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RESEARCH ARTICLE

Warming Temperatures to Expand Spruce Beetle Outbreak Distribution in Northern but Not Southern *Picea* Forests of Western North America

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ABSTRACT

Aim: The biogeography and distribution of irruptive forest insect herbivores are driven by population level responses to host availability, temperature, and precipitation. Because the irruptive dynamics of tree-killing insects such as spruce beetle are regulated by climate, it is imperative to quantify biogeographic drivers and limiters to develop informed predictions and forecasts of future outbreaks. Here, we: (1) identify subcontinental drivers of spruce beetle outbreak distributions, (2) compare drivers and limiters of outbreaks across regions, and (3) develop geospatial hindcasts and forecasts to evaluate the potential for shifts in outbreak activity through time.

Location: Western North American spruce forests spanning 33 to 68 degrees latitude.

Taxon: Spruce beetle (*Dendroctonus rufipennis*) and spruce trees (*Picea* spp.)

Methods: We compiled aerial surveys of spruce beetle-caused tree mortality from 1962 to 2023, forest inventory, and downscaled climate data to develop ensemble machine learning models to investigate patterns of recorded outbreaks and predict the historical and projected distributions of spruce beetle outbreaks.

Results: The distribution of spruce beetle outbreaks are best explained by minimum winter temperature, precipitation as snow, and mean growing season temperatures across western North American. Limiters of outbreaks varied regionally. Host occupancy limited the southern distribution, abundant moisture and diffuse host availability in mixed species forests constrained the western coastal distribution, and minimum winter temperature constrained the northern distribution. Hindcasts and forecasts indicate that the outbreak distribution has expanded in all regions since 1900 and will continue to expand poleward due to projected warming across the boreal.

Conclusions: Understanding how the distributions of forest insect outbreaks respond to fluctuations in climate will dictate the location and severity of outbreaks over the next century. Large-scale irruptions of spruce beetle in forests with historically limited activity will lead to substantial impacts on spruce-dominated landscapes and unknown ramifications for forest processes or long-term disturbance regimes.

1 | Introduction

Population irruptions by insect herbivores shape forest ecosystems. The physical manifestation of these irruptions (i.e., outbreaks) by several forest insect herbivores has caused extensive tree mortality or damage globally (Hicke et al. 2020; van Lierop et al. 2015). Extensive and severe outbreaks can alter ecosystem processes such as carbon cycling (Hicke, Allen, et al. 2012; Kurz et al. 2008) and reshape successional trajectories (Pureswaran et al. 2015; Seidl and Turner 2022). Because the irruption and the population dynamics of insect herbivores are fundamentally regulated by temperature (Bale et al. 2002; Bentz et al. 1991; Robinet and Roques 2010), outbreak dynamics are highly sensitive to shifts in climate (Biedermann et al. 2019; Seidl et al. 2017; Weed et al. 2013). Developing reliable predictions and forecasts for irruption dynamics under projected climate conditions is of paramount importance for land managers, decision makers, and climate adaptation specialists.

Irruptive population dynamics are regulated by cross-scalar drivers and limited by key thresholds, and thus outbreaks exhibit their own unique biogeographic distributions, hereafter 'outbreak distributions'. Distributional differences between species occurrence and outbreaks hold particularly for irruptive species that exhibit two distinct population phases: an extended low-density ('endemic') phase and a short-lived high-density ('epidemic') phase ('alternate attractors'; Holling 1973). Density-independent factors such as temperature and host tree water limitation are widely acknowledged drivers of population irruptions; however, individuals within populations and metapopulations can have variable responses to these drivers (Goodsman et al. 2024; Régnière and Bentz 2007). For example, winter mortality rates can determine whether a population grows or contracts (Safranyik et al. 2010; Safranyik and Carroll 2006); yet observed supercooling points for mountain pine beetle (*Dendroctonus ponderosae*) vary substantially within populations and across space (Bentz and Mullins 1999; Régnière and Bentz 2007). Spatial and temporal patterns of host distributions and climate conditions, combined with variation in density-dependent and independent responses of insects, result in outbreak distributions enclosed within broader species distributions. Given this context, improving our understanding of regional bioclimatic patterns of outbreak distributions is crucial for developing more robust hazard models and more realistic predictions of future insect outbreaks.

Bark beetle outbreak biogeography is fundamentally tied to broad-scale bioclimatic drivers because temperature and precipitation regulate nearly every aspect of bark beetle population dynamics (Bentz et al. 2010). For example, temperature dictates overwintering survival, voltinism (Bentz et al. 1991; Hansen et al. 2001a), phenological and emergence synchrony, and population growth rate (Hansen and Bentz 2003; Powell and Bentz 2009). Precipitation indirectly affects bark beetle population dynamics by mediating host distributions and host susceptibility (Kolb et al. 2016). Since bark beetle population dynamics are influenced by both density dependent and density independent drivers, outbreaks are frequently synchronous across large geographic extents (i.e., Moran effects; Aukema et al. 2008; Moran 1953; Williams and Liebhold 2002). Collectively, these features of bark beetle outbreak dynamics make them an excellent model system for evaluating how climatic change may mediate the distributions of insect herbivore outbreaks.

The North American spruce beetle (*Dendroctonus rufipennis* Kirby) is an irruptive bark beetle that has caused widespread tree mortality to spruce trees (*Picea* spp.) across the contiguous United States (Hart et al. 2017; Veblen et al. 1991), Canada (Zhang et al. 1999), and Alaska (Berg et al. 2006; Werner et al. 2006). Spruce beetle development rate is temperature-dependent and lifecycles vary from 1 to 3 years with univoltine (1 generation per year) and semivoltine (< 1 generation per year) beetles coexisting in the same tree (Bleiker and Willsey 2020; Hansen et al. 2001a, 2001b). Spruce beetle exhibits population phase-dependent host colonisation preferences where endemic beetles are limited to slow growing trees (Hard 1985) and epidemic beetles preferentially colonise vigorous trees (Wallin and Raffa 2004). Outbreak initiation is often linked to an accumulation of defensively-compromised host material following large windfall events (Aukema et al. 2016; Safranyik et al. 1990; Safranyik and Linton 1999), drought (Hart et al. 2017, 2014), or following anomalous warm summer temperatures (Berg et al. 2006). Across North America, spruce beetle outbreak distribution is hypothesised to be limited by the proportion of the population that is univoltine (Bentz et al. 2010; Hansen and Bentz 2003) and overwintering mortality rates (Holsten and Werner 1990), which are both directly determined by temperature. Studies that investigate bark beetle outbreak distributions at longer time scales across broad latitudinal gradients are rare. Based on studies that investigated mountain pine beetle (MPB) and southern pine beetle (SPB; *Dendroctonus frontalis*), we expect low winter temperatures to limit the poleward and elevational extent of the outbreak distribution (SPB: Aoki et al. 2018; MPB: Safranyik et al. 2010), but not the equatorward distribution (Bentz et al. 2010; Bentz and Jönsson 2015; Lombardo et al. 2022). Further, we hypothesise that, as documented in regional studies of spruce beetle and subcontinental studies of other bark beetles, host availability dictates the fundamental niche of the outbreak distribution (Hart et al. 2017; Howe et al. 2024, 2022). Collectively, we hypothesise that while temperature and host occupancy have historically constrained the realised distribution of outbreaks, opportunity exists under projected climate conditions for an expansion of spruce beetle outbreak distribution across broad swaths of host forest that have not historically experienced outbreaks. In this context, quantifying the relative contributions of how host availability, warm and cold temperatures, and precipitation gradients determine spruce beetle outbreak distribution is essential for predicting where future outbreaks may occur in our warming world.

Our objective here is to describe the climatic conditions that determine the outbreak distribution of spruce beetle and assess how climatic change has or may affect the past, current, and future outbreak distribution across western North America. Because one major aim of our study is to forecast how continued climatic warming affects the outbreak distribution, we elected to focus solely on long-term bioclimatic drivers. As a result, we do not include estimates of population pressure (the distance weighted sum of insect activity in the previous

year) in our model, despite its well-documented importance in outbreak models (Aukema et al. 2008; Hart et al. 2017; Howe et al. 2022, 2021; Preisler et al. 2012; Sambaraju et al. 2011; Simard et al. 2012). Measures of population pressure are excellent predictors of where outbreaks may spread following initiation, but their utility is limited outside of the outbreak they describe. Thus, to test our hypotheses, we compiled a spatiotemporally explicit gridded dataset across more than 30° latitude that included descriptors of long-term bioclimatic conditions. Specifically, we compiled spatial estimates of spruce beetle tree mortality collected by aerial observers, host availability from forest inventories, and downscaled historical climatic data to evaluate how host forest and bioclimatic conditions affect the spruce beetle outbreak distribution. We leverage our model to (1) identify how temperature and precipitation limit biogeographic outbreak distributions, (2) compare regional variation in the drivers of outbreak distributions, and (3) develop geospatial hindcasts and forecasts to evaluate shifts in these distributions through time. This work contributes to our understanding of insect herbivore outbreak distributions broadly and supports further hypothesis-based analyses of how temperature mediates spruce beetle outbreak distributions and dynamics.

2 | Methods

2.1 | Overview

We compiled spatially and temporally explicit data (Table 1) to describe the outbreak distribution of spruce beetle. We leveraged these data to construct ensemble machine learning models to identify the relative contribution of drivers and their interactions that influence spruce beetle outbreak distribution. Models were constructed at both the subcontinental and regional scale and a refined thermal envelope was developed to hind and forecast spruce beetle outbreak distribution for six historical 20-year periods (1901–1920...2001–2020) and four future 20-year periods (2021–2040...2081–2100) based on three emissions scenarios.

2.2 | Data Sources and Processing

2.2.1 | Study Resolution

We developed a 0.25-km^2 grid based on the combined bounding box of spruce data sources from Alaska, the Yukon, British Columbia, Alberta, and the contiguous United States. All data were processed in 10,000-km^2 chunks due to processing limitations. All data were intersected with our 0.25-km^2 grid.

2.2.2 | Aerial Surveys

We compiled aerial detection survey data describing the extent of tree damage from insects and diseases. We considered all tree mortality observed from the air to be caused by an irruptive dynamic, as the detection probability of endemic damage is extremely low. We calculated the presence/absence of spruce beetle outbreak populations by intersecting annual polygon and point detection survey data with a 0.25-km^2 grid. Grid cells that contained any visible mortality were listed as affected.

2.2.3 | Forest Structure

We compiled spruce (spp.) basal area estimates from both raster and polygon-based data (see Table 1). Raster-based inventory data were aggregated by upscaling (based on the mean) to 0.25 km^2 and transforming units to m^2/ha. Polygon-based inventory data were aggregated by summing the area-weighted mean (per hectare) of polygons that intersected each cell. In those regions for which we had two sources of data (i.e., British Columbia), we used the higher estimate of spruce basal area because the satellite-based forest inventory (SBFI) underestimates Sitka spruce in coastal British Columbia.

2.2.4 | 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). We extracted raster values using 0.25-km^2 grid cell centroids. Climatic variables, as measured by decadal or multi-decadal gridded data, are proxies for many complex processes that influence bark beetle population dynamics and determine whether a population expands or contracts. Because estimates of how climate determines or affects per capita population-level processes are infeasible to acquire at subcontinental scales, we focus here on long-term gridded data that help describe gradients of host availability and susceptibility as well as the average influence of temperature and precipitation on populations. These indirect measurements such as minimum winter temperature represent excellent proxies for predicting actual population processes such as overwintering mortality. The full list of climatic variables considered are provided in Supplement 1.

2.2.5 | Projected Future Climate

We compiled 20-year climate projections (from ClimateNA) using the 8 General Circulation Model (GCM) ensemble, which has an equilibrium climate sensitivity of 3.4°C (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°C–4.5°C; 2.7°C warming by 2081–2100); medium-high (SSP 3°C–7.0°C; 3.6°C warming by 2081–2100), and high (SSP 5°C–8.5°C; 4.4°C warming by 2081–2100).

2.2.6 | Spruce Suitability Index

We created an estimate of spruce climatic suitability ('spruce suitability index' hereafter) (Jaime et al. 2022) based on spruce basal area and bioclimatic drivers. Spruce suitability index is a unitless measure bounded between 0 and 4 and represents the gradient of bioclimatic conditions associated with higher spruce

TABLE 1 | Model data sources, extent, format and justification for inclusion.

Response	Source(s)	Spatial/temporal extent	Format	Justification
P/A spruce beetle mortality	Aerial detection/overview surveys	Continental United States (1997–2022)[a] Alaska (1986–2022)[b] British Columbia (1961–2022)[c] Alberta (1990–2022)[d] Yukon (1990–2022)[e]	Point/polygon	Response variable
Predictors				
Minimum winter temperatures (°C)	ClimateNA[f]	North America; Historical period: 1901–1920...2001–2020. Future emissions scenarios: 2021–2040...2081–2100 for SSP 2°C–4.5°C, SSP 3°C–7.0°C, SSP 5°C–8.5°C	Raster (800 m)	Cold temperatures cause mortality to larvae and adults
Precipitation as snow (cm)				Snowpack helps insulate larvae and adults from cold
Mean spring and summer temperatures (°C)				Beetle development rate is directly related to growing season temperatures
Climate moisture deficit (mm)				Climate moisture deficit is related to host distribution and likelihood of drought (at broad scales)
Spruce basal area (log[m^2/ha + 1])	Individual tree parameter Maps[g] BC VRI[h] Satellite-based inventory[i]	Continental US/Alaska British Columbia (BC) BC/Alberta/Yukon	Raster (240 m). Polygon. Polygon	Bark beetle outbreak likelihood is tied to host availability
Spruce suitability index (unitless)	Regression model (Supplement 2)	Study Area	Polygon	Bark beetle outbreak likelihood is tied to spruce suitability index

Note: Data sources and links.
[a]USA Detection Survey Data ('Aerial Detection Surveys, USDA Forest Service', 1997).
[b]USA Detection Survey Data ('Aerial Detection Surveys, USDA Forest Service', 1997).
[c]Aerial Overview Surveys (BC).
[d]Aerial Overview Surveys (AB).
[e]Forest Health Aerial Overview (YK).
[f]ClimateNA (Wang et al. 2016).
[g]Individual Tree Species Parameter Maps.
[h]Vegetation Resource Inventory (BC).
[i]Satellite-Based Forest Inventory (Canada); Wulder et al. (2024).

basal area. Models were constructed using a similar machine learning framework as detailed below. Methods and results for our spruce suitability index model are provided in Supplement 2.

2.2.7 | Biogeographic Boundaries

We compiled biogeographic boundaries based on the ecoregions provided by the United States Environmental Protection Agency (North American Ecoregions) and created a depiction of spruce distribution by joining our compiled estimates of spruce basal area and the distribution of spruce in Little's Atlas of United States trees (Little 1971), and buffering the joined polygons by 20 km.

2.2.8 | Preprocessing

All predictors considered were rounded and Winsorised (tails were trimmed at quantiles of 0.005 and 0.995) to control for the distribution and number of distinct observations. For example, precipitation as snow was rounded to the nearest 5 cm and Winsorised to decrease the number of distinct observations from 107 to 41 and to trim the long tail of the distribution and range of precipitation as snow from 0–545 cm to 0–200 cm. These preprocessing steps decrease model overfitting, help us explore model interactions, and allow for easier estimation of prediction errors.

2.3 | Analysis

2.3.1 | Model

We constructed a classification machine learning model stack (i.e., a combination of multiple models; 'classification model' hereafter) with two ensemble models: (1) random forest (Breiman 2001) and (2) gradient boosting (Friedman 2001). Both ensemble models are tree-based and predicated on constructing many simple classification trees in parallel (*bagging*; random forest) or sequentially by reducing residual error (*boosting*; gradient boosting). We used the *ranger* implementation of random forest (Wright and Ziegler 2017) and the *XGBoost* implementation of 'extreme gradient boosting' (Chen et al. 2024; Chen and Guestrin 2016). Both models were constructed using 3-fold cross validation and predictions from each individual model were averaged to compute a final prediction.

2.3.2 | Model Details

Classification models were tuned based on a grid approach (Supplement 3) and variable selection was performed using variable clustering and 'design points' based on holdout models (i.e., testing different combinations of related variables; Supplement 1). Since aerial detection programs contain errors of omission (missing damage caused by insects and pathogens) and commission (incorrect identification) (Coleman et al. 2018), we designed a bootstrapped workflow. For each constructed model, we randomly selected a training and a test dataset using two different stratification methods; (A) numeric; and (B) proportional (Supplement 4). For the numeric stratification method, we randomly selected 10,000 presences and 10,000 absences from each region and 20-year period (sampling was capped at 33% of the total number of observations for each region × period combination). For the proportional stratification method, we randomly selected 10% of presences and an equal number of absences from each region and 20-year period.

2.3.3 | Model Effects

We assessed model effects based on each stratified test dataset. We assessed model performance using confusion matrix metrics, 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) (Fisher et al. 2019), relative mean effects using accumulated local effects (Apley and Zhu 2020), and predictor interaction strength using Friedman's h^2 (higher values correspond to greater interaction strength) (Friedman and Popescu 2008).

2.3.4 | Model Fitting

All models were trained and tested based on data subsampled from Alaska, British Columbia, and the contiguous United States. We constructed models 100 times (50 times for each stratification method) to predict spruce beetle outbreak distribution across the entire compiled extent of spruce forests in western North America. Models were constructed 1000 times (500 times for each stratification method) to estimate the relative mean effects of predictors and associated prediction error based on 95% confidence intervals. Regional models for Alaska, British Columbia, and the contiguous United States as well as models fitted using only data from low or high basal area spruce forests were each constructed 250 times (125 times for each stratification method).

2.3.5 | Thermal Envelope

We developed thermal envelope breakpoints (Supplement 5) to describe the outbreak distribution of spruce beetle based on modelled results and a priori information about spruce beetle biology. Ultimately, we developed our envelope based on mean spring and summer temperature, minimum winter temperature, and climate moisture deficit. Climate moisture deficit was included in the mapped thermal envelope because it helps distinguish between coastal and interior forests but was not included in most tabular summaries. Thermal envelopes were delineated as either 'optimal' (within the breakpoints), 'likely' (outside the envelope, but possibly suitable given our a priori understanding of spruce beetle biology), or 'not suitable'. Together, we refer to spruce forests that are either 'optimal' or 'likely' as 'suitable'. For example, we considered the 'optimal' thermal envelope for mean spring and summer temperature to be 4°C–9.5°C based on model results, while the 'likely' thermal envelope included mean spring and summer temperature between 9.5°C–15°C because: (1) the development time of many *Dendroctonus* sp. is flexible and increasing temperatures are related to either more generations per year or developmental delays

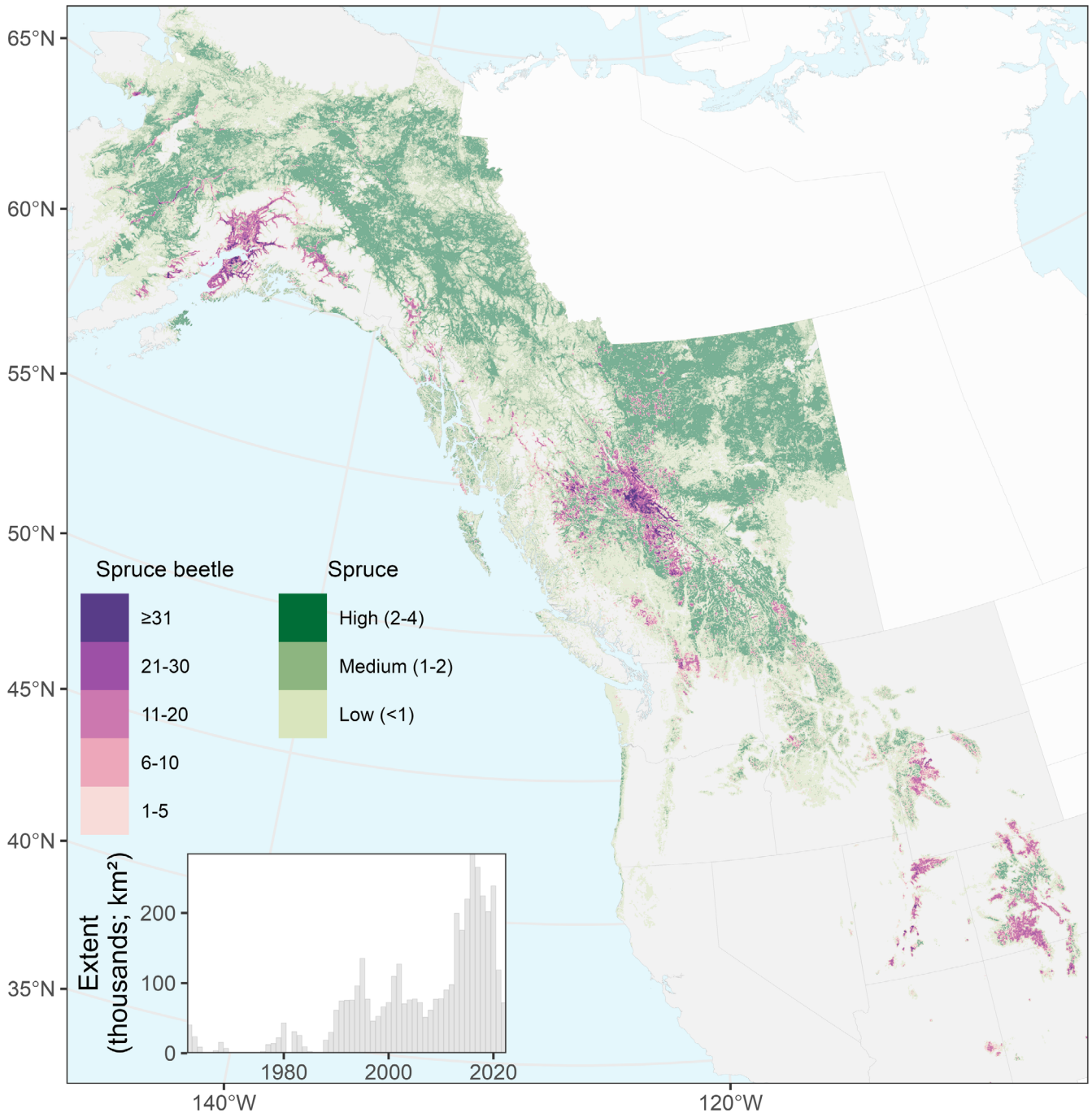

FIGURE 1 | Observed distribution of spruce beetle (pink-purple) and spruce (greens) aggregated at a 5-km^2 resolution. Numbers for spruce beetle correspond to the number observed per cell (anytime between 1961 and 2020 [max = 21 cells × 3 20-year time period]) and the area weighted mean per cell for spruce. Inset depicts the observed extent of spruce beetle per year (per thousand km^2).

through facultative diapause (Bleiker and Willsey 2020; Hansen et al. 2011; Schebeck et al. 2017); (2) field- and laboratory-based studies evaluating the effects of heat on *Dendroctonus* species such as southern pine beetle suggest that chronic extreme heat does not cause high levels of mortality (Lombardo et al. 2022) and laboratory studies suggest that spruce beetles can tolerate temperatures of 43°C (Mitchell and Schmid 1973); and (3) our model results depict that the predicted upper limit of mean spring and summer temperature (where profiles and predictions decrease below 0) tracks the distribution of temperatures across the range of spruce trees (i.e., our dataset contains few observations where host basal area is high and temperatures are warm [Supplement 6]). Finally, we rounded the envelope breakpoints for minimum winter temperature to the nearest 5°C (i.e., −15°C instead of −16°C) for ease of depiction.

2.3.6 | Model Uncertainty

Large-scale spatially and temporally explicit analyses and machine learning models have several sources of uncertainty. First, our models are based on a stratified sample of observations

TABLE 2 | Predicted and observed spruce beetle in each region (no. of pixels) and 20-year time period. Bold face denotes inclusion in model; italic face denotes exclusion. Prediction breakpoints are equivalent to those in Figure 3.

	Binned predictions						
	(0, 0.01)	(0.01, 0.05)	(0.05, 0.1)	(0.1, 0.25)	(0.25, 0.5)	(0.5, 1)	Observations
Alberta							
1961–1980	9246	116,342	102,058	124,268	49,882	12,164	—
1981–2000	2094	108,370	115,949	124,289	54,308	8950	—
2001–2020	359	43,878	96,415	155,110	90,082	28,116	1558
Alaska							
1961–1980	54,952	218,918	142,456	151,316	77,249	37,088	—
1981–2000	52,344	209,791	136,931	142,806	78,189	61,918	66,887
2001–2020	43,995	205,276	145,334	157,340	69,741	60,292	89,522
British Columbia							
1961–1980	21,953	121,623	90,698	141,033	123,783	146,351	38,617
1981–2000	23,368	99,012	80,679	136,545	123,672	182,165	48,468
2001–2020	16,453	68,098	77,291	155,207	140,237	188,056	167,185
CONUS							
1961–1980	5342	13,979	25,418	78,760	84,046	65,546	7
1981–2000	7386	15,335	23,658	71,115	75,491	80,054	15,707
2001–2020	11,339	22,851	35,246	75,185	58,280	70,078	126,088
Yukon							
1961–1980	12,412	135,058	103,662	91,410	20,105	9927	—
1981–2000	7552	132,384	87,864	95,914	32,700	16,160	6614
2001–2020	6322	108,993	85,757	101,833	44,862	24,808	2

that were collected using different protocols and with highly unequal sampling effort across jurisdictions, regions, and 20-year periods. Our decision to develop a bootstrapped modelling approach with two different stratification schemes that under/over sample certain region × period combinations was motivated by this shortcoming. Second, tree-based models do not assume any relationship (e.g., linear) between the independent and dependent variables and instead rely on consensus 'votes' (random forest) or optimization (gradient boosting) of many individual and small tree-based models. Because of this, model prediction uncertainty is difficult to quantify, especially for parameter space combinations (the multi-dimensional combination of all predictors) with low replication. Our decision to develop a boot-strapped modelling approach gives us some ability to quantify within-and-across model uncertainty. Finally, tree-based machine learning models are not robust for predicting new observations outside of the model parameter space, which informs our decision to hindcast and forecast based on thermal envelopes. In total, we are most confident in our predictions from 2001 to 2020, across the contiguous United States, British Columbia, and Southcentral Alaska, and in areas with closer to average bioclimatic conditions (i.e., we are less certain at the distributional extremes for each predictor).

3 | Results

Between 1961 and 2020, irruptive spruce beetle activity was observed across 140,252 km^2 (Figure 1; 561,007 grid cells). Spruce beetle-caused mortality was observed across 9656 km^2 between 1961 and 1980 ($N = 38{,}624$), 34,487 km^2 between 1981 and 2000 ($N = 137{,}949$), 96,108 km^2 between 2001 and 2020 ($N = 384{,}434$). Observations of spruce beetle mortality were highly variable across 20-year time periods and regions (Table 2), reflecting both the intermittent nature of spruce beetle outbreaks and unequal aerial surveying effort across different jurisdictions.

Overall, minimum winter temperature best explained spruce beetle outbreak distribution (Figure 2), followed by precipitation as snow and climate moisture deficit. The relative explanatory power of bioclimatic drivers was consistent across low and high spruce basal area forests (threshold identified at 1.9 $\log[m^2/ha + 1]$) but varied regionally. In Alaska and British Columbia, minimum winter temperature and precipitation as snow provided high explanatory power for spruce beetle outbreak distributions, while across the contiguous United States, spruce basal area ($\log[m^2/ha + 1]$) and mean spring and summer

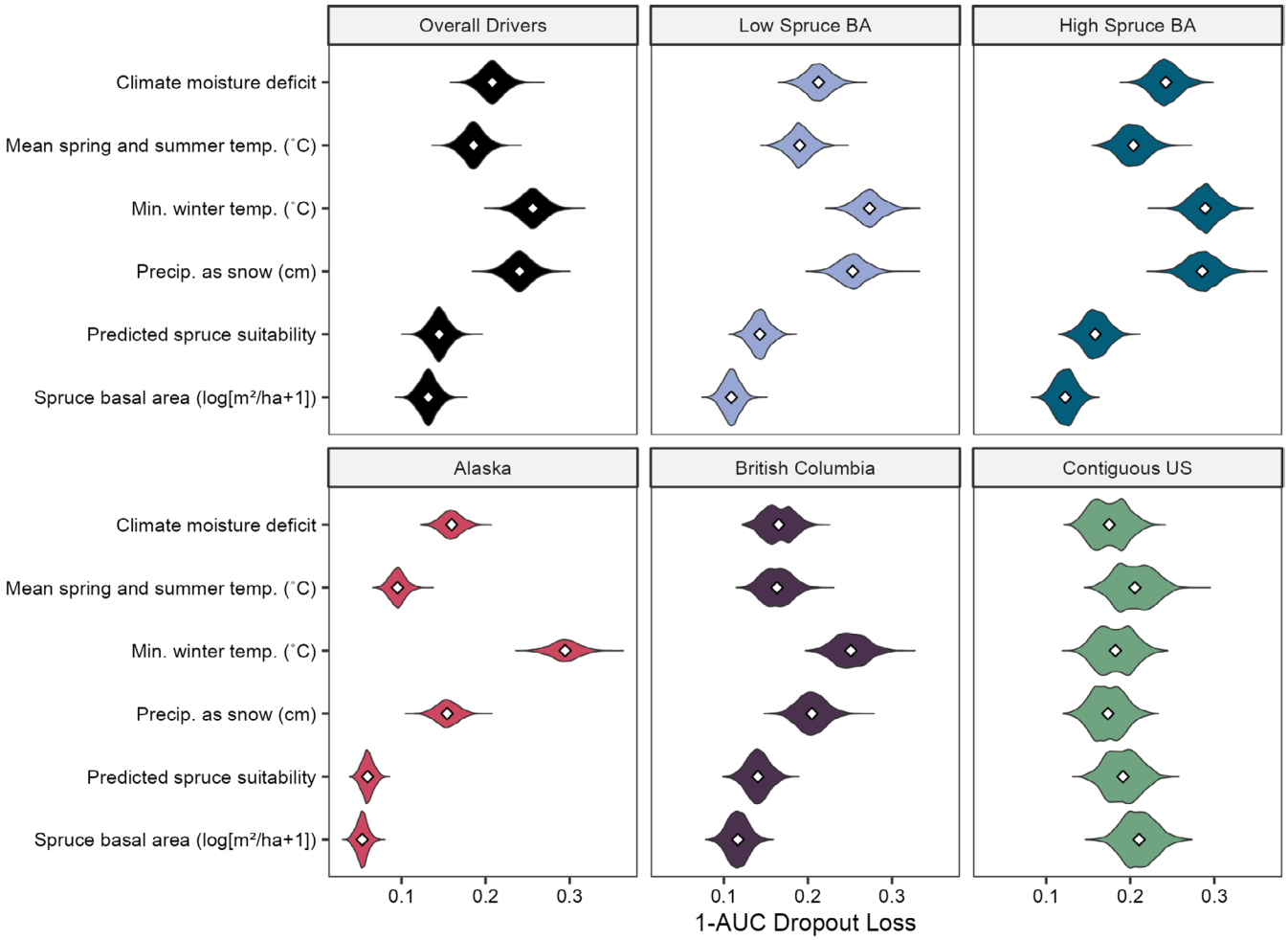

FIGURE 2 | Variable importance (1-AUC [area under the receiver-operator curve]) of predictors included in each model. Points denote mean variable importance.

temperatures (°C) provided better explanatory power (model profiles for each regional model are provided in Supplement 7).

Spruce beetle outbreaks were more likely to be observed in spruce forestlands with minimum winter temperatures between −21°C (Figure 3; Supplement 8; 95% confidence interval = −23, −21) and −6°C (−6, −6), precipitation as snow between 25 cm (5, 25) and 90 cm (85, 90), climate moisture deficit greater than 70 cm (40, 120), mean spring and summer temperatures between 4°C (2.5, 4.5) and 9.5°C (9, 9.5), spruce suitability index greater than 1.5 (1.3, 1.7), and spruce basal area greater than 1.9 log(m^2/ha + 1) (1.7, 2.2). Models indicate that spruce forests across Southcentral Alaska, central British Columbia, the southern Rocky Mountains, and the Wasatch Range are within the current spruce beetle outbreak distribution (prediction ≥ 0.5) (Figure 4; Supplement 9). Models correctly predicted 86% of observed spruce beetle (true positive rate; Table 3). In total, interactions among predictors explained approximately half of prediction variability (Friedman's $h^2 = 0.493 \pm 0.029$; Figure 5; Table 4).

Based on the thermal envelope, most outbreaks (94.9%) occurred in spruce forests with optimal spring and summer temperatures, 94.7% occurred in spruce forests with optimal minimum winter temperatures, and 81.8% occurred in spruce forests with optimal climate moisture deficits (Supplement 5). Further, 89.9% of spruce beetle occurred in spruce forests with optimal temperatures, and 72.8% occurred in spruce forests with optimal temperatures and climate moisture deficit ≥ 70 mm. Across spruce forestlands included in our study area, 54.7% currently (2001–2020) experience optimal mean spring and summer temperatures, while an additional 16.7% experience mean spring and summer temperatures that are warm but likely to support outbreaks (Figure 6; Table 5A,B). In total, 32.6% of spruce forests experienced optimal winter temperatures and an additional 15.3% experienced cool but likely temperatures to support outbreaks.

Between 1901 and 1920, 11.7% of spruce forests were climatically optimal and 18.1% were climatically likely to support spruce beetle outbreaks (Figure 7; Table 5C; Supplement 10). By 2001–2020, 15.5% of spruce forests were optimal and 26.0% were likely to support outbreaks. Forecasted widespread warming across western North America is projected to expand the outbreak distribution of spruce beetle by 2081–2100, as most spruce forests are predicted to experience climatic conditions that are optimal (SSP 2°C–4.5°C = 11.5%; SSP 3°C–7.0°C = 8.5%; SSP 5°C–8.5°C = 6.6%) or likely (SSP 2°C–4.5°C = 47.3%; SSP 3°C–7.0°C = 59.1%; SSP 5°C–8.5°C = 66.0%) to support outbreaks. The relative decrease in optimal climatic conditions associated

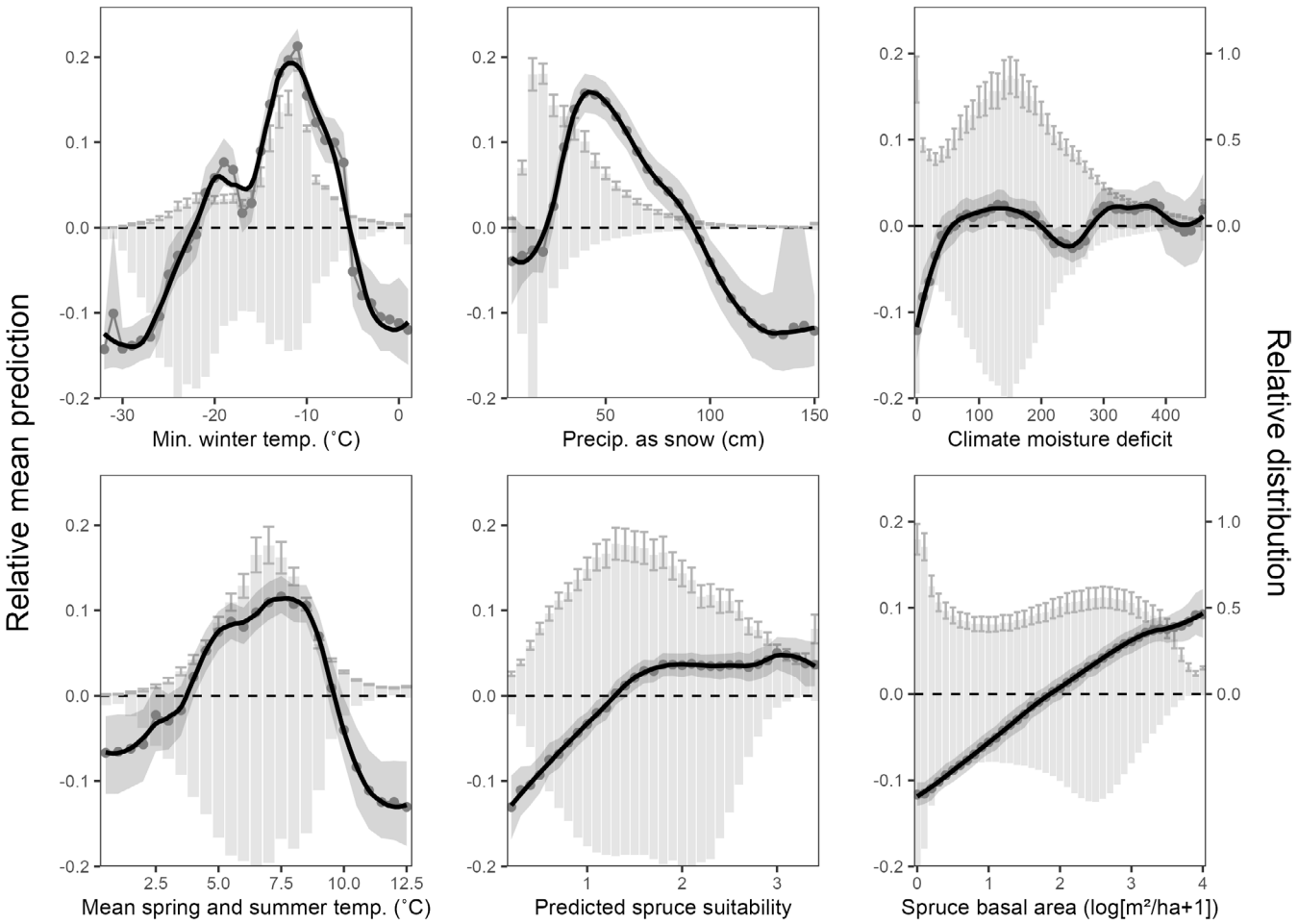

FIGURE 3 | Mean predicted likelihood of observing spruce beetle (±95% confidence interval; lines and ribbons based on 500 models) and the mean relative distribution of each predictor (bars; ±95% confidence interval) across samples (positive values) and the entire dataset (negative values).

with forecasts is predominantly tied to increases in the extent of spruce forestlands that are projected to experience mean spring and summer temperatures between 9.5°C and 15°C. The extent of spruce forestlands that experienced these warm temperatures increased throughout the historical time series from 4.7% in 1901–1920 to 9.2% in 2001–2020 and is projected to continue to increase throughout the century (SSP 2°C–4.5°C = 49.8%; SSP 3°C–7.0°C = 67.0%; SSP 5°C–8.5°C = 74.6%). Warming minimum winter temperatures further contribute as the extent of spruce forestlands that experienced minimum winter temperatures between −20°C and −15°C remained consistent from 1901–1920 to 2001–2020 (20.2%) but is also projected to increase (SSP 2°C–4.5°C = 29.0%; SSP 3°C–7.0°C = 30.6%; SSP 5°C–8.5°C = 27.3%). Such warming is projected to fundamentally alter the geography of spruce beetle outbreak distributions across the ecoregions in our study (Figure 8). For example, in the northern boreal forest, warming is projected to increase the extent of suitable spruce forests from 7.4% to 46.5% by the end of the century (Table 6 [22.3, 75.2]; error estimates in square brackets denote projections based on SSP 2°C–4.5°C and SSP 5°C–8.5°C; see Supplement 11 for map of ecoregions). In contrast, nearly all the southern Rocky Mountains are currently suitable (94.7%) but are projected to decrease in extent (67.2% [80.9–55.6]) because of mean spring and summer temperatures exceeding the upper temperature bounds of 15°C by the end of the century. Finally, the extent of suitable spruce forests in the Pacific coastal temperate rainforest is projected to remain relatively stable (86.4% to 83.0% [86.5, 79.3]) for the remainder of the century.

Observed and projected changes to the extent of suitable spruce forests across our study area are tied to regional variation in what biogeographical features limit spruce beetle outbreak distribution under current climatic conditions (2001–2020). Overall, minimum winter temperature was the greatest limitation of spruce beetle outbreak distribution. Nearly 24.2% of spruce forests were below the minimum winter temperature threshold but were optimal in terms of mean spring and summer temperatures and climate moisture deficits (Table 6). An additional 6.7% of spruce forests experienced suitable minimum winter temperatures < −20°C but mean spring and summer temperatures that were too cold (< 4°C). In the southern Rocky Mountains, climatic conditions were optimal across 214,555 km^2, yet high basal area forests cover only 53,587 km^2. In total, 97.7% of observed spruce forests across the southern Rocky Mountains were suitable for spruce beetle between 2001 and 2020; a relatively large increase from the 88.8% that were suitable at the beginning of the century (1901–1920). Similar limitations were evident across the Cascades and Sierra Nevada mountains and the Canadian Rocky Mountains. In the Pacific coastal temperate rainforest, spruce beetle outbreaks were limited by both host basal area and abundant moisture; climatic conditions were optimal across 264,862 km^2, but high basal area forests cover only 23,571 km^2, and most spruce forests in the Pacific coastal temperate rainforest

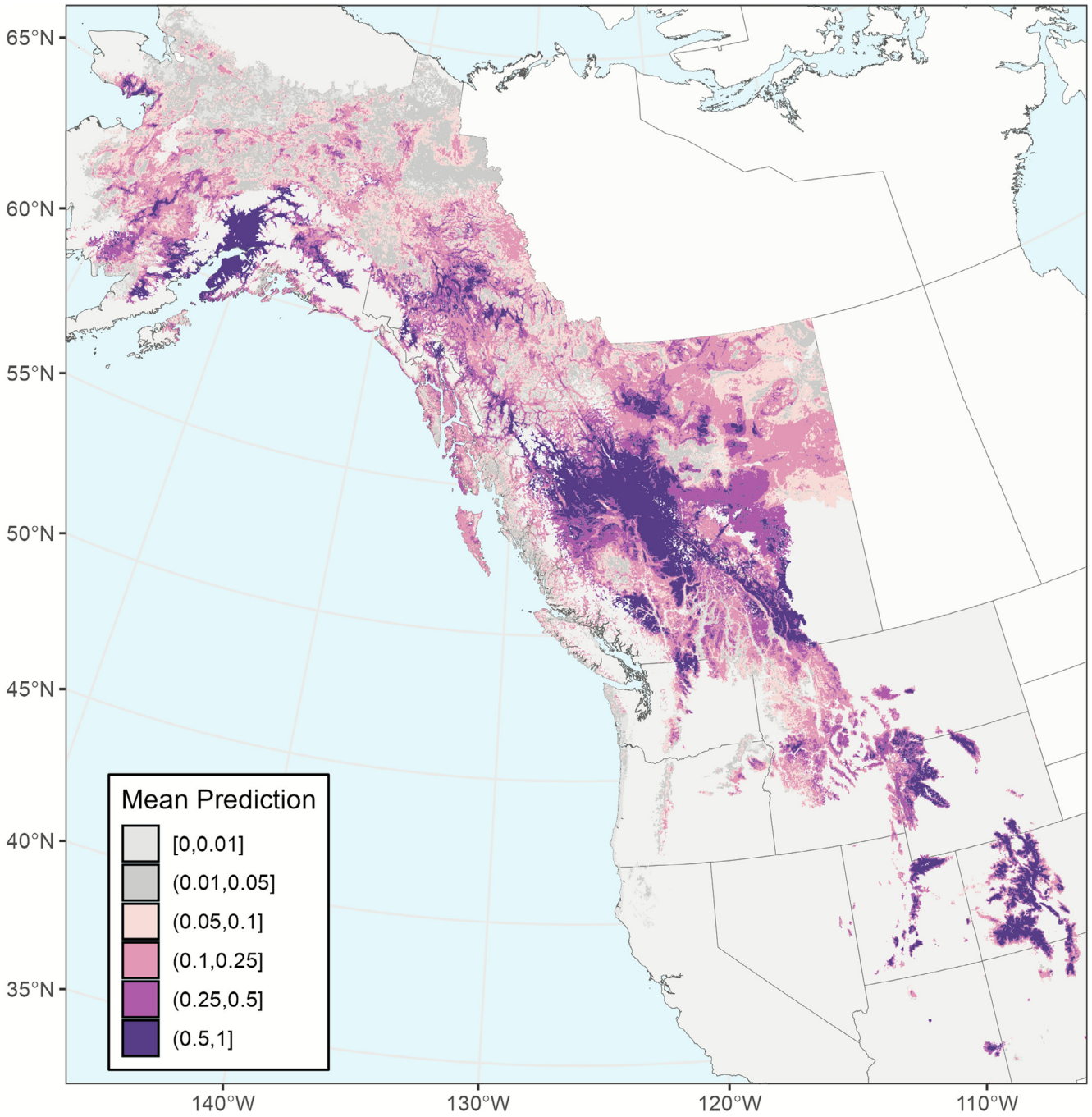

FIGURE 4 | Mean predicted spruce beetle outbreak distribution between 2001 and 2020 aggregated at 5 km^2. Predictions for 1961–1980 and 1981–2000 are provided in Supplement 7.

with optimal thermal conditions (127,309 km^2) also experienced abundant moisture. Only 9373 km^2 of 276,612 km^2 (3%) observed spruce forests were of requisite basal area and experienced optimal bioclimatic conditions for spruce beetle outbreaks in the Pacific coastal temperate rainforest. Finally, spruce beetle outbreak distribution was primarily limited by cold minimum winter temperatures across northern boreal forests as only 19,055 km^2 (3%) of observed spruce forests experienced optimal winter temperatures, 133,032 km^2 (18%) experienced temperatures that were likely too cold, and 588,722 km^2 (79%) experienced winter temperatures that were too cold. Similar patterns were observed across the northern Rocky Mountains (18% optimal; 28% likely too cold; 44% too cold) and northern forests (22% optimal; 46% likely too cold; 32% too cold).

4 | Discussion

Our study demonstrates the specific importance of minimum winter temperature and mean spring and summer temperatures as unifying drivers of spruce beetle outbreak distributions across the North American subcontinent. Additionally, we describe how gradients of host availability and seasonal precipitation regimes further shape outbreak distributions. Results suggest that host

TABLE 3 | Model performance metrics (mean ± SD).

	Overall	Alaska	British Columbia	CONUS	High spruce ba (≥ 1.9 log[m²/ha + 1])	Low spruce ba (< 1.9 log[m²/ha + 1])
Recall/true positive rate	0.858 ± 0.002	0.914 ± 0.003	0.872 ± 0.009	0.814 ± 0.018	0.853 ± 0.006	0.850 ± 0.003
Precision	0.818 ± 0.001	0.912 ± 0.003	0.807 ± 0.005	0.795 ± 0.012	0.800 ± 0.006	0.820 ± 0.005
F1	0.838 ± 0.001	0.913 ± 0.002	0.838 ± 0.007	0.804 ± 0.015	0.826 ± 0.006	0.835 ± 0.003
Accuracy	0.834 ± 0.001	0.913 ± 0.002	0.832 ± 0.007	0.802 ± 0.014	0.820 ± 0.006	0.832 ± 0.003
AUC	0.910 ± 0.001	0.964 ± 0.001	0.909 ± 0.006	0.877 ± 0.014	0.899 ± 0.006	0.907 ± 0.002

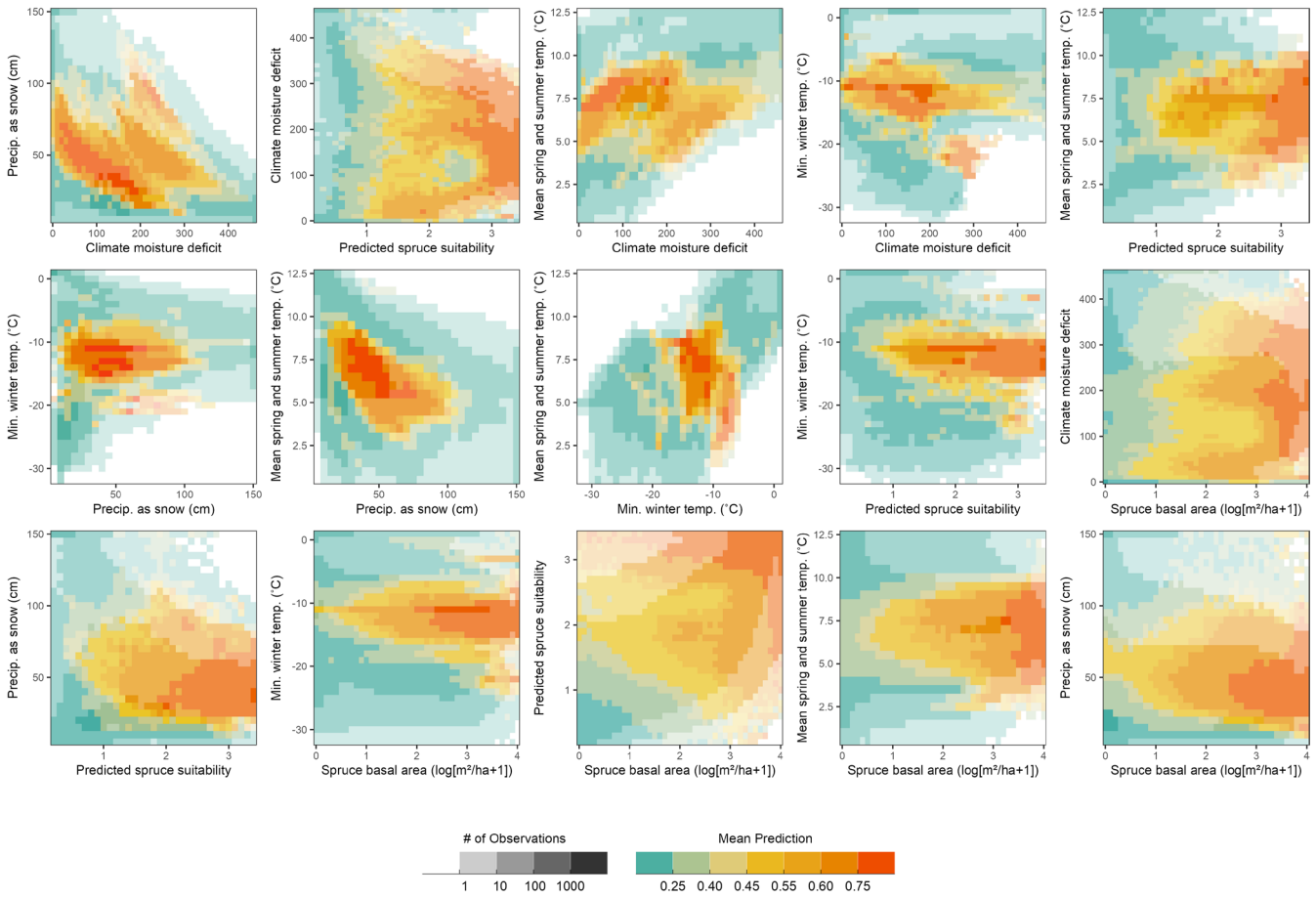

FIGURE 5 | Pairwise interactions between bioclimatic predictors influencing the outbreak distribution of spruce beetle. Panels are ordered by interaction strength (Friedman's h^2). Colour denotes mean prediction and intensity (alpha) denotes the overall number of observations.

availability limits the southern extent of the outbreak distribution, abundant moisture limits the western extent, and minimum winter temperatures limit the northern extent under historical and current climatic conditions. Quantification of these limitations inform projections of future spruce beetle outbreak distributions; suitable climatic conditions for outbreaks across spruce forests rose from 30% to 40% over the twentieth century and are projected to increase to almost 60% (SSP 2°C–4.5°C ~ 40%; SSP 5°C–8.5°C ~ 70%) by the end of the 21st century. Based on emissions scenarios (i.e., SSP 2°C–4.5°C—SSP 5°C–8.5°C), our models predict little to no change in outbreak distributions throughout much of the contiguous United States and southern British Columbia as nearly all suitable host habitat is already climatically suitable for spruce beetle outbreaks. The extent of suitable host habitat is projected to remain at current levels across the Pacific coastal temperate rainforest, although uncertainty remains in how abundant precipitation shapes spruce beetle outbreak likelihood. Finally, warming minimum winter temperatures and mean spring and summer temperatures are projected to substantially increase the poleward distribution of suitable host habitat for spruce beetle outbreaks by the end of the 21st century. Collectively, this work advances our understanding of how host availability and bioclimatic drivers shape the outbreak distributions of irruptive forest insects and how they might shift in the future.

TABLE 4 | Interaction strength (Friedman's $h^2 \pm$ SD; percent of prediction variability explained by interactions) for predictors included in overall model. Diagonals denote one-way interaction strength. In total, 49.3% ± 2.9% of prediction variability was explained by interactions among predictors.

	Climate moisture deficit	Precipitation as snow	Minimum winter temperature (°C)	Spring and summer temperature (°C)	*p* (spruce suitability)	Spruce basal area (log[m²/ha + 1])
Climate moisture deficit	30.4 ± 2.2					
Precipitation as snow	41.0 ± 4.6	29.7 ± 2.2				
Minimum winter temperature (°C)	28.5 ± 4.9	19.1 ± 2.8	28.6 ± 2.2			
Spring and summer temperature (°C)	30.2 ± 4.9	14.4 ± 2.4	13.9 ± 2.3	21.2 ± 2.0		
p (spruce suitability)	33.8 ± 5.5	8.6 ± 2.0	13.0 ± 2.8	21.0 ± 7.3	12.5 ± 1.2	
Spruce basal area (log[m²/ha + 1])	10.4 ± 2.0	2.7 ± 0.9	4.9 ± 1.2	2.9 ± 0.9	4.2 ± 1.1	7.7 ± 0.8

Across scales, temperature is widely regarded as the primary density independent determinant of bark beetle survival, development rate, population dynamics, and outbreak distributions. Indeed, studies have directly linked spruce beetle development rates to spring and summer temperatures (Hansen et al. 2001a, 2001b) and temperature thresholds identified in this study are comparable. For example, a mean spring and summer temperature above 4°C, as identified in our model, corresponds to a mean summer temperature of ~11°C, which is similar to results from a dendrochronological study that identified 10.3°C as a temperature threshold for outbreak probability reaching 50% (Berg et al. 2006). Further, interactions between minimum winter temperatures and snow depth are strongly linked to overwintering survival (Miller and Werner 1987; Rousseau et al. 2012; Schebeck et al. 2017). Our models identified an average minimum winter temperature threshold of −21°C inhibiting outbreaks, similar to a mortality threshold of −25°C for adults and larvae in Alaska (Miller and Werner 1987). Our models also confirm heightened likelihood of outbreaks under greater snow depths (> 50 cm precipitation as snow). The modelling approach detailed in this manuscript effectively identifies relationships between bioclimatic conditions and observed spruce beetle outbreaks but does not attempt to infer how mechanistically temperature affects spruce beetle population dynamics. Thus, it is difficult to compare our results to those at a finer scale, and additional research is needed to reconcile studies that incorporate broad-scale bioclimatic patterns with others that investigate finer scale daily or monthly weather's relations to spruce beetle outbreak dynamics.

Biogeographical gradients of precipitation influence bark beetle outbreak distributions indirectly through host availability and susceptibility. Results from this study confirm that large-scale spruce beetle-caused tree mortality is associated at the stand level with denser and higher volume spruce forests (DeRose et al. 2013; Hansen et al. 2010; Holsten 1984; Schmid and Frye 1976; Werner et al. 2006). The distribution of spruce across western North America is linked to moisture availability, where spruce basal area, persistence, and regeneration are determined and constrained by dry conditions and high climate moisture deficits (Andrus et al. 2018; Hill et al. 2019; Hynes and Hamann 2020; Rehfeldt et al. 2006). Interactions in our models confirm these patterns. Models also indicated that spruce beetle outbreaks were less likely in high-precipitation spruce forests along the Pacific coast. This result may be related to the low likelihood of observing droughty conditions across forests with very low climate moisture deficits, as drought is a well-established inciting driver of outbreaks (Berg et al. 2006; Csank et al. 2016; Hart et al. 2017, 2014; Sherriff et al. 2011). Under normal conditions, spruce chemical and physical defences are an effective barrier to spruce beetle colonisation (Aukema et al. 2016; Davis 2020), but drought can decrease tree resistance (Raffa et al. 2008) and help facilitate an initial population expansion. As with temperature, the long-term measures of precipitation used in this study are not suitable for assessing how short-term fluctuations in precipitation drive spruce beetle outbreak dynamics, nor how variability in snowpack depth and minimum winter temperatures influence outbreak likelihood. Further work is required to integrate biogeographic patterns of host availability, susceptibility, and short-term drivers into a comprehensive framework.

Spruce beetle dynamics in the Pacific coastal temperate rainforest appear to be more nuanced and more difficult to ascribe a single limiting factor to the extent of their outbreak distribution. First, spring and summer temperatures across the Pacific coastal temperate rainforest are near the low end of suitable temperatures identified in this study, especially in coastal Alaska. Previous work suggests that summer temperatures rarely exceed those required for spruce beetles to develop in 1 year (Werner et al. 2006). Second, the extremely wet conditions and resulting low potential evapotranspiration minimises tree stress, allowing vigorous production of tree chemical defences to prevent successful spruce beetle colonisation (Aukema et al. 2016).

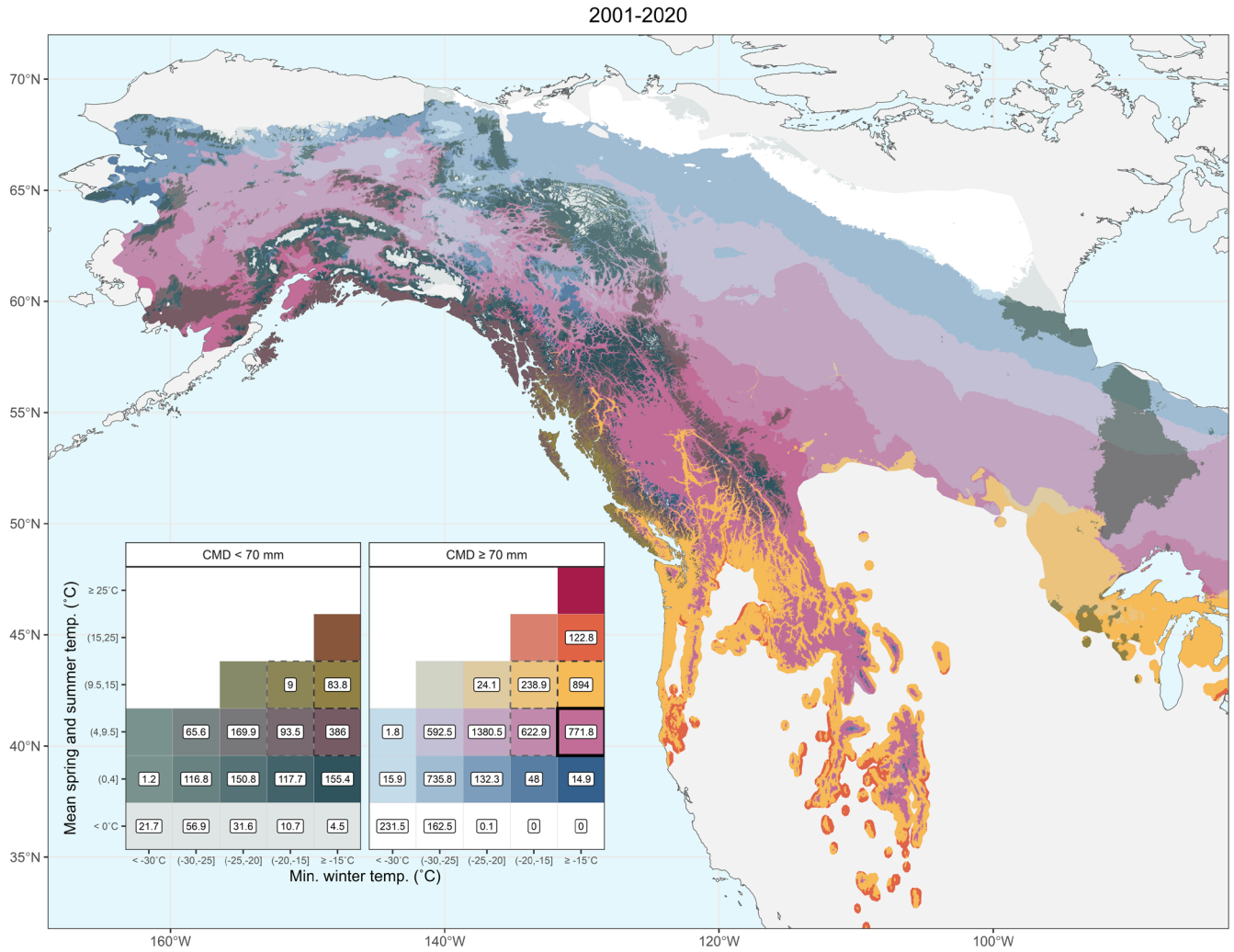

FIGURE 6 | Biogeographic distribution of climate moisture deficit (mm), minimum winter temperature (°C), and mean spring and summer temperature (°C) across spruce forests in western North America between 2001 and 2020. Panel provides the key and the extent of each combination (in thousands of km^2). Black outline depicts the model-based optimal climatic envelope for spruce beetle outbreaks and grey dashed outlines (in the panel) depict the likely climatic envelope for spruce beetle outbreak distribution. CMD = climate moisture deficit.

Third, Sitka spruce (*Picea sitchensis*) is the dominant host species in these cool and high precipitation environments, and past studies found that spruce beetles produce fewer progeny per adult beetle in Sitka spruce than in other hosts like white spruce (*P. glauca*) (Holsten and Werner 1990). Finally, host species occur in relatively low abundances in mixed species stands (e.g., co-occurring with western hemlock [*Tsuga heterophylla*], western redcedar [*Thuja plicata*], as well as other species). Thus, even though models and all emissions scenarios suggest that nearly all spruce forests across the Pacific coastal temperate rainforest will be thermally suitable for spruce beetle outbreaks by the end of the century, further research and monitoring are required to determine the long-term outlook of spruce beetle outbreaks across the region. Forecasts that consider the silvics and landscape arrangement of Sitka spruce, the high degree of projected warming (Lader et al. 2020), and the 'novel' incidence of drought (Bathke et al. 2019) across this ecoregion are necessary.

Recent large-scale irruptions of spruce beetle across the contiguous United States and southern British Columbia reflect the high climatic suitability of spruce forests in these regions. Results from this study confirm that nearly all host forestlands are currently climatically suitable for spruce beetle outbreaks in southern spruce forests (Bentz et al. 2010; DeRose et al. 2013) and thus future outbreaks are tied to host availability. Since spruce beetle preferentially attack mature trees, severe mortality events initially dampen the future likelihood of outbreaks (Hart et al. 2015) and can result in altered forest composition toward unsuitable species (DeRose and Long 2007; Rodman et al. 2022, 2021). Across stands with suitable host material, future spruce beetle outbreaks are tied to the long-term likelihood of initiation events. There remains some debate whether recent outbreaks were primarily triggered by drought (Hart et al. 2017), temperature (Pettit et al. 2020), abiotic disturbances such as windthrows or slides, or some combination, but any of these inciting drivers may contribute to the next spruce beetle outbreak. Projections indicate that southern spruce forests will continue to experience rapid climatic warming, but it remains an open question whether there is an upper thermal performance threshold for spruce beetle where continued summer warming may eventually cause a contraction in the outbreak distribution.

TABLE 5 | (A) Thermal envelope breakpoints; (B) percent of spruce forests in each thermal envelope breakpoint under current (2001–2020) bioclimatic conditions; and (C) percent of spruce forests in each thermal envelope category under past and forecasted bioclimatic conditions. Boldface denotes optimal thermal envelope, while italics denotes conditions that are likely suitable.

(A)

Mean spring and summer temperature (°C)	Percent of spruce forests	Thermal envelope designation	Minimum winter temperature (°C)	Percent of spruce forests	Thermal envelope designation
<0°C	7.0	Cold	< −30	3.6	Cold
(0, 4]	19.9	Cold	(−30, −25]	23.2	Cold
(4, 9.5]	**54.7**	**Optimal**	(−25, −20]	25.3	Cold
(9.5, 15]	*16.7*	*Warm*	*(−20, −15]*	*15.3*	*Cool*
>15	1.6	Hot	**> −15**	**32.6**	**Optimal**

		Mean spring and summer temperature (°C)					
(B)	**Interaction**	**Cold**	**Optimal**	**Warm**	**Hot**	**Total percent**	
Minimum winter temperature (°C)	Cold	22.2	29.6	0.3	—	**Optimal**	15.5
	Cool	2.4	*9.6*	*3.3*	—	*Likely*	26.0
	Optimal	2.3	**15.5**	*13.1*	1.6	Unlikely	58.5

(C)

Period	Optimal			Likely			Unlikely		
1901–1920	**11.7**			*18.1*			70.3		
1921–1940	**11.6**			*20.9*			67.6		
1941–1960	**12.5**			*19.8*			67.7		
1961–1980	**12.3**			*18.5*			69.3		
1961–2000	**14.5**			*22.4*			63.1		
2001–2020	**15.5**			*26.0*			58.5		
Emissions scenarios (SSP)	2°C–4.5°C	3°C–7.0°C	5°C–8.5°C	2°C–4.5°C	3°C–7.0°C	5°C–8.5°C	2°C–4.5°C	3°C–7.0°C	5°C–8.5°C
2021–2040	**13.1**	**12.7**	**12.7**	*30.1*	*29.0*	*30.6*	56.8	58.3	56.6
2041–2060	**12.1**	**12.0**	**11.5**	*36.0*	*37.0*	*40.4*	51.9	51.0	48.1
2061–2080	**11.6**	**10.3**	**9.4**	*41.5*	*48.4*	*52.8*	46.8	41.2	37.7
2081–2100	**10.5**	**8.5**	**6.6**	*47.3*	*59.1*	*66.0*	42.2	32.4	27.4

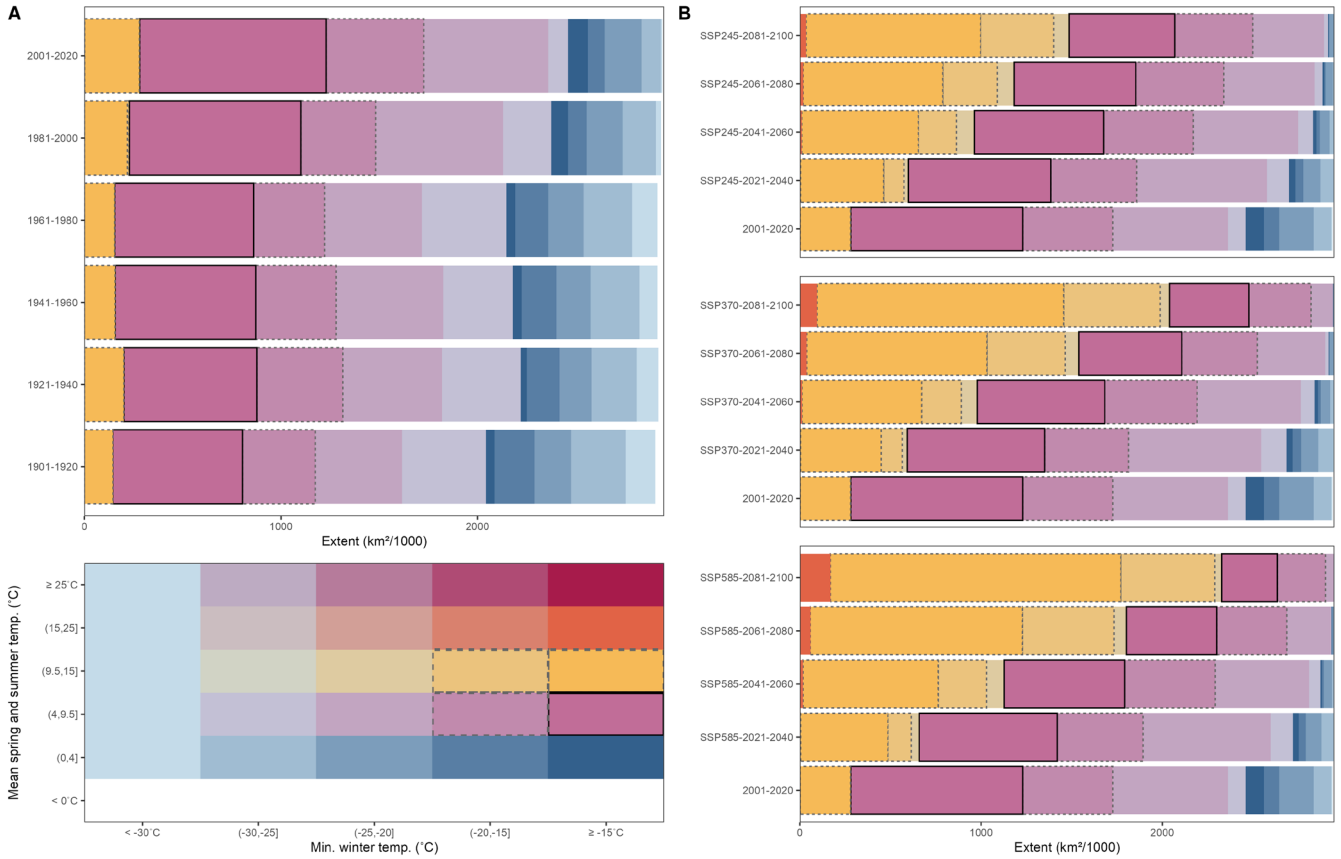

FIGURE 7 | Predicted extent (km^2/1000) of spruce beetle outbreak distribution based on the simplified climatic envelope for (A) historic and (B) projected periods. Black lines denote optimal temperature for spruce beetle outbreak distribution while grey dotted lines denote likely temperatures.

The spruce-dominated boreal forests of North America have rarely experienced spruce beetle outbreaks over the last 200 years (Bleiker and Keeling 2021). Models indicate that the primary limiting factor for spruce beetle outbreaks is minimum winter temperature, which has long been hypothesised (Holsten and Werner 1990; Werner et al. 2006). However, our approach does not allow us to test several non-mutually exclusive hypotheses that may further complicate spruce beetle outbreak dynamics across the boreal forest. First, there is some evidence that there are more predators and competitors of spruce beetles in boreal forests, which may limit irruptive potential (Raffa et al. 2008; Werner and Raffa 2006). Second, the interior boreal forests of Alaska are relatively dry and spruce trees have thin and dry phloem (Werner and Holsten 1985), which is hypothesised to decrease the synchrony of beetle emergence, a key feature that facilitates cooperative attack behaviour (Werner and Raffa 2006). Third, spruce beetles prefer white spruce (*P. glauca*) over black spruce (*P. mariana*) (Holsten and Werner 1990; Werner et al. 2006). Both species are primary components of the boreal forest (Beaudoin et al. 2014; Qian et al. 1998), but black spruce is generally distributed across poorly drained lowlands while white spruce is primarily found on upland or well-drained sites (Viereck et al. 1983). In Interior Alaska, black and white spruce together are estimated to comprise approximately 80% of forested areas (Yarie and Billings 2002). While these factors may affect the long-term trajectory of spruce beetle outbreaks, their effects likely pale in comparison to the rampant warming projected to occur across the boreal forest. Early-century predictions based on the three emissions scenarios considered suggest that the outbreak distribution of spruce beetle will expand to include boreal spruce forests in southwest Alaska, the southern interior of Alaska, and northern Alberta. Mid-century predictions for all three emissions scenarios suggest continued expansion of the outbreak distribution across Interior Alaska, the Yukon, and the prairie provinces. Finally, our models suggest that most spruce forests across North America will be climatically suitable for spruce beetle outbreaks by the end of the 21st century.

Large-scale spruce beetle outbreaks in the boreal forest may alter the extent and composition of boreal spruce forests, shift ecosystem carbon budgets from sink to source, and fundamentally alter disturbance regimes across the boreal forest. Previous outbreaks have been reported to cause conversions from forest to grasslands (Hess et al. 2019), a shift in forest composition toward increasing black spruce dominance (Allen et al. 2006), a shift toward late successional mountain hemlock in the wet Kenai Mountains (Boucher and Mead 2006), or potential physiognomic canopy recovery (Campbell et al. 2019). In addition, large-scale spruce beetle irruptions in the boreal forest would likely shift forests in this region from carbon sinks to carbon sources (Ghimire et al. 2015; Hicke, Allen, et al. 2012; Kurz et al. 2008). Finally, boreal forests are fire-prone landscapes and an expansion of outbreaks may lead to spruce beetle-fire interactions; however, dendrochronological studies found no association between historical spruce beetle outbreaks

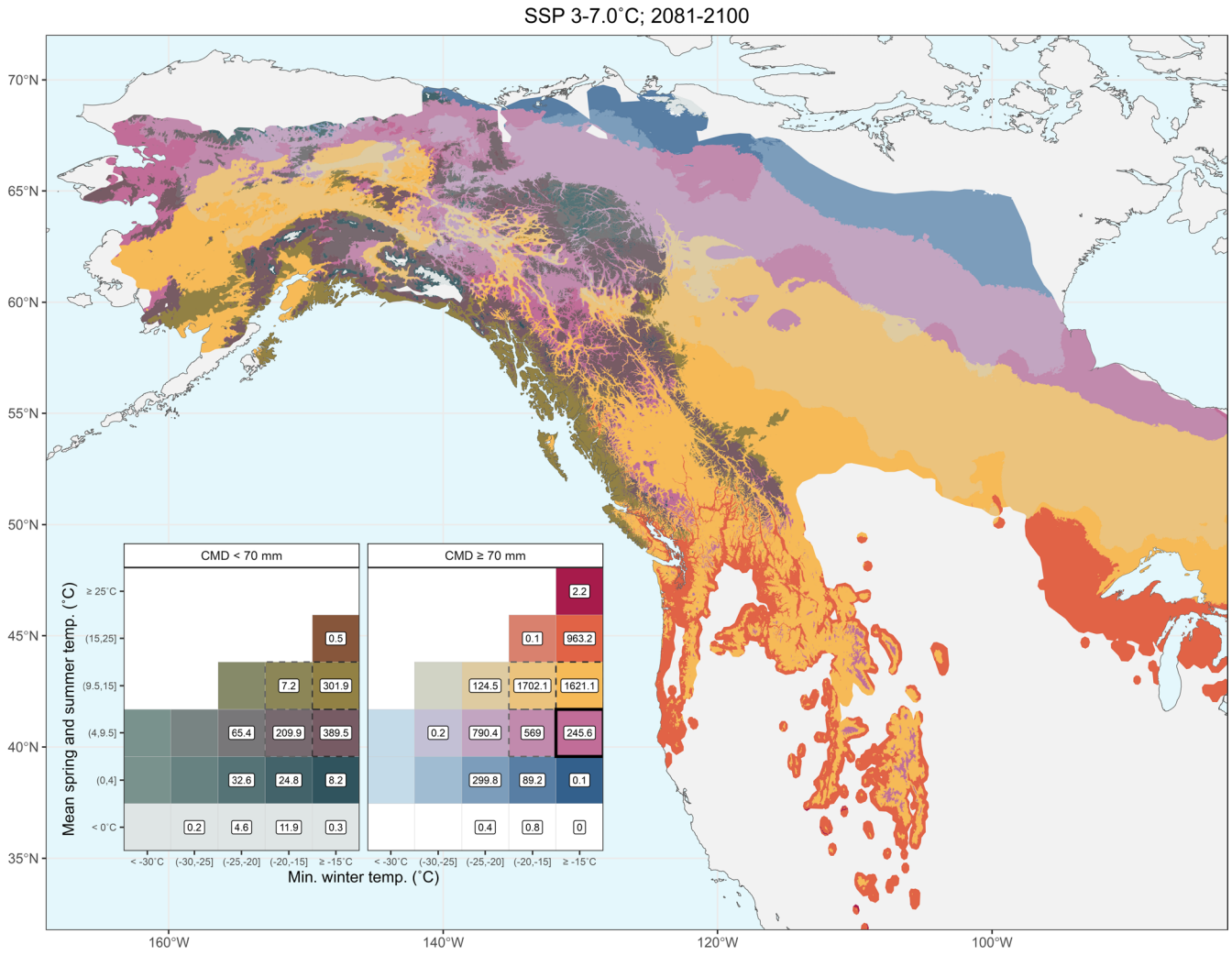

FIGURE 8 | Biogeographic distribution of climate moisture deficit (mm), minimum winter temperature (°C), and mean spring and summer temperature (°C) across western North America between 2081 and 2100 based on the SSP 3°C–7.0°C emissions scenario. Panel provides the key and the extent of each combination (in thousands of km^2). Black outline depicts the model-based optimal climatic envelope for spruce beetle and grey dashed outlines (in the panel) depict the likely climatic envelope for spruce beetle outbreak distribution. Maps for all 20-year periods and emissions scenarios are provided in Supplement 9. CMD = climate moisture deficit.

and fire across the wet Kenai Peninsula of Alaska (Berg and Anderson 2006), similar to other studies in the contiguous United States (Andrus et al. 2016; Hicke, Johnson, et al. 2012). Interactions may be possible due to heightened flammability in black spruce forests (Hansen et al. 2016), a cover type that may rise in dominance following spruce beetle outbreaks. Further research is required to better understand the interaction between spruce beetle and fire disturbance regimes and resultant successional trajectories as both disturbances expand due to warming climate conditions.

5 | Conclusions

An improved understanding of the geography and drivers of spruce beetle outbreaks will help regional monitoring and land management programs assess the risk and impacts of beetle outbreaks to forest resources, anticipate where changing conditions might emerge, and implement proactive management tactics. Aerial insect detection and forest inventory, monitoring, and mapping programs vary greatly across western North America with more established programs and greater data availability at southern latitudes where the distribution of outbreaks is projected to remain stationary and less developed programs and datasets further north where outbreaks are projected to expand. These programs play an important role for insect detection and management by quantifying the extent, characteristics, and susceptibility of host forest cover and detecting and monitoring outbreak initiation, spread, and impacts. Expanded detection and monitoring will be necessary where data is lacking and should prioritise early detection of outbreaks and identify where spruce beetle-caused tree mortality intersects with communities and infrastructure. Managing large-scale outbreaks is not currently feasible; however, silvicultural intervention can reduce impacts and enhance stand resilience through density reductions and the removal of recently infested material. Additionally, spruce beetle impacts can be mitigated with trap-trees, preventive insecticides, and the use of semiochemicals to disrupt spruce beetle behaviour. In stands and landscapes heavily impacted

TABLE 6 | Percent of spruce forests that are suitable (optimal + likely) for spruce beetle outbreaks in each ecoregion based on the thermal envelope. Ecoregion map is provided in Supplement 11.

Ecoregion	1901–1920	1921–1940	1941–1960	1961–1980	1981–2000	2001–2020	2021–2040	2041–2060	2061–2080	2081–2100
Canadian Rocky Mountains	80.1	85.6	82.3	83.3	87.6	89.9	95.0 (95.1–95.4)	95.5 (95.6–94.8)	92.8 (94.9–90.9)	88.3 (93.1–83.4)
Cascades/Sierra Nevada	92.5	89.9	93.8	93.8	91.2	85.1	81.6 (81.5–80.5)	73.5 (74.0–69.6)	62.3 (69.3–57.6)	50.7 (63.5–41.4)
Northern Boreal Forests	1.6	2.7	2.4	1.9	3.9	7.4	8.3 (9.0–9.7)	14.5 (13.9–16.3)	23.5 (17.6–30.9)	46.5 (22.3–75.2)
Northern Forests	16.8	20.6	22.2	18.3	29.5	37.8	37 (40.4–41.1)	54.4 (52.1–61.9)	76 (63.3–80.2)	84.4 (73.4–79.9)
Northern Rocky Mountains	6.7	10.7	9.2	7.1	18.9	32.8	39.6 (42.9–43.2)	58.1 (56.1–62.9)	74.4 (65.4–80.9)	88.1 (73.4–93.9)
Pacific Coastal Temperate Rainforest	74.5	79.9	77.4	75.8	82.6	86.4	88.2 (88.6–88.6)	88.5 (88.3–87.4)	86.5 (87.6–85.5)	83.0 (86.5–79.3)
Southern Rocky Mountains	91.8	93.2	91.8	92.0	93.8	94.7	92.7 (92.7–92.1)	88.2 (89.4–85.6)	78.9 (85.4–74.0)	67.2 (80.9–55.6)
Other	36.1	37.5	38.2	36.8	41.8	41.6	36.2 (36.8–36.0)	35.9 (35.9–39.0)	45.9 (40.8–49.1)	51.0 (45.5–47.8)

by tree mortality, hazard tree removal, fuel hazard mitigation, and managed regeneration may reduce impacts to communities, and future wildfire and spruce beetle risk.

Author Contributions

Michael C. Howe: conceptualisation, data curation, formal analysis, funding acquisition, investigation, methodology, software, visualisation, writing – original draft preparation, writing – review and editing. **Karen Hutten:** conceptualisation, project administration, writing – review and editing. **Jessie Moan:** conceptualisation, project administration, writing – review and editing. **Kellen N. Nelson:** conceptualisation, investigation, funding acquisition, project administration, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available on Dryad. https://doi.org/10.5061/dryad.jm63xsjpk.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** jbi70177-sup-0001-Tables.docx.