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Risk of co-evolved pest damage to non-native Douglas-fir plantations

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ABSTRACT

The high productivity of forests planted with non-native tree species is partly dependent on enemy release, a benefit that may erode as specialist herbivores accumulate over time. The accidental introduction of co-evolved insect herbivores from the native range of the planted tree can thus have severe ecological and economic consequences. Anticipating these risks requires identifying not only which pests can establish and cause damage, but also where damaging outbreaks might occur. Here, we used historical pest damage data from North America to model the climatic suitability for pest damage to Douglas-fir (*Pseudotsuga menziesii*) where it is utilized in plantation forestry in other world regions. We focused on the three most damaging pests of Douglas-fir in its native range: Douglas-fir beetle (*Dendroctonus pseudotsugae*), Douglas-fir tussock moth (*Orgyia pseudotsugata*), and Western spruce budworm (*Choristoneura freemani*). Results show that climatic factors strongly constrain potential establishment of Douglas-fir and other host trees of these pest species, whereas climatic suitability for damage exhibits weaker and species-specific patterns. In two regions where most Douglas-fir is planted outside its native range, Europe and New Zealand, currently planted areas are broadly climatically unsuitable for damaging pest outbreaks. These findings highlight the importance of assessing the climatic niche of pest damage rather than simply modeling the niche of pest establishment when assessing pest invasion risk and provides a framework to inform proactive biosecurity and forest management strategies.

1. Introduction

Escalating global demand for forest products has led to increasing use of plantation forestry worldwide (FAO, 2010, 2020). In many regions, extremely high rates of forest productivity are achieved by planting non-native tree species (Keča et al., 2019). A major contributing factor to the exceptionally high growth rates exhibited by non-native trees (and other non-native plants) is "enemy release" which refers to the decreased impact of co-evolved herbivores and pathogens that are present in a plant species' native range but absent in the introduced range (Keane and Crawley, 2002; Liu and Stiling, 2006). Enemy release can reduce pest and pathogen pressure on introduced species, causing increased productivity of non-native crops but also decreased environmental impacts of invasive plants (Pearse and Rosenheim, 2020, G. D. Martin et al., 2025). The initial advantage conferred by enemy release is, however, rarely permanent and gradually erodes as trees accumulate herbivores over time (Hawkes, 2007). This erosion proceeds both as native herbivores and pathogens expand their host ranges onto introduced trees, but also through invasions of pest species from the trees' native ranges or elsewhere (Crous et al., 2016). Although most tree pest invasions cause limited damage, a small fraction inflict severe damage, undermining the health and value of host trees, and contributing to the increasing social, ecological, and economic costs (Aukema et al., 2011).

In addition to barriers to dispersal, the geographical distribution of herbivorous insects is constrained by two primary factors: the presence of suitable host plants and the availability of suitable climatic conditions (Menéndez, 2007; Weed et al., 2013). Climatic niche models are therefore powerful tools for forecasting the potential distribution of herbivorous insects (Peterson, 2003) and have been widely used to predict the potential for non-native insect herbivores to establish across specific geographic areas (e.g. Lantschner et al., 2017). Implementation of biosecurity measures to successfully prevent invasions, however, requires anticipating not only where non-native insects may establish, but also where they are likely to cause damaging outbreaks—an aspect that is not usually addressed in species distribution modeling (Williams and Liebhold, 2002).

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) exemplifies this

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challenge as one of the most widely planted tree species in plantation forestry globally (Lavender and Hermann, 2014). Native to a vast expanse of western North America, Douglas-fir has been extensively introduced and cultivated in temperate regions worldwide, especially across Europe and New Zealand (Fig. 1). Assessments of insect herbivores feeding on Douglas-fir in its planted range indicate that Douglas-fir has recruited a significantly lower diversity of herbivorous insects compared to its native range despite several decades of extensive planting (Roques et al., 2006; Spiecker et al., 2019).

The initial benefits of enemy release could be adversely affected if it diminishes in the future following long-term cultivation of Douglas-fir in non-native regions. This decline is likely to occur through two mechanisms: first, native or novel generalist herbivores could expand their diet to include Douglas-fir as a host (Pötzelsberger et al., 2021; Roques et al., 2006); and second, coevolved herbivores could become reunited with Douglas-fir following accidental introduction from their native range (Schmid et al., 2014). A good example of such invasion is the accidental introduction of the seed chalcid, *Megastigmus spermotrophus*, (Roques and Skrzypczyńska, 2003), which has already caused significant reductions in Douglas-fir seed viability and productivity in Europe and, to a lesser extent, in New Zealand and other parts of its introduced range (Germano et al., 2025; Lee et al., 2021; Mailleux et al., 2008).

Given the ongoing global movement of goods through trade and travel, further accidental introductions of tree pests are increasingly likely (Brockerhoff and Liebhold, 2017; Fenn-Moltu et al., 2023). Several major insect pests of Douglas-fir from the native North American range have not yet been introduced into the planted ranges of Douglas-fir worldwide. These unintroduced, co-evolved herbivores

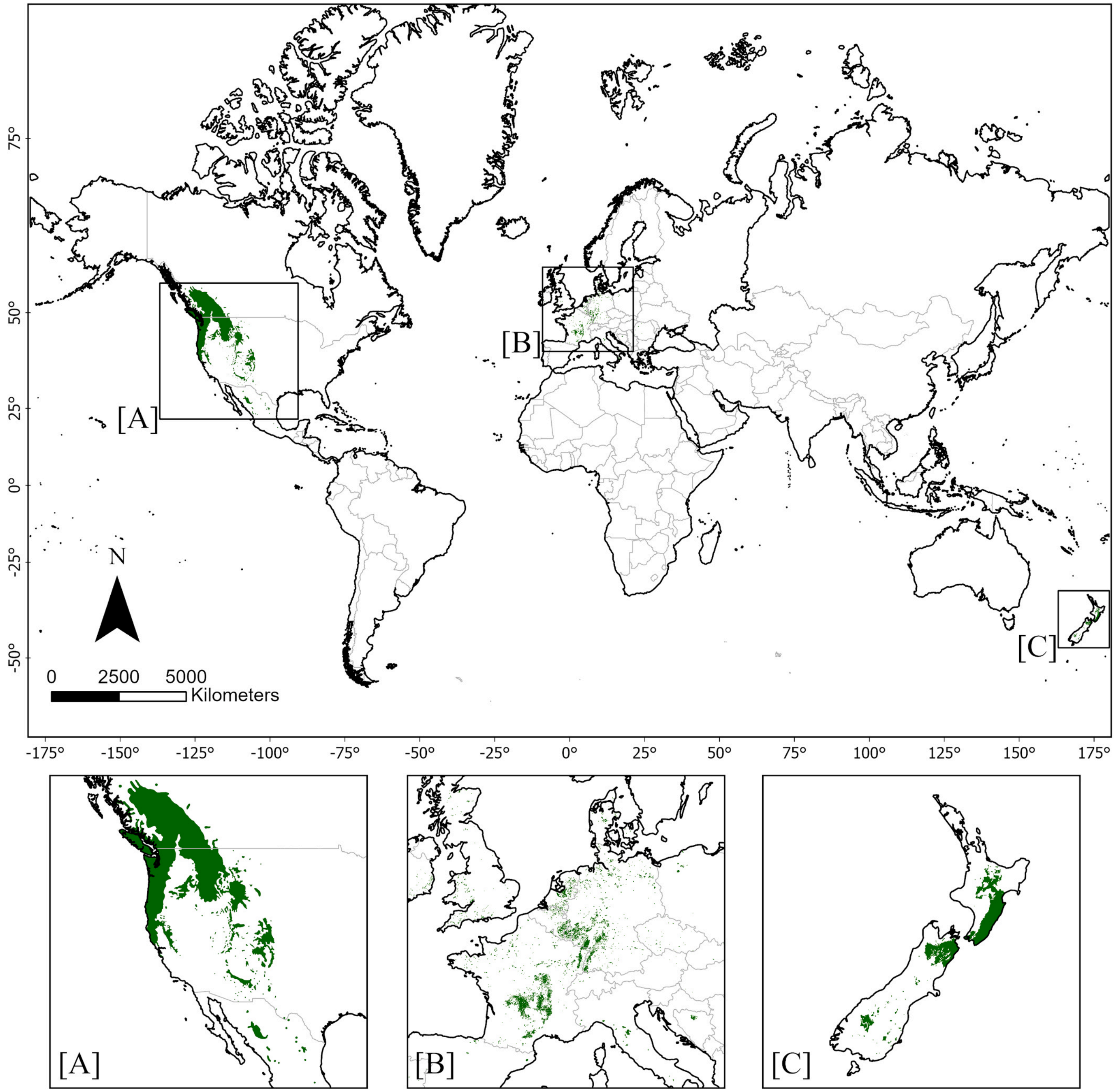


Fig. 1. World map showing the native range of Douglas-fir in [A] North America and its introduced (planted) ranges in [B] Europe and [C] New Zealand (Little, 1971; Ministry for the Environment, 2016; San-Miguel-Ayanz et al., 2016).

represent significant future threats, yet their potential to establish and cause damaging outbreaks outside their native range remains unquantified. Consequently, a pre-emptive risk assessment is essential for safeguarding the economic viability of plantations worldwide and could provide useful guidance to forest biosecurity practices. To address this, we assess global vulnerability of Douglas-fir plantations to the three most damaging North American insect herbivores that cause recurring, economically significant outbreaks to Douglas-fir in its native range: the Douglas-fir beetle (*Dendroctonus pseudotsugae*), the western spruce budworm (*Choristoneura freemani*), and the Douglas-fir tussock moth (*Orgyia pseudotsugata*) (Furniss and Carolin, 1977; Spiecker et al., 2019). Given their recognized potential for damage in Europe, these species are currently listed as quarantine pests that are recommended by EPPO for regulation (EPPO A1 List).

We hypothesize that regions with established Douglas-fir plantations (e.g., in Europe and New Zealand) currently support climatic conditions that are suitable for the establishment of these pests. However, the magnitude of the potential threat, specifically, whether these conditions can trigger damaging pest outbreaks, and the extent of its overlap with the planted range of Douglas-fir, remains undetermined. In this study, we proactively address this uncertainty by applying species distribution models (SDM) to characterize the distinct climatic niches of the three pests and forecast risk of their potential damage to Douglas-fir plantations in its non-native range.

2. Methods

2.1. Data collection and preparation

We generated two spatially thinned occurrence datasets for each of the three pest species to model (1) host range suitability and (2) pest damage risk.

2.1.1. Host tree species occurrence

Spatial coordinates of host tree species were sourced from forest inventory plots located across Canada, the USA, and Mexico. Data for these plots were compiled from the Government of Canada's Multi-Agency Ground Plot (MAGPlot) database (Government of Canada, 2025), the USDA Forest Service Nationwide Forest Inventory and Analysis database (FIADB; USDA Forest Service, 2024), and the Mexican National Forest and Soil Inventory (Gobierno de México, 2020). These data were combined to create occurrence datasets for the host trees of each pest species by selecting inventory plot locations where specific tree species were recorded.

Douglas-fir beetle (DFB) is characterized by its high host specificity, feeding exclusively on Douglas-fir (Schmitz and Gibson, 1996). In contrast, the host datasets for the other two pest species were more diverse. The Douglas-fir tussock moth (DFTM) dataset contained occurrence records for hosts Douglas-fir, grand fir (*Abies grandis*), white fir (*Abies concolor*), and trees recorded simply as "fir spp". (Pederson et al., 2020), while the Western spruce budworm (WSBW) dataset consisted of an even broader range of host tree species including Douglas-fir, grand fir, white fir, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), western larch (*Larix occidentalis*), blue spruce (*Picea pungens*), corkbark fir (*Abies lasiocarpa var. arizonica*), and "fir spp". (Fellin and Dewey, 1982).

The extracted host tree species coordinates were restricted to areas west of the Mississippi River to exclude inventory plots in the east where these tree species occurred outside of their native range. Additionally, we removed all species occurrence records for which bioclimatic variables could not be assigned. This primarily occurred when the intentional 'fuzzing' of FIADB plot coordinates shifted a point's location into the ocean. While some presence coordinates from the FIA database were 'fuzzed' for privacy, previous analyses indicate that use of 'fuzzed' FIADB coordinates does not significantly impact SDM results (Gibson et al., 2014). Because the density of inventory plots varied among Canada, the USA, and Mexico, host tree occurrence records were spatially thinned to a uniform minimum separation distance of 10 km using a random-order, distance-based thinning procedure implemented using the *sf* package in R.

A 200 km buffer was delineated around the host occurrence points for each pest species, within which 10,000 background points were randomly generated. These background points characterize the available climatic conditions and were used for MaxEnt modelling. Pseudo-absence points, similar in number to the host occurrences, were also generated by randomly locating points within a 25 km to 250 km buffer surrounding the host occurrences. These points indicate areas surrounding the known range not currently occupied by the species and were used exclusively for the PCA analysis. All tree occurrence and background coordinates were snapped to a 30 arc second raster to match the bioclimatic raster layer described below.

2.1.2. Pest damage occurrence

Mapped outbreak extents for DFB, DFTM, and WSBW from 1997 to 2023 were compiled across their native ranges in western North America. These data were sourced from the USDA Forest Service's National Insect and Disease Detection Survey database (USDA Forest Service, 2021, Regions 1–6), and from the British Columbia Forest Health Aerial Overview Surveys (AOS; Government of British Columbia, 2025). These programs conduct annual aerial surveys, along with targeted ground truthing, to map visible forest disturbances. This process results in the annual compilation of polygons circumscribing damage attributed to specific damage agents. The host tree occurrences and the outbreak polygons were discretized into 30 arc second raster cells to match the resolution of the bioclimatic rasters described below.

Host tree occurrence raster cells intersecting outbreak cells were classified as "damage presence" and all remaining host locations were classified as "damage absence". A separate 10 km thinning was applied to both classes. Though both DFTM and WSBW are known to be present in Mexico, there is no evidence of outbreaks or damage there (Coleman et al., 2014). Therefore, all Mexican host tree presence cells were classified as damage-absence for these species. In contrast, all DFB host presence and absence cells in Mexico were excluded from the damage dataset because although damage from this species has been reported there (Salinas-Moreno et al., 2010; Salinas-Moreno et al., 2004), comparable aerial surveys are lacking.

2.1.3. Climatic data

Nineteen bioclimatic variables, representing annual temperature and precipitation averaged across three decades (1970–2000), were acquired from the WorldClim 2.1 dataset (Supplementary Table S1, Fick and Hijmans, 2017). This global raster dataset characterizes local climatic conditions at a spatial resolution of 30 arc-seconds (~1 km^2 in mid-latitude world regions).

2.1.4. Forest plantations and Douglas-fir planted range

Global spatial data describing the location of forest plantations were obtained as a shapefile from the *Spatial Database of Planted Trees v2* (SDPT) (Richter et al., 2024) and were rasterized to a 1 km spatial resolution for subsequent analysis. The terrestrial boundaries of Europe (including European countries of former Soviet Union and western Russia) and New Zealand were sourced from the 'World continents' and 'World countries generalized' shapefiles available via ArcGIS Hub (Esri, 2025a, 2025b).

The planted distribution of Douglas-fir was compiled by integrating multiple datasets. For Europe, Douglas-fir occurrence in forest plantations was extracted from the European Forest Atlas, provided in raster form at a native resolution of 1 km (de Rigo et al., 2016; San-Miguel-Ayanz et al., 2016). For New Zealand, Douglas-fir plantation data were obtained from the Ministry for the Environment Data Service in raster format at a native resolution of 100 m (Ministry for the Environment, 2016). These datasets were intersected with the SDPT layer to produce a unified map of the global planted range of Douglas-fir.

2.2. Principal Component Analysis

To visualize the bioclimatic niche of hosts and damage caused by each pest species, we performed a Principal Component Analysis (PCA) using the 19 bioclimatic variables obtained from the WorldClim 2.1 dataset. For each species, a PCA model was estimated using host presence and pseudo-absence records. We then created a biplots of PCA1 vs. PCA2 with points classified as either host absent, host present without damage or host present with pest damage. Separate PCA biplots were generated for each pest species. To more closely focus on the climatic niche of pest damage, we fit a second set of PCA models using data only from where host trees were present. From these, we created biplots plotting where hosts were without damage or hosts were present with pest damage. All analyses were conducted and visualized in R version 4.4 (RStudio Team, 2022) using the *prcomp*, *ggplot2*, and *ggrepel* packages, and final plots were compiled using *patchwork*.

2.3. Climatic niche modelling and validation

Using the curated datasets, we separately modeled the climatic niche of host tree ranges and the niche of damage for each pest species using the MaxEnt algorithm (Phillips et al., 2025) within the *dismo* package in R. For each pest species, host tree distributions were modeled using 19 bioclimatic variables derived from WorldClim 2.1, with the 10,000 randomly generated background points located within 200 km of the host occurrences. To model damage, for each pest species, the extracted damage-presence coordinates served as the presence points, and their full host range (combined set of damage-presence and damage-absence points) were used as the background points in the MaxEnt model.

Model performance was evaluated using a 5-fold cross-validation approach. The full dataset for each species was randomly partitioned into five equal subsets using the *kfold* function in *dismo*. In each of the five iterations, four subsets were used to train the MaxEnt model, and the remaining subset served as an independent test dataset. The trained model was then used to predict suitability values for the test data, and model performance was assessed using the *evaluate* function in *dismo*. For the host range predictions, the MaxEnt models were fit and cross validated using the host presence and background points. However, for the pest damage predictions, although MaxEnt models were fit using background points (damage-presence + damage-absence), model evaluation was conducted using only the damage-absence data. This approach provides a more robust assessment of model performance by testing predictions against confirmed absences rather than potentially suitable background locations.

We calculated the receiver operating characteristic curve and the area under the curve (AUC) across the five cross-validation folds to evaluate the robustness of our species distribution models (Hirzel et al., 2006). Additionally, the True Skill Statistic (TSS), derived from the sensitivity (true positive rate) and specificity (true negative rate) of the models (TSS = Sensitivity + Specificity - 1), was calculated for each model as a measure of classification accuracy (Yoon and Lee, 2023). Finally, the *predict* function was used to generate continuous global climate suitability rasters at the same 30 arc second resolution as the bioclimatic data. We then converted these continuous suitability values into binary predictions of habitat suitability (suitable / unsuitable) by applying the optimal thresholds for each species. The optimal threshold corresponded to the suitability value at which the True Skill Statistic (TSS) for that species was highest.

2.4. Spatial overlap analysis

The raster datasets on the distribution of planted Douglas-fir in Europe and New Zealand (Section 2.1) were overlaid with the Maxent-predicted suitability maps to calculate the proportion of the planted range of Douglas-fir that the model classified as suitable for Douglas-fir and the proportion that the model predicted as suitable for damage from each of the three pests. Predicted pest suitability occurring outside the modeled host distribution was excluded prior to analysis, as pest damage cannot occur in the absence of the host. All spatial data were projected to the Cylindrical Equal Area (sphere) (WKID: 53034) coordinate system and resampled onto a common 1 km^2 grid. Area estimates therefore represent the number of 1 km^2 grid cells. Geodesic area calculations were performed using the '*tabulate area*' function in ArcGIS Pro.

3. Results

3.1. Pest damage extraction

The three pest species exhibited significant variation in cumulative area damaged across their native North American range during the 27-year period (1997–2023) (Fig. 2, Table 1). WSBW recorded the largest impact, with a cumulative damaged area spanning 120,167.38 km^2. DFB affected a total area of 31,656.26 km^2, while DFTM registered the lowest extent of damage at 5080.95 km^2.

3.2. Host-tree extraction

The extraction of host tree coordinates from the inventory datasets across western North America yielded a total of 75,740 plot locations where at least one of the ten host tree species were present (Supplementary Table S2). This dataset comprised 42,918 host-tree coordinates for DFTM, 31,818 for DFB, and 75,653 for WSBW. Spatial thinning (10 km) yielded a total of 8462 host tree coordinates for DFTM, 7879 for DFB, and 12,128 for WSBW. Among the hosts of all the three pest species, Douglas-fir was present most frequently, accounting for 42% of trees recorded. After the separate spatial thinning (10 km) of 'damage presence' and 'damage absence' points, we obtained 204 damage presence points and 5391 damage absence points for DFTM, 2509 presence and 4617 absence points for DFB, and 1946 presence and 2951 absence points for WSBW, used to model pest damage (Supplementary Table S3).

3.3. Principal component analysis

The first two principal components explain between 75.2% (WSBW) and 76.7% (DFTM) of the total variance across all presence and pseudo-absence locations of host trees (Supplementary Figure S1) and reveal clear differences between the three pests. For DFTM, the PC1 axis defines a gradient from cool to hot climates, with positive loadings for most temperature related variables (BIO1, BIO2, BIO3, BIO5, BIO6, BIO8, BIO9, BIO10, BIO11) and the negative side remaining largely empty. The PC2 axis contrasts climates with high precipitation (BIO12, BIO13, BIO16, BIO18, BIO19) with those defined by temperature seasonality (BIO4, BIO7). For DFB, PC1 captures an aridity gradient, with high positive loadings for variables related to summer temperature (BIO2, BIO5, BIO10) and negative loadings associated with summer precipitation. As in DFTM, PC2 contrasts high-precipitation climates with those exhibiting strong temperature seasonality. For WSBW, PC1 distinguishes warmer, climatically stable environments (positive loadings for BIO3, BIO6, BIO11) from highly seasonal climates (negative loadings for BIO4, BIO7). PC2 is primarily associated with precipitation, with positive loadings for BIO12, BIO14, and BIO17, reflecting climates with high year-round rainfall.

Exclusively examining host tree presence locations, we find that the climatic niches of host-ranges of the three pests were fundamentally similar with the first two principal components explaining between 71.4% (WSBW) to 76.1% (DFTM) of the total climatic variance (Fig. 3). PC1 described a primary climatic gradient contrasting warm, wet, and thermally stable environments with cold, dry, and highly continental environments. The positive axis of PC1 was strongly associated with

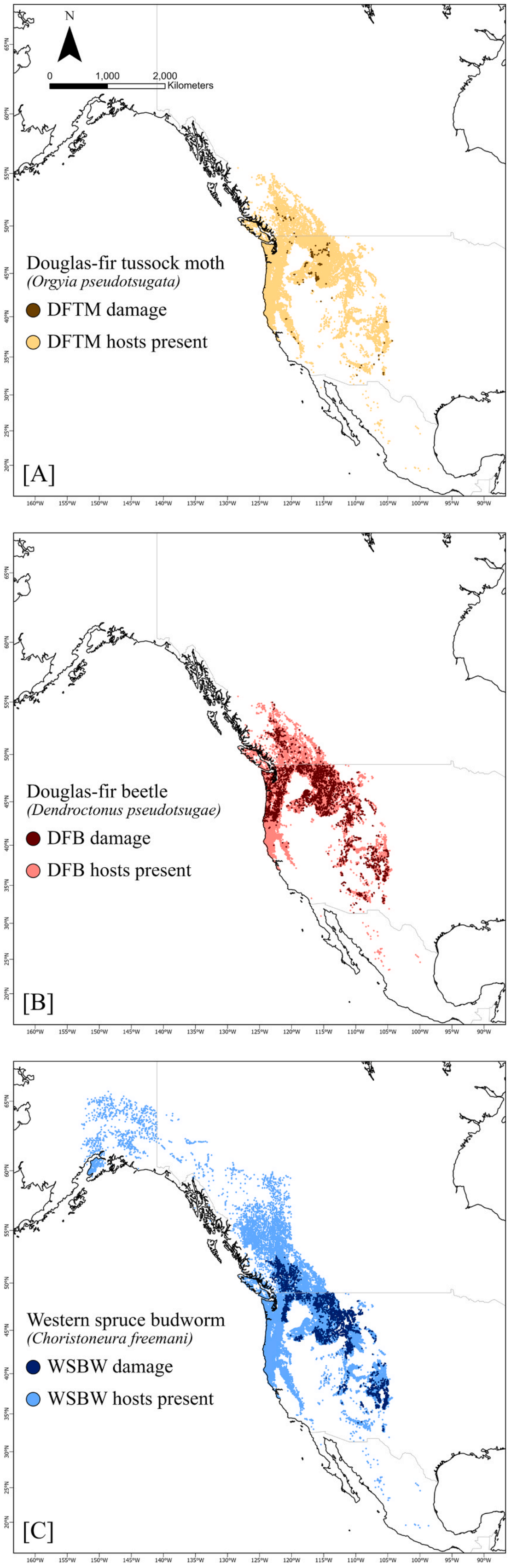


Fig. 2. Map of western North America showing locations of cumulative damage (1997–2023) and presence of hosts for [A] Douglas-fir tussock moth, [B] Douglas-fir beetle, and [C] Western spruce budworm.

Table 1
Cumulative area damaged by Douglas-fir tussock moth (DFTM), Douglas-fir beetle (DFB), and Western spruce budworm (WSBW) in Canada and the USA from 1997 to 2023.

Species	Country	Damage (km^2)
DFTM	Canada	447.73
	USA	4633.22
DFB	Canada	8885.55
	USA	22,770.71
WSBW	Canada	38,565.04
	USA	81,602.34

variables representing annual and extreme temperatures (BIO1, BIO6, BIO9, BIO11) and total and seasonal water availability (BIO12, BIO13, BIO15, BIO16, BIO19), while the negative axis of PC1 was associated with temperature variability or continentality (BIO4, BIO7). PC2 describes a secondary climatic gradient contrasting environments with severe dry-season water limitation characterized by high, sustained maximum warmth and daily thermal stability. PC2 was found to be positively associated with precipitation and aridity (BIO14, BIO17, BIO18) and negatively associated with maximum warmth and thermal stability (BIO2, BIO3, BIO5, BIO8, BIO10).

3.4. *MaxEnt model analysis*

Numbers of presence points of the host species and pest damage, along with corresponding background points used in the MaxEnt modeling, are shown in Table 2. DFTM had the lowest damage incidence, with damage present in only 204 of 8462 host presence points (~2.4%). Damage attributed to WSBW was observed in 1946 of 12,128 host presence points (~16.0%). In contrast, DFB exhibited the highest observed incidence, with 2509 points damaged out of a total of 7879 host presence points (~31.9%). These numbers of damage points were over 13-fold higher for DFB than for DFTM.

Host range model of DFTM was predominantly influenced by BIO5 and BIO19, which collectively explained over 40% of the model's explanatory power (Supplementary Table S4). BIO1, BIO10, and BIO12 accounted for an additional 30%. The host range model of DFB was mainly influenced by BIO5, BIO10 and BIO19, which collectively explained over 65% of the model's explanatory power. In contrast, the main bioclimatic variables contributing to the predictive power of WSBW's host range model were BIO7 (17.53%), BIO10 (29.46%), and BIO19 (11.74%). Host presence models for all three pests demonstrated good discriminatory power, with AUC values ranging from 0.873 ± 0.003 (WSBW) to 0.885 ± 0.001 (DFTM) (Table 3). The resulting True Skill Statistic (TSS) scores confirmed moderate to good overall accuracy, ranging from 0.626 ± 0.006 (WSBW) to 0.663 ± 0.003 (DFTM), indicating that MaxEnt is effective in mapping the potential distribution of these pests.

Damage models for each of the three pests had distinct climatic drivers. The DFB model was primarily driven by BIO3 (12.70%), BIO5 (25.76%), BIO10 (13.72%) and BIO18 (14.78%), while the DFTM model was influenced by BIO5 (11.59%), BIO6 (9.63%), BIO9 (13.01%), BIO14 (16.42%), and BIO15 (9.67%). In contrast, the WSBW damage model was mainly influenced by thermal variables BIO3 (17.08%), BIO5 (13.13%) and BIO11 (19.30%). Models forecasting pest damage were lower in their predictive performance. While the DFTM (AUC = 0.852 ± 0.019, TSS = 0.565 ± 0.037) and WSBW (AUC = 0.858 ± 0.005, TSS = 0.573 ± 0.007) damage models achieved moderate and useful accuracy, the DFB damage model was substantially weaker (AUC 0.662 ± 0.006, TSS = 0.260 ± 0.012). Its low predictive power was driven primarily by poor specificity (0.432 ± 0.026), suggesting that it suffers from a high false-positive rate and a tendency toward over-prediction.

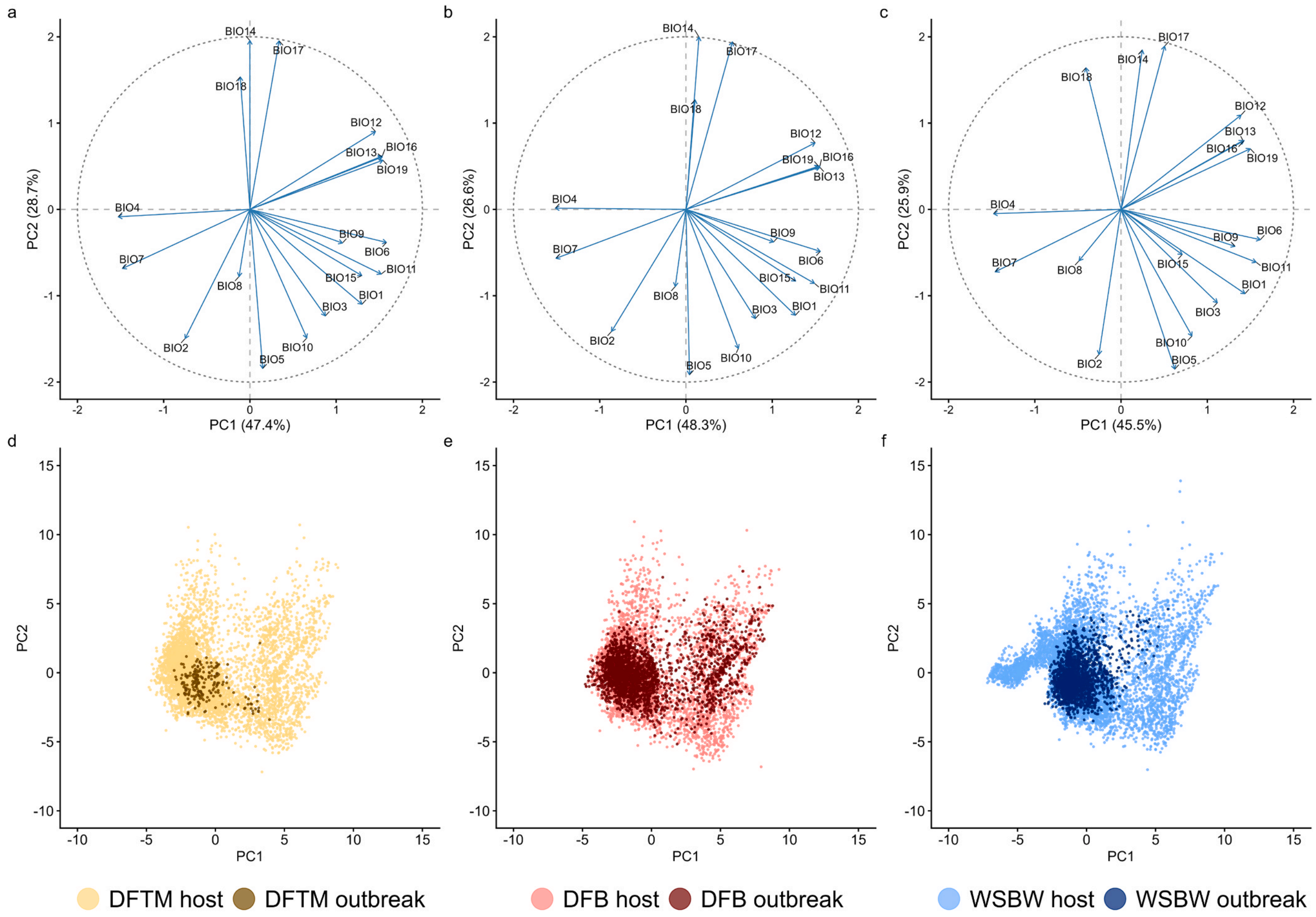


Fig. 3. Summary of principal components analysis (PCA) quantifying the bioclimatic niche of host tree ranges and of pest damage (outbreak). Variable loadings and the distribution of damage presence and absence records along PCA1 and PCA2 axes for Douglas-fir tussock moth (a, d), Douglas-fir beetle (b, e), and western spruce budworm (c, f).

Table 2
Count of presence and background points used for MaxEnt modelling of the native host ranges of Douglas-fir tussock moth (DFTM), Douglas-fir beetle (DFB), and Western spruce budworm (WSBW).

Species	Host range		Pest damage	
	Point type	Count	Point type	Count
DFTM	Presence	8462	Presence	204
	Background	10,000	Background	8462
DFB	Presence	7879	Presence	2509
	Background	10,000	Background	7879
WSBW	Presence	12,128	Presence	1946
	Background	10,000	Background	12,128

3.5. Climatic Suitability Predictions

The three pests had comparable predicted areas suitable for their hosts in Europe, with WSBW hosts being climatically suitable across just over 4.68 M km^2, followed by DFTM and DFB at 3.93 M km^2 and 3.51 M km^2 respectively. In New Zealand, the predicted suitable host ranges of the three pests were also comparable at 0.2 M km^2 for DFB and DFTM and 0.15 M km^2 for WSBW (Table 4). These predicted host suitability ranges exhibited extensive potential reach, covering an average of 41.11% and 71.06% of Europe and New Zealand respectively. Conversely, predicted areas suitable for pest damage varied considerably between species. The highest damage was predicted for DFB at 3.00% of the total land area of Europe, and WSBW and DFTM following with 2.86% and 0.05% respectively. In New Zealand, damage was only predicted for DFB, at just under 4% of the available land area, while New Zealand was found to be entirely climatically unsuitable for DFTM and WSBW outbreaks.

Table 3
MaxEnt evaluation metrics for forecasting host range and pest damage of Douglas-fir tussock moth (DFTM), Douglas-fir beetle (DFB), and Western spruce budworm (WSBW).

Metric	Host range			Pest damage		
	DFTM	DFB	WSBW	DFTM	DFB	WSBW
AUC	0.885 ± 0.001	0.876 ± 0.002	0.873 ± 0.003	0.852 ± 0.019	0.662 ± 0.006	0.858 ± 0.005
Optimal Threshold	0.437	0.444	0.483	0.404	0.529	0.431
Sensitivity at optimal threshold	0.919 ± 004	0.909 ± 006	0.867 ± 006	0.848 ± 0.021	0.828 ± 0.026	0.884 ± 0.011
Specificity at optimal threshold	0.745 ± 004	0.734 ± 003	0.758 ± 0.010	0.717 ± 0.041	0.432 ± 0.026	0.689 ± 0.010
TSS at optimal threshold	0.663 ± 0.003	0.643 ± 0.004	0.626 ± 0.006	0.565 ± 0.037	0.260 ± 0.012	0.573 ± 0.007

The total area of planted forests was estimated at 4098,494 km^2 in Europe and 84,821 km^2 in New Zealand. In Europe, 51.44–68.03% of the area of planted forests was predicted to be climatically suitable for

Table 4

Spatial overlap (km^2 and %) between total land area, planted forest area, and planted Douglas-fir area of Europe and New Zealand with predicted host and pest damage ranges of the pest species.

Species	Region	Area (km^2)	Predicted host range (km^2)	Predicted host range with predicted pest damage (km^2)	Planted forest area (km^2)	Predicted host range within planted forests (km^2)	Predicted host range within planted forests with predicted pest damage (km^2)	Area of planted Douglas-fir (km^2)	Predicted host range with planted Douglas-fir (km^2)	Predicted host range with planted Douglas-fir and predicted damage (km^2)
DFTM	Europe	9836,250	3934,802 (40.00%)	4628 (0.05%)	4098,494	2307,961 (56.31%)	2285 (0.06%)	67,033	66,456 (99.22%)	0 (0.00%)
	NewZealand	261,720	202,231 (77.27%)	0 (0.00%)	84,821	83,756 (98.74%)	0 (0.00%)	18,997	18,749 (98.98%)	0 (0.00%)
DFB	Europe	9836,250	3509,983 (35.68%)	294,922 (3.00%)	4098,494	2108,182 (51.44%)	141,886 (3.46%)	67,033	66,241 (99.19%)	2709 (1.32%)
	NewZealand	261,720	200,634 (76.66%)	9742 (3.72%)	84,821	83,379 (98.30%)	2664 (3.14%)	18,997	18,637 (99.34%)	969 (0.24%)
WSBW	Europe	9836,250	4686,267 (47.64%)	281,050 (2.86%)	4098,494	2788,255 (68.03%)	157,259 (3.84%)	67,033	65,075 (95.61%)	309 (0.55%)
	NewZealand	261,720	155,080 (59.25%)	0 (0.00%)	84,821	61,952 (73.04%)	0 (0.00%)	18,997	17,821 (96.88%)	0 (0.00%)

the host ranges of the three species, compared to New Zealand, where despite the much smaller extent of planted forests, 73.04–98.74% of each species' predicted host range fell within these areas (Fig. 4). Only a small proportion (0.06–3.84%) of Europe's planted forest area was predicted to be suitable for pest damage, while in New Zealand, the predicted pest damage within planted forests was absent for DFTM and WSBW and remained low for DFB (3.14%).

The planted range of Douglas-fir in Europe, was estimated at 67,033 km^2 and occupying 1.64% of the planted forest area of Europe, which is nearly three times larger than its planted range in New Zealand, estimated at 18,997 km^2 and occupying 22.40% of the planted forest area of New Zealand. In both Europe and New Zealand, nearly the entire planted area of Douglas-fir is predicted as climatically suitable for the hosts of the pest species. However, only a very small fraction of this area overlapped with predicted pest damage (Table 4).

4. Discussion

Our analyses on the potential for three key pests to damage non-native Douglas-fir plantations revealed that even though the entire planted area in Europe and New Zealand is climatically suitable for Douglas-fir, damage from these co-evolved pests would be expected only in a small area. The three most damaging insect pests of Douglas-fir in its native range therefore do not appear to be a major threat to plantations in non-native regions, at least under current climatic conditions.

The approach taken in this study stands in contrast with the traditional application of climatic niche models for mapping pest invasion risk that generally predicts where pest species are likely to establish, but not where they are likely to cause damage (Venette et al., 2017, Srivastava et al., 2021). This traditional approach uses pest species occurrence records to fit models of climatic suitability, but pest species generally can only occur in locations where hosts also occur. Thus, traditional pest occurrence SDMs may largely reflect the climatic limits to host plant occurrence rather than the limits of the pest species itself. Here, we separated out the effects of climate on the occurrence of hosts from the effects on pest damage occurrence by fitting two separate models.

4.1. Climatic suitability for host trees

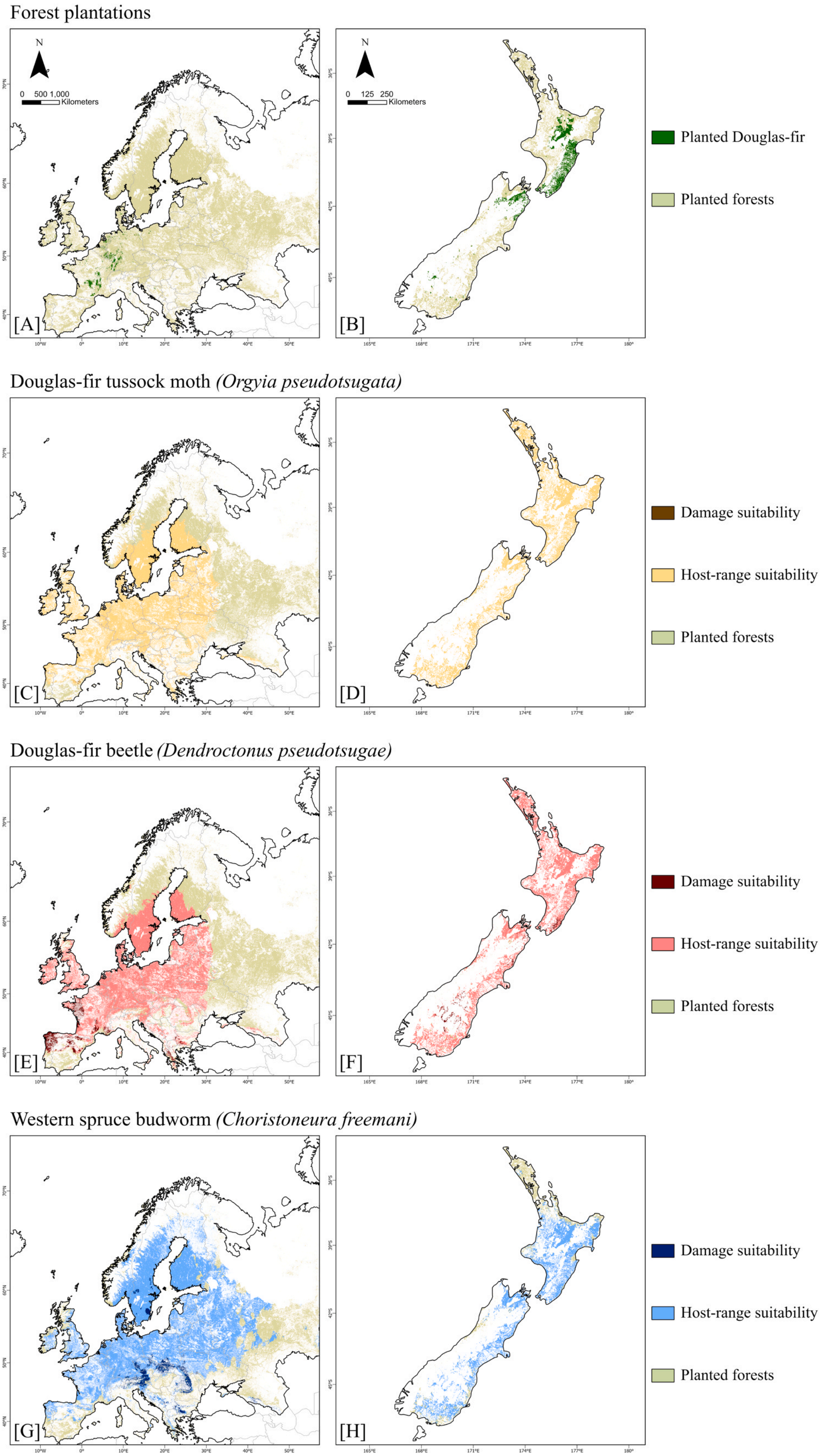
The effect of climate on the occurrence of host tree species is well defined. Specifically, the PCA of bioclimatic variables revealed a 'bi-lobed' distribution of the host ranges in climatic space, reflecting distinct Pacific coast and interior regions of North America (Fig. S1, S2). The native range of Douglas-fir is divided into two climatically distinct regions: *P. menziesii* var. *menziesii* is distributed along Pacific maritime regions while *P. menziesii* var. *glauca* is limited to interior Rocky Mountain regions (Hermann and Lavender, 1990). In this context, the climatic niches of the host trees are primarily captured by a dominant maritime-continental gradient (PC1) and a gradient of summer moisture availability (PC2), which align with the region's west-east and north-south geographic axes, respectively. These findings are consistent with previous work that classified the bioclimatic niches of tree species in western North America, including Douglas-fir (Rehfeldt et al., 2006). Our findings therefore suggest that, despite the vast geographic range of these species, their distribution is mostly governed by two primary climatic drivers, specifically, the transition from maritime stability to interior seasonality and the intensity of summer drought stress.

Our niche modelling analysis confirms that the distributions of host trees of the three pests are influenced by climate. The high accuracy of our host range models (Table 3) can be attributed to the well-defined realized niches of North American host tree species, which are largely conserved with respect to climate (Copenhaver-Parry et al., 2017; Gibson et al., 2014), and also to the comprehensive sampling of forest inventory data available for North America (Magnussen et al., 2007).

In our MaxEnt models, the main bioclimatic variables predicting the host range of WSBW were mean temperature of the warmest quarter, annual temperature range, and winter precipitation. Mean temperature of the warmest quarter reflects sustained summer heat and degree-days, which is linked to the photosynthetic rates of its hosts during the growing season (Duffy et al., 2021). The importance of annual temperature range and winter moisture underscores that the distribution of suitable hosts is restricted by continentality, requiring distinct seasonal changes, and relies on winter precipitation for hydrological recharge (Sophocleous and Perry, 1985). Collectively, our model indicates that the hosts of WSBW are found where summers are warm, winters are wet, and the annual temperature range is within physiological limits.

For DFTM, winter precipitation was the most influential predictor of the potential host range. This underscores the importance of winter moisture in supporting the physiological requirements of its hosts during the dormant and early growing periods (J. Martin et al., 2018). Additional drivers identified were annual moisture and heat availability, including annual and summer temperatures, indicating that the distribution of suitable hosts is influenced by distinct annual thermal cycles and a sensitivity to extremes in temperature (Rosenblad et al., 2023). In summary, our model indicates that the hosts of DFTM are primarily found in regions with sufficient annual and winter precipitation and availability of summer heat.

Host use by DFB is limited to Douglas-fir, whereas DFTM utilizes several other conifer species, in addition to Douglas-fir, as hosts. Despite this difference, the geographical range of DFB hosts is similar to DFTM, and this is reflected in the similarity of bioclimatic drivers of their host



Forest plantations

Douglas-fir tussock moth *(Orgyia pseudotsugata)*

Douglas-fir beetle *(Dendroctonus pseudotsugae)*

Western spruce budworm *(Choristoneura freemani)*

Fig. 4. Area of planted forests and planted Douglas-fir in Europe [A] and New Zealand [B] and MaxEnt predictions of host-ranges and pest damage of Douglas-fir tussock moth [C, D], Douglas-fir beetle [E, F], and Western spruce budworm [G, H].

ranges. The high importance of winter moisture underscores Douglas-fir's adaptation to specific annual precipitation patterns. Additionally, the influence of annual mean temperature and maximum summer temperature indicates that Douglas-fir's range is limited by cumulative heat availability and the extreme heat it can tolerate in the summer.

Our global predictions of Douglas-fir climatic suitability (Fig. 4e, f; Fig S5) generally agree with previous forecasts (Isaac-Renton et al., 2014; Kim et al., 2021; Langdon et al., 2023; Marchi et al., 2025; Watt et al., 2011) and correspond with regions where this species is used in plantation forestry and/or where it is invasive. Europe and New Zealand are the two non-native world regions where Douglas-fir is widely planted (Fig. 1), and a large proportion of these regions were classified as climatically suitable (Table 4, Fig. S5e, f). Douglas-fir is known to be highly invasive in portions of New Zealand and in the Patagonian region of Chile and Argentina (Nuñez and Paritsis, 2018; Peltzer, 2018) which are both predicted to be regions of climatic suitability (Fig. 4d, e). There are two other non-native regions classified as climatically suitable that are worth noting. Large extents of Tasmania and Victoria in southern Australia, are classified as climatically suitable (Fig S4e) but there is relatively little history of Douglas-fir as either a species used in plantation forestry or as an invasive species in that region (Hermann and Lavender, 1999). The other region classified as climatically suitable for Douglas-fir consists of portions of eastern North America, specifically the central Appalachian mountain region of eastern North America as well as Nova Scotia and Newfoundland (Fig S5a). Again, in these regions, there is little history of either invasive populations or plantations though this may be due, in part, to this region being climatically favorable (warm wet summers) for needle disease such as Rhabdocline (*Rhabdocline weirii*) and Swiss needle cast (*Phaeocryptopus gaeumannii*) (Eshenaur, 2017). This result suggests that our model may not account for all of the climatic factors constraining the distribution of Douglas-fir. The prediction of suitability in regions like the Appalachian Mountains and Southern Australia highlights areas where climate is favorable, but other factors such as competition, endemic needle diseases, or historical management choices may have limited Douglas-fir's expansion.

4.2. Climatic suitability for pest damage and influence of biotic interactions

Because herbivorous insects are constrained to the ranges of suitable hosts, our host range predictions also outline the potential limits for these pests, indicating regions that are climatically suitable for them to establish (Fig. S5, S6, S7). While not presented here, occurrence records from the Global Biodiversity Information Facility (GBIF; http://gbif.org) indicate that all three species are broadly distributed throughout the ranges of their hosts; unlike the distribution of damage, WSBW and DFTM occurrence is not limited to the interior portion of the Douglas-fir range.

While the three pest species studied here are present throughout the North American range of their hosts, the geographical range of damage is constrained to specific areas within these host ranges (Figs. 2, 3). Although the geographical ranges of host tree species are broadly similar, pest outbreak distributions are more differentiated. Outbreaks of DFTM and WSBW are constrained to the lobe in climatic space representing the interior region, while DFB damage is more diffuse, occupying both interior and coastal regions of their host range (Fig. 3). In relation to the two Douglas-fir subspecies, this pattern indicates that DFTM and WSBW damage is restricted to *P. menziesii* var. *glauca*, while DFB also affects both subspecies. Together, these results point to a role of climate acting either directly or indirectly (i.e., through effects on host trees or natural enemies) to constrain pest damage within the limits imposed by host distribution alone.

Our niche modelling analysis reveals that the response of pest damage to climate was heterogenous, with two species showing detectable climatic influence. In contrast to the host range predictions, the predicted extent of pest damage was more limited and revealed clear species-specific patterns. An advantage of our outbreak range modelling was the availability of 'true' presence and absence locations for pest damage. While MaxEnt models were fit using automatically generated background points, model evaluation was conducted using confirmed presence and absence locations. Unlike many species distribution models that rely on presence-only data and pseudo-absences or background points, our approach explicitly contrasted locations with confirmed pest damage against sites where hosts were present, but damage was known to be absent (Barbet-Massin, 2012).

Compared to the distribution of its host tree species, the spatial extent of WSBW damage is more narrowly constrained by specific thermal thresholds. The high importance of minimum winter (BIO11) and maximum summer (BIO5) temperature aligns with previous findings that pest outbreak dynamics are affected by overwintering and summer heat stress (Nealis and Régnière, 2021). Overwintering survival of WSBW larvae and subsequent outbreak patterns have been linked to climatic factors, specifically resource exhaustion due to warming during diapause (Régnière and Nealis, 2019; Tai and Carroll, 2022). Additionally, the predictive contribution of daily thermal stability (BIO3) suggests that the pest's impact is not just a result of temporary stress but is instead confined to climatically stable environments. WSBW outbreak dynamics are also known to be influenced by forest composition and proximity to previous outbreaks, which could potentially obscure the extent of climatic influence in observed damage (Senf et al., 2017).

Meanwhile, potential damage by DFTM was mainly predicted by temperature extremes and seasonal moisture limitation. The spatial extent of DFTM damage is likely constrained by winter conditions, particularly by minimum temperatures, which strongly influences overwinter survival of the pest relative to its host (Interagency Tussock Moth Steering Committee, 1973). Winter precipitation likely influences DFTM population dynamics by affecting the rate of predation and parasitization of overwintering eggs (Wickman et al., 1981). The importance of temperature and precipitation conditions during the dry season suggests that drought stress plays a role in shaping geographical variation in DFTM dynamics, potentially influencing both host susceptibility and pest outbreaks. DFTM exhibited the lowest incidence of damage, both in total affected area and in the number of host trees impacted. This aligns with its behavior as an episodic pest, with short-term weather variability acting as a key extrinsic factor regulating mortality and extent of outbreaks (Brookes et al., 1978b; Swetnam et al., 1995). The cyclical damage patterns of DFTM are also strongly influenced by its natural enemies, including the Nuclear Polyhedrosis Virus (NPV), and the parasitoid wasp *Telenomus californicus*, in addition to avian predators, spiders and predatory insects which can potentially limit the extent of observed damage (Brookes et al., 1978a; Vezina and Peterman, 1985; Wickman et al., 1973).

In contrast to the other pests, the DFB model was constrained in its ability to differentiate between regions where it causes damage vs. where hosts are present with no damage, suggesting that climatic predictors alone are insufficient to capture the spatial complexity of outbreaks. The lack of a distinct bioclimatic signal for DFB damage likely reflects its status as an eruptive, disturbance-driven specialist that responds more to short-term local stochastic events than to regional climatic averages. Consequently, while our model accurately predicts host suitability, DFB damage risk remains difficult to quantify using climatic variables, suggesting that its biosecurity risk is more closely tied to forest management and disturbance regimes than to climate. DFB primarily exploits Douglas-fir trees that are physiologically stressed by a combination of factors, including drought, and physical disturbances such as fire or windthrow (Howe et al., 2024a; Powers et al., 1999). These stressors can interact with additional biotic pressures, including Swiss needle cast and root diseases (Kelsey and Manter, 2004; Lan et al., 2026), further increasing host susceptibility. Defoliation from DFTM and WSBW may also act as important precursors to DFB outbreaks (Cole et al., 2022; Negrón et al., 2014). Additionally, as with WSBW and DFTM outbreaks, the spatial proximity of neighboring DFB populations strongly predicts outbreak synchrony (Haynes et al., 2025). These complex interactions between biotic and abiotic factors likely obscure any direct climatic signal in observed damage distributions (Agne et al., 2018).

4.3. Predicted damage risk

A critical focus of this study is the distinction between climatic suitability for host tree establishment versus the risk of damage by the three major Douglas-fir pests. In both Europe and New Zealand, the predicted suitability for host establishment is expansive, encompassing a high proportion of the current planted forest landscape (Table 4). This is particularly pronounced in New Zealand, where nearly the entire extent of the nation's planted forests falls within the predicted host-suitability range, compared to over half of Europe's significantly larger planted forest estate. Despite this widespread suitability for host trees, the climatic requirements for damaging outbreaks are far more restrictive, indicating that most planted forests in both regions are not at risk of significant impacts under current climatic conditions. This disparity is most evident when examining the actual planted range of Douglas-fir. While the species constitutes a higher proportion of the total forest matrix in New Zealand than in Europe, plantations in both regions are located in areas that are classified as climatically suitable for Douglas-fir establishment (Table 1). However, the potential realized risk of damage remains negligible for Douglas-fir plantations in both regions. The overlap between the current Douglas-fir planted area and outbreak-prone regions is confined to a small fraction ($\leq$ 3%) in Europe and is effectively non-existent in New Zealand. From an ecological standpoint, this suggests that while these specialist pests may readily establish across the current planted range, the climatic requirements to transition from endemic presence to outbreak proportions are currently absent from most of the landscape. Consequently, the use of Douglas-fir in plantation forestry in both regions does not appear to be at risk should any of the three pests establish in these regions and none of these three pests can be classified as high-risk species for biosecurity programs. It is important to note that while our models characterize damage within the native range of the pest species, their escape from specialized parasites and pathogens in the planted range of their hosts could theoretically lower the climatic thresholds required for an outbreak. Future research could investigate whether enemy release allows invasive pest populations to reach damaging densities in climatic conditions that would be considered sub-optimal in their native range. Additionally, with anticipated future climatic change, the risk of pest damage in non-native regions is expected to change. Although climatic niche modelling using pest occurrence records to extrapolate impacts based on climate change scenarios is widely practiced (Carvalho et al., 2017; Lobo, 2016), this approach involves a "space-for-time substitution" (Kharouba and Williams, 2024) and invokes substantial uncertainty. The factors that determine when pest populations rise to outbreak levels are complex and involve populations of species at both higher and lower trophic levels and may not be captured from pest occurrence data.

4.4. Limitations

While this study provides a framework for forecasting climatic suitability for Douglas-fir pest outbreaks, some limitations must be acknowledged. First, climatic variables were the primary predictors of damage, yet the critical role of non-climatic factors such as stand age and structure, forest management, host stress, and disturbance events in triggering outbreaks were not incorporated (Canelles et al., 2021; de Groot et al., 2019; Howe et al., 2024b; Marini et al., 2022). Furthermore, our modeling approach assumes niche conservatism; however, invasive or expanding pest populations may exhibit niche shifts in novel environments (Bates and Bertelsmeier, 2021). It should therefore be noted that our finding that most of the area where Douglas-fir is planted is climatically unsuitable for the three focal pests (Table 4) does not mean that these pests would not have impacts on other hosts. For example, Norway spruce (*Picea abies*) is widely distributed in forest plantations through much of Europe and is a known host of WSBW (Fellin and Dewey, 1982) so WSBW damage may be possible in some areas where this tree species occurs. However, our analysis indicated that a relatively small fraction (3.84%) of total forest plantation area (across all tree species) is climatically suitable for WSBW outbreaks (Table 4). We also observed differences in model performance among pest species, with lower accuracy for DFB damage indicating greater uncertainty in its predicted impacts. Additionally, the 1 km^2 spatial resolution of the analysis likely leads to an overestimation of planted forest area and planted Douglas-fir area. Therefore, our results should be interpreted as relative proportions rather than absolute area. Taken together, our projections represent conservative, climate-driven estimates of outbreak potential rather than absolute spatial predictions. Overall, our findings underscore the value of applying niche modelling to host tree occurrence separately from pest damage in order to map emerging biosecurity threats.

5. Conclusions

The exceptional success of non-native tree species in plantation forestry (Keča et al., 2019) can be partially attributed to enemy release, but this escape from herbivory can diminish if co-evolved herbivores from a tree species' native range invade, and are re-united with their hosts (Crous et al., 2016). The use of non-native trees in plantation forestry thus depends upon biosecurity practices that identify high risk pest species and exclude their transport and establishment (Nahrung et al., 2023). While climatic niche modeling is widely applied for predicting environmental suitability and establishment risk of candidate invasive pest species (Srivastava et al., 2021; Venette, 2017), these models generally predict where pest species are likely to establish, but not where they are likely to cause damage. Our study addresses this limitation by first modelling the climatic niche of the insect hosts and then fitting a secondary model to characterize the climatic limits of pest damage within the geographical range of hosts. This global spatial risk assessment reveals that, in major Douglas-fir planting regions such as Europe and New Zealand, currently planted areas are broadly climatically unsuitable for damaging outbreaks of these species. These findings highlight that assessing the climatic niche of pest damage, rather than just the niche of establishment, is essential for accurately evaluating invasion risks. Ultimately, this approach provides a more nuanced framework for informing proactive biosecurity to protect non-native forest resources worldwide.

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CRediT authorship contribution statement

Deepa S. Pureswaran: Writing – review & editing, Resources. **Aditya Ganesh:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Andrew M. Liebhold:** Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123768.

Data availability

All data analyzed here are publicly available.

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