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RESEARCH ARTICLE

Climate, Host Abundance and Spread: Unravelling the Drivers of Forest Pest Distributions in North America

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ABSTRACT

Aim: Forest pathogens, insect pests and parasitic plants are among the most important disturbance agents in forested ecosystems. Understanding where pests occur and where they might occur in the future will be important for understanding their impacts on host trees, and planning for future pest outbreaks.

Location: North America.

Taxon: Insect pests, pathogens and parasitic plants of forest trees.

Methods: Here, we develop and implement a framework to predict the contemporary distributions of 26 pest species that accounts for climate, host abundance and, for non-native species, their spread on the landscape.

Results: We show that pest distributions can be predicted primarily by climatic variables. The abundance of individual host trees had only minor explanatory power, but the summed total of host abundance frequently had greater importance—suggesting forest composition and the relative frequency of hosts and non-hosts place strong limits on pest distributions. Non-native pests were strongly impacted by the distance from their original discovery location in North America, which tended to interact with climate variables—suggesting most non-native pests are not yet at equilibrium with their potential climatic ranges in North America.

Main Conclusions: This work helps to clarify the generalised controls on pest distributions and provide a framework for predicting pest distributions in future climates.

1 | Introduction

Forest pathogens, insect pests and parasitic plants (hereafter, pests) pose major threats to forests globally (Jactel et al. 2020; Panzavolta et al. 2021). While native pests are an important part of forested ecosystems that can facilitate regeneration and remove weakened trees from the gene pool, climate change and land use change can shift the balance in pest and host relationships, resulting in the increased frequency and severity of pest outbreaks, pests expanding their geographic ranges and pests encountering new competent hosts outside their historic ranges (Ramsfield et al. 2016). Likewise, the continued introduction of non-native pests threatens an increasing number of native tree species, many of which lack defences against these pests (Aukema et al. 2010; Gougherty 2023; Nahrung and Carnegie 2020; Santini et al. 2013). Because of their importance to forested ecosystems and the potential for future spread and damage, understanding where pests occur now and where they

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might occur in the future is important for managing and preparing for future pest threats.

Pest distributions are likely determined by a combination of climate, topography, and the occurrence and abundance of host species. Climate has a well-recognised link to pest outbreaks, development and behaviour, and can have complex effects on pests and their interactions with hosts (Haynes, Allstadt, and Klimetzek 2014; Haynes et al. 2022; Lehmann et al. 2020). Many pests undergo multiple lifecycle stages during the course of their development, each of which may have different environmental requirements (Jaworski and Hilszczański 2013; Messenger 1959; Tauber et al. 1998). For many native pests, the interaction between climate and these life stage requirements can limit where within their host ranges pests can occur. Effects of climate can be especially apparent for non-native pests, which may slow their spread as they approach climatic thresholds within their host ranges. The spread of hemlock woolly adelgid (*Adelges tsugae*) in eastern North America provides one such example, as its spread to the northernmost portion of eastern hemlock's range seems to be slowed by its intolerance to cold temperatures (Paradis et al. 2008). The effects of climate on pest distributions are also evident from shifting pest distributions with recent climate change. Globally, crop pest distributions (which also include some forest pests) have been estimated to be shifting poleward at a rate of ~2.7 km/year since 1960 (Bebber, Holmes, and Gurr 2014). Pests can be important bellwethers for climate change, as their short generation times, high reproductive rates and their propensity for long distance dispersal allow them to invade previously inhospitable areas where they may encounter new hosts that could further accelerate their spread.

Pests' reliance on host trees for nutrition, habitat and resources, however, complicates a purely climate-based understanding of pest ranges (Gougherty and Davies 2022a). While biotic interactions are generally assumed to affect species distributions only at fine spatial scales (Wisz et al. 2013), biotrophic pests and obligate parasites, which require hosts to persist, may deviate from this general expectation. The nature of the relationship between host and pest occurrences is generally poorly understood, as different pests may respond to different elements of host geography. Pests with strong host preferences (i.e., whether pests are host specialists or generalists) may primarily rely on one or a few hosts for their occurrence. The known distribution of chestnut blight, for instance, largely follows the historic distribution of its main host (*Castanea dentata*), despite an ability to infect a variety of other eastern North American tree genera. Alternatively, pests without strong preferences may use different hosts in different parts of their geographic ranges and may respond more strongly to aggregate metrics of host occurrence. Oak mistletoe (*Phoradendron leucarpum*), for instance, which occurs throughout much of the southern portions of eastern and western United States and can infect dozens of tree species, appears not to follow the distribution of any particular host species, but appears limited by some combination of total host abundance and climate (Spooner 1983).

While the geographic extent of many pests may be limited by the range of their hosts, at global scales pests seldom occupy the entire geographic ranges of their hosts (Gougherty and Davies 2022b)—just as tree hosts rarely fill their entire climatic ranges (Seliger et al. 2021; Svenning and Skov 2004). Some pests, such as the pathogen associated with oak wilt (*Bretziella fagacearum*), which has ambiguous origins, have distributions that do not clearly align with the occurrence of hosts or evident climatic gradients (Juzwik et al. 2008). Non-native pests may still be spreading on the landscape and so may not yet occupy their entire potential climatic or host ranges. For non-native pests, this non-equilibrium could manifest as a shift in their relationships with climate/hosts with increasing distance from their discovery site. Even native pests, which have presumably co-evolved with hosts for centuries or millennia, and hypothetically could have expanded throughout the range of their hosts, may occupy only a small portion of the ranges of their hosts. Incomplete occupation of an otherwise suitable climatic range suggests interactions between biotic and abiotic controls on pest distributions. Quantifying these relationships can improve our understanding of where pests occur now and where they may occur in the future.

Here, we develop and implement a framework to predict the distribution of select tree pests in North America. Pests are often ideal candidates for this type of distribution modelling, as they frequently have high fecundity, short generation times, high dispersal abilities and their effects can be clearly evident on the landscape. We hypothesise that, like other taxa, pests will respond individualistically to climate and host abundances, but that abiotic variables (i.e., climate and topography) will generally be more important than host abundance given the frequently expected scale dependence of biotic and abiotic variables, and the observation that pests frequently do not fill their entire host ranges. For non-native pests, we expect that the distance from their discovery location will be important, and particularly that this distance will interact with climate and host variables, reflecting the non-equilibrium of non-native pests geographic ranges. These results will help identify any generalities limiting pest distributions and their potential sensitivities to future climate change.

2 | Materials and Methods

2.1 | Pest Species

We include a variety of pest types in our analyses, including insect pests, pathogens and parasitic plants, and a combination of both native and non-native species. We focused on pests known to impact the health or vigour of one or more host trees in North America and for which we were able to find geographic occurrences that covered the entire known northern North American range (United States and Canada) of the pests (see Section 2.2 below). We used previously published lists of forest pests to guide our selection of species for our analyses, including Liebhold et al. (2013), Mech et al. (2019) and Potter et al. (2019). From an initial list of 678 unique pest species, we identified any occurrences in our geographic data sources, detailed below and mapped occurrences in North America. Next, we manually checked each map and selected those pests that had continuous, dense occurrence coverage throughout their geographic ranges for modelling. In total, we considered 26 pests, including 15 insects, 2 pathogens, 9

parasitic plants, of which 16 were native and 10 were non-native (Table 1).

2.2 | Geographic Occurrences

Geographic occurrences used in our models were extracted from the US Department of Agriculture Forest Service (USFS) Forest Insect and Disease Surveys (FIDS) (Forest Health Protection 2023), USFS Forest Inventory and Analysis program (FIA) (Forest Inventory and Analysis Database 2017), Canadian Forest Service Forest Invasive Alien Species database (CanFIAS) (Nealis et al. 2016), British Columbia Aerial Overview Surveys (Ministry of Forests 2023), Ontario Forest Disease and Insect Damage Event databases (Government of Ontario 2023), Quebec Natural Disturbance Data (Ministry of Forests, Wildlife and Parks 2023), the Global Biodiversity Information Facility (GBIF) and MycoPortal (Miller and Bates 2017). Because these data are stored in multiple formats and utilise different geographic projections, several steps were taken to synonymise the occurrence data as detailed below.

The data sources listed above included both polygon and point feature data where pests or their damage was observed. In general, polygons included small continuous areas where the pests were observed attacking trees, while point data represented individual hosts or host populations harbouring pests. Data that were natively stored as polygons were converted to points to simplify their inclusion in the distribution models. To do so, the polygons were overlayed on a base layer raster of North America. Pixels intersecting the polygon were retained as points, regardless of the amount of area covered by the polygon. The raster base layer covered the entire geographic extent of North America at a resolution of 10 arc-minutes. Once assembled, all points were reprojected to an equal Albers projection.

While much of the occurrence data came from federal and state or provincial surveys and thus had some degree of quality control and assurance, we ensured that the occurrences covered the known ranges of the pests by checking against previously published maps and descriptions of pest distributions. These sources included the Alien Forest Pest Explorer (https://mapsweb.lib.purdue.edu/AFPE/), North American Plant Atlas (for parasitic plants) (Kartesz 2015), Forest Service Forest Insect and Disease Leaflets, and the peer-reviewed literature. When occurrences fell far beyond the documented distribution of the pest (e.g., individual occurrences hundreds or thousands of kilometres from the distributions inferred from the above sources), occurrences were individually assessed and removed if deemed unreliable. In total, this step removed <1% of all occurrences considered. Isolated occurrences were retained if they could be verified in the literature. We limited our assessment of spongy moth, *Lymantria dispar*, to the main outbreak area in eastern North America. Although spongy moth has been periodically found in western North America, frequently from pheromone traps, they are actively removed when detected (Régnière, Nealis, and Porter 2009). For all other pests, we included occurrences from their complete geographic ranges in the United States and Canada.

2.3 | Host Information and Abundance Maps

Because pest distributions are likely controlled by a combination of climate (described below), and host occurrences, we sought to identify known hosts of our selected pests and include maps of their abundance in the models. Pest associations were identified from multiple global databases including Centre for Agriculture and Bioscience International (CABI 2023), European Plant Protection Organization (EPPO 2023) and the primary literature (Geils, Wiens, and Hawksworth 2002; Hawksworth, Wiens, and Geils 2002; Liebhold et al. 2013; Potter et al. 2019). We included any recorded host tree, even if considered rare or less preferred, as these could nevertheless impact pest distributions. In addition to individual host abundance maps, we also included the sum of all host abundances in the models, as the aggregate abundance of hosts may better reflect forest composition and the frequencies of hosts and non-hosts, than abundance of any particular host tree. We allowed the aggregate host metric to be unconstrained to capture the intra-pixel variability in host abundances that can emerge from vastly differing forest compositions in individual sample plots in the same pixel.

Tree abundance maps were derived from the US Forest Inventory Analysis (FIA; Forest Inventory and Analysis Database 2017) and Canada's National Forest Inventory (NFI; Gillis et al. 2010) data. For the contiguous United States and Alaska, we used FIA's plot level data (>100,000 plots) to derive relative importance values (RIV) as:

$$\mathrm{RIV}(x) = \frac{50 \times \mathrm{BA}(x)}{\sum \mathrm{BA}(\text{all species} \in \text{plot})} + \frac{50 \times \mathrm{NS}(x)}{\sum \mathrm{NS}(\text{all species} \in \text{plot})}$$

where x is the species in the plot, BA is the basal area, and NS is the number of stems (summed for overstory and understory trees). In monotypic stands, RIV would approach 100%. For Alaska, both coastal and interior inventories were used. For species that spanned the US-Canadian border, we used Canadian NFI which includes 1116 permanent ground plots and remote sensing data (Gillis et al. 2010). The remote sensing component consists of 2×2 km sample units located on a systematic national sampling grid of 20-km, with a total of 13,158 sample units in the first current 10-year (2008–2017) re-measurement survey. The percent composition of species in 2×2 km grids across the country were summarised, which corresponds to the RIV of the FIA. All plot level RIV were rasterised to 20-km cells by averaging FIA plot and NFI grid data, and merging them together.

While the US and Canadian forest surveys cover much of the forested lands in North America, predominantly non-forested areas were not sampled, sometimes resulting in patchy tree abundances in areas with lower forest cover in North America. Because our pest occurrences were assembled independently from the forest surveys, pest occurrences could potentially occur in pixels without forest inventory data. Thus, to prevent a potential spurious relationship between zero or low host abundance and pest occurrences in the models, we interpolated host abundances to unsampled pixels and pixels with few plots. Briefly, for FIA data, when a species was present in 2–3 plots within a 20-km pixel, we used a 3×3 focal

TABLE 1 | Details of pests used in distribution modelling. For introduced pests, the distance from the approximate introduction site was used as a predictor in the models, to capture both spread, and interactions with climate and host variables.

Common name	Species name	Nativity in North America	Taxonomic group	No. host trees included in model	Approximate North American introduction site
Pineapple gall adelgid	*Adelges abietis*	Introduced	Insect	7	Maine, USA
Balsam woolly adelgid	*Adelges piceae*	Introduced	Insect	8	Maine, USA; San Francisco, CA, USA
Hemlock woolly adelgid	*Adelges tsugae*	Introduced	Insect	10	Richmond, VA, USA
Emerald ash borer	*Agrilus planipennis*	Introduced	Insect	8	Detroit, MI, USA
Fir dwarf mistletoe	*Arceuthobium abietinum*	Native	Parasitic plant	10	
Lodgepole pine dwarf mistletoe	*Arceuthobium americanum*	Native	Parasitic plant	12	
Western dwarf mistletoe	*Arceuthobium campylopodum*	Native	Parasitic plant	13	
Pinyon dwarf mistletoe	*Arceuthobium divaricatum*	Native	Parasitic plant	6	
Eastern dwarf mistletoe	*Arceuthobium pusillum*	Native	Parasitic plant	10	
White pine blister rust	*Cronartium ribicola*	Introduced	Pathogen	9	Geneva, NY, USA; Vancouver, BC, CAN
Chestnut blight	*Cryphonectria parasitica*	Introduced	Pathogen	9	New York City, NY, USA
Beech scale	*Cryptococcus fagisuga*	Introduced	Insect	1	Halifax, Nova Scotia, CAN
Southwestern pine beetle	*Dendroctonus barberi*	Native	Insect	2	
Western pine beetle	*Dendroctonus brevicomis*	Native	Insect	2	
Southern pine beetle	*Dendroctonus frontalis*	Native	Insect	19	
Mountain pine beetle	*Dendroctonus ponderosae*	Native	Insect	16	
Douglas-fir beetle	*Dendroctonus pseudotsugae*	Native	Insect	3	
Introduced pine sawfly	*Diprion similis*	Introduced	Insect	14	New Haven, CT, USA
Green spruce aphid	*Elatobium abietinum*	Introduced	Insect	9	Vancouver, BC, CAN
Pinyon pine beetle	*Ips confusus*	Native	Insect	7	
Hemlock looper	*Lambdina fiscellaria*	Native	Insect	33	
Spongy moth	*Lymantria dispar*	Introduced	Insect	137	Medford, MA, USA
Bollean mistletoe	*Phoradendron bolleanum*	Native	Parasitic plant	2	
Desert mistletoe	*Phoradendron californicum*	Native	Parasitic plant	3	
Juniper mistletoe	*Phoradendron juniperinum*	Native	Parasitic plant	10	
Oak mistletoe	*Phoradendron leucarpum*	Native	Parasitic plant	54	

mean and when species were present in only one plot, we used a 5×5 window. For NFI, which tended to be more sparsely sampled, we used a 3×3 focal mean when the number of plots per cell was less than or equal to 3. If the resultant focal mean was a zero (typically near isolated pixels far from the main portion of species distributions), the original value was retained. In effect, applying this procedure 'filled in' host abundances in unsampled pixels that were near adjacent sampled pixels, and smoothed some anomalously values due to unequal sampling effort. While this procedure may introduce some uncertainty into the tree abundance layers, it is a relatively conservative approach that avoids some of the uncertainty that could arise from models of tree abundance (e.g., extrapolation beyond the range and over- or underestimation of observed abundance).

2.4 | Climate Data, Topography and Discovery Distances

Climate data were extracted from the AdaptWest dataset (AdaptWest Project 2022) and aggregated to our 20-km grid to match the resolution of the host abundance maps. We selected six climate variables that lacked strong correlation ($r < 0.7$) that were potentially ecologically meaningful for pest occurrences. These include average winter temperature, average summer and winter precipitation, mean annual relative humidity, annual heat moisture index (calculated as [mean annual temperature + 10]/[mean annual precipitation/1000]) and Hogg's climate moisture index (a metric of drought, calculated as the difference between precipitation and potential evapotranspiration) (Hogg 1994). We also included two metrics of landscape topography, including elevation and topographic ruggedness—a measure of elevational variability within a pixel.

In addition to climate variables and host abundance, for non-native pests we included distance from the initial discovery location in North America as a predictor in the model meant to account for non-native pests still actively spreading on the landscape. We expect this variable to account for the spread of pests on the landscape and to interact with other climatic and host variables. Discovery locations were compiled from the literature and CABI (CABI 2023). We consulted the discovery locations given in Ward, Fei, and Liebhold (2019), which included pest discovery sites in the United States, but we verified whether the first North American discovery sites was actually in Canada, in which case we used the Canadian site. For pests that had separate introductions into eastern and western North America (i.e., *Adelges piceae* and *Cronartium ribicola*), distances were calculated from the nearest eastern or western discovery site. For one pest, *Adelges tsugae*, that is considered native in the west (or at least introduced thousands of years ago), and invasive in the east (introduced separately from Asia), only the distance from the eastern discovery point was included in the model.

2.5 | Models

We used Random Forest (RF) (Breiman 2001) models to predict pest species distributions and infer the importance of the variables included in the model. Since an imbalance between the number of presence and absence points can bias RF model performance (Barbet-Massin et al. 2012; Dar et al. 2021; Senay, Worner, and Ikeda 2013), we generated pseudo-absences equal to the number of occurrence points. The pseudo-absence locations were selected randomly within the United States and Canada but were limited to areas at least 100 km from any presences. This approach is particularly appropriate for pest species, as there are frequently strong sampling effects on pest occurrences.

Random Forest models were fit using the *randomForest* package in R (Liaw and Wiener 2002; R Core Team 2023). Models were fit using 500 trees and mtry parameter (i.e., number of variables considered at each split) assigned to the square root of the number of predictor variables, rounded down. To understand how well pest distributions can be predicted by different sorts of biotic and abiotic data, we fit models using three different subsets of the predictors, including (i) climate and topography ('climate-only'), (ii) individual and aggregate host abundances ('host-only') and (iii) climate, topography and host abundances ('climate/host'). For all invasive pest species models, we included the distance from discovery location in North America, as we expect this variable to interact with both climate and host abundance. We used 5-fold cross validation to separate occurrences into training and testing sets to quantify model performance, which was done by calculating AUC, total error rate, true positive and true negative rates, and the true skill statistic (TSS; Allouche, Tsoar, and Kadmon 2006) on data withheld from model training. Each statistic was calculated for each model run and averaged across the 5-folds. Results and Discussion focus on the climate/host models, unless specifically noted, as these were often the best performing models (based on the validation statistics) and offered the greatest inference regarding the combined influence of host abundance and climate.

After model fitting, we determined variable importance as the mean of the class-specific decreases in node impurity when variables were used for a split. To visualise the relationships between individual predictor variables and the predicted probabilities of each pest species, we generated partial dependence plots for climate and aggregate host abundance. These plots aid in understanding how variables affect the prediction and more specifically show the dependence between the probability of occurrence and the variable investigated, independent of all other variables in the model (Cutler et al. 2007). For non-native pests, we also quantified the interactions between the distance from discovery sites, and the other climate and host abundances variables, as the mean conditional minimum depth. Interactions were quantified using the min_depth_interactions function in the *randomForestExplainer* package (Paluszynska et al. 2017).

Because host abundance sampling and much of the pest data were initially compiled separately in the United States and Canada, we fit an additional model that included country identity as a predictor variable to test if countries had a systematic effect on model fit. For these models, we included both host and climate variables and assessed the rank of the country identity variable, and tested whether the model error rate was significantly different between models with and without country identity, using a paired *t*-test. In general, the country identity variable was not important in the models—for 18 of 26 pests country identity did not rank in the top 50% of variables included in the models and model performance was not significantly different between models with and without country identity ($p = 0.33$).

These results suggest any differences in host or pest sampling between the United States and Canada did not have a meaningful, systematic impact on pest models. These supplemental results are shown in Table S1.

3 | Results

3.1 | Model Performance

Nearly all the models for each of the pests had useful predictive ability and relatively low error rates when tested on data withheld during model training (Figures 1 and 2). In general, the climate-only and climate/host models tended to outperform the host-only models, but many of the host-only models still had high predictive ability (e.g., AUC >0.8, error rate <10%). Across all models, the worst performing was the host-only model for *Phoradendron californicum*, which had low AUC (0.60) and relatively high error rate (40.1%). While the true negative rate (i.e., proportion of absences correctly predicted) was high for this model (near 1.0), it was at the consequence of an ability to predict actual occurrences. *P. californicum*, however, was not representative of the genus as a whole, as models for other *Phoradendron* species tended to perform better. *Dendroctonus brevicomis* followed a similar trend as *P. californicum*, but performed slightly better. The host-only model could not be fit for *Phoradendron bolleanum*, due to its rarity and the narrow distributions and low abundance of its host species.

3.2 | Variable Importance

Although there was substantial variability in the most important variables affecting pests' distributions, some generalities did emerge (Figure 3; Figures S1–S23). For non-native pests, the distance from the discovery site in North America tended to be among the most important variables, with the exception of green spruce aphid (*Elatobium abietinum*), for which winter precipitation and climate moisture index were the most important contributors. All non-native species showed a negative relationship

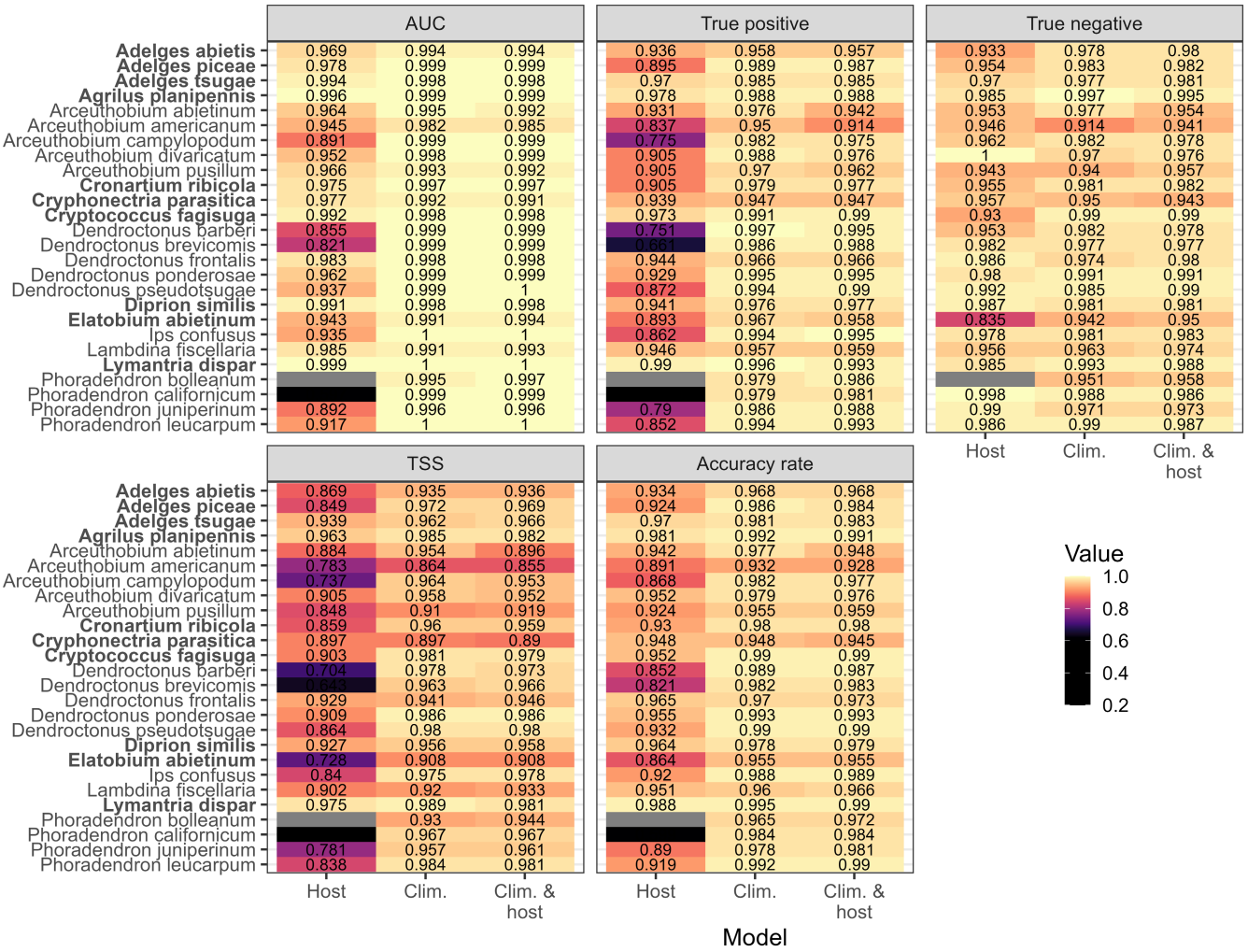

FIGURE 1 | Validation statistics for testing data for 26 North American tree pests. Models were fit with just host abundance data ('Host'), climate and topography ('Clim.') and a combination of host and climate information ('Clim. & Host'). For non-native pests (bold face), the distance from the origin location in North America was included as a predictor in each model. Values represent the mean statistic on testing data for five (cross fold) Random Forest models. Cells are coloured based on their within-pest rank, but note differences between model types are often small. The 'Host' model could not be fit for *Phoradendron bolleanum* as host abundance tended to be low, and in multiple folds, pest and host occurrences did not overlap. AUC is area under the receiver-operating curve, and TSS is true skill statistic. Note the non-linear colour scale.

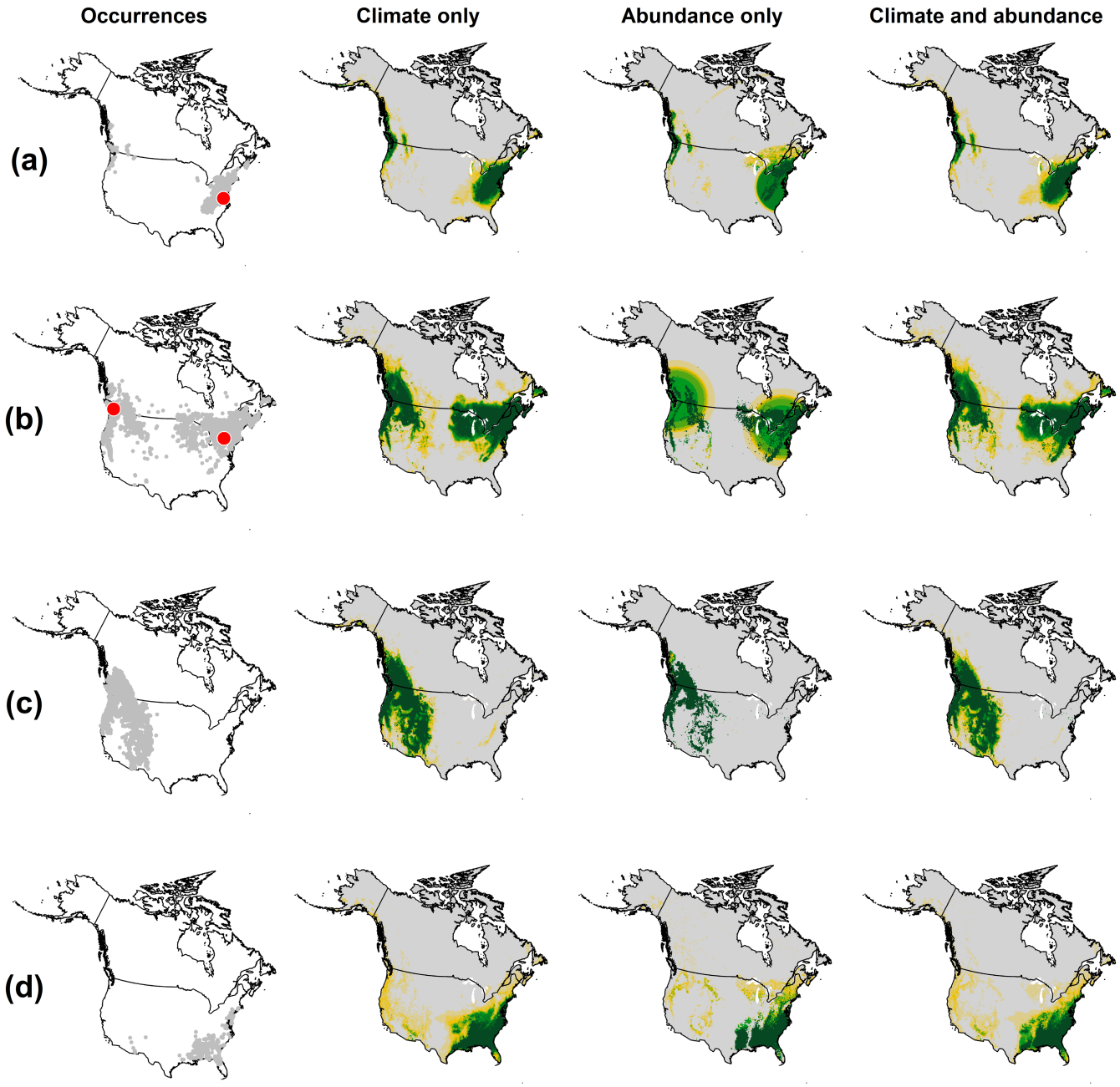

FIGURE 2 | Occurrences, climate-only, abundance-only and climate and abundance models for four example pests: (a) hemlock woolly adelgid, *Adelges tsugae* (b) white pine blister rust, *Cronartium ribicola*, (c) Douglas-fir beetle, *Dendroctonus pseudotsugae* and (d) southern pine beetle *Dendroctonus frontalis*. Red points in (a) and (b) are approximate discovery locations in North America. Geographic distance from discovery locations is included in all models for non-native species.

with distance from the origin site (Figure 4), consistent with many of the pests still spreading on the landscape and the large geographic barriers preventing establishment across the entire North American continent. There was some variability in the steepness of the relationship, with beech scale (*Cryptococcus fagisuga*) having a relatively steep slope and green spruce aphid having a shallower slope. Many of the pests had strong interactions between the distance from the origin site and winter climate, typically average winter temperature, suggesting that winter temperature had a significant effect on pest occurrences, but this was mediated by how far the pest had spread from its origin in North America (Figure S24).

Six of the ten introduced pests were strongly impacted by the abundance of their hosts, with aggregate host abundance frequently having the stronger impact than individual host tree abundances. For *Adelges piceae*, *Agrilus planipennis*, *Cryphonectria parasitica* and *Cronartium ribicola* aggregate host abundance was the first or second most important variable in the model (following distance from the origin site). Each of these pest species attack multiple tree species, but are primarily restricted to a single host genus (i.e., *Abies*, *Fraxinus*, *Castanea* and *Pinus*, respectively). *Diprion similis* and *Lymantria dispar* were each strongly affected by the abundance of individual tree species. *D. similis* was impacted by the abundance of *Pinus strobus*, its main host in eastern

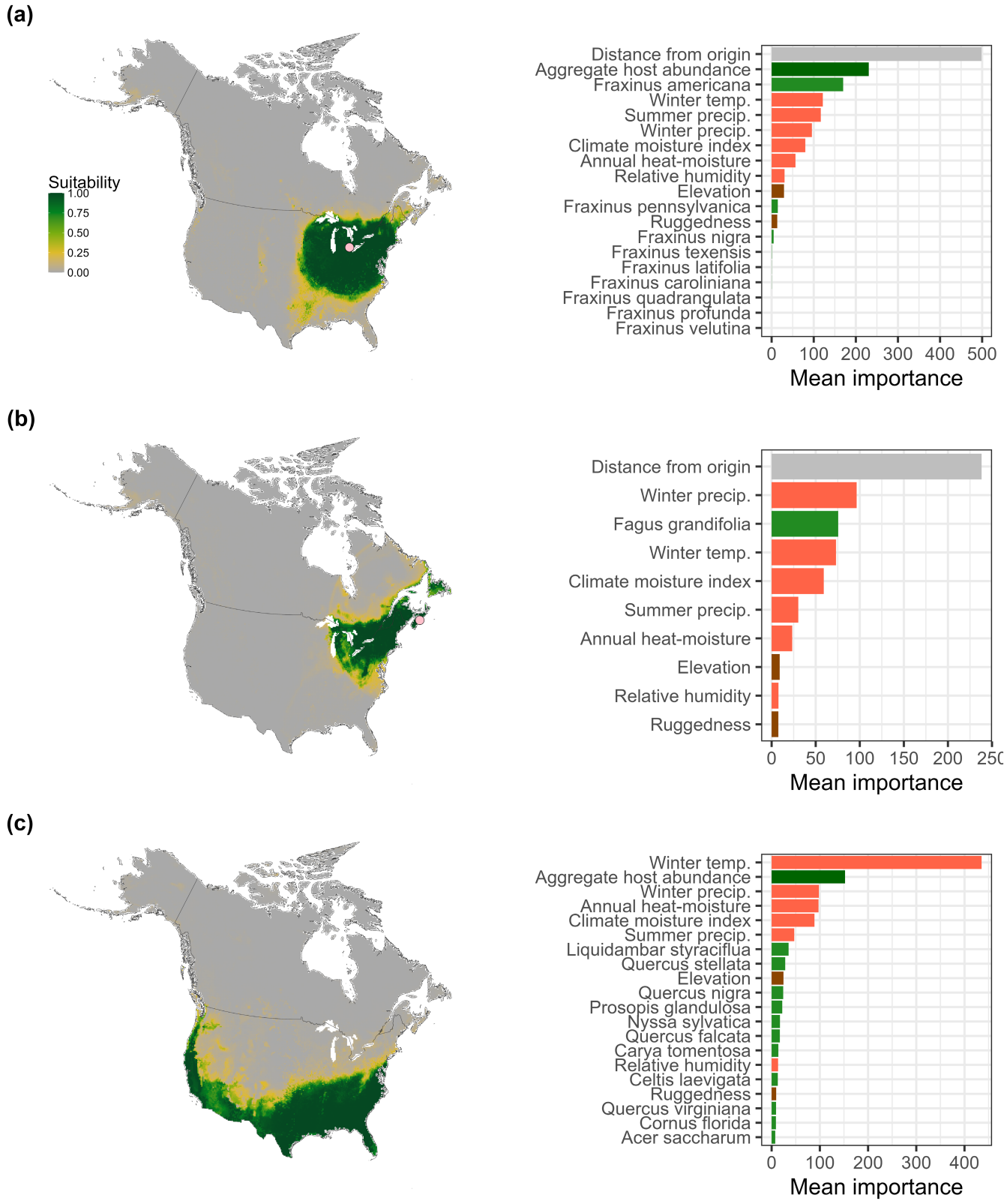

FIGURE 3 | Predicted habitat suitability and variable importance averaged across five Random Forest models including both climate and host abundance for (a) emerald ash borer, *Agrilus planipennis*, (b) beech scale, *Cryptococcus fagisuga* and (c) oak mistletoe, *Phoradendron leucarpum*. If more than 20 predictors are included in the model, only the top 20 are shown. Importance is the average decrease in node impurity when the variables are used for splitting in trees in the Random Forest model. Pink points in (a) and (b) are discovery locations in North America.

North America (Davis et al. 2023). For *Lymantria dispar*, the second most important variable, following distance from the origin location, was sugar maple (*Acer saccharum*)—a host known to be less preferred, but possibly an important component of the forest communities where spongy moth is found, whether or not it is used as a host.

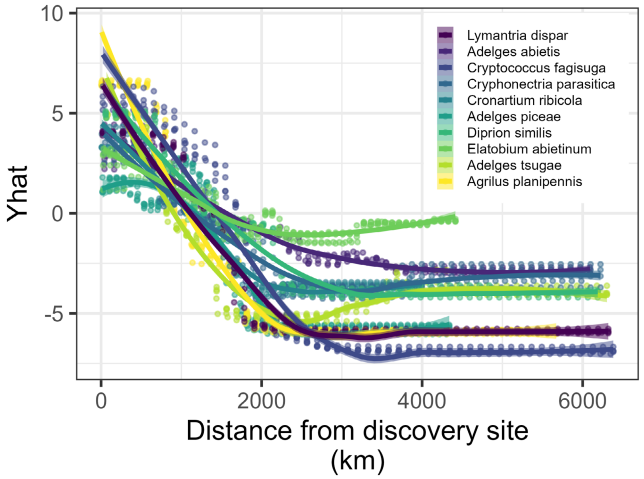

FIGURE 4 | Partial dependence of distance from discover site on pest distributions for 10 non-native tree pests in North America. Points represent one of five Random Forest models used to predict pest distributions. Lines are loess smoothers showing the general trends across the five models. Yhat is the marginal effect of distance on the occurrence of pests. Pest species are ordered based on their time of detection in North America.

Native species were similarly influenced by a combination of host abundance and climate. Of the 16 native species assessed, the most important variable for 11 pests was a climate or topographic variable. Across the five species primarily limited by host abundance, four were dwarf mistletoe species (*Arceuthobium*). Host abundance appeared less important for true mistletoe (*Phoradendron*) species, for which climate or elevation were the top drivers. Across all native pests, aggregate host abundance frequently ranked higher than the abundance of any individual host and was the first or second most important variable for 8 of 16 native pests.

3.3 | Directional Responses to Climate and Host Abundance

Despite some generalities in the most important variables limiting pest ranges, pests varied substantially in their directional responses to host abundance and climate (Figure 5; Figures S25–S32). For instance, although most pests show an increase in their probability of occurrence when host abundance increased from (near) zero, some pests continued to increase while others plateaued or even declined at the highest levels of host abundance (Figure S25). Spongy moth (*Lymantria dispar*), mountain pine beetle (*Dendroctonus ponderosae*) and emerald ash borer (*Agrilus planipennis*), among others, each plateaued at the highest levels of host abundance, suggesting a threshold for the influence of host abundances for these species. Other species had more complex relationships with host abundance. Southwestern pine beetle (*Dendroctonus barberi*) and western pine beetle (*D. brevicomis*) each had more hump-shaped relationships with aggregate host abundances, while green spruce aphid (*Elatobium abietinum*) showed little response to host abundance, likely reflecting its disjunct distribution, and greater sensitivity to topography and climate (Figure 5).

Pest responses to climate tended to be equally complex and species-specific. Most pests showed a unimodal response to winter temperature (Figure 5), with occurrences frequently highest at intermediate temperatures. Responses to elevation varied among the species (Figure S28), but for those species where elevation was an influential variable, there tended to be an increase in occurrence with increasing elevation (e.g., *Arceuthobium americanum*, *Dendroctonus barberi*, *D. ponderosae*, *D. pseudotsugae*, *Ips confusus* and *Phoradendron juniperinum*). Pests with the clearest responses to elevation were western pest species, which experience greater elevation gradients than eastern pest species, that align with forest composition. Pests did not respond consistently to summer precipitation, annual heat moisture, topographic ruggedness, relative humidity or climate moisture index (Figures S26–S31).

4 | Discussion

4.1 | Overview

Tree pathogens, insects and parasitic plants are among the most important disturbance agents shaping forested ecosystems, so understanding where pests occur, and where they could occur, has important implications for planning, management and future monitoring. Here, we assessed the climate, topographic and host constraints on the distributions of 26 important native and non-native pests in North America and show that many pests are limited by a combination of climate and aggregate host abundance. Although we did not attempt to predict pest distribution in future climate, these findings suggest many pests will be sensitive to future shifts in climate and host distributions, which could result in new pest regimes and tree populations being exposed to pests they have not interacted with in the recent past. Combined with the continued introduction of new, damaging pests, impacts in forests are likely to continue to grow and may be exacerbated by future climate and land use change.

4.2 | Role of Climate

Our models consistently showed that climate was a primary constraint on pest distributions and many of the factors we found limiting pest ranges aligned with those reported in the literature. *Phoradendron leucarpum*, a mistletoe species common in the warmer regions of the United States, for instance, was found to be primarily limited by winter temperature, where it occurs only where winter temperatures exceed ~0 to −5°C. Spooner (1983) reports a similar threshold, stating that the northern edge of the species is aligned with a mean minimum January temperature of −4.5°C—very similar to that inferred from our models (Figure 5). Likewise, in a test of winter temperature metrics limiting the distribution of hemlock woolly adelgid (HWA, *Adelges tsugae*), Paradis et al. (2008) showed HWA experienced nearly complete mortality when exposed to mean winter temperature below −5°C. Our models show a similar threshold between −5 and −10°C (Figure 5). Although direct comparisons with the literature were complicated for some species, as studies use a variety of climate metric (e.g., monthly extremes and absolute minimum temperatures), the general importance of winter temperature and precipitation that we found,

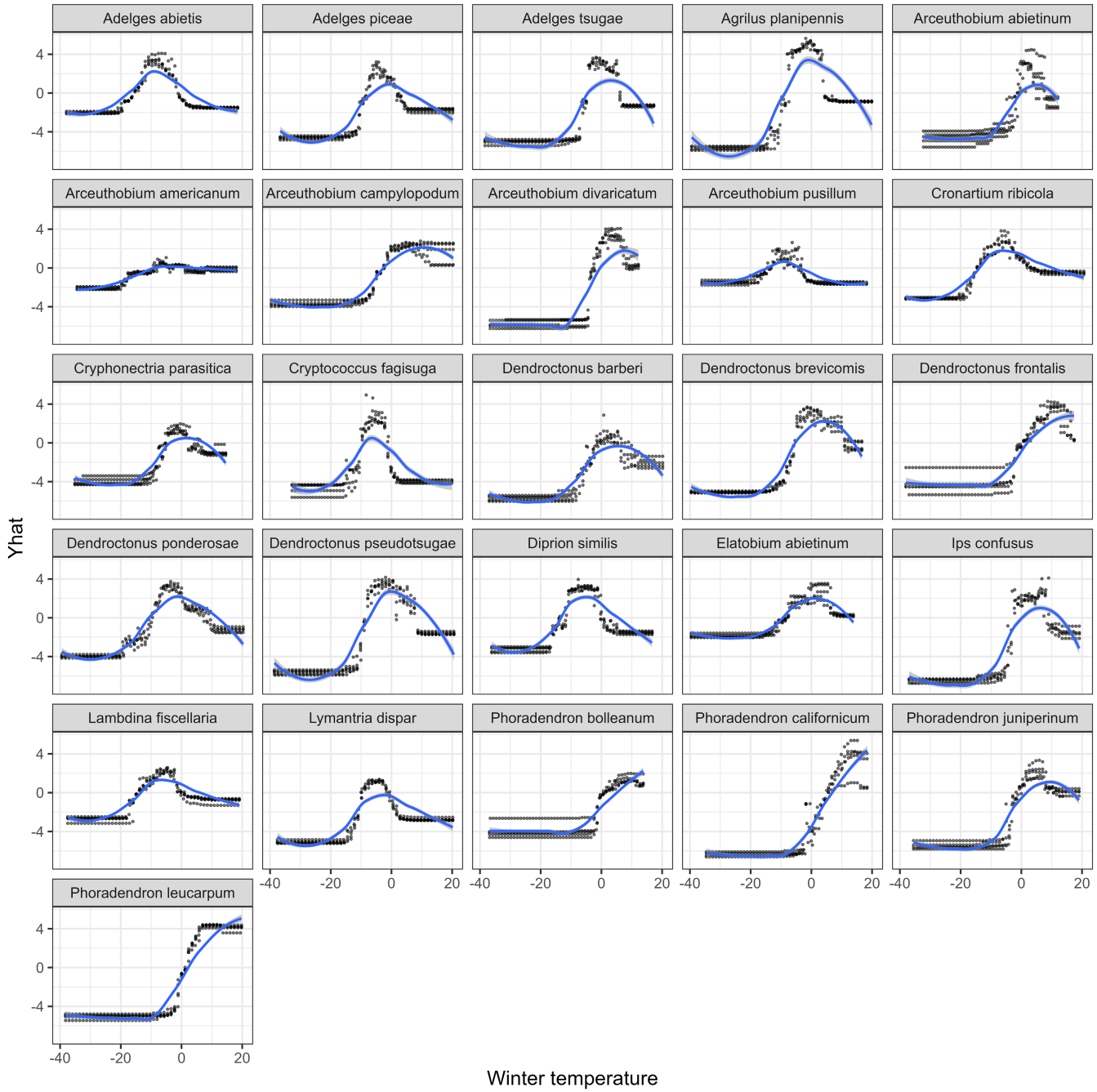

FIGURE 5 | Partial dependence plots for winter temperature for 26 tree pests in North America. Points represent one of five Random Forest models used to predict pest distributions. Blue lines are loess smoothers showing the general trends across the five models. Yhat is the marginal effect of the winter temperature on the occurrence of pests.

was consistent with many pests having physiological limits that align with seasonal extremes.

The important role of climate identified in our models suggests pests may be impacted by future climate change. Several of the pests we assessed have already been noted to be shifting their ranges in response to warming temperatures and shifting precipitation regimes. Southern pine beetle (SPB, *Dendroctonus frontalis*, Figure S13), for instance, has recently been documented as far north as Connecticut—well north of its historic range edge (Dodds et al. 2018). Previous work suggests SPB experiences >90% mortality when air temperature is below −16°C (Ungerer, Ayres, and Lombardero 1999). As winter temperatures have warmed in the eastern United States, suitable climate for SPB has likely expanded northward, allowing SPB to spread to areas that were previously inhospitable. Other non-native pests have also been reported shifting their distributions potentially in response to recent climate change. Recent work has suggested that contemporary climate change has shifted the suitable area available to *Cronartium ribicola* (Figure S9) to higher elevations where it has not occurred until recently (Dudney et al. 2021). The existence of hosts in these newly available regions, for both SPB and *C. ribicola*, illustrate the interplay between climate and host abundance, and tendency for pests not to fill their contemporary

host ranges—leaving some host populations exposed to future risk of invasion as climate shifts.

4.3 | Role of Host Abundances

Despite theoretical expectations that host abundance and occurrence would be a primary constraint on pest distributions—as the pests we assessed were biotrophic or parasitic, requiring hosts to persist over time—the importance of host abundance was inconsistent among pests. Particularly striking was the lack of importance of individual host abundances, despite several of pests we assessed being specialists or having strong generic host preferences (e.g., *Cryptococcus fagisuga*, *Adelges tsugae* and *Elatobium abietinum*) (Figure 3b; Figures S3 and S17). The frequent greater importance of aggregated host abundance seemed to suggest that even minor, or less preferred hosts, can be important for limiting pest distribution and that forest composition (i.e., the relative abundance of hosts and non-hosts) also plays a role (Parker et al. 2015). The potential novel composition of future forests introduces additional uncertainty in how pests will respond to changing climates.

The inconsistent importance of host abundance on pest distribution could be due to multiple methodological or ecological reasons. First, many pests are not constrained solely to forested areas—the primary focus of FIA and NFI sampling—and can occur where host abundance is very low (effectively near zero) as in urban and agricultural areas. Even at low abundance, however, the RF models should be able to distinguish areas of zero host abundance from non-zero abundance, if the simple occurrence of hosts (as opposed to abundance of hosts) was meaningful in predicting pest distributions (Figure S25). The lower importance of host abundances, compared with climate and topography, could also reflect aspects of pest ecology. For instance, it is possible that pest distributions are only limited by host abundances through their interactions with climate. This seems like a plausible explanation, as most pests do not fill the entire geographic ranges of their hosts, but rather are frequently limited to a subset of the regions where hosts are present, even if pests are native and ostensibly have interacted with hosts for millennia. Geographic scale could also be playing a role in the importance of host abundances. At the broadest, global scales, host richness has been shown to play a strong role in limiting tree pest occurrences (Gougherty and Davies 2022a), suggesting a scale dependence to the factors controlling pest distributions.

Finally, the interaction between pests and hosts can also work in the opposite direction—that is, highly impactful pests, could over time reduce the abundance of their hosts (Fei et al. 2019) thereby inversing the expected association between pest occurrence and high host abundance. This may be especially true of non-native pests, which may attack hosts with little to no resistance, but can also be evident among native pests that affect the composition of the forests where they occur. Thus, there may be a temporal component to pests' relationship with host abundance that is not captured by our analyses. The occurrence of chestnut blight, and more recently emerald ash borer (EAB) and hemlock woolly adelgid (HWA), provides clear examples of how relations with host abundance can change over time. For instance, when chestnut blight first appeared in the early twentieth century, chestnut was among the most abundant tree species in the Appalachian Mountains. This likely facilitated the spread of the pathogen through the region. Over the following century, chestnut blight, along with management actions removing hosts ahead of the invasion front, removed chestnut as a major overstory tree, yet the pathogen persists in the region and continues to attack chestnut suckers growing from old stumps. Although the ultimate effects of EAB and HWA on abundance of their hosts are not yet fully realised, these associations could shift in the coming decades. This raises questions regarding the stationarity of the detected associations between host abundances and pest occurrences in models fit with contemporary abundances. For these high impact pests, continued future monitoring will likely be required to conclusively discern whether pest relationships with host abundance are consistent over time.

4.4 | Implications

Although the climate-only models provided good predictive ability, we maintain that including host information in the models is desirable as host variables provide greater inference, and align better with our conceptual understanding of what limits pest distributions (Dang et al. 2021; Koch 2021). While tree host abundance data are generally available for North America, due to the large-scale sampling efforts by US and Canadian Forest Services, we recognise these data only cover tree hosts, and that this type of data is not available for many global regions. While the pests we assessed mostly interact with trees, several were generalists or were otherwise known to utilise other plant types, for which abundance data were not available (e.g., *Lymantria dispar* and *Cronartium ribicola*). Although this may result in an incomplete picture of the biotic niches of these species, any effect they had on the distribution of the pests may have been compensated by climate or available tree host abundances. Future work where hosts are not known or abundance data is not available could consider using species occurrences (e.g., Global Biodiversity Information Facility) to tabulate host richness, which could be another useful host metric for understanding pest distributions.

Perhaps the most consistent effect we found in our models was the negative effect between non-native pest occurrences and the distance from the origin location in North America. This pattern suggests many invasive pests are still spreading on the landscape, and not yet at equilibrium with climate or host abundance and was consistent whether pests had been introduced recently (e.g., *Agrilus planipennis*, Figure 3a) or have been present for hundreds of years (e.g., *Lymantria dispar*, Figure S20). While quarantines and management have constrained the spread of some pests, even pests that have mostly filled the ranges of their host trees in North America (e.g., *Cronartium ribicola*, Figure S9) were responsive to this distance metric, suggesting the interacting effects of spread, host abundance and climate can be felt for decades after the pest has approached its equilibrium in its invaded range. This result is consistent with previous work that showed non-native pest distributions can be adequately inferred using a generalised dispersal kernel seeded from the discovery site (Hudgins, Liebhold, and Leung 2017). Although other approaches have been used to account for

non-equilibrium of non-native species ranges (e.g., Chapman et al. 2019; Gallien et al. 2012; Mainali et al. 2015; Václavík and Meentemeyer 2009), integrating knowledge about the origin site provides added inference on how pest spread can constrain pest distributions independent from climatic and host controls.

Author Contributions

A.V.G. conceived the idea. A.V.G., A.D.W. and I.D. compiled pest occurrences. A.V.G. and A.D.W. compiled host range information. A.P., M.P.P. and S.N.M. compiled host abundance and climate data. A.V.G. and A.D.W. analysed the data and wrote the first draft of the manuscript. All authors contributed to developing the Methods and critically reviewed the manuscript. The use of trade, firm or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the US Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in this work are publicly available at the cited sources. Data frames with climate and host abundances and a script to fit models are available at https://doi.org/10.6084/m9.figshare.25289929.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.