

Spatially explicit forecasts of tree insect and disease incidence across North American forests under future climate scenarios

Received: 9 July 2025

Accepted: 27 July 2026

Published online: 02 September 2026

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Shifts in insect and pathogen pressure with climate change present a potential threat to forest health, carbon sequestration and biodiversity. Here we evaluate climatic effects on insect and pathogen incidence across North America and forecast their future trends under climate scenarios. Using Bayesian hierarchical regression fit to records on more than 1 million trees, we show that warming and drought jointly exacerbate insect and disease incidence in historically colder and wetter regions, while reducing incidence in warmer and drier regions. Models allowing contemporary climate effects to depend on historical climate context better predict observed insect and disease incidence than models assuming quadratic functions of contemporary climate alone. Climate effects on incidence further vary among host species, mediated by tree climatic niches and functional traits, and differ across insect and pathogen taxa. Using ensemble climate projections, we forecast that under the Shared Socioeconomic Pathway 2-4.5 scenario, insect and pathogen incidence will increase across, respectively, 58% and 52% of forest land over the coming decades, with the largest impacts at high latitudes. Incorporating the variability of climate impacts across space and taxa, our work will help in predicting climate-driven insect and pathogen risk for North American forests.

Forest tree insects and pathogens (FIPs) are among the most notable and widespread drivers of disturbance in forest ecosystems¹. Insect and disease outbreaks disrupt forest structure, reduce biodiversity and degrade ecosystem functions, including timber production, carbon storage and nutrient cycling². In North America, FIPs are estimated to affect tens of millions of hectares of forest annually, far exceeding the area affected by wildfire, and result in economic losses of billions of dollars per year^{3,4}. Climate change will probably exacerbate pressure from FIPs by increasing tree susceptibility through drought-induced and heat-induced stress, and accelerating FIP development times^{5,6}. While notable progress has been made in projecting climate responses for some FIPs, predictions are highly variable^{7,8} and fail to capture the

context dependence of climate-driven changes in insect and pathogen pressure^{9,10}. This variability, alongside nonlinearities in species responses to climate have challenged community-wide forecasts of FIP risks in forest ecosystems^{11–13}.

The physiological performance of most organisms increases with temperature up to some optimum and then declines, generating nonlinear thermal response curves¹⁴. Small-bodied FIPs may acclimate more rapidly than their larger-bodied, long-lived hosts, and thus maintain high performance across a wider temperature range¹⁵. Thus, warming can amplify the relative performance gap between trees and FIPs, potentially increasing FIP incidence at temperatures above host thermal optima, while simultaneously decreasing incidence at

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temperatures below host thermal optima. However, thermal responses depend strongly on historical context. Local adaptation of hosts to historically warm environments could shift their thermal optima to higher temperatures. In such cases, warming may enhance host performance relative to FIPs if a trade-off between acclimation and adaptation in FIPs generates a mismatch between host and FIP thermal optima, ultimately reducing FIP incidence¹⁶. In cooler climates, FIP incidence may increase if warming enables the range expansion of previously cold-limited FIPs or if temperatures exceed the thermal optima of locally adapted hosts in historically cold locations^{17,18}.

Drought and excess rainfall can further mediate FIP incidence^{19,20}. Reduced precipitation could increase host susceptibility, particularly in drought-intolerant species²¹, whereas increased rainfall may facilitate pathogen development and spread by relaxing moisture constraints, especially for fungal pathogens in historically dry regions²². Shifts in precipitation regimes can interact with temperature to additionally modify host vulnerability and FIP activity, although the direction of these interaction effects is more difficult to predict^{23,24}. Thus, forecasting shifts in FIP incidence and future impacts of climate change on forest health requires consideration of the nonlinear, context-dependent effects of both precipitation and temperature and their interactions²⁵.

In this study, we leveraged data on FIP occurrence from more than 1 million forest trees to generate predictions of shifting insect and disease incidence with climate change across North American forests. We evaluated two alternative model frameworks using Bayesian hierarchical binomial regression. First, we explored the fit of a relatively simple quadratic term to capture the nonlinear effects of climate. Second, we represented this nonlinearity as the interaction between contemporary and historical climate, reflecting the historical context dependence of climate effects. In both models, we included temperature, precipitation and their interactions as the main effects, and ecological covariates including tree diversity and abundance, host phylogeny and plot identity to adjust for community-level effects on FIP incidence. We then forecasted how projected changes in temperature and precipitation would alter FIP incidence across forest landscapes to identify ecosystems at elevated risk. Integrating information on host functional traits and species climate preference into our models, we further examined how host species attributes may mediate climatic effects on FIP incidence, and identified the tree species most exposed to elevated FIP incidence under future climates.

Results

Historical climate mediates effects of climate change on FIP incidence

Models that incorporated the interaction between contemporary and historical climates consistently outperformed models assuming quadratic terms for climate effects (pathogens: Δ expected log pointwise predictive density = 58.4 ± 25.7 ; insects: Δ expected log pointwise predictive density = 57.7 ± 11.3 ; Supplementary Table 1). More complex models that include both quadratic and interactive terms did not further improve predictive performance (Supplementary Table 1). We suggest that inclusion of the interaction between historical and contemporary climate provides a robust model for predicting the nonlinear effects of climate on FIP incidence and allows for improved forecasting relative to models fitted with polynomial terms; however, as we note below, our main results are not sensitive to exact model specifications.

We show that temperature and precipitation strongly interact to influence FIP incidence (Fig. 1). For pathogens, increasing temperature increases incidence under dry conditions but reduces incidence under wet conditions, leading to elevated disease risks in both hot–dry and cold–wet climates (Fig. 1c). This pattern is consistent with suggestions that trees are highly vulnerable to disease under concurrent heat and drought stress²⁶, and that many foliar pathogens favour moist environments and are limited at high temperature^{9,27}. Insects show

a contrasting climate response (Fig. 1d). Under wetter conditions, warmer temperatures increase insect incidence, which is consistent with the expected benefits of warm and humid environments for insect herbivore development, feeding and reproduction²⁸. However, in dry conditions, warming reduces insect incidence, probably because high temperatures under low humidity impose more severe desiccation stress on insects than their tree hosts^{29,30}. Our results align with a broad literature suggesting additive effects of temperature and precipitation on disease and insect outbreaks^{23,24}, and highlight distinct climate niches for pathogens versus insects, reflecting intrinsic differences in their life histories, ecologies and physiologies³¹.

Despite differences in responses to contemporary climate, the interaction between historical and contemporary climate is consistent for both forest insects and pathogens. Warming promotes FIP incidence in plots with historically cool temperatures and reduces incidence in historically warmer plots (Fig. 2a,b and Supplementary Figs. 1 and 2). Likewise, historically wetter regions experience elevated incidence under drought, and historically dry plots experience elevated incidence with higher rainfall (Fig. 2c,d and Supplementary Figs. 1 and 2). This context dependence may reflect differences in climate tolerance between hosts and their small-bodied FIPs. In historically cool regions, warming may reduce the performance of cold-adapted hosts by pushing local temperature beyond their thermal optima, while enhancing the relative performance of cold-limited FIPs with wider thermal tolerances^{17,18}. In historically warm regions, further warming can suppress FIP activity, but may have little fitness effect on warm-adapted hosts possessing traits that allow them to maintain performance at high temperature²⁷. Similarly, for precipitation, drought stress reduces host performance, especially for drought-intolerant species adapted to wet regions, while in historically dry regions, increases in rainfall are expected to benefit FIPs more immediately than their hosts, increasing near-term FIP incidence and elevating infection and infestation risks²².

We found strong support for the interaction between contemporary and historical temperature in driving the incidence of almost all of the top insect and pathogen species when analysed separately (18 of 20 species from species-specific models fitted to the ten insects and ten pathogens with the most occurrence data). This includes the three most abundant FIP species: *Cronartium quercuum* (pine-oak gall rust), *Nectria coccinea* (fungus associated with beech bark disease) and *Lymantria dispar* (gypsy moth) (Supplementary Fig. 3a). Evidence for a statistical interaction between contemporary and historical precipitation was supported in 12 of 20 FIPs, including beech bark disease and the gypsy moth (Supplementary Fig. 3b). Thus, our results highlight how considering both contemporary and historical climate can better inform predictions of FIP responses to climate change, both at the scale of individual FIPs and across aggregated FIP communities.

Forecasting climate-driven changes in FIP incidence across North American forests

We used our fitted Bayesian models to project FIP incidence under future climate scenarios across North America, restricting projections to regions with historical climates within the range of our fitted data. With this restriction, our projections cover approximately 72% of North American forested land, defined as areas with more than 10% tree canopy cover³². Under a moderate carbon emission scenario (Shared Socioeconomic Pathway (SSP) 2-4.5), our projections indicate that by mid-century (2040–2060), FIP incidence will increase across 58% and 52% of the assessed forested land for insects and pathogens, respectively, with mean increases of 28% and 13% (Fig. 3 and Supplementary Fig. 4). Overall, we predict that 83% of assessed forested lands face elevated threats from insects, pathogens or both under climate change.

Insects are projected to pose a more immediate threat to North American forests, with more than 60% of forested areas experiencing increasing incidence in the near future (by 2040). However, this proportion declines slightly over time, to ~50% by 2100, as precipitation

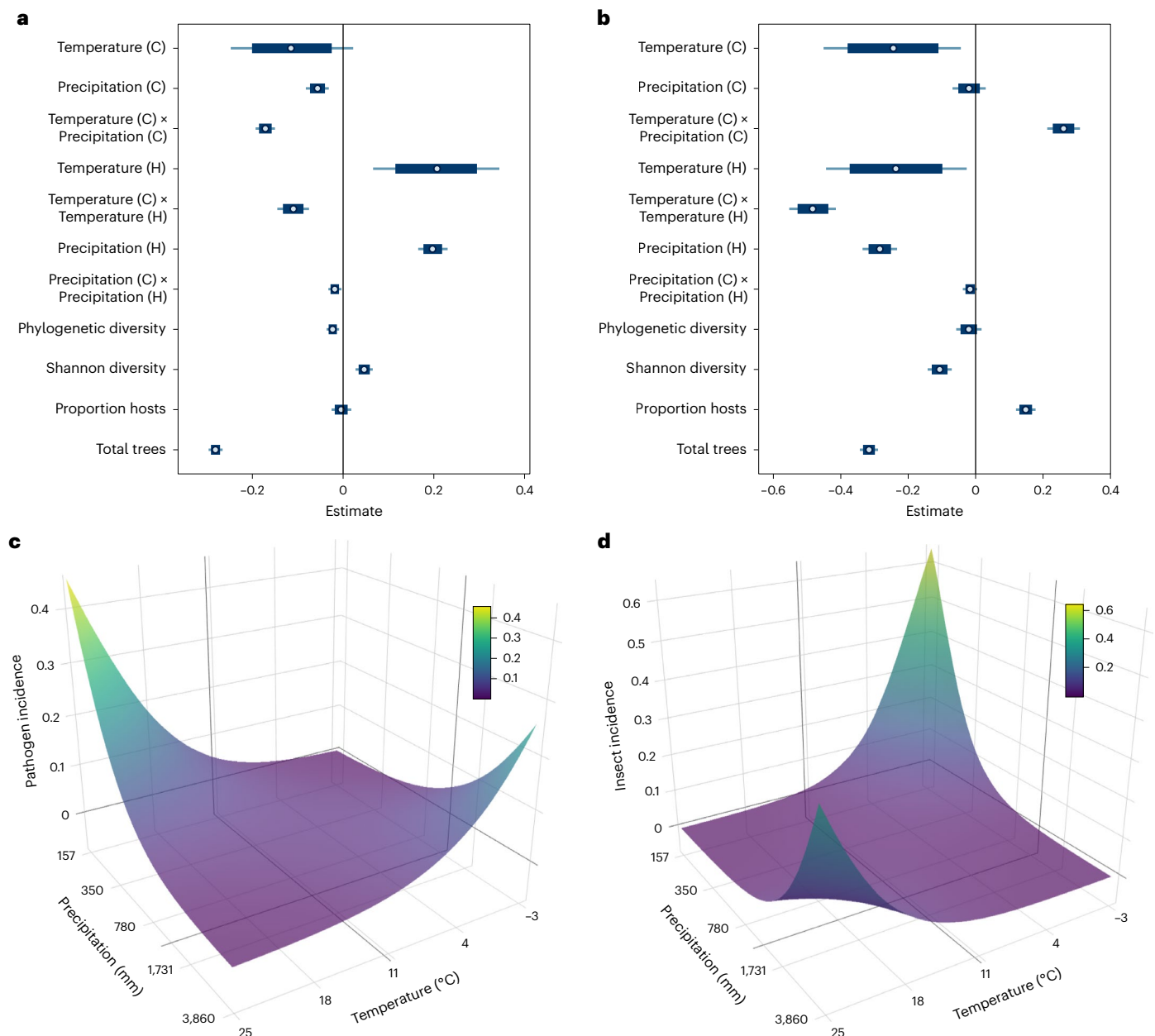


Fig. 1 | Posterior distribution of parameter estimates from the Bayesian model of pathogen and insect incidence, and interactive effects of contemporary temperature and precipitation on pathogen and insect incidence. a,b, Posterior parameter estimates for pathogens (a) and insects (b). The x axis indicates the standardized effect sizes; the points show the posterior medians; and the inner bars and outer lines represent the 80% and 95% credible intervals, respectively. Estimates are based on 40,000 posterior draws from

models fitted to 156,014 tree populations (each a unique host species × plot combination) across 261 tree species in 26,545 plots. **c,d,** Joint effects of contemporary temperature and precipitation on pathogen (c) and insect (d) incidence, with historical climate held constant to facilitate visualization of the temperature × precipitation interaction. Therefore, these response surfaces represent conditional effects and are intended to highlight the shape of the interaction. C, contemporary; H, historical.

changes partly offset warming effects in some regions (Fig. 3e). The average magnitude of increases in incidence is sensitive to carbon emission scenarios, with 32% increases in incidence under SSP2-4.5, rising to 51% under SSP5-8.5 by 2100 (Fig. 3f). The largest increases are projected in high-latitude ecozones, including the eastern Northern Forest and Marine East Coast Forest (Fig. 3d), aligning with previous studies that have suggested warming disproportionately promotes insect herbivory at higher latitude^{33,34}. North American boreal forests are among the most intact forest habitats and critical carbon sinks³⁵, but millions of hectares have been damaged because of pest outbreaks since the early 2000s. Our models suggest that escalating insect incidence over the coming decades could further accelerate

forest loss, potentially shifting these ecosystems from carbon sinks to carbon sources³⁶.

Relative to changes in insect incidence, pathogen incidence is projected to increase more gradually with warming: 41% of forested area is predicted to experience increased incidence by 2040, rising to more than 60% by 2100 under SSP2-4.5 (Fig. 3b). The magnitude of increases in pathogen incidence also intensifies with more extreme emission scenarios, with a 19% increase in incidence under SSP2-4.5 and 39% under SSP5-8.5 (by 2100) (Fig. 3c). Increasing pathogen incidence is particularly pronounced across the North Central Rockies and sub-tropical coniferous forests (Fig. 3a), with potential implication for the pine species that dominate these regions³⁷. However, reduced pathogen

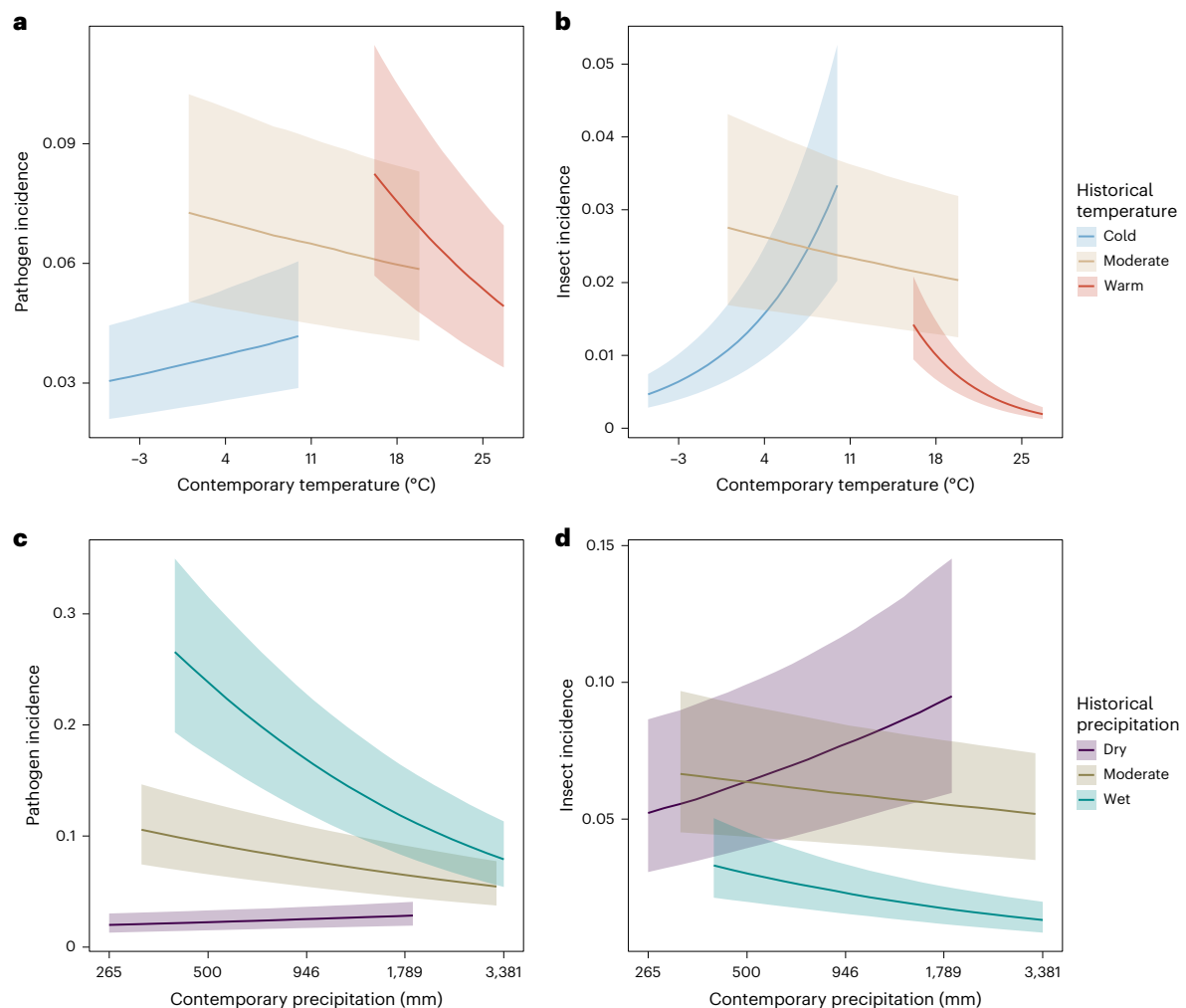


Fig. 2 | Impacts of contemporary temperature and precipitation on the incidence of pathogens and insects across historical climate contexts. **a,b**, Relationships between incidence and temperature for pathogens (**a**) and insects (**b**) are shown for historically cold (<25th percentile of historical temperature), moderate (25th–75th percentile) and warm (>75th percentile) environments. **c,d**, Relationships between incidence and precipitation for pathogens (**c**) and insects (**d**) are shown for historically dry (<25th percentile

of historical precipitation), moderate (25th–75th percentile) and wet (>75th percentile) environments. The lines show posterior median predictions; the shaded areas show the 50% posterior intervals; corresponding predictions with 90% credible intervals are provided in Supplementary Fig. 2. Predictions are conditional on plot-level intercepts to focus on the climate–incidence relationship rather than absolute incidence across plots.

incidence is projected for some regions, such as the Southeastern USA and the West Coast (Fig. 3a).

Using a leave-one-variable-out approach, we show that changes in temperature primarily drive the broad latitudinal trend of increasing FIP incidence, whereas changes in precipitation contribute to local variability and a few emerging hotspots of increasing incidence at lower latitude (Supplementary Fig. 5). Comparing our modelled predictions with independent risk assessments of forest insect and disease from the recent past and present day³⁸ (Methods), we find that forest areas identified as at high insect and disease risk in the past decade are more likely to experience increased FIP incidence under future climate scenarios (predicted changes in FIP incidence: 0.03 versus −0.04 in sites classified as ‘risky’ and ‘non-risky’, respectively; Supplementary Fig. 6), suggesting that the fingerprint of climate warming on FIP incidence is already detectable and that future climate change may further exacerbate observed trends of increasing insect and disease pressure.

Our projections of future FIP incidence were generated holding biotic covariates constant so as to isolate the direct effects of climate change. They represent climate-driven changes in FIP incidence at the tree-population level; aggregate incidence across all trees and species within a plot would depend on additional factors, including tree species

composition and abundance. Because total tree density was an important predictor of FIP incidence in our models, we conducted further analyses to evaluate whether future changes in forest density, using projected forest biomass and tree cover as proxies, would substantially alter our forecasts (Methods). We found that predicted climate-driven changes in pathogen incidence were relatively insensitive to modelled changes in forest structure, although climate-driven increases in insect incidence were intensified in western US mountain regions under scenarios of declining forest density (Supplementary Fig. 7).

Predicting climate change impacts across tree species and FIPs

The effects of climate change on FIP incidence vary markedly among tree species. Trees with a lower species temperature index (STI), typically cold-adapted species, are projected to experience increased FIP incidence under warming, whereas those with a higher STI show reduced FIP incidence. Similarly, trees with a higher species precipitation index (SPI), more drought-intolerant species, experience increased FIP incidence with drought, especially for pathogens (Supplementary Fig. 8). Tree functional traits further mediate the effect of climate. Taller trees and trees with a larger leaf area are commonly assumed to be better adapted to warmer and more productive environments^{39,40}.

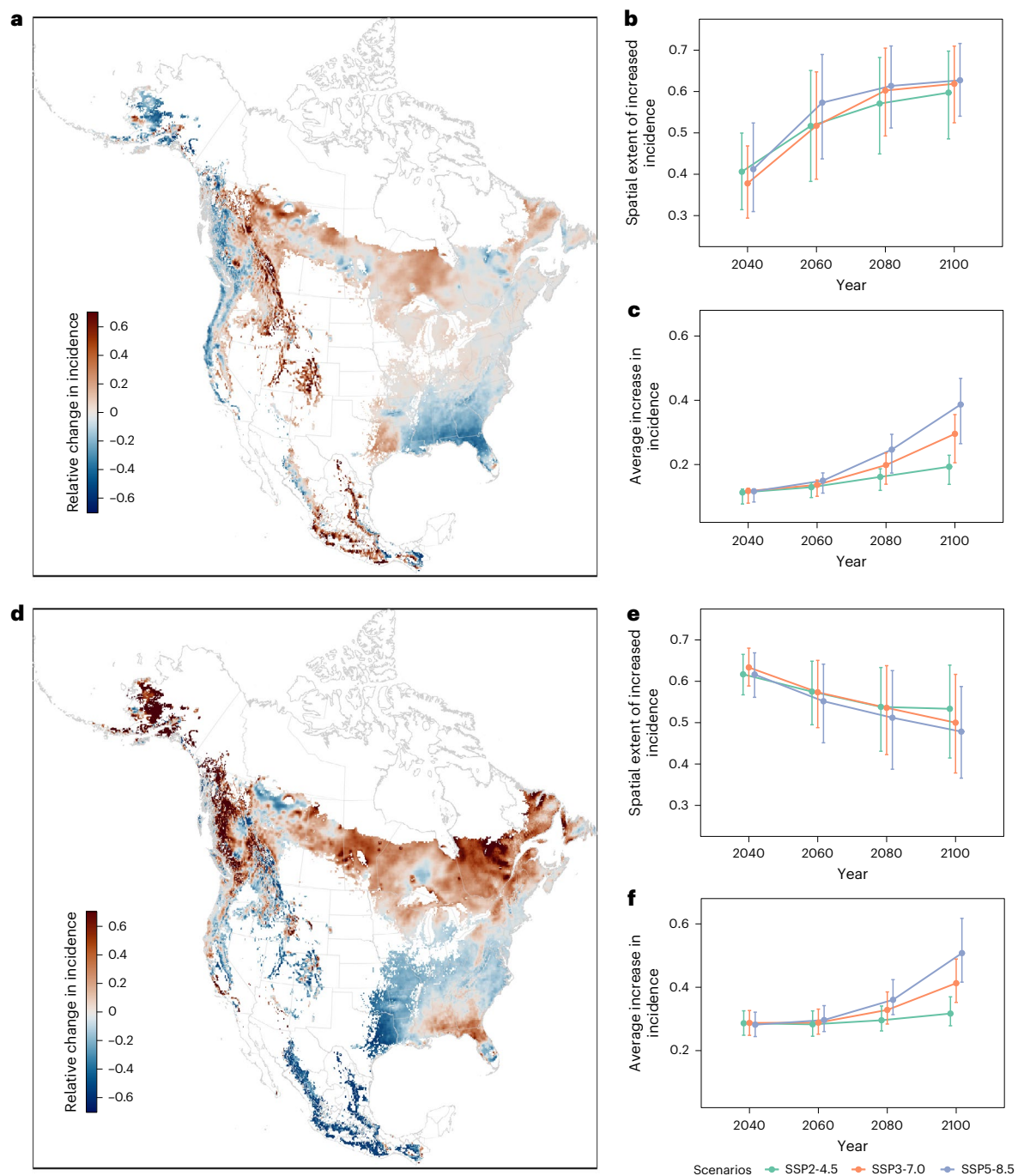


Fig. 3 | Predicted changes in pathogen and insect incidence by 2040–2060 under different climate change scenarios. a,d, Incidence projections for pathogens (a) and insects (d) were generated under SSP2-4.5 scenarios, on land with tree cover greater than 10%. Projections were restricted to regions with historical climate falling in the range of training data. The upper and lower tails of the prediction distribution are presented in Supplementary Fig. 4. **b,e,** The proportion of forested area with increased incidence was calculated for

pathogens (b) and insects (e), representing the spatial extent of increasing FIP risks. **c,f,** The predicted increases in FIP incidence were averaged for pathogens (c) and insects (f) to indicate the severity of FIP risks. **b,c,e,f,** Estimates are based on 194,928 forested grid cells; points show posterior medians and the error bars show the 80% credible intervals, derived from 40,000 posterior draws for each grid cell.

Species with these traits may be able to maintain fitness under scenarios of warming temperatures and increasing precipitation; thus, we might expect them to be less susceptible to elevated FIP incidence. In contrast, species with traits suited to cooler or drier climates may experience a more rapid decline in fitness with warming and increasing rainfall, making them more susceptible to FIPs (Supplementary Fig. 9).

Including host traits improved model performance (Supplementary Table 2) and allowed us to generate tree-species-specific projections

of FIP incidence. We show that, by 2040–2060 under SSP2-4.5, 37% of the modelled tree species are likely to experience a substantial increase in pathogen incidence, with an average increase of 74%, while the remaining species show little change or modest declines. Insects show a similar pattern; 52% of the modelled tree species are projected to experience increased insect incidence, with an average increase of 43% (Fig. 4 and Supplementary Fig. 10). Thus, climate change will probably increase FIP incidence for a large fraction of North American

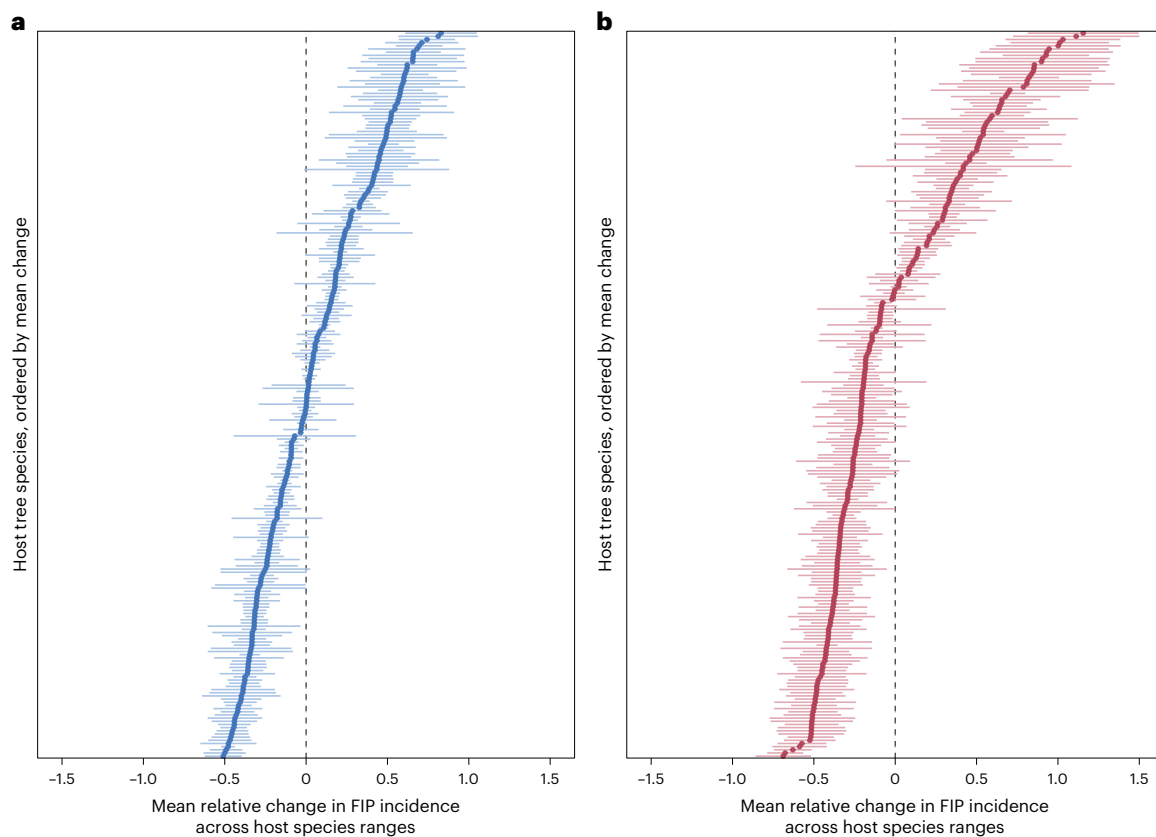


Fig. 4 | Projected changes in insect and pathogen incidence under climate change across host tree species. a,b, Relative changes in insect (a) and pathogen (b) incidence are shown for all host tree species in this study by 2040–2060 under SSP2-4.5. Each point represents one host tree species and shows the mean projected change in incidence across its current geographical range. The horizontal bars show ± 1 s.d. among grid cells within each species' geographical

range. Estimates are derived for 229 host tree species with an average of 21,347 grid cells within each species range. Host tree species are ordered according to mean projected change within each panel. Relative change is indexed as the log ratio between future and current incidence. A version of this figure with host species names is provided in Supplementary Fig. 10.

trees despite variations among host species, some of which may benefit from marginal decreases in FIP incidence, which is consistent with the broader literature on FIP threats in forests^{41,42}.

Species most at risk are typically small-sized to medium-sized and associated with boreal or mountain forested habitats, such as *Salix bebbiana* (gray willow), *Abies lasiocarpa* (Rocky Mountain fir) and *Picea mariana* (black spruce). However, we also identified several species native to the southeastern USA, including *Liriodendron tulipifera* (tulip tree) and *Platanus occidentalis* (American sycamore), which may experience reduced FIP incidence (Fig. 4 and Supplementary Fig. 10). When averaged across tree species, we further estimate that 61% and 69% of forested area will experience increased incidence for pathogens and insects, respectively (Supplementary Fig. 11), which is broadly consistent with our plot-level predictions. Under less restrictive carbon emission scenarios and over longer time frames, FIP incidence is forecast to rise dramatically: by 2080–2100 under SSP5-8.5, the averaged incidence that North American tree species will experience is predicted to approximately double (149% and 90% increases in pathogen and insect incidence, respectively), presenting a severe threat to North American forests (Supplementary Fig. 11).

Incidence was projected to increase by 2040–2060 under SSP2-4.5 for most commonly observed FIPs, including 70% of insects and 50% of pathogens. However, responses can vary spatially within the geographical range of individual FIPs, with incidence increasing in some areas and decreasing in others (Supplementary Fig. 12). Our results are broadly consistent with previous work suggesting that climate change may increase the risk posed by many forest insects and pathogens,

while responses remain taxon-specific^{43,44}. FIPs presenting the greatest future risks include the hemlock woolly adelgid (*Adelges tsugae*), which is projected to increase in incidence across its current cooler range, indicating that warming temperatures may facilitate its northward expansion⁴⁵. The gypsy moth (*L. dispar*) is predicted to increase several-fold in eastern North America, threatening oak-dominated temperate forests⁴⁶. Some FIPs, including Eutypella canker (*Eutypella parasitica*) and Black knot (*Apiosporina morbosa*), are relatively insensitive to climate change in our models, although localized increases in incidence may still occur (Supplementary Fig. 12). Most taxon-specific projections of FIP incidence are positively correlated with the projected changes in overall pathogen or insect incidence; thus, aggregated FIP projections reflect combined responses across multiple FIPs rather than idiosyncratic responses of individual insect or pathogen taxa (Supplementary Fig. 13).

Discussion

In an analysis of more than 1 million trees, we modelled the effects of climate on FIP incidence across common tree species and forested land in North America. We show that climatic effects are predictably and strongly context-dependent: warming and drought elevate FIP incidence in historically colder and wetter regions, respectively, while reducing incidence in historically warmer and drier regions. Using ensemble climate projections, we predict that climate change will probably intensify FIP incidence across most North American forest ecosystems over the coming decades, highlighting the need for strategies to mitigate their potential impacts on forest health¹.

Our analyses help explain the large variability in climate impacts on forest insects and pathogens observed across regions and host trees. While recent work suggested a generally positive effect of warming temperature and shifting precipitation on pest damage in North American forests⁴⁷, FIP responses can be neutral or even dampening in certain cases, for example, if warming temperatures exceed insect or pathogen lethal temperatures, increase host fitness or increase the abundance of natural enemies of insects^{8,9,48}. We show that, on average, FIP incidence increases with warming in historically cold regions but changes little or may even decrease in historically warm regions. Models assuming an interaction between contemporary and historical climate better predict observed FIP incidence than model fits assuming quadratic terms for contemporary climate alone, indicating that a historical climate context provides additional information for forecasting climate impacts^{12,13}. Incorporating this context dependence allows more nuanced projections of increases, declines and uncertainty in changes in FIP incidence across pests, hosts and regions. Our results indicate that climate change will redistribute FIP prevalence across taxa and space, rather than uniformly increase FIP pressure.

We present spatially explicit projections of climate-driven FIP risks for North American forests as a consequence of anthropogenic warming and precipitation changes. We identify vulnerable forest ecosystems, tree species and insects and pathogens with high risk of future outbreaks, allowing for better integrated management strategies, providing guidance for targeted management and enabling risk-based decision-making and resource allocation^{49,50}. We find that invasive FIPs, including hemlock woolly adelgid and the gypsy moth, are especially advantaged by climate change, and thus require extensive monitoring and management to prevent their further range expansion. We suggest that increasing insect incidence represents a more immediate and widespread threat, especially in boreal forests, whereas pathogen incidence may progressively intensify under continued warming and therefore warrants sustained monitoring under climate change.

Our projections represent a critical step towards generating more precise, quantitative assessments of climate impacts on forest health and ecosystem services². Consideration of additional climatic factors, such as atmospheric CO₂, climate variability and extreme weather events, along with the indirect effects of climate change, including shifts in forest tree composition, may further improve the accuracy of forecasts^{6,51,52}. Because the Forest Inventory and Analysis (FIA) data capture commonly observed FIPs and climatic conditions across US forests, the estimated relationships may differ for other FIP assemblages or climate regimes. Our findings can inform management options to maintain forest health in North America, and provide a framework for assessing climate-driven FIP risks globally.

Methods

Forest inventory data

We used forest inventory data from the US Forest Service to assess the relationships between climate and FIP occurrence. The US Forest Service's FIA programme conducts continual surveys of forest attributes nationwide, based on a tessellation of the USA into 6,000-acre hexagons with at least one plot established in each hexagon⁵³. Four subplots of 24-foot fixed radius are surveyed within each primary plot; all trees in the subplots with a diameter at breast height greater than 1.0 inches are visually inspected to record damage (see the FIA database user guide at <https://research.fs.usda.gov/understory/forest-inventory-and-analysis-database-user-guide-nfi> for a full description). Damage is recorded if it is likely to reduce the survival or growth of the tree in the near term, or negatively affect a tree's marketable products. A wide range of damage types and causative agents, including insects, disease, decay and animal herbivory, are recorded and assigned to species level whenever possible. Up to three damaging agents per tree may be

recorded; if there are more than three damaging agents, the three most severe are recorded. Only a very few individual trees are subjected to more than three damaging agents; thus, this survey scheme captures most notable tree damage in the plots⁵⁴.

We used FIA recorded tree damage data from 2013 to 2020, representing survey data for over a million trees from more than 300 species in 26,559 plots across the USA, reporting on the 64 most impactful FIPs (30 insects and 34 pathogens), as well as general insect or pathogen damage not identifiable to a causal species. The 64 identified species account for 51% of all recorded FIP damage in the survey and are broadly representative of the total FIP pressure experienced by trees; the number of individuals recorded as being affected by the 64 FIP species in a given tree population is highly correlated with the number of individuals recorded as being negatively affected by any insect or pathogen, regardless of species (Spearman's $\rho = 0.65$, $P < 0.001$). Importantly, FIP damage recorded at the species level is likely more standardized relative to records of general insect and pathogen damage (where species is non-identifiable), which could be influenced by changes in the survey protocols across inventory regions and over time⁵⁴. While it is possible that FIPs may be misidentified, surveyors receive extensive training on tree damage symptom identification, particularly for common FIPs. In addition, we verified if the reported tree damage represented a known host–FIP association by searching the host–FIP interaction in regional and global databases, and excluded records if the tree was not a recognized host of an FIP, according to Gougherty & Davies⁵⁵. This step removed a small proportion (0.1%) of the total records. We also excluded a few plots located on islands that may have unique tree species.

For each tree species in each plot, we recorded the number of individuals infested by identified insects, the number infected by identified pathogens and separately for each of the most prevalent individual FIPs identified to species. The classification of damage based on visual inspection may overlook root-associated damage; thus, our analyses primarily address FIPs causing above-ground damage. Identification of pathogens in large-scale field surveys is also generally more challenging than that of insects, particularly for taxa with visually subtle symptomology. This potential bias can complicate direct comparisons of absolute pathogen and insect incidence; however, our analyses focus on common FIP taxa with more recognizable symptoms, with insects and pathogens modelled separately; therefore, they are less sensitive to between-group differences in detectability. In total, we recorded FIP incidence (the number of infested trees given the total number of inspected trees) in 156,014 tree populations, representing 261 tree species, across 26,545 forest plots (Supplementary Fig. 14).

Climate data

We collected the following classes of climate data: historical climate in each forest plot; contemporary climate for the year the data were collected; the climate preference for each tree species; and future climate projections across North America. Historical climate data were obtained from WorldClim 1.4 for 1960–1990 at a resolution of 5 arcmin⁵⁶, from which we extracted the average annual mean temperature and annual total precipitation matched to the geographical coordinates of each plot. Contemporary climate was estimated as the mean temperature and total precipitation for each plot for the year the plot was surveyed, extracted from the European Centre for Medium-Range Weather Forecasts Reanalysis v.5 (ERA5) monthly averaged database⁵⁷. We aggregated monthly ERA5 climate data to annual values corresponding to the survey year because many insect outbreaks and pathogen infections are strongly associated with recent climatic conditions, particularly those during the current or immediately preceding growing season²⁵. Although it is common practice to extract contemporary climate from ERA5 and historical baseline from WorldClim, the two climate data sources differ in their resolution and

methods of data generation. By extracting ERA5 climate values for the period corresponding to the WorldClim baseline (1960–1990), we show that the two datasets align closely, with correlation coefficients greater than 0.99 for temperature and greater than 0.85 for precipitation (Supplementary Fig. 15).

We characterized the climate niche for each tree species over their geographical range using Little's Atlas of United States Trees⁵⁸. We calculated the STI as the average annual mean temperature within the geographical range of each species. Similarly, we calculated the SPI as the average precipitation within their geographical range. Little's distribution maps and matching climate niche data were available for 229 tree species, representing 97.3% of records in our database.

We downloaded future climate data as gridded projections for North America at 1-km resolution from AdaptWest⁵⁹. Specifically, we used the ensemble mean projection from eight general-purpose global climate models selected by Mahony et al.⁶⁰ under three emission scenarios: SSP2-4.5, SSP3-7.0 and SSP5-8.5, in Coupled Model Intercomparison Project Phase 6 for the years 2021–2040, 2041–2060, 2061–2080 and 2081–2100. We extracted the projected annual mean temperature and annual total precipitation during these time periods for each SSP. Extraction of climate data was implemented with the terra R package (v.1.7.65).

Plant community, phylogeny and trait data

To adjust for regional and community-level effects on insect and pathogen incidence, we characterized the diversity and abundance of trees along with their phylogenetic relationships within each forest plot, and then nested each plot within a defined 'ecozone'. Tree phylogenetic relationships were obtained by pruning the plant megatree from ref. 61 to the species set included in our analysis, using the phylo.maker function in the V.phyloMaker package (v.0.1.0)⁶². Tree community diversity and phylogenetic structure were quantified using the Shannon index and the mean nearest taxon distance index (MNTD), implemented with the picante R package (v.1.8.2)⁶³, respectively. The total number of trees and the proportion of conspecific individuals within the plot were also recorded. Ecozones were assigned using the level II ecological regions from the North American ecoregion database according to the Commission for Environmental Cooperation in North American Environmental Atlas⁶⁴.

Last, we collated tree functional trait data from the Global Spectrum of Plant Form and Function Dataset⁶⁵. This dataset is based on approximately 1 million records included in the TRY database and additional unpublished data⁶⁶. We used three traits closely aligned with ecological axes of plant growth and survival commonly associated with species' long-term climate adaptation⁶⁷: leaf area, leaf mass per area and adult tree height. Trait data were available for the majority (90%) of tree species in our dataset; for trees without species-level trait data we imputed values using the mean of genus-level or family-level observations.

Bayesian hierarchical modelling

We used Bayesian hierarchical regression fitted to a binomial response to evaluate the relationship between climate and FIP incidence.

First, we modelled climate effects across plots to generate spatially explicit predictions of FIP incidence. Within this framework, we evaluated two model structures. We initially fitted quadratic terms for contemporary climate to capture the nonlinearity of climate responses. We then fitted an alternative model that allows for nonlinearity in climate responses via the interaction between contemporary (current) and historical (historic) climate, which also captures the historical context dependence of climatic effects. We compared model fits using leave-one-out cross-validation, implemented with the loo R package (v.2.6.0). Models were structured as follows:

$$n_{\text{inf}i} \sim \text{Binomial}(n_{\text{total}i}, P_i) \quad (1)$$

$$\begin{aligned} \text{logit}(P_i) = & \alpha + \beta_1 \text{temp.Current}_i + \beta_2 I(\text{temp.Current}_i)^2 \\ & + \beta_3 \text{prec.Current}_i + \beta_4 I(\text{prec.Current}_i)^2 \\ & + \beta_5 \text{temp.Current}_i \times \text{prec.Current}_i + \beta_6 \text{MNTD}_i \\ & + \beta_7 \text{Shannon}_i + \beta_8 \text{Prop.conspecific}_i + \beta_9 \text{Total trees}_i \\ & + u_{\text{hostsp}} + u_{\text{phylogeny}} + u_{\text{Year}} + u_{\text{ecozone}} + u_{\text{plotID}} \end{aligned} \quad (2)$$

$$\begin{aligned} \text{logit}(P_i) = & \alpha + \beta_1 \text{temp.Current}_i + \beta_2 \text{temp.Historic}_i \\ & + \beta_3 \text{temp.Current}_i \times \text{temp.Historic}_i + \beta_4 \text{prec.Current}_i \\ & + \beta_5 \text{prec.Historic}_i + \beta_6 \text{prec.Current}_i \times \text{prec.Historic}_i \\ & + \beta_7 \text{temp.Current}_i \times \text{prec.Current}_i + \beta_8 \text{MNTD}_i \\ & + \beta_9 \text{Shannon}_i + \beta_{10} \text{Prop.conspecific}_i + \beta_{11} \text{Total trees}_i \\ & + u_{\text{hostsp}} + u_{\text{phylogeny}} + u_{\text{Year}} + u_{\text{ecozone}} + u_{\text{plotID}} \end{aligned} \quad (3)$$

where $n_{\text{inf}i}$ is the number of trees attacked and $n_{\text{total}i}$ is the total trees inspected in tree population i . We incorporated the interaction between contemporary temperature and precipitation ($\text{temp.Current}_i \times \text{prec.Current}_i$) to explore the interactive effect of warming and drought. We also included indices of tree community phylogenetic structure (MNTD), species diversity (Shannon), proportion of conspecific individuals (Prop. conspecific) and total number of neighbouring trees (Total trees) as covariates to adjust for potential dilution or amplification effects of biodiversity on FIP incidence⁵⁵. Host tree species identity ($u_{\text{hostsp}i}$), plant phylogeny ($u_{\text{phylogeny}i}$), ecoregion ($u_{\text{ecoregion}i}$), sampling year ($u_{\text{Year}i}$) and plot identity ($u_{\text{plotID}i}$) were fitted as grouping variables with random intercepts to incorporate the spatial, temporal and host-related hierarchical structure of the data.

We fitted models to 156,014 tree populations (representing 261 tree species across 26,545 forest plots), assuming a binomial distribution of incidence (infested versus inspected individuals). We modelled tree-population-level incidence rather than plot-averaged incidence because plot-level incidence depends on both the host species composition and relative abundance within each plot. Modelling incidence at the tree-population-level allows us to account for host identity explicitly and separate climate effects from changes in host composition. Therefore, our model predictions reflect climate-driven changes in potential FIP incidence across tree populations rather than aggregate incidence across all trees in a given location. We assessed model fit using posterior predictive checks and applied a beta-binomial likelihood when diagnostics suggested overdispersion of incidence data. We note that model results were robust to the choice of likelihood.

Second, we modelled the relationship between climate and FIP incidence across tree species to generate host-specific predictions. We focused on interspecific variation in climate responses and examined how climatic effects differ between cold-adapted and warm-adapted species by incorporating the interaction between contemporary temperature and the STI. We also fitted the equivalent interaction term for precipitation (contemporary precipitation and SPI) to examine differences between low-precipitation-adapted and high-precipitation-adapted species (equation (4)). We further included species data on tree height, leaf area and leaf mass per area to explore how host traits mediate species responses. These traits are relatively independent from STI or SPI (correlation coefficient $r < 0.5$) and thus may provide additional information on how climate effects vary among host species (equation (5)). Models were structured as follows:

$$\begin{aligned} \text{logit}(P_i) = & \alpha + \beta_1 \text{temp.Current}_i + \beta_2 \text{STI}_i + \beta_3 \text{STI}_i \times \text{temp.Current}_i \\ & + \beta_4 \text{prec.Current}_i + \beta_5 \text{SPI}_i + \beta_6 \text{SPI}_i \times \text{prec.Current}_i \\ & + \beta_7 \text{temp.Current}_i \times \text{prec.Current}_i + \beta_8 \text{MNTD}_i + \beta_9 \text{Shannon}_i \\ & + \beta_{10} \text{Prop.conspecific}_i + \beta_{11} \text{Total trees}_i + u_{\text{hostsp}i} \\ & + u_{\text{phylogeny}i} + u_{\text{Year}i} + u_{\text{ecozone}i} + u_{\text{plotID}i} \end{aligned} \quad (4)$$

$$\begin{aligned}
\text{logit}(P_i) = & \alpha + \beta_1 \text{temp.Current}_i + \beta_2 \text{STI}_i + \beta_3 \text{STI}_i \times \text{temp.Current}_i \\
& + \beta_4 \text{prec.Current}_i + \beta_5 \text{SPL}_i + \beta_6 \text{SPL}_i \times \text{prec.Current}_i \\
& + \beta_7 \text{temp.Current}_i \times \text{prec.Current}_i + \beta_8 \text{Leaf mass per area}_i \\
& + \beta_9 \text{Leaf area}_i + \beta_{10} \text{Height}_i + \beta_{11} \text{Leaf mass per area}_i \\
& \times \text{temp.Current}_i + \beta_{12} \text{Leaf area}_i \times \text{temp.Current}_i \\
& + \beta_{13} \text{Height}_i \times \text{temp.Current}_i + \beta_{14} \text{Leaf mass per area}_i \\
& \times \text{prec.Current}_i + \beta_{15} \text{Leaf area}_i \times \text{prec.Current}_i \\
& + \beta_{16} \text{Height}_i \times \text{prec.Current}_i + \beta_{17} \text{MNTD}_i + \beta_{18} \text{Shannon}_i \\
& + \beta_{19} \text{Prop.conspecific}_i + \beta_{20} \text{Total trees}_i + u_{\text{hostspj}} \\
& + u_{\text{phylogenyj}} + u_{\text{Yearj}} + u_{\text{ecozonej}} + u_{\text{plotID}}
\end{aligned} \quad (5)$$

Trees with missing trait data were excluded from the model, which was thus fitted to 151,859 tree populations. Model covariates and grouping variables are as described above. As with the plot-level analyses, we compared the performance among models using leave-one-out cross-validation.

We fitted the above models separately to tree pathogens and insects. To further explore variation among individual FIPs, we also refitted our models separately to the FIP species (ten insects and ten pathogens) with the highest prevalence in our data. As individual FIPs only occur on their host trees, we included a binary dummy variable (host versus non-host) as a grouping factor with random intercept. This term captures the structural difference between host and non-host trees (for example, non-host trees have a strongly negative offset, reflecting near-zero incidence) while allowing climate effects to be estimated using a consistent and comparable dataset across insect and pathogen species.

Bayesian models were fitted with Stan⁶⁸ called from brms (v.2.21.0) in R (v.4.2.0)⁶⁹. Contemporary and historical precipitation, the proportion of conspecifics, the total number of trees and plant trait measures were log-transformed. All numerical variables were then scaled to a mean of 0 and s.d. of 1 using z-score standardization before model fitting. We used weakly informative priors assuming a normal distribution with mean 0 and s.d. of 1, and ran four Monte Carlo Markov chains each with 15,000 iterations with 5,000 iterations discarded as warm-up. We verified model convergence by checking if R-hat was near 1.0 and bulk and tail effective sample sizes (bulk-ESS and tail-ESS, respectively) were sufficiently large (Supplementary Fig. 16).

Model projections

With the above fitted models, we projected the shifting incidence in pathogens, insects and individual FIPs across North American forested land and among tree species. We projected FIP incidence at a spatial resolution of 5 arcmin for computing efficiency and to match with the climate data used to train our models. We restricted our projection to ‘forested’ land, defined as grid cells with a tree cover more than 10% based on global tree cover data 2010 (ref. 70) following ref. 32. Additionally, to avoid extrapolating beyond the data, we constrained projections to regions with historical climates (temperature and precipitation) falling within the range represented in our training data. This constraint excluded climatically distinct regions, including the northern Canadian boreal forest and southern Mexican tropical forests, but nonetheless allows projections for more than 72% of forested land across North America.

We generated projections under current and future climate conditions using the posterior distribution of parameters extracted from models fitted with equation (2) (models with quadratic terms) and equation (3) (models with interaction terms). We then calculated the relative changes in incidence as $\frac{P_{\text{future}} - P_{\text{current}}}{P_{\text{current}}}$ where P is the probability of occurrence (that is, incidence). For all projections, non-climatic covariates, including tree species diversity, conspecific proportion, host

phylogenetic diversity and total tree abundance, were fixed at their observed mean values in the fitted data. The same values were used for all grid cells both within and outside the FIA plots, and were held constant between current and future projections. Thus, model projections quantify climate-driven changes in FIP incidence independent of additional possible changes to forest structure. For each cell, we calculated the median and 80% credible intervals of the posterior predictive distribution. We summarized the proportion of land areas with increased FIP incidence to quantify the spatial extent of increased risks, and calculated the mean increases in incidence in these areas to quantify the magnitude of increases. Projections were generated using the brms (v.2.21.0) and ggEffects (v.1.5.2) packages, and visualized using the terra (v.1.7.65) package in R.

To evaluate the robustness of projections to model specifications, we compared projected changes in FIP incidence from the quadratic model (equation (2)) and the interaction model (equation (3)). The projections from the two models were highly consistent across grid cells, with Pearson’s correlation coefficients of 0.92 for pathogens and 0.95 for insects (Supplementary Fig. 17). Because the interaction model showed higher predictive performance, we report projections from this model in the main text.

To explore the sensitivity of our projections to potential changes in forest structure, we conducted an additional analysis in which we incorporated two independent proxies of forest density into our models: above-ground vegetation biomass and potential tree cover. Vegetation biomass was estimated using the MC2 dynamic global vegetation model across the conterminous US; this model simulates how vegetation grows and responds to climate and wildfire at monthly time steps⁷¹. Potential tree cover was derived using machine learning models trained with bioclimatic variables and incorporates natural disturbance regime estimated as the difference between observed and potential tree cover in intact areas⁷². These two variables provide complementary predictions of forest dynamics under future climate regimes. We extracted values of biomass and tree cover for 2015–2020 at each of our plot coordinates, and refitted our Bayesian regression models including these variables. In the refitted models, both insect and pathogen incidence were affected by potential tree cover; insect incidence was additionally affected by vegetation biomass. We then used predicted biomass and tree cover for 2040–2060 to generate an additional set of projections of FIP incidence. Projections with and without including these estimates of forest density were highly correlated for pathogens (Pearson $r = 0.94$) and moderately correlated for insects ($r = 0.47$), with projections that incorporate forest density tending to yield equal or higher estimates of future FIP incidence (Supplementary Fig. 7). Thus, our projection of climate-change-induced FIP risks is probably an underestimate, although we acknowledge that projecting forest structure is inherently complex; the models used in this study do not fully capture processes such as species turnover or management interventions.

We explored how well climate effects estimated from plot-level data transfer to the spatial resolution of the project grid by fitting additional models for insects and pathogens in which we aggregated plot-level incidence to grid-cell means. Each grid cell was represented by between 1 and 9 plots; predictors including contemporary, historical climate and biotic covariates were averaged for each cell. We then refitted our model to the aggregated dataset and incorporated grid-cell identity as a grouping effect to account for cell-specific intercept variation (such as those induced by difference in sampling intensity). Climate-effect estimates from the grid-cell models were highly consistent with those from the plot-level models (Supplementary Fig. 18), supporting the scalability of the inferred climate–FIP relationships.

To project the potential changes in FIP incidence that individual tree species may experience under future climates, we considered tree species’ climate preference, traits and how these attributes mediated climate effects, using the posterior distribution of parameters from models fit with equation (5). We restricted our projections to within

tree species' geographical extents according to Little's range map, capturing the heterogeneity of climate change experienced by the different tree species.

We compared projections generated from our species-level models (equation (5)) to those from plot-level models (equation (3)) by averaging projected changes in FIP incidence across tree species for each grid cell, again restricting species-level projections to Little's range maps.

Lastly, we generated projections for incidence of individual FIPs, based on the refitted models for each of the top most prevalent insects and pathogens. We limited our projections to the geographical range of each FIP using state-level or province-level records from the Centre for Agriculture and Bioscience International (CABI) database. We also extended the projection across all forested lands, assuming potential FIP range expansion. However, because individual models and CABI range data were available only for a subset of major FIP species, we could not aggregate predictions across FIPs to generate projections of overall risk.

Validation of model projections

Validating projections is challenging. However, given recent historical climate warming, forests projected to experience increased FIP incidence in the future may have already been exposed to elevated FIP pressure over recent decades. Therefore, we examined whether recent increases in FIPs coincide with our projections of future increases in FIP incidence.

We collected FIP risk assessments from the updated National Insect and Disease Risk Map (NIDRM) (2012), a strategic assessment and database of FIP risks developed by the US Forest Health Assessment & Applied Sciences Team³⁸. NIDRM evaluates the potential for tree mortality caused by forest insects and diseases for the period 2013–2027, classifying forest sites into either 'risk' or 'non-risk' categories. A site is designated as at risk if at least 25% of the standing live basal area (greater than one inch in diameter) is expected to die within 15 years because of FIP activity. The NIDRM was updated in 2018 to remove invalid risk areas; we used the updated data in our analysis. As different risk assessment models are applied to the conterminous USA, Alaska and Hawaii, we restricted our analysis to the conterminous USA³⁸.

To compare our projections with the NIDRM dataset, we adjusted the resolution and the coordinate reference system of the NIDRM risk map to align with our projected FIP incidence (that is, Fig. 3a), using the project function in the terra R package (v.1.7.65). We then classified grid cells into risk and non-risk groups according to the NIDRM 2013–2027 classification system. For each cell, we extracted and averaged the predicted increases in insect and pathogen incidence. We compared predicted FIP risks between risk and non-risk cells using a two-sample Student's *t*-test.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All primary data are from publicly available sources: forest insect and pathogen damage records from the US Forest Service Forest Inventory and Analysis database⁵³ (www.fs.usda.gov/research/products/dataandtools/tools/fia-datamart), historical climate from WorldClim 1.4⁵⁶, contemporary climate from ERA5⁵⁷, projected climate from the AdaptWest project⁵⁹, forest tree cover from the global tree cover dataset for 2010⁷⁰, ecoregions from the North American ecological regions database⁶⁴, tree range maps from Little's Atlas of United States trees⁵⁸, the tree phylogeny from ref. 61, tree functional traits from the Global Spectrum of Plant Form and Function dataset⁶⁵ and forest insect and pathogen ranges from the CABI database (www.cabidigitallibrary.org, subscription required). The processed data required to reproduce

the analyses are available via Zenodo at <https://doi.org/10.5281/zenodo.21480977> (ref. 73).

Code availability

The R code associated with the study is available via Zenodo at <https://doi.org/10.5281/zenodo.21480977> (ref. 73).

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Acknowledgements

We thank E. M. Wolkovich for valuable edits and comments on a previous version of our manuscript. The findings and conclusions in

this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

Author contributions

Z.W. and T.J.D. conceived the study and designed the methodology. Z.W., A.V.G. and T.J.D. assembled and curated the datasets used in the study. Z.W. performed the analyses and created the visualizations. T.J.D. acquired the funding. Z.W. wrote the original draft and Z.W., A.V.G. and T.J.D. reviewed and edited the manuscript.

Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada (to T.J.D.).

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-026-03163-6>.

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Peer review information *Nature Ecology & Evolution* thanks Andrew Latimer and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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