

Warming temperatures and shifting precipitation patterns may exacerbate pest damage in North American forests

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Climate change is expected to alter the extent and severity of forest pest damage, with substantial economic and ecological consequences, but predicting future pest impacts is challenging because of complex feedbacks among climate, pests and host trees. Here we use 20 years of data from the conterminous USA to assess how bioclimatic and biotic factors have influenced forest damage by 30 high-impact pest species and to identify ecological signals in those relationships. We found consistency in pest damage responses to maximum temperature in the warmest month, including recent average conditions and shifts from a historical baseline. Mean damage from focal pest species tends to be higher in regions with moderate maximum temperatures and in regions with faster rates of warming. In certain cases, the direction and magnitude of relationships between climate and forest damage vary by pest guild, native status and region of occurrence. Our findings provide empirical support for expectations of climate-induced stress to host trees and temperature-boosted pest performance, leading to increased pest damage in future forests.

In the past several decades, global temperatures have warmed and precipitation patterns have shifted at a pace without recent historical precedent^{1,2}. These changes in climate are already having numerous ecological effects on plant species, such as advancing spring phenology^{3,4} and impacting the timing and intensity of species interactions⁵. Climate change impacts on species interactions are of particular concern, as mutualistic or antagonistic species could partially dictate where plants may survive and thrive in future climates. Impacts of antagonistic species—specifically, phytophagous insects, tree pathogens and plant parasites (hereafter, referred to collectively as pests)—are frequently predicted to become more severe with climate change, especially as short-lived, highly fecund pests could adapt more quickly than their long-lived host trees⁶, which may become physiologically stressed from increasing temperatures and more frequent periods of drought⁷. Shifts in climate away from historical levels could surpass the environmental

tolerance thresholds of host trees^{8,9} and affect pest performance¹⁰. Understanding how contemporary climate change affects the amount of pest damage is of paramount economic and ecological importance, as pests are already among the primary disturbance agents in forests¹¹ and can contribute to accelerated host tree mortality and reduced forest productivity¹².

Changes in climate conditions can exacerbate forest pest damage through several potential mechanisms: direct effects on pest population dynamics (such as survival, reproduction and dispersal), indirect effects on host trees that increase their vulnerability to pest attacks or a combination of both direct and indirect effects^{13–15}. Insect physiology and metabolic rates are highly sensitive to temperature, and phytophagous insect populations are directly linked to seasonal thermal conditions. For example, winter temperatures interact with physiological limits through cold tolerance and cold-induced mortality^{16,17}, whereas

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summer temperatures may dictate the timing and sequence of specific temperature-dependent developmental processes for pests such as bark beetles¹⁸ (Curculionidae: Scolytinae). Warming winter temperatures can increase overwintering survival and facilitate population growth¹⁹. Meanwhile, warming spring and summer temperatures in temperate and boreal forests can accelerate insect development rates and increase reproductive potential, facilitating population growth and range expansions²⁰. However, there is an upper threshold in maximum temperature conditions for many insect species; for example, one study²¹ found that performance—encompassing development, fitness and survival—of several pest guilds (including leaf chewers, sap suckers, bark and wood borers and pathogens) declines after temperatures exceed ~30 °C. Sporulation and colonization success of tree pathogens also depend on temperature, precipitation, soil moisture and relative humidity²². Climatic warming is generally expected to amplify the prevalence of many pests by reducing generation times and increasing growth rates, fecundity, survival and dispersal^{23,24}. However, there remains considerable uncertainty when making predictions about the spatiotemporal effects of climate change as a result of the idiosyncrasies of individual pest dynamics, as well as an incomplete understanding of potentially interacting relationships among several pest species.

Climate change may also intensify pest damage through impacts on host tree vigour—trees can experience higher levels of physiological stress under new climate conditions, which may increase their susceptibility to pest attacks^{18,25}. Increasing mean and maximum summer temperatures, along with decreasing precipitation, for instance, can induce heat and/or drought stress in many tree species^{25,26}. Pest impacts can be particularly amplified when host trees are abundant, when forest communities have low species richness^{27,28} or in certain ecoregions²⁹. Regardless of the precise mechanism (pest population growth associated with increased demographic rates versus higher susceptibility of host trees caused by physiological stress versus a combination of both scenarios), climate change has the potential to greatly exacerbate the amount of pest damage. Thus, there is a pressing need to develop a predictive understanding of how climate change influences pest damage and to assess generalities in how pest damage responds to bioclimatic factors.

Results

Quantifying the effects of climate and other factors on forest pest damage

We assessed the significance, direction and magnitude of the effects of mean climate conditions, climate anomalies, tree species abundance and richness, spatiotemporal pest dynamics and ecoregion on forest damage caused by 30 pest species in the USA (Extended Data Table 1). Specifically, we explored the relationships between pest damage and 15 variables (Table 1; Methods), which included five bioclimatic metrics calculated within a multiyear window (hereafter, climate window) and as an anomaly from long-term historical means (hereafter, climate anomaly), host tree relative abundance, tree species richness (Extended Data Fig. 1), two county-level damage metrics intended to represent spatial and temporal pest dynamics, respectively³⁰, and ecoregion (Extended Data Fig. 2). On the basis of previous studies, we expected the 15 predictor variables to have ecological relevance to the focal pest species^{19,31,32}, although we also anticipated that responses would be individualistic, given differences in pest physiology, feeding guilds, geographic distributions and host tree species. We further selected individual bioclimatic metrics that minimized collinearity among the predictor variables (see Methods for a detailed explanation of variable selection).

Using data from the annual Insect and Disease Surveys (IDS) of the US Department of Agriculture (USDA) Forest Service, we quantified pest damage into two response metrics (Fig. 1 and Extended Data Fig. 3): damage footprint (the total spatial extent (ha) of forest damage) and refined damage (a refinement of the footprint metric (ha) based on

Table 1 | List of 15 predictor variables used to explain variation in pest damage

Category	Predictor variable	Description
Climate window	Mean monthly temperature range	Bioclimatic metrics calculated within a multiyear window (ranging 2–6 years)
	Maximum temperature in the warmest month	
	Minimum temperature in the coldest month	
	Precipitation in the wettest month	
	Precipitation in the driest month	
Climate anomaly	Mean monthly temperature range	Bioclimatic metrics calculated as an anomaly from a long-term historical climate period (spanning 1980–1999)
	Maximum temperature in the warmest month	
	Minimum temperature in the coldest month	
	Precipitation in the wettest month	
	Precipitation in the driest month	
Tree-related	Host tree relative abundance	Proportion of aggregated host tree species basal area
	Tree species richness	Mean number of tree species
Spatiotemporal pest dynamics	Total county-level damage	Total amount of pest-specific damage within the county; may be spatially correlated with pest population density
	Difference in county-level damage from the previous year	Difference ($t_0 - t_{-1}$) in the total amount of county-level pest damage (t_0) from the previous year (t_{-1}); may be temporally correlated with pest population density change
Ecoregion	Ecoregion	Ecoregion (categorical) from the USDA Forest Service EcoMap ^{33,90}

the aerial surveyor’s estimate of the percentage area affected). We ran a total of 58 linear mixed effects models, comprising 30 damage footprint models and 28 refined damage models (Extended Data Table 2). We then applied a meta-analytical approach to quantify generalities by standardizing slope coefficient estimates across the models, while accounting for uncertainty from individual models. To ensure that model results were robust, models were spatiotemporally cross-validated and residuals were checked for spatial autocorrelation (Methods; Extended Data Fig. 4). Trends in the significance, magnitude and direction of relationships with predictor variables were generally consistent between the two damage metrics, and we therefore focused on presenting results in the main text that were supported by both sets of models, unless noted otherwise. For each predictor variable, we considered the mean effect size to be the standardized mean magnitude (absolute value) of its slope coefficient values (Extended Data Table 3), which quantified overall impact without differentiating between positive versus negative effects, and we considered the mean effect to be the standardized mean of its slope coefficient estimates (Extended Data Table 4), which indicated consensus in the direction (positive or negative) of the relationship. In addition to assessing generalities across all 30 pest species, we further

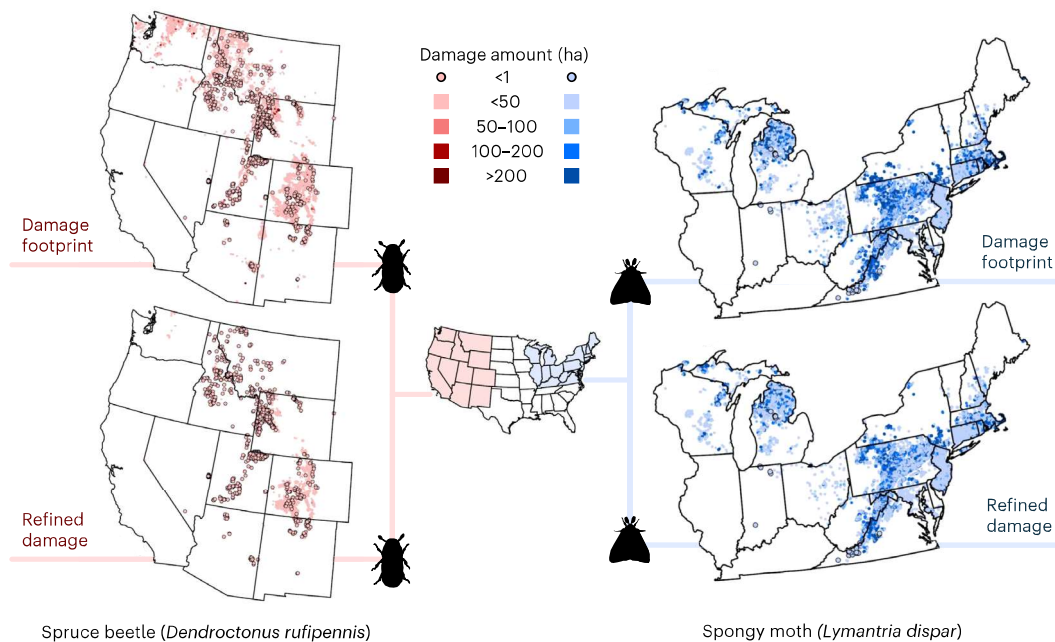


Fig. 1 | Maps of 2000–2019 IDS data for the conterminous USA, showing the extent and amount of tree damage from two focal pest species. The IDS damage records included both polygons (areas of widespread damage with discrete boundaries) and points (fine-scale damage involving a limited number of trees). For this study, we compiled the IDS damage records into two response metrics: damage footprint (ha), which was calculated for all records and represented the total amount of forested area (ha) within the polygons or within

50 m of points; and refined damage (ha), which was calculated for the subset of records with additional surveyor information and incorporated the surveyor's estimate of the percentage area affected within the polygons. The maps display IDS damage records attributed to spruce beetle (*Dendroctonus rufipennis*; red gradient) in the western USA (left column) and spongy moth (*Lymantria dispar*; blue gradient) in the eastern USA (right column).

compared trends between bark beetles versus defoliators, between native versus non-native pests and among the three primary regions where pests occurred (western USA versus nationwide versus eastern USA). It should be noted that our analyses are focused on forested areas with extant pest damage and whether the mean amount of damage was influenced by the predictor variables under consideration; thus, we emphasize that we are not attempting to model pest damage occurrence or abundance, pest outbreaks or pest population parameters (such as population growth rates).

Effects of mean climate conditions and climate anomalies

As expected, there was considerable variability in how climate influenced the amount of damage from individual pest species (Figs. 2 and 3), but several generalities did emerge. Both climate window and climate anomaly variables were important in explaining pest damage in nearly every model, and they had similar aggregated mean effect sizes across all pest species (standardized mean magnitudes = 0.16 (95% confidence interval (CI) = 0.13–0.18) for climate window variables versus 0.16 (95% CI = 0.13–0.19) for climate anomaly variables (Extended Data Table 3); $P = 0.83$ for between-group differences). There were significant differences ($P < 0.001$) among the mean effect sizes of the individual climate variables, with the highest magnitude values corresponding to the climate window and climate anomaly metrics for maximum temperature in the warmest month (standardized mean magnitudes = 0.21 (95% CI = 0.14–0.28) and 0.28 (95% CI = 0.19–0.37), respectively). These two metrics were also frequently significant and their mean effects on pest damage were negative (standardized mean = -0.13 (95% CI = -0.22 to -0.03)) and positive (standardized mean = 0.15 (95% CI = 0.02 – 0.28)), respectively (Extended Data Table 4)—indicating higher pest damage in regions where maximum temperatures were moderate but increasing (Figs. 4 and 5 and Extended Data Figs. 5 and 6). For many of the models, significant relationships between pest damage and the climate window versus climate anomaly metric

of the same bioclimatic variable were frequently in opposite directions (such as positive versus negative), although interactions were infrequently significant and inconsistent.

In many cases, the relative influence of the climate window and climate anomaly metrics (Extended Data Table 3) differed for bark beetles versus defoliators, for native versus non-native status and among the three primary regions where pests occurred (western USA versus nationwide versus eastern USA). Among the ten individual climate variables, a climate window metric (such as maximum temperature in the warmest month and minimum temperature in the coldest month) had a consistently greater impact (higher standardized mean magnitude) on pest damage by defoliators and nationwide species. In contrast, a climate anomaly metric (such as change in maximum temperature in the warmest month and change in minimum temperature in the coldest month) was the most impactful climate variable for bark beetles, native species, western species and eastern species.

Comparing trends in mean effects (Extended Data Table 4) and significant relationships with climate metrics (Fig. 4 and Extended Data Fig. 5) for groups of pest species, we observed that damage by bark beetles tended to be higher in regions where minimum temperature in the coldest month was warming or where precipitation in the wettest month was relatively low or decreasing, whereas damage by defoliators and nationwide species tended to be higher in regions where minimum temperature in the coldest month was decreasing. In addition, many of the eastern species often caused greater damage in regions with relatively high mean monthly temperature ranges and relatively warm minimum temperatures in the coldest month.

Effects of tree species, pest dynamics and ecoregion

The two tree-related predictor variables (host tree relative abundance and tree species richness; Table 1) were not as frequently important and generally had less influence on pest damage (standardized mean

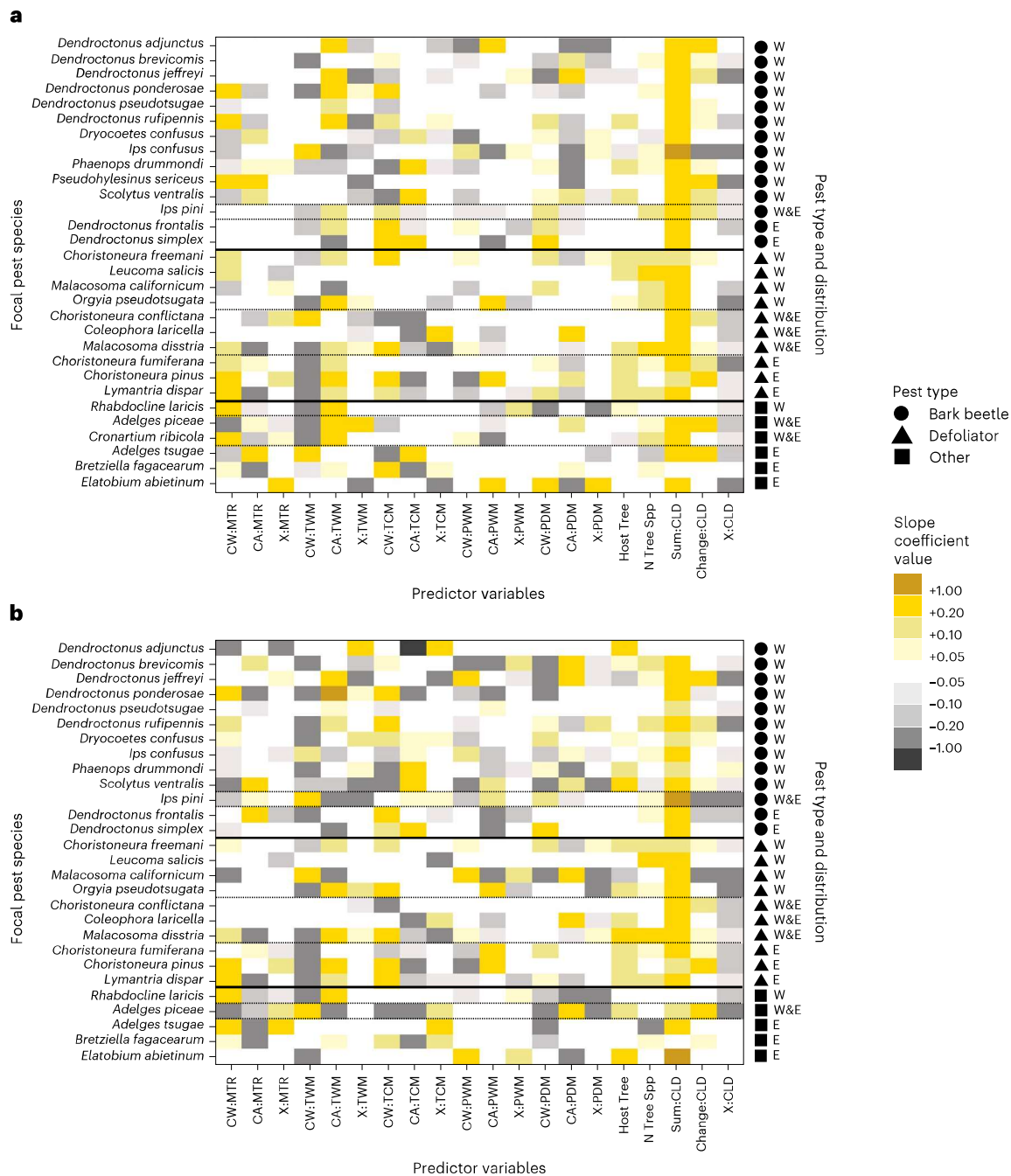


Fig. 2 | Heat maps showing slope coefficient values associated with 14 predictor variables and their interactions for the two response metrics.

a, b. Heatmaps are from linear mixed effects models of damage footprint (**a**) and refined damage (**b**). Each row corresponds to individual focal pest species (listed by scientific name (left axis) and arranged by pest type and distribution within the USA (right axis)), and each column corresponds to individual predictor variables (listed by abbreviated code along bottom axis) and their interactions (indicated by X), which include ten climate metrics—mean temperature range (MTR), maximum temperature in the warmest month (TWM), minimum temperature in the coldest month (TCM), precipitation in the driest month (PDM) and

precipitation in the wettest month (PWM) calculated within a climate window (CW) and as a climate anomaly (CA); two tree-related metrics—host tree relative abundance (Host Tree) and mean tree species richness (N Tree Spp); and two county-level damage (CLD) metrics—total pest-specific damage during the survey year (Sum) and the difference in total pest-specific damage from the previous year (Change). The colour of each cell indicates the slope coefficient value; those that were not considered statistically significant (95% CIs overlapped 0) are white. Bold horizontal lines delineate the three pest types and dotted lines within those divisions further delineate the three pest regional distributions (western USA (W) versus both western and eastern USA (W&E) versus eastern USA (E)).

magnitude = 0.08 (95% CI = 0.06–0.10)) compared with the climate window and climate anomaly variables. Pest damage tended to increase with tree species richness (standardized mean = 0.07 (95% CI = 0.02–0.11)) and host tree relative abundance (standardized mean = 0.05 (95% CI = 0.02–0.08)), regardless of pest type, native status or regional distribution. However, the strongest and most consistently positive

relationships were with defoliators (standardized means = 0.13 (95% CI = 0.01–0.24) for tree species richness and 0.12 (95% CI = 0.07–0.16) for host tree relative abundance). Meanwhile, the two variables representing spatiotemporal pest dynamics (Table 1), plus their interaction, were more frequently important in explaining pest damage than any other set of predictor variables, and total county-level damage

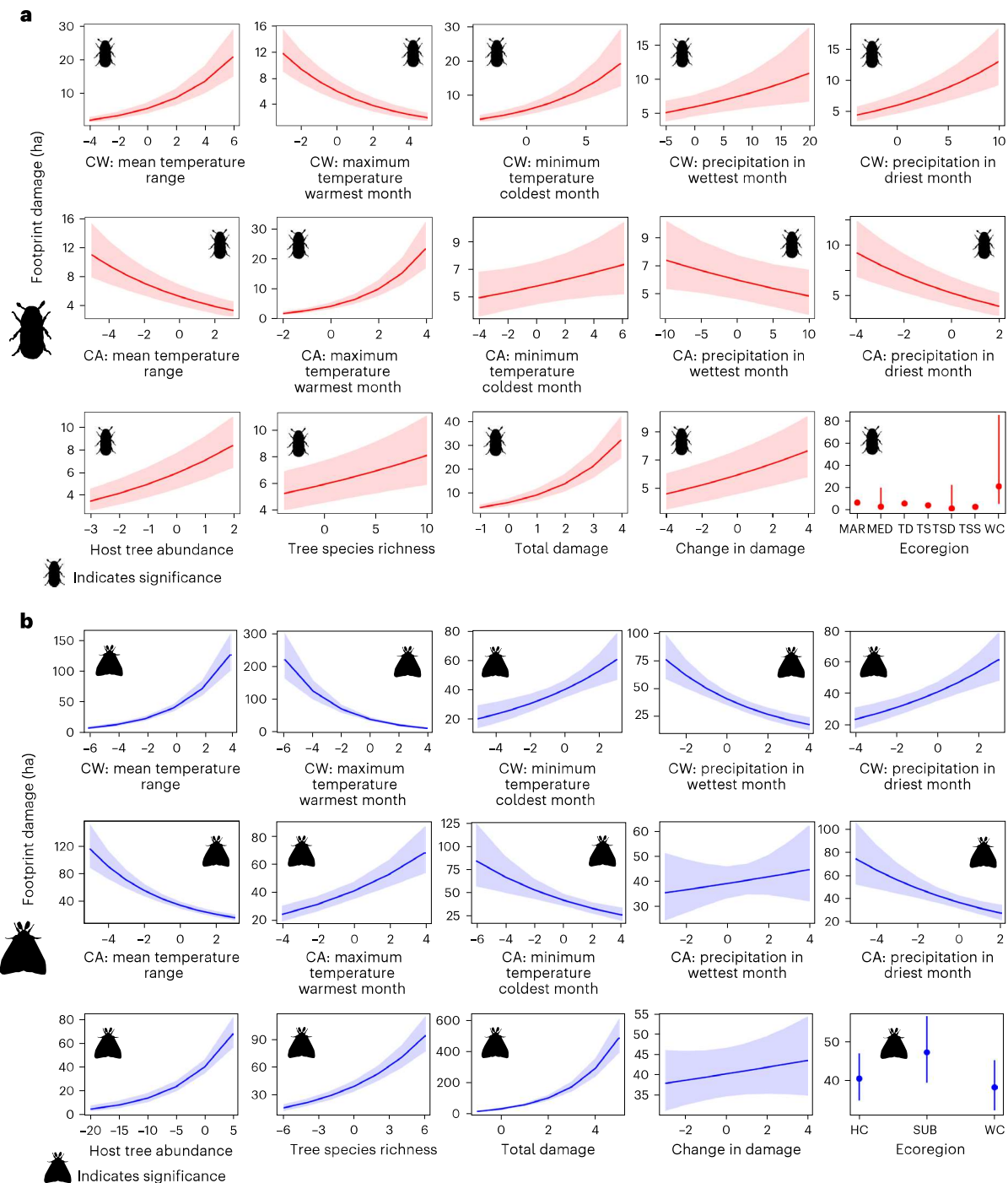


Fig. 3 | Plots of marginal effects for each predictor variable from damage footprint models for two focal pest species. a, b. The top set of plots (a) shows relationships in red with the damage footprint metric for spruce beetle (*D. rufipennis*) and the bottom set of plots (b) shows relationships in blue with the damage footprint metric for spongy moth (*L. dispar*). For both sets of plots: the response variable (y axis) was log-transformed in the linear mixed effects model, but back-transformed here to show the marginal effects; all continuous predictor variables ($n = 14$; x axis) are scaled and centred, except for the climate anomaly (CA; $n = 5$) and change in total county-level pest damage ($n = 1$) variables, which were only scaled and not centred (such that 0 reflects no change); the line or dot represents the mean predicted response; and the shading or vertical whisker represents the 95% CI. The individual predictor variables include ten climate

metrics—mean temperature range, maximum temperature in the warmest month, minimum temperature in the coldest month, precipitation in the driest month and precipitation in the wettest month calculated within a climate window (CW; top row) and as a climate anomaly (middle row); two tree-related metrics (bottom row)—host tree relative abundance and mean tree species richness; two county-level damage metrics (bottom row)—total pest damage during the survey year (total damage) and the difference in total pest damage from the previous year (change in damage); and ecoregion with ecoregion codes corresponding to Extended Data Fig. 2). An alternate version of this figure which includes observed values as data points can be accessed from the online data repository <https://doi.org/10.6084/m9.figshare.26426608> (ref. 95).

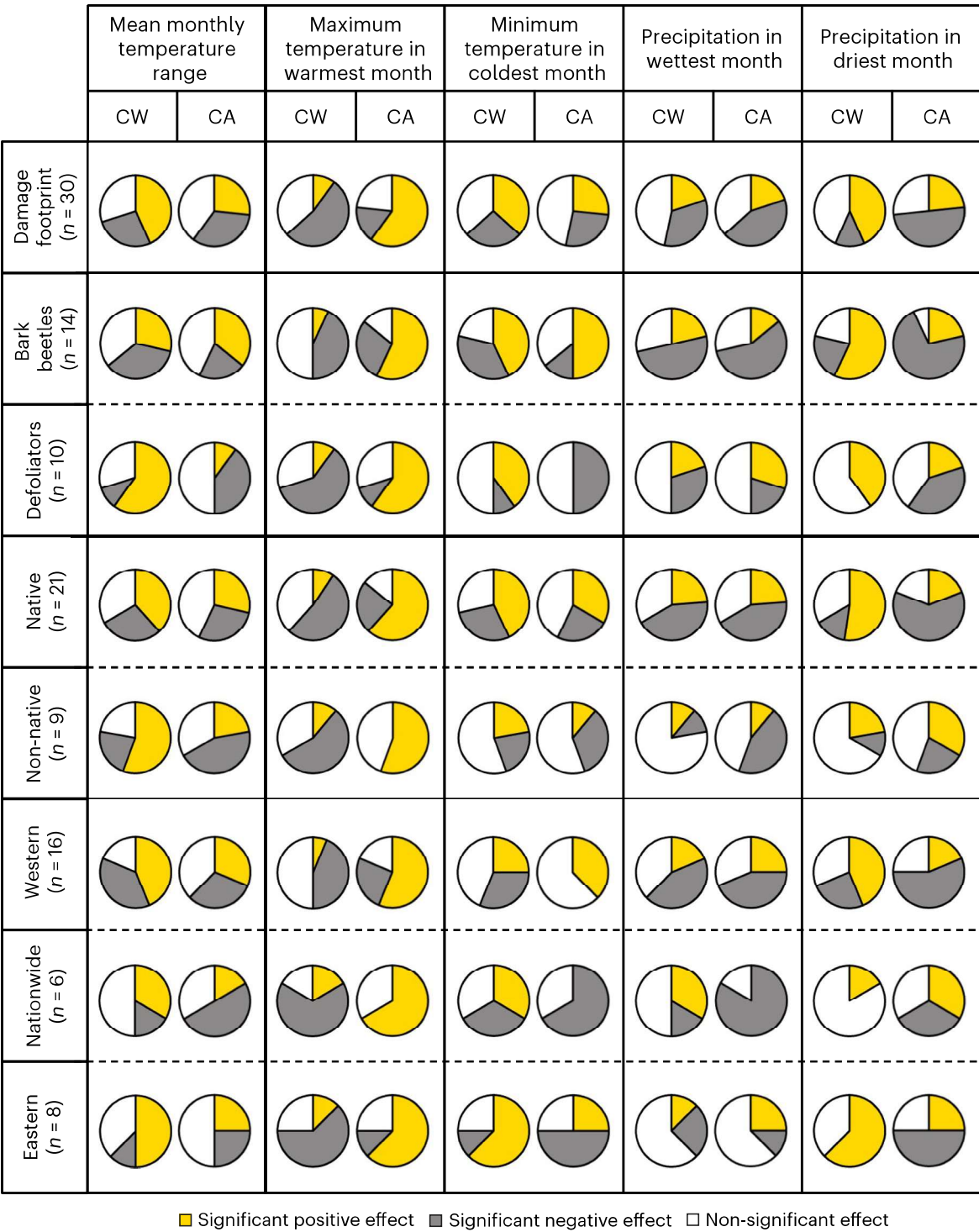


Fig. 4 | Diagram of significance and direction of each climate variable for all damage footprint models and for specific groups of pest species. Columns correspond to the climate window (CW) and climate anomaly (CA) metrics of the five bioclimatic metrics. Rows correspond to different groupings of the focal pest species, including all damage footprint models, bark beetles versus defoliators, native versus non-native species and western versus nationwide versus eastern species. Pie charts indicate the proportion of significant positive relationships (gold), significant negative relationships (grey) and non-significant relationships (white).

(which may be spatially correlated with pest population density) had the highest mean effect sizes (standardized mean magnitude = 0.51 (95% CI = 0.36–0.66)) of all the individual continuous predictor variables ($P < 0.0001$ for between-group differences). Both county-level damage variables had consistently positive effects (standardized means = 0.51 (95% CI = 0.36–0.66) and 0.09 (95% CI = 0.02–0.15))—indicating that the mean amount of pest damage was greater when there was more overall damage in the surrounding county or when the amount of county-level damage had increased from the previous year—and the interaction between the two variables almost always had a negative relationship (Fig. 2). Finally, ecoregion had a moderate influence on pest damage and potentially accounted for systematic differences in regional forest composition and structure³³, although the significance and direction of effects varied by pest species and response metric.

Discussion

Here we present a comprehensive analysis of how the amount of forest pest damage in the conterminous USA over the past 20 years has been influenced by contemporary climate conditions and recent climate change, while also accounting for the effects of host tree abundance, forest diversity, spatiotemporal pest dynamics and ecoregion. Despite differences in pest physiologies and life histories, climatic tolerances, natural population cycling, geographic distributions, native status, host tree associations, potential sampling effects and damage metrics, we found notable consistency in how pest damage responded to metrics of maximum temperature in the warmest month—in particular, the tendency for pest damage to be higher in regions with moderate maximum temperatures and regions that were experiencing the greatest rate of warming (Fig. 5 and Extended Data Fig. 6). The particular importance of temperature extremes—which aligns with expectations for climate-induced stress to host trees²⁵ and temperature-boosted pest performance⁴⁵—has important implications for understanding current trends in forest pest damage across North America and for predicting potential pest impacts as regional climates continue to warm and experience shifts in precipitation patterns.

Several generalities were evident when synthesizing model results across all 30 pest species. First, damage from all pest species in our study exhibited significant responses to climate in the time period immediately preceding the damage, the anomaly from historical levels or both—even when accounting for host tree abundances, spatiotemporal pest dynamics and differences among ecoregions. This finding highlights the importance of climate in explaining the amount of forest pest damage across North America, and it is consistent with many other studies that have linked climate to pest damage caused by bark beetles^{34,35}, defoliating insects^{31,36,37} and various pathogens³⁸. Although there was variability in the particular climate variables that influenced forest damage caused by the various pest species, we further found that maximum temperature in the warmest month was frequently among the most important predictor variables impacting mean damage amounts, given a forested area was damaged by pests. This finding aligns with studies that link high temperature extremes with pest outbreaks³⁹. Interestingly, the effects of several bioclimatic variables often manifested in opposing directions when assessed as climate windows versus climate anomalies, implying that several mechanisms could potentially be amplifying and dampening pest damage simultaneously. While our study cannot ascribe climate effects directly to tree stress or pest population dynamics, our results nevertheless indicate that these emergent macroscale effects are strikingly similar across diverse pest species.

Accounting for recent climate change improved our ability to model pest damage, as we found that climate anomaly metrics were important in explaining trends in forest damage caused by nearly all pest species in our study. Specifically, our models indicated that pest damage may be highest in regions where climate conditions are moving away from long-term baselines. This finding implies that climate impacts on pest damage may not be stationary, but rather contingent on their deviation from historical levels. Because climate anomalies were generally not correlated strongly with the climate windows, our results further suggest that failing to account for recent climate shifts may leave an incomplete picture of how climate influences pest damage. It is also worth noting that our estimates of climate impacts on

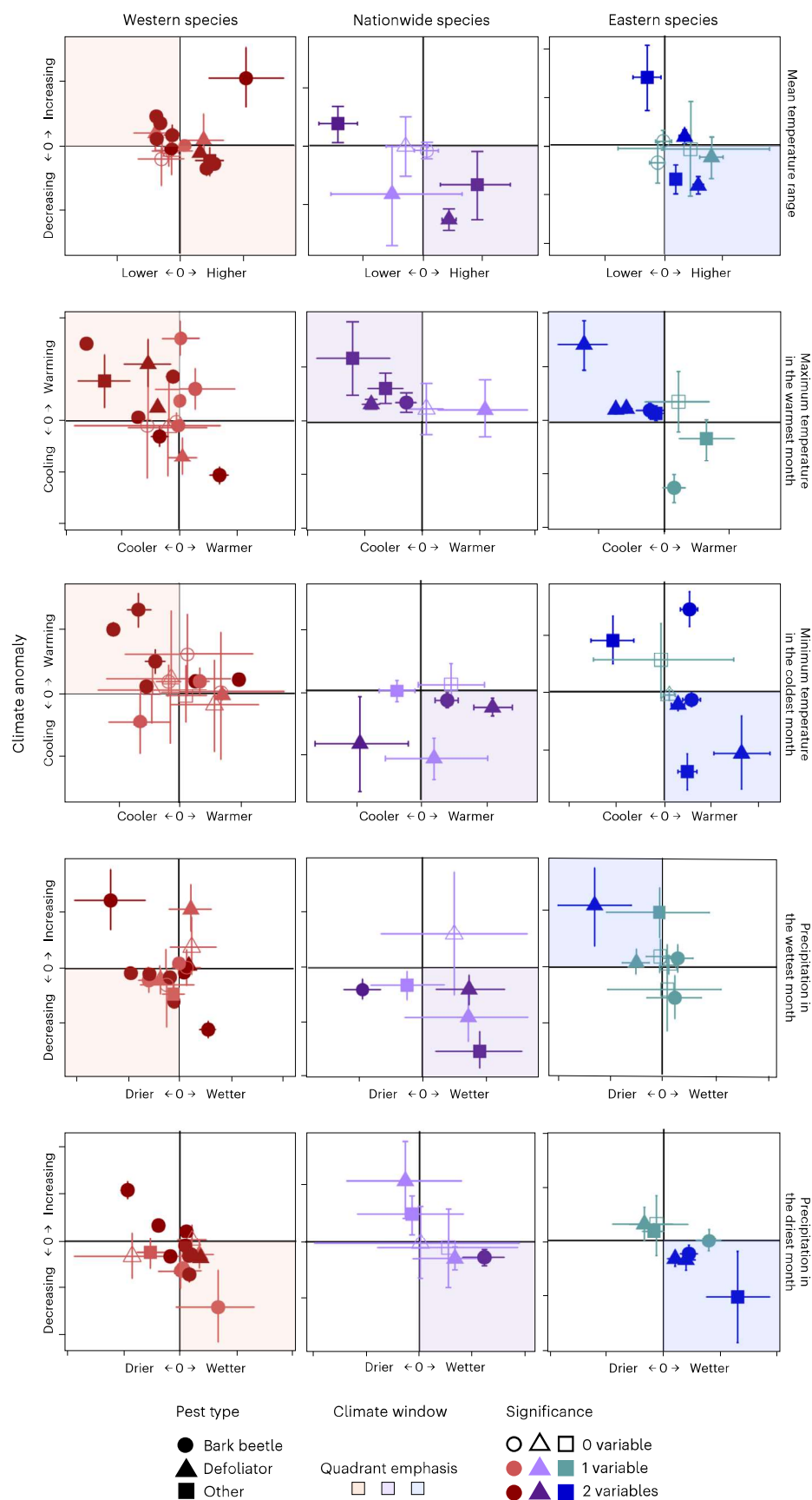
pest damage should be considered conservative, as we controlled for systematic differences among states, survey years and ecoregions, each of which could be accounting for some of the variability in the climate metrics. Although further work may be needed to specifically link climate anomalies to pest and host tree physiologies and life histories, our ability to predict potential pest outbreaks in the future will probably be improved by first understanding how forest damage has already begun to intensify with recent climate shifts.

Damage associated with the focal pest species tended to have consistently significant positive relationships with host tree relative abundance and tree species richness. Given a forested area damaged by pests, the mean damage amount was greatest in regions with relatively high proportions of host tree basal area and relatively high numbers of tree species. The positive relationship with host relative abundance is probably related to host density effects aligning with the resource concentration hypothesis⁴⁰, as well as greater potential for tree pest species to colonize and spread in forest stands with high host abundance⁴¹. However, the association between greater pest damage and higher tree species richness is contrary to the frequently reported ‘dilution effect’ of biodiversity on forest pests⁴². Although this finding did not support our expectation for associational resistance in mixed forests^{43,44}, the response of insect herbivory to forest diversity may be scale-dependent and is often species-specific and highly variable^{45,46}, especially for non-native forest insects and pathogens that have not yet reached equilibrium with host trees or climate conditions⁴⁷ (and thus caution is necessary when interpreting these results). A positive effect of tree species richness is consistent with other recent studies, which have provided evidence for associational susceptibility and documented increased damage in tree mixtures compared with monocultures^{48,49}, possibly reflecting effects of forest composition and evolutionary relatedness on pest damage, independent from tree species richness. Furthermore, ecoregions often varied significantly in their individual effects on pest damage, similar to the differences in forest damage rates among ecoregions noted by previous studies²⁹. We conjecture that the ecoregions characterized by more heterogeneous, continuous and deciduous forests with plentiful host tree availability (including warm continental, hot continental and subtropical ecoregions) allowed for increased pest damage by facilitating spread of pest populations^{41,50}, especially for more generalist pest species. Other landscape-scale characteristics that distinguish the eastern versus western ecoregions and may influence pest damage extent or severity include landscape patterns and configuration (such as fragmentation and connectivity), stand size, stand age and composition, forest density and history of forest management practices^{51–54}.

Some of the variation in responses to climate variables that we detected among pest species was attributable to the pest type, their native versus non-native status and the geographic regions where they occurred. Differences between bark beetles and defoliators are probably related to diverging physiological or life history traits^{55,56}, as well as their relative sensitivities to climate factors. Bark beetles, for instance, may be more influenced by indirect climate effects on host trees than defoliators, which may respond more directly (positively or negatively) to shifts in temperature and precipitation⁵⁷. Phenology and life history also interact to play an important role in determining which life stages are most exposed (and thus vulnerable) to climate change⁵⁸. Differences between native and non-native species may stem from their

Fig. 5 | Quadrant plots of slope coefficient values corresponding to the five bioclimatic metrics from the damage footprint models. Within each plot, coordinates of the points reflect mean slope coefficient values for each bioclimatic metric (mean temperature range, maximum temperature in the warmest month, minimum temperature in the coldest month, precipitation in the wettest month and precipitation in the driest month), calculated within a climate window (CW; x axis) and as a climate anomaly (CA; y axis), from the 30 damage footprint models. Horizontal and vertical lines represent 95% CIs

of the slope coefficients for the climate window variable and climate anomaly variable, respectively. If the 95% CI overlaps 0, then that slope coefficient value is not considered statistically significant (as reflected by the colour and fill of the point). Pest type is denoted by the shape of the point, and pest distribution within the USA is delineated by columns and colour themes. Axes labels describe the climate conditions associated with each quadrant, and shading of a single quadrant (quadrant emphasis) indicates that quadrant contains the greatest number of significant points.



co-evolutionary histories (or lack thereof) with native trees. In particular, native pests adapted to prevailing regional climate conditions may be more responsive to climate shifts than non-native pests that have not yet reached equilibrium with climate or host geographies. Meanwhile, differences among the primary geographic regions where pests occurred are probably driven partially by variation in climate trends in the western versus eastern USA³⁹, as well as differences in forest types and forest cover. We also note that the underlying mechanisms responsible for certain differences between pest types and among geographic regions may partially coincide, as they were conflated to a degree; for example, 12 of the 17 western species were bark beetles, 4 of the 7 nationwide species were defoliators and 5 of the 10 eastern species were defoliators.

On the basis of our model results, mean effects of the predictor variables were not as frequently significant as their effect sizes, probably reflecting species-specific responses; thus, we advise caution in inferring directional effects and making generalizations across larger groups of species. However, we can tentatively identify climate conditions that were often associated with the highest amounts of pest damage for particular pest types and distributions within the USA. For instance, despite some inconsistency from interspecific variation, bark beetles tended to cause higher mean damage at forested sites with relatively cool or increasingly warmer maximum temperatures, increasingly warmer minimum temperatures and relatively low or decreasing precipitation during the rainy season. This finding is similar to several studies focused on the response of western bark beetles to climate change^{18,34}, aligning with expectations for bark beetles to benefit from drought-stressed trees that may have a reduced ability to resist infestation^{10,21}. In addition, many of the pest species in the eastern USA tended to cause higher mean damage at forested sites with relatively high mean monthly temperature variability, relatively cool or increasingly warmer maximum temperatures, or relatively warm minimum temperatures. Several of these relationships are similar to those found by previous studies of an eastern forest-defoliating species¹⁴ and expected for a suite of insect pests in the forests of northeastern North America²⁴.

The elaborate ecological interplay among abiotic stressors, host trees, tree diseases and insect pests poses a considerable challenge for fully understanding climate impacts on pest damage⁶⁰. In our study, several metrics were customized to correspond to the focal pest species, but our overall modelling approach was to use a single general set of predictor variables for all pest species to identify broad generalities in how pest damage is influenced by bioclimatic metrics, which entailed deliberately sacrificing the complexity of certain species-specific dynamics. Although we found a few consistent signals across the 30 pest species, we propose considering additional factors before attempting to make spatially explicit predictions of species-specific damage under future climate scenarios. A more individualistic approach is probably needed to develop a better mechanistic understanding of how individual pest species will respond to warming temperatures and changing precipitation regimes⁶¹. The selected climate variables included in our analyses capture extreme temperature and precipitation dynamics that may limit or exacerbate pest damage, but based on R^2 values for individual models (Extended Data Table 2), these could yet be improved with the inclusion of other variables. Thus, the next step in this line of enquiry could be to further customize models to account for additional environmental or climatic variables important for individual pest species. For example, species-dependent components of pest damage to consider include the additive and interactive effects of non-climate drivers, such as windthrow⁶² and fire⁶³. It would also be valuable to integrate spatially explicit pest population dynamics over time^{64,65} or a more flexible neighbourhood approach that could explicitly account for pest spread. In our linear mixed effects models, we accounted for systematic differences between regions and years, which could manifest from abiotic (sampling) or biotic (population

cycling) processes, by incorporating random effects of US state by survey year, and we included interacting variables of county-level pest damage to serve as spatiotemporal proxies of pest dynamics in an effort to control for correlated differences in pest damage across space and time (which may result from spatial autocorrelation and density dependence). However, inference of climate effects on pest damage could be improved by designing species-specific models that more directly account for annual local abundance and further incorporate biological interactions with other forest pest species⁵⁶ and with parasitoids or other biological control agents⁶⁶. Alternatively, modelling several pest species simultaneously could highlight the importance of different pest traits that may interact with climate to affect damage. For introduced non-native species, it may also be valuable to account for an 'invasional lag' associated with species that have not yet fully filled their potential distribution⁶⁷. Finally, disaggregating the host tree information (by considering the relative abundances of each host tree species rather than a single aggregated metric for all host tree species, as done here) may be a useful strategy to better elucidate relationships with host tree abundance⁶⁸. Determining whether certain host tree species are particularly vulnerable versus resistant to pest attacks associated with climate change could aid in crafting forest management plans⁴¹.

Looking to future climate conditions, our results provide broad insights that can help to anticipate impacts and develop pest management plans for regions where forest pest damage may be exacerbated by climate change across North America, based on expected changes in seasonal temperatures and precipitation patterns. Even modest changes in climate can have rapid impacts through strong direct effects on the abundance of forest insects and pathogens¹³. Bioclimatic metrics that were important in our models are expected to continue shifting in the future. Maximum temperatures are predicted to continue rising throughout North America through the end of the century⁶⁹, while precipitation patterns may be more variable, with declining precipitation in parts of western North America and increased precipitation in much of the east⁷⁰. Under such future conditions, forests in northern regions (where maximum temperatures are projected to increase the most) could be at the greatest risk of exacerbated pest damage.

Methods

Overview of study system

Our study focused on forest pests (including phytophagous insects and tree pathogens) that occur in North America and cause damage to native tree species. To quantify forest pest damage, we used data from the IDS of the USDA Forest Service^{71,72}, which identify areas with tree mortality and defoliation caused by insect and disease activity. Digital mobile sketch mapping allows for polygon geometry, which is used for damage areas where boundaries are discrete and obvious, and point geometry, which is used for small clusters of damage involving a limited number of trees⁷². Surveyors define the extent of an area experiencing pest damage and can further estimate the percentage range of the area within polygons that is affected⁶³. Note that IDS data do not indicate where pest damage is truly absent versus unsurveyed, precluding analyses that require the inclusion of non-damaged areas; however, this dataset currently represents the best source of information for forest pest damage on a nationwide spatial scale and relatively long-term temporal scale. Overall accuracy for aerial detection survey observations is >70%, with particularly high levels of accuracy for damage type observations of tree mortality and defoliation⁷³, and these data are used in national summaries of forest pest conditions⁷⁴. To optimize the number of years of IDS data and the amount of high-quality data (from digital mobile sketch mapping), the temporal extent of our data ranged from 2000 to 2019, and as a result of data limitations, our spatial extent was limited to the conterminous USA.

Within the IDS data, more than 140 pest species were identified by surveyors as causing tree damage, but we focused on a subset of 30 species for our study (Extended Data Table 1). To select our focal species,

we first mapped all occurrences of each IDS damage agent (focusing exclusively on insects and pathogens) and prioritized consideration of pest species with a large number ($n > 900$) and high density of records that spanned their known geographic ranges within the conterminous United States. We eliminated pest species with few records or strong state-level sampling biases, as well as those that occurred over a small geographic area. Initial sample sizes for the pest species that met our criteria ranged from 920 records for satin moth (*Leucoma salicis*) to over 1.2 million records for mountain pine beetle (*Dendroctonus ponderosae*) and their spatial extents ranged from 2 to 30 US states. Of the 30 total focal pest species, most were classified as either bark beetles ($n = 14$) or defoliators ($n = 10$), while the remaining pest species were classified as a collective 'other' pest type consisting of sap feeders ($n = 3$), foliage/shoot diseases ($n = 1$), rusts ($n = 1$) and wilts ($n = 1$). Most of the focal pest species ($n = 21$) were considered native to North America, with 8 species concentrated in the eastern USA, 6 species occurring in both the eastern and western USA and 16 species concentrated in the western USA. All species in our study are considered important agents of biological disturbance in North American forests¹³.

Data compilation and processing of response variables

We assembled 2000–2019 IDS data corresponding to each focal pest species and selected all polygon and point records with damage types relating to either defoliation or mortality. Although we used 20 consecutive years of IDS data, these were not structured as time-series data, as individual sites were not surveyed through time. To reduce survey biases, we removed polygons greater than 1,600 ha, as surveyors occasionally recorded very large areas of low-intensity damage ($n = 7,829$ records across all pest species; ranging from 0% to 3.2% of the initial sample size per pest species). For each polygon record, we calculated the proportion of forest cover within the polygon using National Land Cover Database⁷⁵ (NLCD) data from the year closest to the survey year (Extended Data Fig. 3). We considered forest cover to comprise the following NLCD land cover classes: deciduous forest, evergreen forest, mixed forest and woody wetlands. Point records were assumed to have 100% forest cover.

For our response variable, we combined mortality and defoliation records for each species and, to incorporate varying amounts of detailed information available for each damage record, we considered two metrics (Fig. 1 and Extended Data Fig. 3): (1) damage footprint (ha), defined as the total spatial extent of forest affected by either mortality or defoliation; and (2) refined damage (ha), a refinement of the footprint metric that incorporated the surveyor's estimate of the percentage area affected. All damage records had a corresponding footprint value ((1) above), which was calculated as the product of the proportion of forest cover and size (ha) associated with the polygon or point. Any polygons with 0% forest cover were removed from our dataset before any further processing or analyses. For the subset of polygons with information on percentage damage, we calculated the refined damage metric ((2) above) as the product of the footprint value and the midpoint of the percentage range indicated by either a percentage affected code (1 for 1–3%, 2 for 4–10%, 3 for 11–29%, 4 for 30–50% and 5 for >50%) or legacy pattern code (1 | 2 for >50%, 3 | 4 for <50%), the latter of which links contemporary data standards to the legacy standards. Point records were assumed to have 100% damage.

Data compilation of predictor variables

Our focal predictor variables for this study included two sets of bioclimatic metrics, calculated within a multiyear window (range = 2–6 years) and as an anomaly from long-term historical means. To model the effects of climate variability and extremes on pest damage, we focused on five bioclimatic metrics⁷⁶: (1) mean monthly temperature range, (2) maximum temperature in the warmest month, (3) minimum temperature in the coldest month, (4) precipitation in the wettest

month and (5) precipitation in the driest month. These bioclimatic metrics were selected to represent acute, extreme climate conditions which probably have immediate, short-term repercussions and biological importance for the focal pest species and/or their host tree species. For example, maximum temperature in the warmest month is representative of extreme heat conditions and high temperatures, whereas precipitation in the driest month is representative of drought conditions and low precipitation amounts. In addition, we specifically chose these five bioclimatic metrics to minimize collinearity, with $\sim 95\%$ of the 1,350 total pairwise correlations ($((2 \text{ sets} \times 5 \text{ bioclimatic metrics}) \times 9 \text{ possible correlations})/2 \text{ replicate pairs} \times 30 \text{ pest species})$ below the threshold of concern ($-0.7 < r < 0.7$)⁷⁷.

We obtained PRISM climate data^{78,79} for monthly minimum temperatures, monthly maximum temperatures and monthly total precipitation. Using spatial raster packages (including raster v.3.6-2.6, exactextractr v.0.10.0 and terra v.1.7-78)^{80–82} in the R Statistical Software program⁸³ (v.4.3.1), we extracted the mean PRISM climate value for each month within each damage polygon record and for each damage point record associated with each focal pest species, and then averaged the mean monthly minimum temperatures, monthly maximum temperatures and monthly total precipitation values across all years within five distinct multiyear climate windows (consisting of the survey year and 1–5 preceding years) and across all years within a long-term historical climate period spanning 1980–1999. We then used the biovars function from the dismo R package⁸⁴ (v.1.3-14) to calculate the five bioclimatic metrics for each multiyear climate window, which eventually served as our climate window variables, and from the long-term historical climate period. To obtain our climate anomaly variables, which were intended to represent recent deviations in climate conditions, we subtracted the bioclimatic metrics for the long-term historical climate period from the bioclimatic metrics for each multiyear climate window. The specific time period (spanning 2–6 years) used for the climate window and climate anomaly variables was determined at a subsequent step in the statistical analysis process.

In addition to the ten focal climate variables, which reflected both contemporary climate and recent climatic shifts, we included two tree metrics, two county-level damage metrics related to spatiotemporal pest dynamics and a single categorical ecoregion designation as predictor variables. For the tree metrics, we used 324 tree species basal area maps modelled at a 250-m resolution by ref. 85 to calculate individual tree species relative abundance and overall tree species richness. The latter values were achieved by stacking the 324 tree species basal area maps, converting basal area to occurrence (0 or 1) and summing the occurrences, which resulted in a single raster containing the number of tree species present in each cell (Extended Data Fig. 1). We then calculated the proportion of aggregated host tree species basal area (as the total host tree species basal area divided by all tree species basal area) and mean tree species richness within each polygon record or within a 50-m radius around each point record. Host tree species information was compiled for each focal pest species using a variety of sources that included the CABI Digital Library⁸⁶, EPPO global database⁸⁷ and refs. 88,89.

Given the known population cycling and temporal outbreak dynamics exhibited by many of our focal pest species, we sought to include predictor variables that would account for potential effects of density dependence across space and time. However, for most of our focal pest species, there were no existing datasets of pest population sizes or densities matching the entire spatial and temporal extent of the IDS data. Instead, for each pest species, we calculated the total amount (ha) of damage (total forest cover (ha) that experienced either mortality or defoliation) summed across the county during the survey year (t_0) and the difference in that metric ($t_0 - t_{-1}$) from the previous year (t_{-1}). Total county-level damage was intended to reflect local pest density levels (assuming high spatial correlation with population density³⁰), and we conjectured that a positive, negative, or zero difference between

the preceding year and survey year would reflect increasing, decreasing or stable trends, respectively, in local pest density levels (assuming high temporal correlation with population density change). While these metrics are not entirely decoupled from the response variables, they merit inclusion because of their function in linking local-scale processes to dynamics at broader spatial and temporal scales (for example, during outbreaks), which probably improves the accuracy of our estimates of climate and host effects. Given that many pest species exhibit strong spatial and temporal autocorrelation in their population dynamics, we expected strong positive effects associated with both county-level damage metrics. Damage records for which there were no corresponding county-level data of any pest species from the previous year were removed before analyses, as we could not determine whether the county had no pest damage or simply had not been surveyed.

Finally, we assigned an ecoregion from the USDA Forest Service EcoMap^{33,90} (Extended Data Fig. 2) to each damage record associated with each focal pest species. By incorporating ecoregion as a categorical predictor variable, we aimed to account for sampling variation that could be attributed to differences in forest structure/connectivity (such as continuous versus fragmented stands) and composition (such as homogenous versus heterogeneous stands) among the ecoregions of the USA. Large-scale spatial autocorrelation in pest prevalence may have also been captured by the ecoregion variable.

Statistical analysis

To analyse the effects of the 15 predictor variables (comprising climate windows, climate anomalies, tree-related metrics, spatiotemporal pest dynamics and ecoregion) on pest damage, we used linear mixed effects models using the *lmer* function from the *lme4* R package⁹¹ (v.1.1-35.5). For each focal pest species, there were two possible response variables—damage footprint and refined damage. To ensure that model results were robust, we only fit models with at least 600 pest damage records. In all models, we did the following: log-transformed the response variable; included the same set of 15 predictor variables (with the total number of parameters depending on the number of ecoregions); scaled all continuous predictor variables; additionally centred the climate window, tree-related and total county-level damage predictor variables (so that the mean value of the predictor variable was equal to 0); specified interactions between each pair of climate window and climate anomaly metrics for each bioclimatic variable; allowed an interaction between the total amount of damage at the county level and the difference in total county-level damage from the previous year; and incorporated random effects of US state by survey year. The random effects were intended to account for any systematic differences among US states and survey years due to potential state-level and annual variation in IDS design, IDS sampling effort and IDS surveyor bias. For each model, the optimal time span used to calculate the climate window and climate anomaly variables was determined using model selection, based on Akaike information criterion values, and showed no trend among the five options: 2 years (16% of the total models), 3 years (19%), 4 years (22%), 5 years (5%) and 6 years (38%).

Ultimately, we examined the results of 58 total linear mixed effects models for the 30 focal pest species (Extended Data Table 2). To perform model checking and generate visual diagnostics plots for each model, we used the *check_model* function from the R package *performance*⁹² (v.0.11.0), which performs posterior predictive checks, checks the assumption of linear relationships, checks the assumption of equal variance (homoscedasticity), identifies influential observations, evaluates for potential collinearity among predictors, determines if the residuals are normally distributed and checks for normality of the random effects. All models passed our inspection of their diagnostics plots. Collinearity among the continuous predictor variables varied by individual model, but 99.96% of the 5,278 total pairwise correlations ((14 continuous predictor variables × 13 possible correlations)/2 replicate pairs × 58 models) were below the

threshold of concern ($-0.7 < r < 0.7$)⁷⁷. We further evaluated model fit based on the marginal and conditional R^2 values (Extended Data Table 2), which ranged from 0.03 to 0.43 (mean = 0.13) and 0.13 to 0.75 (mean = 0.40), respectively.

To determine whether predictor variables were statistically significant within each linear mixed effects model, we calculated the 95% CIs for each slope coefficient estimate using the *confint* function from the R package *stats*⁸³ (v.4.3.1). If the 95% CI for a slope coefficient estimate did not overlap 0, then the corresponding predictor variable was considered statistically significant. In addition, to assess trends in relationships across models, we used a meta-analytical approach and calculated the standardized mean magnitude (absolute value) and standardized mean values of the slope coefficient estimates for each numerical predictor variable. We used the *metagen* function from the R package *meta*⁹³ (v.8.2-1), which uses an inverse variance method to conduct a random effects meta-analysis based on estimates and their standard errors. Each model slope coefficient was treated as a 'study' and assigned a contribution weight based on the 95% CI of the mean estimate to account for uncertainty from the individual models. For all focal pest species and for each pest type, distribution or native status, we additionally tested for statistically significant variation among effect sizes of the predictor variables by performing subgroup analyses and evaluating between-group differences in standardized mean magnitude values. Subgroups were designated as either aggregated groups of predictor variables (n subgroups = 4 (grouping the five climate window metrics, five climate anomaly metrics, two tree-related metrics and two county-level damage metrics, respectively) or 2 (grouping the five climate window metrics and five climate anomaly metrics, respectively)) or individual predictor variables (n subgroups = 14 (all metrics) or 10 (climate metrics only)).

Model cross-validation and spatial autocorrelation assessment

To ensure the parameter estimates and fit of our models were robust, we performed a spatially and temporally structured fourfold cross-validation on the 58 models and assessed whether parameters changed signs and if model fit was consistent. To do so, we split data for each pest by state and year and assigned observations within each state–year to one of four folds to be used for testing—this ensured that state–years were represented proportionally in both training and testing data. State–years with fewer than four occurrences were not included in the cross-validation. For each training set, we refit the 58 models (hereafter, referred to as 'reduced' models) and compared each to the corresponding full model containing all data. For comparisons, we assessed root mean square error (RMSE) of the full and reduced models and tallied the number of climate parameters that switched signs (indicating that the interpretation of the variables changed) between the full and reduced models. Direct comparisons between the full and reduced models were complicated because the full models did not have data set aside for testing. Thus, we compared RMSE between the full models (which necessarily only had training data available) to the reduced models on training and testing data. Because the focus of our study is the interpretation garnered from the complete dataset, we solely presented results in the main text from the full models (where no data were withheld for cross-validation). Results of the cross-validation are shown in Extended Data Fig. 4.

To test the ability of our full models to account for spatial autocorrelation in our response metrics, we calculated Moran's index on model residuals. To do so, we split observations for each model by year and assigned each damage polygon the latitude and longitude of its centroid. We then transformed the coordinates to an equidistant conic coordinate system and used the *moranfast* R package⁹⁴ (v.1.0) to calculate Moran's I for all years with at least ten records. Generally, Moran's I will be low (near or < -1) when values are spatially dispersed and high (near or > 1) when clustered. Results of the spatial autocorrelation tests are shown in Extended Data Fig. 4.

Reporting summary

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

Data availability

All data used in this study are freely and publicly available at the cited sources. IDS data were obtained from the USDA Forest Service (<https://www.fs.usda.gov/science-technology/data-tools-products/fhp-mapping-reporting/detection-surveys>; accessed July 2023). Climate data were obtained from PRISM (<https://prism.oregonstate.edu/recent/>; accessed August 2023). Tree species basal area maps were obtained from ref. 85 (<https://doi.org/10.2737/RDS-2013-0013>; accessed October 2023). Ecoregion shapefiles were obtained from the USDA Forest Service (<https://data.fs.usda.gov/geodata/edw/datasets.php>; accessed December 2023). Processed data and all model outputs (including coefficients for all temporal windows) associated with the study are available via figshare at <https://doi.org/10.6084/m9.figshare.26426608> (ref. 95).

Code availability

The R code associated with the study is available via figshare at <https://doi.org/10.6084/m9.figshare.26426608> (ref. 95).

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Author contributions

H.L.C. co-developed the methods, handled data compilation and processing, performed the statistical analyses, generated the figures and cowrote the paper. K.M.P. provided insight into the IDS data and contributed to editing the paper. M.P.P., A.M.P. and S.N.M. provided input on methods and contributed to editing the paper. A.V.G. conceived the study, co-developed the methods and co-wrote the paper.

Competing interests

The authors declare no competing interests.

Additional information

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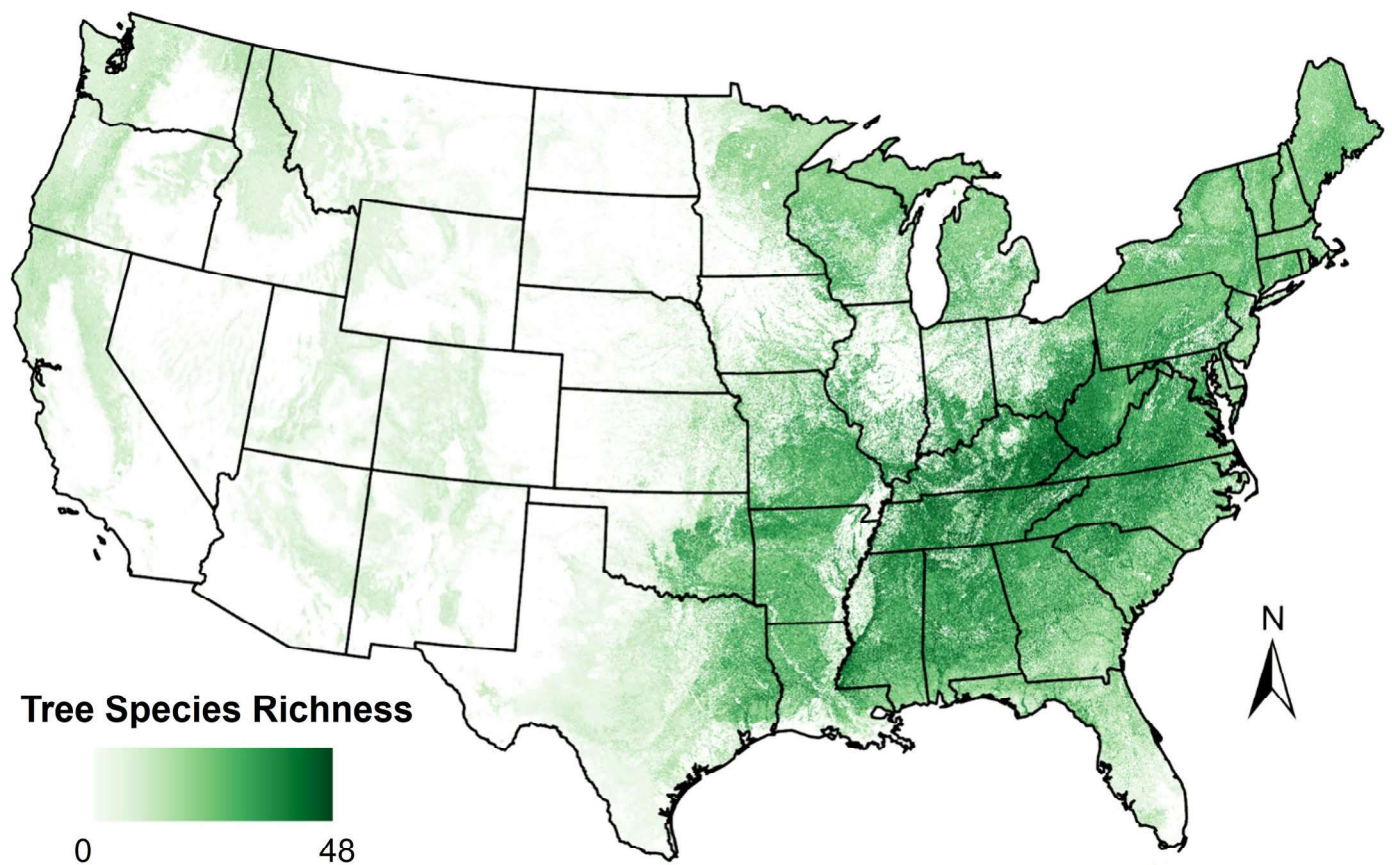
Correspondence and requests for materials should be addressed to Andrew V. Gougherty.

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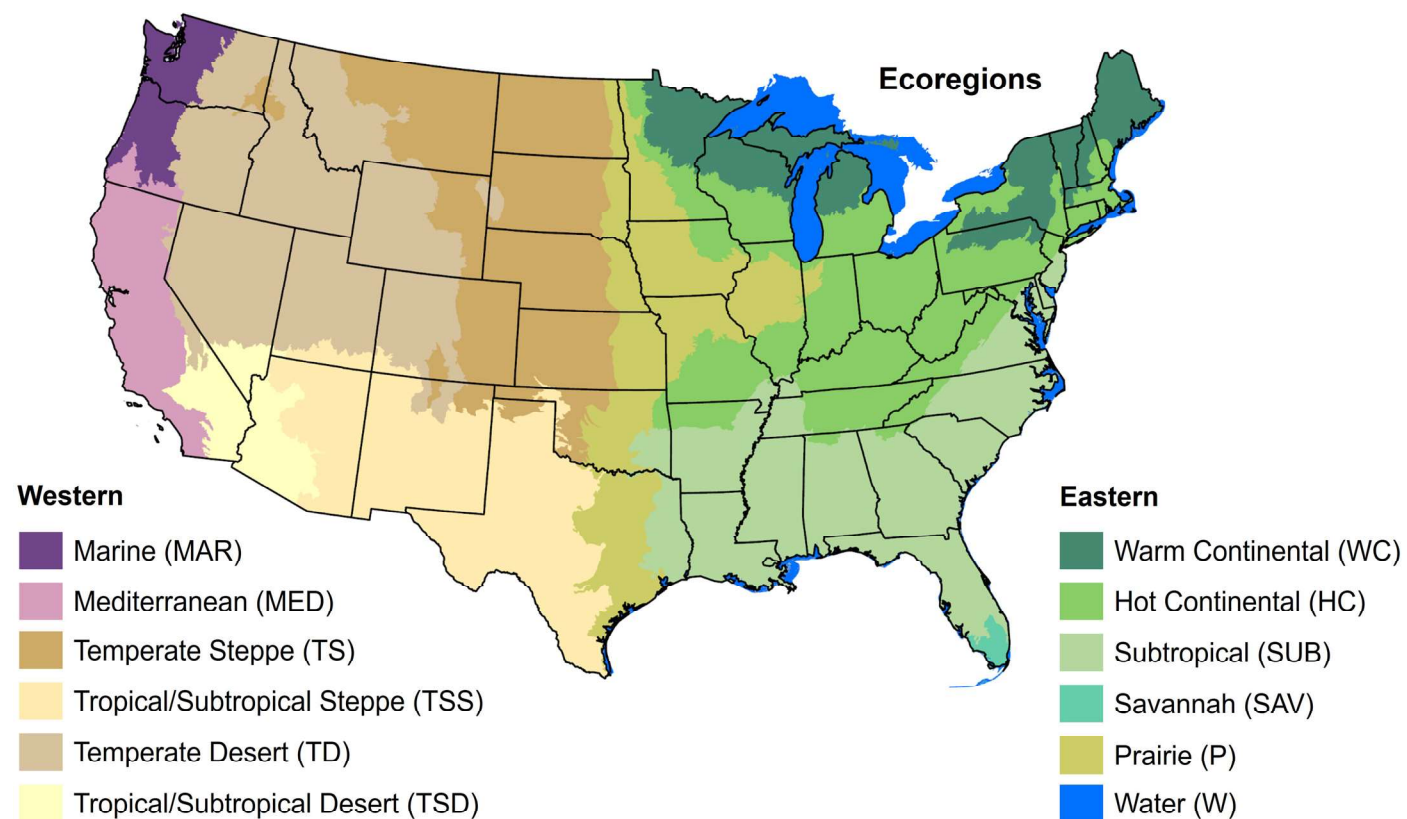
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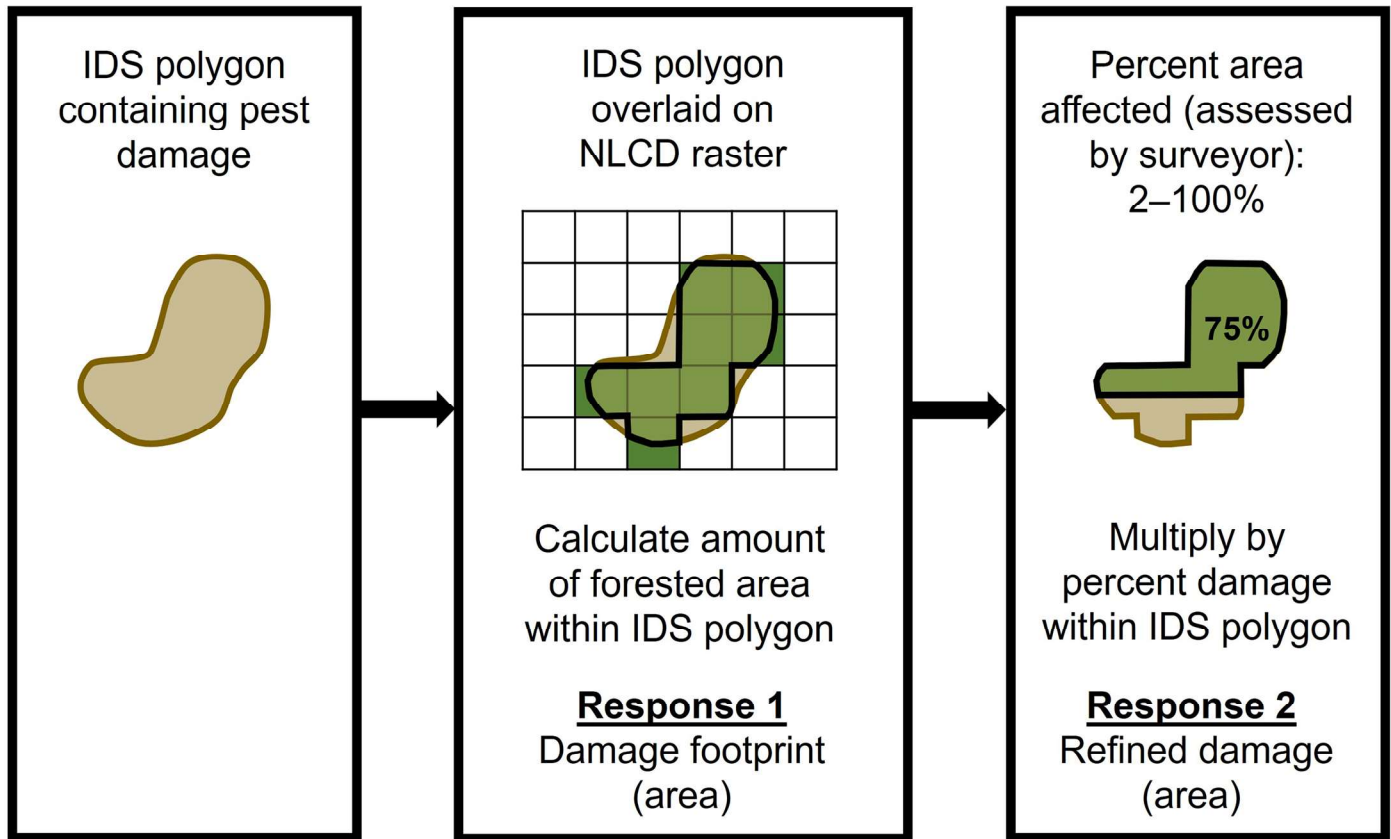
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Extended Data Fig. 1 | Map of tree species richness across the conterminous United States of America. This map was created by stacking the 324 tree species basal area maps modeled at a 250-m resolution by Wilson et al.⁸⁵, and converting basal area to occurrence, resulting in a single raster containing the number of tree species present in each cell.

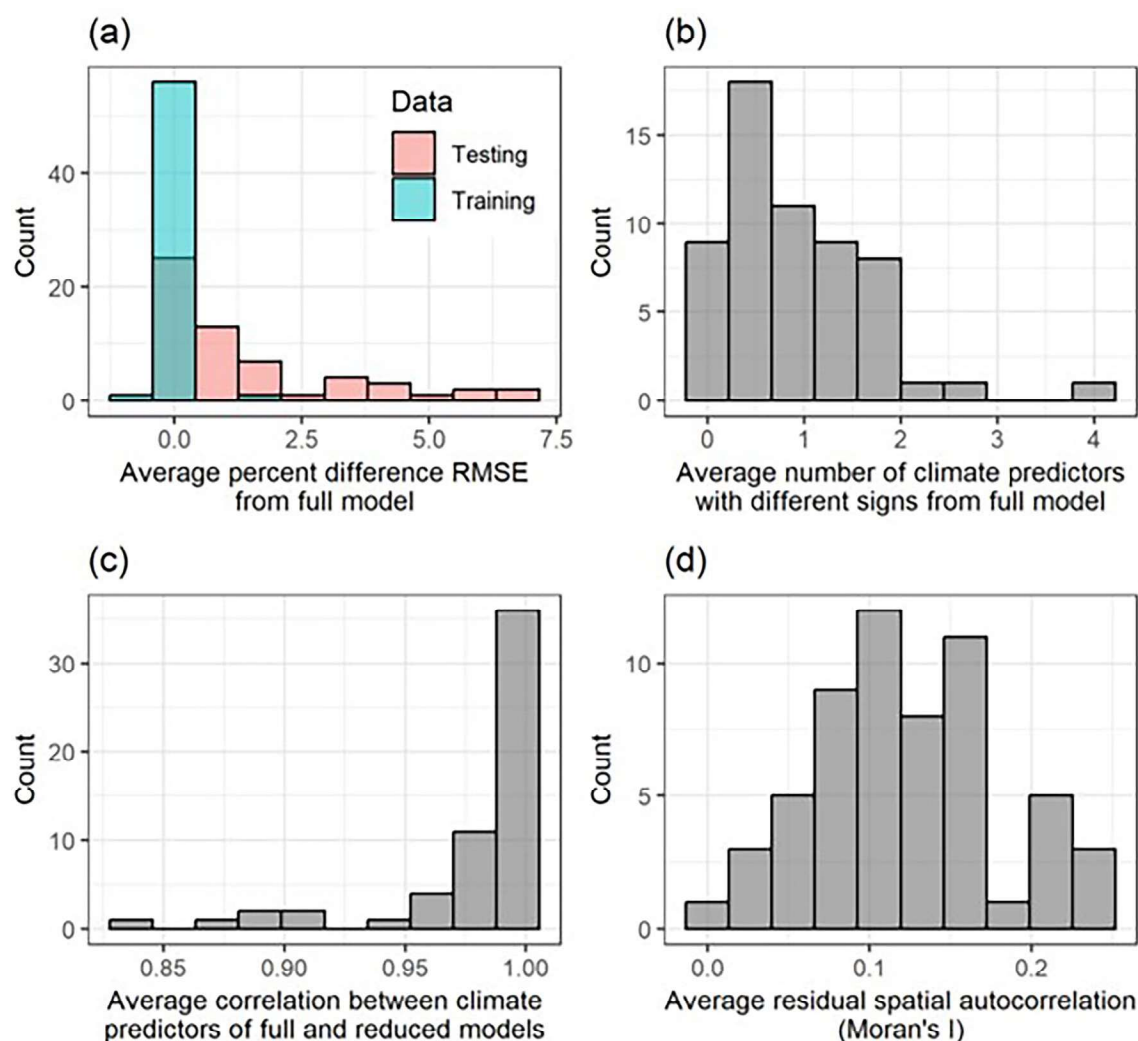


Extended Data Fig. 2 | Map of ecoregions within the conterminous United States of America. These ecoregions (N = 11, excluding water) correspond to ecosystem divisions delineated in the USDA Forest Service EcoMap^{33,90}.



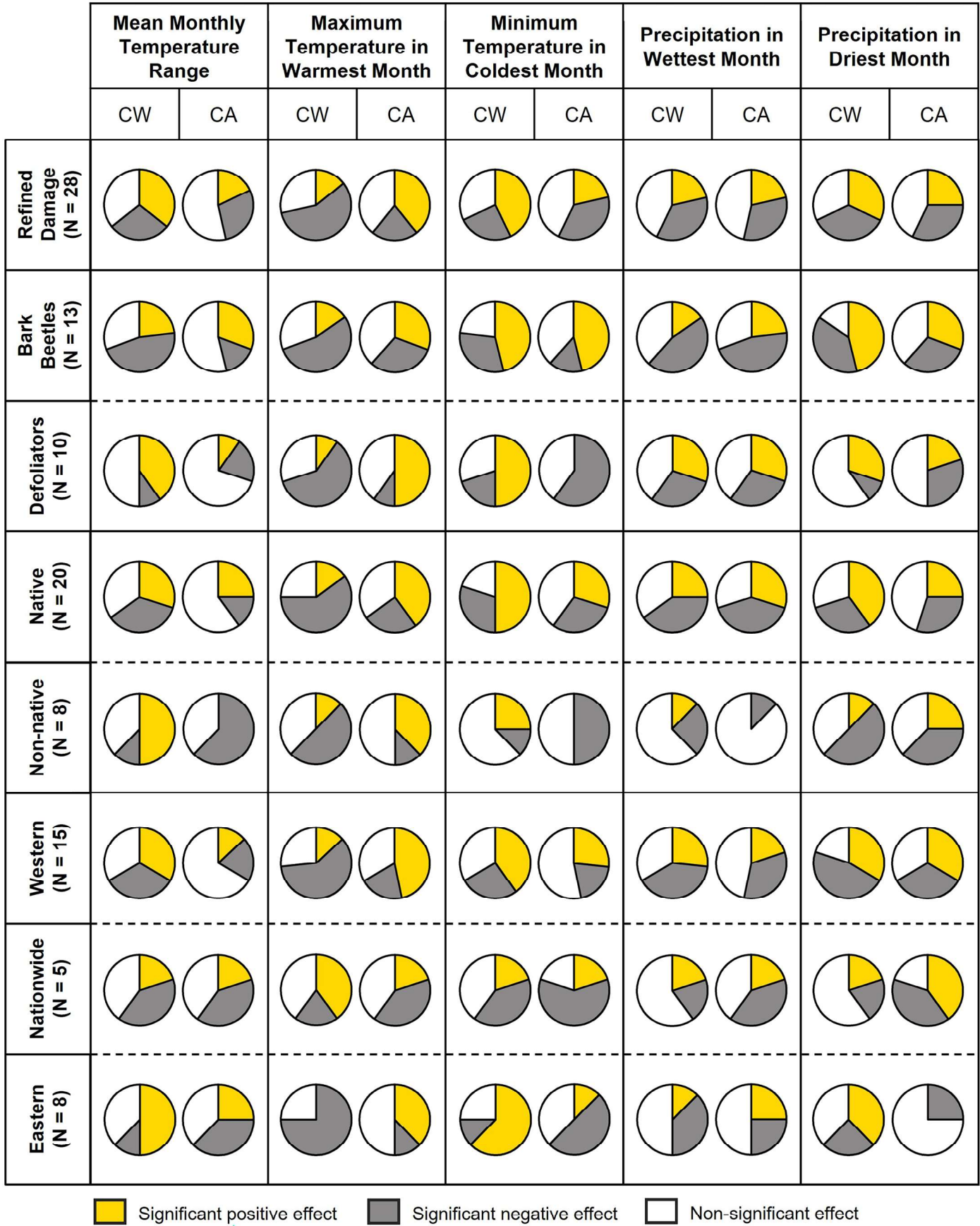
Extended Data Fig. 3 | Conceptual diagram of the Insect and Disease Survey (IDS) data processing. IDS polygons (box 1) represent areas with discrete boundaries that contain tree mortality or defoliation damage caused by insect and disease activity. For each IDS polygon, we calculated a damage footprint metric (Response 1) as the proportion of forest cover within the polygon using National Land Cover Database⁷⁵ (NLCD) data from the year closest to the survey year (box 2). For the subset of polygons with information on percent damage

(the percent area showing damage within the polygon) provided by the surveyor, we additionally calculated a refined damage metric (Response 2) as the product of Response 1 and the midpoint of the percent range (box 3) indicated by either a percent affected code (1 = 1–3%, 2 = 4–10%, 3 = 11–29%, 4 = 30–50%, 5 = > 50%) or legacy pattern code (1 | 2 = > 50%, 3 | 4 = < 50%), the latter of which links contemporary data standards to the legacy standards.



Extended Data Fig. 4 | Results of cross-validation and spatial autocorrelation analyses. Models were cross-validated by splitting observations by state-year and then assigning each record to one of four folds. Using this spatial-temporal structure ensured state-years were contributing to each fold in proportion to their total data. Models were then retrained, but with one fold withheld for testing. The retrained ‘reduced’ models were compared to the ‘full’ model (with no data withheld) by assessing (a) percent difference in root mean square error (RMSE), (b) the average number of climate predictors with different signs

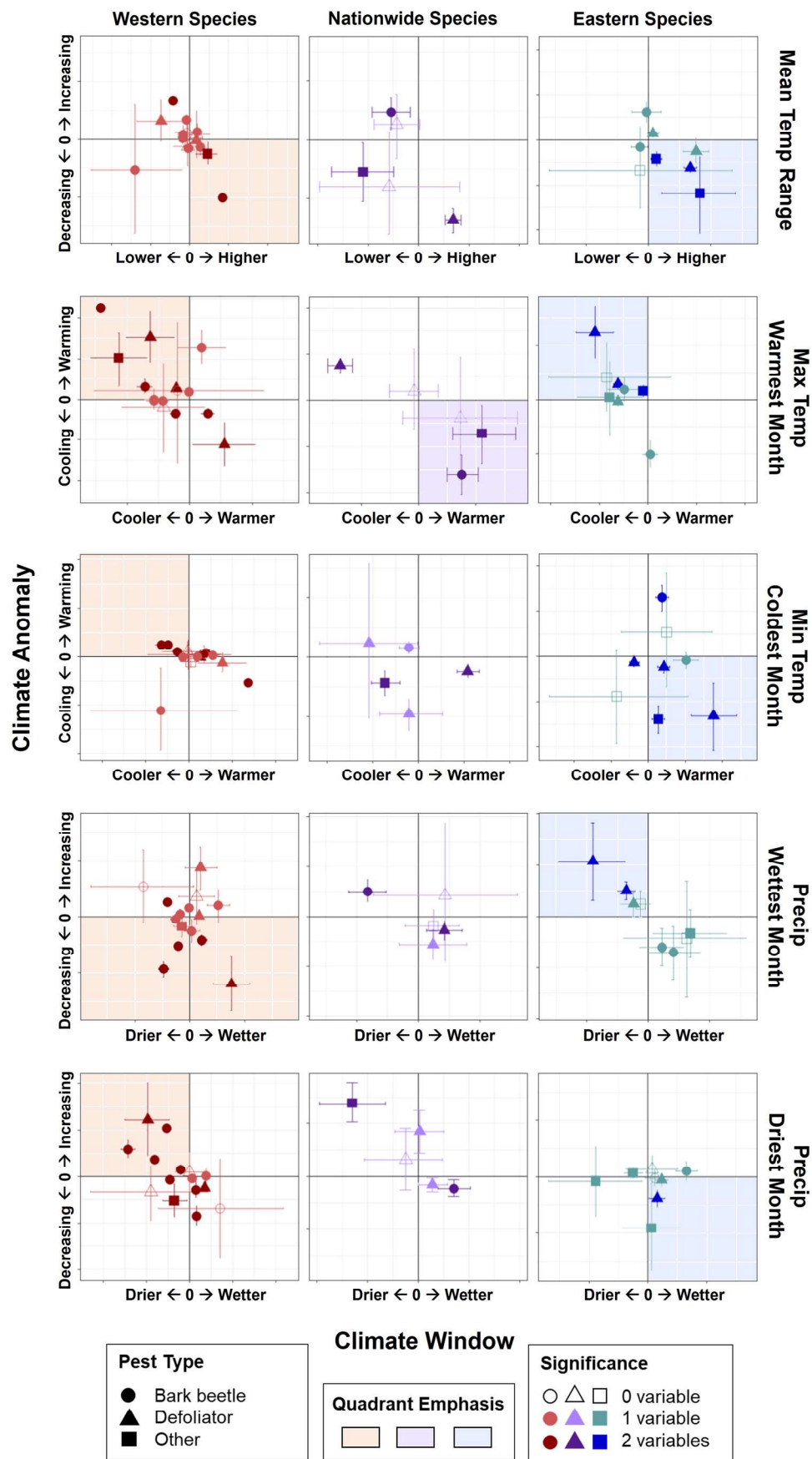
compared to the full model, and (c) the correlation between climate predictors in the full and reduced models. Each of these plots indicate that models trained on the full dataset were generally robust to data being withheld. (d) Spatial autocorrelation was calculated on the residuals of the full models. Generally, lower values (near or <-1) indicate residuals were dispersed, while higher values (near or >1) indicate clustering. This plot indicates that most models had relatively low residual spatial autocorrelation. In each histogram, counts are the number of models.



Extended Data Fig. 5|See next page for caption.

Extended Data Fig. 5 | Diagram of significance and direction of each climate variable for all refined damage models and for specific groups of pest species. Columns correspond to the climate window ('CW') and climate anomaly ('CA') metrics of the five bioclimatic metrics. Rows correspond to different groupings of the focal pest species, including all refined damage models, bark beetles *vs.*

defoliators, native *vs.* non-native species, and western *vs.* nationwide *vs.* eastern species. Pie charts indicate the proportion of significant positive relationships (gold), significant negative relationships (gray), and non-significant relationships (white).



Extended Data Fig. 6 | See next page for caption.

Extended Data Fig. 6 | Quadrant plots of slope coefficient values corresponding to the five bioclimatic metrics from the refined damage models. Within each plot, coordinates of the points reflect mean slope coefficient values for each bioclimatic metric (mean temperature range, maximum temperature in the warmest month, minimum temperature in the coldest month, precipitation in the wettest month, and precipitation in the driest month), calculated within a climate window (x-axis) and as a climate anomaly (y-axis), from the 28 refined damage models. Horizontal and vertical lines represent 95% confidence intervals of the slope coefficients for the

climate window variable and climate anomaly variable, respectively. If the 95% confidence interval overlaps 0, then that slope coefficient value is not considered statistically significant (as reflected by the color and fill of the point). Pest type is denoted by the shape of the point, and pest distribution within the USA is delineated by columns and color themes. Axes labels describe the climate conditions associated with each quadrant, and shading of a single quadrant ('Quadrant Emphasis') indicates that quadrant contains the greatest number of significant points.

Extended Data Table 1 | List of 30 focal pest species in our study

Scientific Name	Common Name	Taxonomy	Type	Native	Range	States	Years
<i>Rhabdocline laricis</i>	larch needle cast	Fungi: Helotiales	X	0	W	4	11
<i>Bretziella fagacearum</i>	oak wilt	Fungi: Microascales	X	0	E	11	19
<i>Cronartium ribicola</i>	white pine blister rust	Fungi: Pucciniales	X	0	W&E	12	20
<i>Dendroctonus adjunctus</i>	roundheaded pine beetle	Insecta: Coleoptera	BB	1	W	5	17
<i>Dendroctonus brevicornis</i>	western pine beetle	Insecta: Coleoptera	BB	1	W	12	20
<i>Dendroctonus frontalis</i>	southern pine beetle	Insecta: Coleoptera	BB	1	E	17	20
<i>Dendroctonus jeffreyi</i>	Jeffrey pine beetle	Insecta: Coleoptera	BB	1	W	2	20
<i>Dendroctonus ponderosae</i>	mountain pine beetle	Insecta: Coleoptera	BB	1	W	14	20
<i>Dendroctonus pseudotsugae</i>	Douglas-fir beetle	Insecta: Coleoptera	BB	1	W	12	20
<i>Dendroctonus rufipennis</i>	spruce beetle	Insecta: Coleoptera	BB	1	W	14	20
<i>Dendroctonus simplex</i>	eastern larch beetle	Insecta: Coleoptera	BB	1	E	4	17
<i>Dryocoetes confusus</i>	western balsam bark beetle	Insecta: Coleoptera	BB	1	W	10	20
<i>Ips confusus</i>	pinyon ips	Insecta: Coleoptera	BB	1	W	8	20
<i>Ips pini</i>	pine engraver	Insecta: Coleoptera	BB	1	W&E	14	20
<i>Phaenops drummondi</i>	flatheaded fir borer	Insecta: Coleoptera	BB	1	W	4	11
<i>Pseudohylesinus sericeus</i>	silver fir beetle	Insecta: Coleoptera	BB	1	W	2	20
<i>Scolytus ventralis</i>	fir engraver	Insecta: Coleoptera	BB	1	W	11	20
<i>Adelges piceae</i>	balsam woolly adelgid	Insecta: Hemiptera	X	0	W&E	9	20
<i>Adelges tsugae</i>	hemlock woolly adelgid	Insecta: Hemiptera	X	0	E	14	20
<i>Elatobium abietinum</i>	spruce aphid	Insecta: Hemiptera	X	0	E	5	17
<i>Choristoneura conflictana</i>	large aspen tortrix	Insecta: Lepidoptera	DF	1	W&E	9	18
<i>Choristoneura freemani</i>	western spruce budworm	Insecta: Lepidoptera	DF	1	W	11	20
<i>Choristoneura fumiferana</i>	spruce budworm	Insecta: Lepidoptera	DF	1	E	4	20
<i>Choristoneura pinus</i>	jack pine budworm	Insecta: Lepidoptera	DF	1	E	3	20
<i>Coleophora laricella</i>	larch casebearer	Insecta: Lepidoptera	DF	0	W&E	10	20
<i>Leucoma salicis</i>	satin moth	Insecta: Lepidoptera	DF	0	W	5	20
<i>Lymantria dispar</i>	spongy moth	Insecta: Lepidoptera	DF	0	E	18	20
<i>Malacosoma californicum</i>	western tent caterpillar	Insecta: Lepidoptera	DF	1	W	6	20
<i>Malacosoma disstria</i>	forest tent caterpillar	Insecta: Lepidoptera	DF	1	W&E	30	20
<i>Orgyia pseudotsugata</i>	Douglas-fir tussock moth	Insecta: Lepidoptera	DF	1	W	11	20

For each pest species, we provide the scientific name, common name, and taxonomic information, including kingdom (for fungi) or class (for insects) and order. We also indicate the type (BB = bark beetle, DF = defoliator, X = other), native status (1 = native, 0 = non-native), primary range or distribution within the USA (W = western USA, W&E = nationwide, E = eastern USA), number of states in which the pest occurred, and number of survey years in which the pest was recorded.

Extended Data Table 2 | List of model information corresponding to the 30 focal pest species in our study

Scientific Name	Response	Sample Size	Climate Window	Marginal R ²	Conditional R ²
<i>Rhabdocline laricis</i>	damage footprint	4,909	6	0.07	0.13
<i>Rhabdocline laricis</i>	refined damage	3,824	6	0.07	0.24
<i>Bretziella fagacearum</i>	damage footprint	25,071	4	0.04	0.73
<i>Bretziella fagacearum</i>	refined damage	25,033	5	0.03	0.67
<i>Cronartium ribicola</i>	damage footprint	7,807	6	0.12	0.33
<i>Dendroctonus adjunctus</i>	damage footprint	4,170	6	0.17	0.53
<i>Dendroctonus adjunctus</i>	refined damage	636	3	0.21	0.44
<i>Dendroctonus brevicomis</i>	damage footprint	220,964	4	0.08	0.29
<i>Dendroctonus brevicomis</i>	refined damage	60,339	2	0.13	0.35
<i>Dendroctonus frontalis</i>	damage footprint	24,553	6	0.04	0.66
<i>Dendroctonus frontalis</i>	refined damage	12,580	6	0.09	0.64
<i>Dendroctonus jeffreyi</i>	damage footprint	18,475	2	0.08	0.23
<i>Dendroctonus jeffreyi</i>	refined damage	9,096	4	0.09	0.38
<i>Dendroctonus ponderosae</i>	damage footprint	1,209,153	6	0.19	0.43
<i>Dendroctonus ponderosae</i>	refined damage	572,050	4	0.14	0.47
<i>Dendroctonus pseudotsugae</i>	damage footprint	382,131	6	0.06	0.36
<i>Dendroctonus pseudotsugae</i>	refined damage	70,852	2	0.03	0.47
<i>Dendroctonus rufipennis</i>	damage footprint	64,470	4	0.09	0.39
<i>Dendroctonus rufipennis</i>	refined damage	29,026	2	0.06	0.24
<i>Dendroctonus simplex</i>	damage footprint	17,719	4	0.14	0.34
<i>Dendroctonus simplex</i>	refined damage	17,698	4	0.12	0.44
<i>Dryocoetes confusus</i>	damage footprint	52,759	2	0.05	0.39
<i>Dryocoetes confusus</i>	refined damage	16,174	3	0.04	0.45
<i>Ips confusus</i>	damage footprint	35,420	3	0.08	0.39
<i>Ips confusus</i>	refined damage	12,095	6	0.05	0.56
<i>Ips pini</i>	damage footprint	29,099	6	0.10	0.37
<i>Ips pini</i>	refined damage	8,026	3	0.21	0.75
<i>Phaenops drummondi</i>	damage footprint	17,731	3	0.12	0.28
<i>Phaenops drummondi</i>	refined damage	11,179	3	0.10	0.40
<i>Pseudohylesinus sericeus</i>	damage footprint	1,157	6	0.30	0.38
<i>Scolytus ventralis</i>	damage footprint	270,797	6	0.08	0.27
<i>Scolytus ventralis</i>	refined damage	92,802	5	0.10	0.25
<i>Adelges piceae</i>	damage footprint	12,999	6	0.11	0.39
<i>Adelges piceae</i>	refined damage	7,005	3	0.12	0.43
<i>Adelges tsugae</i>	damage footprint	3,136	2	0.20	0.46
<i>Adelges tsugae</i>	refined damage	962	6	0.43	0.51
<i>Elatobium abietinum</i>	damage footprint	3,044	4	0.16	0.41
<i>Elatobium abietinum</i>	refined damage	1,435	6	0.12	0.33
<i>Choristoneura conflictana</i>	damage footprint	1,370	4	0.29	0.51
<i>Choristoneura conflictana</i>	refined damage	1,172	2	0.19	0.42
<i>Choristoneura freemani</i>	damage footprint	167,268	6	0.05	0.18
<i>Choristoneura freemani</i>	refined damage	123,189	6	0.06	0.25
<i>Choristoneura fumiferana</i>	damage footprint	18,260	6	0.12	0.31
<i>Choristoneura fumiferana</i>	refined damage	17,984	6	0.11	0.46
<i>Choristoneura pinus</i>	damage footprint	4,177	2	0.24	0.47
<i>Choristoneura pinus</i>	refined damage	4,082	2	0.29	0.56
<i>Coleophora laricella</i>	damage footprint	6,086	3	0.12	0.35
<i>Coleophora laricella</i>	refined damage	5,526	3	0.13	0.45
<i>Leucoma salicis</i>	damage footprint	920	5	0.25	0.36
<i>Leucoma salicis</i>	refined damage	676	6	0.26	0.36
<i>Lymantria dispar dispar</i>	damage footprint	34,476	4	0.11	0.36
<i>Lymantria dispar dispar</i>	refined damage	32,958	4	0.12	0.40
<i>Malacosoma californicum</i>	damage footprint	3,635	3	0.09	0.33
<i>Malacosoma californicum</i>	refined damage	923	3	0.21	0.23
<i>Malacosoma disstria</i>	damage footprint	36,763	4	0.21	0.44
<i>Malacosoma disstria</i>	refined damage	35,944	4	0.20	0.51
<i>Orgyia pseudotsugata</i>	damage footprint	3,301	6	0.15	0.36
<i>Orgyia pseudotsugata</i>	refined damage	2,569	6	0.15	0.36

For each pest species (see Extended Data Table 1 for common names) and response metric, we provide the sample size (number of combined polygon and point records), the number of years in the climate window (inclusive of the survey year), and the marginal and conditional R² values.

Extended Data Table 3 | Effect sizes of the slope coefficients for the climate window and anomaly metrics of the five bioclimatic variables

Pest Groups	Model Response	Climate Metric	All	MTR	TWM	TCM	PWM	PDM
All pest spp.	Footprint	Window	0.16 [0.13; 0.18]	0.16 [0.12; 0.20]	0.21 [0.14; 0.28]	0.20 [0.14; 0.25]	0.09 [0.06; 0.12]	0.13 [0.09; 0.18]
		Anomaly	0.16 [0.13; 0.19]	0.10 [0.07; 0.14]	0.28 [0.19; 0.37]	0.15 [0.08; 0.22]	0.12 [0.08; 0.16]	0.16 [0.11; 0.20]
	Refined	Window	0.19 [0.16; 0.22]	0.14 [0.09; 0.20]	0.25 [0.19; 0.32]	0.25 [0.17; 0.33]	0.12 [0.09; 0.15]	0.18 [0.12; 0.25]
		Anomaly	0.19 [0.16; 0.22]	0.15 [0.10; 0.21]	0.27 [0.15; 0.38]	0.21 [0.12; 0.29]	0.15 [0.10; 0.19]	0.17 [0.10; 0.23]
Bark beetles	Footprint	Window	0.14 [0.11; 0.17]	0.13 [0.07; 0.19]	0.15 [0.04; 0.25]	0.18 [0.13; 0.23]	0.11 [0.06; 0.17]	0.14 [0.07; 0.22]
		Anomaly	0.17 [0.12; 0.21]	0.09 [0.04; 0.14]	0.31 [0.15; 0.47]	0.13 [0.03; 0.23]	0.10 [0.04; 0.17]	0.20 [0.10; 0.30]
	Refined	Window	0.19 [0.15; 0.23]	0.12 [0.04; 0.20]	0.23 [0.11; 0.34]	0.25 [0.14; 0.36]	0.13 [0.08; 0.18]	0.22 [0.11; 0.34]
		Anomaly	0.19 [0.13; 0.24]	0.16 [0.06; 0.25]	0.28 [0.08; 0.49]	0.19 [0.04; 0.34]	0.14 [0.08; 0.21]	0.16 [0.05; 0.26]
Defoliators	Footprint	Window	0.17 [0.13; 0.21]	0.18 [0.11; 0.26]	0.25 [0.12; 0.39]	0.24 [0.08; 0.39]	0.08 [0.04; 0.12]	0.12 [0.07; 0.17]
		Anomaly	0.13 [0.09; 0.17]	0.11 [0.04; 0.17]	0.24 [0.09; 0.39]	0.13 [0.01; 0.26]	0.11 [0.02; 0.19]	0.13 [0.08; 0.17]
	Refined	Window	0.19 [0.14; 0.23]	0.16 [0.06; 0.26]	0.27 [0.16; 0.38]	0.29 [0.10; 0.48]	0.11 [0.06; 0.17]	0.11 [0.03; 0.18]
		Anomaly	0.17 [0.12; 0.22]	0.13 [0.05; 0.21]	0.26 [0.08; 0.45]	0.17 [0.03; 0.30]	0.19 [0.08; 0.30]	0.13 [0.05; 0.22]
Native spp.	Footprint	Window	0.16 [0.13; 0.18]	0.15 [0.10; 0.19]	0.20 [0.11; 0.29]	0.20 [0.14; 0.27]	0.10 [0.06; 0.15]	0.13 [0.08; 0.18]
		Anomaly	0.16 [0.12; 0.19]	0.09 [0.05; 0.13]	0.30 [0.19; 0.42]	0.12 [0.04; 0.19]	0.11 [0.05; 0.16]	0.16 [0.10; 0.23]
	Refined	Window	0.20 [0.16; 0.23]	0.13 [0.07; 0.19]	0.25 [0.17; 0.34]	0.28 [0.18; 0.38]	0.14 [0.09; 0.18]	0.19 [0.11; 0.27]
		Anomaly	0.19 [0.14; 0.23]	0.14 [0.08; 0.21]	0.30 [0.15; 0.45]	0.17 [0.07; 0.28]	0.16 [0.10; 0.23]	0.14 [0.07; 0.22]
Non-native spp.	Footprint	Window	0.16 [0.12; 0.20]	0.21 [0.13; 0.28]	0.23 [0.09; 0.37]	0.17 [0.06; 0.28]	0.06 [0.02; 0.10]	0.14 [0.02; 0.26]
		Anomaly	0.17 [0.12; 0.21]	0.14 [0.05; 0.23]	0.20 [0.09; 0.31]	0.22 [0.03; 0.41]	0.16 [0.07; 0.24]	0.12 [0.07; 0.17]
	Refined	Window	0.16 [0.12; 0.21]	0.19 [0.08; 0.29]	0.26 [0.09; 0.42]	0.17 [0.06; 0.28]	0.07 [0.03; 0.10]	0.14 [0.03; 0.25]
		Anomaly	0.20 [0.14; 0.25]	0.18 [0.06; 0.29]	0.12 [0.05; 0.19]	0.29 [0.10; 0.49]	0.10 [0.07; 0.14]	0.25 [0.09; 0.40]
Western spp.	Footprint	Window	0.15 [0.12; 0.18]	0.16 [0.11; 0.21]	0.17 [0.07; 0.28]	0.16 [0.11; 0.21]	0.10 [0.05; 0.15]	0.14 [0.08; 0.21]
		Anomaly	0.15 [0.12; 0.19]	0.09 [0.05; 0.13]	0.31 [0.17; 0.45]	0.07 [0.03; 0.11]	0.11 [0.04; 0.17]	0.20 [0.12; 0.29]
	Refined	Window	0.19 [0.15; 0.23]	0.14 [0.06; 0.21]	0.26 [0.15; 0.36]	0.21 [0.11; 0.31]	0.13 [0.07; 0.18]	0.23 [0.12; 0.34]
		Anomaly	0.18 [0.13; 0.23]	0.13 [0.05; 0.21]	0.31 [0.12; 0.50]	0.14 [0.04; 0.24]	0.15 [0.07; 0.22]	0.19 [0.10; 0.29]
Nationwide spp.	Footprint	Window	0.14 [0.09; 0.19]	0.15 [0.01; 0.29]	0.25 [0.07; 0.44]	0.23 [0.09; 0.38]	0.08 [0.05; 0.10]	0.07 [0.02; 0.12]
		Anomaly	0.13 [0.09; 0.18]	0.11 [0.00; 0.21]	0.21 [0.09; 0.32]	0.14 [0.00; 0.32]	0.14 [0.04; 0.24]	0.08 [0.03; 0.12]
	Refined	Window	0.17 [0.11; 0.23]	0.13 [0.10; 0.17]	0.25 [0.06; 0.44]	0.32 [0.05; 0.59]	0.10 [0.03; 0.16]	0.12 [0.00; 0.27]
		Anomaly	0.18 [0.13; 0.24]	0.14 [0.03; 0.26]	0.25 [0.04; 0.46]	0.21 [0.00; 0.42]	0.12 [0.06; 0.17]	0.23 [0.00; 0.49]
Eastern spp.	Footprint	Window	0.19 [0.14; 0.25]	0.17 [0.06; 0.28]	0.24 [0.08; 0.40]	0.29 [0.09; 0.49]	0.09 [0.01; 0.18]	0.18 [0.06; 0.29]
		Anomaly	0.20 [0.14; 0.26]	0.14 [0.04; 0.24]	0.25 [0.05; 0.46]	0.35 [0.11; 0.58]	0.15 [0.02; 0.27]	0.10 [0.05; 0.15]
	Refined	Window	0.20 [0.14; 0.25]	0.17 [0.03; 0.31]	0.25 [0.10; 0.40]	0.32 [0.11; 0.53]	0.13 [0.06; 0.20]	0.14 [0.04; 0.23]
		Anomaly	0.20 [0.14; 0.27]	0.21 [0.09; 0.32]	0.20 [0.02; 0.39]	0.36 [0.11; 0.60]	0.17 [0.10; 0.24]	0.07 [0.00; 0.14]

For both the damage footprint ('Footprint') and refined damage ('Refined') models, we used a meta-analytic approach to calculate the standardized mean magnitude (absolute value) of the slope coefficients in aggregate ('All') and individually for the five bioclimatic variables: mean temperature range ('MTR'), maximum temperature in the warmest month ('TWM'), minimum temperature in the coldest month ('TCM'), precipitation in the driest month ('PDM'), and precipitation in the wettest month ('PWM'). For each standardized mean magnitude value, the corresponding 95% confidence interval follows in brackets.

Extended Data Table 4 | Standardized means of the slope coefficients for the climate window and anomaly metrics of the five bioclimatic variables

Pest Groups	Model Response	Climate Metric	All	MTR	TWM	TCM	PWM	PDM
All pest spp.	Footprint	Window	-0.01 [-0.04; 0.03]	0.03 [-0.04; 0.11]	-0.13 [-0.22; -0.03]	0.05 [-0.04; 0.15]	-0.03 [-0.08; 0.02]	0.04 [-0.03; 0.11]
		Anomaly	0.01 [-0.03; 0.05]	-0.01 [-0.07; 0.04]	0.15 [0.02; 0.27]	0.00 [-0.10; 0.10]	-0.01 [-0.08; 0.05]	-0.06 [-0.13; 0.02]
	Refined	Window	-0.02 [-0.07; 0.02]	0.03 [-0.05; 0.11]	-0.16 [-0.27; -0.06]	0.09 [-0.03; 0.22]	-0.00 [-0.07; 0.07]	-0.06 [-0.16; 0.03]
		Anomaly	-0.01 [-0.05; 0.04]	-0.05 [-0.13; 0.03]	0.09 [-0.06; 0.24]	-0.08 [-0.20; 0.05]	-0.02 [-0.10; 0.05]	0.02 [-0.07; 0.12]
Bark beetles	Footprint	Window	-0.02 [-0.06; 0.03]	-0.01 [-0.11; 0.10]	-0.08 [-0.21; 0.05]	0.02 [-0.10; 0.14]	-0.06 [-0.14; 0.03]	0.04 [-0.08; 0.15]
		Anomaly	0.02 [-0.04; 0.08]	0.02 [-0.06; 0.10]	0.10 [-0.13; 0.34]	0.10 [-0.02; 0.21]	-0.05 [-0.14; 0.04]	-0.09 [-0.24; 0.07]
	Refined	Window	-0.04 [-0.10; 0.03]	-0.02 [-0.13; 0.10]	-0.14 [-0.30; 0.01]	0.09 [-0.09; 0.27]	-0.04 [-0.14; 0.06]	-0.05 [-0.23; 0.13]
		Anomaly	0.014 [-0.06; 0.09]	0.02 [-0.11; 0.15]	0.06 [-0.20; 0.33]	0.04 [-0.16; 0.24]	-0.06 [-0.17; 0.05]	0.02 [-0.12; 0.16]
Defoliators	Footprint	Window	0.02 [-0.05; 0.08]	0.10 [-0.03; 0.24]	-0.18 [-0.37; 0.02]	0.14 [-0.08; 0.36]	-0.01 [-0.11; 0.09]	0.08 [-0.00; 0.16]
		Anomaly	-0.01 [-0.07; 0.05]	-0.07 [-0.16; 0.02]	0.16 [-0.04; 0.37]	-0.12 [-0.25; 0.01]	0.05 [-0.07; 0.17]	-0.05 [-0.15; 0.05]
	Refined	Window	0.01 [-0.07; 0.08]	0.07 [-0.08; 0.22]	-0.19 [-0.37; -0.00]	0.15 [-0.13; 0.43]	0.03 [-0.10; 0.16]	0.02 [-0.11; 0.14]
		Anomaly	-0.00 [-0.07; 0.07]	-0.07 [-0.18; 0.04]	0.12 [-0.14; 0.38]	-0.14 [-0.30; 0.02]	0.05 [-0.13; 0.24]	0.03 [-0.13; 0.19]
Native spp.	Footprint	Window	-0.01 [-0.05; 0.04]	0.02 [-0.07; 0.11]	-0.12 [-0.24; -0.00]	0.07 [-0.05; 0.19]	-0.04 [-0.11; 0.02]	0.05 [-0.03; 0.12]
		Anomaly	0.02 [-0.03; 0.06]	-0.01 [-0.07; 0.06]	0.14 [-0.04; 0.31]	0.03 [-0.07; 0.13]	-0.01 [-0.08; 0.07]	-0.07 [-0.18; 0.03]
	Refined	Window	-0.02 [-0.07; 0.03]	0.01 [-0.09; 0.10]	-0.16 [-0.28; -0.03]	0.12 [-0.04; 0.29]	-0.02 [-0.10; 0.07]	-0.04 [-0.16; 0.09]
		Anomaly	0.02 [-0.04; 0.07]	-0.01 [-0.10; 0.08]	0.09 [-0.11; 0.29]	-0.01 [-0.15; 0.13]	-0.02 [-0.13; 0.08]	0.03 [-0.07; 0.13]
Non-native spp.	Footprint	Window	-0.01 [-0.08; 0.05]	0.06 [-0.11; 0.24]	-0.14 [-0.35; 0.07]	0.00 [-0.18; 0.19]	-0.00 [-0.07; 0.06]	0.00 [-0.18; 0.19]
		Anomaly	0.00 [-0.07; 0.08]	-0.03 [-0.18; 0.11]	0.17 [0.01; 0.33]	-0.05 [-0.31; 0.20]	-0.03 [-0.19; 0.13]	-0.01 [-0.15; 0.13]
	Refined	Window	-0.03 [-0.10; 0.04]	0.10 [-0.08; 0.28]	-0.18 [-0.42; 0.07]	-0.00 [-0.19; 0.19]	0.00 [-0.08; 0.09]	-0.12 [-0.27; 0.03]
		Anomaly	-0.07 [-0.16; 0.01]	-0.16 [-0.31; -0.01]	0.09 [-0.08; 0.25]	-0.26 [-0.49; -0.02]	-0.02 [-0.12; 0.08]	-0.01 [-0.28; 0.27]
Western spp.	Footprint	Window	-0.03 [-0.08; 0.01]	0.02 [-0.09; 0.12]	-0.11 [-0.25; 0.01]	-0.01 [-0.11; 0.09]	-0.05 [-0.12; 0.02]	-0.01 [-0.11; 0.10]
		Anomaly	0.02 [-0.03; 0.07]	0.02 [-0.05; 0.09]	0.15 [-0.05; 0.36]	0.06 [0.01; 0.10]	-0.02 [-0.10; 0.07]	-0.10 [-0.24; 0.04]
	Refined	Window	-0.05 [-0.11; 0.01]	0.01 [-0.11; 0.13]	-0.19 [-0.34; -0.04]	0.08 [-0.07; 0.22]	-0.01 [-0.11; 0.09]	-0.13 [-0.29; 0.02]
		Anomaly	0.02 [-0.04; 0.09]	-0.01 [-0.12; 0.10]	0.17 [-0.08; 0.41]	-0.02 [-0.15; 0.12]	-0.04 [-0.15; 0.08]	0.02 [-0.14; 0.17]
Nationwide spp.	Footprint	Window	-0.01 [-0.08; 0.07]	-0.03 [-0.25; 0.19]	-0.14 [-0.46; 0.19]	0.07 [-0.22; 0.36]	0.02 [-0.06; 0.10]	0.05 [-0.02; 0.11]
		Anomaly	-0.02 [-0.09; 0.05]	-0.08 [-0.21; 0.05]	0.21 [0.09; 0.32]	-0.13 [-0.32; 0.06]	-0.11 [-0.25; 0.02]	0.03 [-0.11; 0.16]
	Refined	Window	-0.01 [-0.11; 0.08]	-0.07 [-0.24; 0.11]	0.06 [-0.32; 0.44]	-0.09 [-0.60; 0.42]	0.01 [-0.13; 0.15]	-0.02 [-0.25; 0.22]
		Anomaly	-0.04 [-0.13; 0.06]	-0.08 [-0.27; 0.12]	-0.11 [-0.46; 0.25]	-0.16 [-0.45; 0.13]	-0.03 [-0.12; 0.14]	0.17 [-0.18; 0.51]
Eastern spp.	Footprint	Window	0.04 [-0.04; 0.13]	0.11 [-0.05; 0.27]	-0.13 [-0.37; 0.12]	0.16 [-0.15; 0.47]	-0.04 [-0.16; 0.09]	0.12 [-0.05; 0.30]
		Anomaly	0.01 [-0.08; 0.11]	-0.03 [-0.20; 0.14]	0.07 [-0.24; 0.37]	0.00 [-0.39; 0.40]	0.07 [-0.11; 0.26]	-0.04 [-0.16; 0.08]
	Refined	Window	0.03 [-0.06; 0.12]	0.14 [-0.02; 0.31]	-0.25 [-0.41; -0.09]	0.23 [-0.07; 0.53]	-0.01 [-0.17; 0.16]	0.05 [-0.11; 0.21]
		Anomaly	-0.05 [-0.14; 0.04]	-0.13 [-0.34; 0.09]	0.07 [-0.19; 0.32]	-0.14 [-0.53; 0.24]	0.01 [-0.19; 0.20]	-0.03 [-0.13; 0.07]

For both the damage footprint ('Footprint') and refined damage ('Refined') models, we used a meta-analytic approach to calculate the standardized mean of the slope coefficients in aggregate ('All') and individually for the five bioclimatic variables: mean temperature range ('MTR'), maximum temperature in the warmest month ('TWM'), minimum temperature in the coldest month ('TCM'), precipitation in the driest month ('PDM'), and precipitation in the wettest month ('PWM'). For each standardized mean value, the corresponding 95% confidence interval follows in brackets.