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Research article

Patterns and drivers of biotic disturbance hotspots in western United States coniferous forests

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Globally, forest disturbances caused by herbivorous insects and plant pathogens (i.e. biotic disturbances) have increased since the 1990s, a trend linked in part to climate warming. With increases in biotic disturbance activity, an emerging ecological phenomenon has been documented: biotic disturbance 'hotspots', or areas where two or more biotic disturbance agents co-occur in space and time. Biotic disturbance hotspots may have important implications for forest resilience, particularly if they erode mechanisms of post-disturbance forest recovery. The factors leading to hotspot occurrence, however, remain poorly understood. We characterized the patterns and drivers of biotic disturbance hotspots occurring from 2000 to 2020 across three broad forested regions in the western United States (US; the Southern Rockies, Middle Rockies, and Cascades). Using Bayesian spatio-temporal models, we evaluated whether hotspots can be predicted from predisposing factors expected to increase forest susceptibility to biotic disturbance (i.e. forest composition, topography, and average climate), as well as inciting factors known to trigger individual bark beetle and pathogen outbreaks (i.e. annual weather). Biotic disturbance hotspots exhibited distinct spatio-temporal patterns and trends within each region. Forest structure and composition were the strongest and most consistent drivers of hotspots. Other factors varied in their importance by region, reflecting regional differences in biophysical context. Relative to the predictor variables included in our models, estimated spatio-temporal random effects were more closely correlated with model predictions, suggesting that dynamic factors such as outbreak spread strongly shape patterns of biotic disturbance hotspots. Our results illustrate the widespread nature of biotic disturbance hotspots across western US coniferous forests and demonstrate the importance of forest structure and regional outbreak dynamics in anticipating hotspots at regional scales. These findings provide a deeper understanding of interacting forest disturbances and have important implications for the resilience of forests during a period marked by continued increases in disturbance activity.

Keywords: Bark beetle, disturbance interactions, plant pathogen, spatio-temporal model, temperate forest, tree mortality

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Introduction

Forest disturbances play a critical role in shaping the structure and function of temperate forests worldwide, along with the ecosystem services these forests provide (Thom and Seidl 2016). Globally, biotic disturbance activity (i.e. outbreaks of insects and plant pathogens) has been increasing since the late 1990s (Kautz et al. 2017), linked in part to the sensitivity of biotic agents to changing climate (Bentz et al. 2010, Weed et al. 2013, Seidl et al. 2017). While region- and species-specific trends vary, biotic disturbance activity is expected to continue to increase as climates become warmer and drier (Bentz et al. 2010, Kautz et al. 2017, McNichol et al. 2022, Lantschner and Corley 2023).

As disturbance regimes change in response to changing climate, interactions among disturbances are increasingly important to consider (Turner 2010, Buma 2015, Burton et al. 2020). Multiple disturbances can interact via the legacies of prior disturbances affecting subsequent disturbances or ecological patterns and processes (Peterson 2002). Some disturbances can interact to produce compound effects that may alter mechanisms or rates of ecosystem recovery (Paine et al. 1998). In the western United States (US), one disturbance interaction emerging in recent decades is the occurrence of biotic disturbance 'hotspots', areas where two or more distinct biotic disturbances overlap in space and time (Harvey et al. 2023). Between 1997 and 2019, ~ 5–18% of the area affected by biotic disturbance each year in western US forests were hotspots (Harvey et al. 2023). Yet, the causes and consequences of biotic disturbance hotspots remain poorly understood.

Biotic disturbance hotspots may have important implications for forest resilience, particularly if they result in compound or synergistic effects (Paine et al. 1998). Tree-killing bark beetles and many plant pathogens are specialists, feeding on or infecting a specific host tree genus or species, and in the case of bark beetles, also preferentially attacking older and larger host trees (Raffa et al. 2008). In forests affected by a single biotic disturbance, the selective mortality of particular species and sizes of trees often results in abundant surviving non-host and/or understory trees that facilitate rapid post-disturbance growth responses (Veblen et al. 1991, Buonanduci et al. 2023), providing continuity in forest functional attributes such as live carbon stocks (Pfeifer et al. 2011). In forests affected by biotic disturbance hotspots, however, the synchronous mortality of multiple host tree species has the potential to dampen compensatory growth responses that might otherwise provide stability in forest function (Harvey et al. 2023). These effects are likely to be exacerbated in areas subject to increasing climate stress, further decreasing rates of forest recovery and increasing the likelihood that mechanisms of forest resilience could break down.

Biotic disturbance and associated tree mortality is a complex process, with numerous factors shaping both the activity and effects of biotic agents ultimately contributing to tree death. As a conceptual framework, both 'predisposing' and 'inciting' factors can drive biotic disturbance activity (Manion 1981). Long-term or persistent factors, including host availability, forest structure, and average climatic conditions, can predispose locations to biotic disturbance activity (Raffa et al. 2008). Short-term factors, including annual weather conditions, can then incite biotic disturbance activity through various mechanisms. For example, warm temperatures below supraoptimal temperature thresholds affect insect physiology, leading to increased survivorship, reproduction, and reproductive synchrony, all of which can facilitate insect outbreaks (Bentz et al. 1991, Hansen et al. 2001, Tobin et al. 2014). Warm and dry conditions also stress potential host trees, reducing resources allocated to defense (Mattson and Haack 1987, Gaylord et al. 2013, Huang et al. 2020). Predisposing and inciting factors can both shape biotic disturbance activity, with their relative influence being context dependent.

Spatial overlaps in biotic disturbances may occur due to shared drivers, mechanistic links between agents, or random chance. Temporally synchronous hotspots may occur when individual biotic agents respond to shared broad-scale drivers, such as multiple bark beetle outbreaks occurring synchronously in response to regional increases in temperature (i.e. the 'Moran effect'; Moran 1953, Peltonen et al. 2002, Bentz et al. 2010, Chapman et al. 2012, Preisler et al. 2012, Hart et al. 2017). Conversely, temporally lagged hotspots may occur due to mechanistic links between disturbance agents, such as when defoliating insects reduce tree vigor, thereby increasing host tree susceptibility to subsequent bark beetle attacks (Hadley and Veblen 1993, Cole et al. 2022). Even in the absence of shared or linked mechanisms, some overlap of biotic disturbance agents is expected to occur randomly due to an overall increase in biotic disturbance activity within a finite forested area. Despite the increasing potential for overlap and interaction of biotic disturbance agents, the broad-scale factors associated with biotic disturbance hotspots remain understudied.

Here, we characterize the spatio-temporal patterns and drivers of biotic disturbance hotspots across three broad forested regions in the western US that span differing gradients of forest types and bioclimatic conditions. We focus on temporally synchronous hotspots of tree-killing biotic agents that target a variety of host tree species and that are not expected to be mechanistically linked (Table 1). We examine predisposing factors expected to increase forest susceptibility to biotic disturbance (i.e. forest composition, topography, and climate), as well as inciting factors known to trigger individual bark beetle and pathogen outbreaks (i.e. annual weather conditions; Table 2). Using this framework, we ask: Can the occurrence of biotic disturbance hotspots be predicted from predisposing and inciting factors known to favor individual biotic disturbance agents?

Methods

Study regions

We studied three broad forested regions within the western US: the Southern Rockies, Middle Rockies, and Cascades.

Table 1. Tree-killing biotic agents and multi-species complexes used to identify biotic disturbance hotspots. [a]Subalpine fir mortality complex includes the effects of western balsam bark beetle activity, *Armillaria* root rot, and other mortality agents (Harvey et al. 2021). We treated western balsam bark beetle and subalpine fir mortality complex as separate agents when identifying hotspots; however, because our definition of hotspots required that two or more distinct host tree species be affected, we do not expect that doing so inflated our detection of hotspots. [b]Five-needle pine decline includes the effects of mountain pine beetle activity and white pine blister rust. We treated mountain pine beetle and five-needle pine decline as separate agents when identifying hotspots; however, as noted above, we do not expect that doing so inflated our detection of hotspots.

Common name	Scientific name	Host tree species
Bark beetles		
Western pine beetle	*Dendroctonus brevicomis*	Ponderosa pine
Jeffrey pine beetle	*Dendroctonus jeffreyi*	Jeffrey pine
Mountain pine beetle	*Dendroctonus ponderosae*	All pine species; primarily lodgepole, ponderosa, western white, sugar, limber, and whitebark pines
Douglas-fir beetle		Douglas-fir
Spruce beetle	*Dendroctonus rufipennis*	Engelmann spruce, Sitka spruce, Brewer spruce
Western balsam bark beetle	*Dryocoetes confusus*	Primarily subalpine fir; occasionally other true firs, Engelmann spruce, and lodgepole pine
Pinyon ips	*Ips confusus*	Pinyon pine
Pine engraver	*Ips pini*	All pine species; primarily ponderosa, lodgepole, and Jeffrey pines
Ips engraver beetles	*Ips* spp.	All pine species
Silver fir beetle	*Pseudohylesinus sericeus*	Primarily Pacific silver fir; occasionally other true firs, Douglas-fir, western hemlock, and Sitka spruce
True fir bark beetles	*Scolytus* spp.	True firs
Douglas-fir engraver	*Scolytus unispinosus*	Douglas-fir
Fir engraver	*Scolytus ventralis*	Primarily grand fir, white fir, red fir, and noble fir; occasionally Douglas-fir, subalpine fir, and western hemlock
Multi-agent mortality 'complexes'		
Subalpine fir mortality complex[a]		Subalpine fir
Five-needle pine decline[b]		Five-needle pines; primarily limber, Rocky Mountain bristlecone, and whitebark pines
Pinyon pine mortality		Pinyon pine

These regions are all mountainous, dominated by conifer forests, and comparable in their spatial extents (each 134 000–144 000 km^2), but span a range of forest types and bioclimatic conditions (Rollins 2009). The topography, climate, and forest types characterizing these regions are described in the Supporting information.

Biotic disturbance data

Forest insect and disease impacts are mapped annually through aerial detection surveys (ADS) conducted by the USDA Forest Service. During ADS, trained observers are flown systematically over forested areas in small aircraft; observers delineate areas of forest damage on maps while characterizing the type of damage (i.e. identifying both host tree species and disturbance agent). Ground-truthing has found that binary (presence/absence) ADS classifications are approximately 70% accurate when aggregated to 200–1000 m raster cells, which is generally considered sufficient for broad-scale monitoring (Johnson and Ross 2008, Backsen and Howell 2013, Coleman et al. 2018).

We obtained ADS data within each of our study regions for the period 1999–2021 from the USDA Forest Health Protection program database (USDA 2022a). We filtered the data to include 13 tree-killing Scolytinae species and three multi-agent mortality complexes among which mechanistic links are not expected (Table 1). Because damage from these agents is typically detected one year following host tree infestation or infection (when foliage of attacked trees begins to fade), we attributed ADS detections in a given year to the preceding year (i.e. detection data for 1999–2021 were attributed to 1998–2020; Meddens et al. 2012, Backsen and Howell 2013). We rasterized the ADS polygon data to 510-m cells containing binary indicators for presence/absence of each disturbance agent, with zeros assigned only to cells that were surveyed but lacked detection. A 510-m resolution was selected as a moderately coarse grain to improve ADS classification accuracy while remaining compatible with finer-grained 30-m datasets used in our analysis. All rasters were generated in the USGS contiguous USA Albers projection using the 'raster' package (Hijmans et al. 2022) in R (R Core Team 2023).

To quantify hotspot occurrence, we identified spatiotemporal overlaps in disturbance activity attributed to the 16 biotic agents included in our study (Table 1). First, we defined a hotspot as any 510-m raster cell in which damage caused by ≥ 2 biotic agents and affecting ≥ 2 host tree species was detected within a three-year window, including the focal year and prior two years. We used a relatively short three-year window to define hotspots because our goal was to identify temporally synchronous hotspots that may result in compound or synergistic effects, following Harvey et al. (2023). For a cell to be designated a hotspot in a given focal year, at least one of the co-occurring agents must have been detected within that focal year. To increase the computational efficiency of our models, we aggregated these moderate-resolution (510 m) rasters by a factor of 10, with

Table 2. Potential predictor variables for hotspot occurrence and prevalence, and hypothesized associations.

Category	Predictor variable	Description	Temporally variable?	Expected direction of effect and justification	
Predisposing factors					
Forest composition	Host tree co-occurrence	Number of 510-m subcells containing $\geq$ 2 potential host tree species	No	+	Increased potential for hotspot occurrence in areas where host trees tend to co-occur
	Host tree basal area (m^2 ha^{-1})	Average total basal area of host species within subcells containing $\geq$ 2 potential host tree species	No	+	Increased susceptibility to bark beetle outbreak
	Host tree richness	Average host species richness within subcells containing $\geq$ 2 potential host tree species	No	+	Increased susceptibility to co-occurring biotic agents
Topography	Heat load index	Index of potential direct incident radiation	No	+	Increased moisture stress for host trees
	Topographic wetness index	Index of the long-term moisture availability of a given site in the landscape	No	-	Decreased moisture stress for host trees
Average climate	Annual actual evapotranspiration (AET; mm)	Average annual AET, expressed as 30-year normals (1991–2020)	No	+	Increased vegetation productivity
	Summer maximum vapor pressure deficit (VPD; hPa)	Average daily maximums for June–August, expressed as 30-year normals (1991–2020)	No	+	Increased moisture stress for host trees
	Winter minimum temperature (°C)	Average daily minimums for December–February, expressed as 30-year normals (1991–2020)	No	+	Increased overwinter survival for bark beetles
Inciting factors					
Weather	Summer maximum vapor pressure deficit (VPD; hPa)	Average daily maximums for June–August, averaged over the 3-year hotspot detection window and expressed as deviations from 30-year normals	Yes	+	Increased moisture stress for host trees
	Winter minimum temperature (°C)	Average daily minimums for December–February, averaged over the 3-year hotspot detection window and expressed as deviations from 30-year normals	Yes	+	Increased overwinter survival for bark beetles

each aggregated 5.1-km cell expressing a binary indicator for hotspot detection in one or more 510-m subcells (hereafter referred to as hotspot occurrence) as well as a count of 510-m subcells in which hotspots were detected (hereafter referred to as hotspot prevalence). To express hotspot prevalence at the 5.1-km scale as a proportion, we also quantified the number of subcells with the potential for hotspot detection. Subcells had the potential for hotspot detection if they were surveyed every year of the three-year hotspot window and were likely to contain $\geq$ 2 co-occurring host tree species (based on host tree data described in the following section). After accounting for the three-year hotspot detection window, our final dataset included focal years 2000–2020.

Potential predictors of hotspots

As potential predictors of hotspots, we considered predisposing factors expected to increase forest susceptibility to biotic disturbance as well as inciting factors known to trigger individual biotic disturbance events (Table 2; Supporting information).

Forest composition was characterized using the USDA Forest Service Individual Tree Species Parameter (ITSP) database (USDA 2022b), which provides species-specific basal area rasters modeled from USFS Forest Inventory and Analysis plot data; 30-m Landsat satellite imagery; and local climate, terrain, and soils. The ITSP data, which are publicly distributed at a 240-m resolution, represent tree species conditions across the US in approximately 2002 (Krist 2014), thus corresponding to the beginning of our biotic disturbance dataset. We obtained basal area rasters for each potential host tree species occurring in our study regions from the ITSP database (Supporting information). We converted these basal area rasters to binary presence/absence rasters for each species, where we defined presence as > 1 m^2 ha^{-1} host basal area following Tutland et al. (2023). We converted all species-specific rasters from a 240-m resolution to a 510-m resolution by first disaggregating to a 30-m resolution and then aggregating to a 510-m resolution, with aggregated basal area and presence quantified as the average and maximum, respectively, of 30-m subcells. We then calculated total host basal area and richness within each 510-m cell by summing all host species basal area and presence rasters, respectively. Finally, we aggregated host tree presence, basal area, and richness to a 5.1-km scale, where host co-occurrence was quantified as the number of 510-m subcells containing two or more host tree species, and basal area and richness were averaged across those subcells containing two or more host tree species.

Topography was characterized using a 30-m resolution digital elevation model obtained from the USGS LANDFIRE database (Rollins 2009). Heat load index, an index of potential direct incident radiation ranging from 0 (coolest) to 1 (hottest), was calculated using the 'spatialEco' package (Evans 2021, R Core Team 2023) in R following McCune and Keon (2002) and McCune (2007). Topographic wetness index, an index of long-term moisture availability, was calculated in ArcMap (ESRI 2019) according to Beven and Kirkby (1979). Higher values of the topographic wetness index indicate topographically wetter areas and lower values indicate topographically drier areas. Both indices were aggregated to a 5.1-km scale by averaging all 30-m subcells.

As an index of site productivity and moisture stress, climatic water balance data were obtained from the TerraClimate database (Abatzoglou et al. 2018). We obtained actual evapotranspiration (AET) rasters at a resolution of 1/24 degree (approximately 4 km) on a monthly time step for the period 1991–2020. AET represents the amount of water lost from a surface due to evaporation and transpiration and is used as a proxy for plant productivity (Stephenson 1990). We summed monthly actual evapotranspiration by calendar year and averaged the annual rasters to derive a 30-year climate normal. Finally, we rescaled all rasters from their native 1/24-degree resolution by first resampling to a 510-m resolution and then aggregating to a 5.1-km resolution.

Additional climate and weather data were obtained from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) database (PRISM Climate Group 2022). We obtained 30-year (1991–2020) climate normals and annual weather values at a resolution of 1/24 degree (approximately 4 km), which we rescaled to 5.1-km cells via resampling and aggregation, as described above. Summer maximum vapor pressure deficit (VPD) was calculated by averaging values for June–August of a given year, and winter minimum temperature was calculated by averaging values for December of the prior year through February of the focal year. Annual weather values were converted to annual anomalies by subtracting the corresponding 30-year climate normals, and anomalies were averaged across the three-year window corresponding to the temporal window used for hotspot detection (e.g. for focal year 2007, anomalies were averaged for years 2005–2007).

Statistical analysis

We used Bayesian spatio-temporal regression models, fit separately to each study region, to evaluate the relative influence of predisposing and inciting factors on hotspot occurrence and prevalence at the 5.1-km scale. The discrete response (count of subcells in which hotspots were detected) for cell location s and year t was modeled as a zero-inflated ('hurdle' model) binomial random variable Y_{st}. The probability density function takes the following form:

$$P\left(Y_{st}\right)=\begin{cases}1-p_{st}, & \text{if } Y_{st}=0\\ p_{st}\left(\dfrac{\text{Binomial}(Y_{st}\mid N_{st},\pi_{st})}{1-\text{Binomial}(0\mid N_{\text{st}},\pi_{st})}\right), & \text{if } Y_{st}>0\end{cases}$$

Here, p_{st} is the probability of hotspot occurrence (i.e. hotspot detection in at least one subcell), N_{st} is the number of subcells with the potential for hotspot detection, and π_{st} is the success probability in the binomial function used for positive counts. The probability of occurrence (Bernoulli) and positive prevalence count (binomial) were estimated as separate processes, each linked to covariates and random effects as follows:

$$\text{logit}\left(p_{st}\right)=\gamma_t+\boldsymbol{\beta}\boldsymbol{X}_{st}+\in_{st}$$

$$\text{logit}\left(\pi_{st}\right)=\eta_t+\boldsymbol{\theta}\boldsymbol{X}_{st}+\omega_{st}$$

Here, the linear predictors for occurrence and prevalence are modeled as functions of time-varying intercepts γ_t and η_t respectively, covariates $\boldsymbol{X}_{st}$, and spatio-temporal random effects $\in_{st}$ and ω_{st}, respectively. The time-varying intercepts are modeled as year-specific random walks as follows (for γ_t, with η_t following an analogous form):

$$\gamma_t\sim\text{Normal}\left(\gamma_{t-1},\sigma_\gamma\right)$$

The spatio-temporal random effects are modeled as stationary autoregressive Gaussian random fields as follows (for $\in_{st}$, with ω_{st} following an analogous form):

$$\in_{s,t>1}=\phi\in_{s,t-1}+\sqrt{1-\phi^2\delta_{st}}$$

$$\in_{s,t=1}\sim\text{MVN}\left(0,\Sigma_\delta\right)$$

$$\delta_{st}\sim\text{MVN}\left(0,\Sigma_\delta\right)$$

Here, ϕ $(0<\phi<1)$ is the temporal autoregression parameter for the Gaussian random field. The spatial covariance matrix Σ_δ is modeled using a Matérn covariance function parameterized by marginal standard deviation σ_δ and practical range r (the distance at which the spatial correlation drops to approximately 0.1) (Lindgren et al. 2011).

We fit these models in a Bayesian framework using the integrated nested Laplace approximation (INLA) and stochastic partial differential equation (SPDE) approaches (Lindgren et al. 2011, Blangiardo and Cameletti 2015) (Supporting information). We used penalized complexity priors for the marginal standard deviations and practical ranges of the Gaussian random fields, which shrink the marginal variance toward zero and the practical range toward infinity (Fuglstad et al. 2019). The penalized complexity prior approach avoids spatial overfitting and can reduce the potential for spatial confounding between autocorrelated covariates and spatio-temporal random effects (Mäkinen et al. 2022). We used uninformative priors for all other parameters (Krainski et al. 2019). Models were fit using the 'R-INLA' package (www.r-inla.org) in R.

We fit models using only data from those 5.1-km cells within which ≥ 25% of subcells had the potential for hotspot detection (i.e. ≥ 25% of subcells both [a] contained ≥ 2 host tree species and [b] were surveyed each year of the three-year hotspot detection window). All potential predictor variables, with the exception of host co-occurrence, were included as covariates in both the Bernoulli model of hotspot occurrence and binomial model of hotspot prevalence. The prevalence of host co-occurrence is in many cases equal to N_{st}, the number of subcells with the potential for hotspot detection (though the two are not always equal, with N_{st} accounting not only for host co-occurrence but also for whether each subcell was surveyed each year). Since N_{st} is explicitly included in our binomial model of hotspot prevalence, we excluded the prevalence of host co-occurrence as a covariate in that model. We checked for multicollinearity among covariates using variance inflation factors (Zuur et al. 2010).

To enable comparison of the magnitude of coefficients within each regional model, we standardized all covariates within each regional dataset by subtracting their means and dividing by their standard deviations. A covariate was considered a statistically important predictor if the 95% credible interval for the coefficient did not include zero. Because we expected the effects of inciting factors (i.e. annual weather anomalies) might vary with predisposing climate, we considered interaction terms between weather anomalies and their corresponding climate normals. We added interaction terms to each model only if they were statistically important predictors and they improved model fit (i.e. decreased model Deviance Information Criterion by > 10). We calculated randomized quantile residuals for our zero-inflated binomial models following Bai et al. (2021) and validated each model using standard regression diagnostics. To verify inferences drawn from our models were not affected by spatial autocorrelation, we evaluated residual autocorrelation using Moran's I (Cliff and Ord 1981) and empirical variograms calculated using the 'gstat' package in R (Pebesma 2004).

Results

Observed hotspots

Hotspot occurrence (presence/absence) and prevalence (the proportion of subcells in which hotspots were detected; a measure of local hotspot magnitude) exhibited distinct spatial and temporal patterns within each study region (Fig. 1–3). Across all 5.1-km cells with the potential for hotspot detection, annual rates of hotspot occurrence ranged from 3 to 38% in the Southern Rockies, from < 1 to 49% in the Middle Rockies, and from 10 to 28% in the Cascades (Fig. 1–3). Within those 5.1-km cells in which hotspot occurrence was detected, average annual hotspot prevalence ranged from 3 to 14% in the Southern Rockies, from 2 to 15% in the Middle Rockies, and from 5 to 16% in the Cascades (Fig. 1–3). In both the Southern Rockies and Middle Rockies, hotspot occurrence and prevalence peaked between 2003 and 2008, whereas occurrence and prevalence in the Cascades peaked around 2009 and again from 2014 to 2017 (Fig. 1–3).

The individual biotic agents and multi-species complexes contributing to hotspot occurrence varied by region (Supporting information). In the Southern Rockies, mountain pine beetle, subalpine fir mortality, and spruce beetle were the most common agents contributing to hotspot occurrence; at the 510-m scale, mountain pine beetle was detected in 49% of hotspots, while subalpine fir mortality and spruce beetle were detected in 28% and 27% of hotspots, respectively. In the Middle Rockies, mountain pine beetle, five-needle pine decline, and subalpine fir mortality were the most common agents, being detected in 67%, 21%, and 19% of hotspots, respectively. In the Cascades, fir engraver, mountain pine beetle, and western pine beetle were most common and were detected in 53%, 41%, and 23% of hotspots, respectively.

Effects of predisposing and inciting factors

Hotspot occurrence (presence/absence) and prevalence (local magnitude) were affected by each of the predisposing factors considered in our analysis, with the strength and direction of effects varying by region (Fig. 4; Supporting information). Forest composition had the strongest and most consistent effect on hotspot occurrence and prevalence; across study regions, hotspot occurrence consistently increased with host co-occurrence (number of subcells containing two or more host tree species; a measure of the extent of host species overlap), and hotspot occurrence and prevalence both consistently increased with total host basal area and richness (Fig. 4). Decreases in hotspot occurrence and prevalence were consistently linked with increases in normal summer VPD and topographic heat load, though the magnitude of the effect of topographic heat load was small (Fig. 4).

All other predisposing factors considered in our analysis had variable effects across regions. Hotspot occurrence decreased with increasing topographic wetness in the Southern Rockies and Cascades, whereas hotspot prevalence increased with topographic wetness in the Middle Rockies. Hotspots decreased with increasing normal AET in the Middle Rockies but strongly increased with normal AET in the Cascades; in the Southern Rockies, effects of AET were mixed, with hotspot occurrence increasing but hotspot prevalence decreasing with increasing AET (Fig. 4). Finally, hotspot occurrence and prevalence decreased with normal winter minimum temperature in the Southern Rockies, whereas normal winter temperature had no detectable effect in the Middle Rockies (Fig. 4). Winter temperature normals could not be included in the models for the Cascades due to collinearity with AET (Fig. 4).

Across study regions, inciting factors had the strongest effects in the Southern Rockies (Fig. 4). Hotspot occurrence and prevalence increased with increasing winter temperature

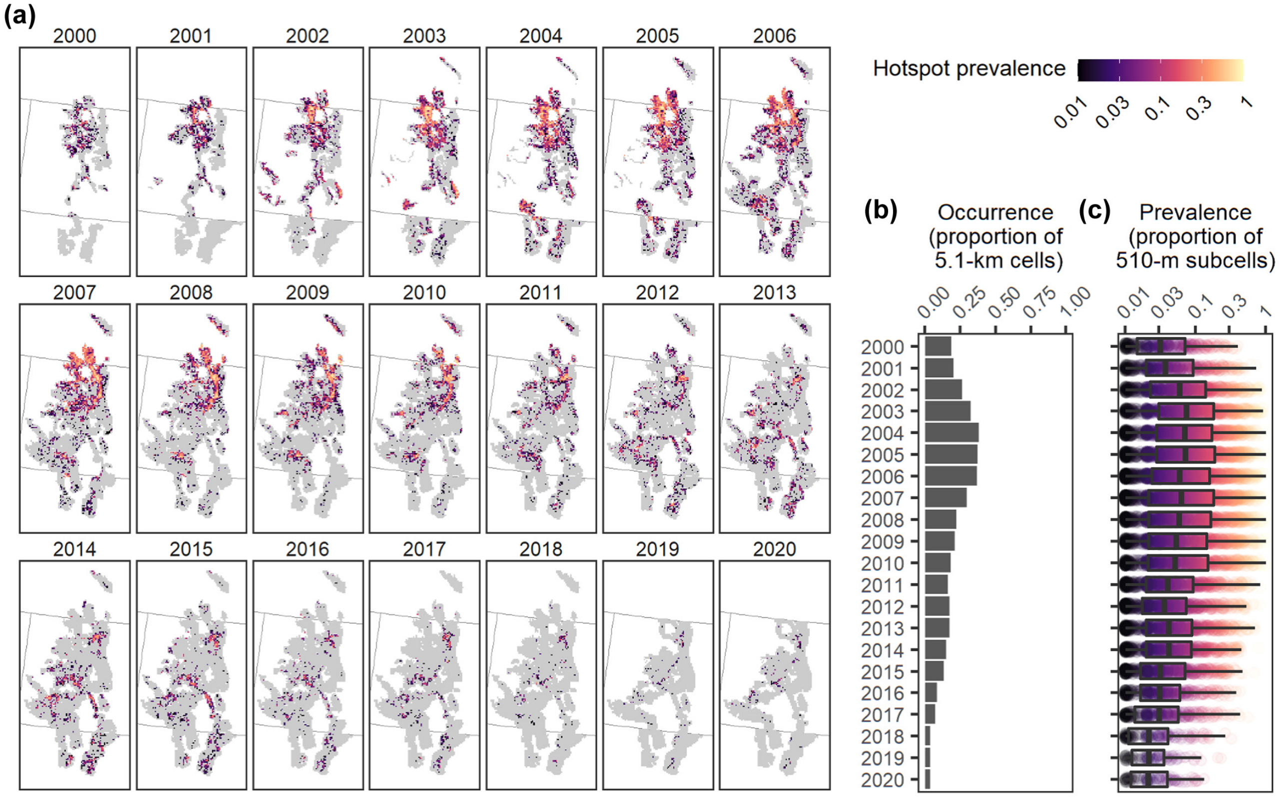

Figure 1. Hotspots in the Southern Rockies region, US (EPA Level III Ecoregion 21). (a) Observed spatio-temporal patterns of hotspot occurrence (presence/absence) and prevalence (local magnitude) within 5.1-km cells with the potential for hotspot detection. Surveyed cells in which zero hotspots were detected are shown in light gray; for those cells in which ≥ 1 hotspots were detected, hotspot prevalence is expressed as the proportion of 510-m subcells in which hotspots were detected. Thin gray lines represent US state boundaries. (b) Observed temporal patterns of hotspot occurrence. (c) Observed temporal patterns of hotspot prevalence within those 5.1-km cells in which ≥ 1 hotspots were detected. Note the log-transformed scales in (a) and (c).

anomalies in the Southern Rockies, with the negative interaction between normals and anomalies suggesting that winter temperature anomalies have weaker effects in locations with warmer normal winter temperatures (Fig. 4). Similarly, hotspot prevalence increased with summer VPD anomalies in the Southern Rockies, with the positive interaction between normals and anomalies suggesting that summer VPD anomalies have stronger effects in locations with greater normal summer VPD (Fig. 4). We detected no effect of inciting factors on hotspot occurrence in either the Middle Rockies or Cascades (Fig. 4). Hotspot prevalence decreased with increasing winter temperature anomalies in the Middle Rockies, increased with winter temperature anomalies in the Cascades, and increased with summer VPD anomalies in both regions, though the magnitudes of these effects were all relatively modest (Fig. 4).

Spatio-temporal random effects

Compared to the fixed effects estimated in our models, the temporal and spatio-temporal random effects were greater in magnitude and more closely correlated with model-predicted hotspot occurrence and prevalence (Fig. 5; Supporting information). Odds ratios associated with a one standard deviation increase in estimated random effects ranged from 11.3 to 30.1 for hotspot occurrence and from 2.7 to 3.8 for prevalence. In contrast, odds ratios associated with a one standard deviation increase in estimated fixed effects only ranged from 2.3 to 4.5 for hotspot occurrence and from 1.8 to 2.2 for prevalence. Overall, odds ratios for random effects were 1.5–13.1 times greater than those for corresponding fixed effects (Supporting information).

The temporal and spatio-temporal random effects estimated in our models reflect the distinct patterns and trends in hotspots across our study regions (Supporting information). Peaks in the time-varying random intercepts largely corresponded with peaks in the observed hotspots data (Supporting information). The estimated practical range r (distance at which spatial autocorrelation approaches zero) varied from 55 to 85 km across regions for hotspot occurrence and from 35 to 40 km across regions for hotspot prevalence. Spatial patterns of hotspots were strongly persistent from year to year, with the temporal autoregression parameter ϕ for the spatial random fields varying from 0.88 to 0.93 across all models. Our models accounted for most of the spatio-temporal correlation in our data, with empirical variograms of model residuals suggesting some residual autocorrelation, but only at very short distances (i.e. ≤ 10 km) relative to the extents of our study regions (Supporting information).

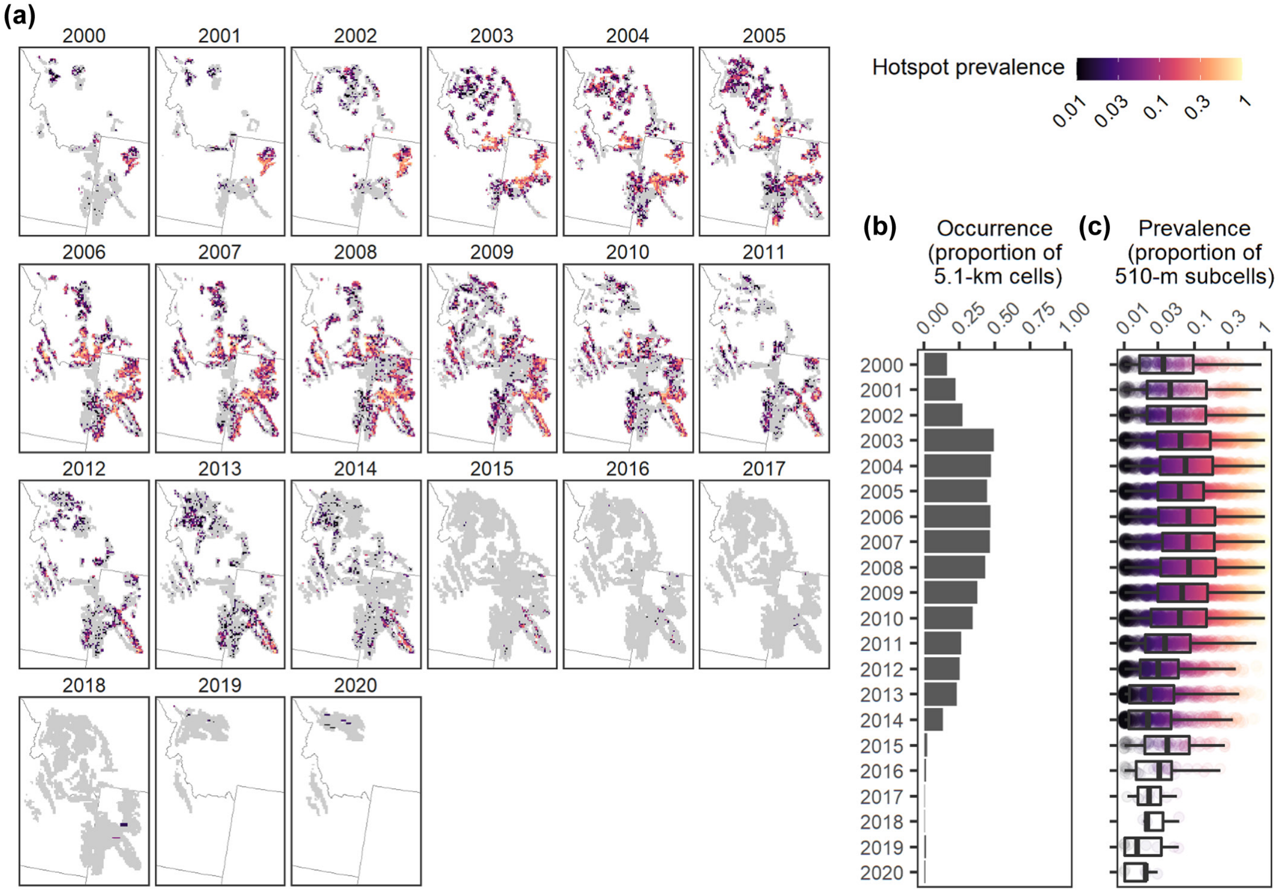

Figure 2. Hotspots in the Middle Rockies region, US (EPA Level III Ecoregion 17). (a) Observed spatio-temporal patterns of hotspot occurrence (presence/absence) and prevalence (local magnitude) within 5.1-km cells with the potential for hotspot detection. Surveyed cells in which zero hotspots were detected are shown in light gray; for those cells in which ≥ 1 hotspots were detected, hotspot prevalence is expressed as the proportion of 510-m subcells in which hotspots were detected. Thin gray lines represent US state boundaries. (b) Observed temporal patterns of hotspot occurrence. (c) Observed temporal patterns of hotspot prevalence within those 5.1-km cells in which ≥ 1 hotspots were detected. Note the log-transformed scales in (a) and (c).

Discussion

Our study investigates the patterns, trends, and drivers of biotic disturbance hotspots across three forested regions in the western US. Biotic disturbance hotspots occurred widely throughout the western US in the early part of the 21st century (2000–2020), with distinct patterns characterizing each of our three study regions. Using a spatio-temporal modeling approach, we found that predisposing and inciting factors both contributed to hotspot occurrence, with forest composition and structure being consistent drivers and other effects varying with the unique biophysical characteristics of each region. Relative to the predictor variables included in our analysis, we found that the random spatio-temporal effects estimated in our models were stronger and more closely correlated with hotspot predictions, suggesting that dynamic factors such as outbreak spread strongly shape patterns of biotic disturbance hotspots. These findings provide an understanding of interacting biotic disturbance agents in the western US during a period when climate and biotic disturbance regimes were both changing.

Hotspots occur widely and have implications for forest resilience

The widespread nature of biotic disturbance hotspots across the western US carries important implications for forest resilience in a period of increasing biotic disturbance activity. Biotic disturbance hotspots are an emerging ecological phenomenon (Harvey et al. 2023), and this study provides a foundational understanding of their spatial and temporal patterns in recent decades. While interannual trends varied regionally, each of our study regions experienced years in which hotspots were detected within ≥ 28% of 5.1-km cells with the potential for hotspot occurrence, with annual occurrence rates as high as 49% observed in the Middle Rockies. Forest disturbances caused by a single host-specific agent are often followed by robust compensatory responses facilitated by increased growth of surviving non-host trees (Veblen et al. 1991, Buonanduci et al. 2023). These compensatory responses underpin forest recovery and continuity in forest function (Romme et al. 1986), serving as important mechanisms of forest resilience. In forests affected by biotic disturbance hotspots, however, compensatory responses could be

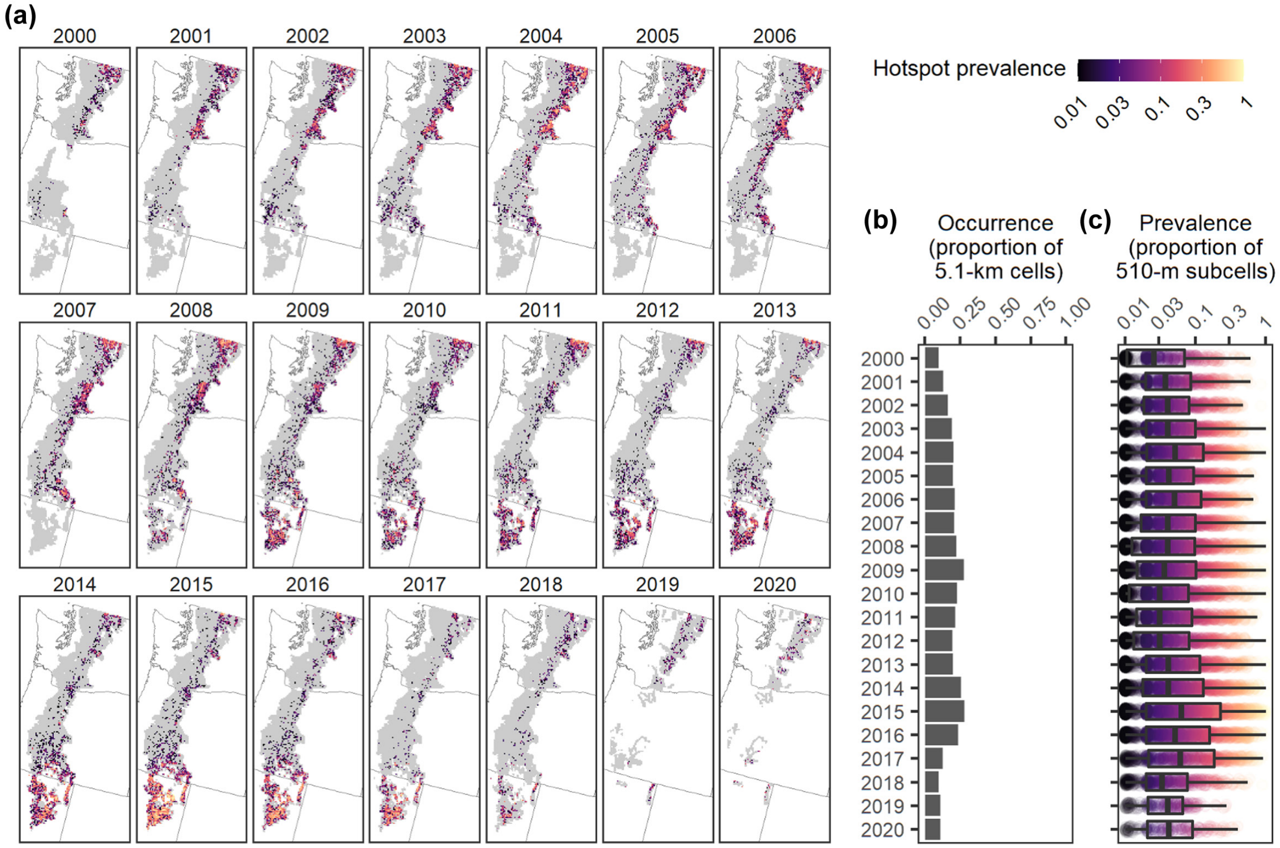

Figure 3. Hotspots in the Cascades region, US (EPA Level III Ecoregions 4, 9, and 77). (a) Observed spatio-temporal patterns of hotspot occurrence (presence/absence) and prevalence (local magnitude) within 5.1-km cells with the potential for hotspot detection. Surveyed cells in which zero hotspots were detected are shown in light gray; for those cells in which ≥ 1 hotspots were detected, hotspot prevalence is expressed as the proportion of 510-m subcells in which hotspots were detected. Thin gray lines represent US state boundaries. (b) Observed temporal patterns of hotspot occurrence. (c) Observed temporal patterns of hotspot prevalence within those 5.1-km cells in which ≥ 1 hotspots were detected. Note the log-transformed scales in (a) and (c).

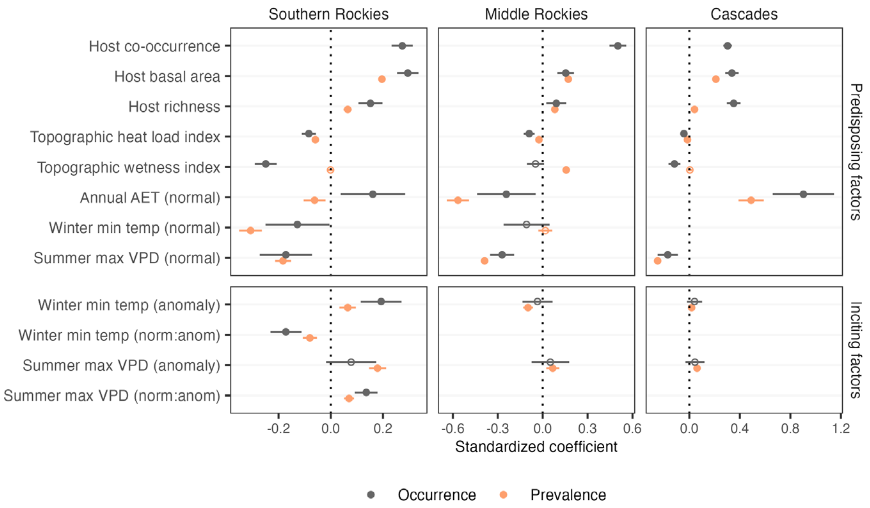

Figure 4. Effects of covariates on hotspot occurrence and prevalence. Dots represent posterior means and horizontal lines represent 95% credible intervals. Closed circles represent statistically important predictors and open circles represent predictors that are not statistically important. Blank spaces indicate covariates not evaluated in a particular model. The effects for each predictor are per one standard deviation within each region-specific dataset. AET, actual evapotranspiration; VPD, vapor pressure deficit.

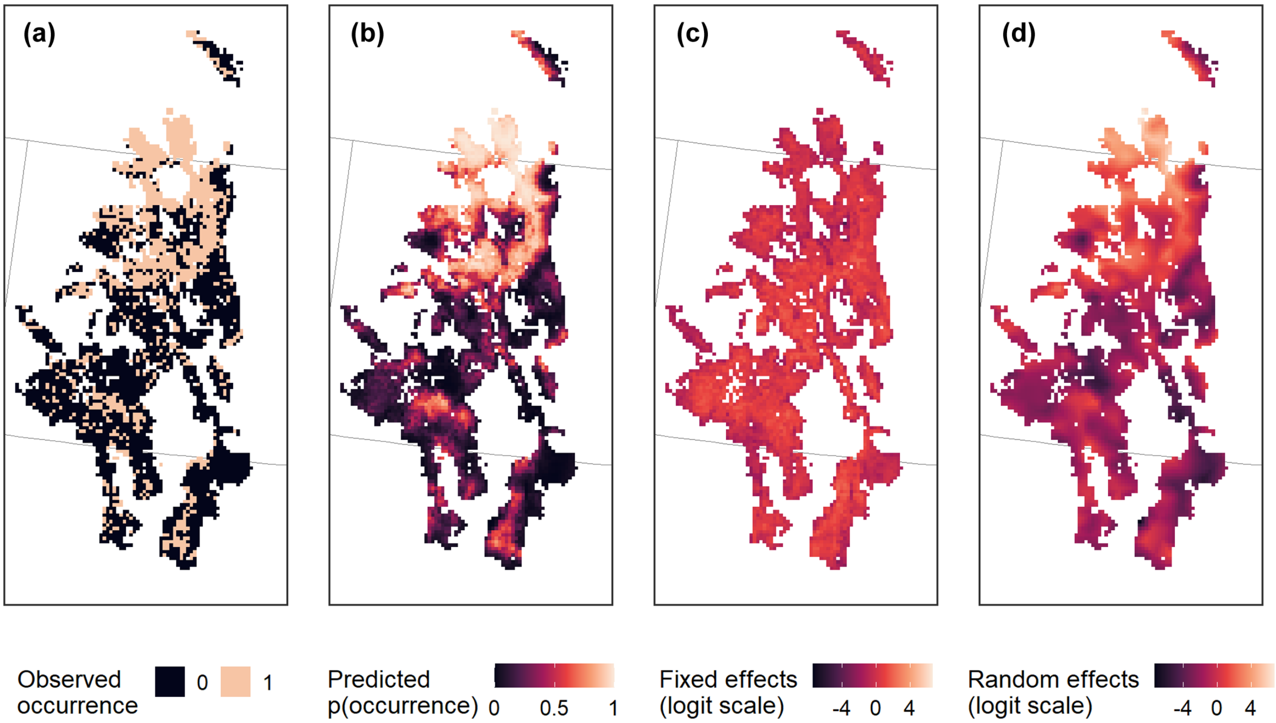

Figure 5. Illustrative comparison of (a) observed hotspot occurrence, (b) predicted probability of hotspot occurrence, (c) fixed effects of all covariates, and (d) random temporal and spatio-temporal effects. Hotspot occurrence in the Southern Rockies in 2007 is shown here as a representative example. Note the visual correspondence between (a), (b), and (d), reflecting the strong influence of spatio-temporal random effects in our models.

eroded due to the spatially synchronous mortality of multiple host tree species. Compared to forest disturbances caused by single biotic agents, overall tree mortality may not necessarily be more severe in areas affected by hotspots (Tutland et al. 2023); however, the mechanisms and rates of forest recovery are likely to be altered (Harvey et al. 2023). Thus, the widespread nature of biotic disturbance hotspots has important implications for forest resilience as climate continues to change and biotic disturbance activity continues to increase.

Forest composition and structure are consistent drivers of biotic disturbance hotspots, while other factors vary with biophysical context

Biotic disturbance hotspots are strongly and consistently driven by the abundance, richness, and spatial distributions of host trees. Even after constraining our analysis to those areas where hotspots could potentially be detected (i.e. surveyed areas where two or more potential host tree species were likely to be present), hotspot occurrence and prevalence increased with host basal area and richness, suggesting that forested areas characterized by a greater amount of host biomass and number of host tree species are most susceptible to biotic disturbance hotspots. Individually, biotic agents are most likely to occur where host tree basal area is high (Shore et al. 2000, Fettig et al. 2007), and it logically follows that the likelihood of overlapping biotic agents is greatest where multiple host species co-occur and host basal area is high. Forest types vary strongly along elevational gradients in each of our study regions, thus our finding that hotspots varied with climate normals also likely reflects the climatic niches of individual host tree species and thus the influence of host species distributions on hotspot occurrence. For example, the most prevalent biotic agents contributing to hotspot occurrence in our study regions were those known to attack pine, fir, and spruce trees (Table 1, Supporting information). Pine, fir, and spruce largely tend to co-occur at higher elevations in our study regions, where climate is characterized by lower summer VPD and winter temperature. Thus, our finding that hotspot occurrence increased in areas characterized by lower winter temperature and summer VPD could be attributed to the increasing overlap of pine/spruce/fir at higher elevations.

The effects of other predisposing and inciting factors were variable, reflecting the unique biophysical characteristics of each region. For example, the variable effects of annual AET (a proxy for plant productivity) across regions likely stems from their differing levels of productivity. The western Cascades are some of the most productive forest ecosystems in the world (Waring and Franklin 1979, Watson et al. 2015, Spies et al. 2018), with greater annual AET and host basal area than both the Middle and Southern Rockies (Supporting information). It is possible that the differing effects of AET observed across our study regions are related to the complex growth–defense tradeoffs that occur in host plants (Herms and Mattson 1992, Kane and Kolb

2010, Vázquez-González et al. 2020). Since tree-killing bark beetles prefer mature hosts with thicker phloem (Amman 1969), high growth rates may increase infestation probability (Cooper et al. 2018) in areas where productivity is generally high. Conversely, in areas where productivity is generally more limited, growth–defense tradeoffs may be amplified (Vázquez-González et al. 2020), and host trees may allocate more resources to defense rather than growth. This tradeoff could potentially explain the positive association between annual AET and hotspots that we observed in the Cascades, a highly productive region, versus the negative and mixed associations observed in the less-productive Middle and Southern Rockies (Watson et al. 2015).

Similarly, our finding that inciting factors (i.e. annual weather anomalies) were most important for predicting hotspots in the Southern Rockies likely stems from the differing climate conditions characterizing each of the study regions. For example, winter minimum temperatures generally increase from the Middle Rockies to the Southern Rockies to the Cascades (Supporting information). Concurrently, overwintering survivorship of tree-killing bark beetles, which as a group are a dominant biotic disturbance agent across all regions, is generally lowest in the Middle Rockies and highest in the Cascades, with the Southern Rockies falling in-between (Bentz et al. 2010). Annual weather anomalies are likely to have a greater influence on biotic disturbance activity in areas where climate straddles important temperature thresholds for bark beetle survival and reproduction (Raffa et al. 2008, Bentz et al. 2010). Thus, it is possible that weather anomalies could be more likely to incite hotspot occurrence in the Southern Rockies where climate conditions suitable to bark beetle outbreak fall within an intermediate range and where proximity to temperature thresholds is therefore important. Although winter minimum temperatures in the Southern Rockies were not likely cold enough during our study period to be lethal to mountain pine beetle (the most common agent contributing to hotspots in this region), warm winter temperatures may also allow for earlier emergence and potential decreases in the duration of subsequent beetle generations, thus providing favorable conditions for beetle population growth (Chapman et al. 2012, Bentz et al. 2014).

Dynamic factors, including outbreak spread, play an important role in shaping biotic disturbance hotspots

The temporal and spatio-temporal random effects estimated in our models contributed strongly to model predictions and closely mirrored observed hotspot patterns and trends, suggesting that dynamic factors such as outbreak spread play an important role in shaping biotic disturbance hotspots. Biotic disturbances are stochastic processes, with local and regional population pressure of biotic agents strongly shaping the dynamics of bark beetle and plant pathogen outbreaks (Raffa et al. 2008, Preisler et al. 2012, Linnakoski et al. 2019, Howe et al. 2021). The strong spatio-temporal correlation in our dataset and high year-to-year persistence of hotspots suggest that biotic disturbance hotspots are also stochastic processes that can emerge as a by-product of the dynamic nature of individual outbreaks. We found that temporal and spatio-temporal random effects were more closely correlated with hotspot occurrence and prevalence than the covariates included in our models, suggesting that the strongest predictor of hotspot occurrence at any given location and time is whether other hotspots occurred nearby or in a previous year.

Each of the three study regions was affected by broad-scale, synchronous bark beetle outbreaks and increasing wildfire activity during our study period (2000–2020), likely contributing to the patterns and trends in hotspots that we observed. In particular, regional outbreaks of mountain pine beetle have been well-documented across the western US in the early part of the 21st century (Raffa et al. 2008, Chapman et al. 2012, Preisler et al. 2012), and mountain pine beetle was a primary contributor to hotspot occurrence across our study regions. The temporal trends estimated in our models, particularly the peaks in hotspots occurring from 2003 to 2008 in the Southern and Middle Rockies (Supporting information), mirror the rapid growth followed by decline in mountain pine beetle populations observed in these regions (Chapman et al. 2012, Meddens et al. 2012). Rapid depletion of available live host biomass with outbreak progression often plays a key role in ending regional-scale outbreaks (Raffa et al. 2008), as sufficient live host trees are necessary to sustain bark beetle populations. Similarly, the spatial legacies of wildfire can strongly shape the likelihood and patterns of bark beetle and pathogen outbreaks, either through host tree injury that may increase host susceptibility to subsequent colonization or infestation, or through host tree mortality that may decrease the availability of live host biomass required for subsequent outbreaks (Simler-Williamson et al. 2021, Howe et al. 2024). Because species-specific and temporally explicit tree biomass estimates are not currently available at the spatial resolutions and extents modeled in our study, we were only able to include one static estimate of host tree basal area in our models. Thus, while we were not able to explicitly account for the loss in live host biomass caused by regional-scale outbreak or wildfire activity, the random effects estimated in our models effectively capture these trends.

Study limitations and directions for future research

Aerial detection surveys provide critical data for broad-scale mapping of biotic forest disturbances but are not without limitations. Despite efforts to standardize data collection procedures (McConnell et al. 2000), aerial sketchmapping is inherently subjective in nature (Johnson and Wittwer 2008). Semi-automated satellite remote sensing approaches offer an improvement over ADS data in terms of spatio-temporal coverage and resolution (Rodman et al. 2021). However, ADS data perform better with respect to damage attribution and offer sufficient accuracy at coarse scales, thus remaining the best available option for monitoring interactions among biotic disturbance agents across regional extents.

We took a broad approach in our analysis, lumping numerous tree-killing biotic agents and host tree species. By design, our results reflect the patterns and drivers of biotic disturbance hotspots generally, rather than specific combinations of biotic agents. Some biotic disturbance agents may be more likely to co-occur in space and time (e.g. agents targeting commonly co-occurring host trees and responding to similar environmental conditions), while others may be less likely to co-occur (e.g. agents targeting less commonly co-occurring host trees, responding to different environmental conditions, and/or functioning as competitors). Therefore, further research could focus on specific combinations of agents that may be of interest, such as the mountain pine beetle and spruce beetle, two species that occur widely throughout North America, tend to co-occur due to the extensive overlap of their host genera, respond similarly to many climatic drivers, and can each cause widespread tree mortality during regional outbreaks (Bentz et al. 2022, Harvey et al. 2023, Andrus et al. 2025). Additionally, we focused on temporally synchronous overlaps of agents that are not expected to be mechanistically linked. Future research could also focus on temporally lagged hotspots that may be occurring due to expected or novel mechanistic links.

Finally, our study focused on regional-scale patterns and trends. We identified biotic disturbance hotspots at a coarse spatial resolution (i.e. co-occurrence within 510-m or 26-ha grid cells, further aggregated to 5.1-km or 2600-ha grid cells) to reduce model complexity and enable modeling these patterns over broad spatial extents. Our methodology harnessed a variety of data products to represent potential drivers of hotspots (i.e. forest composition, topography, climate, and weather), which required aggregating these data to a common spatial scale. The process of aggregating or 'coarse-graining' data has the potential to result in a loss of information, in particular an inability to account for extreme events or conditions occurring at finer scales, and is a common challenge in balancing tradeoffs between model grain and extent (Newman et al. 2019). Complementary research at finer spatial scales will be important for further elucidating the mechanisms driving hotspots and the ways in which forests respond.

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Author contributions

Michele S. Buonanduci: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Project administration (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Sarah J. Hart**: Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal). **Patrick C. Tobin**: Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal). **Brian J. Harvey**: Conceptualization (equal); Funding acquisition (equal); Project administration (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data and code are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.15398140.

Supporting information

The Supporting information associated with this article is available with the online version.

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