communications earth & environment

Article

A Nature Portfolio journal

https://doi.org/10.1038/s43247-026-03301-9

Future climate will not save high-elevation white pines

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Diseases are threatening forests worldwide. In North America, white pine blister rust (WPBR) is one of the most damaging tree epidemics. To understand patterns in the current and future risk for high-elevation five-needle white pine species (High-5), we compiled data from independent studies across the western U.S. to estimate WPBR risk. Contrary to previous predictions, the future climate is not expected to reduce the prevalence of WPBR risk on High-5 species in the western U.S. The prevalence of WPBR is predicted to increase, with most distributions of the High-5 species projected to experience elevated WPBR prevalence over the next century. Temperature and moisture conditions ensure that while some newly invaded areas are projected to experience regular periods of elevated risk, others can expect intermittent episodes of high risk. Restoration in impacted areas and proactive management in regions at increased risk are warranted to ensure High-5 population sustainability and ecosystem function.

Climate change poses a significant threat to ecosystems by altering environmental conditions that affect plant disease risk[1–5]. Rising temperatures, shifting precipitation patterns[5–7], and elevated atmospheric CO_2 levels may create conditions that favor or hinder the spread and pathogenicity of plant pathogens[5,8,9]. Shifting the location of climate optima in space, climate change will lead to changes in patterns of disease prevalence[10–12]. Globally, diseases are increasingly threatening natural and managed forests[13]. As a result, there is a pressing need to understand the specific mechanisms by which future climate influences plant disease dynamics, including changes in pathogen distribution and host susceptibility, as well as interactions with insect vectors. Here, we evaluate disease prevalence across large geographic ranges to understand the potential for future climate-induced changes in forest disease risk.

High-elevation five-needle white pine (High-5, hereafter) forests in the United States (U.S.) are characterized by pines that thrive in harsh, high-altitude environments. These forests are found throughout the mountainous areas of the western U.S. and can include whitebark pine (*Pinus albicaulis* Engelm.; PIAL), limber pine (*P. flexilis* James; PIFL2), southwestern white pine (*P. strobiformis* Engelm.; PIST), Rocky Mountain bristlecone pine (*P. aristata* Engelm.; PIAR), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey; PILO), and foxtail pine (*P. balfouriana* Grev. & Balf.; PIBA). The High-5 tend to be slow-growing and long-lived, often having a disproportionately large effect on ecosystem function and biodiversity relative to their abundance (i.e., serving as keystone species) and defining ecosystem structure and functional dynamics (i.e., serving as foundation species)[14]. Tree mortality in High-5 forests over the past decades has been attributed primarily to the disease white pine blister rust (WPBR) and climate-driven increases in drought stress, mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) outbreaks, and changing fire regimes[15,16].

Caused by the pathogenic fungus *Cronartium ribicola* (J.C. Fischer ex Rabh.), WPBR is one of North America's most damaging tree diseases[17,18]. Since the pathogen's introduction to western North America around 1910 in the Pacific Northwest[19], *C. ribicola* continues to spread and infect new populations of white pines[20] as primary hosts. *Ribes* spp. (Grossulariaceae) and forbs in the family Orobanchaceae are alternate hosts that the pathogen requires to complete its life cycle[21]. Each of the High-5 species has been infected in at least a portion of their natural distributions, except the Great Basin bristlecone pine[16]. Nevertheless, in controlled inoculation studies, Great Basin bristlecone pine was susceptible to the disease[16]. The impacts of WPBR were the primary driver for the recent listing of whitebark pine as threatened under the Endangered Species Act[22].

Climate influences the dynamics of WPBR through its effects on the interactions between the pathogen, host plants, and environmental conditions[1,16,23,24]. The number and frequency of *C. ribicola* infections in pine hosts, as well as disease severity, are not uniform across the landscape. This is

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due in part to the distance from the point of introduction, the biology of the pathogen and its hosts, and the environmental conditions required for successful spore production, transport, germination, and infection. *Cronartium ribicola* is an obligate biotroph with a complex life cycle that involves five spore stages and two hosts; there is no tree-to-tree transmission[18]. Each of the five spore stages has specific temperature and moisture requirements for development, dissemination, and germination[19,25–28]. The disease spreads rapidly through host ranges in the moist forests of the northwest and northern U.S. Rocky Mountains. It continues to spread, albeit more slowly, into the drier habitats of the southern Rocky Mountains, the Great Basin, and the southwest[29].

It has been hypothesized that warmer and drier conditions would reduce the prevalence of WPBR, as the pathogen requires cool, moist conditions to facilitate infection[1,18,30]. Consistent with this hypothesis, studies in the Rocky Mountains have found that trees in more arid habitats are less likely to be infected with WPBR[31,32]. However, for trees already infected in areas experiencing increasing aridity, the likelihood of developing severe symptoms and mortality increases[32]. In contrast, Dudney et al. (2021)[7] proposed that increased aridity contributed to an uphill shift of WPBR in the Southern Sierra Nevada Mountains. Additionally, warming temperatures may exacerbate WPBR in moist habitats by extending the growing season, allowing for greater canker expansion[33] and a longer infectious season[34]. These findings suggest that the effects of climate change on WPBR prevalence and severity are likely to be an outcome of complex interactions between environmental factors and the biology of the pathogen and hosts[16,29].

Past studies suggest that WPBR in trees may have reached the limits of the outbreak due to climatic conditions[1,30,35], while others suggest suitable conditions exist beyond the current WPBR distribution[36]. While disjunct disease infection centers have occurred, providing evidence for at least occasional long-distance spore dispersal[37–39], the predominant advancement of the disease across western North America is a pattern of contiguous spread from the point of introduction in the Pacific Northwest over time[29]. This progression of disease on western North American pine hosts suggests a dominance of local spore dispersal punctuated by several long-distance infection events[29,32,40]. While data on the density of *C. ribicola* spores in forests across western North America are lacking, it is expected that higher quantities of *C. ribicola* spores are likely in areas with a greater number of locally diseased hosts and active sporulation than in areas with lower disease prevalence and therefore lower inoculum levels. Experimental data reveal a dose-response relationship between spore density and infection frequencies for both host types under ideal infection conditions[41,42]. Consequently, in addition to climatic factors, limited inoculum availability may currently play a role in southern locations where WPBR prevalence is low[36].

The primary objective of our study is to understand the conditions that have contributed to the prevalence of WPBR in whitebark pine and across all High-5 species, and to determine whether these conditions are likely to reduce or increase disease incidence in the future. With both the primary (i.e., white pines) and secondary (e.g., *Ribes spp.*) host groups co-occurring throughout the High-5 range and low disease resistance in white pines, the major determinants of risk are the prevalence of inoculum[43] and the conditions associated with spore production, dispersal, and host infection[44].

We evaluated disease occurrence across the western U.S. to understand where and when suitable conditions for WPBR will decline or become enhanced in the near future (2030-2099). We estimate the risk of WPBR for areas where we have observed low disease incidence and presumed low inoculum, and for regions where the disease was established at higher levels and inoculum was assumed to be high (Fig. 1)[45]. We focus on the current distribution of the High-5 species, which can be divided into areas where the disease is invading (INV) or established (EST). Here, the difference between invading and established WPBR was determined by observed disease prevalence[16,29]. We defined invading regions as those characterized by low WPBR prevalence, likely due to a combination of a low inoculum and conditions that limited disease on the pines. Established areas were characterized by high WPBR prevalence and presumed inoculum levels. Although both invading and established characteristics occur at small scales across the High-5 landscape, ecoregions were delineated based on patterns of WPBR prevalence observed at larger scales (~ 10-20 km). In addition to a model for each of the two geographic areas based on observed disease prevalence, we also parameterized models with different ranges in climate data based on the forest health assessment date. Seasonal means for 5-, 10-, or 20-year climate periods preceding the assessment date were explored, recognizing that the timeframe influencing disease susceptibility is complex and has yet to be defined.

The disease, WPBR, kills trees of all ages and has had a profound impact on the white pine forestry industry[35,46]. Impacts on high-elevation white pine species in mountain and treeline landscapes are now recognized as jeopardizing watershed health and biodiversity[14,18,35]. *Cronartium ribicola* is widespread across North America following unsuccessful eradication attempts[18,35,47]. A commitment to managing whitebark, limber pine, and the other High-5 species is warranted and requires the development of tools that integrate information about the disease across regions. Estimates of future WPBR risk can aid in tailoring management treatments for greater efficacy.

Results

Risk models indicate the probability of observing conditions suitable for WPBR in areas with an observed low ($P(WPBR)_{INV}$) or high ($P(WPBR)_{EST}$) prevalence of WPBR. Models for both the invading and established regions were also developed using climate summaries for the 5, 10, or 20 years prior to the WPBR assessments. Risk ranged from 0 to 1, with higher values indicating conditions more suitable for WPBR on trees. Model performance, measured by the area under the curve (AUC), ranged from 0.67 to 0.96, and the accuracy of detecting WPBR, when present, ranged from 76 to 99% for the training data and 71 to 94% for the test data. The mean square error was similar across climate summaries and was lower for the $P(WPBR)_{INV}$ compared to the $P(WPBR)_{EST}$. Model accuracies were higher for the $P(WPBR)_{INV}$ compared to the $P(WPBR)_{EST}$. The prevalence of WPBR was significantly lower in the Invading dataset than in the Established dataset, and this difference, combined with variation in sample sizes,

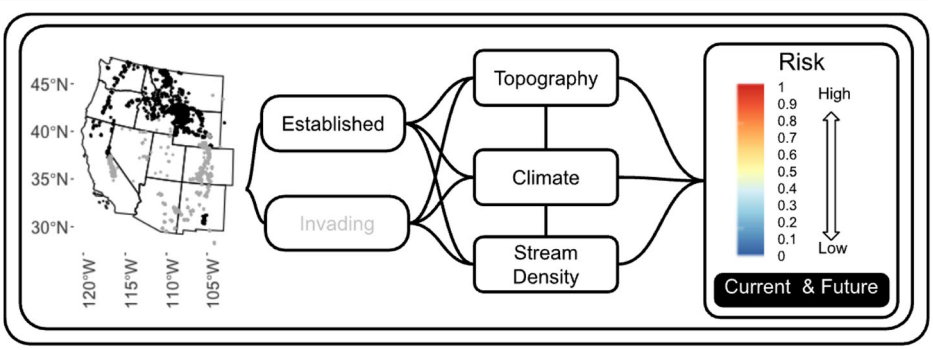

Fig. 1 | The project workflow. The presence and absence of WPBR have been recorded in regions where the presumed inoculum was low (gray) and high (black). Studies have shown that climatic conditions can play a significant role in disease incidence[1,18,30] and could be useful in determining current and future risk.

Table. 1 | Model performance for the P(WPBR)

Models:	$P(WPBR)_{INV}$			$P(WPBR)_{EST}$		
Performance	5 (Yrs)	10 (Yrs)	20 (Yrs)	5 (Yrs)	10 (Yrs)	20 (Yrs)
OOB MSE	8.95	7.81	7.23	28.87	21.09	17.54
AUC	0.84	0.96	0.96	0.67	0.83	0.83
Test Accuracy	99%	99%	99%	76%	97%	97%
Training Accuracy	88%	94%	91%	71%	79%	82%

The performance of models that were parameterized with data from regions with low ($P(WPBR)_{INV}$) and high ($P(WPBR)_{EST}$) prevalence of WPBR.

topographic and regional distribution of samples, and climate patterns, justified the use of separate models. Across models, both short-term (5 and 10-year) and long-term (20-year) climate summaries were important and showed consistent patterns (Table 1).

Stream density (STREAM_DEN), topography, hardiness zone (H_Zone), precipitation (PRCP), air temperature (T), vapor pressure deficit (VPD), and relative humidity (RH) were included in both $P(WPBR)_{INV}$ and $P(WPBR)_{EST}$ models (Table 2 and Fig. 2). Short-term effects on $P(WPBR)_{INV}$ were dominated by fall PRCP, while spring, summer, and fall climates were more influential for the 10 and 20-year climate windows. Summer PRCP, spring Tmin, and fall VPD were important in some $P(WPBR)_{EST}$ models.

The relationship between the P(WPBR) and climate variables for both the Invading and Established models generally indicated that probabilities increased with moisture and decreased with temperature (Supplementary Fig. 1). The P(WPBR) increased with stream density, precipitation, and vapor pressure deficit. Hardiness zone and air temperature were negatively correlated with the P(WPBR) (Supplementary Fig. 1). The highest risk was at VPDs of approximately 700 Pa and 1400 Pa, and the P(WPBR) declined at lower and higher VPDs in both models. The drivers of the $P(WPBR)_{INV}$ and the $P(WPBR)_{EST}$ were similar but exhibited differences in their magnitude and sensitivity to topography and climate. The magnitude of the $P(WPBR)_{INV}$ was half the $P(WPBR)_{EST}$. Although the $P(WPBR)_{INV}$ declined with RH, the $P(WPBR)_{EST}$ increased with RH. The $P(WPBR)_{INV}$ was most sensitive to topography, minimum temperature, and VPD, and the $P(WPBR)_{EST}$ was most sensitive to stream density, precipitation, and RH. The differences in the primary drivers of $P(WPBR)_{INV}$ and $P(WPBR)_{EST}$ (Table 2) suggest that WPBR dynamics differ between the established and invading regions, where there were notable differences in the current prevalence of WPBR. Altogether, the models' performance indicated that landscape attributes and climate could be used to understand conditions that supported WPBR prevalence at the landscape scale, which differ across the two regions.

P(WPBR) Across the High-5 Range

The probability of observing conditions suitable for WPBR from 1980 to 2023, across the High-5 landscape, differed between the $P(WPBR)_{INV}$ and $P(WPBR)_{EST}$ models (Fig. 2). The $P(WPBR)_{INV}$ was below 0.5 for all of the southern High-5 range (1980-2023), and the $P(WPBR)_{EST}$ was greater than 0.6 for the majority (97%) of the High-5 range (Fig. 2a, b). The standard deviation among the models developed using 5, 10, and 20-year climate data was low (0-0.2) for both $P(WPBR)_{INV}$ and $P(WPBR)_{EST}$ (Fig. 2c, d). Given consistent model performance across climate summaries (5, 10, and 20 years) and low variability across climate summaries (Fig. 2c, d), results are presented as ensembles of models developed with the contemporary climate for both the invading and established models. Comparing the $P(WPBR)_{INV}$ to the $P(WPBR)_{EST}$, where the two models overlap, there was a significant positive correlation ($R^2 = 0.1$; $P < 0.001$). The high (> 0.5) $P(WPBR)_{EST}$ across the entire U.S. High-5 range suggests that if inoculum becomes widely abundant in the southern landscapes, conditions would be conducive to WPBR across the entire range.

Table. 2 | Variable importance for P(WPBR)

Models:		$P(WPBR)_{INV}$			$P(WPBR)_{EST}$		
Variables		5 (Yrs)	10 (Yrs)	20 (Yrs)	5 (Yrs)	10 (Yrs)	20 (Yrs)
STREAM_DEN (Km Km^{-2})		X			X		
H_ZONE			X				
TPI		X	X				
TRI		X			X		
PRCP (mm)	spring		X	X		X	
	summer		X			X	X
	fall	X					
Tmax (°C)	spring		X	X			X
	summer						
	fall					X	X
Tmin (°C)	spring		X			X	X
	summer		X	X		X	
	fall		X	X	X	X	
VPD (Pa)	spring						
	summer		X	X		X	X
	fall		X		X	X	X
VPDmax (Pa)	spring						
	summer		X	X			
	fall		X			X	
RH (%)	spring		X			X	X
	summer		X				X
	fall		X	X	X		

Important variables for models parameterized with data from regions with low ($P(WPBR)_{INV}$) and high ($P(WPBR)_{EST}$) WPBR prevalence.

Future P(WPBR) Across the High-5 Range

From 2030 to 2099, $P(WPBR)_{INV}$ ranged between 0.01 and 0.75 (Fig. 3). Although less than 2% of years had a mean annual $P(WPBR)_{INV}$ greater than 0.5 across the southern portion of the U.S. High-5 range, the average increased by 4% compared to the mean for 1980-2023, while the minimum increased by 28%. The $P(WPBR)_{EST}$ ranged from 0.3 to 0.8 from 2030 to 2099 (Fig. 4), and the mean annual average across the southern portion of the U.S. High-5 range increased by ~ 2% compared to the average for 1980-2023. Both models indicate that increased precipitation, combined with changes in temperature, VPD, and RH, will enhance the risk of WPBR in the future.

The mean annual $P(WPBR)_{INV}$ varied between 2030 and 2099 with climate patterns and peaked between 2024 and 2050 (Fig. 3a). The Southern Rockies, the Great Basin, and the Southern Sierra Nevada consistently had higher average $P(WPBR)_{INV}$ relative to the Southwest (Fig. 5b). The mean annual $P(WPBR)_{INV}$ for the species ranges were indicated by the areas they occupied. The risk for PIBA and PIAL was the highest, followed by PIFL2, PILO, and PIAR; PIST was consistently lower (Fig. 5). Although the mean annual $P(WPBR)_{INV}$ was low across the southern portion of the U.S. High-5 range ($P(WPBR) < 0.5$), there were increases projected for the future for most regions and species.

Unlike $P(WPBR)_{INV}$, $P(WPBR)_{EST}$ was elevated ($P(WPBR) > 0.5$) across the High-5 (Fig. 5). The mean annual $P(WPBR)_{EST}$ declined between 2030-2050 and began increasing between 2070-2099 (Fig. 4a). The WPBR risk was highest for PIAL, PIAR, and PIFL2 ranges associated with the Crown of the Continent, Pacific Northwest, Greater Yellowstone Ecosystem, and Southern Rockies. For both models, PIST maintained the lowest risk. The $P(WPBR)_{EST}$ was higher in the north compared to the southern areas of the U.S. High-5 range. The average

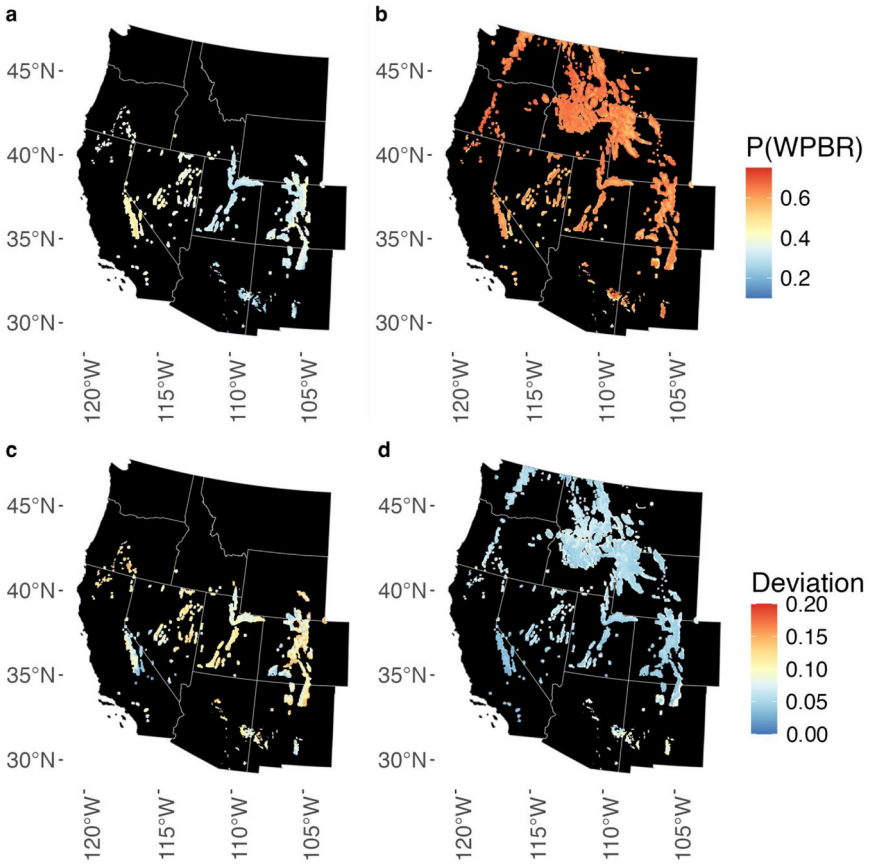

Fig. 2 | The probability of WPBR in the western U.S. from 1980 to 2023. The mean ensemble estimates of the probability of WPBR from models parameterized with data from (**a**) areas with low ($P(WPBR)_{INV}$) and (**b**) high ($P(WPBR)_{EST}$) observed prevalence of WPBR. The standard deviation in (**c**) $P(WPBR)_{INV}$ and (**d**) $P(WPBR)_{EST}$ across the High-5 range among models developed with 5-, 10-, and 20-year climate windows was low in the western U.S. from 1980 to 2023.

$P(WPBR)_{EST}$ for the southern areas was greater than that projected by $P(WPBR)_{INV}$.

Elevated Risk

We evaluated the proportion of the landscape at an elevated risk (P(WPBR) > 0.5) annually to understand the temporal dynamics of landscape risk across regions and species distributions (Supplementary Fig. 2). A percentage of the southern High-5 landscape showed elevated $P(WPBR)_{INV}$ 2030 - 2099, with an average of 13% (10 S.D.) with elevated risk annually and a minimum of ~1% of the landscape falling into the elevated risk category in any given year (Fig. 6a). Infrequently, the percentage of the landscape with elevated $P(WPBR)_{INV}$ reached 59% of the southern High-5 U.S. range (Fig. 6a).

The average proportion of the U.S. High-5 distribution at elevated $P(WPBR)_{EST}$ ranged from 72% to 99% (Fig. 6a). Elevated $P(WPBR)_{EST}$ was also not distributed evenly across the southern portion of the U.S. High-5 range (Supplementary Fig. 3). In the Crown of the Continent, Greater Yellowstone Ecosystems, Pacific Northwest, and the Southern Rockies, an elevated risk was projected to affect > 99% of the High-5 distribution in peak years (Supplementary Fig. 3). Uniquely, the Southwest High-5 range exhibited the greatest year-to-year variation in the proportion of the land area projected to be at elevated risk for $P(WPBR)_{EST}$, ranging from 10% to 98%, suggesting that local wave-year patterns of infection were prominent (Supplementary Fig. 3f).

Elevated risk also varied across species' ranges (Supplementary Fig. 4). All High-5 species in the southern portion of the U.S. High-5 were projected to have some part of their distribution encounter conditions conducive to infection this century for both the $P(WPBR)_{INV}$ and the $P(WPBR)_{EST}$. With the $P(WPBR)_{INV}$, all species experienced high year-to-year variation in risk, with the PIBA and PIAL distributions showing strong positive trends. The lowest $P(WPBR)_{INV}$ was observed for the PIST range, corresponding to patterns observed over the Southwestern High-5 range. With the $P(WPBR)_{EST}$, PIST was projected to experience significant year-to-year variation in risk, with less than 25% and up to 99% of its distribution exposed to elevated risk in any given year. A lower percentage of the U.S. PIST distribution was at elevated risk for WPBR than any other High-5 species. In the western U.S., each High-5 species was projected to experience at least one year with conditions conducive to elevated $P(WPBR)_{EST}$ across 75-100% of their distributions this century (Supplementary Fig. 4).

Refugia

Although there were areas with persistently elevated risk, locations that did not experience high risk until the future were indicative of potential High-5 WPBR refugia (Fig. 7). If the disease expands into them at sufficient levels, most of these areas were projected to have conditions conducive to supporting the development of elevated $P(WPBR)_{EST}$. If WPBR were to become established across the entire High-5 range, refugia would become ephemeral. Similarly, some areas may serve as short-term High-5 refugia, consistently exhibiting low $P(WPBR)_{INV}$. Still, if the disease prevalence increased, they might no longer be considered low-risk based on the $P(WPBR)_{EST}$ (Fig. 7). Alternatively, some areas are projected to have fewer wave-years of high risk than others (Fig. 6b,c) and may also serve as WPBR refugia for High-5. While all regions are projected to be exposed to at least one episode of elevated risk this century, some areas have a potential for High-5 refugia from WPBR in the U.S, which may occur at a smaller scale in the future.

Discussion

The disease WPBR poses substantial risks across the High-5 landscapes, varying regionally and by species, as well as over time. While the $P(WPBR)_{INV}$ explored risk in landscapes with currently low prevalence of WPBR due to a combination of conditions that may be inhibiting the spread of the disease on trees and potentially low inoculum levels, the $P(WPBR)_{EST}$ showed concerning probabilities for areas currently with high WPBR

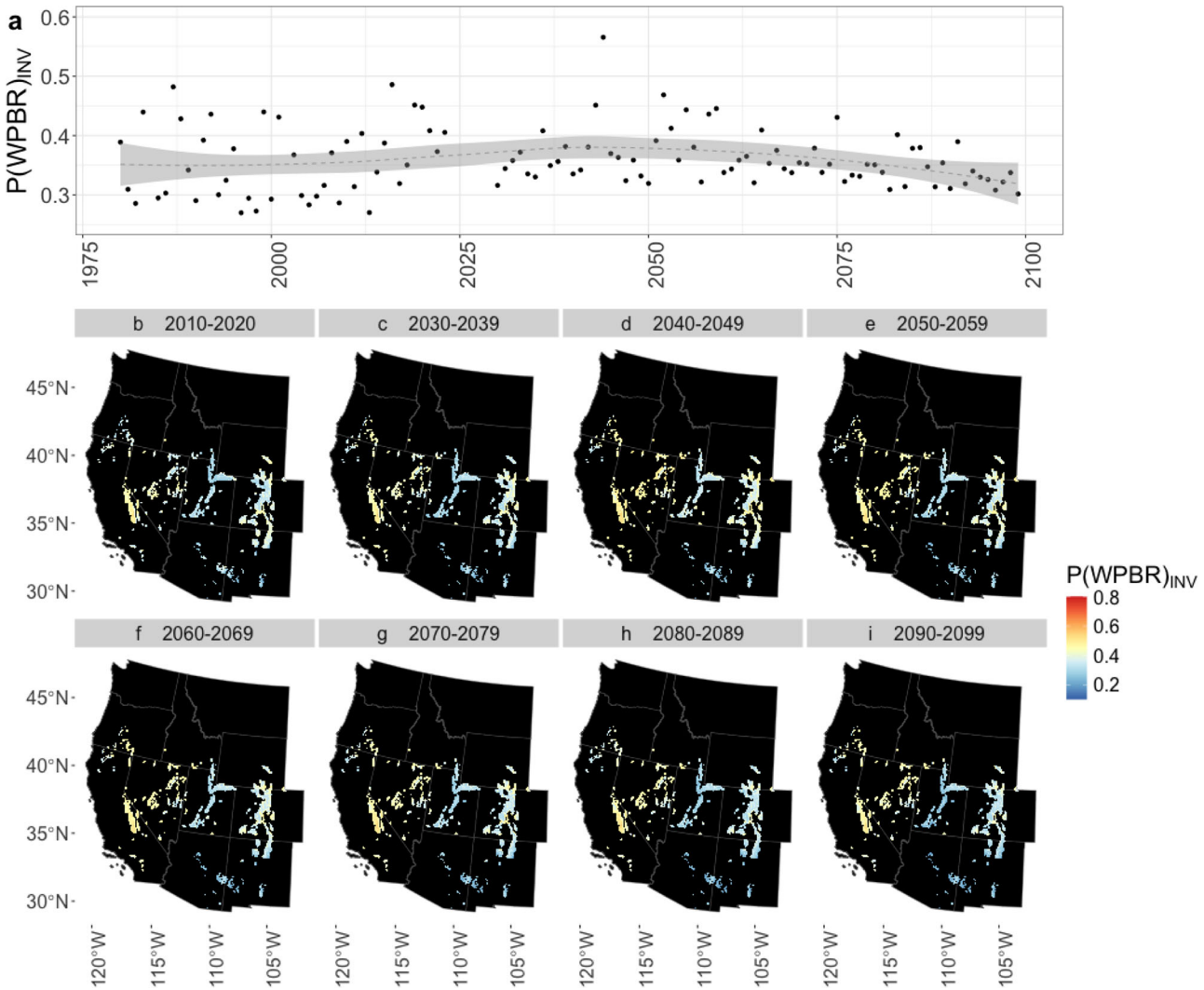

Fig. 3 | The $P(WPBR)_{INV}$ in southern portion of the western U.S. from 2010 to 2099. The (**a**) average ensemble annual estimates of WPBR risk for areas with low prevalence of WPBR ($P(WPBR)_{INV}$) for the southern portion of the U.S. High-5 range and the average decadal risk in (**b**) 2010- 2020, (**c**) 2030 s, (**d**) 2040 s, (**e**) 2050 s, (**f**) 2060 s, (**g**) 2070 s, (**h**) 2080 s, and the (**i**) 2090 s.

prevalence, where inoculum was unlikely to be limiting disease risk. Regardless of presumed spore exposure, both WPBR risk models demonstrated that suitable climatic conditions exist beyond the current WPBR distribution. This aligns with the expectation that WPBR will eventually fill its climatic niche, which these analyses suggest includes most of the High-5 U.S. distribution, despite the current distribution[36,48,49]. The $P(WPBR)_{INV}$ may be more realistic in regions where disease prevalence is low, and the $P(WPBR)_{EST}$ is likely a worst-case scenario for a future where prevalence becomes high across all ecoregions. Although future climates do not reduce the prevalence of conditions conducive to WPBR on high-elevation white pine species in the western U.S, localized areas of consistently low projected WPBR risk, and areas that may be exposed to only infrequent episodes of high risk, may serve as refugia, albeit possibly ephemerally, from severe WPBR impacts even if management interventions are not implemented.

Drivers of WPBR Risk

The risk of WPBR as modeled was driven by climatic conditions and topography across the western U.S[1,18,30] and shown to differ across areas with current low ($P(WPBR)_{INV}$) and high ($P(WPBR)_{EST}$) disease prevalence. Given the interacting components of the pathogen, the environment, primary pine hosts, and secondary *Ribes* hosts, it is essential to consider the influence of topographic and climatic variables on the entire disease system. Free water or saturated air is required for spore germination and infection at specific times in the disease cycle[27], which is consistent with the sensitivity of P(WPBR) to precipitation, relative humidity, and VPD. Yet the relationship with precipitation was complex, given that frequent and hard rains can wash spores away prior to infection events, suggesting a nonlinear relationship. High temperatures are also known to constrain spore production and germination[27]. Temperatures above approximately 28 °C generally limit spore germination[27], consistent with a negative correlation between temperature and P(WPBR).

The first WPBR spore stage occurring on the secondary hosts, e.g., *Ribes*, is often referred to as the repeating stage, as urediniospores can reinfect other *Ribes* throughout the growing season, building up inoculum that transitions to the teliospore stage and finally the basidiospore stage, which infects pines[18]. Stream density is a reasonable proxy for *Ribes* density since several susceptible species grow in riparian and streamside habitats[36]. Therefore, the significance of stream density to P(WPBR) likely reflects a higher prevalence of susceptible *Ribes* plants as well as the conditions conducive to spore production on those hosts. Similarly, variation in topographic terrain ruggedness is a reasonable indicator or proxy for microenvironment frequencies that favor conditions such as cool air pockets and prolonged moisture durations, as well as a wider range of microsites for hosts.

Rust pathogens grow and obtain nutrients only from living, vigorous host plants, so factors that favor the growth of susceptible hosts also

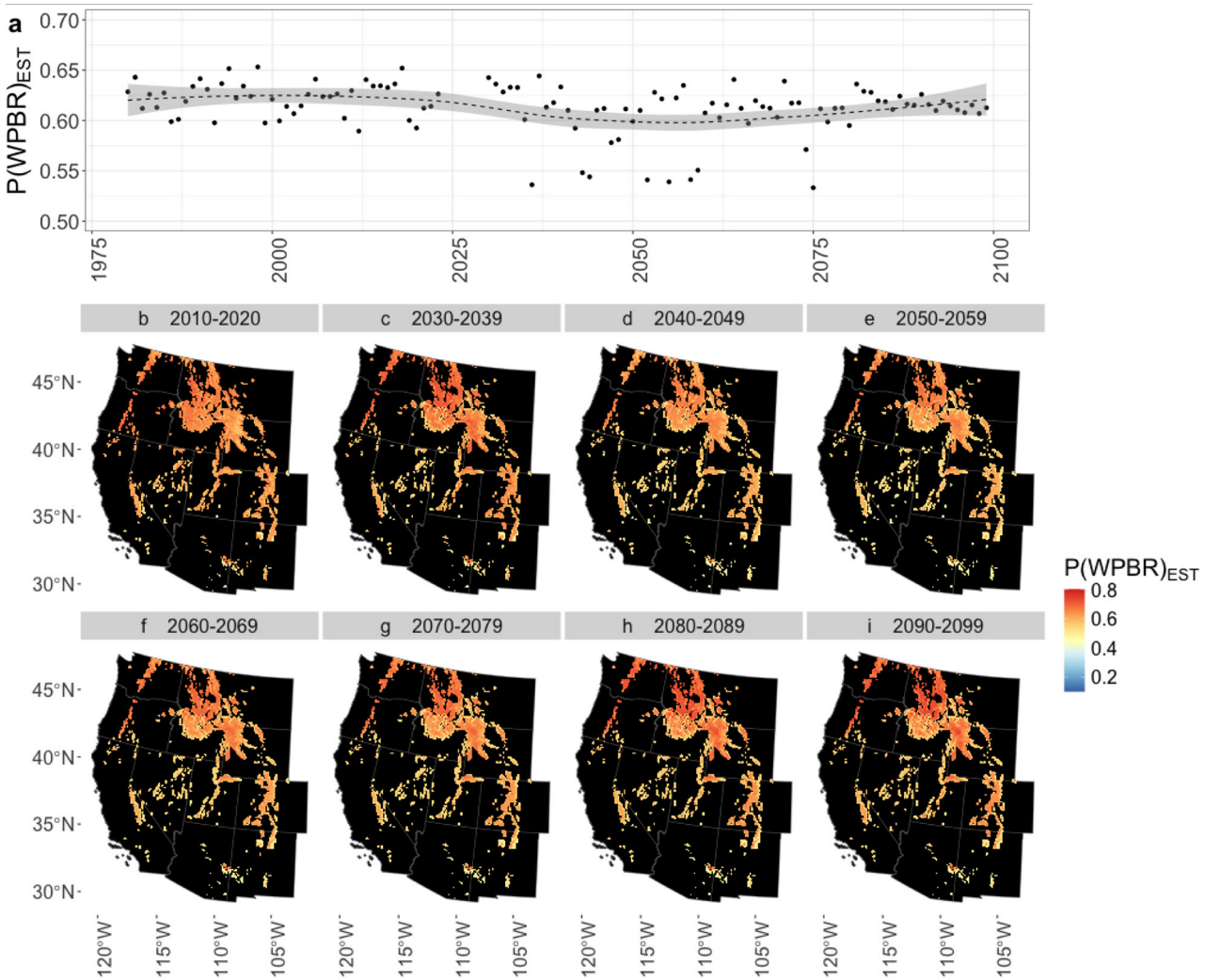

Fig. 4 | The $P(WPBR)_{EST}$ in the western U.S. from 2010 to 2099. The (**a**) average ensemble annual estimates of WPBR risk ($P(WPBR)_{EST}$) for the entire U.S. High-5 range, and decadal average of risk in (**b**) 2010- 2020, (**c**) 2030 s, (**d**) 2040 s, (**e**) 2050 s, (**f**) 2060 s, (**g**) 2070 s, (**h**) 2080 s, and the (**i**) 2090 s.

support pathogen development. Vapor pressure deficit directly influences the growth of trees and shrubs, as do topographic variables[50]. The high value of P(WPBR) at a VPDmax of approximately 1400 Pa could reflect conditions that are favorable to pine host growth and density, given that 1400 Pa reflects a moderate evaporative demand and good growing conditions for plants[50].

While climate and topography have a significant impact on risk, the magnitude and persistence of WPBR into the future will be determined by both inoculum levels and the capacity to support sufficient disease prevalence to establish the disease across large regions. For this to occur annually, conditions must be met for each spore stage, including the infection of pines. While the disease is perennial and progressive on the pines, *C. ribicola* colonization is limited to the deciduous leaves of the alternate hosts and is shed with leaf abscission each autumn. Therefore, the alternate hosts must be newly infected each year for basidiospore production in late summer for new pine infections to occur. Infection of the alternate hosts with aeciospores, followed by the sequence of conditions suitable for basidiospore formation and pine infection, must all occur during a single growing season. If the alternate host infection occurs in an otherwise disease-free area, and subsequent environmental conditions favor basidiospore production and pine infection, the pathogen introduction becomes established as perennial mycelium in pine tissues; if not, the local pathogen population goes extinct[35]. A failed *C. ribicola* founding event was suspected to have occurred in Utah, where Ribes infections were observed, yet no subsequent disease was detected on pines[39]; WPBR has still not been found on pines in the state[16]. In contrast, the founding of a disjunct infection center in southern New Mexico spurred a rapid intensification of the disease, suggesting that inoculum availability rather than environmental conditions had previously limited WPBR presence in the area[35]. The risk of infection of the pine host is associated with a sequence of suitable environmental conditions that lead to basidiospore abundance, which in turn is a function of initial aeciospore availability[43].

Wave-Years

Counter to prior predictions[1,30], future climate will unlikely impede the pathogen's advancement and intensification if disease prevalence and, therefore, inoculum becomes sufficient to establish the disease across the entire High-5 range. As the pathogen spreads, all regions face at least one episode of elevated WPBR risk across the southern U.S. High-5 range before 2099, even in areas currently with low disease prevalence. Our models reveal considerable interannual variation in large-scale elevated WPBR risk, suggesting wave years could become more frequent, especially in some regions. Most regions experienced large-scale elevated WPBR risk nearly annually. In contrast, the Southwest was projected to exhibit a more pronounced pattern of wave-years, with less frequent large-scale elevated risks of new infections. As pine hosts experience more frequent wave years, the accumulation of infections will result in an increase in disease severity and mortality[32]. In areas already severely

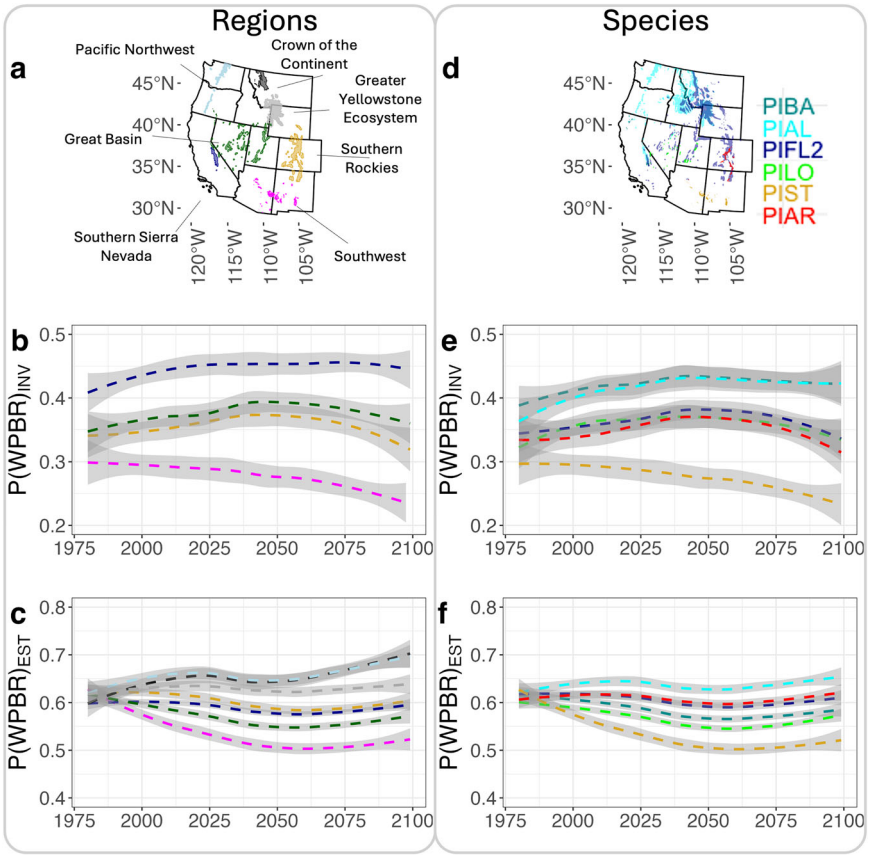

Fig. 5 | The mean annual probability of WPBR in the western U.S. from 1980 to 2099. a Focal High-5 regions and smoothed trend (loess) in (**b**) $P(WPBR)_{INV}$ and (**c**) $P(WPBR)_{EST}$ for each region. **d** High-5 species ranges and smoothed trend (loess) in (**e**) $P(WPBR)_{INV}$ southern portions of each species range and (**f**) $P(WPBR)_{EST}$ for each U.S. species range. The susceptible High-5 white pines include whitebark pine (*Pinus albicaulis* Engelm.; PIAL), foxtail pine (*Pinus balfouriana;* PIBA), limber pine (*Pinus flexilis* James; PIFL2), Great Basin bristlecone Pine (*Pinus longaeva*; PILO), southwestern white pine (*Pinus strobiformis* Engelm.; PIST), and Rocky Mountain bristlecone pine (*Pinus aristata*; PIAR).

impacted, climate change offers little reprieve from elevated disease prevalence this century, though minor risk reductions may facilitate strategic restoration efforts later.

Refugia

The High-5 species are projected to experience differential effects of climate change depending on the level of WPBR and the associated risk in the future. Although the risk is widespread, some isolated areas remain at low risk, or are projected to have infrequent wave years of elevated risk, and may serve as WPBR refugia for the High-5. Refugia occur in dispersed, isolated locations throughout the High-5 distribution where conditions render the environment less suitable for the disease in most years[35]. These areas of refugia may not coincide with those that offer refuge to the High-5 species from the direct impacts of climate change. The refugia along the trailing edge of a species' range are most vulnerable to range contractions as environmental conditions exceed the species' physiological tolerances[51,52]. Among the High-5, southwestern white pine is the exception, as its core distribution is in Mexico, and some areas of WPBR refugia are projected in the northern extent of its range in the Southwestern U.S., provided inoculum levels remain low. However, Shirk et al. (2018)[53] project that the southwestern white pine populations in Arizona and New Mexico will be extirpated in the future except for a few high-elevation climate refugia. Rocky Mountain bristlecone pine may be capable of occupying the southwestern WPBR refugia areas with future climatic suitability, potentially enabling colonization if seed dispersal is sufficient to facilitate migration[54] or with human-assisted migration. Limber pine in the Great Basin has been observed tracking cold air drainages, migrating downslope into ravines as temperatures rise[55]. Unfortunately, these cool, moist habitats favor the growth of WPBR's alternate hosts and may not be WPBR refugia as the disease spreads[16,56].

Management Implications

Management actions that are most likely to succeed in mitigating WPBR impacts and promoting High-5 population sustainability will depend, in part, on current and future levels of WPBR[57,58]. Proactive and restoration strategies have been developed for the High-5[57,59,60]. Both have the same long-term management goal of sustaining, restoring, and promoting self-sustaining, evolutionarily stable pine populations in the presence of WPBR and other stressors, thereby supporting ecosystem processes and services into the future. Proactive strategies promote pine regeneration to increase population size, genetic diversity, and adaptive capacity to maintain forest health in areas currently with low WPBR prevalence and presumed low *C. ribicola* inoculum[58,61]. Alternatively, restoration strategies target impacted populations to re-establish viable pine populations, natural processes, and ecosystem services[57,60,62]. For both types of management strategies, interventions can include regenerating stands through planting or direct seeding; identifying, developing, and deploying WPBR-resistant seed sources; and implementing silvicultural treatments to increase resilience (e.g., generating a diverse mosaic of stand ages across a landscape to enhance forest adaptation and mitigating pine mortality by other factors)[16,60,62]. However, some treatments are less effective in populations highly impacted by WPBR. For example, in stands with high overstory mortality by WPBR, treatments relying on natural regeneration processes will be constrained by limited seed availability and high seedling mortality[63], and some mechanisms of genetic resistance to WPBR in planting stocks can be less effective under high WPBR pressure[41]. In forests with low current impacts but increasing vulnerability, opportunities for proactive silvicultural interventions before or upon increases in WPBR prevalence can increase adaptive capacity and accelerate High-5 evolution, potentially avoiding population declines that could lead to extirpation[16,59,60]. Knowledge of the current and future level of WPBR risk can aid land managers in designing and prioritizing effective action plans for their landscapes[57,58].

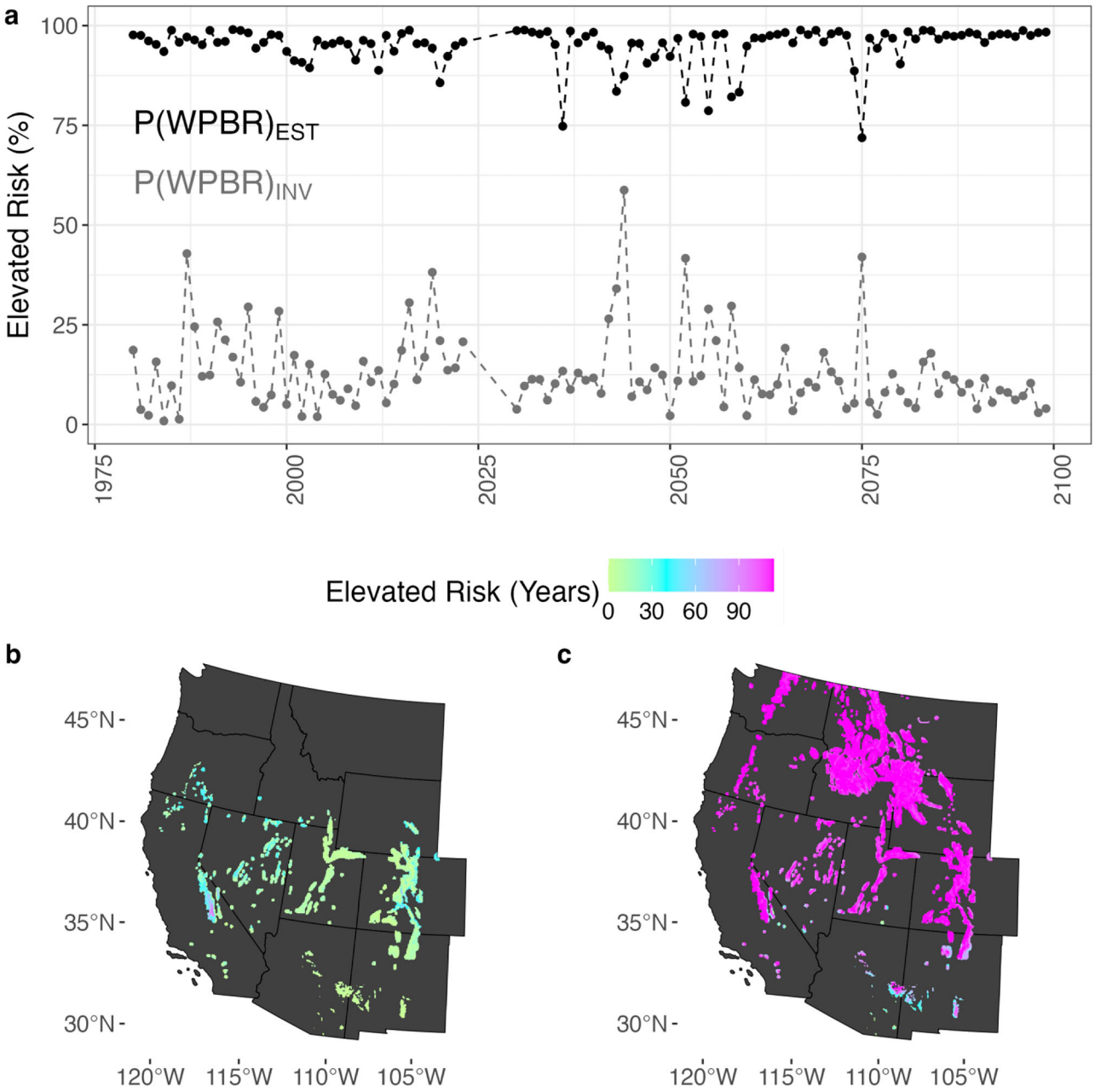

Fig. 6 | Elevated risk of WPBR in the western U.S. from 1980 to 2099. a The percentage of the southern portions of the U.S. High-5 range at elevated risk (P(WPBR) > 0.5) for the $P(WPBR)_{INV}$ (gray) and the entire U.S. High-5 range at elevated risk for the $P(WPBR)_{EST}$ (black). The number of years within the study period (1980-2023, 2030-2099) at elevated risk for (**b**) the $P(WPBR)_{INV}$ and (**c**) the $P(WPBR)_{EST}$.

In addition to WPBR, High-5 forests are under pressure from other major disturbances that are leading to increased mortality and population decreases. Mountain pine beetle outbreaks are also accelerating declines in the High-5. Although ponderosa pine (*Pinus ponderosa* Lawson) and lodgepole pine (*Pinus contorta* Douglas) are the most common host species, most western pines are suitable hosts for the mountain pine beetle. Increasing minimum winter temperatures in the past few decades have led to higher survival rates of overwintering broods in some high-elevation and high-latitude forests, resulting in elevated High-5 mortality[64]. Because mountain pine beetles attack and kill larger trees, advanced regeneration and new seedling germinants can support forest recovery. However, in the presence of WPBR, which kills trees of all ages, forest recovery after bark beetle outbreaks is jeopardized[16]. The mountain pine beetle alone has not threatened the persistence of High-5 species; however, in combination with WPBR, it is an additive mortality factor that can significantly affect the adaptive capacity and trajectory of High-5 populations[16].

Given that *C. ribicola* is now a permanent North American resident, and the projected persistence and increase in conditions suitable for the disease, continued commitment to managing whitebark and limber pine is warranted, as are expanded efforts for the other High-5 species that are also at elevated risk. A science foundation to support management is needed to identify and increase genetic resistance to WPBR in pine populations, bolster population sizes, and mitigate additive mortality factors[16,57,60,62]. As the frequency of WPBR-resistant genotypes increases in pine populations through natural selection and planting, there will be a concomitant decrease in disease incidence, severity, and tree mortality, thereby providing a pathway for adaptation to WPBR and viable High-5 populations in the future.

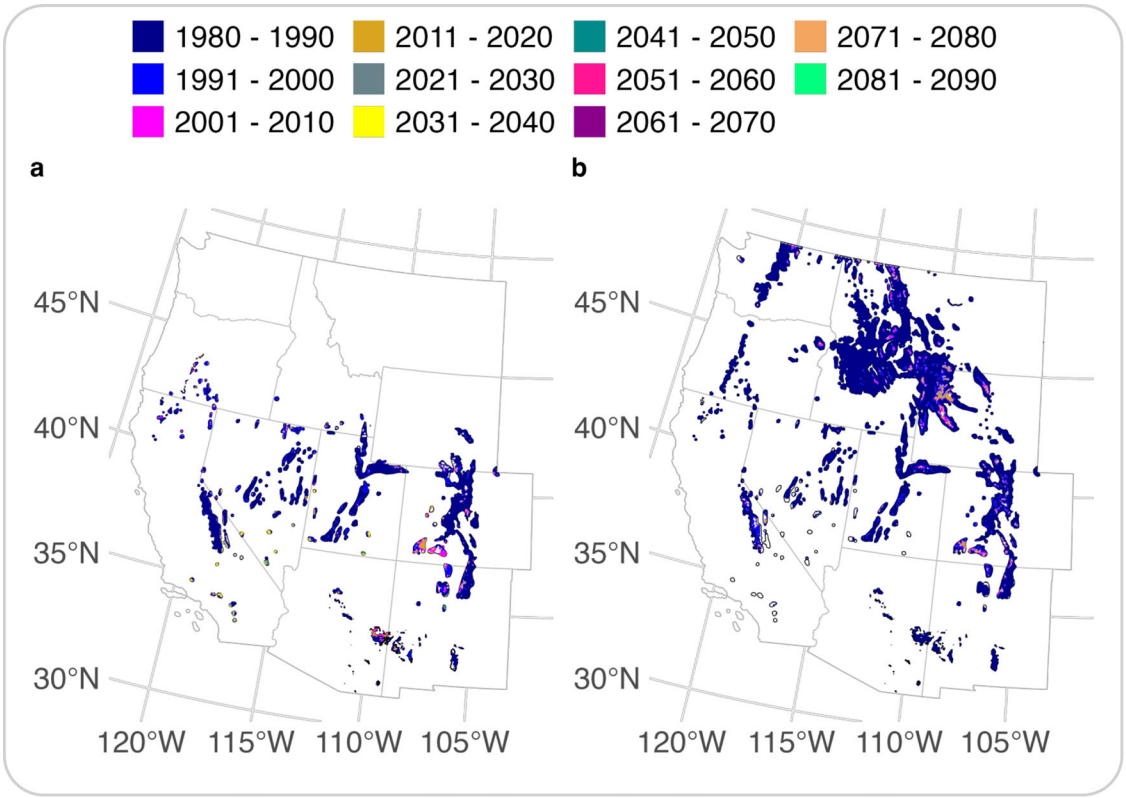

Fig. 7 | WPBR Refugia. Contour maps of the High-5 range indicating the first year when P(WPBR) was (**a**) greater than 0.5 for the $P(WPBR)_{INV}$ and (**b**) greater than 0.65 for the $P(WPBR)_{EST}$.

Methods

Disease Occurrence Data

We harmonized WPBR data (n = 6678) for focal species from independent studies and reports from 1995-2020 (Supplementary Fig. 5 and Supplementary Table 1)[65]. We developed a point database that compiles information on WPBR presence and absence across the High-5 species distributions in the U.S.[45,65]. Sample points were categorized based on WPBR prevalence at scales > 10 km^2, inferred inoculum abundance across the broader landscape, and the duration of pathogen presence[29,45]. Data from areas with low prevalence and presumed inoculum were included in the Invading dataset. Data from regions with high prevalence and presumed inoculum were included in the Established dataset. Due to the spatial distribution of the Invading dataset, these locations were confined to the U.S. southern High-5, representing conditions associated with this range. The Established dataset included conditions that spanned the range of climatic conditions observed across the U.S. High-5 range, though at different prevalence rates.

We obtained static and dynamic information for all sample locations to explore the conditions associated with WPBR on trees (Supplementary Table 2). Static variables included stream density (STREAM_DEN; km km^{-2}) and topographic characteristics. Using the USGS National Hydrography Dataset (NHD)[66], we estimate stream density to use as a proxy for the *Ribes* species commonly occurring in riparian corridors[67]. Topographic information included elevation[68], and the topographic position index (TPI) and the terrain ruggedness index (TRI)[69,70] were calculated using the *spatialEco* package.

Dynamic variables accurately described the climate. We recorded the USDA plant hardiness zone (H_ZONE) for each sampling location and determined the Plant Hardiness Zone annually from 1980 to 2023 using the minimum winter temperature. Daily daymet climate data were obtained to calculate average climatic conditions[71]. From the daily data, we calculated seasonal conditions (April to November) based on the assessment date of the plot data. We measured the conditions for each climate variable by season: spring (April - May), summer (June - August), and fall (September - October).

Modeling Approach

We employed the machine learning algorithm Random Forests (RF) to evaluate the conditions associated with the presence and absence of WPBR on the High-5 species across the western U.S. A series of bootstrapped datasets was used to generate independent regression trees (n = 500); at each node, a random sample of predictor variables was selected for use. We utilized the R package randomForest[72] to create 500 regression trees using WPBR presence/absence data from the High-5 database. Prior to model fitting, the data were divided into training (70%) and testing (30%) sets. Climate, topographic, and the presence/absence of WPBR were included as predictors in a preliminary step, in which we first estimated RF models using a series of subsets of the candidate independent variables, using a modified backward elimination procedure with the package *VSURF*[73]. The VSURF approach was used to minimize the number of predictors required, both for efficiency and to avoid overfitting[74]. The VSURF is a three-step variable selection procedure. The first step eliminates irrelevant variables from the dataset; the second step selects all variables related to the response; and the third step refines the selection by removing redundancy among the variables selected in the second step. Following the model fit with the chosen variables from VSURF, we used the testing dataset to measure model accuracy by producing a confusion matrix with the caret package[75]. We explored bi-weekly to seasonal dynamic variables (Supplementary Table 2) to identify the strongest predictors of WPBR presence. Variables with high importance were primary determinants of the conditions associated with WPBR risk. We used the mean decrease in accuracy and the mean decrease in Gini to measure variable importance. These essential values reveal which factors significantly impact the probability of conditions conducive to WPBR in the High-5 species.

Models were parameterized for climate data based on the assessment date and the seasonal means for 5, 10, and 20 years before the assessment

date. This was done, recognizing that the timeframe that influences disease susceptibility is complex and has yet to be defined. If the models behaved similarly, with low standard deviations in the probability of WPBR occurrence (P(WPBR)), we used an ensemble of models developed from 5-, 10-, and 20-year climate summaries. Ensembles were the mean P(WPBR) across the 5, 10, and 20-year climate summaries. We also parameterized models with data from the Invading dataset ($P(WPBR)_{INV}$) or the Established dataset ($P(WPBR)_{EST}$). We defined an Invading region to project the $P(WPBR)_{INV}$ for ecoregions with low inferred inoculum abundance[29]. We defined the Invading region, where WPBR was still spreading in the High-5 landscape, based on the analysis of Jacobi et al. (2018)[29]. The boundary of the Invading region was delineated by ecoregion boundaries that best approximated the WPBR establishment history at a landscape scale[4]. This included the southern portion of the High-5 range in the U.S[29], extending from 31° to 44° latitude. Parameterizing the model for the southern areas with the Invading dataset added resolution to near-term risk analysis for regions with low inferred current inoculum abundance.

We downloaded gridMET climate data using climateR to project models in space for 1980-2023[76]. Using gridded climate data, we predicted annual probabilities of WPBR across the range of High-5 white pines. While there was a loss of spatial detail with the use of gridMET, this product provided a more seamless transition to climate change projections. We downloaded climate change projections from the College of Global Change and Earth System Science, Beijing Normal University (Beijing Normal University Earth System Model, BNU-ESM), the Canadian Centre for Climate Modelling and Analysis (CanESM2), the National Center for Atmospheric Research (CCSM4), the Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancées en Calcul Scientifique (CNRM-CM5), and the Institut Pierre-Simon Laplace (IPSL-CM5B-LR) for 2030-2099 using the package climateR[77]. These models are a subset of widely evaluated climate models. They are used to study natural climate variability[78–80], and carbon-climate feedbacks at interannual to interdecadal time scales[81–83].

Using the gridded climate data, we predicted annual probabilities of suitable conditions for WPBR infection across the range of High-5 white pines. Models were projected over the High-5 range, which was delineated by the union of tree species distribution maps from Little's "Atlas of United States Trees" series available in R for the High-5 species[53,54,84–87]. The whitebark and limber pine species ranges were obtained from the Whitebark Pine Ecosystem Foundation (whitebarkfound.org), and the range for southwestern white pine was an adapted version from Shirk et al. (2018)[53,88].

Because of differences in the distribution of sample points used to develop models, the Invading model was projected only for the southern portions of the High-5 range, while the Established Model was projected for the entire High-5 range within the U.S. The Invading model was projected on the southern High-5 range to assess conditions conducive to WPBR presence under limited disease prevalence and presumed inoculum availability. The Established model was projected to assess the probability of conditions conducive to WPBR presence, assuming high prevalence and abundant inoculum availability. These risk models were projected to the current spatial distribution of High-5 species, neglecting potential climate-driven shifts in their geographic range[53,54,84,85,87]. Consequently, this analysis addresses the risk of WPBR to extant trees and those projected to be established within the current species ranges during this century. Given the longevity of the High-5 species, it is reasonable to assume that their legacy distributions will persist beyond 2100[89].

To provide information on the changes in P(WPBR) for the High-5 distributions in specific areas, we summarized model output for essential areas of management concern, including the Greater Yellowstone Ecosystem, Crown of the Continent Ecosystem, Pacific Northwest, Great Basin, Southern Sierra Nevada, Southern Rocky Mountains, and Southwestern U.S. These areas were defined using ecoregions across the conterminous United States[90,91]. We visualized temporal trends in the probability of WPBR over time using locally estimated scatterplot smoothing (LOESS). This approach is a nonparametric method for smoothing a time series that makes no assumptions about the underlying structure of the data. LOESS uses local regression to fit a smooth curve through a scatterplot of data. We calculated the global annual mean in the probability of WPBR using the terra package in R[92] and used ggplot2 to generate loess plots[93].

Using the WPBR risk, we identified potential wave years by determining the fraction of the landscape with an elevated risk (P(WPBR) > 0.5). Refugia status was determined by identifying cells with a P(WPBR) less than 0.5 for the $P(WPBR)_{INV}$ and less than 0.65 for the established models, and creating a contour map of the year the threshold was reached. To meet the criteria for refugia, areas had to remain below the threshold.

Data availability

Malone, S.L., A.W. Schoettle, K.S. Burns, H.S. Kearns, J.E. Stewart, M. Newcomb, and C.M. Cleaver. (2025). White Pine Blister Rust (WPBR) Plot Data from the Western United States ver 2. Environmental Data Initiative. https://doi.org/10.6073/pasta/70d7cd56799fc79668343e48e87bb9ef[65]. Malone, S.L., A.W. Schoettle, K.S. Burns, H.S. Kearns, J.E. Stewart, M. Newcomb, and C.M. Cleaver (2026) RustMapper: White Pine Blister Rust Risk in the Western United States 1980-2023. Environmental Data Initiative. https://doi.org/10.6073/pasta/677bc02adfe51760f752494cac74d11e[94]. Malone, S.L., A.W. Schoettle, K.S. Burns, H.S. Kearns, J.E. Stewart, M. Newcomb, and C.M. Cleaver. (2026). RustMapper: White Pine Blister Rust Risk in the Western United States, 2030-2099 ver 1. Environmental Data Initiative. https://doi.org/10.6073/pasta/0a5a5880cdba8761c3f2de32f4575804[89].

Code availability

The code for RustMapper can be found here: Sparkle Malone. (2026). Malone-Disturbance-Ecology-Lab/RUSTMapper: Future climate will not save high-elevation white pines. Zenodo. https://doi.org/10.5281/zenodo.18234106

Received: 3 February 2025; Accepted: 4 February 2026;
Published online: 06 March 2026

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Acknowledgements

This work was supported by funding from the U.S. Forest Service through the Western Wildland Environmental Threat Assessment Center (WWETAC) grant under agreement 19-JV-11221633-129. The contributions of U.S. Government employees to this research were partially supported by their respective agencies. The Yale School for the Environment and the Yale Center for Natural Carbon Capture provided additional support. The findings and conclusions in this paper are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. The authors extend their gratitude to Anthony Culpepper of the Mountain Studies Institute for his assistance with GIS analysis and to Angel Chen for her efforts in publishing the final data products.

Author contributions

SLM and AWS conceived the project idea. AWS and KSB harmonized data from various independent studies, while SLM collected auxiliary data, developed models, and maintained the code. AWS also reviewed analyses and collaborated with SLM on data visualization. Expert reviews were provided by KSB, HSJK, JES, MN, and CMC. The manuscript was written, reviewed, and edited collectively by SLM, AWS, KSB, HSJK, JES, MN, and CMC.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s43247-026-03301-9.

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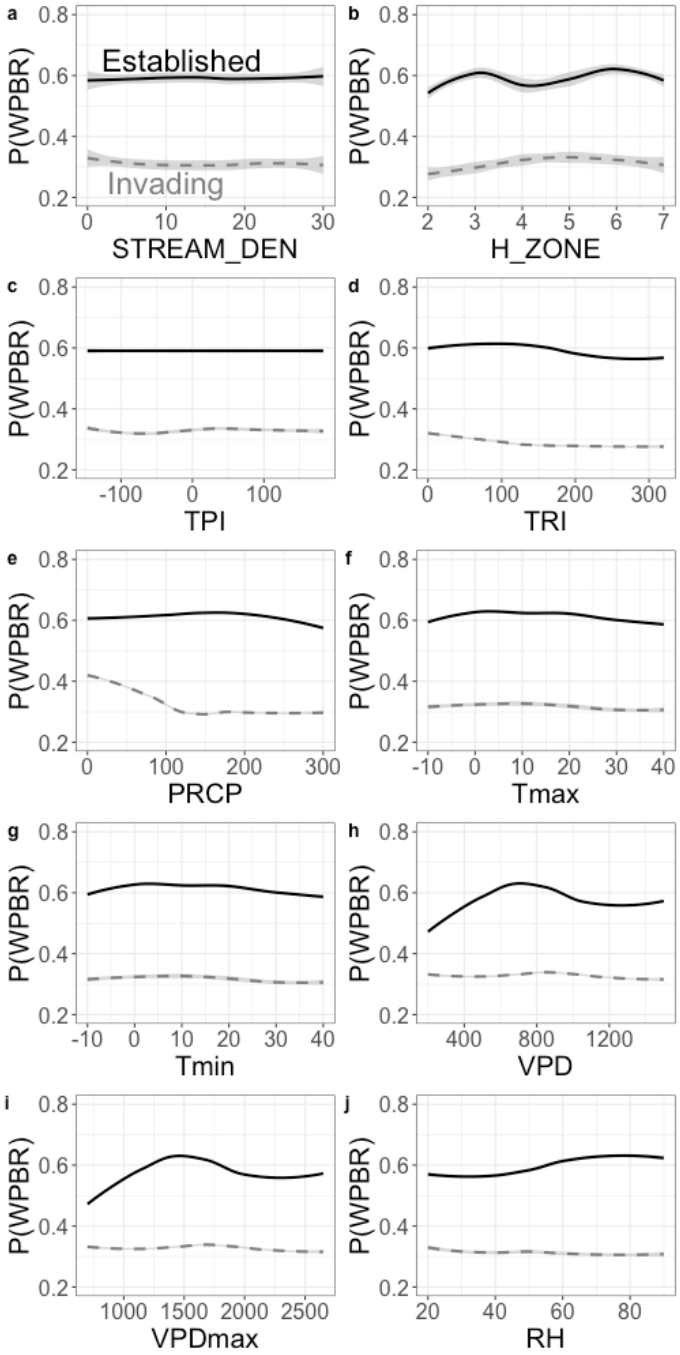
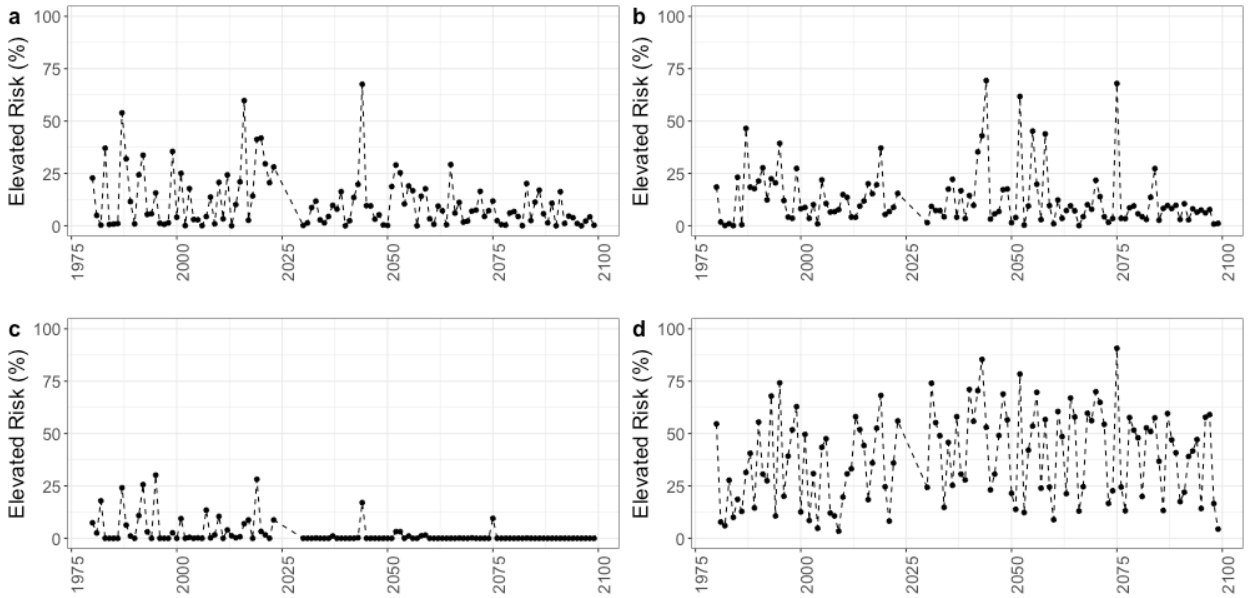
Peer review information *Communications Earth and Environment* thanks the anonymous reviewers for their contribution to the peer review of this work. Primary Handling Editors: Mengjie Wang. A peer review file is available.

Supplementary Information

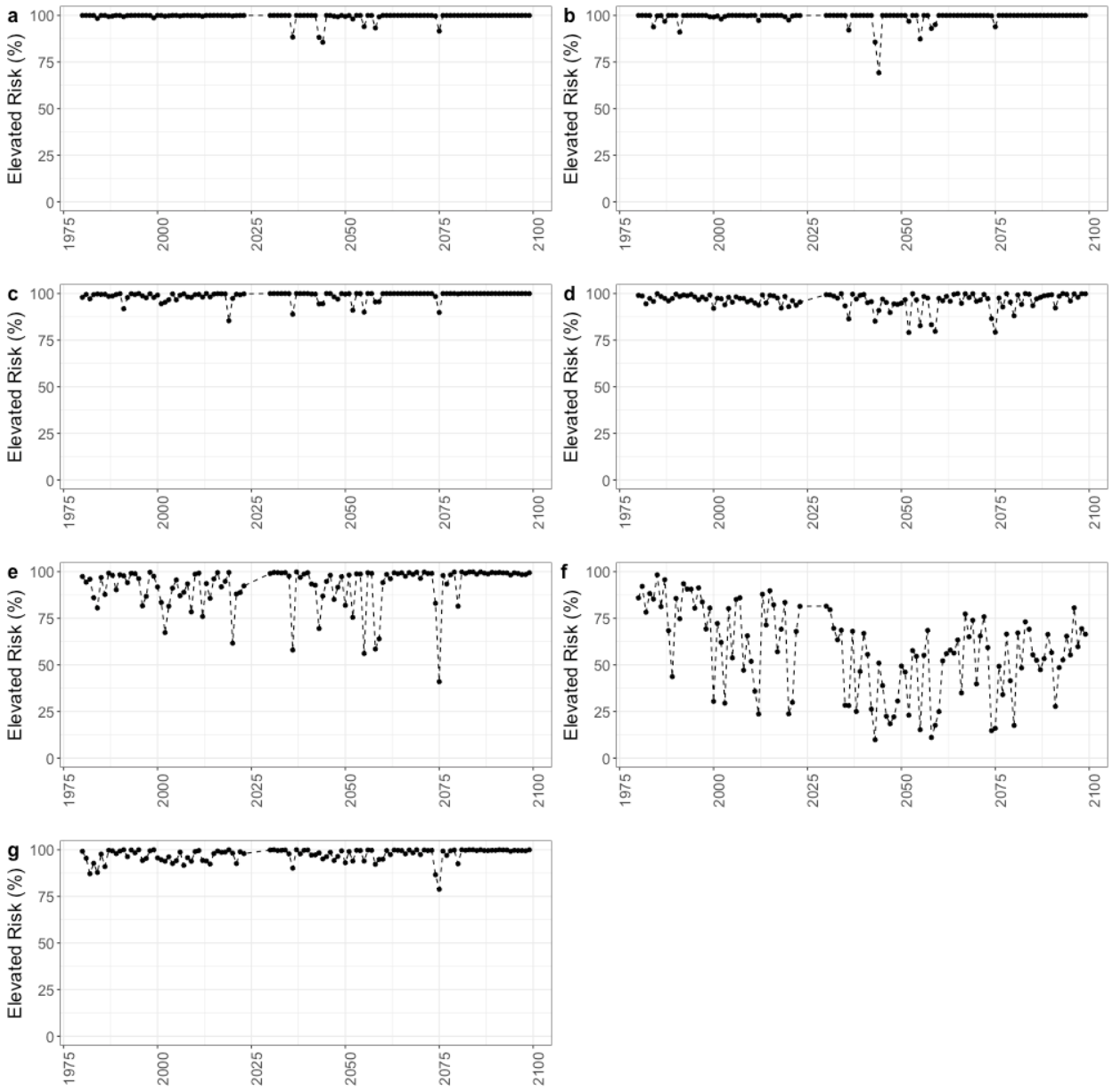


Supplementary Figure 1. Sensitivity analysis for models of WPBR risk in regions where inoculum was presumed high (black) and low (gray). Landscape variation in (a) stream density (STREAM_DEN), (b) hardiness zone (H_Zone), (c) topographic position index (TPI), (d) topographic roughness index (TRI),

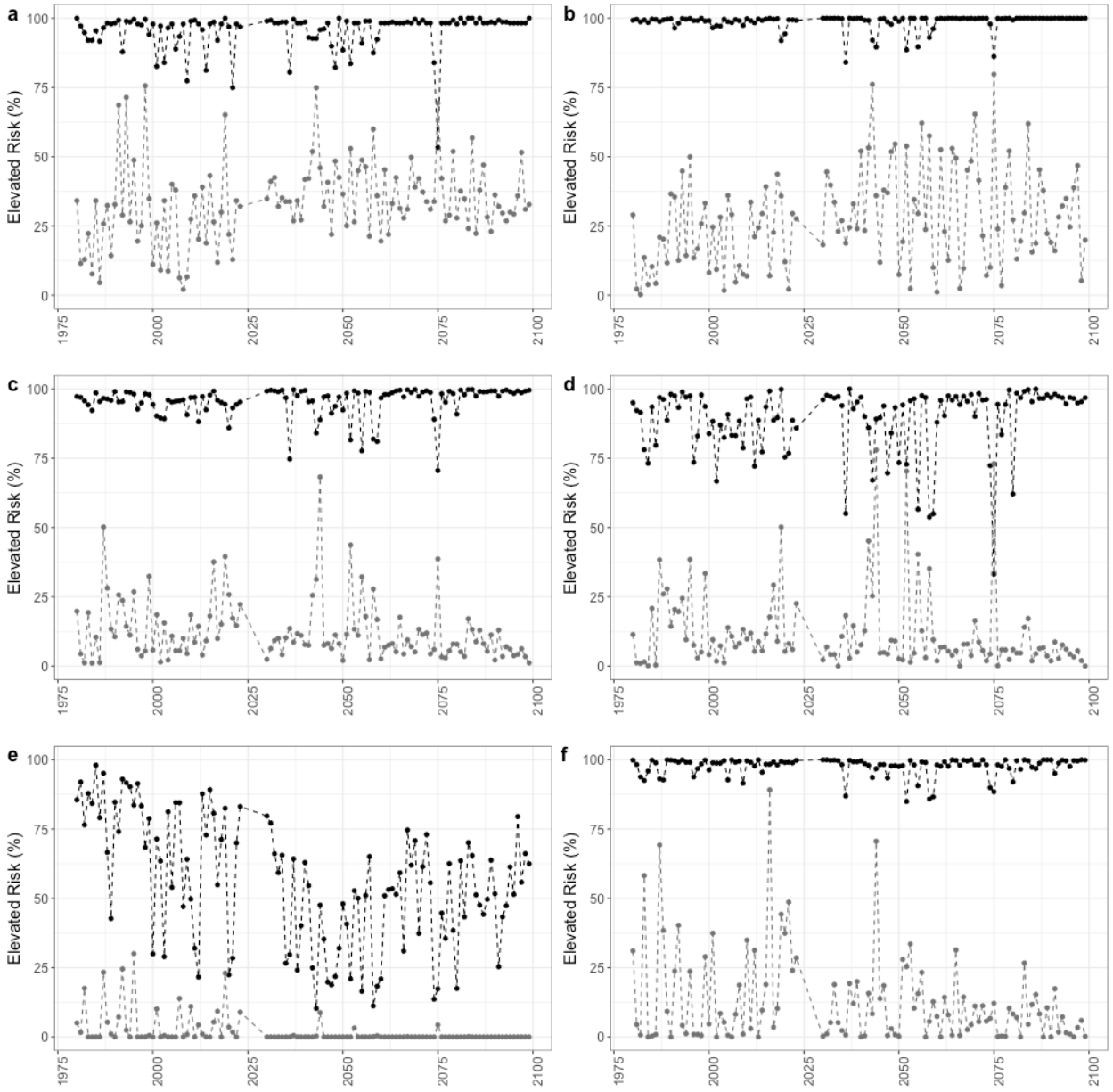
(e) precipitation (PRCP), (f) maximum (Tmax) and (g) minimum temperature (Tmin), (h) vapor pressure deficit (VPD), (i) maximum vapor pressure deficit (VPDmax), and (j) relative humidity (RH) explained patterns in risk.



Supplementary Figure 2. The percentage of the landscape at elevated risk ($P(WPBR_{INV}) > 0.5$) for (a) the Southern Rockies, (b) the Great Basin, (c) the Southwest, and (d) the Southern Sierra Nevada.



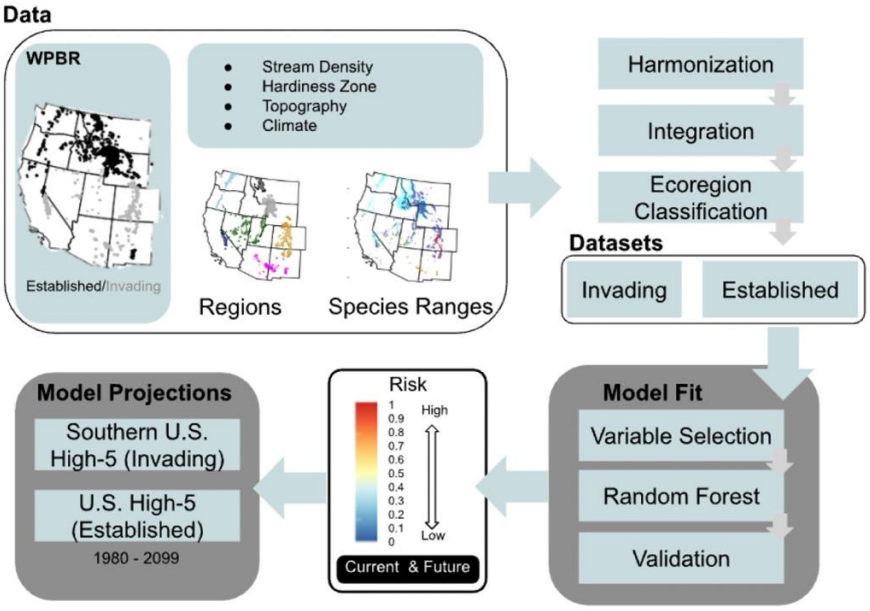
Supplementary Figure 3. The percentage of the landscape at elevated risk ($P(WPBR_{EST}) > 0.5$) for (a) the Pacific Northwest, (b) the Crown of the Continent, (c) the Greater Yellowstone Ecosystem, (d) the Southern Rockies, (e) the Great Basin, (f) the Southwest, and (g) the Southern Sierra Nevada.



Supplementary Figure 4. The percentage of species ranges at elevated risk $P(WPBR_{EST}) > 0.5$ (black) and $P(WPBR_{INV}) > 0.5$ (gray) for: (a) foxtail pine (*Pinus balfouriana;* PIBA), (b) whitebark pine (*Pinus albicaulis* Engelm.; PIAL), (c) limber pine (*Pinus flexilis* James; PIFL2), (d) Great Basin bristlecone pine (*Pinus longaeva*; PILO), (e) southwestern white pine (*Pinus strobiformis* Engelm.; PIST) and (f) Rocky Mountain bristlecone pine (*Pinus aristata*; PIAR). It is important to note that the U.S. ranges for each

22 species are projected for $P(WPBR_{EST})$ and only the southern U.S. portions of each species' range for

23 $P(WPBR_{INV})$.



Supplementary Figure 5. Project workflow showing steps from data acquisition to mode projections for the invading and established models.

Supplementary Table 1. Data contributors were from diverse institutions. Contributed data included plots (Φ), Forest Health Protection trip reports, and professional observations (Y). [45]

Institution (Contributor)	Sample Type
USDA Forest Service, Forest Health Protection, Region 2 (Kelly Burns)	ΦY
Greater Yellowstone Coordinating Committee	Φ
University of California at Berkeley (Joan Dudney)	Φ
USDA Forest Service, Forest Health Protection, Region 3 (David A. Conklin)	ΦY
Humboldt State University (Jenell I. Jackson, Erick S. Jules)	Φ
USDA Forest Service, Rocky Mountain Research Station (Robert Keane, Anna Schoettle)	ΦY
USDA Forest Service, Forest Health Protection, Region 1 (Sandra Kegley)	Φ
Northern Rocky Mountain Science Center, USGS, Glacier National Park (KC Kendall)	Φ
USDA Forest Service, Rocky Mountain Research Station (Jennifer G. Klutsch)	Φ
USDA Forest Service, Forest Health Protection, Region 1 (Lockman)	Φ
USDI National Park Service, Sierra Nevada Network, Inventory & Monitoring Division (Jonathan C.B. Nesmith)	Φ
The University of Montana (Maria Newcomb)	Φ
USDI National Park Service, Greater Yellowstone Inventory and Monitoring Network (Erin Shanahan)	Φ
USDA Forest Service, Pacific Northwest Region 6 (Robin Shoal)	Φ
USDA Forest Service (R. Simons)	Φ
Northern Arizona University (Jonathan P. Smith, Christopher E. Looney, Betsy A Goodrich, Kristen Waring)	Φ
British Columbia Ministry of Forests, Vancouver Forest Region (Stefan Zeglen)	Φ
USDA Forest Service, Pacific Northwest Research Station (Detlev R. Vogler)	YΦ
University of Colorado at Denver (Diana F. Tomback, Laurel A. Sindewald)	Φ
University of Colorado Boulder (Robert Andrus)	Y
USDA Forest Service, Forest Health Protection, Region 2 (Jim Blodgett, Kelly Burns)	YΦ
USDA Forest Service, Forest Health Protection, Region 3 (Greg Reynolds, Nick Wilhelmi)	Y
USDA Forest Service, Forest Health Protection, Region 4 (John Guyon, Angel Saavedra)	Φ
USDA Forest Service, Forest Health Protection, Region 5 (Danny Cluck, Cynthia Snyder)	Φ
USDI National Park Service (John Boetsch, Rob Daley, Jonny Nesmith, Regina Rochefort, Sean Smith)	Φ
USDA Forest Service, Forest Health Protection, Region 6 (Kristen Chadwick, Brendt Oblinger)	Φ
USDA Forest Service, Rocky Mountain Research Station (Brian Geils)	YΦ
USDA Forest Service, Forest Health Protection, Region 1 Hi5 Database	Φ
USDA Forest Service, Forest Health Protection, Region 4 (James T. Hoffman)	Y

Supplementary Table 2. Static and dynamic variables for evaluating white pine blister rust (WPBR) risk across the High-5 range. Dynamic variables were defined bi-weekly to seasonally.

Variables	**Description**	**Abbreviation**
Stream Density (Static)	The total length of streams (km)/ total area of a cell (km^2) determined by the USGS National Hydrography Dataset	STREAM_DEN
Elevation (Static)	Shuttle Radar Topography Mission (SRTM), the Global Multi-resolution Terrain Elevation Data, and the ETOPO1 global relief model	ELEV
Topographic position index (Static)	Topographic slope positions are determined using mean deviations [92].	TPI
Terrain ruggedness index (Static)	An index that denotes terrain heterogeneity [93].	TRI
Plant Hardiness Zone (Dynamic)	Minimum winter temperature, divided into 10 °F zones.	H_ZONE
Air Temperature (°C; Dynamic)	Maximum temperature	Tmin
	Minimum temperature	Tmax
	Average temperature	Tmean
Precipitation (mm; Dynamic)	Average total precipitation	PRCP
Relative Humidity (%; Dynamic)	Average relative humidity	RH
Growing Degree Day (days; Dynamic)	The number of days in each month where the daily average air temperature is greater than 5 °C	GDD
Vapor Pressure Deficit (Pa; Dynamic)	Average vapor pressure deficit	VPD
	Maximum vapor pressure deficit	VPDmax