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# RustMapper: White Pine Blister Rust Risk Across High Elevation Forests in the Western United States

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White pine blister rust (WPBR) is one of North America's most damaging tree epidemics. Aggregating data from more than 80 independent studies across the western U.S. from 1995–2024, we estimate WPBR risk for high-elevation five-needle pine species (High-5) from 1980–2023 in the adaptive management tool RustMapper. WPBR risk is the probability of observing WPBR on the High-5. Stream density, topography, hardness zone, precipitation, air temperature, vapor pressure deficit, and relative humidity were critical in estimating WPBR risk. WPBR risk increased with moisture and declined with temperature. Across the High-5 range, suitable conditions were found in areas where the disease had not yet invaded and throughout regions where the disease was well established. As a result, the mean risk for WPBR was much higher in the north (~0.6) compared to the southern portions of the High-5 range (~0.15). These findings indicate cautious optimism for disease mitigation success in regions where the disease is established and urgency for proactive management where WPBR occurrence is currently low.

## Background & Summary

White pine blister rust (WPBR), caused by the non-native pathogenic fungus *Cronartium ribicola* (J.C. Fischer ex Rabh.), is one of the most damaging tree epidemics in North America<sup>1,2</sup>. Since its introduction to western North America around 1910 into the Pacific Northwest via infected nursery stock imported from France<sup>3</sup>, *C. ribicola* continues to spread and infect new populations of five-needle white pines. The incidence of *C. ribicola* infection is not uniform on the landscape due in part to the distance from the point of introduction, the biology of the pathogen and hosts, and the environmental conditions required for successful spore production, transport, germination, and infection<sup>4</sup>.

Past efforts to contain the spread of *C. ribicola* failed<sup>5</sup>; the pathogen is now a permanent resident of North America. While its spread cannot be curtailed, management interventions can reduce the impacts of the disease on pine populations and ecosystem services. WPBR risk or hazard, host species adaptive capacity, and forest health condition of populations and ecosystems can affect the likelihood of treatment effectiveness<sup>6–8</sup>. Consequently, incorporation of these factors into management frameworks to prioritize limited resources has been recommended<sup>7,9,10</sup>. However, reliable geographic projections of current and future WPBR risk still need to be improved for efficient management planning<sup>10</sup>.

It has been hypothesized that warmer and drier conditions may reduce the prevalence of WPBR due to the pathogen's requirement for cool, moist conditions to facilitate infection<sup>2,11–13</sup>. Consistent with this hypothesis, studies in the Rocky Mountains have found that trees in more arid habitats are less likely to be infected by *C. ribicola*<sup>14,15</sup>. However, for trees already infected in areas experiencing increasing aridity, the likelihood of developing severe symptoms and mortality rises<sup>15</sup>. In contrast, Dudney *et al.* (2021) proposed that increased aridity

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| Source   | Institution (Contributor)                                                                                  | Sample Type |
|----------|------------------------------------------------------------------------------------------------------------|-------------|
| 15,61–63 | USDA Forest Service, Forest Health Protection, Region 2 (Kelly Burns)                                      | ΦY          |
| 64       | Greater Yellowstone Coordinating Committee                                                                 | Φ           |
| 65       | University of California at Berkeley (Joan Dudney)                                                         | Φ           |
| 66       | USDA Forest Service, Forest Health Protection, Region 3 (David A. Conklin)                                 | ΦY          |
| 67–70    | Humboldt State University (Jenell I. Jackson, Erick S. Jules)                                              | Φ           |
| 71,72    | USDA Forest Service, Rocky Mountain Research Station (Robert Keane, Anna Schoettle)                        | ΦY          |
| 73,74    | USDA Forest Service, Forest Health Protection, Region 1 (Sandra Kegley)                                    | Φ           |
| 75       | Northern Rocky Mountain Science Center, USGS, Glacier National Park (KC Kendall)                           | Φ           |
| 76       | USDA Forest Service, Rocky Mountain Research Station (Jennifer G. Klutsch)                                 | Φ           |
| 77       | USDA Forest Service, Forest Health Protection, Region 1 (Lockman)                                          | Φ           |
| 78       | USDI National Park Service, Sierra Nevada Network, Inventory & Monitoring Division (Jonathan C.B. Nesmith) | Φ           |
| 79       | The University of Montana (Maria Newcomb)                                                                  | Φ           |
| 80       | USDI National Park Service, Greater Yellowstone Inventory and Monitoring Network (Erin Shanahan)           | Φ           |
| 81       | USDA Forest Service, Pacific Northwest Region 6 (Robin Shoal)                                              | Φ           |
| 82       | USDA Forest Service (R. Simons)                                                                            | Φ           |
| 83–87 ** | Northern Arizona University (Jonathan P. Smith, Christopher E. Looney, Betsy A Goodrich, Kristen Waring)   | Φ           |
| 88       | British Columbia Ministry of Forests, Vancouver Forest Region (Stefan Zeglen)                              | Φ           |
| 89       | USDA Forest Service, Pacific Northwest Research Station (Detlev R. Vogler)                                 | YΦ          |
| 90       | University of Colorado at Denver (Diana F. Tomback, Laurel A. Sindewald)                                   | Φ           |
| **       | University of Colorado Boulder (Robert Andrus)                                                             | Y           |
| 15,29 ** | 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           |
| 91 **    | USDA Forest Service, Forest Health Protection, Region 6 (Kristen Chadwick, Brendt Oblinger)                | Φ           |
| 92 **    | USDA Forest Service, Rocky Mountain Research Station (Brian Geils)                                         | YΦ          |
| 93,94 ** | Colorado State University (Jane Stewart, Christy M. Cleaver, Holly S.J. Kearns, Olga Kozhar)               | YΦ          |
| 95,96 ** | University of California Davis (Patricia Maloney)                                                          | Φ           |
| **       | USDI Bureau of Land Management (Dana Perkins)                                                              | Φ           |
| **       | USDA Forest Service, Forest Health Protection, Region 1 Hi5 Database                                       | Φ           |
| **       | USDA Forest Service, Forest Health Protection, Region 4 (James T. Hoffman)                                 | Y           |

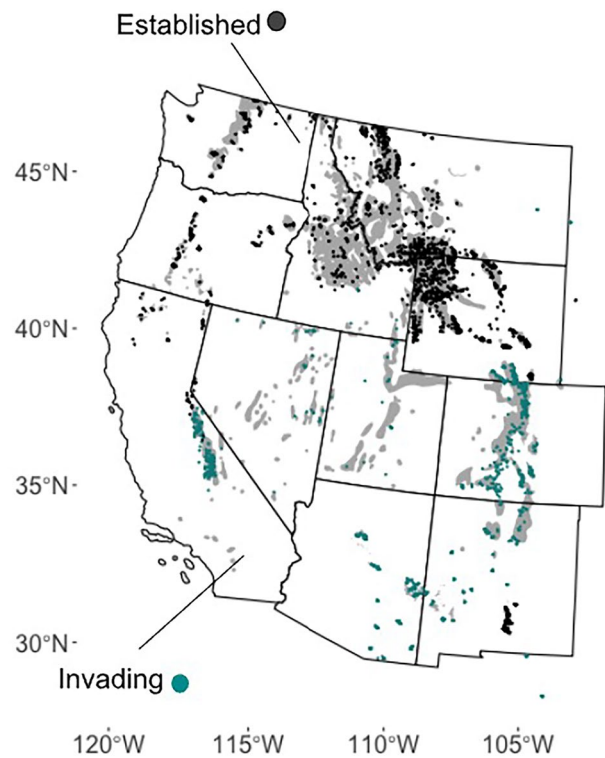
**Table 1.** Data sources include published and unpublished data (\*\*) from diverse institutions. Contributed data included plots (Φ), Forest Health Protection trip reports, and professional observations (Y).

contributed to a shift in WPBR prevalence uphill in the Southern Sierra Nevada Mountains<sup>16</sup>. Additionally, warming temperatures may exacerbate WPBR in moist habitats by extending the growing season, allowing for a longer infectious season<sup>17</sup> and greater canker expansion<sup>18</sup>. These findings suggest that understanding WPBR risk will be complex but provide support for customizing landscape restoration strategies by local climatic factors<sup>4,9,19</sup>.

To understand patterns in disease risk, we evaluate the conditions that have contributed to the presence of WPBR in high-elevation five-needle white pines (High-5, hereafter) to project risk across the High-5 distribution for improved analyses of large-scale patterns. With host groups co-occurring throughout the High-5 range and low genetic disease resistance in white pines, the major determinants of risk are the prevalence of *C. ribicola* inoculum<sup>20</sup> and the conditions associated with spore production, dispersal, and host infection<sup>21</sup>. Past studies suggest that WPBR in trees may have reached the limits of the outbreak due to climatic constraints<sup>11–13</sup>, while others suggest suitable conditions exist beyond the current disease distribution<sup>22</sup>. In this study, we evaluate where conditions have been suitable for WPBR occurrence from 1980 to 2023 in a tool called RustMapper.

## Methods

**WPBR Pathosystem.** The *Cronartium ribicola* life cycle is complex, involving two hosts and five spore stages. The primary infection of pine hosts occurs via fungal infection through needle stomata. Following an incubation period of one or more years, the rust fungus colonizes stem tissues<sup>23,24</sup>, initiating the formation of spermatia and, subsequently, aecia, which erupt through the bark during the spring and summer months, causing the characteristic canker. As the disease progresses, the canker elongates, spreading along the branch toward the main stem and, in many cases, may result in girdling lesions that lead to branch dieback or tree mortality<sup>25,26</sup>. Upon rupture of the aecia, airborne aeciospores are released, potentially infecting alternate hosts, most commonly *Ribes* species, provided environmental conditions are favorable. On the alternate hosts, *C. ribicola* produces uredinia, which may undergo multiple generations (ranging from one to seven), followed by the formation



**Fig. 1** Sample points that recorded the presence or absence of WPBR within the landscape where the disease had been established for decades (black; n = 3926; Established dataset) and in areas with low inferred inoculum abundance at the time of measurement (blue; n = 2752; Invading dataset) based on Jacobi *et al.*<sup>4</sup>. The range of the susceptible High-5 species is shown in gray.

| Variables                            | Description                                                                                                                     | Abbreviation |
|--------------------------------------|---------------------------------------------------------------------------------------------------------------------------------|--------------|
| Stream Density (Static)              | The total length of streams (km)/ total area of a cell (km <sup>2</sup> ) 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 <sup>97</sup> .                                                | TPI          |
| Terrain ruggedness index (Static)    | An index that denotes terrain heterogeneity <sup>43</sup> .                                                                     | 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       |

**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.

of telia. Basidiospores, released from the telia mid-summer through fall, are the only spore type capable of initiating new infections on pine hosts. Importantly, there is no direct transmission of *C. ribicola* between pine trees; the pathogen's lifecycle is obligately heteroecious, requiring both pine and alternate hosts to complete its development. *C. ribicola* colonizes the deciduous leaves of alternate hosts, where it sporulates, but the pathogen does not cause significant impact to the plant, as the infected leaves are shed annually.

Airborne basidiospores can move relatively short distances from alternate hosts to pines<sup>27</sup>. However, new disjunct infection centers are likely initiated by long-distance aeciospore transport, infection of the alternate host, and subsequent basidiospore production and infection of the pines, conditions permitting. Aeciospores produced on the pine host can travel several hundred kilometers to infect a susceptible alternate host<sup>3</sup>. Analysis of atmospheric currents suggests that an isolated infection center on southwestern white pine (*P. strobiformis*



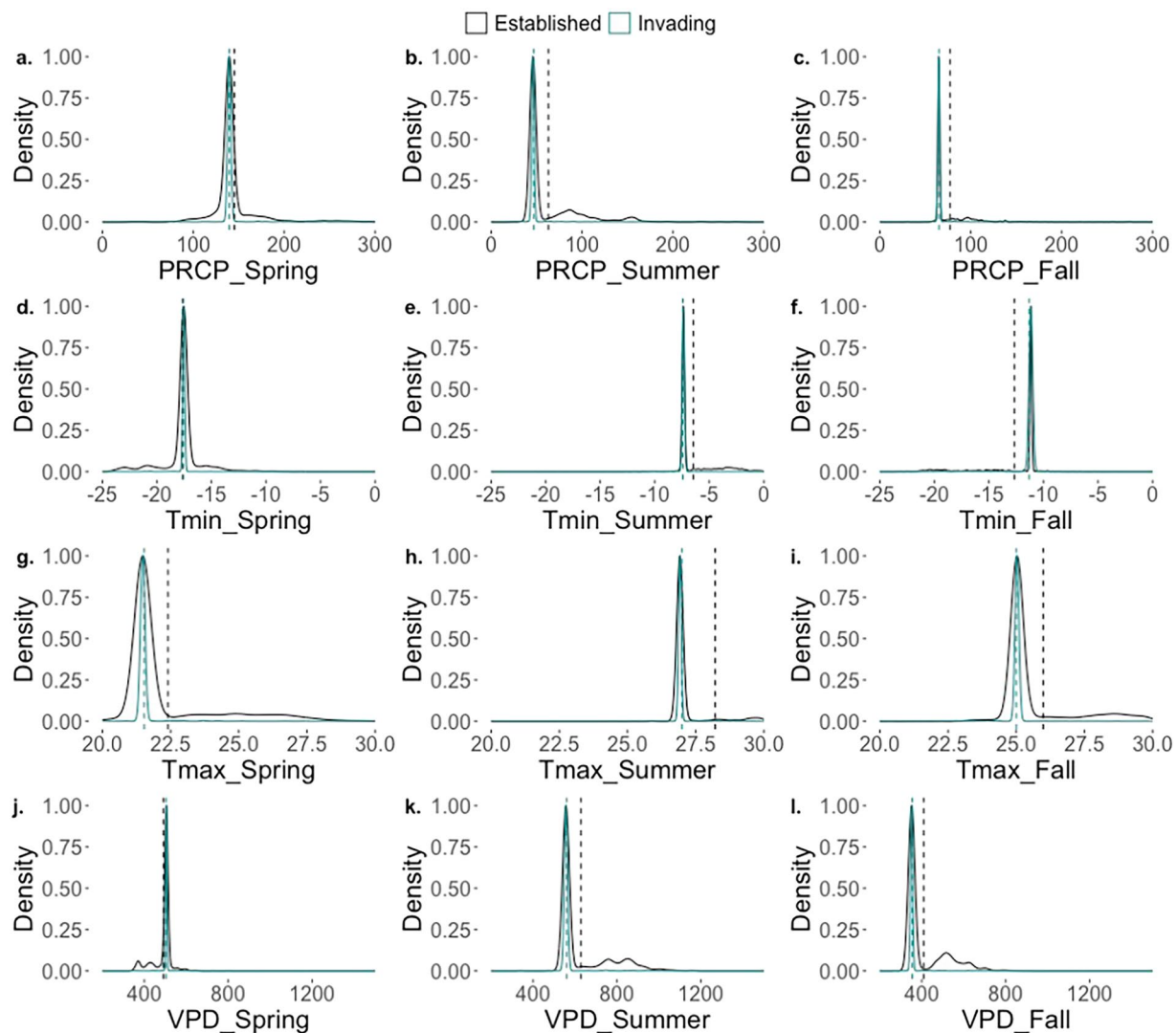
**Fig. 2** The Invading region (blue) for the High-5 range (blue and gray) in the U.S. The Invading region, 31°–44° latitude, as defined by the intersection of ecoregions and the High-5 range with low inferred inoculum abundance<sup>4</sup>.

Engelm.) in southern New Mexico originated from aeciospores transported in the upper atmosphere from central California<sup>28</sup>. Long-distance transport of spores may also explain the recent disjunct infection center in south Colorado on Rocky Mountain bristlecone pine (*P. aristata* Engelm.) and limber pine (*P. flexilis* James)<sup>29</sup>. These successful colonizations demonstrate that areas once thought too dry for the disease can be exposed to inoculum and be environmentally suitable for infections and disease development on pines.

In contrast, a failed founding event has been documented in Utah. Alternate hosts (*Ribes inerme* Rydb.) were found infected with *C. ribicola* in 2005 at a site 257 km south of the closest known diseased pines<sup>30</sup>, yet there is still no evidence of diseased five-needle pines in all of Utah<sup>9</sup>. These patterns of infection and disease indicate that areas at and beyond the current geographic extent of WPBR on pines have some level of exposure to inoculum. In plant pathology, inoculum refers to the part of the pathogen that can cause infection<sup>31</sup>. The risk of infection of the pine host and subsequent disease development is associated with environmental conditions and basidiospore inoculum abundance, which is a function of aeciospore availability<sup>20</sup>. Exposure of the alternate hosts to higher levels of aeciospores is more likely in areas with more regionally infected trees with active sporulating cankers. The occurrence of “wave years”, intense and widespread WPBR infection, is typically driven by episodic environmental conditions that favor abundant inoculum production and infection<sup>11,26,27</sup>.

**Study system.** The focal High-5 species included whitebark pine (*P. albicaulis* Engelm.; PIAL), limber pine (*P. flexilis* James; PIFL2), foxtail pine (*P. balfouriana* Grev. & Balf.; PIBA), Great Basin bristlecone pine (*P. longaeva* D.K. Bailey; PILO), southwestern white pine (*P. strobiformis* Engelm.; PIST), and Rocky Mountain bristlecone pine (*P. aristata* Engelm.; PIAR). We harmonized WPBR data for focal species from independent studies and reports (Table 1) from 1995–2020 across the Western U.S. (Fig. 1). Data sources included published and unpublished data from various federal agencies, universities, and the Hi5 Database (Table 1)<sup>32</sup>. Only data collected by forest health professionals with expertise in field disease detection were included due to the skill and experience required to identify WPBR infections on the High-5 species correctly. The majority of the data were from plot-based studies (73%). While the study designs varied, all plots used in this analysis recorded the location, assessment date, species present, and presence/absence of WPBR on High-5 species within plots. Inconsistencies in reporting methods for other disease metrics precluded including those measures in our analyses while retaining robust sampling across the western U.S. In addition to plot-based data, we also utilized trip reports from Forest Health Protection (FHP) professionals. Trip reports record insect and disease findings and relevant management options for recreation sites, administrative sites, certification stands, project areas, analysis areas, or other areas of interest. Trip reports were included for locations where more recent plot data were unavailable. We developed a point database compiling information on WPBR presence and absence throughout the High-5 species distributions in the U.S.<sup>9</sup>.

Our nearly 6678 WPBR sample points were categorized based on inferred inoculum abundance across the greater landscape and length of pathogen presence<sup>4</sup>. Therefore, areas with presumed low inoculum were included in the Invading dataset, and regions with presumed high inoculum were included in the Established dataset. The Invading dataset occurred mainly across the southern range of the High-5 (31°–44° latitude),



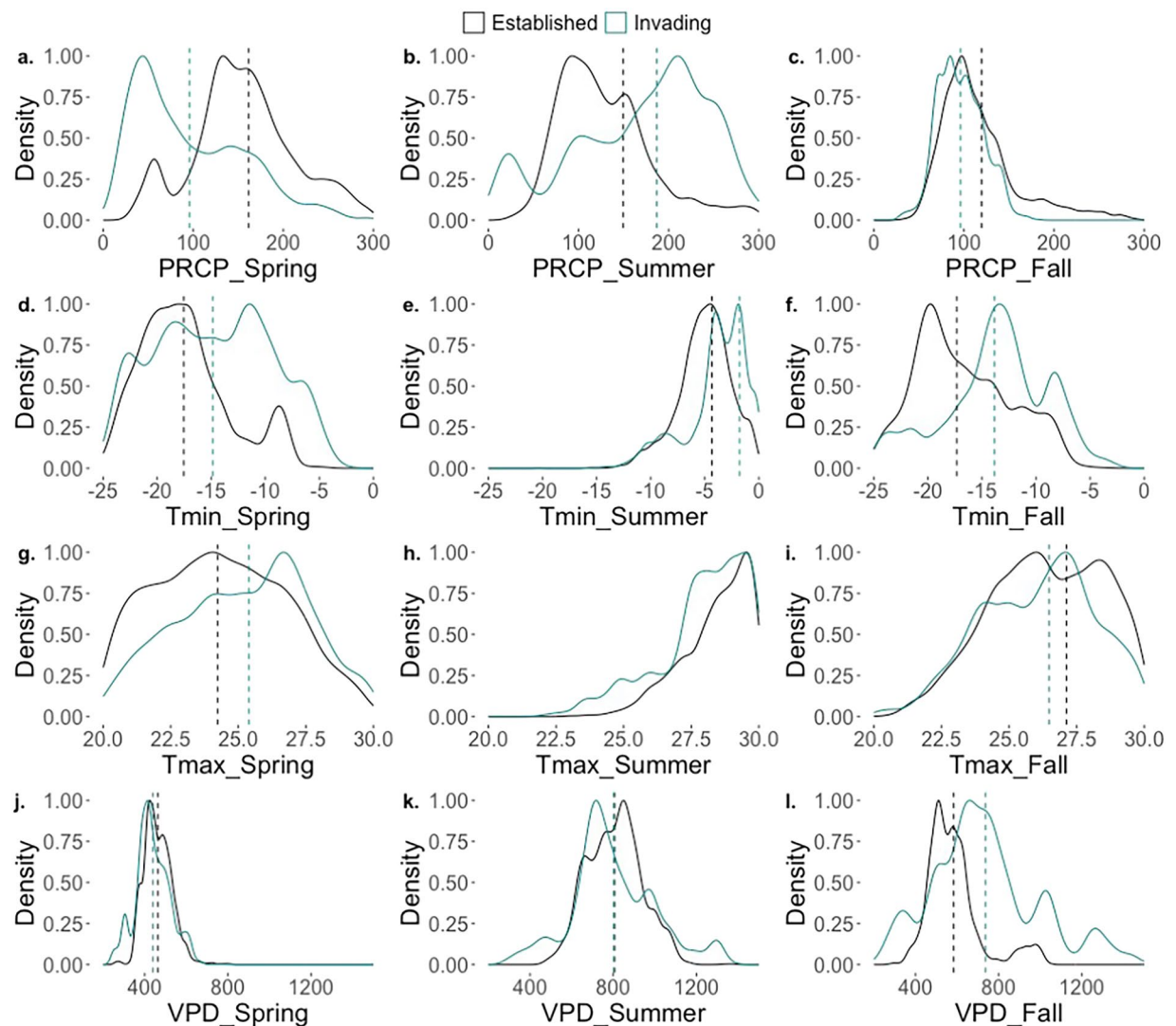
**Fig. 3** Climate summaries (5-Year) for (a–c) precipitation (mm), (d–f) minimum temperature (°C), (g–i) maximum temperature (°C), and (j–l) vapor pressure deficit (Pa) by season (spring, summer, and fall) indicate that the climate associated with sample locations in areas with presumed low inoculum (blue; Invading dataset) and where the disease was established (black; Established dataset) differ. Vertical lines denote the mean.

where the disease had not been detected or present over the last 25 years. The one exception is the Sacramento Mountains of south-central New Mexico, where a disjunct WPBR outbreak, discovered in 1990, has become an area of high WPBR impacts<sup>28</sup>. WPBR data from this mountain range was included in the Established, not the Invading dataset. In contrast, the Established dataset was generally distributed in the more northern High-5 region closer to the point of disease introduction to western North America (Fig. 1), where the pathogen had been present for a long time (>25 years), and the disease was well established.

**Modeling approach.** We employed the machine learning algorithm Random Forests (RF) to evaluate the conditions associated with the presence or absence of WPBR on the High-5 species across the western U.S. The RF algorithm was introduced by Breiman 2001<sup>33</sup>. A series of bootstrapped datasets are used to generate independent regression trees; at each node, a random sample of predictor variables was selected for use. We utilized the R package randomForest<sup>34</sup> to create 500 regression trees using WPBR presence/absence datasets. The fit of each RF model was evaluated with the out-of-bag mean square error (OOB MSE), and variable importance was computed as the amount of prediction error increased when a particular predictor was permuted. Initially, 500 RF trees were generated using all possible predictor variables. The overall model fit was evaluated with the average of the 500 OOB MSEs from the final model, and variable importance was calculated as the average rank of each predictor variable for the 500 models.

Prior to fitting each model, the data was divided into training (70%) and testing (30%) for Established and Invading models. Climate, topographic, and presence/absence of WPBR were included as predictors in a preliminary step where we first estimated RF models with a series of subsets of the candidate independent variables

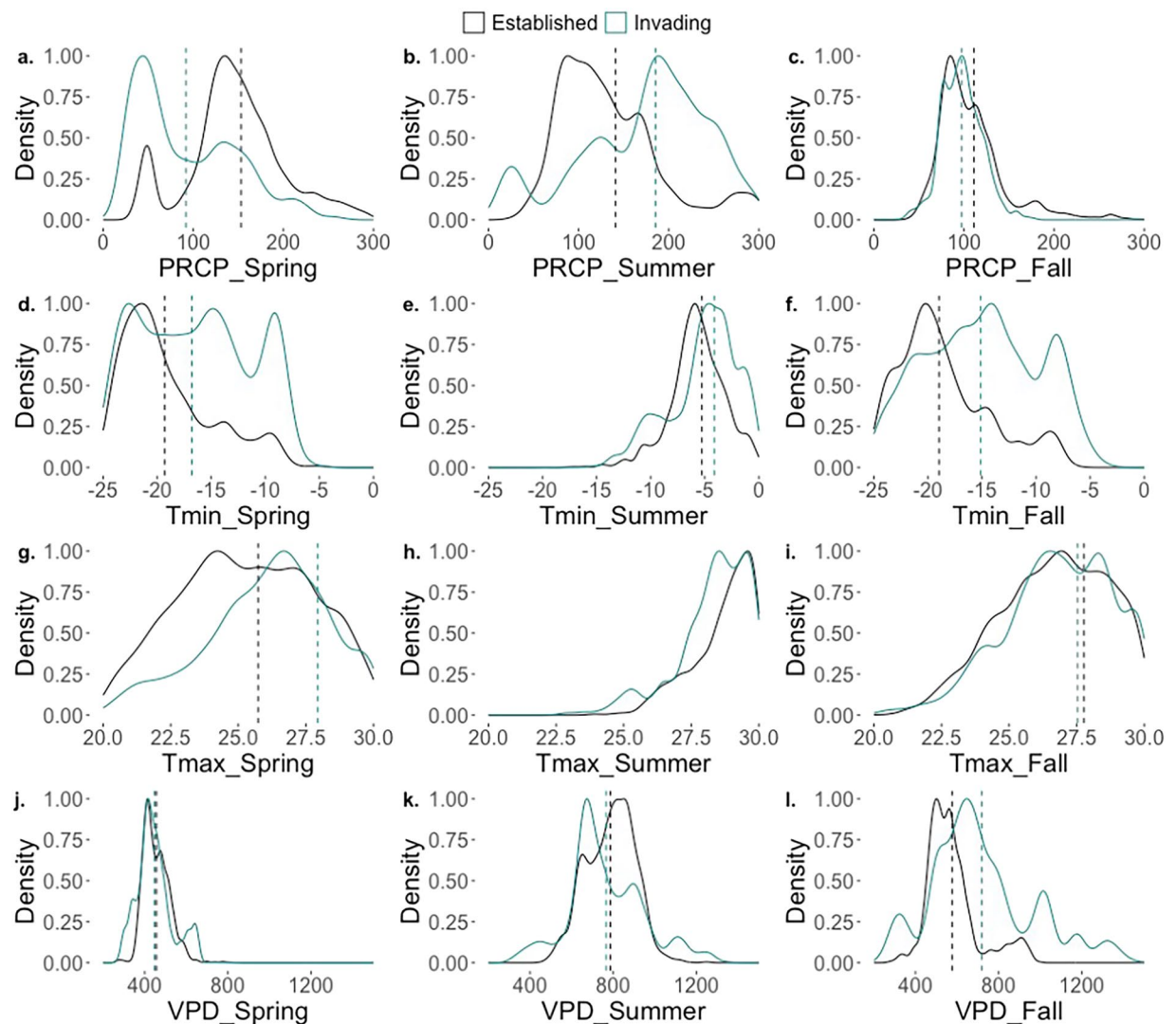




**Fig. 4** Climate summaries (10-Year) for (a–c) precipitation (mm), (d–f) minimum temperature (°C), (g–i) maximum temperature (°C), and (j–l) vapor pressure deficit (Pa) by season (spring, summer, and fall) indicate that the climate associated with sample locations in areas with presumed low inoculum (blue; Invading dataset) and where the disease was established (black; Established dataset) differ. Vertical lines denote the mean.

using a modified backward elimination procedure with the package *VSURF*<sup>35</sup>. This process reduced the number of variables considered from >100 to less than 10. We explored bi-weekly to seasonal dynamic variables to identify the strongest predictors of WPBR presence. Variables with high importance were primary determinants of the conditions associated with WPBR risk. Variables with low importance or that were highly correlated with more important variables were omitted from the model. 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. The *VSURF* approach was used to minimize the number of predictors required for both efficiency and to avoid overfitting<sup>36</sup>. 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 in the variables selected by the second step. Following the model fit with the chosen variables from *VSURF*, we used the testing dataset to measure model accuracy using a confusion matrix from the *caret* package<sup>37</sup>.

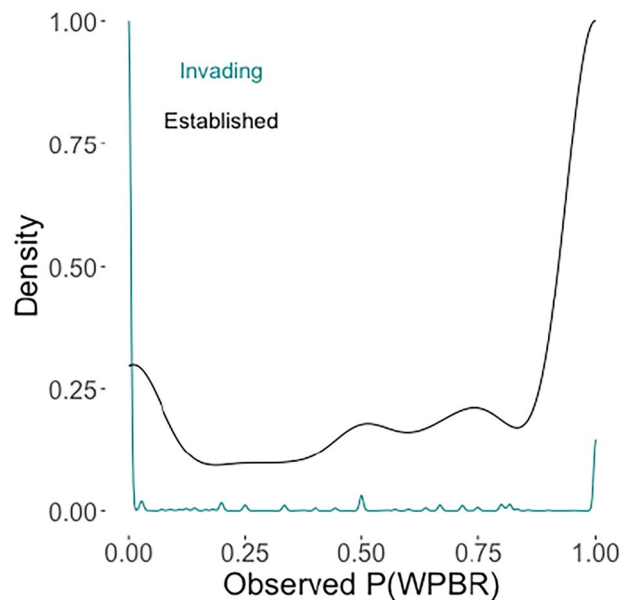
We used static and dynamic variables in models to define the conditions associated with WPBR on trees (Table 2). Static variables included stream density (*STREAM\_DEN*) and topographic characteristics. We measured stream density across the western U.S. with the USGS National Hydrography Dataset (NHD)<sup>38</sup>. Stream density is the total length of streams (km) divided by the area of each cell and was estimated by creating a ~1 km grid across the western U.S. and measuring the total length of streams within each grid by taking the intersection of the NHD vector file and the grid using the *sf* and *terra* packages in R<sup>39,40</sup>. The total stream length was divided by the area to get stream density in km km<sup>-2</sup>. Stream density was used as a proxy for *Ribes* species commonly occurring in riparian corridors, including *Ribes hudsonianum* Richardson and *R. inerme*, both highly susceptible



**Fig. 5** Climate summaries (20-Year) for (a–c) precipitation (mm), (d–f) minimum temperature (°C), (g–i) maximum temperature (°C), and (j–l) vapor pressure deficit (Pa) by season (spring, summer, and fall) indicate that the climate associated with sample locations in areas with presumed low inoculum (blue; Invading dataset) and where the disease was established (black; Established dataset) differ. Vertical lines denote the mean.

species in western states restricted to moist sites<sup>41</sup>. Topographic information was obtained with the package *elevatr* for each WPBR sampling location<sup>42</sup>. The *elevatr* package provides access to digital elevation models from the Shuttle Radar Topography Mission (SRTM), the Global Multi-resolution Terrain Elevation Data, and theETOPO1 global relief model. An elevation raster layer was downloaded using the function `get_elev_raster`, and the topographic position index (TPI) and the terrain ruggedness index (TRI) were calculated using the *spatialEco* package. The TPI calculates topographic position using mean deviations within a specified window ( $s = 29$ ), and the TRI is the topographic roughness index<sup>43</sup>. Topographic information was extracted for all WPBR sample points.

Dynamic variables were descriptive of 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<sup>44</sup>. Daymet provided gridded daily weather and climatology variables (daily minimum and maximum temperature, precipitation, vapor pressure deficit, shortwave radiation, snow water equivalent, and day length) by interpolating ground-based observations through statistical modeling techniques<sup>44</sup>. The daymet data products are produced on a 1 km × 1 km gridded surface over continental North America and Hawaii from 1980 through the end of the most recent full calendar year. We downloaded daymet data for locations using the *daymetR* package<sup>45</sup>. From daily data, we calculated seasonal conditions (April to November) based on the assessment date. We measured the conditions for each climate variable by season: spring (April – May), summer (June – August), and fall (September – October).



**Fig. 6** The observed WPBR occurrence was estimated from the Invading plot data (a,b) where inoculum was presumed low ( $WPBR_{INV}$ ) and (c,d) for the Established dataset ( $WPBR_{EST}$ ). Occurrence estimates are only shown for areas where point data was available.

| Models:           | $P(WPBR)_{INV}$ |          |          | $P(WPBR)_{EST}$ |          |          |
|-------------------|-----------------|----------|----------|-----------------|----------|----------|
| Climate Summaries | 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     |
| Training Accuracy | 99%             | 99%      | 99%      | 76%             | 97%      | 97%      |
| Test Accuracy     | 88%             | 94%      | 91%      | 71%             | 79%      | 82%      |

**Table 3.** Performance of the random forest models of WPBR risk for models parameterized with plot data in areas with presumed low inoculum ( $P(WPBR)_{INV}$ ) and data from areas where WPBR was well established ( $P(WPBR)_{EST}$ ).

The spatial resolution of daymet data was advantageous for capturing high-resolution patterns in the climate at sample locations<sup>46</sup>. At a 1 km resolution, daymet offered fine-grained information that included small-scale climate features and processes that could affect the presence of WPBR<sup>46</sup> and has been shown to capture crucial ecological processes in white pines<sup>15,47,48</sup>. The resolution of daymet was high enough to capture conditions that can affect exposure and susceptibility to WPBR<sup>48</sup>, and the resolution was also sufficient to bridge the gap between high-resolution data used to predict outcomes at more extensive spatial ranges. When developing models, high-resolution data generally leads to more accurate and detailed responses to conditions, particularly for capturing small-scale phenomena. Low-resolution data is more cost-effective for large-area monitoring and climate change projections, though they may lack detail. Studies have shown that information is lost with decreased resolution<sup>49,50</sup>.

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 with 5, 10, and 20-year climate summaries. Ensembles were the mean  $P(WPBR)$  across the 5, 10, and 20-year climate summaries. This approach would either integrate short-term and long-term climate effects or identify whether short or long-term effects were more relevant. 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<sup>4</sup>. We defined the Invading region, where WPBR was still invading the High-5 landscape, based on the analysis of Jacobi *et al.*, 2018<sup>4</sup>. The boundary of the Invading region was delineated by ecoregion boundaries that best approximated the WPBR establishment history at a landscape scale<sup>4</sup>. This included the southern portion of the High-5 range in the U.S.<sup>4</sup> extending from 31°–44° latitude (Fig. 2). Parameterizing the model for the southern areas with the Invading dataset added resolution to near-term risk analysis for regions with low inferred inoculum abundance.

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<sup>51–56</sup>. The whitebark



| Models:                           |        | P(WPBR) <sub>INV</sub> |          |          | P(WPBR) <sub>EST</sub> |          |          |
|-----------------------------------|--------|------------------------|----------|----------|------------------------|----------|----------|
| Variables                         |        | 5 (Yrs)                | 10 (Yrs) | 20 (Yrs) | 5 (Yrs)                | 10 (Yrs) | 20 (Yrs) |
| STREAM_DEN (km km <sup>-2</sup> ) |        | 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                      |          |          |

**Table 4.** Important variables for the random forest models of WPBR risk for models parameterized with the Invading dataset in areas with low presumed inoculum (P(WPBR)<sub>INV</sub>) and the Established dataset from areas where WPBR was well established (P(WPBR)<sub>EST</sub>).

and limber pine species ranges were obtained from the Whitebark Pine Ecosystem Foundation (whitebark-found.org), and the range for southwestern white pine was an adapted version from Shirk *et al.*, (2018)<sup>54,57</sup>. The P(WPBR)<sub>EST</sub> was projected over the entire U.S. High-5 range (31°–49° latitude) to assess the probability of conditions conducive to WPBR presence, assuming abundant inoculum availability. The Invading model was projected on the southern High-5 range in the Invading region to determine conditions conducive to WPBR presence under presumed low inoculum availability (Fig. 2). Consequently, this analysis addresses the risk of WPBR to extant forests.

We downloaded gridMET climate data using to project models in space for 1980–2023<sup>58</sup>. While gridMET will not capture microclimates that arise at spatial scales finer than the native resolution (~4 km), this study is focused on understanding landscape-level risk. 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, a future area of research.

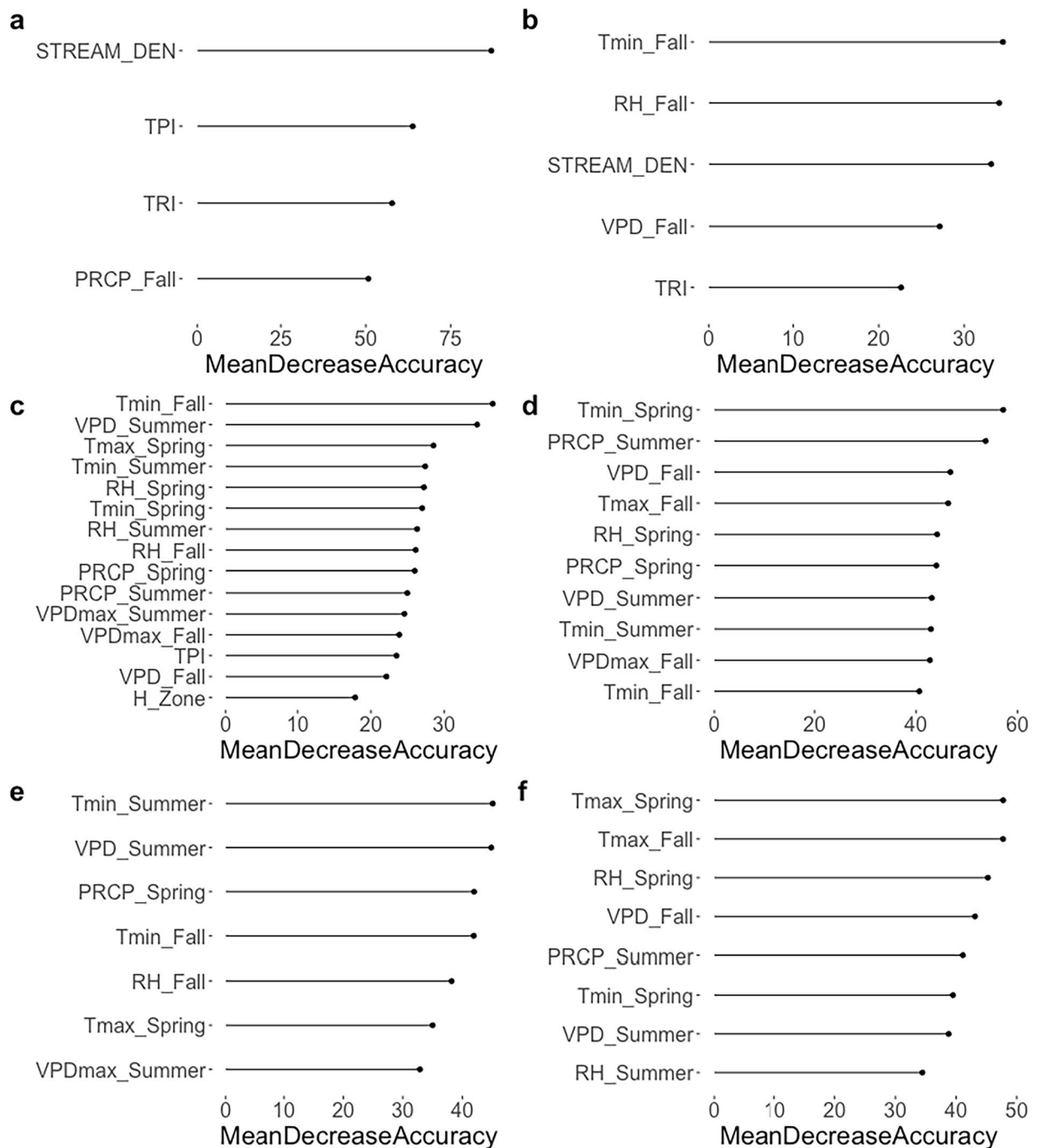
### Data Records

RustMapper comprises the ensemble P(WPBR) risk layers archived in the Environmental Data Initiative (EDI) repository. The RustMapper consists of 1. annual (1980–2023) P(WPBR)<sub>INV</sub> based on 5, 10, and 20-year climate summaries; and 2. annual P(WPBR)<sub>EST</sub> based on 5, 10, and 20-year climate summaries<sup>59</sup>. The model values are the probability of rust occurrence, ranging from 0 to 1. Higher values denote a greater likelihood of WPBR. Spatial models were estimated with gridMET climate data at 4 × 4 km resolution in GeoTIFF format. Metadata with details of data architecture and attributes was also included.

### Technical Validation

Data were distributed across the western U.S., where the High-5 occurred in regions that represented gradients in precipitation, temperature, vapor pressure deficit, and relative humidity (Fig. 1; Table 2). There were noticeable differences in climate for the Established and Invading datasets (Figs. 3–5). While warm and dry conditions were generally associated with the Invading dataset, conditions for the Established dataset were skewed towards lower temperatures and more precipitation in the spring and fall. Vapor pressure deficit was lower for the Established dataset than the Invading dataset in the fall. Similar temporal and regional patterns were found across the 5-year (Fig. 3), 10-year (Fig. 4), and 20-year climate summaries (Fig. 5). Differences in the conditions in the Invading and Established datasets prompted the development of separate models to estimate the probability of observing conditions associated with the occurrence of WPBR.

The Invading dataset comprised sample points distributed across the southern areas of the western U.S. (Fig. 1). Most of the sample points (83%) had no rust present, making the total WPBR occurrence ~0.17, though this varied in space, ranging from 0 to 1 with a mean of 0.17 (Fig. 6). Unlike the Invading data, most of the

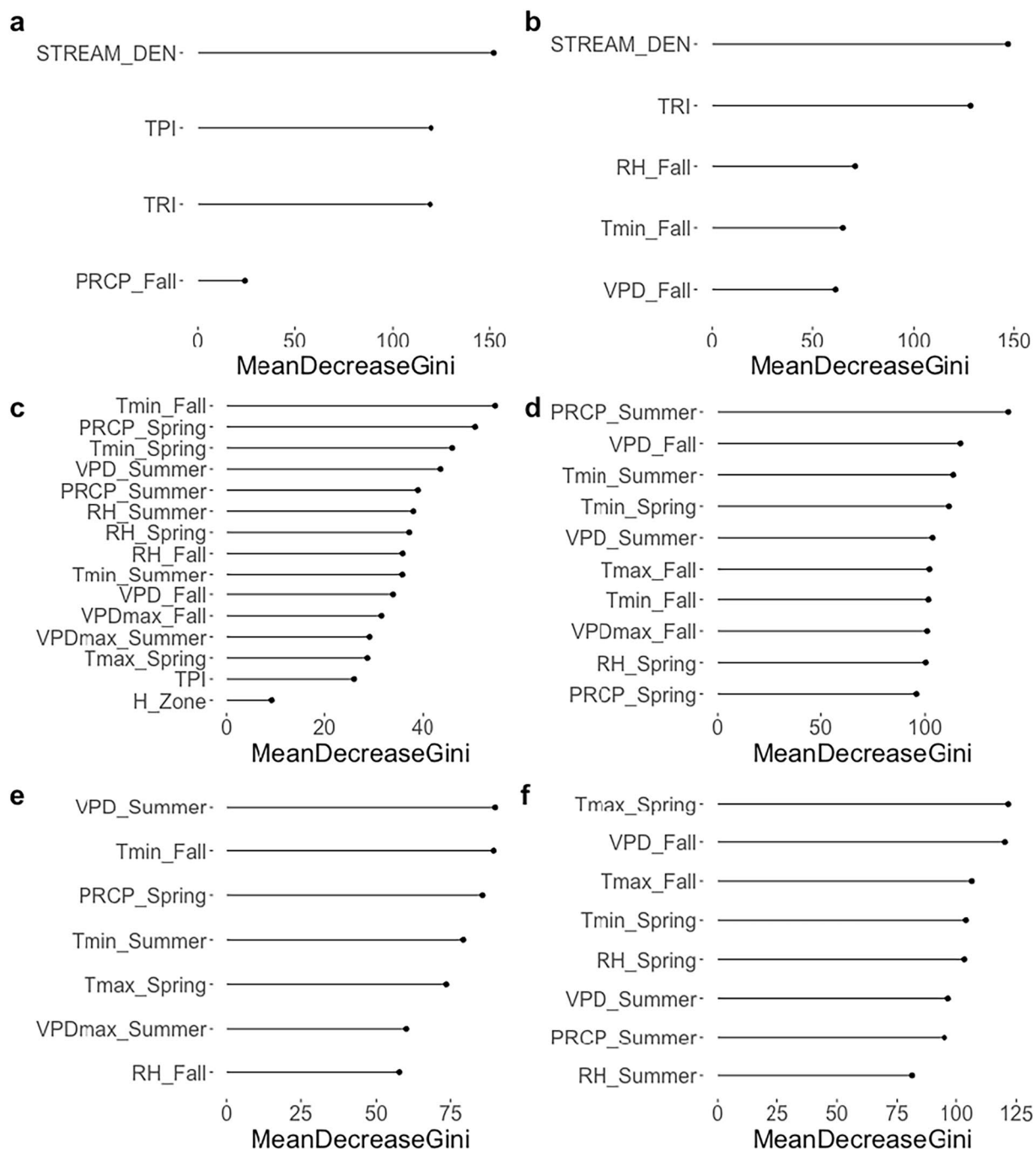


**Fig. 7** Variable importance plots, the mean decrease in accuracy for the Invading ( $P(WPBR)_{INV}$ ) and Established ( $P(WPBR)_{EST}$ ) models, respectively, for (a,b) 5-year climate summaries, (c,d) 10-year climate summaries, and (e,f) 20-year climate summaries in the western U.S.

Established data had rust present (70%) (Fig. 6). WPBR occurrence for the Established data also varied in space and ranged from 0 to 1, with a mean of 0.70.

Across the western U.S., we estimate the probability of WPBR using presence/absence data (Table 3). Model performance measured by area under the curve (AUC) ranged between 0.67 to 0.96, and the accuracy of detecting WPBR where it was present ranged between 76–99% for the training data and 71–94% for the testing dataset. The error was lower for the  $P(WPBR)_{INV}$  compared to the  $P(WPBR)_{EST}$  with higher accuracies compared to the  $P(WPBR)_{EST}$ . The occurrence of WPBR was much lower for the Invading dataset than the Established dataset, and combined with the differences in sample sizes and climate patterns, separate models were appropriate.

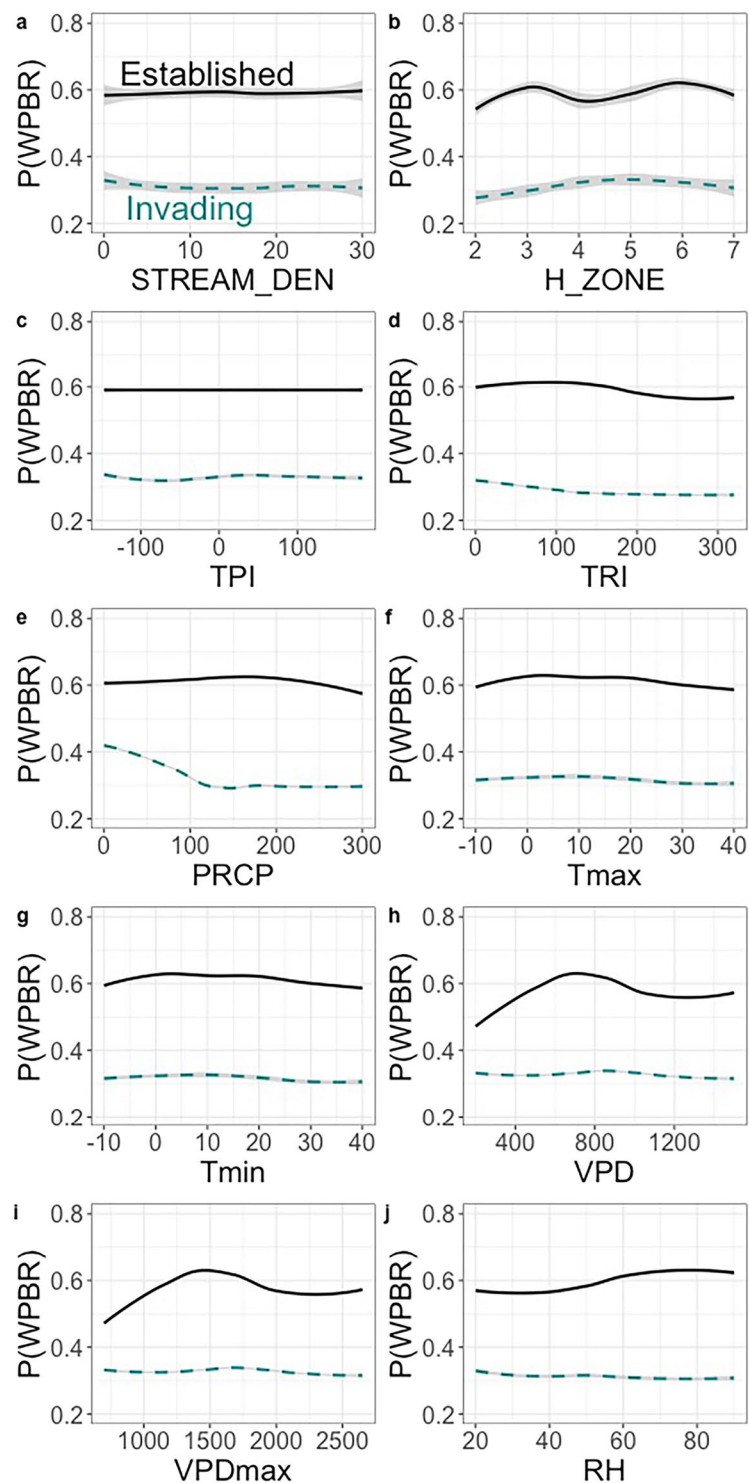
Across models, both short-term (5 and 10-year) and long-term (20-year) climate summaries were important (Table 4). Stream density (STREAM\_DEN), topography, hardiness zone (H\_Zone), precipitation (PRCP), temperature (T), vapor pressure deficit (VPD), and relative humidity (RH) were included in both  $P(WPBR)_{INV}$  and



**Fig. 8** Variable importance plots, the mean decrease in the Gini for the Invading ( $P(WPBR)_{INV}$ ) and Established ( $P(WPBR)_{EST}$ ) models, respectively, for (a,b) 5-year climate summaries, (c,d) 10-year climate summaries, and (e,f) 20-year climate summaries in the western U.S.

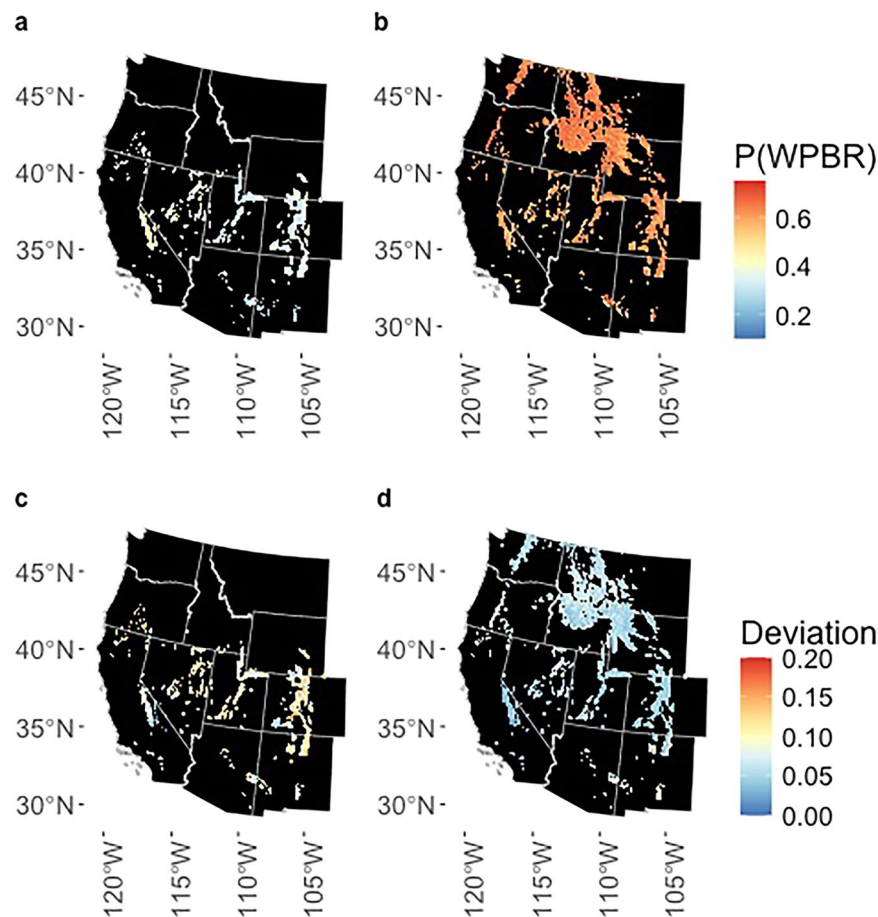
$P(WPBR)_{EST}$  models (Table 4 and Figs. 7, 8). Short-term effects on  $P(WPBR)_{INV}$  were dominated by fall PRCP, while spring, summer, and fall climate was more influential for the 10 and 20-year risk. Summer PRCP, spring Tmin, and fall VPD were important in some  $P(WPBR)_{EST}$  models. Altogether, model performance indicated that landscape attributes and climate summaries could be used to understand conditions that have supported WPBR at the landscape scale where the disease is invading and was well established.

The relationship between the  $P(WPBR)$  and climate variables generally indicated that probabilities increased with moisture and declined with temperature (Fig. 9). The  $P(WPBR)$  increased with stream density, precipitation, and vapor pressure deficit. Hardiness zone and temperature were negatively correlated with the  $P(WPBR)$  (Fig. 9). The highest values were at a VPD of approximately 700 Pa and a VPDmax of approximately 1400 Pa, and the  $P(WPBR)$  declined at lower and higher values in both models. The drivers of the  $P(WPBR)_{INV}$  and the  $P(WPBR)_{EST}$  were similar but exhibited significant differences in their magnitude and sensitivity to topography



**Fig. 9** Sensitivity analysis for models of WPBR risk in areas with low inferred inoculum (blue) and where the disease was established (black). Landscape variation in (a) stream density (STREAM\_DEN), (b) hardness zone (H\_ZONE), (c) topographic position index (TPI), (d) topographic roughness index (TRI), (e) precipitation (PRCP), (f) maximum (Tmax) and (g) minimum (Tmin) temperature, (h) vapor pressure deficit (VPD), (i) maximum vapor pressure deficit (VPDmax), and (j) relative humidity (RH) explained patterns in WPBR risk.

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 vapor pressure deficit, and the  $P(WPBR)_{EST}$  was most sensitive to stream density, precipitation,



**Fig. 10** RustMapper ensemble estimates of the probability of WPBR from models parameterized from (a) areas with low inoculum ( $P(WPBR)_{INV}$ ) and (b) areas where WPBR is well established ( $P(WPBR)_{EST}$ ). The standard deviation in (c)  $P(WPBR)_{INV}$  and (d)  $P(WPBR)_{EST}$  across the High-5 range was low in the western U.S. for 1980–2023.

| Year                       | P(WPBR) <sub>INV</sub> 1980–2023 |      |       | P(WPBR) <sub>EST</sub> 1980–2023 |      |       |
|----------------------------|----------------------------------|------|-------|----------------------------------|------|-------|
| Region                     | Range                            | Mean | >0.50 | Range                            | Mean | >0.50 |
| Total U.S. High-5 Range    | —                                | —    | —     | 0.36–0.83                        | 0.63 | 0.97  |
| Southern U.S. High-5 Range | 0.16–0.6                         | 0.39 | 0.221 | 0.47–0.76                        | 0.61 | 0.99  |

**Table 5.** The mean  $P(WPBR)$  1980–2023 by region for the total U.S. High-5 range and the southern portion of the U.S. High-5 range. Results are displayed for the Invading model ( $P(WPBR)_{INV}$ ) and the Established model ( $P(WPBR)_{EST}$ ).

and relative humidity. The small differences in the primary drivers of  $P(WPBR)_{INV}$  and  $P(WPBR)_{EST}$  (Table 4, Figs. 7, 8) suggests that the WPBR dynamics may be slightly different in the northern and southern landscapes. The magnitude of the probability of observing conditions suitable for WPBR across the High-5 landscape differed between the  $P(WPBR)_{INV}$  and  $P(WPBR)_{EST}$  models (Figs. 9, 10; Table 5). While the  $P(WPBR)_{INV}$  in 1980–2023 was below 0.6 for all of the southern High-5 range,  $P(WPBR)_{EST}$  was greater than 0.5 for the majority (97%) of the High-5 range. The standard deviation across models that were developed using 5, 10, and 20-year climate data was low (0–0.2) for both the  $P(WPBR)_{INV}$  and the  $P(WPBR)_{EST}$ . Given the consistent model performance across climate summaries (5, 10, and 20 years), combined with low variability across climate summaries (Fig. 9c,d), results are presented as ensembles of models developed with climate summaries of different lengths 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 introduced, there are conditions conducive to WPBR across the whole range.



## Usage Notes

Management interventions can reduce the impacts of WPBR on High-5 populations and the ecosystem services they provide<sup>6</sup>. Current and projected forest conditions can affect the likelihood of success of some treatment actions<sup>7</sup>. Proactive management offers the opportunity to prepare healthy populations for resilience before extensive ecological impacts occur. The proactive strategy focuses on activities to promote pine regeneration to increase population size, genetic diversity, and adaptive capacity to maintain forest health. Alternatively, restoration strategies target impacted populations to re-establish viable pine populations, natural processes, and ecosystem services<sup>8,10,60</sup>. For both management approaches, 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).

Decision frameworks require tools that allow managers to prioritize limited resources. RustMapper integrates information on WPBR risk that can be used in mitigation planning for proactive and restoration strategies across boundaries. While the  $P(WPBR)_{INV}$  is more appropriate for regions with low presumed inoculum, the  $P(WPBR)_{EST}$  should be used in areas with presumed high inoculum. The  $P(WPBR)_{EST}$  projections for the more southern U.S. landscapes provide a preview of possible risks if pathogen spread continues and inoculum levels increase. RustMapper can be used to understand current and future risks, identify regions with consistently low risk now and in the future (refugia), define the risk level of specific areas, and select treatment options based on risk and relative chances of success. RustMapper makes this information accessible to resource managers for focused applications and decision support.

## Code availability

The code for RustMapper can be found here: Sparkle Malone. (2025). Malone-Disturbance-Ecology-Lab/ RUSTMapper: RustMapper: White Pine Blister Rust Risk Across High Elevation Forests in the Western United States (RUSTMapper). Zenodo. <https://doi.org/10.5281/zenodo.15212542>.

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## Author contributions

S.L.M. and A.W.S. conceived the project idea. A.W.S. and K.S.B. harmonized data from various independent studies, while S.L.M. collected auxiliary data, developed models, and maintained the code. A.W.S. reviewed analyses and collaborated with S.L.M. on data visualization. Expert reviews were provided by K.S.B., H.S.J.K., J.E.S., M.N. and C.M.C. The manuscript was written, reviewed, and edited collectively by S.L.M., A.W.S., K.S.B., H.S.J.K., J.E.S., M.N. and C.M.C.

## Competing interests

The authors declare no competing interests.

## Additional information

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