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Predicting Present and Future Suitable Climate Spaces (Potential Distributions) for an Armillaria Root Disease Pathogen (*Armillaria solidipes*) and Its Host, Douglas-fir (*Pseudotsuga menziesii*), Under Changing Climates

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Climate change and associated disturbances are expected to exacerbate forest root diseases because of altered distributions of existing and emerging forest pathogens and predisposition of trees due to climatic maladaptation and other disturbances. Predictions of suitable climate space (potential geographic distribution) for forest pathogens and host trees under contemporary and future climate scenarios will guide the selection of appropriate management practices by forest managers to minimize adverse impacts of forest disease within forest ecosystems. A native pathogen (*Armillaria solidipes*) that causes Armillaria root disease of conifers in North America is used to demonstrate bioclimatic models (maps) that predict suitable climate space for both pathogen and a primary host (*Pseudotsuga menziesii*, Douglas-fir) under contemporary and future climate scenarios. Armillaria root disease caused by *A. solidipes* is a primary cause of lost productivity and reduced carbon sequestration in coniferous forests of North America, and its impact is expected to increase under climate change due to tree maladaptation. Contemporary prediction models of suitable climate space were produced using Maximum Entropy algorithms that integrate climatic data with 382 georeferenced occurrence locations for DNA sequence-confirmed *A. solidipes*. A similar approach was used for visually identified *P. menziesii* from 11,826 georeferenced locations to predict its climatic requirements. From the contemporary models, data were extrapolated through future climate scenarios to forecast changes in geographic areas where native *A. solidipes* and *P. menziesii* will be climatically adapted. Armillaria

root disease is expected to increase in geographic areas where predictions suggest *A. solidipes* is well adapted and *P. menziesii* is maladapted within its current range. By predicting areas at risk for Armillaria root disease, forest managers can deploy suitable strategies to reduce damage from the disease.

Keywords: climate change, drought, potential distribution, root disease, species distribution modeling, tree maladaptation

INTRODUCTION

Armillaria root disease, caused by *Armillaria* spp., is a leading cause of growth loss and mortality of a diverse range of horticultural and timber trees in many temperate regions around the world (e.g., Heinzelmann et al., 2019). In coniferous forests of North America, *Armillaria solidipes* (formerly North American *A. ostoyae*) is a native pathogen that causes Armillaria root disease that negatively impacts growth and survival of many conifer species (Ferguson et al., 2003; Lockman and Kearns, 2016) including *Pseudotsuga menziesii* (Douglas-fir), which is a dominant component of many forest stands in western North America and an important tree for ecological, sociological, and economic purposes.

Changing climate, extreme weather events (e.g., drought, high temperatures), and/or other disturbances (e.g., fire, insect attack, and forest management activities) are causing increased disease severity by *A. solidipes* on stressed *P. menziesii* (Morrison, 2011; Murray and Leslie, 2021). Armillaria root disease, in conjunction with the adverse impacts from climate and extreme weather events, can predispose trees to attack by other biotic agents including bark beetles (e.g., Hertert et al., 1975; Kulhavy et al., 1984; Tkacz and Schmitz, 1986), which can result in tree mortality and increased availability of nutritional substrates for inoculum of *Armillaria* species that can, in turn, contribute to future disease on the site. When characterizing the ecological role of *Armillaria* in western North America, it is crucial to consider that *Armillaria* also behaves as a saprophyte, colonizing trees that succumbed to other abiotic and biotic causes. Thus, careful observations are required to determine the interactive role of Armillaria root disease in relation to climate, extreme weather, and other interacting biotic/abiotic factors (Kubiak et al., 2017). While Armillaria root disease is well known for its negative impacts on tree health, causing economic impact and reduced carbon sequestration potential of forests, it is important to note that *Armillaria* can also contribute ecological benefits, which include nutrient cycling, habitat formation (e.g., nesting cavities), and food for wildlife, such as small birds and mammals (e.g., Steeger and Hitchcock, 1998; Parsons et al., 2003; Heinzelmann et al., 2019).

Although information is generally lacking on the incidence and spread of Armillaria root disease over time and space in association with climate and extreme weather events, the known spatial occurrence of *A. solidipes* from extensive sampling offers a unique opportunity to apply bioclimatic modeling to identify climatic components associated with its occurrence. Output from these models can be coupled with GIS to project maps that show the predicted suitable climate space (potential distribution or realized climate niche) across geographic areas, and when coupled with output from general circulation models (GCMs) show predicted future distributions of suitable climate spaces for *P. menziesii* and *A. solidipes*. Understanding the host-pathogen interaction under changing climates allows for predictions of the potential distributions of *P. menziesii* and *A. solidipes* across current and future landscapes to inform Armillaria root disease management.

Armillaria occurs primarily below ground, which represents a distinct environment that is relatively stable from minor weather fluctuations. Below-ground conditions (e.g., soil temperature and moisture) and microclimate can affect *A. solidipes*, soil microbial communities, and/or *P. menziesii*. These below-ground, climatic conditions are influenced by latitude/longitude, elevation, slope, aspect, topography, drainage, soil properties, crown cover, etc. The distribution of Armillaria root disease on a site is largely attributable to soil environments and microclimates that vary within and/or among stands. In addition, the occurrence of *A. solidipes* is associated with plant association groups or habitat types (i.e., well-defined associations of trees, shrubs, and herbaceous plants) that reflect soil temperature (e.g., represented by overstory trees) and moisture (e.g., represented understory plants) in conifer forests of western North America (e.g., McDonald et al., 2000; Kim et al., 2010). At the broadscale, bioclimatic models (e.g., MaxEnt: Maximum entropy species distribution modeling) can use presence-only survey data to project potential distribution of both pathogen and host tree species based on major climatic factors (e.g., 19 bioclimatic variables from the WorldClim) for contemporary or projected future time periods (Phillips et al., 2006). Furthermore, climate layers of projected future climates based on different greenhouse emission scenarios can be used to predict future potential distribution of both pathogen and host tree species under different projected climate scenarios.

In western North America, Armillaria root disease caused by *A. solidipes* is common on trees that are ecophysiologically maladapted (stressed by environmental factors), which can be attributed to climatic maladaptation and/or other disturbances (McDonald et al., 1987a; McDonald, 1990; Murray and Leslie, 2021). Projections of climate change in the northwestern United States predict an increase in the frequency and intensity of drought and higher temperatures that will result in more stressful environmental conditions for forest trees (Chmura et al., 2011). Thus, a reasonable approach toward predicting climate change impacts on Armillaria root disease at the broad scale is to use bioclimatic models to predict the realized climatic niche for the *P. menziesii* and *A. solidipes* pathosystem (e.g., Rehfeldt et al., 2006; Klopfenstein et al., 2009). Although *P. menziesii* spans a

wide geographic (19–44°N latitude and 100–118°W longitude; Hermann and Lavender, 1990) and climatic range in western North America, it is considered a specialist in terms of its climatic requirements for populations, making individual stands especially vulnerable to climate-induced stresses (e.g., Weiskittel et al., 2012; Rehfeldt et al., 2014b).

Our goals were to (1) predict suitable climate spaces (potential distributions) for *P. menziesii* and *A. solidipes* across western North America for contemporary climate and projected climate for the average of years 2081–2100; and (2) draw inferences from comparisons of the prediction models for the host (*P. menziesii*) and pathogen (*A. solidipes*) to predict geographic areas where *P. menziesii* will become maladapted due to climate change, which will likely exacerbate Armillaria root disease in areas where *A. solidipes* remains climatically adapted. We used georeferenced occurrence locations for visually identified *P. menziesii* and DNA sequence-confirmed *A. solidipes* in combination with location-specific climate data for bioclimatic modeling to predict where *A. solidipes* is likely to occur and cause increased disease pressure on maladapted and/or stressed *P. menziesii* under changing climatic conditions.

MATERIALS AND METHODS

Pseudotsuga menziesii Location Data

A total of 11,826 locations of *P. menziesii* were used from selected "fuzzy" coordinates obtained from Forest Inventory Analyses (FIA) data (Rehfeldt et al., 2014a) within the continental United States (locations from Canada and Mexico were not included because the FIA data are only available for the contiguous United States) (**Figure 1A**).

Armillaria solidipes Surveys, Identification, and Location Data

Briefly, surveys for Armillaria root disease pathogens require collection of *Armillaria* mycelia (e.g., mycelial fan, rhizomorph, or basidiocarp) for *Armillaria* identification via DNA sequences (e.g., Kim et al., 2000, 2006; Ross-Davis et al., 2012; Elías-Román et al., 2013; Klopfenstein et al., 2017). Careful examination of symptoms and signs can confirm that *Armillaria* is acting as a pathogen on the host. In addition, precise locations of identified *Armillaria* collections were recorded so that bioclimatic modeling can be applied to determine climatic influences on Armillaria root disease pathogens.

Armillaria solidipes point locations were collected from previous studies of distribution and ecology from the states/provinces of Washington, Oregon, Idaho, Montana, Utah, Wyoming, South Dakota, Arizona, Colorado, New Mexico, British Columbia (BC, Canada), and Chihuahua (Mexico) (McDonald et al., 1987b, 2011; Shaw, 1989; Omdal et al., 1995; McDonald, 1998, unpublished data; Kim et al., 2000; Ferguson et al., 2003; Van der Star et al., 2003; Worrall et al., 2004; Hanna et al., 2007, 2008, 2009, 2014; Blodgett and Lundquist, 2011; Klopfenstein et al., 2012; Berbee et al., 2014, 2015; Hoffman et al., 2014; Blodgett et al., 2015 and Hanna, unpublished data). For *Armillaria* surveys, the main lateral roots of diverse trees were excavated and inspected, and *Armillaria* samples were collected as mycelial fans under the bark, rhizomorphs, basidiocarps, and/or decayed wood. Isolates were established in culture and were confirmed as *A. solidipes* using basidiocarp morphology (e.g., some Canadian locations) and DNA-based species identification (e.g., Kim et al., 2000, 2006; Ross-Davis et al., 2012; Elías-Román et al., 2013; Klopfenstein et al., 2017). From these studies, *A. solidipes* isolates were recorded from 382 distinct locations throughout western North America (**Figure 1B**).

Climate Data and Bioclimatic Variables

Climate-based, species-distribution models using MaxEnt and 19 bioclimatic variables (**Table 1**) from Worldclim version 2.1 (Fick and Hijmans, 2017) were created for both host (*P. menziesii*) (**Figure 2**) and pathogen (*A. solidipes*) (**Figure 3**) for the contemporary (1970–2000) and future time periods (2081–2100) using Coupled Model Intercomparison Project phase 6 (CMIP6) (Eyring et al., 2016) data consisting of two different Shared Socioeconomic Pathways (SSPs) paired with The Canadian Earth System model version 5 (CanESM5) GCM (Swart et al., 2019) using 2.5-min data. In general, five SSPs narratives describe the broad socioeconomic trends that could shape future society and we chose to use two scenarios: SSP2-4.5 ("middle of the road" world where trends do not shift markedly from historical patterns) and SSP5-8.5 ("fossil-fueled development," which follows path of rapid and unconstrained growth in economic output and fossil fuel-based energy use). In addition, change in climate suitability for *P. menziesii* from the contemporary time period to the future time period for both SSPs (SSP2-4.5 and SSP5-8.5) were visually compared (**Figure 4**).

MaxEnt Modeling

To allow calculations in suitability models, input data for MaxEnt consisted of SWD (samples with data) files for each species that linked geographic coordinates (presence point locations) with climate variable values for each of the 19 bioclimatic variables. The models used 19 bioclimatic variables in three sets of 2.5-min, interpolation grids from worldclim.org (Fick and Hijmans, 2017). MaxEnt also uses SWD files of background locations or "pseudo-absences" to "train" the models. For the *P. menziesii* model, 292,639 actual absence point locations were used as background data. MaxEnt's logistic output (an index of probability from 0 to 1) was chosen for easier conceptualization compared to MaxEnt's raw exponential model. For the *A. solidipes* model, background points were created from 10,000 randomly selected geographical locations within the geographic range of the collected isolates.

MaxEnt parameters included cross-validation with 20 replicate runs to generate statistical data. Quantum GIS (QGIS)[1] was used to create the final outputs using MaxEnt's cumulative output. Each cumulative value is the sum of probabilities of cells less than or equal to the cell grid, times 100. MaxEnt's cumulative output was chosen for easier conceptualization compared to MaxEnt's logistic (an index of probability from 0 to 1) or raw exponential output. Totals of 11,826 and 382 locations were used for *P. menziesii* and *A. solidipes*, respectively.

[1] http://www.qgis.org/en/site/

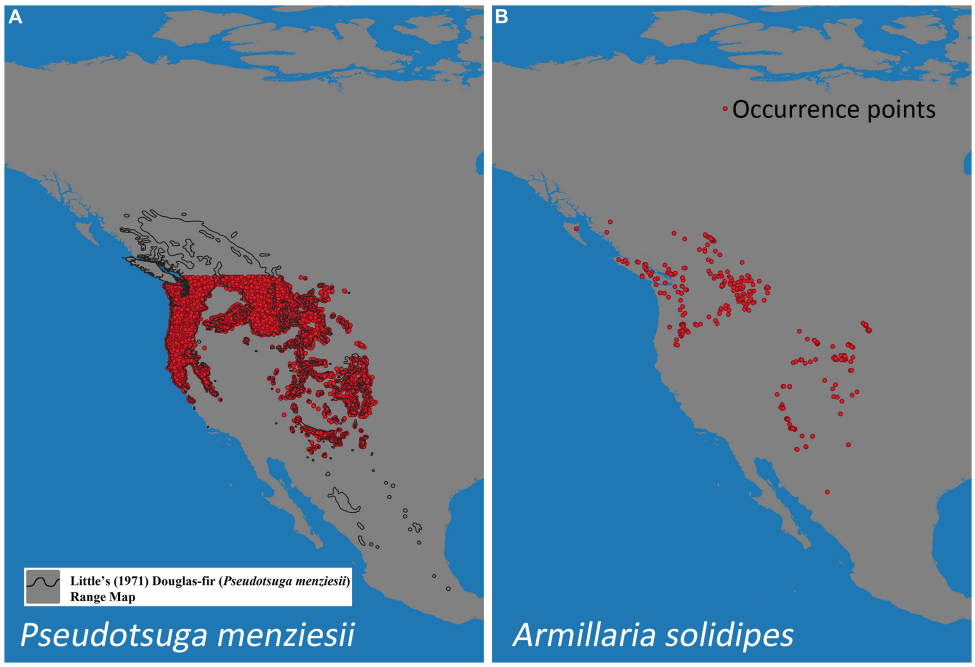

FIGURE 1 | Occurrence points of *Pseudotsuga menziesii* **(A)** and *Armillaria solidipes* **(B)** in North America. The black outline **(A)** designates Little's (1971) *P. menziesii* range map.

To evaluate the reliability of the model, the receiver operating characteristic (ROC) curve of the jackknife method was used (Dorfman et al., 1992). The areas under the ROC curve (AUC) values (ranging from 0 to 1) were generated to calculate model performance (e.g., prediction accuracy) based on true-positive, false-positive, true-negative, and false-negative rates. Higher AUC values (> 0.9) indicate higher reliability of the model (Wiley et al., 2003). Permutation importance (resulting from the values of each environmental variable on training presence and background data being randomly permuted, the model then re-evaluated on the permuted data; resulting drop in training AUC is normalized to percentages) of 19 bioclimatic variables derived from the WorldClim database used to model suitable climate space (potential distribution) based on known occurrence points for *P. menziesii* and *A. solidipes* (**Table 1**).

RESULTS

The MaxEnt bioclimatic model using all occurrence records of *P. menziesii* (N = 11,826) and *A. solidipes* (N = 382) (**Figures 1A,B**, respectively) shows a prediction where many geographic areas throughout the North America have some degree of probability of suitable climate (i.e., possesses a climate suitable for species survival) for both *P. menziesii* and *A. solidipes* (**Figures 2**, **3**, respectively). With 1.0 representing a perfect value and 0.5 representing presence by chance, the average test AUC ± standard deviation values, based on 20 replicate runs, were 0.953 ± 0.002 for *P. menziesii* and 0.960 ± 0.010 for *A. solidipes*.

For the *P. menziesii* model, the major bioclimatic variables (i.e., > 10%) of permutation importance were mean temperature of warmest quarter (Bio10), precipitation of coldest quarter (Bio19), and precipitation of driest quarter (Bio17). For the *A. solidipes* model, temperature annual range (Bio7), maximum temperature of warmest month (Bio5), annual mean temperature (Bio1), and minimum temperature of coldest month (Bio6) were the major bioclimatic variables (**Table 1**).

The predicted contemporary distribution of *P. menziesii* is consistent with the actual range of this tree species reported by Little (1971) (**Figure 2A**). The predicted contemporary distribution of *A. solidipes* shows a geographically wide distribution with more suitable habitat in the wetter forests of the Pacific Northwest and with pockets in the southwestern United States, which appear to be associated with areas that have monsoon seasons (**Figure 3A**). In general, the bioclimatic models predict that the contemporary suitable climatic space (potential distribution) of *A. solidipes* has considerable overlap with that of *P. menziesii* (e.g., northern Idaho, northern Cascade Mountains, Rocky Mountains, etc.).

The models predicted future suitable climate spaces for Year 2081–2100 under two climate scenarios, SSP2-4.5 and SSP5-8.5, are shown in **Figures 2B,C**, **3B,C** respectively. For both *P. menziesii* and *A. solidipes*, the suitable habitat shifts northwest toward more northern and coastal areas. Notably, for *P. menziesii*, the suitable climate space shifts considerably northward and is much smaller in size under the SSP5-8.5 model compared to the SSP2-4.5 model (**Figures 2B,C**). Predicted changes in climate suitability for *P. menziesii* in western North America from contemporary (1970–2000) to

TABLE 1 | Summary of MaxEnt's permutation importance value for each of the contemporary 19 bioclimatic variables (Bio1–Bio19) derived from the WorldClim (worldclim.org) database (1970–2000) used to model suitable climate space (potential distribution) based on occurrence points of *Pseudotsuga menziesii* and *Armillaria solidipes*.

Variable (Units)		*Pseudotsuga menziesii*	*Armillaria solidipes*
Bio1	Annual mean temperature (°C)	0.9	**12.7**
Bio2	Mean diurnal range [Mean of monthly (max temp - min temp)] (°C)	0.2	1
Bio3	Isothermality (Bio2/Bio7) (× 100)	0.5	0.7
Bio4	Temperature seasonality (SD × 100, Coefficient of variation) (°C)	9.7	1.2
Bio5	Maximum temperature of warmest month (°C)	0.8	**16.6**
Bio6	Minimum temperature of coldest month (°C)	4.4	**12.5**
Bio7	Temperature annual range (Bio5-Bio6) (°C)	3.8	**38.8**
Bio8	Mean temperature of wettest quarter (°C)	1.2	0.6
Bio9	Mean temperature of driest quarter (°C)	1.5	4.1
Bio10	Mean temperature of warmest quarter (°C)	**35**	0.2
Bio11	Mean temperature of coldest quarter (°C)	4	0
Bio12	Annual precipitation (mm)	2.8	0.5
Bio13	Precipitation of wettest month (mm)	2.2	0.3
Bio14	Precipitation of driest month (mm)	3.2	3.8
Bio15	Precipitation seasonality (Coefficient of variation) (-)	1.6	0.6
Bio16	Precipitation of wettest quarter (mm)	0.5	0.1
Bio17	Precipitation of driest quarter (mm)	**10.8**	0.7
Bio18	Precipitation of warmest quarter (mm)	4.8	4.9
Bio19	Precipitation of coldest quarter (mm)	**12**	0.8

Variables with the greatest permutation importance (> 10%) are in bold.

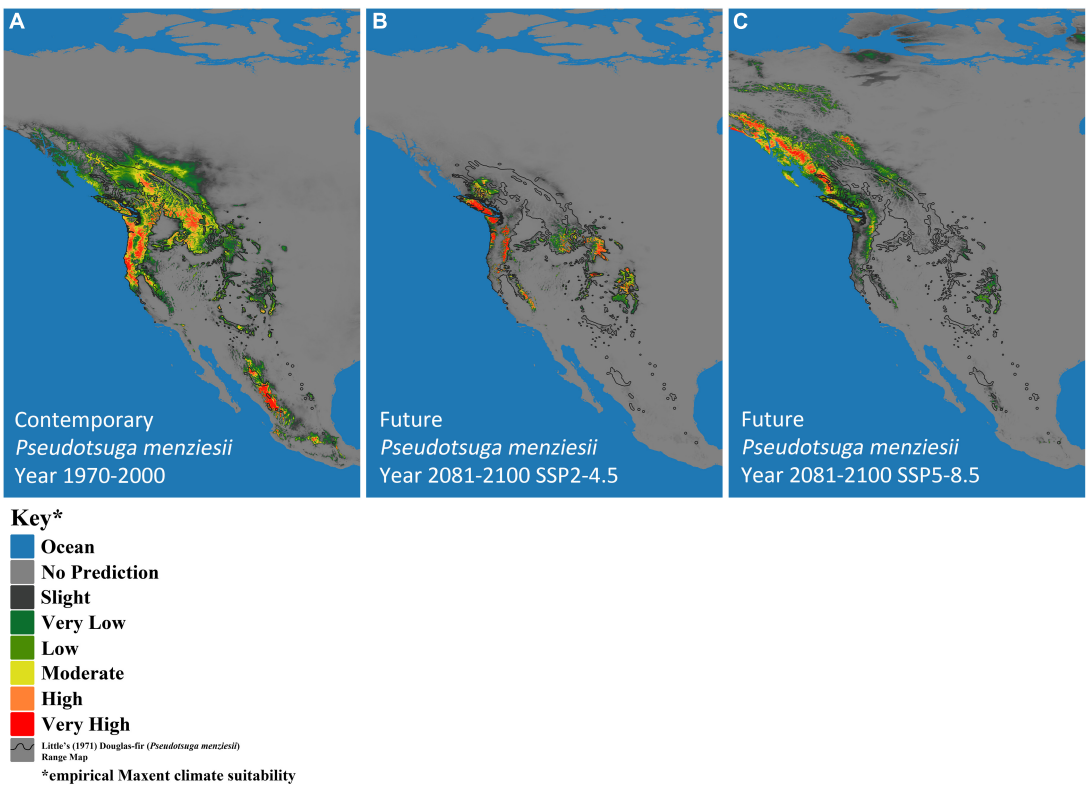

FIGURE 2 | MaxEnt-based, bioclimatic models for *Pseudotsuga menziesii* (Douglas-fir) in western North America. **(A)** Contemporary years (1970–2000), and two future models show two Shared Socioeconomic Pathway (SSP) scenarios (SSP2-4.5 and SSP5-8.5), **(B)** SSP2-4.5 and **(C)** SSP5-8.5. Darkest gray represents predicted empirical MaxEnt climate suitability, with dark green, light green, yellow, orange, and red indicating increased probability of climatic suitability, respectively. The black outline designates Little's (1971) *P. menziesii* range map.

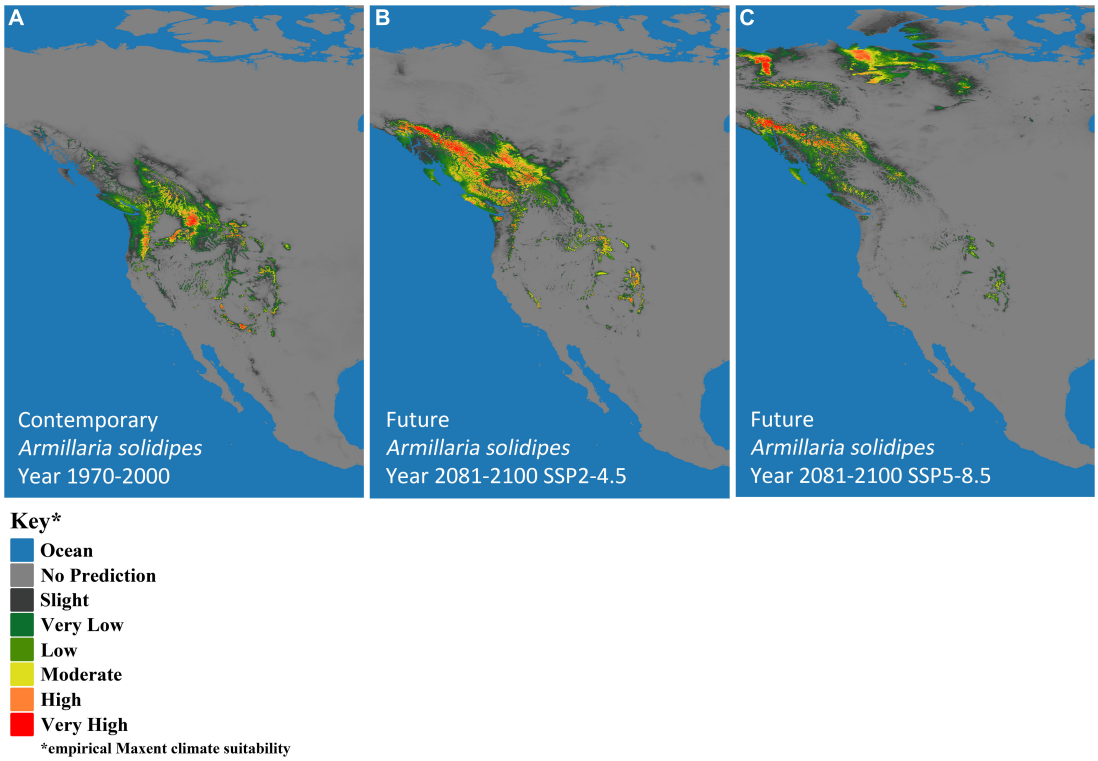

FIGURE 3 | MaxEnt-based, bioclimatic models for *Armillaria solidipes* in western North America. **(A)** Contemporary years (1970–2000) and two future models show two Shared Socioeconomic Pathway (SSP) scenarios (SSP2-4.5 and SSP5-8.5), **(B)** SSP2-4.5 and **(C)** SSP5-8.5. Darkest gray represents predicted empirical MaxEnt climate suitability, with dark green, light green, yellow, orange, and red indicating increased probability of climatic suitability, respectively.

future (2081–2100) models for both SSPs (SSP2-4.5 and SSP5-8.5) are shown in **Figures 4A,B**. Both future climate scenarios indicate increasing probability of disappearing climate suitability (i.e., ecophysiologically maladapted trees) for *P. menziesii* within its current range. Distributions of suitable climate space for *P. menziesii* in the Rocky Mountains that can be observed in **Figure 4A** are conspicuously absent under the more severe climate-change model of SSP5-8.5 (**Figure 4B**), though some climate suitability is observed in northern coastal regions.

When comparing the SSP2-4.5 and SSP5-8.5 models for *A. solidipes*, differences in suitable climate space are striking. In **Figure 3B** (SSP-4.5), the suitable climate space shifts northward and toward coastal areas, fairly similar to the *P. menziesii* suitable climate space predicted under the SSP2-4.5 model. However, the suitable climate space predicted under the SSP5-8.5 model highlights a new northern region of climatic suitability that coincides with newly identified areas with potential climatic suitability for *P. menziesii* under the same model (**Figure 3C**).

DISCUSSION

This study provides a sound approach for predicting potential forest disease incidence and potential severity under contemporary and changing climate scenarios. We used presence-only occurrence data for *A. solidipes* and both presence and absence (as background data) occurrence data for *P. menziesii* to produce predictions of potential contemporary and future distributions of these species using MaxEnt modeling. Predicted shifts in suitable climate space for both *P. menziesii* and *A. solidipes* are highly correlated as the predicted change in climate suitability moves dramatically northward for years 2081–2100 using both SSPs (SSP2-4.5 and SSP5-8.5). The results from this study strongly suggest that Armillaria root disease will be exacerbated in many areas where *P. menziesii* is predicted to become increasingly maladapted and extreme weather events will likely become more common. Predicting the potential distribution of both pathogen (*A. solidipes*) and a primary host (*P. menziesii*) under contemporary and future climate scenarios is critical to deploy suitable strategies to reduce damage from the disease.

In this study, the MaxEnt models performed remarkably well, based on the high AUC values (0.953 for *P. menziesii* and 0.960 for *A. solidipes*) that indicate high reliability and predictive accuracy. This approach seems to be quite reliable, especially given the relatively limited occurrence data for *A. solidipes*. In addition, MaxEnt is a robust predictor of collinearity in model training and highly correlated variables have little impact on the model output (Feng et al., 2019). This study predicts areas at risk for Armillaria root disease using the MaxEnt model, which works well with limited number of presence-only occurrence data (Phillips et al., 2006). Unlike *P. menziesii* (N = 11,826),

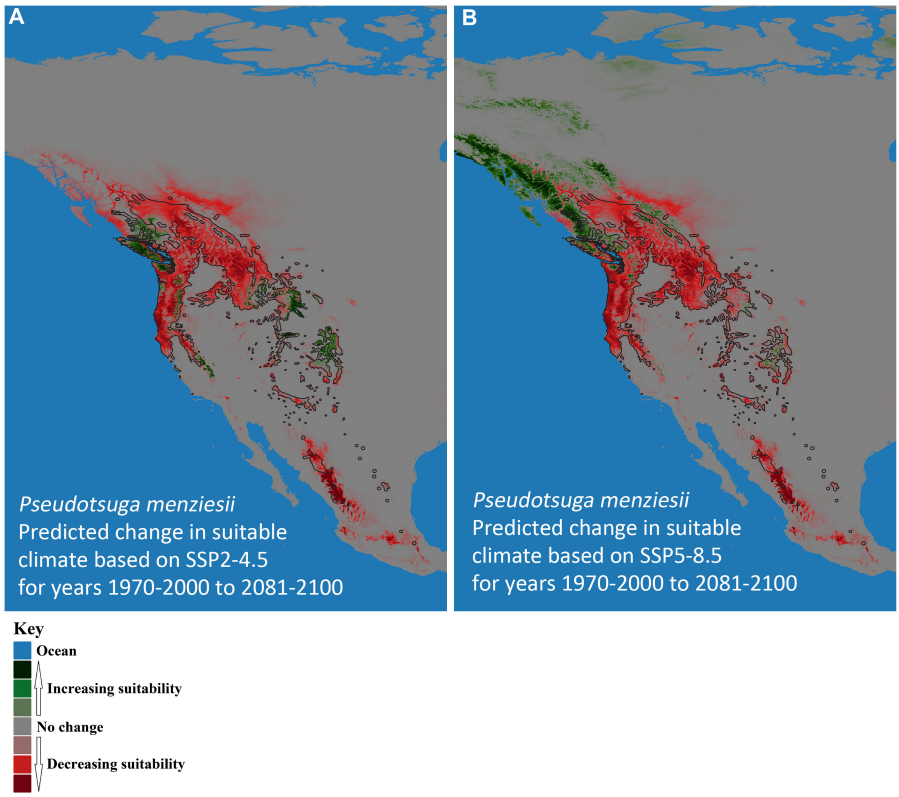

FIGURE 4 | Predicted change in climate suitability for *Pseudotsuga menziesii* (Douglas-fir) in western North America from contemporary (1970–2000) to future (2081–2100) models. **(A)** Shared Socioeconomic Pathway (SSP) SSP2-4.5 and **(B)** SSP5-8.5. Pink to dark red, respectively, indicates increasing probability of disappearing climate suitability (i.e., ecophysiologically maladapted trees), while light green to dark green, respectively, represents predictions of new climatically suitable areas. The black outline designates Little's (1971) *P. menziesii* range map.

the acquisition of occurrence data for *A. solidipes* (N = 382) required highly labor-intensive work including excavation of lateral roots, pathogen isolation, and DNA sequence-based identification to confirm occurrence (Klopfenstein et al., 2009). In addition, absence data for *Armillaria* are difficult to obtain and confirm with certainty. For these reasons, MaxEnt was applied to compare both host (*P. menziesii*) and pathogen (*A. solidipes*) using the same modeling parameters, although the model slightly overpredicts the suitable climate space compared to a presence/absence model (see Rehfeldt et al., 2014a for a climate niche model of *P. menziesii* based on a Random Forests classification algorithm). Overall, under the contemporary climate, the predicted potential distribution of *P. menziesii* using the MaxEnt is generally congruent with the established range map of *P. menziesii* within the continental United States (Little, 1971). Recently, MaxEnt bioclimatic models have been widely used to investigate the suitable climate space of other plants and plant pathogens, with high predictive performance (e.g., Kumar and Stohlgren, 2009; Khanum et al., 2013; Remya et al., 2015; Stewart et al., 2018, 2020; Tang et al., 2021).

Several other critical variables can be implemented to improve the precision of these prediction models for *P. menziesii* and *A. solidipes*. For *P. menziesii*, the MaxEnt models were based on presence and absence data at the species level. However, *P. menziesii* exhibits climatic adaptation at the intraspecies level where a given population within the species is genetically adapted to persist only over a portion of the climate range occupied by the species as a whole (e.g., Weiskittel et al., 2012; Rehfeldt et al., 2014a). Because our bioclimatic models do not explicitly include intraspecies adaptive structure (i.e., climate types), they likely underestimate the extent of climatic maladaptation within the species under predicted climate change. Of special note, *P. menziesii* with higher levels of drought tolerance were also associated with higher levels of resistance to Armillaria root disease, caused by *A. solidipes* (Cruickshank and Filipescu, 2017). Furthermore, summer droughts were associated with increased *A. solidipes*-caused mortality of *P. menziesii* in southern BC, Canada (Murray and Leslie, 2021). These findings further support that climatic maladaptation of *P. menziesii* will lead to increased infection by *A. solidipes*. Thus, predictions of *P. menziesii* maladaptation under future climate scenarios likely underestimate the extent of maladaptation and associated increased susceptibility to Armillaria root disease. However, east of the Cascade Range, *P. menziesii* is one of the most susceptible tree species to Armillaria root disease (Morrison, 1981; Robinson and Morrison, 2001), but the faster growing coastal variety of *P. menziesii* succumbs less often to *A. solidipes* infection (Johnson et al., 1972; Robinson and Morrison, 2001).

In addition, the population structure of *A. solidipes* is unknown; however, an individual *A. solidipes* genet (vegetative clone) can reside on a site up to ca. 1900–8650 years (Ferguson et al., 2003), suggesting that this root pathogen may possess a broad tolerance for changing climatic conditions. To address genetic differences within the species, population-level data are needed for both host and pathogen to refine climate-based models. Additional predictive variables (e.g., soil types, soil temperature and moisture, drainage properties/patterns, solar radiation, predictions of other *Armillaria* species, soil microbial communities, etc.) will affect the suitable climate distribution of *A. solidipes*, and this information could improve the resolution of predictive maps.

Reliable, long-term records are unavailable for quantifying Armillaria root disease levels because of difficulties associated with below-ground surveying, sampling, and identifying *Armillaria* spp. Long-term monitoring for Armillaria root disease in relation to weather/climate factors would provide an opportunity to directly determine climatic influences on the impact of the disease; however, such studies are complex because tree maturity and other stand conditions also change over time. Long-term monitoring is needed to further establish any climatic relationships with *P. menziesii* maladaptation, *A. solidipes* growth/survival, and Armillaria root disease of *P. menziesii*. Monitoring must also consider that the majority of *P. menziesii* associated with Armillaria root disease show no readily observable symptoms, except slower growth (Morrison et al., 2000; Cruickshank et al., 2011). In addition, evidence suggests complex interactions among *Armillaria* spp., in which some *Armillaria* sp. may serve as a biocontrol against more pathogenic *Armillaria* sp. under favorable site conditions (e.g., *A. altimontana* vs. *A. solidipes*) (Hanna, 2005; Warwell et al., 2019). For this reason, bioclimatic modeling of *Armillaria* spp. that are currently existing as saprophytes in a non-pathogenic mode is also warranted. Monitoring data need to include presence/absence of accurately identified *A. solidipes*, some measure of abundance (inoculum), and virulence of *Armillaria* to allow further refinements of climate-Armillaria root disease predictions. Continued surveys are also needed to further validate the relationship of Armillaria root disease with maladapted forest trees at diverse geographic locations.

Although the ranges of *P. menziesii* and *A. solidipes* show considerable overlap, *P. menziesii* extends further south into Mexico (Oaxaca) and it can exist in different regions with distinct climatic niches where *A. solidipes* does not occur (Cannon et al., 2008). Any differences in the ranges of *P. menziesii* and *A. solidipes* likely explain why the important climate variables (permutation importance > 10%) were different for *P. menziesii* and *A. solidipes* models. Mean temperature of warmest quarter (Bio10), precipitation of coldest quarter (Bio19), and precipitation of driest quarter (Bio17) are the significant variables to predict contemporary distribution for *P. menziesii*; whereas, temperature annual range (Bio7), maximum temperature of warmest month (Bio5), annual mean temperature (Bio1), and minimum temperature of coldest month (Bio6) were the major variables for *A. solidipes*. Among climate variables affecting *P. menziesii* distribution, the mean temperature of warmest quarter (Bio10) showed a greatest contribution (35%) followed by the precipitation of coldest (12%) and driest (10.8%) quarters. A previous study (Rehfeldt et al., 2014b) also found that temperature- and precipitation-related variables were important to predict species distribution of *P. menziesii*.

The climatic variables related to temperature demonstrated significant roles in the spatial distribution of *A. solidipes* in this study. Because *A. solidipes* can exhibit an extremely long-term occupancy of a site (e.g., Ferguson et al., 2003), this root pathogen apparently has the capacity of broad tolerance for changing climatic conditions. However, within a site, *A. solidipes* spreads predominately via vegetative growth of rhizomorphs, and the rate of *Armillaria* rhizomorph growth varies dependent on climatic factors, but warmer winters could extend the period for rhizomorph growth (e.g., Rishbeth, 1978; Van Der Kamp, 1993; Peet et al., 1996; Cruickshank et al., 1997). In situations where *Armillaria* spread via basidiospores, higher precipitation and temperatures in autumn will likely favor production of *Armillaria* basidiocarps, especially in Boreal regions (Ferguson et al., 2003; Heinzelmann et al., 2019). In general, growth and dispersal of *Armillaria* may specifically benefit from mild and moist seasons, while hot and dry seasons may increase host stress that allows *Armillaria* to overcome host defenses (Heinzelmann et al., 2019), which suggests that seasonal climates are important factors that contribute to Armillaria root disease.

Although predictions of future suitable climate space for *P. menziesii* and *A. solidipes* are dependent on the accuracy of the projected climate grids, the trends indicate that suitable climate space for both species will move northward and toward higher elevations under both SSP2-4.5 and SSP5-8.5 pathways. Under SSP2-4.5 and SSP5-8.5 conditions, while suitable climate for *A. solidipes* is predicted to decrease in many areas of the inland western United States and BC, Canada, *A. solidipes* will remain adapted to many areas of this region, where it will likely still persist and likely contribute significantly to decreased forest health and increased mortality where maladapted hosts remain. However, these models do not take adaptation into account, but it is presumed unlikely that either of these relatively long-lived species can dramatically adapt within such a short period time. A plausible hypothesis is that maladaptation (stress) caused by climate change can predispose host trees and result in increased susceptibility to root pathogens (e.g., Kliejunas et al., 2009; Sturrock et al., 2011).

The science-based information to predict potential distribution of Armillaria root disease pathogens and host trees under present and future climate scenarios will inform strategies to reduce Armillaria root disease. For example, predictive models will help identify tree populations at risk and prioritize species and seed source selection to address the objectives of adaptive management. In general, tree species/populations that are predicted to be adapted to future climates can be selected for or planted within sites that are expected to have suitable climate for the *Armillaria* pathogen. Many existing or naturally regenerated tree populations that exhibit a moderate-to-high degree of phenotypic plasticity for climatic adaptability

(i.e., generalists), such as *P. monticola*, will likely experience less stress from climatic maladaptation and should also exhibit higher resistance/tolerance to Armillaria root disease. Other forest management practices that reduce tree stress, such as increased spacing, may also reduce impacts of Armillaria root disease under a changing climate.

CONCLUSION

Contemporary and future predictions of suitable climate space of *P. menziesii* and *A. solidipes* generated by MaxEnt modeling is an informative tool that can be used to help reduce impacts from Armillaria root disease under changing climates. It is important to note, however, predicted suitable climate space for a species does not necessarily correspond to the future distribution of that species. Although the co-occurrence of suitable climate space for the pathogen and its host does not necessarily result in disease, it is a likely prerequisite for disease. As discussed above, future species distribution and the occurrence of disease will depend on many factors, such as population structure, migration, regeneration, competition, susceptibility to insect attack and diseases, and other interacting factors. The realized distribution of a species will be determined by the interactions among diverse biological, climatic, and environmental factors. Regardless, this study provides an approach to examine the influence of climate on the distribution of an Armillaria root disease pathogen (*A. solidipes*) and its host tree (*P. menziesii*). Such approaches are especially useful in determining areas with climate where *Armillaria* pathogens should not occur, and of course, Armillaria root disease will not occur in areas where the *Armillaria* pathogen does not occur. The climate-based modeling methods developed from this study can also be used to model other important forest pathogens and examine the potential for invasive species to occupy new geographic areas under contemporary and future climates.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article and further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

NK, JH, JS, MW, GM, and M-SK designed the study and collected a partial *Armillaria solidipes* data. M-SK, NK, JS, and JH wrote the first draft of the manuscript. JH performed the data analyses. All authors contributed to manuscripts revision and approved the submitted version.

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