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BIOCLIMATIC MODELING PREDICTS POTENTIAL DISTRIBUTION OF *ARMILLARIA SOLIDIPES* AND *PSEUDOTSUGA MENZIESII* (DOUGLAS-FIR) UNDER CONTEMPORARY AND CHANGING CLIMATES IN THE INTERIOR WESTERN USA

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INTRODUCTION

Pseudotsuga menziesii (Douglas-fir) is a dominant component of forest stands in much of western North America. It is an important tree to the timber industry, yielding more timber than any other species in North America. It is also extremely important for wildlife as habitat and food. Many small birds and mammals feed on its seeds. *Armillaria solidipes* [pending vote to conserve *A. ostoyae* (Redhead *et al.* 2011)] is also a key component of forest stands throughout much of western North America (Hanna 2005). It is an aggressive pathogen of conifers causing tree mortality and growth loss (Cruickshank 2000). In particular, *P. menziesii* (and specifically the inland subspecies) is one species along with *Abies grandis* (grand fir) and *A. lasiocarpa* (subalpine fir) that can have the highest rates of susceptibly to *A. solidipes* (McDonald *et al.* 1987a). These species have a long history of co-evolution and co-distribution over millions of years. Under the host/stress/saprogen concept, disease develops when these secondary pathogens already on-site invade host tissue after environmental stress (Houston 1992). These stressors include climate, human disturbance, arthropod pests, and other pathogens. Such diseases are believed to increase in severity and prevalence under climate change as trees become progressively maladapted to their environments (Kliejunas *et al.* 2009). In this study, we use DNA-based methods to confirm species identification and utilize location-specific climate data for bioclimatic modeling to predict where *A. solidipes* is likely to occur and cause increased disease pressure on *P. menziesii* under changing climatic conditions.

OBJECTIVES

The objectives of this study are to 1) determine suitable climate space (potential distribution/realized climate niche) for *Armillaria solidipes* across inland North America for contemporary climate and projected climate for the average of years 2061-2080; 2) determine suitable climate space (potential distribution/realized climate niche) for *P. menziesii* across inland North America for contemporary climate and projected climate for the average of years 2061-2080; and 3) make comparisons between the prediction models of the pathogen and host to examine potential maladaptation pressures caused by climate change.

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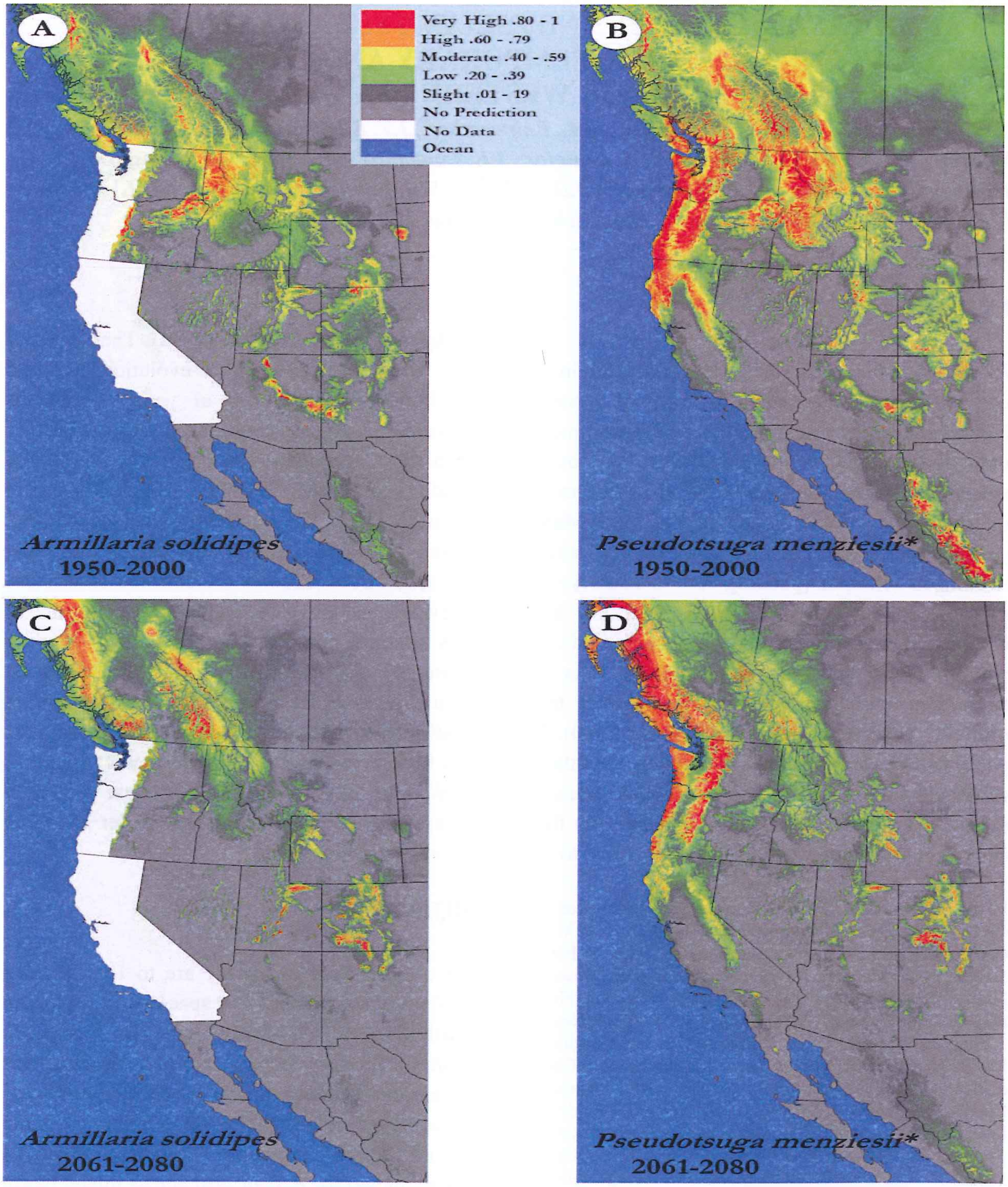

Figure 1. *Maximum Entropy bioclimate model of suitable climate space (potential distribution) for* ***A****: predicted contemporary (1950-2000) Armillaria solidipies,* ***B****: predicted contemporary (1950-2000) Pseudotsuga menziesii,* ***C****: predicted for the years 2061-2080 Armillaria solidipes,* ***D****: predicted for the years 2061-2080 Pseudotsuga menziesii. Areas of lowest to highest suitability of climate space are indicated by dark grey, light green, yellow, orange, and red. *Predicted climate suitability of Pseudotsuga menziesii based solely on U.S.A. locations. Therefore, Canadian and Mexican predictions are less accurate.*

METHODS

Climate-based, species-distribution models using Maximum Entropy (MaxEnt) were created using the techniques described in Phillips *et al.* 2006 and Klopfenstein *et al.* 2009: Figure 1, A - *A. solidipes* contemporary (1950-2000) predicted suitable climate; B -*P. menziesii* contemporary (1950-2000) predicted suitable climate, C - *A. solidipes* year 2061-2080 predicted suitable climate; and D - *P. menziesii* year 2061-2080 predicted suitable climate. The models used 19 bioclimatic variables (e.g., annual mean temperature, maximum temperature of warmest month, annual precipitation, precipitation of wettest month, precipitation of coldest quarter, etc.) in two sets of interpolation grids (ca. 1-km^2 resolution) from worldclim.org (Hijmans 2005). One set contained environmental data for contemporary climate (based on data from 1950-2000) and the other had climate projection grids for the years 2061-2080 based on data from the Intergovernmental Panel on Climate Change/Coupled Model Intercomparison Project Phase 5 (IPCC/CMIP5). For the 2061-2080 predictions we used the representative concentration pathway 8.5 (RCP8.5), which represents a "business-as-usual" continued rise in CO_2 greenhouse-gas scenario and the global circulation model (GCM) HadGEM2-ES (Collins *et al.* 2008; Riahi *et al.* 2011).

To allow calculations in suitability models, input data for MaxEnt consisted of SWD "samples with data" files for each species that linked climate variable values for each of the 19 bioclimatic variables with geographic coordinates (presence point localities). *Armillaria solidipes* point locations were collected from previous studies of distribution and ecology from the states/provinces of Washington, Oregon, Idaho, Montana, Utah, Wyoming, Arizona, Colorado, New Mexico, British Columbia, and Chihuahua (McDonald *et al.* 1987b; Shaw 1989; Omdal *et al.* 1995; McDonald *et al.* 1998; Kim 1999; Kim *et al.* 2000; Ferguson *et al.* 2003; Worrall *et al.* 2004; Hanna 2005; Hanna *et al.* 2007; Hanna *et al.* 2008a; Hanna *et al.* 2008b; Blodgett and Lundquist 2011; McDonald *et al.* 2011; Klopfenstein *et al.* 2012; Hanna *et al.* 2014; Hoffman *et al.* 2014; Blodgett *et al.* 2015; and Hanna *et al.* unpublished data). From these studies, *A. solidipes* isolates were recorded from 378 distinct locations throughout inland western North America. The isolates were confirmed as *A. solidipes* using DNA-based species identification at the Forestry Science Laboratory, Rocky Mountain Research Station in Moscow, Idaho using similar techniques as described by Kim *et al.* (2006), Ross-Davis *et al.* (2012), and/or Elías-Román *et al.* (2013). Many isolates were also identified by somatic incompatibly testing and/or basidiocarp morphology. For *P. menziesii*, a total of 12,152 locations were used from selected 'fuzzy' coordinates obtained from Forest Inventory Analyses data (please refer to Rehfeldt *et al.* 2014 for information about how these points were selected) within the continental USA. Locations from Canada and Mexico were not included. MaxEnt also uses SWD files of background locations or "pseudo-absences" to "train" the models. For the *A. solidipes* model, background points were created from 10,000 randomly selected locations within the geographic range of the collected isolates. 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.

Armillaria solidipes predictions for coastal areas of Oregon and Washington are not shown (white areas) due to lacking occurrence records for this area, which indicates that additional distribution data for *A. solidipes* are needed for these areas (see below). California is also not shown (white) because *A. solidipes* has not been recorded in California (Baumgartner and Rizzo 2001).

RESULTS, DISCUSSION, AND FUTURE WORK

Two results are obvious from the models (Figure 1). Predicted suitable climate for *A. solidipes* and *P. menziesii* are highly correlated and the predicted change in climate suitability moves dramatically northward (and toward higher elevations) for year 2070 using the RCP8.5 "business as usual" scenario. MaxEnt is better suited for presence only data and over predicts *P. menziesii* compared to a presence/absence model (see Rehfeldt *et al.* 2014 for a climate niche model of *P. menziesii* based on a Random Forests classification algorithm). Nevertheless, absence data for Armillaria are difficult to obtain and if available difficult to confirm with certainty. Thus, we used MaxEnt to compare both pathogen and host using the same modeling parameters. These models do not take adaptation into account, but it is presumed unlikely that either of these relatively long-lived species can adapt dramatically within such a short time. A plausible hypothesis, shared by others (Kliejunas *et al.* 2009; Sturrock *et al.* 2011) is as hosts become maladapted (stressed) due to changing climates they will have a higher likelihood of susceptibility to many pathogens. While suitable climate is predicted to decrease in many areas of the inland west for *A. solidipes*, the pathogen will likely persist in many areas of the interior west, where will likely contribute significantly to tree mortality and growth loss it where maladapted hosts remain.

A number of projects could be implemented to improve the predictive capabilities of these *A. solidipes* prediction models, including: 1) removal of bias by using bias grids and/or collection of additional isolates from under-represented areas, 2) adding additional predictive variables (i.e. soil types, solar radiation, and/or predictions of other *Armillaria* spp), and 3) obtaining population-level data to run independent predictions based on separate populations.

While *A. solidipes* is well known to exist west of the Cascade Range, our models are unreliable sources of prediction for this area because we lack knowledge of specific geographic occurrences west of the Cascade Range. Furthermore, it is well established that climate and ecological behavior of *A. solidipes* is different in regions west of the Cascades compared with the interior western North America. However, Douglas-fir is one of the most susceptible tree species east of the Cascade Range (Morrison 1981; Robinson and Morrison 2001), but the coastal variety of Douglas-fir seldom succumbs to infection (Johnson *et al.* 1972; Robinson and Morrison 2001). To address these differences, population-level data are needed for both host and pathogen to refine climate-based models. Genetic variation within *A. solidipes* has already been demonstrated, but only on the basis of a few genes (Hanna 2005; Hanna *et al.* 2007; Hanna *et al.* 2012). It is now feasible to incorporate whole-genome variation data to better determine population structure.

The climate-based modeling methods developed from this project 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.

Predicting the distribution of fungal species relies strongly on DNA-based identification methods to verify fungal species and/or populations. Furthermore, fungal taxonomy continue to change over time. Thus, living specimens are important to obtain the quantity and quality of DNA needed for fungal identification and population analyses. The availability of living cultures allow us to update/verify species identification of cultures collected in the past. For example, many of the isolates and data used to complete this study are from the USDA Forest Service-RMRS forest fungi collection located in Moscow, Idaho. This collection houses over 15,000 living specimens and associated collection data including many Armillaria specimens collected over the past 30 years. Future support is needed to maintain such invaluable collections, in which fungal isolates are associated with a specific time, place, and climate. These collections are critical to understanding species distribution changes under climate change (Ashiglar *et al.* 2014).

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