Bioclimatic modeling of *Armillaria altimontana* in western North America

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Introduction

Relatively little is known about the ecology and distribution of *Armillaria altimontana* compared with some other *Armillaria* species in North America. After first being recognized as an unnamed North American Biological Species X based on mating tests (Anderson and Ullrich 1979), *A. altimontana* was subsequently formally described by Brazee et al. (2012). While *A. altimontana* is occasionally found as a pathogen causing Armillaria root disease, it is often only found in a saprophytic state as rhizomorphs on diverse coniferous and broad-leaved trees and shrubs. A previous study suggests that *A. altimontana* found in this saprophytic state may also function as an *in situ* biological control agent for Armillaria root disease caused by *A. solidipes* (Warwell et al. 2019). Subsequent studies have compared the *A. solidipes* and *A. altimontana* genomes and their associated soil microbiomes (microbial communities) to gain insights into their ecological functions (Ibarra Caballero et al. 2023). *Armillaria altimontana* occurs widely across the northwestern USA to southern British Columbia, Canada (Figure 1A). Efforts are underway to better understand the ecology and distribution of *A. altimontana*. Recently, bioclimatic modeling using MaxEnt (Maximum Entropy) have been used to model suitable climate for forest pathogens and their hosts (e.g., Klopfenstein et al. 2009, Stewart et al. 2017, Hanna et al. 2020, Kim et al. 2021, Kim et al. 2023). These models can be projected for different future time periods, using a combination of emissions scenarios and global circulation models, to predict suitable habitat (potential distribution) for a species under future-climate scenarios. Such information provides valuable insights into geographic regions where *A. altimontana* is predicted to potentially occur under various climate scenarios, which can guide forest management in decisions to promote desirable outcomes for forest ecosystems in the future.

Objectives

The objectives of this project are to (i) use survey data to evaluate and refine bioclimatic models for predicting the suitable climate space (the geographic area that is climatically suitable for a species' survival) for *A. altimontana*; and (ii) project this information to future time periods under different climate scenarios to better understand influences of changing climates on *A. altimontana* and associated microbes that may represent an important management tool to help protect forest ecosystems against Armillaria root disease caused by *A. solidipes*.

Methods

For this study, MaxEnt bioclimatic modeling (Phillips et al. 2006) was coupled with 139 GPS locations of DNA sequence-confirmed *A. altimontana*, collected from basidiocarps, wood samples, mycelial fans, and rhizomorphs, to produce models that predict its suitable climate space/potential distribution (Figure 1A, Figure 2A-D). MaxEnt bioclimatic modeling and evaluation methods largely followed the protocol of Kim et al. (2021, 2023), in which WorldClim version 2.1 (Fick and Hijmans, 2017) provided 19 bioclimatic variables that were used in the species distribution model for *A. altimontana* under the contemporary (1970–2000) time period (Figure 1B). The model was computed from 20 replicate runs using cross-validation and scored an average area under curve (AUC) score of 0.978 with a standard deviation of 0.010. An AUC score of 1 represents a perfect model, while values below 0.5 are worse than random.

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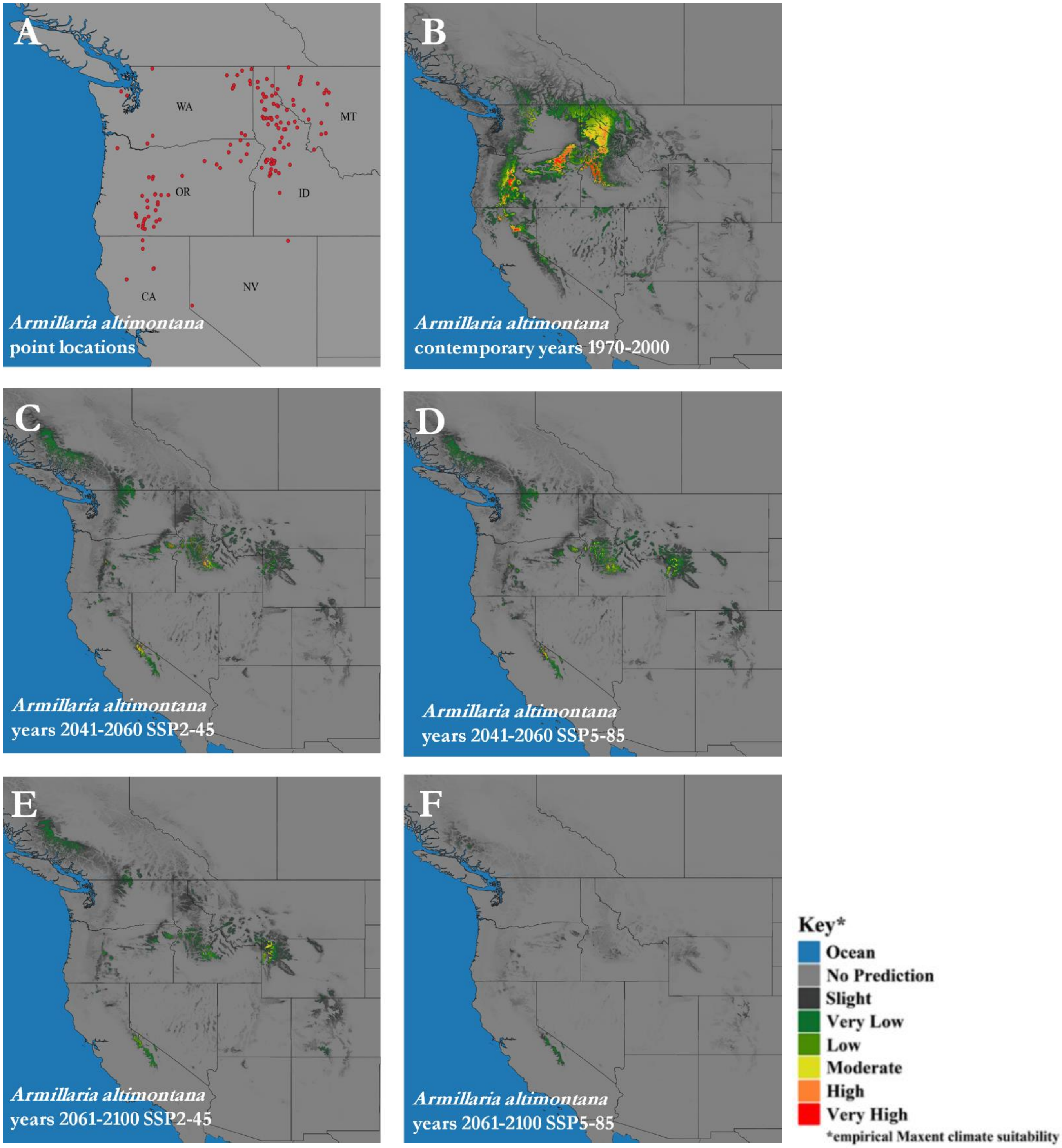

Figure 1A-F: A: *Armillaria altimontana* GPS point locations used for the models, where the presence of *A. altimontana* has been confirmed using DNA-based identification methods. B: Contemporary bioclimatic prediction model for the years 1970–2000. C-F: Bioclimatic predictive distribution models based on two future climate emissions scenarios (SSP2-45 and SSP5-85) and projected for two future time periods (years 2041–2060 and years 2061–2100) using 30-sec resolution (~1 km) CMIP6 downscaled data (WorldClim v2.1). Derived from Kim et al. (2023).

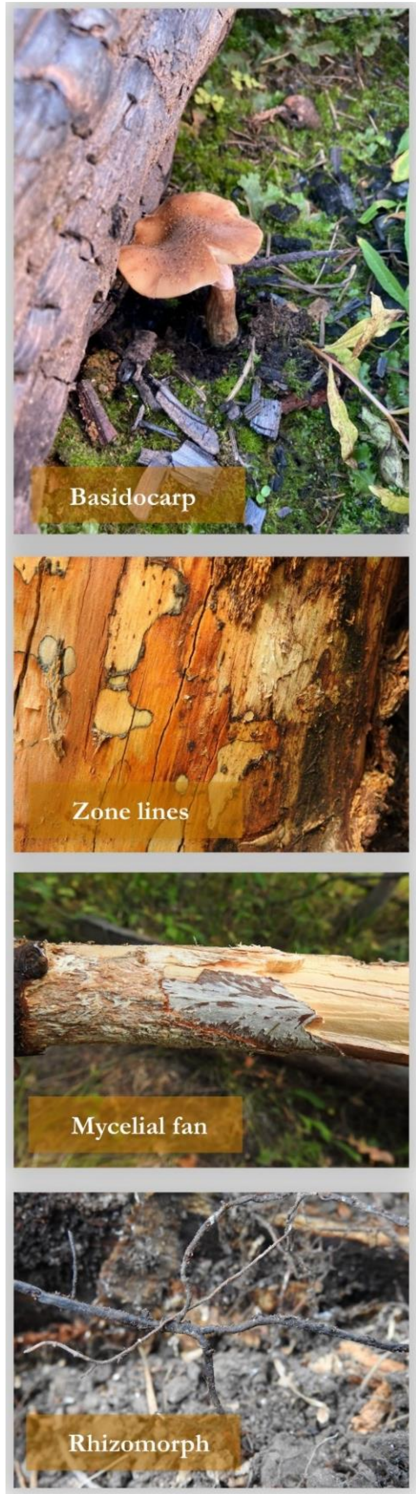

Figure 2: Signs of *Armillaria altimontana*. Derived from Kim et al. (2023).

Predictive distribution models based on future-climate scenarios were also projected for two future time periods (years 2041–2060 and years 2061–2100) using 30-second (ca, 1-km) resolution CMIP6 downscaled data (WorldClim v2.1) (Figure 1C-E). Two different Shared Socioeconomic Pathways (SSPs) were paired with the "Canadian Ocean Ecosystem model" (CanESM5-CanOE) GCM (Christian et al. 2022). In general, five SSPs narratives describe the broad socioeconomic trends that could shape future society, and we applied two scenarios: SSP2-4.5 ("middle of the road" world, where trends do not shift markedly from historical patterns) and SSP5-8.5 ("fossilfueled development" that follows path of rapid and unconstrained growth in economic output and fossil fuel-based energy use) (Figure 3).

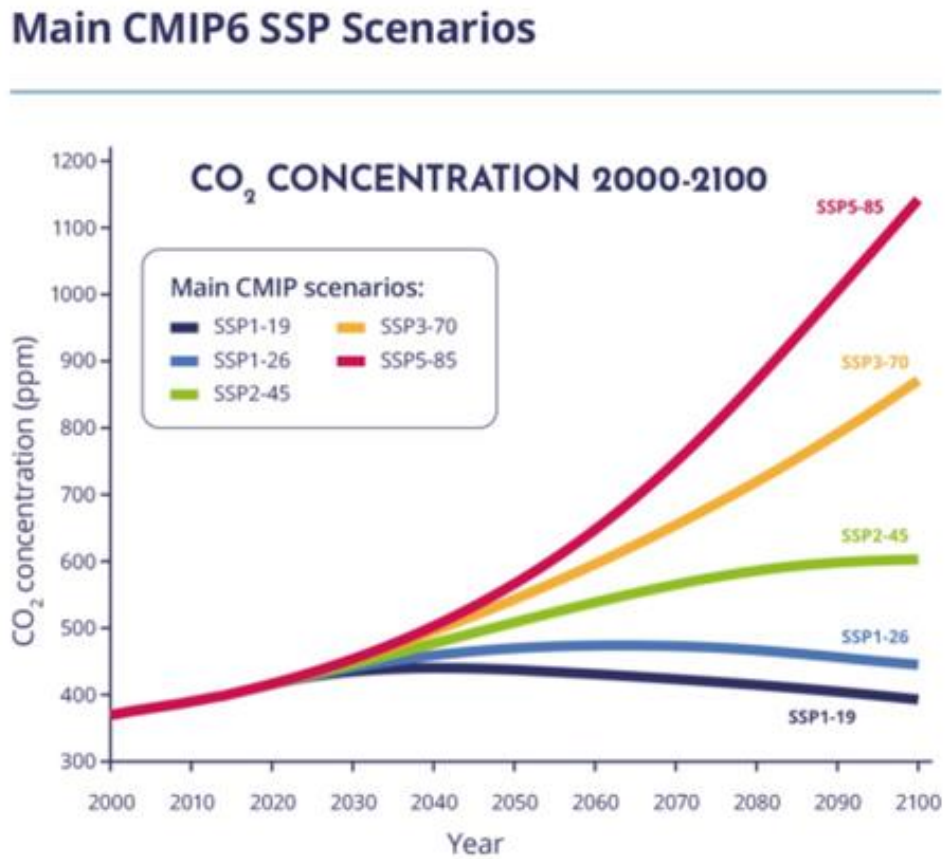

Figure 3: Comparison of CMIP6 SSP emissions scenarios. SSP2-45 (some carbon mitigation and a declining population) and SSP5-85 ("business as usual" scenario) were used for this study. From: "CONSTRAIN (2020) ZERO IN ON: A new generation of climate models, COVID-19 and the Paris Agreement," by D. Rosen, A. Nauels, K.B. Tokarska, C. McKenna, C.-F. Schleussner, J. Rogelj, and P. Forster, 2020, The CONSTRAIN Project Annual Report 2020, DOI:10.5281/zenodo.4282461. CC BY 4.0.

Results and discussion

The contemporary prediction from the MaxEnt bioclimatic models (Figure 1B) largely concur with the *A. altimontana* occurrence data found from surveys (Figure 1A). These predictions show a high probability of suitable climate space (potential distribution) for *A. altimontana* in diverse geographic areas, such as northwestern Montana, northern Idaho, northeastern Washington, northeastern Oregon, and the Oregon Cascade Mountains of the USA, and southern British Columbia, Canada. Interestingly, the projected range of *A. altimontana* overlaps the range of western white pine (*Pinus monticola*) in many areas. Based on the overlapping ranges and the mutualistic ecology of *A. altimontana* and western white pine, we hypothesize that these two ecosystem components may have a long co-evolutionary history; however, more in-depth studies are needed to examine this hypothesis. The results of the future models indicate that *A. altimontana* may have a substantially reduced range in the future, if the predicted models of future climate come to fruition (Figures 1C-F). Unfortunately, this trend parallels the predictions of many host species as well (Rehfeldt et al. 2006, Rehfeldt et al. 2009, Hanna et al. 2016, Kim et al. 2021). Climate mitigation measures must be a top priority to sustain future healthy forest ecosystems that have any resemblance to those of the present and past.

As previous work has demonstrated, *A*. *altimontana* can potentially function as an *in situ* biological control agent against Armillaria root disease caused by *A*. *solidipes* (Warwell et al. 2019). However, many questions remain about how to enhance biological control activities of *A*. *altimontana*. For the purposes of this discussion, widespread inoculation of forests with *A*. *altimontana* is deemed impractical, and the ecological requirements of *A*. *altimontana* must also be considered. Instead, activities to encourage *in situ* biological control of Armillaria root disease should focus on areas where *A*. *altimontana* (and associated beneficial microbes) and the pathogen (*A*. *solidipes*) already co-occur. First, surveys are needed to determine the geographic distribution and climatic/environmental requirements of the putative biocontrol agent (*A*. *altimontana*) and the Armillaria root disease pathogen (*A*. *solidipes*) for identifying areas/sites where the putative biocontrol agent(s) and pathogen naturally co-occur. Second, the ecological conditions where *A*. *altimontana* functions as a biological control agent must be better characterized. Third, the influence of interacting microbes and other ecosystem components must be better understood (e.g., Ibarra Caballero et al. 2023). With this information, management techniques can be developed to encourage *A*. *altimontana* and other beneficial microbes in sites where they co-occur with the pathogenic *A*. *solidipes*. Examples of management methods that should be evaluated for increasing biological control of Armillaria root disease include minimizing site disturbances, increasing organic matter in the soil, adjusting soil pH, increasing vegetation that serves as hosts for *A*. *altimontana* but not *A*. *solidipes* (e.g., hardwoods and shrubs), using prescribed burning, or other activities that could favor *A*. *altimontana* and/or suppress *A*. *solidipes*. Although more studies are needed to unleash the full potential of *in situ* biological control for Armillaria root disease by *A*. *altimontana* and associated microbes, the benefits of such studies are warranted because of the extensive mortality and growth loss associated with Armillaria root disease, which subsequently exacerbates climate change.

One long-term goal of studies toward understanding ecological interactions of *A*. *altimontana* is the development of novel, ecologically friendly approaches for forest management to reduce Armillaria root disease and increase forest productivity (C sequestration) and sustainability. Such studies can help determine which management activities (e.g., prescribed fire, organic matter retention, soil pH adjustments, favoring/planting appropriate tree species, thinning, etc.) will promote beneficial functions of *A*. *altimontana* and associated microbes, while decreasing detrimental activities of *A*. *solidipes* or other forest root pathogens, while also preparing for climate change.

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