MAXIMUM ENTROPY-BASED BIOCLIMATIC MODELS PREDICT AREAS OF CURRENT AND FUTURE SUITABLE HABITAT FOR *ARMILLARIA* SPECIES IN WESTERN OREGON AND WESTERN WASHINGTON

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Introduction

Climate change is predicted to increase the impacts of Armillaria root disease as host trees become maladapted to their environment, escalating tree stress, and potentially increasing susceptibly to *Armillaria* pathogens (e.g., Klopfenstein et al. 2009, Kliejunas et al. 2009, Kliejunas 2011, Sturrock et al. 2011, Dempster 2017, Kubiak et al. 2017, Aslam & Magel 2018). Powerful statistical bioclimatic modeling methods [e.g., Maximum entropy (Maxent)] are available to determine probable suitable climate space and potential distribution for *Armillaria* species for contemporary and future time periods, even with minimal presence data (Phillips et al. 2006, Pearson et al. 2007, Klopfenstein 2009a). Currently, only limited information is available on *Armillaria* spp. in western Washington and western Oregon, yet this region is expected to experience strong climate-change influences. In 2016, a collaborative project was initiated to determine the distribution of *Armillaria* species in the region under changing climates.

Objectives

(1) Isolate, culture, and identify *Armillaria* species from collections/surveys throughout western Washington and western Oregon.

(2) Predict current suitable climate space (potential distribution) of six *Armillaria* species identified in the region and project the distributions for future time periods under several climate-change scenarios.

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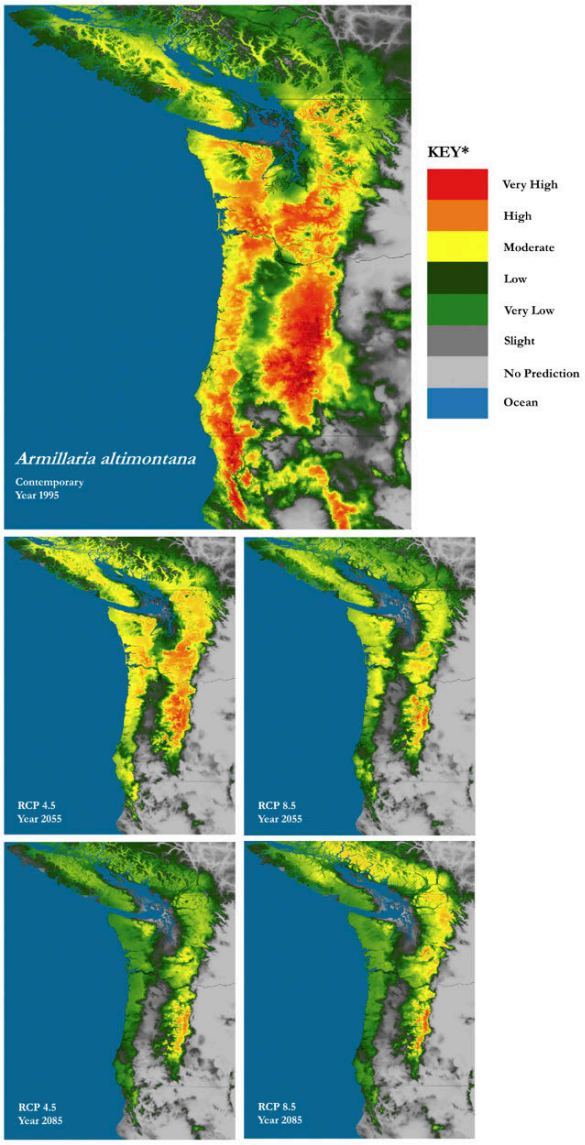
Methods

Roots of trees and shrubs as well as basal portions of tree trunks were examined, and samples (e.g., rhizomorphs, mycelial fans, rotten wood) of *Armillaria* species were collected along with precise location information and associated environmental data. Cultured *Armillaria* isolates from western Washington, western Oregon, and northern California were then identified based on DNA sequence-based methods (e.g., translation elongation factor 1 alpha gene; *tef1*; Ross-Davis et al. 2012, Elías-Román et al. 2013, Klopfenstein et al. 2017). Over 200 isolates were collected from 2016 to 2018 and many additional isolates (ca. 100 that had been archived and curated by James B. Donley at the RMRS Forest Pathology Laboratory in Moscow, ID, USA) were re-evaluated after long-term storage at -80˚C from the USDA Forest Service-RMRS forest fungi collection in Moscow, Idaho (Zambino 2004, Ashiglar et al. 2014). These older isolates had been collected by Dave Shaw (1989) and Geral McDonald (1989-2003). These archived *A. solidipes* collections and three additional collections from southern British Columbia (location information was available in GenBank) were identified with IGS-1 sequence data (Kim et al. 2006). *Armillaria solidipes* IGS-1 data has been found to be adequate for its positive identification within the region, but it is less reliable for the other five *Armillaria* species found in the region (Kim et al. 2006, Hanna et al. 2007b).

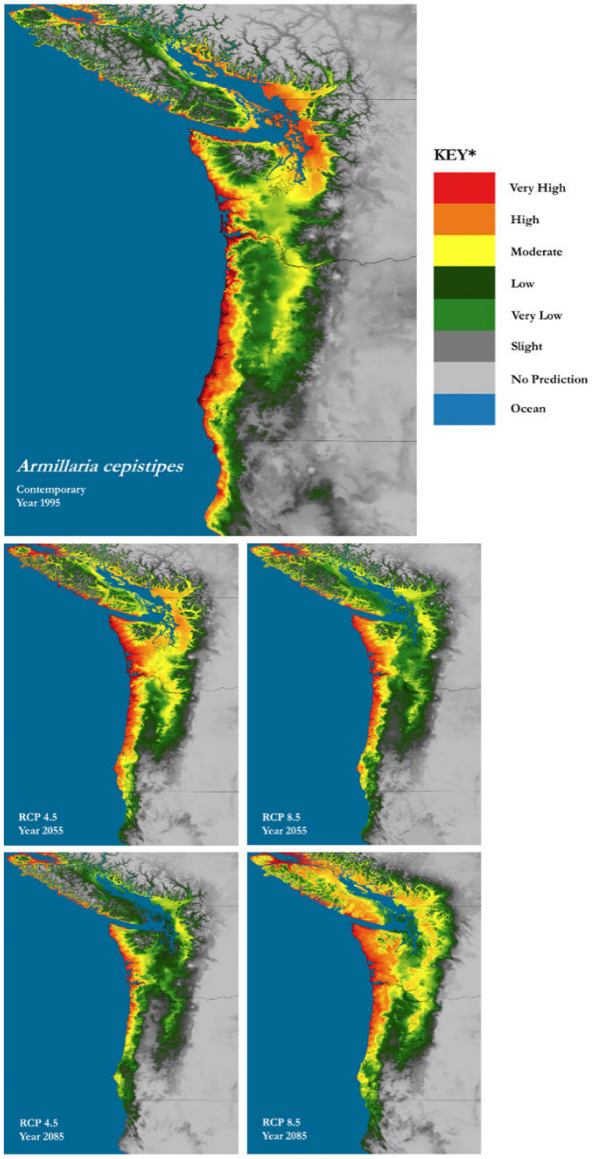
Figure 1a: *Armillaria altimontana.*



Using these positively identified *Armillaria* isolates, a dataset of coordinates was created for use in bioclimatic modeling. Duplicate isolates of the same *Armillaria* species were eliminated if the geographic coordinates of their origin was within 0.25 km. Based on this reduced isolate set, a total of 13 locations for *A. altimontana*, 13 locations for *A. cepistipes*, 35 locations for *A. gallica*, 13 locations for *A. nabsnona*, 37 locations for *A. sinapina*, and 27 locations for *A. solidipes* were used for bioclimatic modeling. Locations used for modeling are denoted as small black dots on the maps (Figure 1a-f).

Bioclimatic models for each *Armillaria* species were created using Maxent software (Phillips et al. 2006). Input data for Maxent calculations in suitability models consisted of "samples with data" (SWD) files for each species that linked climate variable values for each of 26 bioclimatic variables with geographic coordinates (presence point localities). Additional input into Maxent included sets of interpolation grids (ca. 1-km^2 resolution) for current and projected climate data for North America (CMIP5 scenarios) provided by the AdaptWest Project (Wang et al. 2016). These climate data grids consisted of a set based on contemporary climate normals for the year 1995 (an average from 1981-2010) and two future sets for year 2055 (average from 2041-2070) and year 2085 (average from 2071-2100). For the future climate data, we chose a single

Figure 1b: *Armillaria cepistipes.*



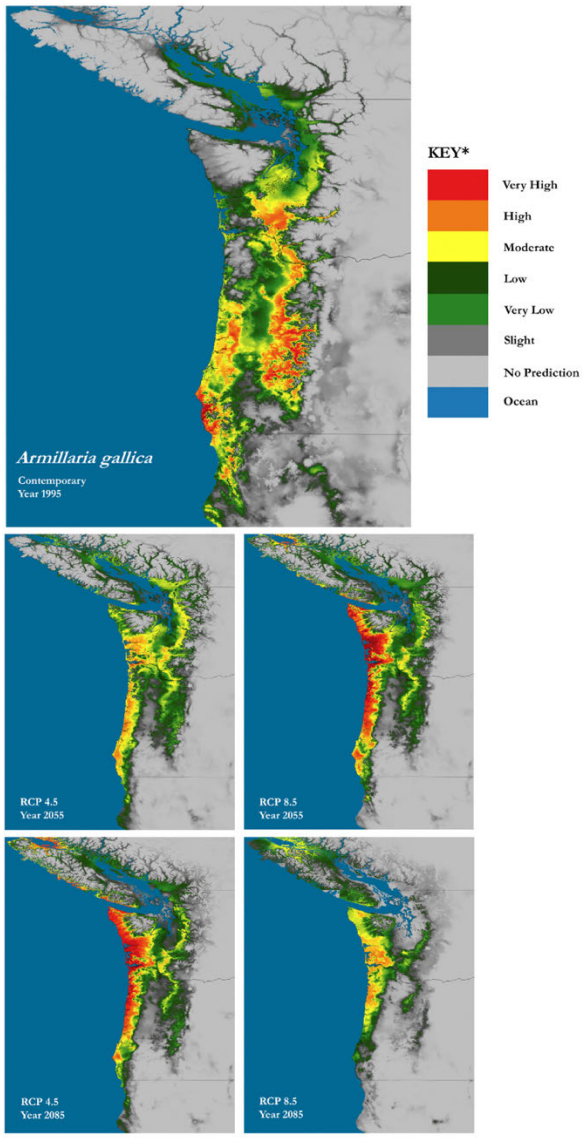
atmosphere-ocean general circulation model (AOGCM), the Hadley Global Environment Model 2 - Earth System (HadGEM2-ES), rather than an ensemble of dissimilar models (Bellouin et al. 2007, Collins et al. 2011, Martin et al. 2011). HadGEM2-ES is one of the eight available datasets from the AdaptWest Project; it fits in the middle of climate model genealogy for CMIP5 (performs similarly to ensemble models) and has been shown to be a top performer for the Pacific Northwest USA (Knutti et al. 2013, Rupp et al. 2013, Wang et al. 2016). The gridded climate layers were unprojected from Lambert Conformal Conic to an acceptable format for Maxent in degrees of latitude and longitude and then clipped to 28.5˚ W, 40˚ N, 120˚ W, 51˚ N so that random background points selected by Maxent would be within the study area of *Armillaria* locations. In all, grids for 26 biologically relevant variables, including seasonal and annual means, extremes, growing and chilling degree days, snow fall, potential evapotranspiration, and several drought indices were used for modeling.

Additional settings for each Maxent model included 10 replicates with the bootstrapping method (sampling with replacement) and a 25% test percentage. "Random seed" was also selected. Maxent uses background locations (pseudo-absences) to train the models. Background points for each model were created from 10,000 randomly selected geographical locations within the geographic range of the collected isolates. Maxent's cumulative output (an index of probability from 0 to 100) was chosen for easier conceptualization compared to Maxent's raw exponential model. A model for each *Armillaria* species was created for the contemporary time frame (year 1995) and then projected to future time periods (year 2055 and year 2085) using two different representative concentration pathways (RCPs – see Figure 2). This combination of six *Armillaria* species, a contemporary time period, two future time periods using two different RCPs produced 30 different outcomes (Figure 1a-f).

Results and Discussion

Six *Armillaria* species from western Oregon and western Washington were identified: *A. solidipes*, *A. sinapina*, *A. gallica*, *A. nabsnona*, *A. cepistipes*, and *A. altimontana*. These *Armillaria* species appeared to have a range of ecological roles from pathogen to saprophyte. Generally, *A. solidipes* is known as an aggressive pathogen of conifers that causes significant growth loss and mortality; whereas, *A. gallica*, *A. sinapina*, *A. nabsnona*, *A. cepistipes*, and *A. altimontana* have been commonly characterized as primarily saprophytic with weak/variable pathogenicity (Gregory et al. 1991). However, recent observations suggest

Figure 1c: *Armillaria gallica.*



that these less aggressive species can also be associated with root disease and/or deteriorating forest health, which frequently results in tree mortality (e.g., Dettman & van der Kamp 2001, Hanna et al. 2007a, Klopfenstein et al. 2009b, Kim et al. 2010, Cleary et al. 2012, Nelson et al. 2013, Klopfenstein et al. 2014, Burns et al. 2016, Kim et al. 2017, personal observations - J. W. Hanna).

Of the six *Armillaria* species, a low number of occurrence records was obtained for three species (*A. altimontana*, *A. cepistipes*, and *A. nabsnona*), with 13 occurrence records for each species; however, Maxent has been shown to be one of the best performing models for low numbers of presence records (Wisz et al. 2008). Pearson et al. (2007) had successful results with as few as five occurrence records, while Proosdij et al. (2016) indicates 13 occurrence records as a minimum to model "widespread" species. Nevertheless, our models performed well according to the AUC statistics. AUC values 0.5 to 0.6 represent a failed model, while 0.6 to 0.7 is poor, 0.7 to 0.8 is fair, 0.8 to 0.9 is good, and 0.9 to 1 is excellent model performance (Swets 1988). The following AUC values were obtained for the species models: *A. altimontana* = 0.896 (good), *A. cepistipes* = 0.922 (excellent), *A. gallica* = 0.965 (excellent), *A. nabsnona* = 0.895 (good), *A. sinapina* = 0.934 (excellent), and *A. solidipes* = 0.937 (excellent). The predicted species distribution range indicates that *A. cepistipes* and *A. nabsnona* are perhaps more widespread than previously reported (Banik et al. 1996, Volk et al. 1996). The projected future distributions for *A. cepistipes* and *A. nabsnona* also show predicted occurrences along the coastal areas. *Armillaria gallica* and *A. sinapina*, the two most commonly found species in our study, show substantial reductions in predicted climatically suitable areas under the projected future-climate scenarios. If *A. sinapina* cannot adapt to the predicted future climate, it may become rare or extirpated in the region by the year 2085. Likewise, the prediction for *A. altimontana* shows a substantial reduction in predicted range by the year 2085. Noteworthy is that *A. altimontana* has been shown to have potential benefits to growth and survival of western white pine (*Pinus monticola*) in north Idaho and exerts potential biocontrol against the pathogenic species, *A. solidipes* (Warwell et al. 2019). As for predictions for *A. solidipes* "the most aggressive destroyer of forests*," suitability decreases in its southern range but increases in the north by the year 2085 (* quote from Phil Cannon). The information from these models will contribute to management strategies for reducing detrimental impacts and increasing the benefits of these ecologically important fungal species.

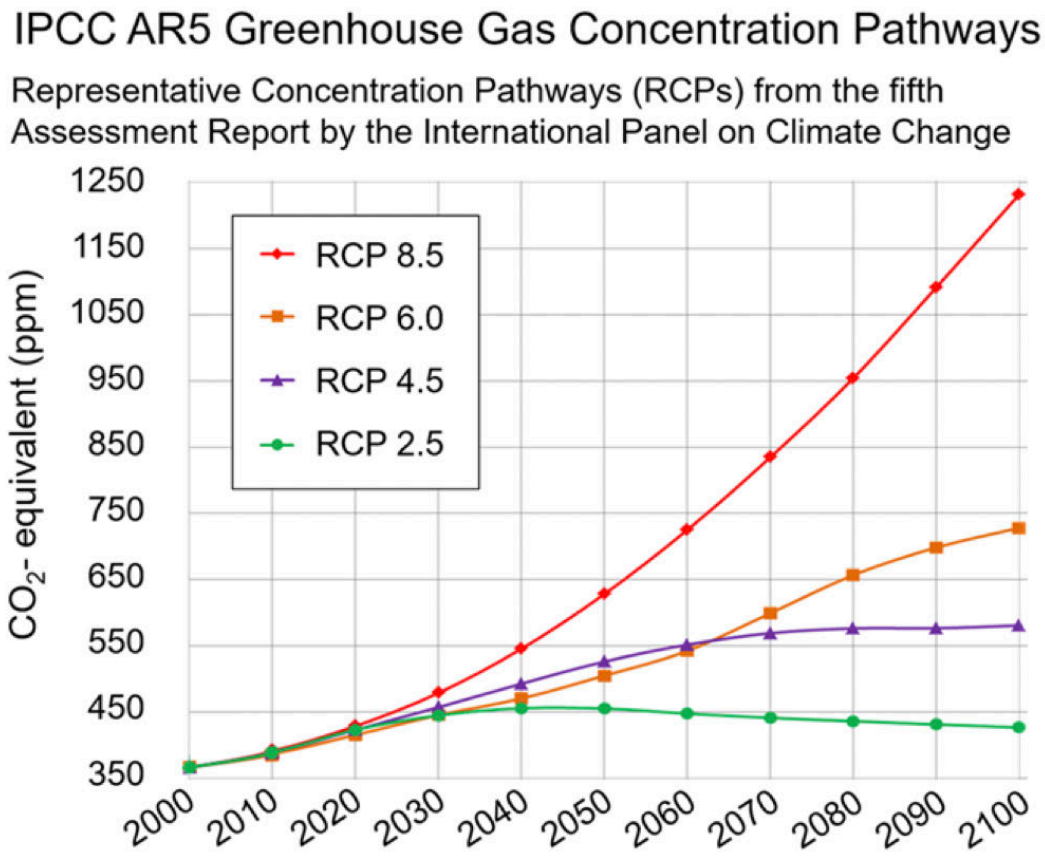


Figure 2: *Differences in RCPs (Representative Concentration Pathways) 4.5 and 8.5 for future time periods. RCPs are greenhouse gas concentration (not emissions) trajectories adopted by the IPCC for its fifth Assessment Report (AR5) in 2014. It supersedes Special Report on Emissions Scenarios (SRES) projections published in 2000. In general terms, RCP 8.5 represents a rampant increase in fossil fuel energy use by the end of the century, and no mitigation to control CO_2 concentrations. While, RCP 4.5 represents a future where energy use increases; however, there is a substantial growth in renewable energy resources by the year 2050. "The Beginner's Guide to Representative Concentration Pathways" by G.P. Wayne provides informative details. https://skepticalscience.com/docs/RCP_Guide.pdf.*

Future Work

In addition to acquiring more occurrence points for *A. altimontana*, *A. cepistipes,* and *A. nabsnona*, studies on predicted *Armillaria* distributions could be improved by obtaining population-level data to run independent predictions based on separate populations. Differing populations within species may be adapted to differing climatic niches. These studies are also critically limited by the dearth of *Armillaria* distribution data from California. *Armillaria* species in California are likely adapted to climates that relate to the future climate scenarios for the Pacific Northwest, USA. Location data based on current methods to identify *Armillaria* species in California are unavailable, because it has been nearly 20 years since the distribution of *Armillaria* in California was published (Baumgartner & Rizzo 2001). Finally, predictions of future climates are continually improving and new atmosphere-ocean general circulation models and representative concentration pathways (or similar scenarios) will improve the models based on predicted future climates. For example, data not included in current estimates of climate change (e.g. currently available climate grids/surfaces; Wang et al. 2016, Fick & Hijmans 2017, and others) include invasive

earthworms in the boreal forests that change global carbon dynamics (Lubbers et al. 2013) and increased CO_2 sensitivity with increasing temperatures (Friedrich et al. 2016). In addition, our predictions are based on climate averages; however, increases in the occurrence and intensity in extreme climate events will also likely impact species survival and distribution (Rahmstorf & Coumou 2011).

Figure 1d: *Armillaria nabsnona.*

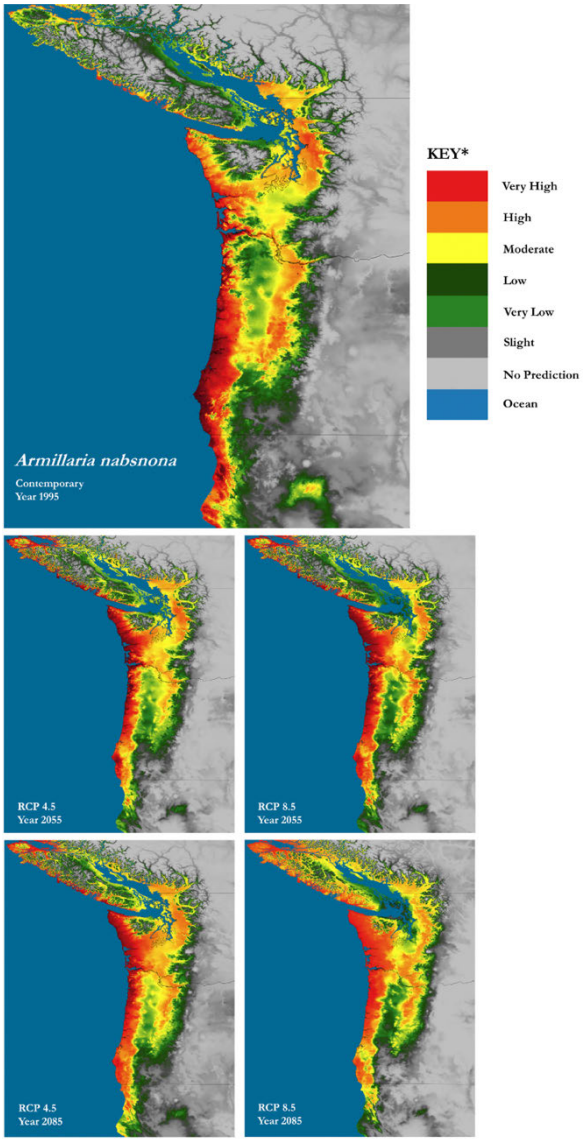


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Figure 1e: *Armillaria sinapina.*

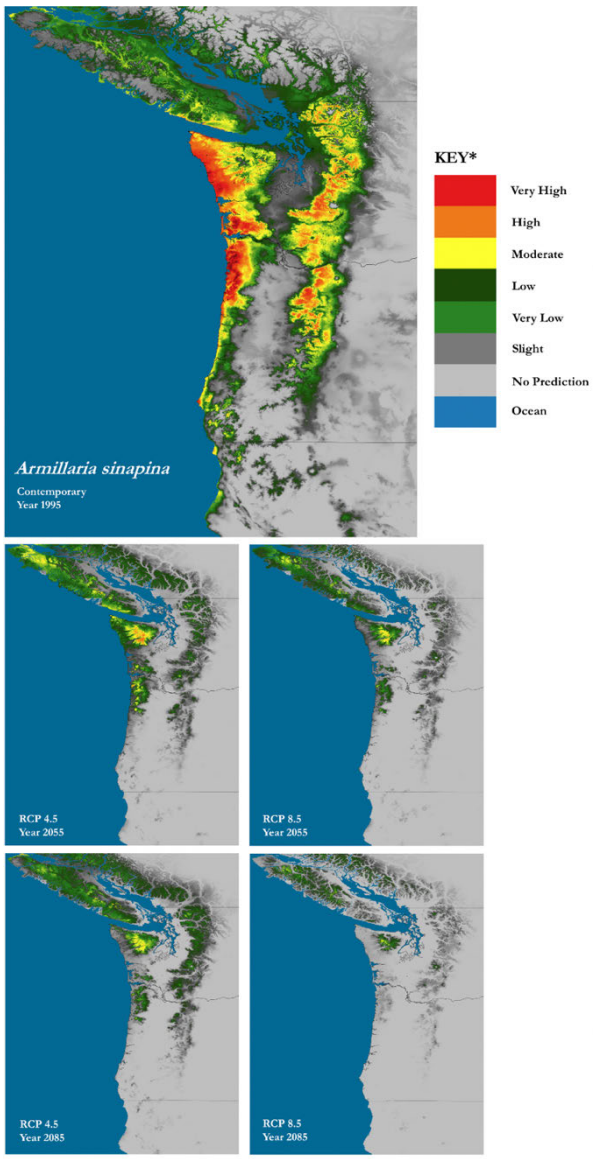

Figure 1f: *Armillaria solidipes.*

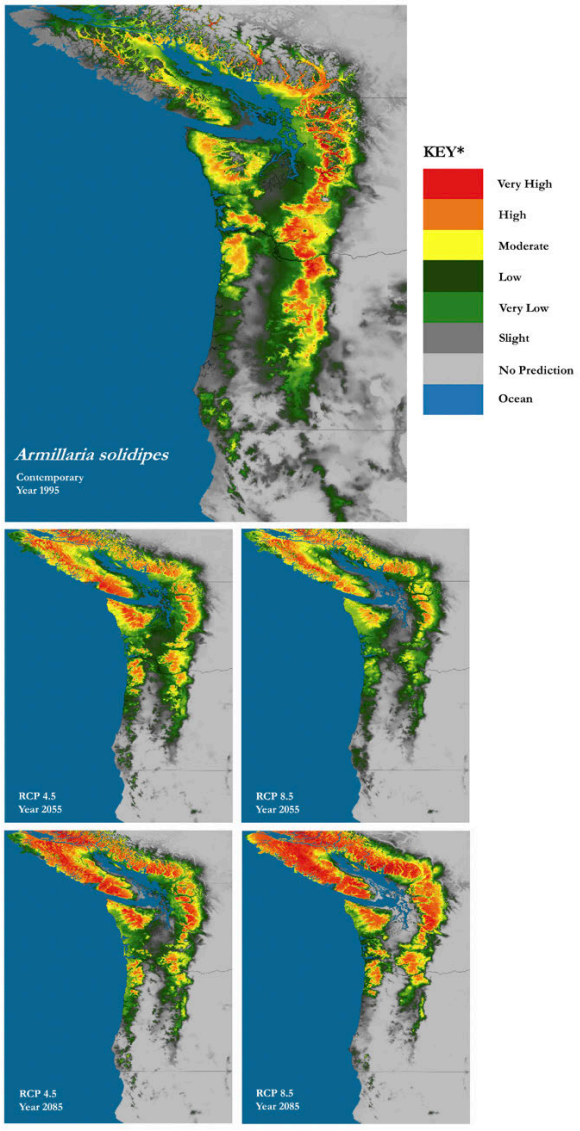

Figure 1a-f: *Maximum Entropy bioclimatic model of suitable climate space (potential distribution) for six* Armillaria *species. Largest map on top is a model of suitable climate space based on climate normals from 1981 to 2010. Smaller sets of four future models show two different RCPs [Representative concentration pathways, RCP4.5 and RCP8.5 (see Figure 2)] for the years 2055 and 2085. Darkest gray represents predicted suitable climate space, with light green, yellow, orange, and red indicating increased suitability, respectively. Small black dots represent collection locations for corresponding* Armillaria *species maps that were used to produce the models. Listed years represent averages, 1995 = climate normals from years 1981-2010, 2055 = years 2041-2071, 2085 = years 2071-2100.*

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