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Southwestern white pine (*Pinus strobiformis*) species distribution models project a large range shift and contraction due to regional climatic changes

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ABSTRACT

Southwestern white pine (*Pinus strobiformis;* SWWP) is a conifer species that occurs at mid to high elevations in the mountains of Arizona, New Mexico, and northern Mexico. A key component of mixed conifer forests in the region, SWWP is an important species for wildlife and biodiversity. The dual threats of the non-native fungal pathogen that causes white pine blister rust (WPBR) and a warmer, drier projected future climate have created an uncertain future for SWWP. In this study, we used a novel multi-scale optimization approach including an ensemble of four species distribution modeling methods to explore the relationship between SWWP occurrence and environmental variables based on climate, soil, and topography. Spatial projections of these models reflecting the present climate provide an improved range map for this species that can be used to guide field data collection and monitoring of WPBR outbreaks. Future projections based on two emissions scenarios and an ensemble of 15 general circulation models project a large range shift and range contraction by 2080. Changes in the future distribution were particularly extreme under the higher emissions scenario, with a more than 1000 km northerly shift in the mean latitude and 500 m increase in the mean elevation of the species' suitable habitat. This coincided with a range contraction of over 60% and a significant increase in habitat fragmentation. The ability of SWWP to realize its projected future range will depend on colonization at the leading edge of the range shift, including dispersal dynamics, resistance to WPBR, competition with other species, and genetic adaptations to local climate. Our results provide information that can be used to guide monitoring efforts and inform conservation planning for this keystone species.

1. Introduction

The southwestern white pine (*Pinus strobiformis*; SWWP), the southernmost white pine (*Pinus* subgenus *strobus*) species in the United States, occurs primarily at mid to high elevations in the Rocky Mountains of Arizona and New Mexico as well as the Sierra Madre ranges of Mexico (Fig. 1). At least one species of white pine occurs in every high mountain region of western North America, where they play important ecological roles (Tomback and Achuff, 2010). Their large, nutritious seeds are important dietary components for many birds and mammals (Tomback and Achuff, 2010).

The southwestern white pine is currently considered a 'species of least concern' with a stable population trend (Kyne et al., 2013). However, it is highly susceptible to white pine blister rust (WPBR; Kinloch and Dupper, 2001; Schoettle and Sniezko, 2007), caused by the fungus C*ronartium ribicola*. This pathogen was first introduced to North America from Asia in the late 1800s (Kinloch, 2003). Since then, it has spread throughout the range of most white pine species and caused more than 90% mortality in some affected areas (Campbell and Antos, 2000). WPBR has recently spread into parts of Arizona and New Mexico (Hawksworth, 1990; Wilson et al., 2014), posing an increasing threat as it enters the core of the SWWP range. The threat is particularly acute given that genetic resistance to WPBR has been found in only a small percentage of SWWP trees to date, leaving most of the population vulnerable to mortality (Sniezko and Kegley, 2008).

In addition to the increasing threat from WPBR, climatic changes in the region also pose risks to the future viability of SWWP populations. Climate across the range of SWWP is expected to become warmer and

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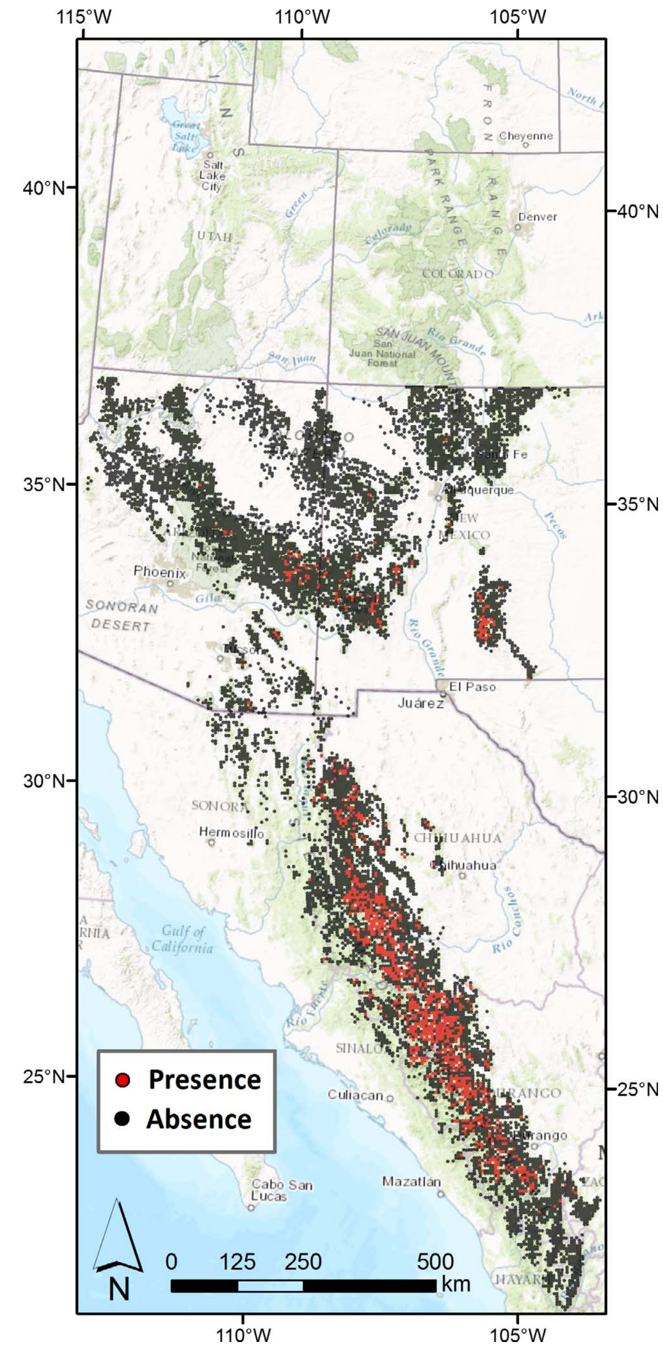

Fig. 1. Study area and sampling sites for southwestern white pine (*Pinus strobiformis*). The study area encompassed 193.4 Mha in the southwestern United States and Mexico. Field surveys to detect the presence (red dots, n = 1077) or absence (black dots, n = 9071) of southwestern white pine were limited to Arizona, New Mexico, and northwestern Mexico. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

drier with increasing drought frequency (Seager and Vecchi, 2010). This may put SWWP at a competitive disadvantage because it is more drought sensitive than potential competitors like Douglas-fir (*Pseudotsuga mensiesii*) and Ponderosa Pine (*Pinus ponderosa*; Barton and Teeri, 1993). Phenological events are also highly sensitive to changes in temperature regimes (Richardson et al., 2013). For example, budburst in many temperate and boreal tree species, including SWWP, is regulated by a winter chilling and spring forcing (i.e. thermal time). In a warmer future climate, the chilling requirement may take longer to achieve, leading to a delay in budburst and thereby reducing growth and ultimately survival (Harrington and Gould, 2015).

Currently, the distribution of SWWP has only been delimited by expert opinion (Little, 1971), and the environmental variables controlling its distribution are poorly understood. Efforts are underway to genetically sample the population to identify loci associated with WPBR resistance (Sniezko and Kegley, 2008) as well as adaptations to climate variability (Goodrich et al., 2016). In addition, monitoring efforts are tracking the spread and severity of WPBR outbreaks. To support these efforts, more accurate range maps of the SWWP distribution are required. In addition, greater understanding of the relationship between SWWP distribution and environmental controls will improve our ecological knowledge of this poorly understood species. Projecting those relationships into the future given climate change projections for the region will help inform conservation planning to mitigate the impacts of SWWP range shifts and range contractions. For example, assisted migration and assisted gene flow (Aitken et al., 2008) are strategies being explored to maximize WPBR resistance and adaptation to a rapidly changing regional climate.

To meet these needs, the goals of this study were to (1) model the relationship between observed patterns of SWWP occurrence and environmental variables related to climate, topography, and soil, (2) apply the model to the current landscape and recent climate to produce a continuous probability of occurrence map for SWWP, (3) project the model into the future based on future climate projections, and (4) assess the potential future distribution of SWWP habitat.

2. Material and methods

2.1. Study area

Our study area (Fig. 1) comprised 193.4 Mha encompassing nearly the entire historical distribution of SWWP, plus potentially suitable future habitat areas in Colorado and Utah. The elevation of the study area varied from sea level to over 4400 m. At the lowest elevations, the climate is warm and dry, with mean annual temperature (MAT) reaching as high as 26.3C and mean annual precipitation (MAP) as low as 6.5 cm. At the highest elevations, the climate is cool and wet, with MAT as low as 1.2C and MAP as high as 204.1 cm. The lower elevations are generally covered in sparse desert scrub vegetation, including a variety of shrubs, grasses, forbs, and cacti. At progressively higher elevations, pinyon-juniper woodlands, ponderosa pine forests, dry and wet mixed conifer forests and spruce fir forests predominate. Areas above treeline are covered in sparse alpine tundra vegetation.

2.2. Occurrence data collection

We evaluated SWWP occurrence at 6308 sites in the US and 7590 sites in Mexico (surveyed once between 2001 and 2015). The US sites consisted of all Forest Inventory and Analysis (Smith, 2002) program plots maintained by the US Forest Service in Arizona and New Mexico. The Mexican sites consisted of National Forest and Soil Inventory plots in temperate forests of the Sierra Madre Occidental range. Both sets of plots were based on the same design consisting of four circular 400 m^2 subplots. The center subplot was surrounded by three outer subplots spaced 45.14 m apart. Plots were distributed in forested areas in a regular grid approximately 5 km × 5 km (Fig. 1). We defined presence as the occurrence of one or more live SWWP seedlings, saplings, or mature trees in any subplot.

Species distribution models are sensitive to the geographic distribution of absences relative to presences (Barve et al., 2011). We constrained the geographic scope of our analysis by removing absences from level III ecoregions (Environmental Protection Agency, 2010) where no presence locations were recorded. This resulted in the removal of 3750 absence locations occurring primarily in low elevation areas unsuitable for SWWP.