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Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Realized climate niches

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ABSTRACT

The Random Forests classification algorithm was used to predict the occurrence of the realized climate niche for two sub-specific varieties of *Pinus ponderosa* and three varieties of *Pseudotsuga menziesii* from presence-absence data in forest inventory ground plots. Analyses were based on ca. 271,000 observations for *P. ponderosa* and ca. 426,000 observations for *P. menziesii*, with ca. 6% of the observations in each dataset recording the presence of one of the varieties. Classification errors to the respective databases attributable to fitting the models were ca. 5%, most of which were from falsely predicting varietal occurrence. Confusion in classifying varieties was nil. The primary drivers of the niche model were summer precipitation, winter precipitation and summer degree-days >5 C for the varieties of *P. ponderosa* and the summer-winter temperature differential, summer maximum temperatures and summer precipitation for the varieties of *P. menziesii*. Projected impacts of global warming using output from an ensemble of 17 general circulation models were greater for *P. ponderosa* than for *P. menziesii* and for varieties of both species from inland climates than from coastal. Projected impacts imply dire consequences for the varieties of *P. menziesii* occurring in Mexico.

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1. Introduction

Ingrained in the foundations of biogeography is the concept that plant distributions are limited by climate, with species flourishing within a relatively narrow range of climatic conditions (see Dansereau, 1957). Entrenched in evolutionary biology is the concept that genetic variation within wide-ranging plant species has been molded by climate to produce clines that parallel climate gradients (see Morgenstern, 1996). The climate, however, is warming and will continue to warm at unprecedented rates (Hansen et al., 2012). As climate-change progresses, disruption of species distributions is inevitable (see Thomas, 2010), but the impact will vary among species largely because of intraspecific clines of different steepness (Rehfeldt, 1994; Sorensen and Weber, 1994). Impacts to forests are occurring presently (e.g., Breshears et al., 2005; Allen et al., 2010; Worrall et al., 2013) and are projected to continue (e.g. Iverson et al., 2008; Rehfeldt et al., 2006). Strategies, options and guidelines are needed by forest managers for accommodating the changing climate such that forest health, growth and productivity are maintained (e.g., Ledig and Kitzmiller, 1992; Mátýas, 1994; Rehfeldt et al., 1999; Pedlar et al., 2012).

The conclusion of many researchers is that climate change impacts on North American tree species involve contraction of ranges at trailing edges, the southern and low-altitudinal limits of distribution, with expansion at leading edges in the north and at higher elevations (e.g., Lavergne et al., 2010; Worrall et al., 2013). Yet, even where projected species are expected to persist, genotypes appropriate for the new climates invariably occur elsewhere today (St Clair and Howe, 2007; Rehfeldt and Jaquish,

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2010; Joyce and Rehfeldt, 2013). To mitigate the adaptation and dispersal lags that accompany plant migrations, proactive management must be a component of the challenge facing forest managers (see Rehfeldt et al., 1999, 2001, 2002; Ledig et al., 2010; Sáenz-Romero et al., 2012b).

Our focus is on the potential impacts of the changing climate on the sub-specific varieties of *Pseudotsuga menziesii* and *Pinus ponderosa*, two of western North America's most widely distributed and economically important forest trees. Both species are comprised of varieties long-recognized by taxonomists: *P. p.* vars. *ponderosa* and *scopulorum*, and *P. m.* vars. *menziesii* and *glauca*. Varieties *ponderosa* and *menziesii* tend to occupy coastal regions while vars. *scopulorum* and *glauca* tend to be interior (Fig. 1). In *P. menziesii*, an unnamed third variety occurs in central and southern Mexico (Reyes-Hernández et al., 2006). The disparate evolutionary histories of the varieties of these species (e.g., Latta and Mitton, 1999; Gugger et al., 2010; Wei et al., 2011) portend disparate responses to historical climates and, therefore, deserve recognition when impacts from climate change are considered.

Our analytical approach first defines statistically the realized climate niche, that is, the climate profile (*sensu* Rehfeldt et al., 2006), such that climatically suitable habitat can be mapped. The second step defines the climatic clines that link intraspecific genetic variation to climate gradients occurring within the climate profile. Completion of these steps allows the climate profile and intraspecific genetic variation to be projected into future climate space provided by emissions scenarios of General Circulation Models (GCM). The results then can be used to develop seed transfer protocols suited to reforestation in a changing climate. This approach parallels those used for *Larix occidentalis* (Rehfeldt and Jaquish, 2010) and *Pinus strobus* (Joyce and Rehfeldt, 2013).

Analyses and discussion of this work are presented in three tandem papers in this issue of Forest Ecology and Management. The objectives of the present paper, PART 1 of the series, are (a) to develop from a comprehensive database techniques for predicting the occurrence of the contemporary realized climate niche of the sub-specific varieties of *P. menziesii* and *P. ponderosa*, and (b) to project the niche into mid-century climates representative of GCMs such that potential impacts can be quantified at both the trailing and leading edges.

The results of PART 1 provide a statistical framework for the second paper of this series (PART 2, Rehfeldt et al., 2014a), the objectives of which are (a) to synthesize disparate provenance test data so that the clines in genetic variability that occur within varieties can be described and mapped within the climate niche, and (b) to project genetic variation into mid-century climate space. PART 3 of the series (Rehfeldt et al., 2014b) integrates the results of PARTS 1 and 2, synthesizes potential impacts to natural ecosystems, and considers management options for promoting long-term persistence and health consistent with ecosystem resilience.

2. Methods

2.1. Climate data

Throughout this series, all point and gridded climate estimates were obtained from the thin plate spline surfaces of Crookston and Rehfeldt (2008) for North America >13.9° latitude. These climate surfaces produce monthly estimates of temperature and precipitation normals for 1961–1990. From the monthlies, twenty variables are derived directly, but additional variables can be constructed from temperature-precipitation interactions (see Rehfeldt et al.,

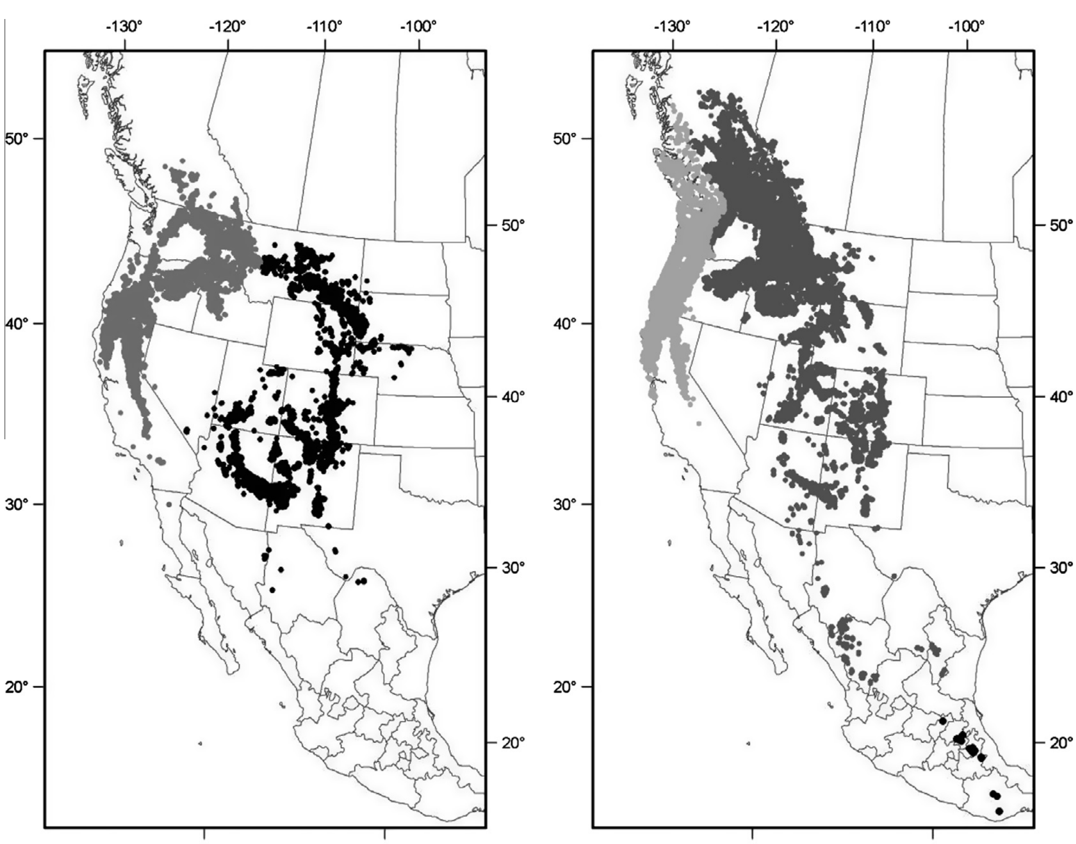

Fig. 1. Presence of ground plots (dots) of the varieties of *Pinus ponderosa* (left) and *Pseudotsuga menziesii* (right). Left panel: *P. p.* var. *ponderosa* (gray), var. *scopulorum* (black). Right panel: *P. m.* var. *menziesii* (light gray), var. *glauca* (dark gray), and unnamed Mexican variety (black).