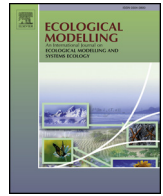




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Diverging distribution of seedlings and mature trees reflects recent climate change in British Columbia

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ABSTRACT

The composition and health of forests across western North America have shown signs of change over the last half-century associated with altered climate conditions. Most models developed to predict responses to variation in climate assume that the ecological distribution of adult trees provides a sound basis for projecting potential shifts in a species' range. Under a dynamic climate, however, recently established seedlings may more closely reflect changes in climate conditions. This study combined the simple, widely tested physiological model 3-PG with an empirical regeneration dataset, composed of 21,097 plots, to assess regional scale changes in tree species distributions across British Columbia, Canada. We geographically registered all plot locations to correspond with topographically-adjusted 1 km monthly climatic data for the period 2000–2009. By comparing the distribution of seedlings to that of mature trees present in an earlier period (1950–1975), we could assess where alterations in the environment have occurred, and the extent to which changes may make a species vulnerable to replacement in some places or likely to regenerate and migrate elsewhere. Decision tree models were developed to assess the relative importance of suboptimal temperatures, frost, soil water deficits and evaporative demand on the growth and distribution of four widely distributed species: Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and subalpine fir (*Abies lasiocarpa*). Tree responses varied by species, with areas suitable for lodgepole pine experiencing the largest relative increase in summer drought and areas dominated by western larch experiencing the least. Those areas modelled as suitable for species range expansions occurred 79% (SD = 16%) of the time in places where seedlings of a designated species were predicted in 2000–2009 using the regeneration dataset. We conclude that employing seedling surveys in concert with tree surveys provide valuable ecological insights when predicting species responses to climate shifts.

1. Introduction

Forest ecosystems provide many important ecological benefits, including habitat for wildlife and a continued source of clean water and air (Bonan, 2008; Spittlehouse, 2008). Many local communities depend on forests for timber as well as for their cultural and spiritual values (Millennium Ecosystem Assessment, 2005). Maintaining these ecosystem services requires an improved understanding of how forests are responding to a changing climate.

Increases in disturbances caused by insect attacks (Raffa et al., 2008; Anderegg et al., 2015), diseases (Ramsfield et al., 2016; Woods et al., 2010), and wildfires (Westerling et al., 2006) are associated with climatic variation over recent decades (IPCC, 2014). Small changes in temperature and precipitation impact seedlings more than adult trees,

whereas the opposite is the case with bark beetles and wind storms. The life stage of a species individual matters in predicting the future composition of a forest (Bose et al., 2016; Bell et al., 2014; Niinemets, 2010).

In some parts of a species' range, a shift in climate may induce stress, while elsewhere conditions may improve, fostering range expansion (Mathys et al., 2017; Coops et al., 2011; Rehfeldt et al., 2014; Gray and Hamann, 2013). Most species distribution modelling efforts attempt to include a large part, if not all, of a species' natural range. In doing this, there is an underlying assumption that the climatic envelope encompassing the species' range represents those niches where a species is able to survive in the presence of the existing complement of organisms. This complement includes not only other tree species but biological agents that limit tree growth and survival, including native

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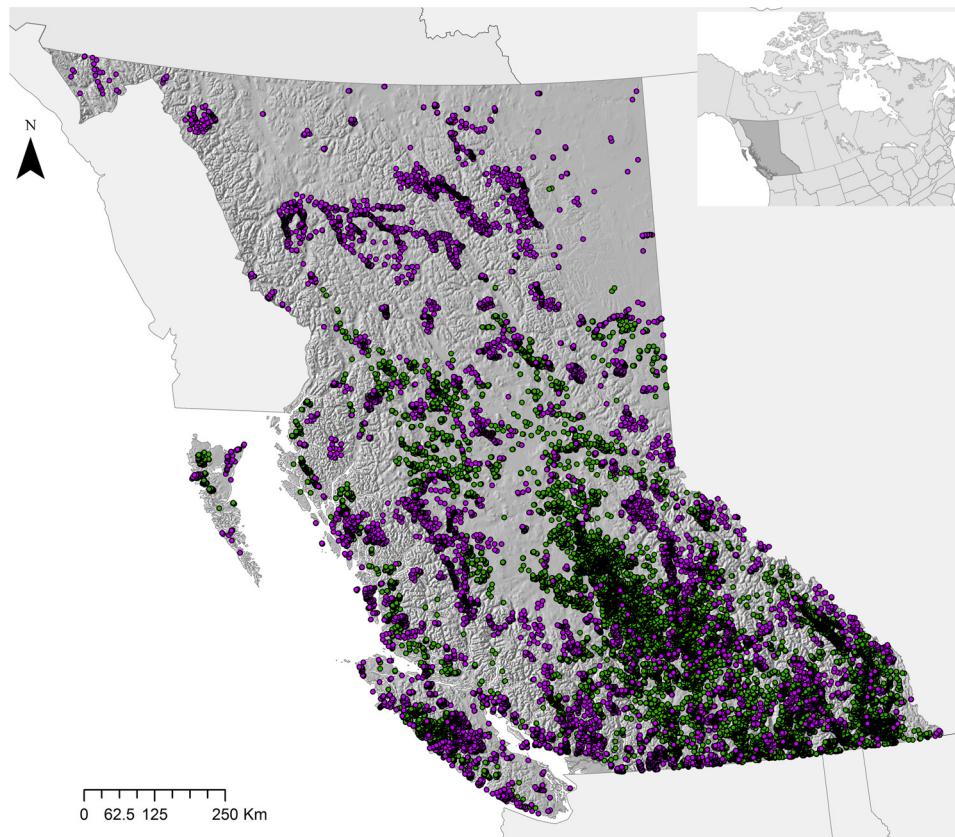


Fig. 1. Location of the survey plots of mature trees (purple) and seedlings (green) in British Columbia (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

and introduced herbivores and pathogens. Climate change may reduce niche space, not necessarily because a species might not grow as well, but because previously benign relationships become lethal.

The response of different tree species to climate can be characterized by quantifying relationships between species occurrence and environmental variables (Guisan and Thuiller, 2005). Data mining approaches such as random forest algorithms have also been employed, first to accurately assess current patterns of a species' distribution and then to demarcate probable future habitat (Rehfeldt et al., 2014; Iverson et al., 2008). For example, Gray and Hamann (2013) used a climate-envelope model with random forest algorithm to map the potential future distribution of major tree species in western North America. Coops et al. (2009) introduced a hybrid modelling approach that compared the environmental sensitivities of different western tree species with those predicted using a process-based model parameterized for a single, widely-distributed conifer (*Pseudotsuga menziesii*). An alternative approach, based on the observed growth of different populations observed in common garden experiments, has been used to predict responses to assisted migration of different genotypes under a changing climate (Wang et al., 2010; O'Neill et al., 2008). Unfortunately, data requirements for genetics-based models limit the approach to a few widely studied species (Aitken and Bemmels, 2016).

Although the majority of biologically-based climate-response models rely on species occurrence data acquired for mature trees, Nitschke and Innes (2008) provide a notable exception by modelling species' responses within their regeneration niche. We believe that a modelling approach based on the distribution of tree seedlings has merit because the fate of seedlings at the front or rear margin of a species distribution is a more sensitive harbinger of the future than the response of mature trees (Malcolm et al., 2002; Bell et al., 2014; Bose et al., 2016). By incorporating tree seedlings in species distribution models, we gain insights as to how climatic variation affects

reproductive success in both previously established and newly occupied niches (Bose et al., 2016). To date, the paucity of seedling data has limited our ability both to assess and model the effects of climate change on forest composition at large spatial scales (Blanco et al., 2009; Weiskittel et al., 2011; Parmesan et al., 2011).

In this study, we took advantage of databases available both on seedlings and established trees. Using a hybrid model developed by Coops et al. (2009), we combined these geographically-registered datasets with physiologically-defined climatic variables to run decision tree models for both seedlings and mature trees of four widely-distributed species in British Columbia (BC). This hybrid model allowed us to combine process-based modeling with sophisticated machine learning algorithms by relating species occurrences with the relative importance of four environmental limitations on photosynthesis rather than simply employing climatic data.

In an earlier study, Mathys et al. (2014) mapped the baseline distribution of native tree species using climate and soil information with an average accuracy of 84%. The objective of this study was to refine these models to evaluate the extent that predicted tree species shifts were in agreement with seedling observations of four species. We focused the area analysed on BC and selected interior and coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco and *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*, lodgepole pine (*Pinus contorta* (Dougl.)), western larch (*Larix occidentalis* (Nutt)), and subalpine fir (*Abies lasiocarpa* (Hook.)) for the analysis. Finally, we inferred changes in environmental constraints on species distributions over the past decade compared to baseline conditions (1950–1975).

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