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Statistical performance and behaviour of environmentally-sensitive composite models of lodgepole pine growth

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ABSTRACT

New initiatives are emerging to rehabilitate vast expanses of lodgepole pine (*Pinus contorta* var. *latifolia*) recently affected by insect outbreaks and wildfires across western North America. By assessing potential long-term changes in productivity, environmentally-sensitive models of tree growth can help to make informed decisions about where lodgepole pine will likely thrive and how it will respond to silvicultural treatments under future environmental conditions. It remains a challenge, however, to produce models that are practical to apply, statistically robust, and representative of real-world complexity. In this study, we developed composite models of aboveground biomass growth of lodgepole pine, with the purpose of assessing the statistical performance and behaviour of models covering a range of complexity. Adding complexity, including environmental sensitivity, did not appreciably increase explained variance over that of models based on tree size, stand competition, and site conditions alone. Nevertheless, Akaike's Information Criterion and cross-validation results offered no reason to dismiss the most complex model, which additionally considered insects, pathogens, heat, water, nitrogen deposition, and carbon dioxide concentration, and interactions among covariates. For models that represented environmental sensitivity, average predictions of growth increased between historical and future periods, but the increases were not significant at the 95% confidence level. Despite consistency in the overall average future change in growth among environmentally-sensitive models, the consideration of interactions among environmental variables caused fundamental changes in the magnitude and spatial pattern of future predictions, suggesting that interactive responses of tree growth to changing climate and atmospheric composition remain an important knowledge gap, that can likely only be constrained by improved coordination of field sampling and experimentation.

1. Introduction

Plans to optimize timber supply, conserve protected areas, and mitigate greenhouse gas emissions in the forest sector face increasing uncertainty in forest health and productivity under continued environmental changes (Spittlehouse & Stewart, 2003; Metsaranta et al., 2011; Lobianco et al., 2016; Tian et al., 2016). Forests are already experiencing changes in growth (Girardin et al., 2016; Hember et al., 2017a), mortality (van Mantgem et al., 2009; Hember et al., 2017b), and the activity of insects and pathogens (Kurz et al., 2008; Woods et al., 2010; Kolb et al., 2016). Continued changes in climate and atmospheric composition are likely to introduce new opportunities, new problems, and greater volatility in the forest sector, demanding improved predictive capabilities. The ongoing use of empirical yield curves is increasingly inappropriate because they do not account for projected future global environmental changes, or the impacts of extreme regional climate events.

Nowhere is this more evident than forests of western North America, where epidemic levels of Mountain Pine Beetle and wildfires have killed large expanses of lodgepole pine (*Pinus contorta* Dougl. Ex Loud. var. *latifolia* Engelm.), altering species composition, timber supply, and carbon stocks (Burton, 2006; Kurz et al., 2008; Hawkins et al., 2012). Lodgepole pine remains an important component of unsalvaged stands and a primary candidate for rehabilitation in salvaged stands, emphasizing a need to better understand in the short term, how rates of regeneration will be affected by continuing environmental change.

Approaches to predict climate change impacts on forest biomass production range from process-based models (Arora et al., 2016; Dymond et al., 2016; Mathys et al., 2017), hybrid models (Ashraf et al., 2015; Seely et al., 2015), and statistical models (Nigh et al., 2004; Crookston et al., 2010; Cortini et al., 2011; McLane et al., 2011). These

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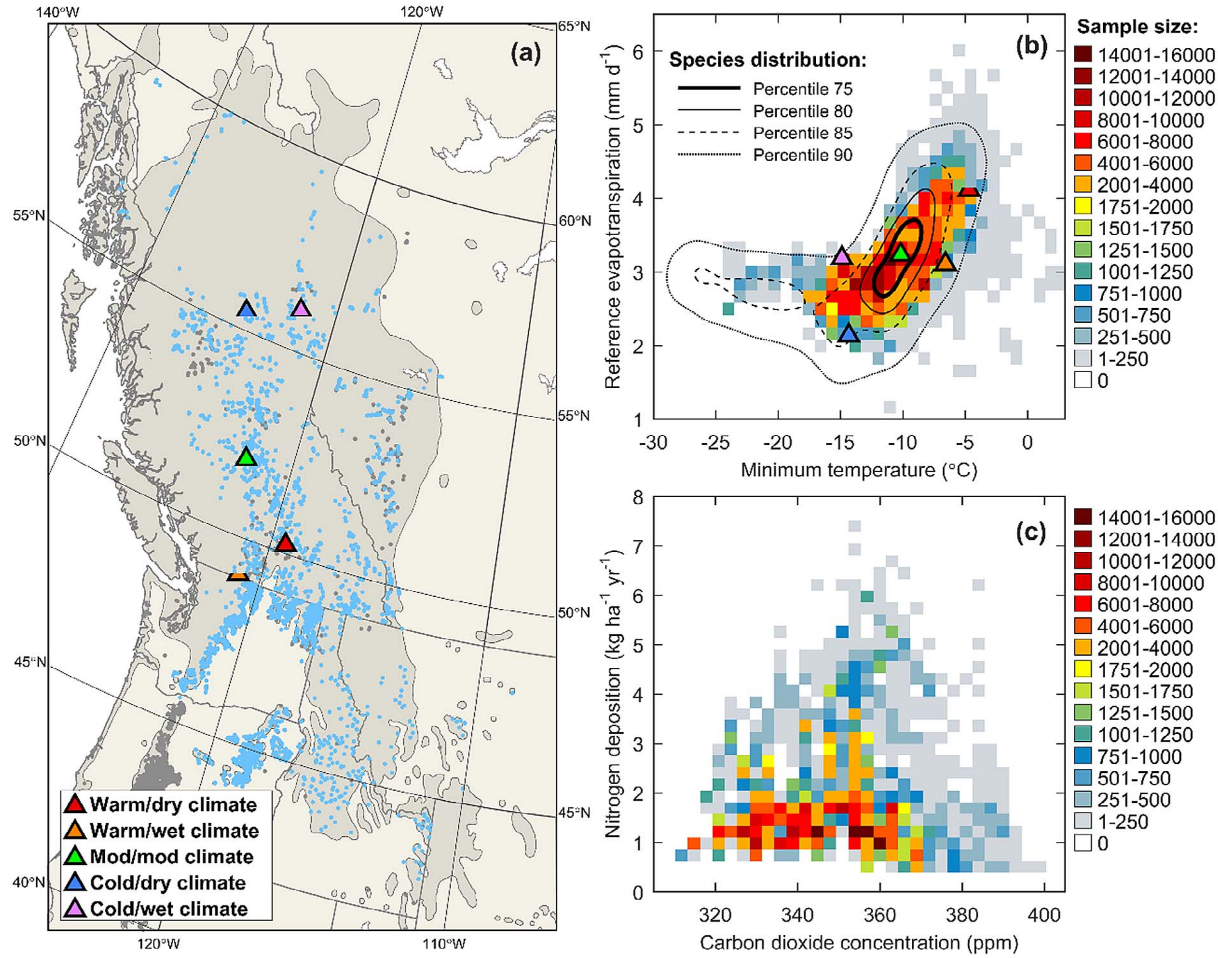

Fig. 1. Study area and field plot sampling in dimensions of (a) geographic space, (b) climate and (c) in atmospheric composition space. In (a), shading indicates the range of Lodgepole pine (Little 1971), grey symbols indicate all lodgepole pine growth observations, blue symbols indicate a subset of observations in the final analysis (see text for reasons behind exclusion). In (b), black counters indicate where the species exists in the dimensions of reference evapotranspiration and minimum temperature according to species fraction maps (Wilson et al., 2013; Beaudoin et al., 2014).

approaches do not always agree on the magnitude or even the direction of regional responses under future environmental change scenarios. While Arora et al. (2016) and Nigh et al. (2004) project increases in productivity, Coops and Waring (2011), McLane et al. (2011), and Seely et al. (2015) project decreases in forest productivity over large expanses of the range of lodgepole pine.

Statistical models are well suited to estimate the sensitivity of trees to recent historical environmental change, which can be used to test hypotheses, to evaluate assumptions in process-based models, and to predict the response of tree growth to current and projected scenarios. Early studies in forestry developed ‘composite’ models to predict the growth rate of individual trees (Stage, 1973; Wykoff, 1990; Monserud and Sterba, 1996). Versions of this approach form the basis for analyzing growth in many subsequent studies (Lacerte et al., 2006; Yang et al., 2009; Crookston et al., 2010; Caspersen et al., 2011; Martin-Benito et al., 2011; Kint et al., 2012; Pokharel and Dech, 2012; Yue and Kahle, 2014; Ford et al., 2016). Such models focus on the behaviour of individual species, and provide a practical method of projecting future tree growth based on interrelationships between biotic and abiotic factors (Stephenson, 1998; Pretzsch and Biber, 2010).

Model specification is an important criterion when evaluating growth models because the influence of omitted-variable bias on the representation of environmental sensitivity is not well understood. In general, we expect simpler models to exhibit low variance and high bias, and more complex models to exhibit high variance and low bias. With respect to tree growth, models that do not simultaneously account for ontogeny, competition, site conditions, biological agents, climate, and atmospheric composition are underspecified. Interactive effects on growth are common in experiments, but they are rarely tested in composite growth models. Competitive status of trees and environmental conditions may affect growth interactively, with important implications for the representation of varying planting density, thinning, and nutrient management (Trouvé et al., 2014; Guillemot et al., 2015; Primicia et al., 2015; Sánchez-Salguero et al., 2015; Carnwath and Nelson, 2016). Site conditions are also a fundamental component of landscape variation of growth (Coops et al., 2007; Buma and Barrett, 2015; Smith et al., 2016). Surface hydrology and microclimate, for example, are closely related to terrain position. Yet, because these processes are, for the most part, not inherently represented in advanced climate datasets, terrain and climate variables may also affect growth interactively.

Despite this demand to develop comprehensive predictive tools, ideal model specification must be weighed against practical limitations, including availability and quality of the independent variables, properties of the sample, the influence of multicollinearity on the variance of the regression coefficients, and overall performance and utility of the model. Whether ideal specification of growth models is supported by historical field plot measurements has not been thoroughly investigated.

In this study, we developed composite models of individual-tree growth of lodgepole pine. The purpose of the study was to add environmentally-sensitive composite models to the arsenal of approaches