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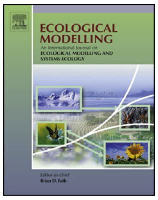

Validation and application of a forest gap model to the southern Rocky Mountains

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ABSTRACT

Rocky Mountain forests are highly important for their part in carbon cycling and carbon storage as well as ecosystem services such as water retention and storage and recreational values. These forests are shaped by complex interactions among vegetation, climate, and disturbances. Thus, climate change and shifting disturbances may lead to significant changes in species composition and biomass. Individual tree-based modeling allows various climate change scenarios and their effects on forest dynamics to be tested. We use an updated individual-based gap model, the University of Virginia Forest Model Enhanced (UVAFME) at four sites in the southern Rocky Mountains. UVAFME is quantitatively and qualitatively validated at these sites against inventory data and descriptions of vegetation zonation and successional dynamics. Results show that UVAFME can be used to reasonably simulate the expected change in species composition with elevation for the southern Rocky Mountains region. UVAFME output on size structure (stems size class^{-1} ha^{-1}) and species-specific biomass (tonnes C ha^{-1}) is comparable to forest inventory data at these locations. UVAFME can also simulate successional dynamics to accurately predict changes in species dominance with landscape age. We then perform a hypothetical climate sensitivity test in which temperature is first increased linearly by 2 °C over 100 years, stabilized for 200 years, cooled back to present climate values over 100 years, and again stabilized for 200 years. Results show that elevated temperatures within the southern Rocky Mountains may lead to decreases in biomass and shifts upslope in species composition, especially that of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*). At some ecotones these changes are also likely to be fairly long lasting for at least 100 years. The results from these tests suggest that UVAFME and other individual-based gap models can be used to inform forest management and climate mitigation strategies for this region.

1. Introduction

Forests in the Rocky Mountains are a crucial part of the North American carbon budget (Schimel et al., 2002), but increases in disturbances such as insect outbreaks and fire, in conjunction with climate change, threaten their vitality (Joyce et al., 2014). Mean annual temperatures in the western United States have increased by 2 °C since 1950 (Meehl et al., 2012), and the higher elevations are warming faster than the rest of the landscape (Wang et al., 2014). It is predicted that this warming trend will continue, and that by the end of this century, nearly 50% of the western US landscape will have climate profiles with no current analog (Bentz et al., 2010; Rehfeldt et al., 2006).

Water-limited systems, such as much of the western US, are vulnerable to drought resulting from warmer temperatures (Hicke et al., 2002). Recently, there have been large-scale die-off events related to rising temperatures and water stress in western forests (Anderegg et al., 2012; Hicke and Zeppel, 2013; Joyce et al., 2014;

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McDowell and Allen, 2015). A severe drought in northern New Mexico in the 1950s resulted in widespread mortality of ponderosa pine (*Pinus ponderosa*) and a shift upwards in the transition zone between pinyon pine (*P. edulis*)-juniper (*Juniperus* spp.) woodland and ponderosa pine forest (Allen and Breshears, 1998), and a regional-scale drought from 2002 to 2003 within the western US resulted in high mortality of pinyon pine (Breshears et al., 2005). Trees are more vulnerable to drought at higher temperatures (Adams et al., 2009). Thus, even if the frequency of prolonged low-precipitation intervals across the Rocky Mountains does not increase in the future, higher temperatures could lead to drought effects through increased water demand, which may then lead to higher tree mortality.

Vegetation patterns of the Rocky Mountains are strongly driven by climate, particularly by elevation gradients in temperature and moisture (Bugmann, 2001a; Peet, 1981). Disturbances are also dominant and integral components of the Rocky Mountains that affect the species composition, size-structure, and stand age of vegetation (Hadley and Veblen, 1993; Sibold et al., 2007; Veblen et al., 1994). Major disturbances include fire, windthrow, and insect outbreaks (Peet, 1981), which can affect and interact with each other (Dale et al., 2001; Jenkins et al., 2012; Rasmussen et al., 1996; Veblen et al., 1994). Climate change is predicted to result in an increase in the frequency and severity of disturbances within the Rocky Mountains (Bentz et al., 2010; Dale et al., 2001), further influencing the future of western forests.

It is difficult to predict how vegetation will respond to climate change alone and with concurrent disturbances (Fettig et al., 2013; Raffa et al., 2008). Plants are able to respond to changing climate at multiple spatial and temporal scales. Over short time and space scales, plants may respond to water stress through stomatal closure, leading to lower transpiration and canopy conductance (Katul et al., 2012). Over longer time and space scales, changing climate may lead to shifts in the locations of species' optimal ranges (Shugart and Woodward, 2011). Increasing disturbances are expected to accelerate these shifts by opening up canopies, allowing for more rapid transitions from historical tree demographics to dominance by new, more climate-appropriate tree species at a given locale (McKenzie et al., 2009). In mountainous regions, however, high-elevation species may be unable to move to upslope locations if their expected range shifts exceed the mountain heights (Bell et al., 2014; Hannah et al., 2002), which may result in local extinction of subalpine species.

The complex interactions between climate, vegetation, and disturbances in this region make parsing the relative effects of these drivers difficult (Fettig et al., 2013; Joyce et al., 2014; Raffa et al., 2008). Gap models are based on the forest dynamics involved in the competitive aftermath of the death of a large, dominant tree (Shugart, 1984; Watt, 1947) and are able to simulate small-scale tree responses to their environment, climate, and disturbances, tree to tree competition, as well as larger-scale successional dynamics (Shugart and Woodward, 2011). For these reasons, they have been successfully used to study the response of forests to shifting climate and disturbance regimes (Bugmann, 2001b; Keane et al., 2001; Lasch and Lindner, 1995; Shuman and Shugart, 2009). Since the creation of the original gap model, JABOWA (Botkin et al., 1972), others like it have been developed, each with its own set of governing processes and assumptions (Bugmann, 2001b; Bugmann and Solomon, 2000). In general, the relatively simple equations and moderate number of parameters of forest gap models make them adaptable to a wide range of forest types (Waldrop et al., 1986). Good practice is testing to ensure that models are performing well in new locations and climates.

The University of Virginia Forest Model Enhanced (UVAFME) derives from the individual-based gap model, FAREAST, which was initially produced by a fusion of functions from the FORSKA model of Swedish forests (Leemans and Prentice, 1987) and the FORET model (Shugart and West, 1977) of Southern Appalachians (USA). FAREAST was originally developed by Yan and Shugart (2005) for use in China and subsequently boreal Eurasia, and has been successfully applied and tested within the Russian boreal forest. The model was validated against maps of species composition and vegetation types across all of boreal Russia (Shuman et al., 2015, 2014) and model output compared favorably to the bioclimatic envelope model, RuBCLiM when applied at 31,000 sites across Russia (Shuman et al., 2015). The version of UVAFME presented here has updated functionality and processing, described in detail within the methods section, and has been adapted for use in the Rocky Mountains landscape. The equations previously used in UVAFME to calculate the temperature limitation and the overall effect of environmental stressors on diameter increment growth have been criticized in the ecological modeling literature (Bugmann, 2001b). We have thus modified these equations to better reflect vegetation dynamics within the Rocky Mountains. We have also updated the soil moisture modeling within UVAMFE to reflect a mountainous environment highly influenced by snow accumulation and melt (Serreze et al., 1999). Finally, we have added a new fire module that simulates the species- and tree size-specific responses to varying levels of fire intensity, a crucial part of simulating forest dynamics within the disturbance-dominated Rocky Mountains (Schumacher et al., 2006; Veblen, 2000).

Other forest and landscape models have been previously applied within the Rocky Mountains, such as FireBGC (Keane et al., 1996), ForClim (Bugmann, 2001a) and LandClim (Schumacher et al., 2006; Temperli et al., 2015). Our study builds on these previous studies through the use of a model that includes simulation of the annual growth and response of individual trees to fire and wind throw, as well as the inclusion of nitrogen cycling and vegetation response to nutrient availability (Foster et al., 2015; Shuman et al., 2015; Yan and Shugart, 2005). This study is also a stepping stone for future model development within the region, including the creation of an individual tree-based submodel for prediction of bark beetle-related mortality (Foster et al., *in review*).

The goals of this study are to evaluate the performance of UVAFME within the southern Rocky Mountains and to determine how increasing temperatures may affect the vegetation within this region. After the tests on UVAFME's performance we conduct a temperature sensitivity test to investigate how species zonation and species-specific biomass within the region may respond to increasing temperatures. In this sensitivity test, we also cool temperature back to present values after a period of stabilization at the elevated values. This cooling is conducted to determine how lasting the vegetative response to increasing temperatures might be, even under conditions of reverse climate cooling. This theoretical experiment is designed to test both the model's sensitivity to climate as well as the individual response of vegetation to changing temperature alone. Previous research with UVAFME in the southern Rocky Mountains (Foster et al., 2015) found evidence for cyclic behavior in the subalpine zone in the absence of disturbances. This study builds on Foster et al. (2015) through the study of how fire and windthrow disturbances as well as warming temperatures affect Rocky Mountain vegetation dynamics. One of the benefits of individual-based, height-structured forest models such as UVAFME is their ability to modify individual tree drivers and disentangle different factors affecting forest dyanmics (Purves and Pacala, 2008). This type of temperature sensitivity test has not been conducted in this region as of yet, and is only possible with an individual tree-based model, such as UVAFME, capable of capturing the interactions between climate, vegetation, and disturbances at multiple spatiotemporal scales.