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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.

2. Methods

2.1. Study area

We focus on the climate response of the broader southern Rocky Mountains region (Bassman et al., 2003) as well as specific forest dynamics at four subalpine sites in the Wyoming and Colorado Rocky Mountains (Fig. 1). These specific sites are the USDA Forest Service's Glacier Lakes Ecosystem Experimental Site (GLEES), Niwot Ridge/US NR1, USDA Forest Service's Fraser Experimental Forest (FEF), and Wolf Creek Pass. GLEES is located east of the continental divide in the Snowy Range, near Centennial WY (41°22′30″N, 106°15′30″W, 3200–3500 m). It is dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), with some lodgepole pine (*Pinus contorta*) and limber pine (*P. flexilis*) (Regan et al., 1997). Average annual precipitation is about 1000 mm, and mean annual temperature is about −0.5 °C (NCDC, 2015). Niwot Ridge is located 50 miles west of Boulder, CO at 40°1′58.44″N, 105°32′45.60″W. It is situated on the eastern slope of the Colorado Front Range at elevations from 3020 to 3810 m. Annual precipitation is about 700 mm and mean annual temperature is about 2.7 °C (NCDC, 2015). The vegetation at this site is also typical of a subalpine forest in this region, dominated by subalpine fir, Engelmann spruce, and lodgepole pine (Sacks et al., 2006). FEF is located on the west slope of the continental divide, at 39°50′50″N, 105°54′42″W and elevations from 2700 to 3400 m. Average precipitation at this site is about 500 mm and average temperature is about 1 °C (Elder, 2006, 2005). Vegetation at this site consists of Engelmann spruce, subalpine fir, and lodgepole pine (Stottlemyer and Troendle, 2001). Wolf Creek is also west of the continental divide and is located in the San Juan Mountains, in southern Colorado at 37°29′24″N, 106°50′24″ and at elevations from 2800 to 3600 m. Average precipitation at Wolf Creek is about 1100 mm and average temperature is about 1.5 °C (NCDC, 2015). Vegetation at this site is comprised of Engelmann spruce, subalpine fir, quaking aspen (*Populus tremuloides*), and Douglas-fir (*Pseudotsuga menziesii*).

2.2. Inventory data

Forest inventory data on species, diameter at breast height (DBH), and tree status (i.e. alive, dead, infested, etc.) for each tree were collected at GLEES between 1989 and 1991 and between 2010 and 2012, in 143 plots ranging from 100 to 200 m^2 in size. Inventory data in the form of species, DBH, and status were also collected at Wolf Creek Pass in 2015 in 78 400 m^2 plots. We use these inventory data to quantitatively validate model performance at these two sites. For the GLEES data, some plots had been sampled during both inventory periods; in these cases, we used only the data from the latest sampling date. We did not have inventory data for either Niwot Ridge or FEF, and thus compared model output at those sites to qualitative descriptions of species composition and successional trajectories for the region.

2.3. Model description

UVAFME simulates the establishment, growth, and death (see Fig. 2 for a schematic of UVAFME) of individual trees on independent plots, or "gaps", about the area of influence of a dominant tree crown (500 m^2). The average of several hundred of these simulated plots represents change in species composition, biomass, and structure of a forested landscape through time. Please note that the use of "landscape" in this paper refers to the aggregated behavior of many spatially non-contagious sample plots – a quasi-equilibrium landscape (Shugart and Woodward, 2011). A landscape-level dynamic response in this sense differs strongly from the dynamics of a single plot. Landscape responses can demonstrate complex dynamics, inertial effects, hysteresis, and multiple stable states not apparent in the dynamics at the plot scale (see Chapter 5 of Shugart and Woodward 2011 for a review of these issues). The species composition and biomass of each simulated plot, and as such of the whole landscape (i.e. several hundred plots), are affected by competition among individual trees for resources. Competition is simulated through species- and tree size-specific differences in shade, drought, nutrient, and temperature tolerances. UVAFME also simulates tree mortality and tree response to disturbances by fire and windthrow. A detailed description of the equations and methods used in UVAFME can be found in the Supplementary Material. Inputs to UVAFME include climate information (mean monthly temperature minima and maxima and precipitation), site and soil information, and species-specific parameters such as drought, temperature, shade, and nutrient tolerances, maximum height, and maximum DBH. UVAFME output includes the species, DBH, and height of each tree on each plot, making it directly comparable to forest inventory data. Output from UVAFME can then be aggregated to derive forest characteristics such as biomass (tonnes C ha^{-1}), basal area (m^2 ha^{-1}), size structure (stems size $class^{-1}$ ha^{-1}), species composition, and LAI. Thus, output from UVAFME can be used to make inferences about the effects of various management, climate, or disturbance scenarios on vegetation composition and structure.

2.4. Model updates and parameterization

UVAFME was first parameterized to the southern Rocky Mountains with climate, site, soil, and species information from the US Forest Service, the National Climatic Data Center (Menne et al., 2012a,b; NCDC, 2015), Burns and Honkala (1990), and other scientific literature as in Foster et al. (2015) (see Table A1 in the Appendix A for a list of species parameters). The inputs for month-specific environmental lapse rates (i.e. change in temperature with elevation; °C km^{-1}) were developed using mean monthly temperature for years ranging from 1967 to 2014 for an average of 26 years at 15 sites across the Colorado and Wyoming Rocky Mountains and at elevations ranging from 1690 to 3414 m. Change in precipitation with elevation (mm km^{-1}) was derived from Marr (1961). These values are comparable to lapse rates found in other studies (Daubenmire, 1943; Peet, 1981), and are used to run UVAFME at different elevations within the region. Species-specific growing degree day (GDD, i.e. annual sum of mean daily temperatures above 5 °C) tolerances were also developed using this lapse rate and information from Peet (1981) and Marr (1961) on the elevation zones of southern Rocky Mountains species. For example, Engelmann spruce (*Picea engelmannii*) is documented as surviving at elevations between 2438 and 3353 m (CSFS, 2016). We utilized our lapse rate and the temperature data across all 15 weather stations to calculate average GDD at 2438 m and 3353 m, thus calculating an average maximum and minimum GDD, respectively, for Engelmann spruce.

Forest dynamics within the southern Rocky Mountains are highly influenced by disturbances such as fire and windthrow, as well as snowpack accumulation and melt dynamics (Serreze et al., 1999; Sibold et al., 2007; Veblen et al., 1994). Previous versions of UVAFME did not include any snow accumulation or melt, and included only stand-replacing wildfire, which is not realistic for the study region. Additionally, previous equations relating tree growth to temperature and other environmental stressors have been criticized in the recent literature (Bugmann, 2001b). To address these concerns, we made several modifications to UVAFME appropriate to the study region. UVAFME simulates soil moisture and soil decomposition processes through a coupled three-layer (organic, A, and B layers) soil bucket model. Inputs to the soil layers come in the form of precipitation from the climate subroutine, and carbon and nitrogen inputs from the tree growth and death subroutines.

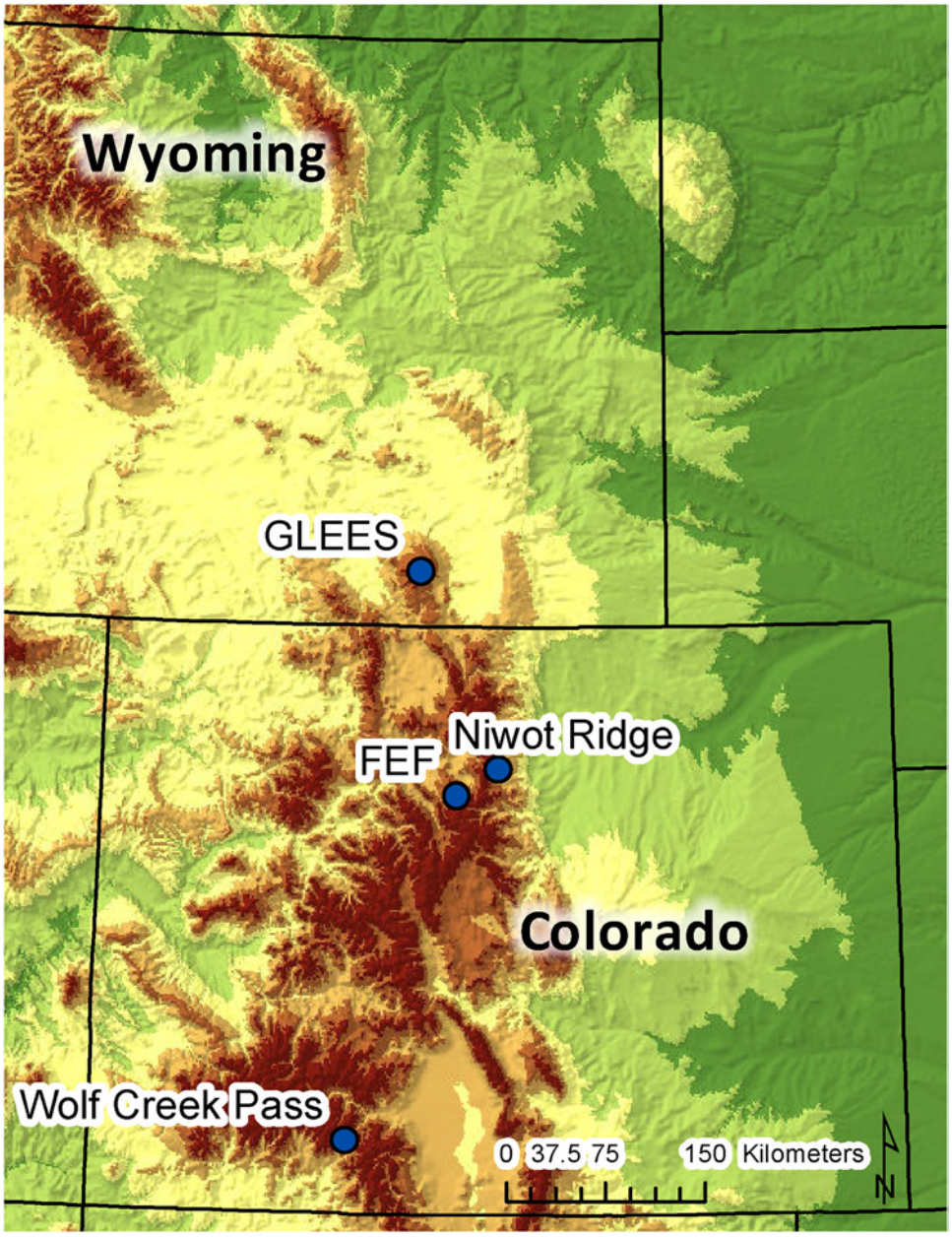

Fig. 1. Map of study sites.

UVAFME then simulates soil moisture, C, and N in each soil layer based on these inputs, input soil characteristics (i.e. field capacity, wilting point, slope, etc.), and daily potential evapotranspiration (PET), calculated in the climate subroutine. This nutrient cycling and tree growth response to nitrogen availability is a key feature of UVAFME not present in other similar models such as LandClim (Schumacher et al., 2006). A simple snowmelt submodel (Eq. 1) was implemented within the soil subroutine of this version of UVAFME using degree-day method equations from Singh et al. (2000) in order to simulate accumulation and melting of snow. If the air temperature is below 5 °C, precipitation for that day is assumed to be snow, and is accumulated in the snowpack. If the temperature is above the base temperature (t_b, generally set to 0 °C), the thaw for that day (M, in mm) is calculated as:

$$M = c_m (t_a - t_c) \quad (1)$$

where c_m is the melt factor (mm degree-dayC^{-1}), based on site characteristics (DeWalle et al., 2002), and t_a is the mean air temperature (°C). This meltwater is then transferred to the surface water layer for further soil moisture modeling (see the Supplementary Material for a complete description of the soil moisture subroutine within UVAFME). The addition of snowpack accumulation and snowmelt within UVAFME allows for better representation of soil moisture dynamics within the Rocky Mountain subalpine zone, where most of the precipitation falls as snow in the fall and winter, and melts in spring and summer (Serreze et al., 1999).

To better track vegetation response to changing climate conditions, we modified the original equation for the effect of growing degree-days (GDD) on tree growth from a parabolic response curve (Eq. (2)) to an asymptotic response curve (Eq. (3)).

$$f_{temp} = \begin{cases} 0, \; GDD \le DD_{min} \\ 0, \; GDD \ge DD_{max} \\ \left(\frac{GDD - DD_{min}}{DD_{opt} - DD_{min}}^{a}\right)\left(\frac{DD_{max} - GDD}{DD_{max} - DD_{opt}}^{b}\right), \; DD_{min} < GDD < DD_{max} \end{cases} \quad (2)$$

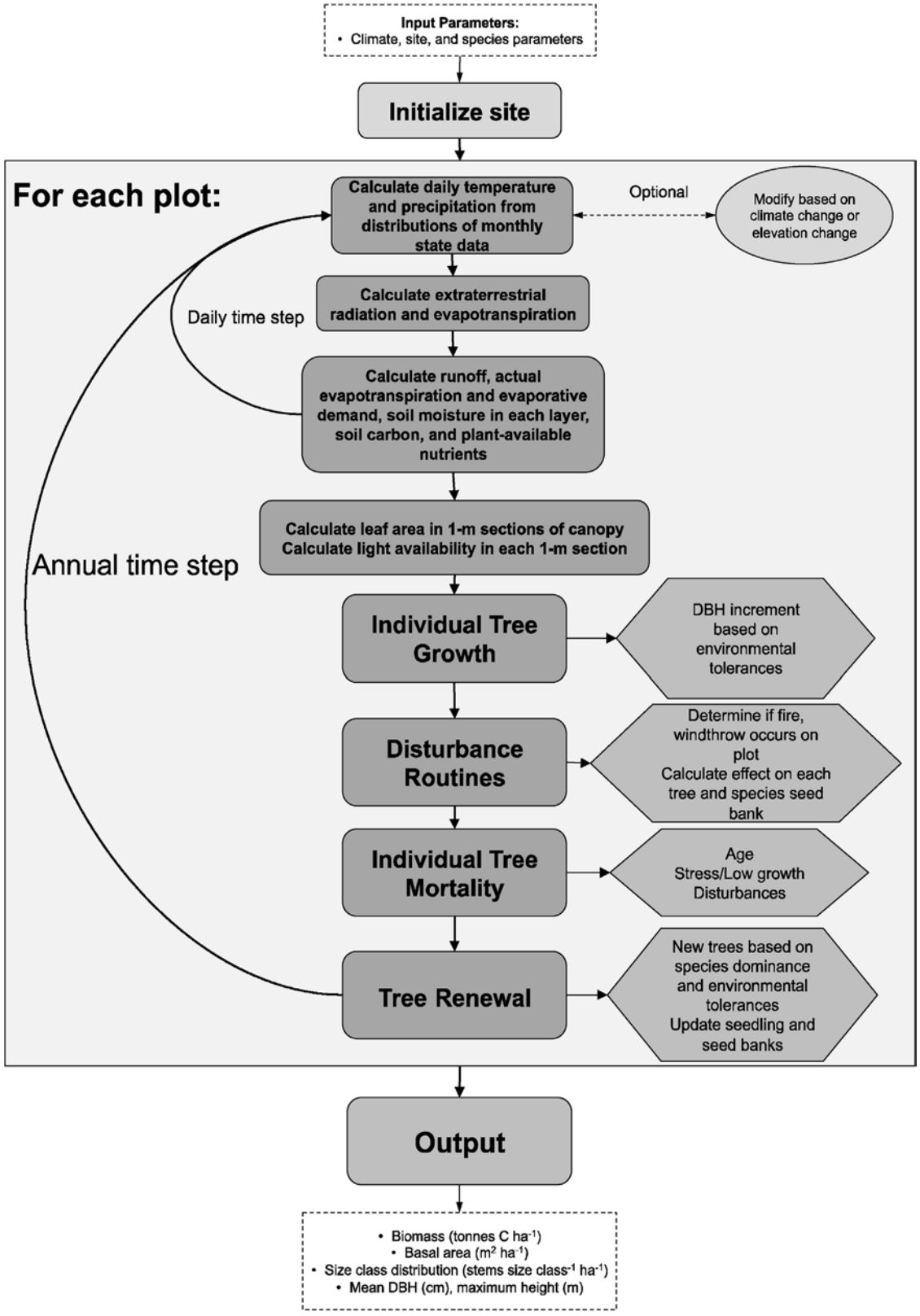

Fig. 2. Schematic of UVAFME.

$$f_{temp} = \begin{cases} 0, \; GDD \le DD_{min} \\ 1, \; GDD \ge DD_{opt} \\ \left(\frac{GDD - DD_{min}}{DD_{opt} - DD_{min}}^{a}\right)\left(\frac{DD_{max} - GDD}{DD_{max} - DD_{opt}}^{b}\right), \; DD_{min} < GDD < DD_{opt} \end{cases} \quad (3)$$

where f_{temp} is the effect of GDD on tree growth, GDD is the annual growing degree day sum that year, $DD_{\min}$, DD_{opt}, and $DD_{\max}$ are the minimum, optimum, and maximum tolerable growing degree day sums, $a = \left(DD_{opt} - DD_{min}\right) / \left(DD_{max} - DD_{min}\right)$, and $b = \left(DD_{max} - DD_{opt}\right) / \left(DD_{max} - DD_{min}\right)$.

This change means that trees are negatively affected by growing degree-days below their optimum tolerable GDD, but unaffected by growing degree-days above DD_{opt}. The parabolic temperature response curve (Eq. (2)) has been criticized for predicting extremely low growth at species' warmest range limits, in contrast to empirical studies, which often find that, in the absence of drought, trees grow quite well at their warmer range limits (Bugmann, 2001b; Korzukhin et al., 1989; Loehle, 2000). By using an asymptotic temperature response curve, simulated trees that are experiencing high temperatures are only negatively affected by potential increases in drought stress and tree – tree competition. The switch from parabolic to asymptotic allows for a move away from a "climate envelope" approach to species distribution modeling. Whereas in "climate envelope" modeling trees cannot grow beyond the upper GDD limit, in our updated model trees are allowed to grow outside this boundary, given adequate above- and belowground resources. This modification allows for testing of species responses to increasing temperatures without a need to assume trees cannot grow at temperatures above their normal range.

FAREAST originally used the multiplicative method (Eq. (4)) to aggregate the different growth-limiting factors (i.e. shade, drought, temperature, and nutrient stress, all 0–1 in scale) to create an overall growth-limiting factor. In this method, each factor is multiplied together and the final factor is used to reduce annual optimal diameter increment growth, based on allometric equations, to an actual increment growth for that year.

$$f_{growth} = f_{shade} \cdot f_{drought} \cdot f_{temp} \cdot f_{nutrient} \quad (4)$$

$$f_{growth} = \min\left(f_{shade}, f_{drought}, f_{temp}, f_{nutrient}\right) \quad (5)$$

The multiplicative method has been criticized for resulting in growth rates that are far too low (Bugmann, 2001b). A key issue with this method is that the more growth-limiting factors considered, the harsher the environment becomes with respect to annual tree growth. We, as did Pastor and Post (1986), calculate growth-limitation in this version of UVAFME using a Liebig's Law of the Minimum approach. Here, the smallest of the stress-specific growth factors is chosen as the overall growth-limiting factor (Eq. (5)), meaning that an individual tree's growth is hindered by only the most limiting environmental factor. This method is more representative of tree response to stressors, especially in the Rocky Mountain region, where many of the species have adapted to the harsh climate and conditions of the high elevations (Daubenmire, 1978).

Mortality by disturbance is an essential element of forest dynamics in this region (Veblen, 2000). This version of UVAFME includes disturbances by windthrow and fire. A future version will include bark beetle disturbance (Foster et al., *in review*). Site-specific fire return interval, fire intensity, and wind return interval input parameters were estimated based on information in the literature (Veblen, 2000; Veblen et al., 1994). These values were based on the subalpine zone being characterized by low frequency (i.e. 300 years or longer return intervals), stand-replacing fires and occasional high-intensity windstorm events (Veblen, 2000). For these elevation tests, fire frequency was increased linearly with decreasing elevation until 2000 m, where it was decreased with elevation. In contrast, fire intensity was decreased with elevation. Windthrow frequency was decreased with elevation. Because these estimates are not based on empirical data they may add some uncertainty to our simulations. However, our intent was to simulate the general shift from a subalpine zone dominated by high intensity, low frequency disturbance events, to forests of the lower elevations, which experience more moderate, higher-frequency disturbances by fire (Veblen, 2000).

The effect of fire on tree mortality and tree regeneration within the Rocky Mountains depends both on tree species as well as tree size (Ryan and Reinhardt, 1988). Fires significantly affect species composition and size structure (Sibold et al., 2007; Veblen et al., 1994), and are an important feature of modeling forest dynamics in this region (Schumacher et al., 2006; Temperli et al., 2015). The fire module for UVAFME was updated so that the size- and species-level effects of fire on tree mortality and regeneration could be simulated. Previously, if a fire occurred on an individual plot, or "gap", it would kill all trees on that plot. In this new module, fire kills trees based on size and a species-specific bark thickness coefficient, and affects the regeneration of trees based on a species-specific fire regeneration parameter. Fire in UVAFME is stochastic and based on the site-specific fire return interval (FRI). Each year and for each plot, a random number is called between 0 and 1.0, and if this number is lower than 1/FRI, fire occurs on that plot (see the Supplementary Material for further information). With fire occurrence, UVAFME first calculates the intensity level of the fire (f_{cat}) using a normally distributed random number between 0.0 and 12.0, with a site-specific mean corresponding to the site's average fire intensity. Low-intensity surface fires have a fire category between 0.0 and 4.0, moderate-intensity fires have a fire category between 5.0 and 8.0, and high-intensity crown fires have a fire category between 9.0 and 12.0. UVAFME then calculates which trees will die and which will survive. The model first calculates the scorch height of the fire (Eq. (6)) and percent of crown volume scorched of each tree (Eq. (7)) based on equations from Keane et al. (2011) and Van Wagner (1973).

$$SH = \frac{a \cdot FI^{1.1667}}{\left(T_{kill} - T_{amb}\right)\left[b \cdot FI + c \cdot U^3\right]^{0.5}} \quad (6)$$

$$CK = 100\frac{CS\left(2CL - CS\right)}{CL^2} \quad (7)$$

where SH is the scorch height of the fire (m), CK is the percent crown volume scorched (%), CL is the crown length (m), CS is the scorch length (m; calculated as $CS = SH - (H_{tree} - Z_{bole})$, where H_{tree} is the total tree height (m), and Z_{bole} is the crown depth (m)), and FI is the fire intensity (kW m^{-1}, calculated as $FI = 1000 f_{cat}$). The empirical parameters a (0.74183 m $^{\circ}$C^{-1}), b (0.025574 (kW m^{-1})$^{4/3}$), and c (0.021433 km^{-1} h (kW m^{-1})$^{7/9}$), are based on values from Keane et al. (2011), as are the values for the ambient fire temperature (T_{amb}, 20 $^{\circ}$C) and lethal fire temperature (T_{kill}, 60 $^{\circ}$C). The exponent in the numerator of the equation for scorch height (Eq. (6)) is from Van Wagner (1973), based on a two-thirds power law relationship between scorch height and fire intensity. Wind speed (U, km hr^{-1}) is a randomly generated value between 0 and 32.0, based on the default value in Reinhardt and Crookston (2003).

All trees less than 12.7 cm in diameter die regardless of fire intensity or bark thickness, based on Bonan (1989). Trees larger than 12.7 cm may die based on percent scorch volume (CK), bark thickness, and tree diameter. Species-specific bark thickness coefficients (b_{thick}, cm bark cm DBH^{-1}) are adapted from values in Keane et al. (2011). The probability for tree mortality (Eq. (8)), based on

the fire mortality from Ryan and Reinhardt (1988) and Keane et al. (2011), is calculated as:

$$p_{fire} = \frac{1}{1 + e^{\left[-1.941+6.32\left(1-e^{-b_{thick}DBH}\right)-0.00053CK^2\right]}} \quad (8)$$

where p_{fire} is the probability of mortality due to cambial death and percent of crown scorch. These equations have been successfully used to predict crown scorch and fire mortality within forests of the western United States (Hood et al., 2007; Keane et al., 2011; Reinhardt and Crookston, 2003; Ryan and Reinhardt, 1988), and are a valuable addition to UVAFME's disturbance submodels.

The seedbank for each species is also affected by fire, based on species-specific fire regeneration values (1–6; 1 being the most tolerant, and 6 being the least tolerant). If the fire category (f_{cat}) is 11.0 or higher, a five-year wait occurs before new seedlings and saplings can regenerate (Harvey et al., 2016; Johnstone and Chapin, 2006). Otherwise, each species' seedbank is multiplied by the variable f_{fire}, which ranges from 0.001 to 100.0, depending on the species' regeneration tolerance to fire. Thus, fire increases the seedbank of species that have a high regeneration tolerance to fire, and decreases the seedbank of species that have a low regeneration tolerance to fire. More information on the updated fire submodel can be found in the supplementary material.

2.5. Model evaluation

To determine whether the updated UVAFME accurately simulates forest dynamics of the Rocky Mountains, we conducted several tests of the model's performance. We first ran the model at successive elevations at both GLEES and Wolf Creek in order to determine if UVAFME can predict the expected change in species composition with elevation (Daubenmire, 1943). Results from elevation tests for the area within and surrounding GLEES and Wolf Creek represent zonation for the northern and southern extent of the study area, respectively. Even though in reality the specific locations at which we ran the elevation tests are not comprised of the full elevation range used and may not include all species present, we were interested in determining how well UVAFME is able to predict the general species zonation within the region (Daubenmire, 1943; Marr, 1961; Peet, 1981). In these tests, UVAFME was run from 1600 m to 3600 m at 100 m intervals as in Foster et al. (2015). Tests presented here include disturbances by fire and windthrow.

Model evaluation involves both model verification, in which the model is tested against a set of observations that were used during parameterization, and model validation, in which model output is compared to an independent set of observations, not used to structure or parameterize the model (Mankin et al., 1977; Shugart, 1984; Shuman et al., 2014). We performed model calibration during the verification phase, with small changes in parameter values and internal processes (for example, increasing the number of years a tree can survive at extremely low diameter increment growth) at two elevations (2400 and 3400 m) at GLEES prior to conducting the validation elevation tests. Other than at these two elevations at this location, all additional validation tests are independent of observational data. At each of the 20 elevations, and at both sites, 200 independent plots were run in a Monte Carlo-style simulation from bare ground for 500 years. Model output at year 500 averaged over all 200 plots reflects the average expected species composition for a mature forest landscape at that elevation. In simulations as long as 3000 years, we found that 500 years capture the forest dynamic responses when disturbances by fire and windthrow are included. The eleven major tree species found in the southern Rocky Mountains were allowed to grow at each elevation except for pinyon pine (*P. edulis*) at GLEES and lodgepole pine (*P. contorta*) at Wolf Creek, as the geographical ranges of these species do not intersect with these sites. In this test, UVAFME computed which species should grow and dominate at each elevation zone as well as which species should fail to prosper at a particular elevation. The resultant species zonations arise from the resource requirements and climate tolerances of each species as well as competition among trees of different species. We compared the pattern of species composition (based on biomass at year 500) with elevation to descriptions of zonation expected in a typical mountainside in the southern Rocky Mountains (Marr, 1961; Peet, 1981).

We also compared UVAFME-simulated biomass and size structure to forest inventory data from GLEES and Wolf Creek, and conducted *t*-tests (for biomass) and linear regressions (for size structure) to determine if model-derived data was significantly different from inventory data on forest structure and composition. Only species present in a particular site's inventory data were allowed to grow at that site. For these validation tests, the model was used to simulate 200 independent plots for 500 years at both Wolf Creek and GLEES. Within the inventory data, species-specific aboveground biomass (tonnes C) for each tree above 3 cm DBH was calculated using updated diameter – biomass equations from Chojnacky et al. (2014). These data were then aggregated to create species-specific biomass (tonnes C ha^{-1}) for each inventory plot. The current version of UVAFME does not contain disturbances by bark beetles. Information on the bark beetle infestation status of each tree on each plot was collected along with the inventory data, and we included trees denoted as "beetle killed" in the biomass and size structure calculations for each site. Plot-specific data on stand age for either site were lacking; however, as both sites are unmanaged (J. Negron, *pers.comm.*; J. Sibold, *pers. comm.*), it was assumed that the forests at each location were at a quasi-equilibrium state and model output at 500 years was compared to the inventory data.

As a final model test, UVAFME was used to simulate forest dynamics at all four test sites (Fig. 1) from bare ground for 500 years on 200 independent plots to determine if successional dynamics and the time series of species-specific biomass changes over time predicted by UVAFME at each site corresponded to typical successional changes for the subalpine zone in the region (Aplet et al., 1988; Daubenmire, 1978; Veblen, 1986). Similarly, only species present in the inventory data (GLEES and Wolf Creek) and site descriptions (Niwot Ridge and FEF) were allowed to grow at a given site.

2.6. Climate sensitivity test

We conducted a temperature sensitivity test at GLEES to determine the effect of temperature change alone on the general species zonation of the southern Rocky Mountains region. We ran the model for 1100 years, using 200 independent plots, from 1600 m to 3600 m at 100 m intervals, as in our elevation validation tests. In these sensitivity simulations, the model was run with current climate conditions until year 500. At year 500 a 2 °C linear increase in temperature was employed over 100 years (i.e. 0.02 °C/year), after which climate was allowed to stabilize at these new values for 200 years. At year 800, we employed a 2 °C linear decrease in temperature over 100 years, back to current historical values. We then allowed this climate to stabilize for another 200 years. Daily temperature and precipitation in UVAFME are sampled from input distributions (i.e. mean and standard deviation) of monthly precipitation and monthly minimum and maximum temperatures. For this sensitivity test the linear temperature change was applied only to each site's mean monthly minimum and maximum temperature values, with the standard deviations for these values held at historical levels, thus retaining historical temperature variability. The 2 °C increase was chosen as it is a conservative estimate for climate change (IPCC, 2014), as well as the "tolerable change" value proposed by the UN Climate Change Conference in Paris

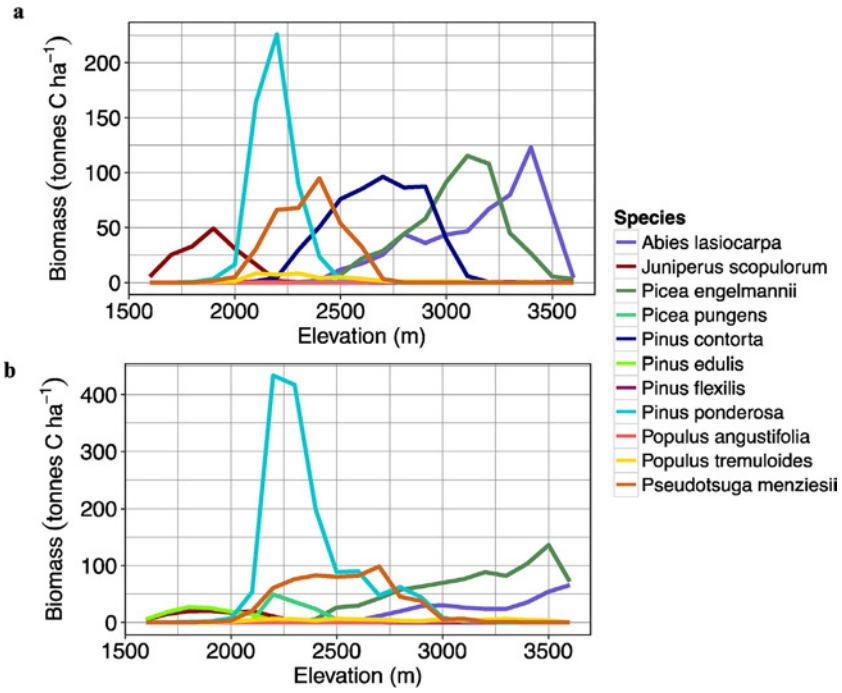

Fig. 3. UVAFME-simulated biomass (tonnes C ha^{-1}) at year 500 of eleven Rocky Mountain species at different elevations at (a) the northern site, GLEES, and (b) the southern site, Wolf Creek. UVAFME was run every 100 m from 1600 m to 3600 m with species- and size-specific effects of fire and windthrow.

in December 2015. This model investigation inspected how the biomass and species composition may change with increasing temperatures alone, and whether there is any inertial response in the transition back to its current state. We did not include change in precipitation in these simulations, so any increase in drought-related stress would be due to increasing temperatures affecting evapotranspiration and thus soil moisture.

3. Results

3.1. Model evaluation

In simulations at successive elevations at GLEES and Wolf Creek, a pinyon pine (*P. edulis*) and/or juniper (*J. scopulorum*) woodland is modeled to exist at lower elevations, giving way to a conspicuous ponderosa pine (*P. ponderosa*) belt at about 2000 m (Fig. 3). Douglas-fir is predicted to prosper between about 2000 and 2700 m at GLEES (Fig. 3a), and up to 3000 m at Wolf Creek (Fig. 3b). Ponderosa pine (*P. ponderosa*) is predicted to have a wider range at Wolf Creek than it does at GLEES. Finally, a subalpine zone, dominated by subalpine fir (*A. lasiocarpa*) and Engelmann spruce (*P. engelmannii*), is modeled to exist at elevations above 3000 m at both sites. Model simulations also predict a zone with Engelmann spruce, subalpine fir, and lodgepole pine (*P. contorta*) between 2700 m and 3000 m at GLEES.

Local-scale model output on species-specific biomass within the subalpine zone at both GLEES (3115 m) and Wolf Creek (3100 m) compared fairly well with inventory data at those sites (Fig. 4). There was no statistically significant difference between simulated and measured Engelmann spruce biomass at either test site (Table 1). While the measured and simulated biomass values of most of the subdominant species at each site did statistically differ, in general the relative dominance of each species was similar between simulated and inventory values (Fig. 4). Total biomass at each site was not significantly different between inventory and simulated values (Table 1).

UVAFME also performed well at predicting the tree size class distribution at GLEES and Wolf Creek for trees with a DBH larger than 20 cm at Wolf Creek and for all size classes at GLEES (Fig. 5). At

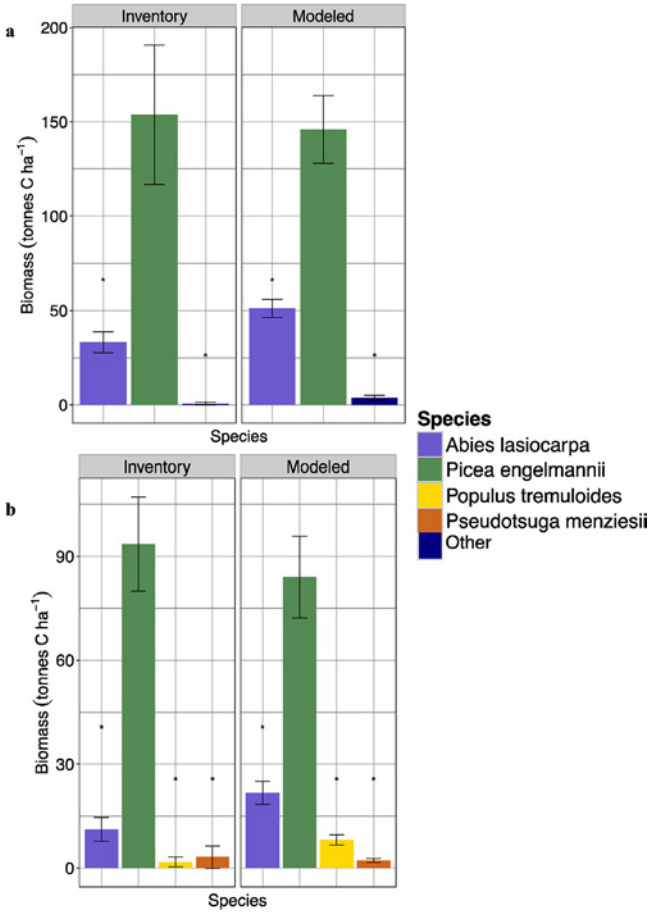

Fig. 4. UVAFME-simulated biomass (tonnes C ha^{-1}) at year 500 compared with inventory biomass for (a) GLEES (3115 m) and (b) Wolf Creek (3100 m). Error bars correspond to 95% confidence intervals and stars indicate significant differences ($p < 0.05$) between modeled and inventory biomass.

Table 1
Results of *t*-tests comparing UVAFME-simulated biomass at year 500 and inventory-derived biomass at GLEES and Wolf Creek for the subalpine zone at 3115 and 3100 m.

Site	Species	Modeled Biomass (tonnes C ha^{-1})	Inventory Biomass (tonnes C ha^{-1})	*t*-statistic	p-value
GLEES	*Picea engelmannii*	145.97	153.76	−0.36	0.718
	Abies lasiocarpa	51.09	33.16	4.69	<0.001
	Other	3.60	0.57	3.77	<0.001
	Total	200.66	187.49	0.61	0.543
Wolf Creek Pass	*Picea engelmannii*	84.02	93.55	−1.04	0.301
	Abies lasiocarpa	21.70	11.16	4.33	<0.001
	Populus tremuloides	8.17	1.76	6.12	<0.001
	Pseudotsuga menziesii	2.18	3.17	−0.59	0.558
	Total	116.07	109.65	0.76	0.449

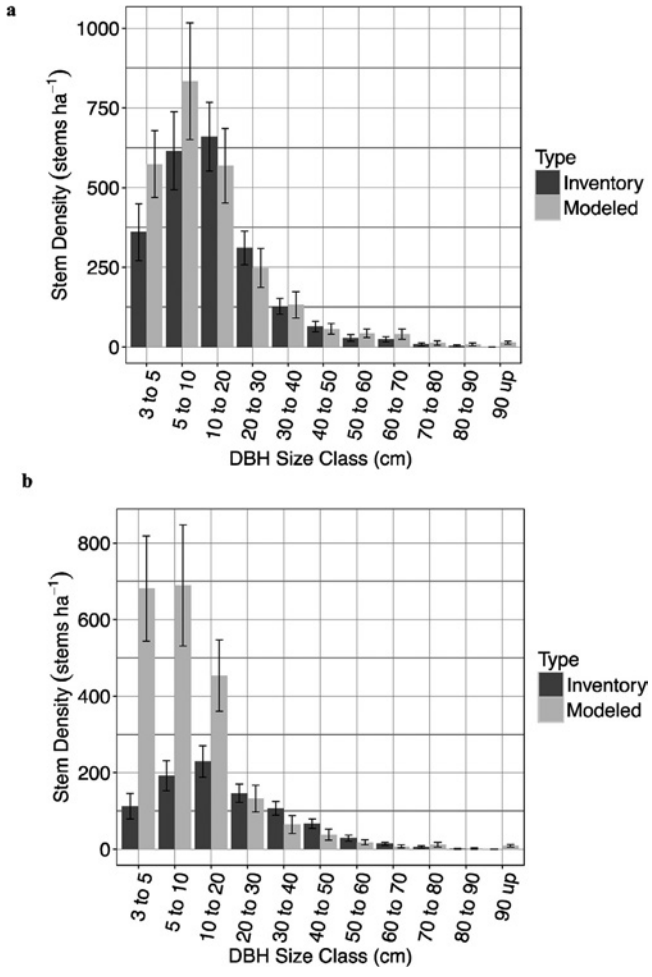

Fig. 5. UVAFME-simulated total stem count (trees ha^{-1}) at year 500 compared with inventory-derived stem count for (a) GLEES (3115 m) and (b) Wolf Creek (3100 m). Error bars correspond to 95% confidence intervals.

GLEES, a linear regression of modeled versus measured stem count had no significant difference from an intercept of zero ($t = 0.221$, $p = 0.83$) and a slope of 1 (95% confidence interval: 0.67, 1.33). At Wolf Creek, the linear regression had no significant difference from a zero intercept ($t = 1.893$, $p = 0.09$), however the slope was significantly different from 1 (95% confidence interval: 0.08, 0.37). The simulated stem count in the smaller size classes (below a DBH of 20 cm) at Wolf Creek was larger than the measured stem count, leading to the positive slope in the linear regression.

In simulations from bare ground to year 500 across all sites, Engelmann spruce and subalpine fir coexist for the first one hundred years, with Engelmann spruce eventually attaining dominance by year 200 (Fig. 6). At Niwot Ridge and FEF (Fig. 6b, c) there is a higher occurrence of lodgepole pine (*Pinus contorta*). Aspen (*Populus tremuloides*) is consistently present throughout the time series at FEF, Niwot Ridge, and Wolf Creek.

3.2. Temperature sensitivity test

There were considerable differences in the modeled species zonation between current climate conditions at GLEES (Fig. 7a) and those conditions with elevated temperatures (Fig. 7b). The ponderosa pine zone shifted upslope, with decreased biomass in its previous range, concurrent with increasing temperatures (see Fig. B1 in the Appendix A for a difference plot). The juniper woodland also shifted upwards in elevation, and declined in biomass between 1600 and 1900 m. Douglas-fir also shifted upwards in elevation, encroaching on the original subalpine zone. Lodgepole pine and subalpine fir biomass were considerably reduced throughout their original range, and the dominance of Engelmann spruce shifted upwards. Though we did not simulate drought through decreasing precipitation, increasing temperatures led to increasing evaporative demand (i.e. PET; for the simulation at 2500 m PET increased by about 10% during the warming years; see Fig. B2a in the Appendix A) at historical levels of rainfall, which caused soils to dry (at 2500 m soil dryness indices increased by about 125%; Fig. B2b). This soil drying caused several spikes of moisture stress-related mortality at both 2100 and 2500 m during the warming period (see Figs. B3, B4a in the Appendix A).

By year 1100 (once temperature had returned to current values) some of the landscape had recovered to what it had been under current climate conditions (Fig. 7c). Time series results which tracked the climate response at specific elevations show that the ponderosa pine zone was in the initial stages of regaining the biomass it had lost due to increasing temperatures (Fig. 8a, b), although it did not shift completely back downwards in elevation by the end of the simulation (Fig. 7c; Fig. B1b). At 2500 m, mortality due to moisture stress declined after climate cooling, however mortality due to shade stress increased (Fig. B4b). The juniper woodland regrew at the lower elevations, though it retained biomass at higher elevations than it had before climate change was implemented (Fig. 7c; Fig. B1b). Douglas-fir retreated from the original subalpine zone, and while lodgepole pine, subalpine fir, and Engelmann spruce were not completely restored to their original biomass values, the general species mix of the subalpine zone was restored after climate cooled again (Fig. 8c). Within the subalpine zone at 3100 m, mortality due to cold stress declined during the climate warming period, however mortality due to nutrient stress and shade stress increased during the latter half of the warming period, continuing into the cooling and stabilization periods (Fig. B5). Even though in general, the change in species composition with elevation at year 1100 (Fig. 7c) looks similar to that at year 500 (Fig. 7a), snapshots of individual elevations show substantial and lasting changes due to the applied temperature changes (Fig. 8b, c).

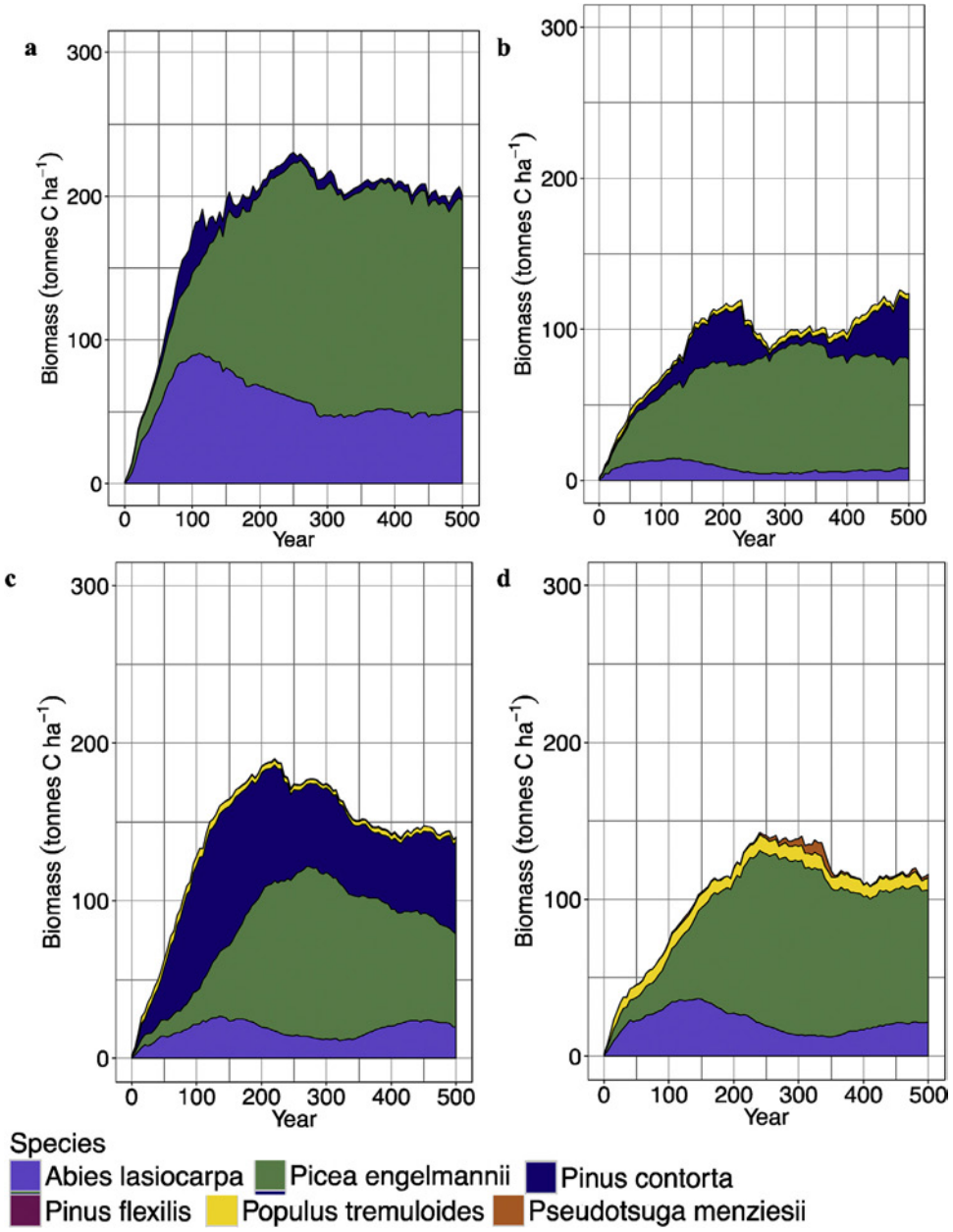

Fig. 6. Model-simulated biomass (tonnes C ha^{-1}) at (a) GLEES (3115 m), (b) Fraser Forest (2900 m), (c) Niwot Ridge (3020 m), and (d) Wolf Creek (3100 m).

4. Discussion

4.1. Model evaluation

The tests presented in this study were conducted with prior calibration at only two elevations (2400 and 3400 m) at GLEES. The model was not "tuned" (i.e. fitted to existing inventory data) in order to achieve higher accuracy at any other elevation or site, and was not compared to inventory data prior to conducting the validation tests. This independence between model parameterization/calibration and the validation datasets increases the robustness of the validation tests as well as our confidence in UVAFME's applicability at other locations within the Rocky Mountains. Simulation of species zonation (Fig. 3) requires that the model's internal logic and parameterization reflect actual forest dynamics in the region. UVAFME-output on species composition with elevation (Fig. 3) for forests at the northernmost (GLEES) and southernmost (Wolf Creek) study sites is comparable to what is found on a typical mountainside in the southern Rocky Mountains (Daubenmire, 1943; Marr, 1961; Peet, 1981). At both sites, juniper/pinyon pine woodlands transition to pondersa pine and Douglas-fir forests, then to a lodgepole pine zone (at GLEES), and finally to a high-elevation spruce-fir zone (Fig. 3). In reality, GLEES and Wolf Creek are subalpine sites with elevations that range from a minimum of 3200 and 2800 m to a maximum of 3500 and 3600 m, respectively, and the species mixture in the lower-elevation areas surrounding GLEES is atypical for the southern Rocky Mountains (Knight 1994; Dillon et al., 2005). However, by using the climate and site data from each location along with the calculated region-wide lapse rates, we are able to explore dynamics for typical mountainsides and for hypothetical forests at all elevation zones.

Differences between simulated species zonation and actual zonation at GLEES arise from microclimate and topographical effects due to the surrounding mountains (Dillon et al., 2005). In the areas surrounding GLEES, there are only rare instances of Douglas-fir and ponderosa pine, which is atypical for this area of Rocky

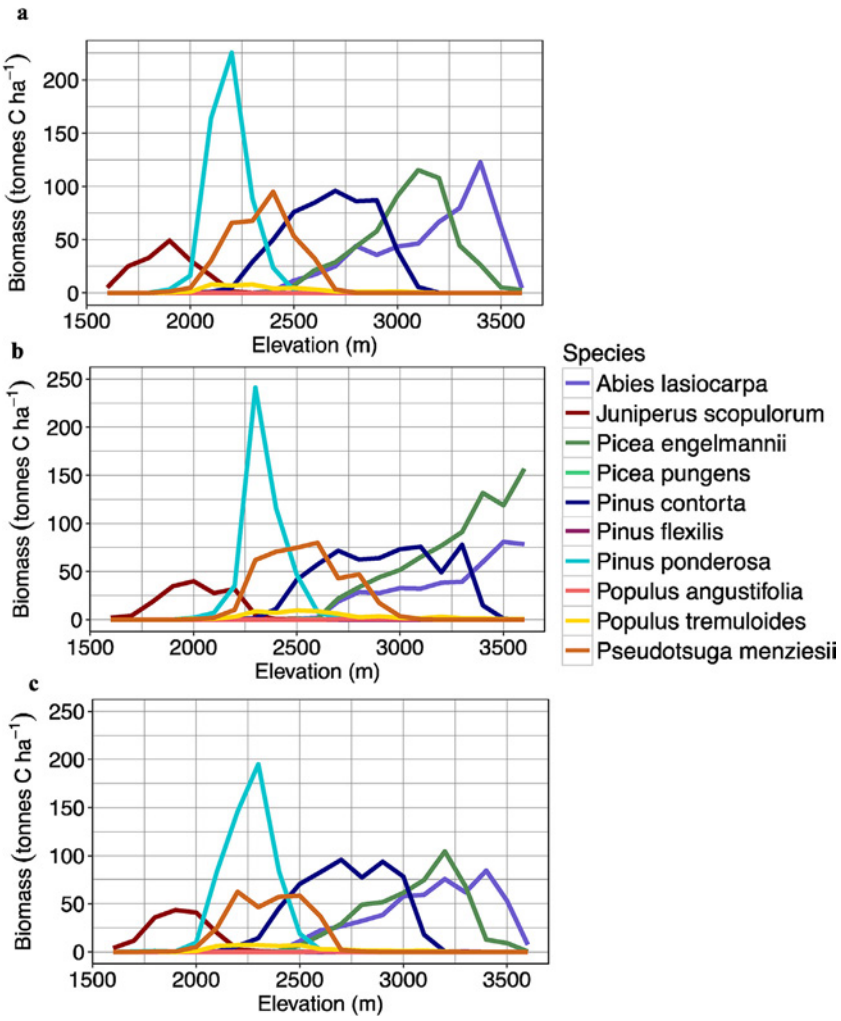

Fig. 7. UVAFME-simulated biomass (tonnes C ha^{-1}) of ten Rocky Mountain species at different elevations at GLEES at (a) year 500 with present climate, (b) year 800 after 200 years at 2 °C warmer temperatures, and (c) year 1100 after 200 years at 2 °C cooling back to current climate.

Mountains (Dillon et al., 2005). Due to the high elevations of nearby intermountain basins, grassland and shrubland zones transition directly into lodgepole pine forest around 2700 m (Dillon et al., 2005; Knight, 1994). The model-predicted location of the spruce-fir zone (3000 m), however, agrees well with what exists in reality at GLEES, and the overall zonation predicted at GLEES agrees well with expected species composition for a typical mountainside in the southern Rockies (Daubenmire, 1943; Marr, 1961; Peet, 1981). The results of these elevation tests demonstrate UVAFME's ability to simulate tree – tree competition for resources and species-specific environmental responses in the Rocky Mountains, as well as the species-specific responses to fire disturbance.

The results of the elevation test at GLEES are similar to those in Foster et al. (2015), but with some striking differences. Tests by Foster et al. (2015) conducted at GLEES were done without disturbances by windthrow and fire, resulting in very high biomass in the subalpine zone (2600–3600 m), and an underrepresentation of lodgepole pine (increase in biomass of ~84 t C ha^{-1} at year 500 at 2600 m with disturbances compared to without (Fig. B6)). The elevation tests in this study were conducted with fire and windthrow, with higher fire probability (but lower intensity) in the montane zone (2200–2500 m), and higher windthrow in the subalpine zone. The inclusion of windthrow and the new fire module resulted in lower biomass of Engelmann spruce, and slightly higher biomass of ponderosa pine and lodgepole pine. Most notably, lodgepole pine biomass increased considerably and its distribution shifted upslope in this elevation test relative to the test without disturbances (Fig. 3a; Foster et al. (2015)). These results are similar to findings by Bugmann (2001a) and Schumacher et al. (2006). Bugmann (2001a) found that the addition of disturbances in model runs of ForClim in the Colorado Front Range resulted in higher biomass of lodgepole pine as well as ponderosa pine. Though it was not tested without disturbances, in simulations with LandClim in this same region, increased fire frequency compared to historical fire disturbance also resulted in higher biomass of lodgepole pine (Schumacher et al., 2006). Lodgepole pine is disturbance-adapted, recolonizing quickly after wildfire (Sibold et al., 2007), so it follows that the addition of fire disturbance or increased fire disturbance would increase its dominance. It is clear that disturbances are important factors to include in forest gap models, especially in the Rocky Mountains, where disturbances are fundamental drivers of forest dynamics (Edburg et al., 2012; Frank et al., 2014; Hansen, 2013; Veblen et al., 1994). Future work with UVAFME in this region will include disturbances by bark beetles such as the spruce beetle (*Dendroctonus rufipennis*), which infests Engelmann spruce in the subalpine zone and greatly affects forest composition and structure (Bentz et al., 2010). It is expected that the inclusion of bark beetles such as the spruce beetle will reduce host species biomass, and allow for greater upslope migration of lower elevation, non-host species (i.e. Douglas-fir) under warming temperatures (Foster et al., *in review*; Temperli et al., 2015).

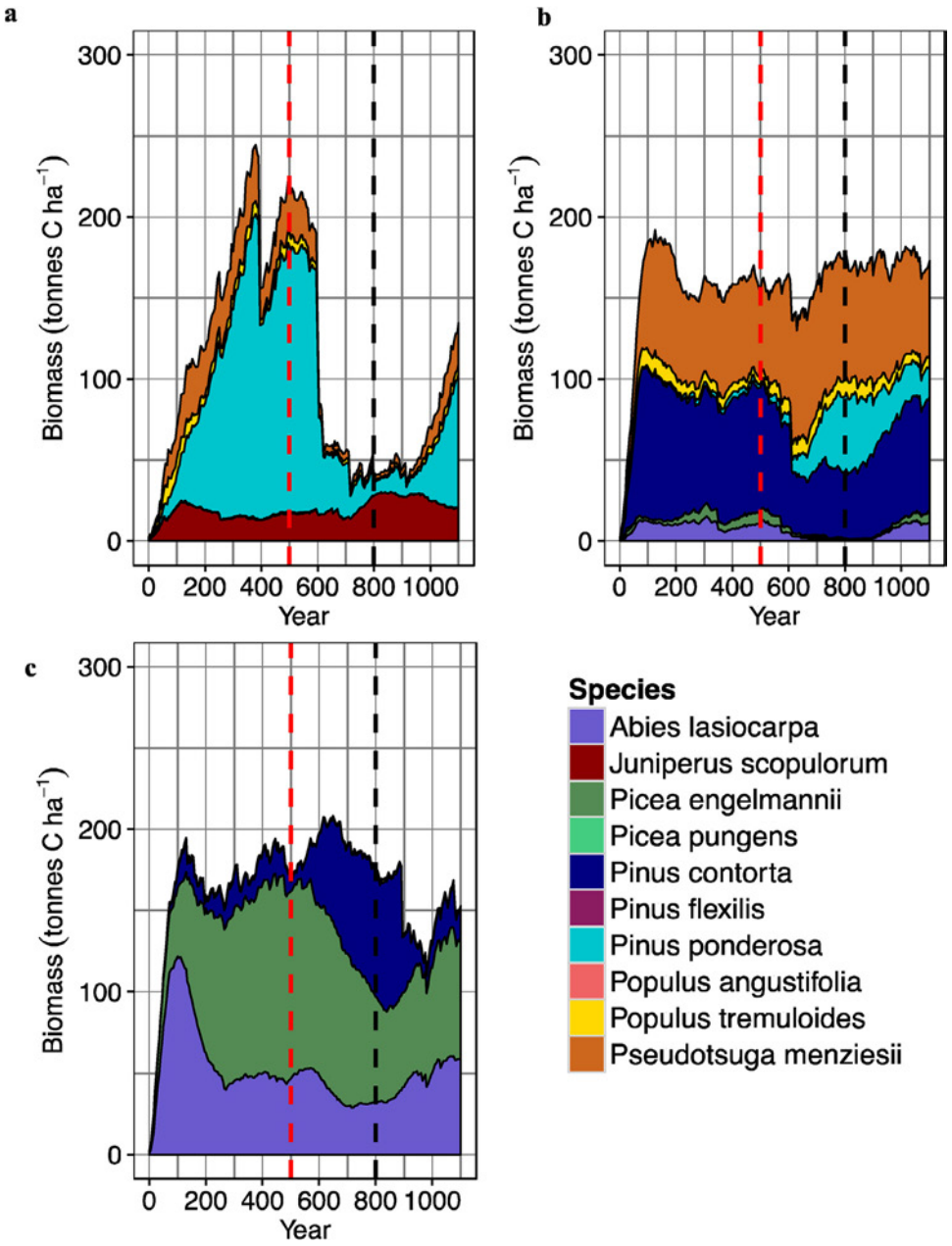

Fig. 8. Model-simulated biomass (tonnes C ha^{-1}) at GLEES under the climate change scenario at (a) 2100 m, (b) 2500 m, and (c) 3100 m. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to the start of a 2 °C cooling over 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The differences between the elevation tests at GLEES and at Wolf Creek are chiefly in the subalpine zone. Whereas the biomass dominance of lodgepole pine, Engelmann spruce, and subalpine fir are shown as three distinct peaks at GLEES, the biomass of Engelmann spruce and subalpine fir at Wolf Creek is more evenly distributed between 2700 and 3400 m (Fig. 3). This difference is likely due to the climate differences between the two sites. Wolf Creek is considerably warmer and wetter than is GLEES, potentially leading to less decline in subalpine fir and Engelmann spruce at high elevations. There is also a higher level of Douglas-fir biomass above 2600 m at Wolf Creek, which could be due to its warmer, wetter climate (Burns and Honkala, 1990). These differences between model output for each elevation test indicate that UVAFME is sensitive to site-level differences in site and climate characteristics, while still maintaining realistic representations of species-specific tolerances and tree competition.

The quantitative validation tests (Figs. 4 and 5; Table 1) show that UVAFME can simulate tree response to local-scale environmental conditions and can predict site-specific biomass, species composition, and size structure for trees 20 cm and above at both sites, and for all size classes at GLEES. It is not clear why there were differences between modeled and measured values in the smaller size classes and in the biomass of the subdominant species (Figs. 4 and 5). Tree establishment in high elevation ecosystems such as the subalpine zone are highly influenced by local-scale conditions (Elliott and Kipfmueller, 2010). It is thus possible that small-scale differences in climate, disturbances (e.g. fire, animal browsing, etc.), or site conditions, not captured by our generalized method of parameterization, would result in differences in the abundance of small stems and in the proportion of subdominant species, which are generally present as small, subcanopy trees (Cairns and Moen, 2004; Keane et al., 2011; Ryan and Reinhardt,

1988). Even with an overestimation of small stems at Wolf Creek the fact that UVAFME does correctly predict larger size classes indicates that it is capturing appropriate thinning mechanisms.

UVAFME also predicts the expected successional dynamics within the subalpine zone. A time series of model-simulated biomass at all four locations is typical of the subalpine zone in the region (Aplet et al., 1988; Daubenmire, 1978; Veblen, 1986) (Fig. 6). The model also predicts slightly different biomass and species composition at each site, arising from differences in climate and site characteristics. The higher biomass of lodgepole pine, which is common on xeric sites (Veblen, 1986), at FEF and Niwot Ridge (Fig. 6b, c) may be a result of relatively drier climates at these sites compared to GLEES or Wolf Creek (Fig. 6a, d).

These tests showcase UVAFME's ability to simulate expected forest dynamics, even at disparate locations within the Rocky Mountains, each with their own set of climate conditions, site characteristics, and species composition. The input parameters on climate and soil conditions and species presence for these sites varied, but UVAFME was not reformatted across the sites, demonstrating its broad applicability within the study area. Because UVAFME can reliably model species distributions and forest dynamics under current climate conditions in the Rocky Mountains, it has potential as a useful tool for predicting the response of vegetation within this region to changing climate.

4.2. Temperature sensitivity

The decline in juniper biomass and the shift upwards in the ponderosa pine – juniper transition zone seen under increasing temperatures (Fig. 7a, b) has also been documented in field studies of sites undergoing water stress (Allen and Breshears, 1998; Breshears et al., 2005). Bell et al. (2014) predicted changes in climatic suitability over the next century within the western US and found that ponderosa pine is likely to shift upslope due to its current proximity to areas that will remain or become climatically suitable. In the sensitivity test shown here it declined in biomass in the lower elevations and shifted upslope due to increasing temperatures and subsequent increasing soil dryness (Figs. B2b ; B3 ; B4a). Ponderosa pine also failed to completely regain biomass in the lower elevations (Figs. 7 c, 8 a) after temperature cooling. In contrast, it maintained biomass within its new climate-induced range (2100–2700 m; Fig. 7c). This lasting zonation change is particularly evident in the upper limits of the species' original range (2500 m, Fig. 8b), and may in part be due to ponderosa pine's growth habit.

Ponderosa pine can grow fairly quickly given adequate environmental conditions, especially compared to the slow and steady growth of high elevation species such as Engelmann spruce (Burns and Honkala, 1990). Because of this, the small increase in temperature we employed likely gave ponderosa pine a competitive advantage over other species (see Fig. B7). Combined with the presence of stand-replacing disturbances, this competitive advantage allowed it to shift upslope and increase in biomass, a change that was lasting even after climate had cooled. This competitive advantage is evidenced in the increase in shade stress mortality after climate cooling (Fig. B4b), which can be interpreted as increased light competition between trees after moisture is no longer limiting. Within the time period of one or two centuries the effects of only a 2 °C increase had noticeable effects on the biomass and distribution of species within the montane zone.

The subalpine zone (3000–3600 m) also experienced significant changes due to elevated temperatures (Fig. 7b). Subalpine fir and Engelmann spruce declined in biomass throughout their original elevation zones (Fig. B1a), potentially due to competition with lodgepole pine and Douglas-fir, which both shifted upslope with increasing temperatures. This increase in Douglas-fir and decrease in Engelmann spruce with increasing temperatures has also been seen in other modeling studies within the western US (Notaro et al., 2012; Temperli et al., 2015). Even after climate had cooled again (Fig. 7c), the biomass and composition of the subalpine zone remained altered from that under historical temperature conditions (Fig. 7a; Fig B1b in the Appendix A); neither Engelmann spruce nor subalpine fir completely regained the biomass they lost in the 3000–3400 m zone. It is important to note that the increase in Engelmann spruce biomass with increasing temperatures at 3400 m and above is only possible for mountains that reach that elevation and have adequate soils for tree establishment. Bell et al. (2014) predicted that climate suitability in mountain ecosystems will likely decline for species in their current ranges as well as in nearby areas where they may be able to migrate. They found that there may be significant reduction in climatically suitable areas for high elevation species, and that there will not be adequate geographical area to offset the loss of habitat.

These predictions of potential future biomass and species composition can be used to determine the possible futures of the Rocky Mountains landscape. A critical driver of vegetation dynamics in the Rocky Mountains that we did not include in this sensitivity test was increasing disturbances. Disturbances by fire and insect outbreak are predicted to increase in frequency and severity with climate change (Bentz et al., 2010; Dale et al., 2001; Jolly et al., 2015). Annual wildfire suppression in the last ten years has cost the US upwards of $1.7 billion (Jolly et al., 2015) and outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*D. rufipennis*) have affected over 1.9 million ha since 1996 in Colorado alone (USFS, 2015). Given that the inclusion of historical rates of disturbances in this elevation test resulted in significant differences in biomass and species composition compared to previous work (Fig. 3a; Foster et al. (2015)), it is likely that an increase in the frequency or severity of disturbances in combination with changes in climate would lead to even further changes in the vegetation of the Rocky Mountains, such as enhanced mortality and upslope migration (Notaro et al., 2012; Schumacher et al., 2006; Temperli et al., 2015). Further application of UVAFME within the southern Rocky Mountains will investigate the effects of increasing fires and spruce beetle infestations on Rocky Mountains vegetation (Foster et al. *in review*).

The tests presented here did not include changes to precipitation, thus any increase in drought-related stress within our climate simulations were due to increasing atmospheric demand at current levels of water availability. Similar to what we found under elevated temperatures (Figs. 7 b; 8 b) if there is a concurrent increase in the frequency of prolonged low-precipitation intervals in this region, it is expected that tree mortality and changes in species composition would increase further, potentially leading to an even higher biomass of ponderosa pine and Douglas-fir in the upper elevations (Allen and Breshears, 1998; Breshears et al., 2005). This invasion of these lower elevation species into the subalpine zone may result in a concurrent reduction in subalpine species through increasing competition for above- and belowground resources. In our sensitivity test, we assumed that species present at a site were available for colonization at all elevations potentially allowing for faster upslope shifts in species composition than would occur in reality. Studies have documented tree migration rates in response to climatic change at 2–5 km/decade, and more recently at 1 km/year for species of the northeastern United States (Davis, 1989; Woodall et al., 2009). With these migration rates, it is feasible that within the span of 200 years the tree species modeled in our temperature sensitivity test could migrate and establish.

The updates made to the calculation of the effect of temperature (in the form of GDD) on tree growth move UVAFME further away from climate envelope or niche-based models. Niche-based models generally use data on species distributions and their relationship with environmental or climatic predictors to project future

species composition (Morin and Thuiller, 2009). Unlike process-based models (such as UVAFME), envelope models do not consider between-tree competition, individual tree mortality and growth, or phenotypic plasticity (Keane et al., 2001; Morin and Thuiller, 2009). With such rigid controls on where and how certain species grow, niche-based models tend to predict stronger levels of extinction under changing climate than do process-based models (Morin and Thuiller, 2009). The fact that we see tree mortality and species shifts in our simulation, even without the restriction of tree growth at higher temperatures, points to the importance of individual tree competition. Forest gap models like UVAFME, which explicitly consider the responses and interactions of individual trees are thus valuable tools for projecting the future of vegetation under changing climate and disturbance regimes. Gap models also allow for testing of the separate responses of vegetation to changes in temperature, precipitation, and various disturbances – an important step in understanding vegetation response to the combination of these regime shifts. Our temperature sensitivity test investigated the complicated vegetative response to increasing temperatures alone, without further complication by concurrent increasing disturbances. This type of test is difficult to conduct in the field, especially when considering centuries-long forest dynamics. With individual-based modeling and the ability to explicitly modify important vegetation drivers, we can begin to parse the relative effects of these drivers.

UVAFME, whose original version was broadly applied across boreal Russia, has been updated to better reflect forest dynamics and their response to climate and fire disturbance within the southern Rocky Mountains. The validation tests presented here show that the model can be used to simulate biomass, species composition, and stand structure at various sites within the Wyoming and Colorado Rocky Mountains. UVAFME is a valuable model that can be used to study the variations in stand age, species composition, size structure, and biomass given different climate and disturbance conditions. Additionally, due to the tree-level modeling within UVAFME, model output can compare directly to inventory and high-resolution remote sensing data, allowing for unique methods of model initialization and validation, and other model-data intercomparisons (Shugart et al., 2015).

5. Conclusions

High elevation ecotones are highly controlled by climate, and can be seen as “barometers” for climatic change (Loehle, 2000; Malanson et al., 2007). Within the Rocky Mountains many factors, including natural disturbances, the harsh conditions of the landscape, and species zonation, make predicting vegetation response to climate change difficult (Fettig et al., 2013). Forest gap models have been successfully used to study vegetation response to climate and disturbances across a wide variety of ecosystems (Bonan, 1989; Bugmann, 2001a; Huth and Ditzer, 2000; Kercher and Axelrod, 1984). UVAFME has been significantly updated from its original version (FAREAST; Yan and Shugart (2005)) with improved handling of climate and moisture dynamics and a new fire disturbance routine. This new version was tested across four sites in the southern Rocky Mountains. The model accurately simulates the forest structure and dynamics of the subalpine zone as well as the greater Rocky Mountain landscape. We have shown that as little as a 2 °C increase in ambient temperature is likely to significantly affect the vegetation of the Rocky Mountains, leading to changes in species dominance, shifts upslope in forest ecotones, and decreases in biomass. These changes are also likely to be fairly long lasting even after climate cooling at some elevations. This 2 °C increase coincides with the outcomes of the UN Climate Change Conference in Paris in December 2015 in which the key result was the agreement to keep global average temperature change below 2 °C. While we cannot speak to the efficacy of this plan, it is clear that even this level of climate change may have significant negative impacts on vegetation, and the Rocky Mountains landscape in particular. The use of individual-based gap models to project the future of forest landscapes will continue to increase in value in the coming years. Ultimately, we hope that UVAFME will be used to project the many complex and varied scenarios (such as increasing or decreasing precipitation, wildfire, etc.) that are a potential for vegetation of the western US as well as other forest ecosystems.

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Appendix A. Species Parameter Table.

Species Parameter Table.

Table A1
Relevant parameter input for the eleven species used in UVAFME simulations. AGE_{max}, DBH_{max}, and H_{max} are the species-specific maximum age (yr), diameter at breast height (cm), and height (m); *s* and *g* are growth parameters; ρ_w is the wood bulk density (tonnes m^{-3}); l_c is the specific leaf area ratio (tonnes C ha^{-1}); DD_{min}, DD_{opt}, and DD_{max}, are the minimum, optimum, and maximum growing degree days for the species; *shade* is the relative shade tolerance of the species, from 1 to 5, 5 being the least tolerant; *drought* is the relative drought tolerance of the species, from 1 to 6, 6 being the least tolerant; *nutrient* is the relative nutrient availability tolerance of the species, from 1 to 3, 3 being the least tolerant. All parameter inputs are derived from information in Burns and Honkala (1990) unless otherwise denoted with a superscript (*: wood bulk density derived from USFS Western Core Table Reports; †: specific leaf area ratios derived from default model values; ¶: minimum, maximum, and optimum GDD values are derived from environmental lapse rates derived from climate data and CSFS (2016)).

Species Name	AGE_{max}	DBH_{max} (cm)	H_{max} (m)	s	g	ρ_w*	l_c†	DD_{min}¶	DD_{opt}¶	DD_{max}¶	shade	drought	nutrient
Abies lasiocarpa	250	61	30	1.03	1.041	0.43	0.5	200	500	1665	1	5	3
Juniperus scopulorum	300	43	15	0.69	0.455	0.46	0.5	800	1900	3200	4	1	1
Picea engelmanii	500	95	40	1	0.689	0.45	0.5	250	600	1665	2	4	1
Picea pungens	600	150	38	0.52	0.55	0.45	0.5	600	1550	2300	3	3	3
Pinus contorta	400	46	27	0.58	1.19	0.45	0.5	450	900	2500	4	3	1
Pinus edulis	400	46	10.7	0.46	0.256	0.45	0.5	800	1900	3200	5	2	1
Pinus ponderosa	600	127	40	0.56	0.579	0.45	0.5	800	1600	2500	3	3	1
Pinus flexilis	900	90	15	0.33	0.157	0.46	0.5	300	1600	3000	3	3	3
Populus tremuloides	200	75	22	0.61	0.986	0.42	0.316	350	1500	2200	5	3	2
Populus angustifolia	200	76	18	0.47	0.82	0.42	0.316	600	1550	2500	5	5	2
Pseudotsuga menziesii	400	152	49	0.66	1.054	0.48	0.5	700	1400	2300	3	3	1

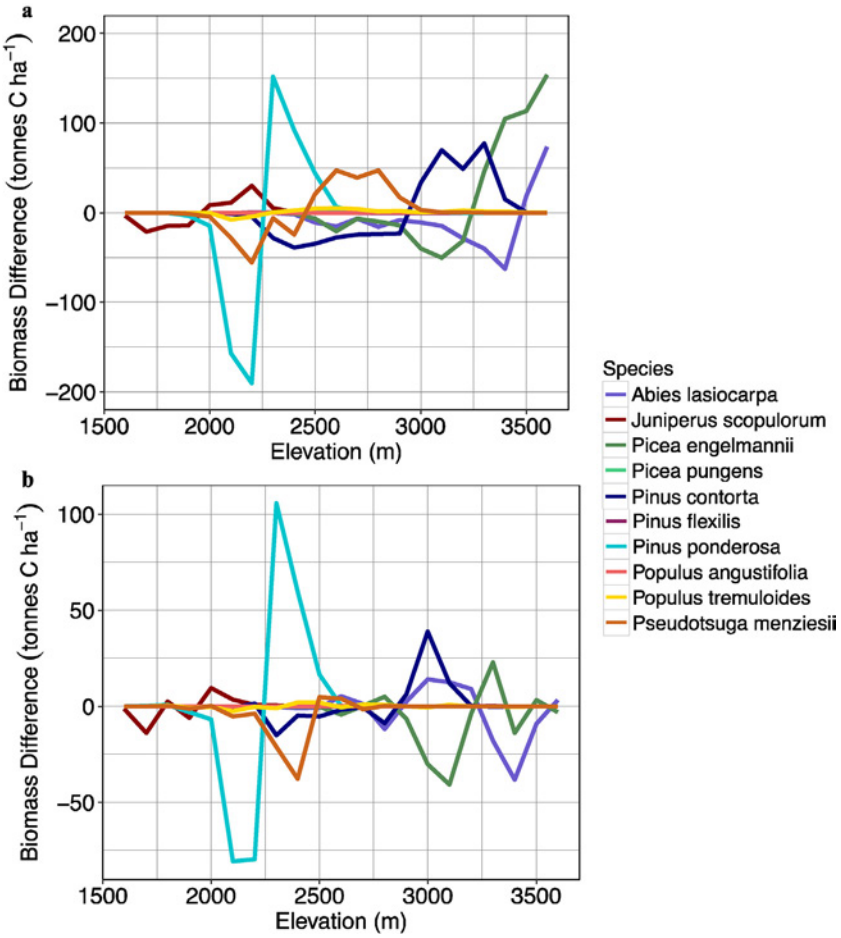

Fig. B1. Biomass difference (tonnes C ha^{-1}) between UVAFME climate simulations at different elevations at GLEES for (a) year 800 after 200 years at 2 °C warmer temperatures minus year 500 with present climate; and (b) year 1100 after 200 years at 2 °C cooling back to current climate minus year 500 with present climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

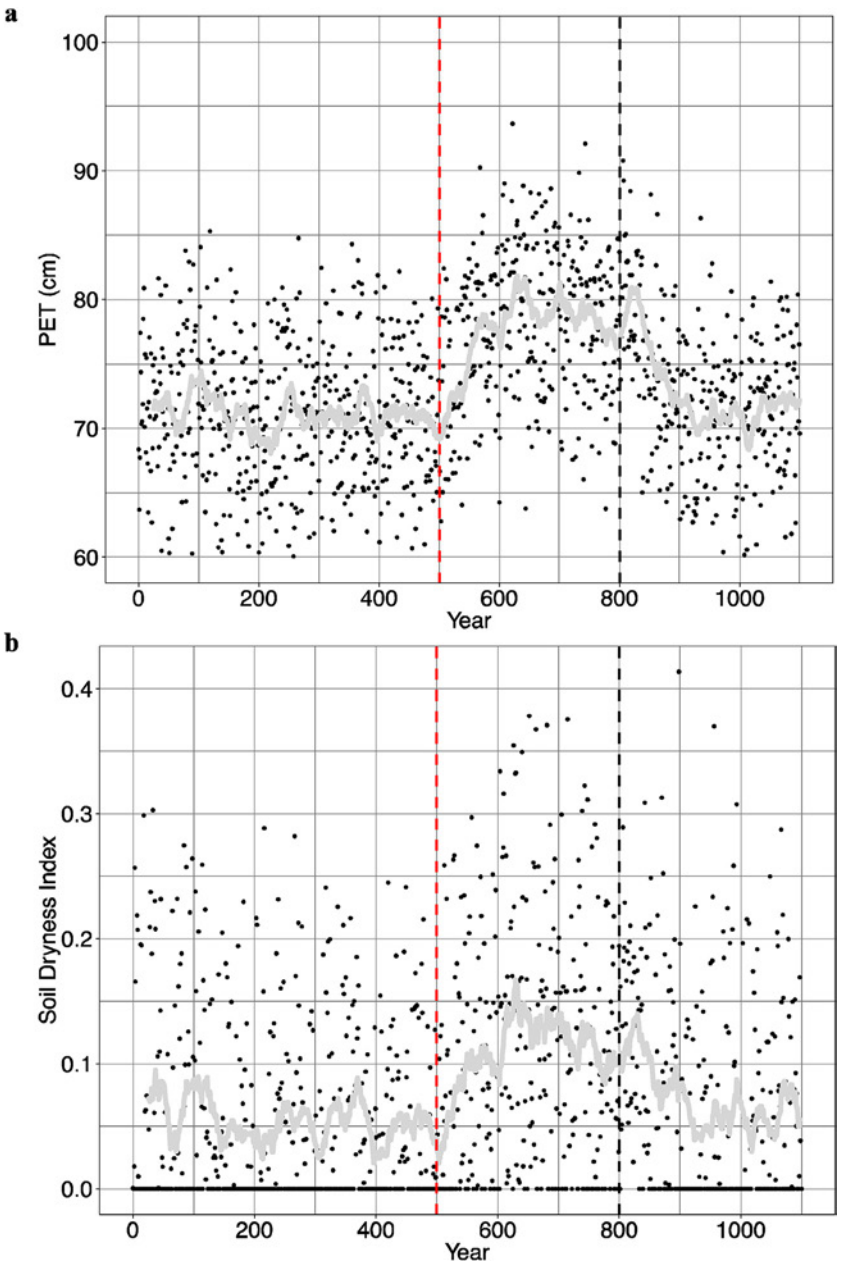

Fig. B2. (a) PET (cm) and (b) soil dryness index (0–1) for climate simulations at GLEES at 2100 m along with 25-year running averages in grey. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to the start of a 2 °C cooling over 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

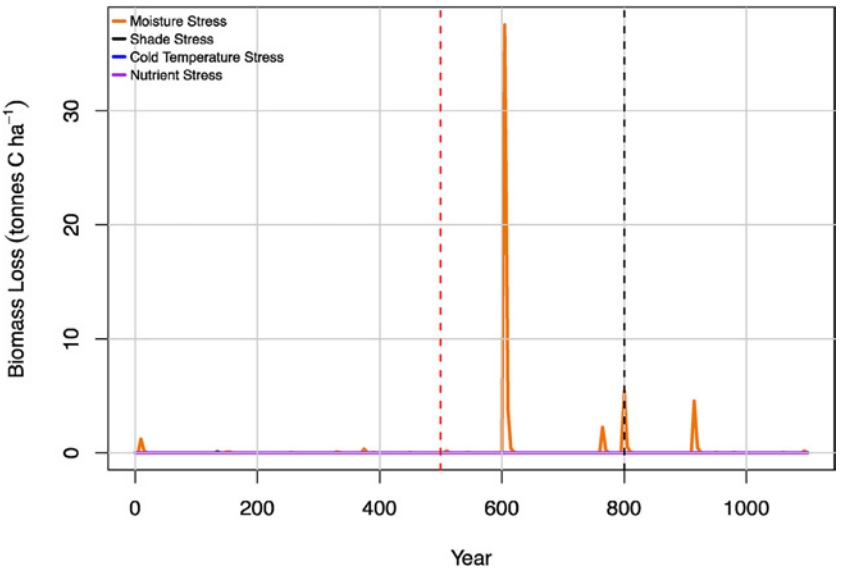

Fig. B3. Biomass loss (tonnes C ha^{-1}) due to different stress types during climate simulations at GLEES at 2100 m. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to year 800 and the start of a 2 °C cooling over 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

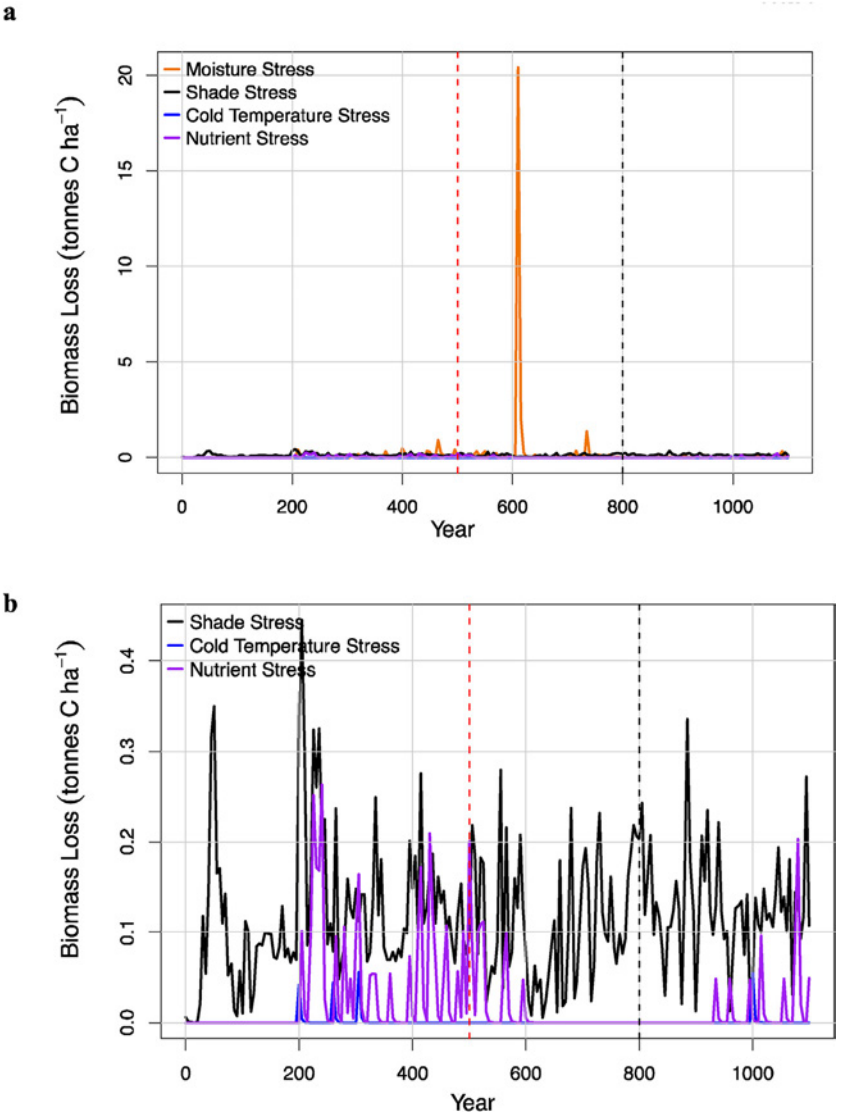

Fig. B4. Biomass loss (tonnes C ha^{-1}) due to different stress types (all stress types included in graph (a); moisture stress removed for graph (b) for readability of other stress types) during climate simulations at GLEES at 2500 m. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to year 800 and the start of a 2 °C cooling over 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

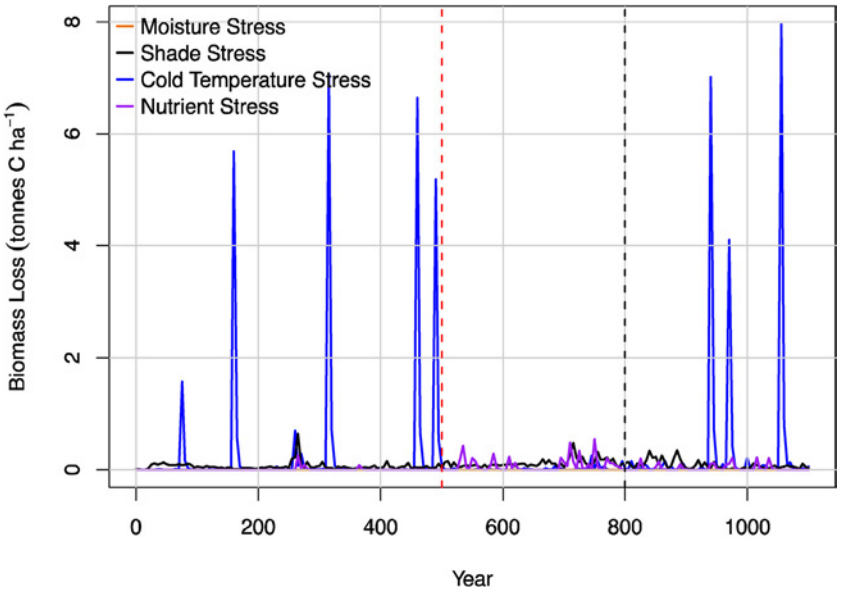

Fig. B5. Biomass loss (tonnes C ha^{-1}) due to different stress types during climate simulations at GLEES at 3100 m. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to year 800 and the start of a 2 °C cooling over 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

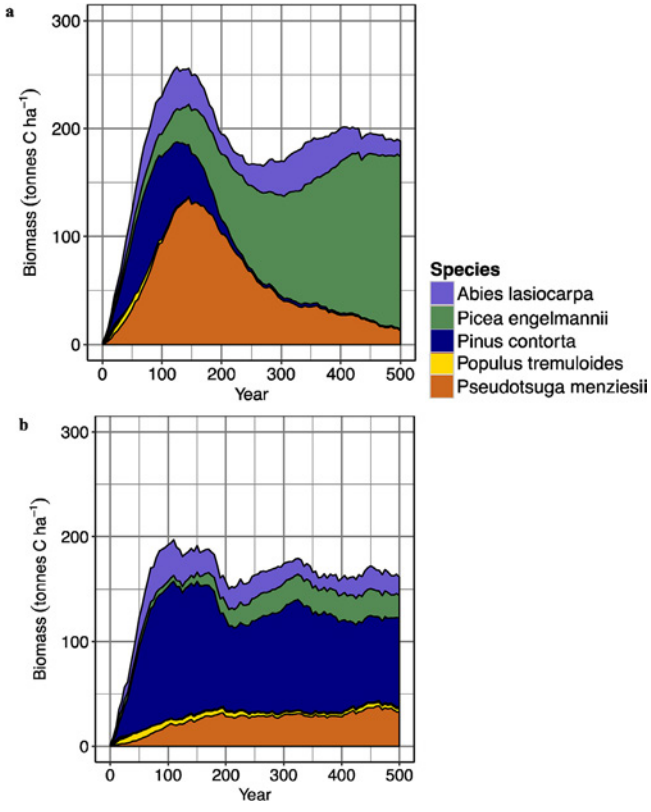

Fig. B6. Biomass (tonnes C ha^{-1}) development over time at 2600 m at GLEES under historical temperature conditions with (a) no disturbances; and (b) disturbances by fire and windthrow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

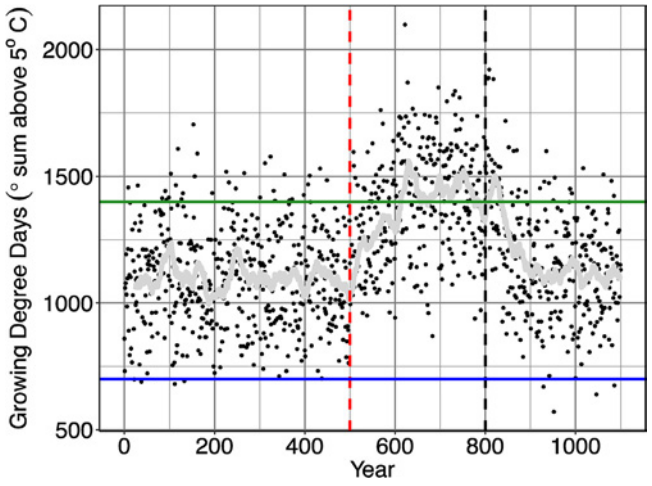

Fig. B7. Growing degree days (degree sum above 5° C) for climate simulations at GLEES at 2500 m along with a 25-year running average in grey. The red dashed line corresponds to year 500 and the start of a 2 °C increase in temperature over 100 years; the black dashed line corresponds to the start of a 2 °C cooling over 100 years. The blue and green horizontal lines correspond to the degree-day minimum and optimum values, respectively, for ponderosa pine (*Pinus ponderosa*) (see Table A1 for exact values). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.02.019.

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