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Christian Temperli
University of Colorado Boulder

Thomas T. Veblen
University of Colorado Boulder

Sarah J. Hart
University of Colorado Boulder

Dominik Kulakowski
Clark University, DKulakowski@clarku.edu

Alan J. Tepley
Conservation and Research Center (National Zoo)

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Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model

Christian Temperli,[1,4,†] Thomas T. Veblen,[1] Sarah J. Hart,[1] Dominik Kulakowski,[2] and Alan J. Tepley[3]

[1]*Department of Geography, University of Colorado, Campus Box 260, Boulder, Colorado 80309-260 USA*
[2]*Graduate School of Geography, Clark University, Worcester, Massachusetts 01610-1477 USA*
[3]*Smithsonian Conservation Biology Institute, Front Royal, Virginia 22630 USA*

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Abstract. The risk of bark beetle outbreaks is widely predicted to increase because of a warming climate that accelerates temperature-driven beetle population growth and drought stress that impairs host tree defenses. However, few if any studies have explicitly evaluated climatically enhanced beetle population dynamics in relation to climate-driven changes in forest composition and structure that may alter forest suitability for beetle infestation. We synthesized current understanding of the interactions among climate, spruce beetles (*Dendroctonus rufipennis*) and forest dynamics to parameterize and further advance the bark beetle module of a dynamic forest landscape model (LandClim) that also integrates fire and wind disturbance and climate-driven forest succession. We applied the model to a subalpine watershed in northwestern Colorado to examine the mechanisms and feedbacks that may lead to shifts in forest composition and spruce beetle disturbance under three climate change scenarios. Simulation results suggest increased drought- and beetle-induced reduction of large Engelmann spruce (*Picea engelmannii*) trees while Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) increased in dominance throughout the study area under all climate change scenarios. This shift in forest composition and structure counterbalances the enhancing effects of accelerated beetle population development and increased drought-induced susceptibility of spruce to beetles. As a result, we projected a long-term decrease in beetle-induced spruce mortality to below historical values under all climate scenarios at low elevations (<2800 m asl). Beetle-induced spruce mortality above 2800 m asl and under moderate climate change was slightly higher and more variable than under historical conditions but decreased to 36% and 6% of historical values under intermediate and extreme climate change, respectively. Because mechanisms driving beetle disturbance dynamics are similar across different bark beetle species, we argue that the depletion of host trees due to drought and beetle disturbance may also be important in other climate-sensitive beetle-host systems. We advocate for the consideration of climate-driven shifts in forest and disturbance dynamics in devising adaptive management strategies.

Key words: climate change; *Dendroctonus rufipennis*; forest dynamics; landscape model LandClim; northwestern Colorado; *Picea engelmannii*.

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[4] Present address: Resource Analysis, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.

† **E-mail:** christian.temperli@wsl.ch

INTRODUCTION

Bark beetles (Curculionidae: Scolytinae) are the most important biotic disturbance agents and key drivers of the dynamics of northern hemisphere conifer forests (Raffa et al. 2008). Populations of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the spruce beetle (*Dendroctonus rufipennis* Kirby) have recently erupted to region-wide outbreaks in western North America causing widespread tree mortality and affecting forest ecosystem services (Price et al. 2010, Meddens et al. 2012, Hansen 2014, Hart et al. 2014*a*, Negrón and Fettig 2014). The extent and severity of bark beetle outbreaks is determined by various interactions among forest composition and structure, climate, and other disturbance agents such as fire and blowdown (Raffa et al. 2008, Bentz et al. 2010, Jenkins et al. 2014). There is abundant quantitative information on the direct effects of weather and interannual climate variations that may lead to large-scale outbreaks (Sherriff et al. 2011, Chapman et al. 2012, Bentz et al. 2014, Hart et al. 2014*a*). In contrast, the indirect and long-term interactions and feedbacks mediated by changes in forest composition and structure are largely unknown, particularly under a warming climate (Bentz et al. 2010, Turner 2010).

Spruce beetles are the most widespread bark beetle species in subalpine spruce-fir (*Picea engelmannii* Parry ex Elgelm.-*Abies lasiocarpa* [Hooker] Nutt.) forests of western North America (Jenkins et al. 2014), and spruce beetle outbreaks are currently expanding in the Colorado Rocky Mountains (Colorado State Forest Service 2014). The development of spruce beetle broods is temperature dependent (Hansen et al. 2001, Bentz et al. 2010) with beetles requiring two years to complete larval, pupal and adult development when relatively cool summer temperatures prevail (semivoltine life-cycle). Under warmer conditions univoltine generations develop, which may accelerate beetle population growth and facilitate escape from parasites and predators (Jenkins et al. 2014). For extensive spruce beetle outbreaks to occur, favorable temperatures need to be maintained over several years and must coincide with susceptible host forests, i.e., older and drought-stressed forest stands dominated by large spruce (Schmid and Frye 1977, Hart et al. 2014*b*, Jenkins et al. 2014). In addition, an abundance of large, downed trees following wind disturbance provides an ideal breeding substrate for beetles, which has commonly been associated with outbreak initiation (Schmid and Frye 1977, Schmid 1981).

Given these interacting drivers, climate change may alter spruce beetle disturbance in several ways. Projected warmer temperatures will likely accelerate beetle population growth, allowing outbreaks to occur at higher elevations and latitudes than today (Bentz et al. 2010, DeRose et al. 2013). In the short term, increased drought-stress may weaken tree defenses and increase susceptibility to beetles (Bigler et al. 2006, McDowell et al. 2011, Hart et al. 2014*a*). Over longer time frames (decades to centuries) climate change may affect beetle disturbance indirectly (Bentz et al. 2010). For example, expanding populations of drought-adapted Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and ponderosa pine (*Pinus ponderosa* Douglas ex Lawson) at the expense of cold and wet-adapted spruce and fir (Rehfeldt et al. 2006) may reduce the susceptibility of subalpine forests to spruce beetles in the long term. Increased fire and beetle disturbance due to climate warming may hasten such vegetation shifts, resulting in a negative feedback mediated by a depletion of susceptible hosts and a greater portion of the landscape in early seral stages (Veblen et al. 1991, Westerling et al. 2011, Hart et al. 2015). These stages are typified by high proportions of the non-host aspen (*Populus tremuloides* Michx) and subalpine fir, and younger, smaller trees that are less susceptible to subsequent bark beetle disturbance and blowdown. Thus, interactions among recurring disturbances may attenuate the potential for spruce beetle outbreak in the long term (Bigler et al. 2005, Kulakowski et al. 2012, Hart et al. 2014*b*).

While these short-term, direct and long-term, indirect effects of climate change on beetle disturbance have been documented individually, their relative importance under various scenarios of climate change in western North America is unclear. We hypothesize that forest composition and structure will be altered due to direct effects of climate on tree growth and survival and due to climate-sensitive disturbances by beetles and fire, and that these changes will reduce forest susceptibility to subsequent beetle disturbance (Bebi et al. 2003, Rehfeldt et al. 2006, Kulakowski et al. 2012). Consequently, warming temperatures and increased drought-stress may not result in widespread spruce beetle disturbance in the long term, as a result of a reduced abundance of susceptible host trees (cf. Økland and Berryman 2004, Temperli et al. 2013).

To test this hypothesis and reveal the underlying mechanisms and their relative importance, a simulation approach that integrates climate-sensitive forest succession and disturbance interactions over a wide range of spatial and temporal scales is required. Dynamic forest landscape models (FLM) that simulate forest and disturbance dynamics based on spatially explicit input of topographic, climate and other environmental data have been developed to meet such objectives (Scheller and Mladenoff 2007, Seidl et al. 2011). Here, we used the climate-sensitive FLM LandClim (Schumacher et al. 2004) that integrates patch-scale forest succession with landscape-scale bark beetle, wind and fire disturbance (Schumacher et al. 2006, Temperli et al. 2013). Using the latest research we adapted the model to represent spruce beetle disturbance in the Colorado Rocky Mountains and applied it to project forest dynamics and bark beetle disturbance under a range of climate change scenarios.

METHODS

LandClim model

LandClim is a spatially explicit stochastic landscape model that combines fine-grained forest dynamics with broad-scale bark beetle, fire and wind disturbance to simulate a dynamic forest landscape in response to climate, topography and soil properties (Schumacher et al. 2004). Recruitment, growth, mortality and competition among age cohorts of different tree species are simulated with a simplified gap-model (Bugmann 2001) in response to monthly mean temperature, drought (a function of temperature, precipitation, and soil water-holding capacity) and light-availability in 25 × 25 m cells at a yearly time step. Assuming trees within an age cohort to be the same size, the model tracks the number of stems, the above-ground whole tree biomass and derived variables such as diameter at breast height (DBH) for each age cohort. Seed dispersal and disturbances link individual cells across the simulated landscape (typically 10–100 km^2) and act on recruitment and mortality on a decadal time step. Here we provide a brief overview and refer to Schumacher (2004) and Temperli et al. (2013) for detailed descriptions of LandClim.

Beetle and fire disturbance regimes emerge from climate-forest interactions. The LandClim beetle module uses bioclimatic and forest stand structural variables to assess beetle population dynamics and forest susceptibility to bark beetle disturbance. These assessments are used to simulate the extent, occurrence and severity of beetle-induced tree mortality. While the beetle module was designed and structured to be generally applicable for northern hemisphere climate-sensitive bark beetle-host systems, it was originally parameterized to represent disturbances by the European spruce bark beetle (*Ips typographus* Linnaeus) in Norway spruce (*Picea abies* Karst.; Temperli et al. 2013). Here, we parameterized the beetle module for *D. rufipennis* in Engelmann spruce (*P. engelmannii*).

Fire spread is simulated using a cell-to-cell-percolation model with spread probability dependent on the presence and moisture content of fuels in three size classes. Fire-induced mortality is a function of (1) bark thickness that depends on tree species and tree size and (2) crown scorch that in turn is a function of drought, available fuel biomass and tree size (Schumacher et al. 2006). Wind disturbance is simulated stochastically based on user-defined frequency and patch size distributions. In blowdown patches, the probability of wind-induced mortality increases with tree size. Blown down spruce trees increase the susceptibility of a forest patch (cell) to spruce beetle infestation in the decade wind disturbance occurs. For subsequent decades wind disturbance reduces susceptibility to beetle infestation via the reduction of large susceptible spruce (Temperli et al. 2013). LandClim has previously been applied to reconstruct and project forest and disturbance dynamics including historical fire regimes in the Colorado Front Range (Schumacher et al. 2006, Henne et al. 2013).

Model parameterization

Parameters that specify life history and responses of tree species to environmental drivers

(Schumacher et al. 2004) were available from Schumacher et al. (2006) for the five most common conifers in the Colorado Rocky Mountains (Engelmann spruce, subalpine fir, lodgepole pine, Douglas-fir and ponderosa pine). For trembling aspen we derived a new set of parameters from relevant literature (Appendix A: Table A1).

To adapt the LandClim beetle model to *D. rufipennis* we synthesized findings from recent spruce beetle research to (1) re-parameterize the relationships used to assess forest susceptibility to beetles, (2) assess temperature-dependent beetle population development and (3) parameterize an improved beetle dispersal routine. Here, we summarize the parameterization of these relationships and refer to Appendix A for additional details.

Following operational stand rating systems (Schmid and Frye 1976, Shore and Safranyik 1992, Reynolds and Holsten 1994), susceptibility to infestation at the level of individual cells (S_{cell}) is assessed based on drought-mediated tree resistance (S_{dr}), the DBH of the largest spruce cohort in the cell (S_{dbh}), the basal area share of spruce (S_s), and the amount of wind thrown spruce biomass (S_w). S_{dr}, S_{dbh} and S_s were modeled with logistic functions. The assessment of S_{dr} was based on the LandClim-inherent and cell-specific drought index (Bugmann and Cramer 1998, Schumacher et al. 2004) and drought-dependent spruce beetle outbreak probabilities in northwestern Colorado (Hart et al. 2014*a*). S_{dbh} was related to spruce DBH based on the DBH-dependent, tree-level infestation probabilities found by Hart et al. (2014*b*) and S_s is based on Schmid and Frye's (1976) spruce share-specific hazard rating scores. Because no quantitative data were available to relate S_w to wind thrown spruce biomass we adapted the simple linear relationship of the original model (Temperli et al. 2013). We combined S_{dr}, S_{dbh}, S_s and S_w additively to obtain the cell-specific susceptibility index S_{cell}. The effect of wind thrown spruce (S_w) was weighted four times more than the effects of the other susceptibility factors (Appendix A: Eq. A9; Dyer and Taylor 1971, Reynolds and Holsten 1994). A sensitivity test showed that the dynamics of simulated spruce beetle disturbance under climate change are robust under this weighting (Appendix A: Figs. A7–A9).

Temperature-dependent beetle population development is modelled using index *G*, which is scaled between 0 and 1 and can be considered as a proxy for the potential number of bark beetles that are able to develop per season, contingent on the temperature sum (Temperli et al. 2013). We first calculated the proportion of univoltine (as opposed to semivoltine) spruce beetles (P_u) for each cell based on annual degree day sums using an approximation of the spruce beetle phenology model previously used in the BioSIM simulation model (Appendix A: Fig. A8; Hansen et al., *unpublished manuscript*; Bentz et al. 2010). We accounted for accelerated beetle population growth and concurrent increasing beetle mortality rates with increasing P_u due to density-dependent competition and parasite pressure by relating *G* to P_u using a logistic function (Hansen and Bentz 2003, Wallin and Raffa 2004).

To parameterize beetle dispersal (Appendix A: Eq. A1) we relied on results of mark-recapture experiments that indicate that the yearly spruce beetle dispersal distance ranges between 90 and 300 m (Werner and Holsten 1997). Assuming that the probability of spruce beetles flying 300 m is 0.01 allowed us to calculate decadal (the time step of the beetle model), distance-dependent dispersal probabilities.

To estimate the importance of beetle pressure arising from beetle population dynamics in relation to forest susceptibility and to apply LandClim under climate change scenarios, we selected a case study landscape that is representative of subalpine forests of northwestern Colorado. The study landscape is a 39.7 km^2 watershed within the Routt National Forest of northwestern Colorado (Fig. 1) where fire and spruce beetle outbreak history was reconstructed in previous studies (Veblen et al. 1994, Eisenhart and Veblen 2000, Kulakowski and Veblen 2002). The watershed encompasses elevations between 2200 and 3340 m asl and is dominated by aspen and mixed-conifer (mostly Douglas-fir and lodgepole pine) forests at lower elevations (ca. $<$2800 m asl) and Engelmann spruce and subalpine fir at higher elevations (Fig. 1A, B; LANDFIRE, Ryan and Opperman 2013). Similar to many subalpine forests of northwestern Colorado, the lower elevation aspen, mixed conifer forests regenerated following fire in the late 19th century, while the higher elevation

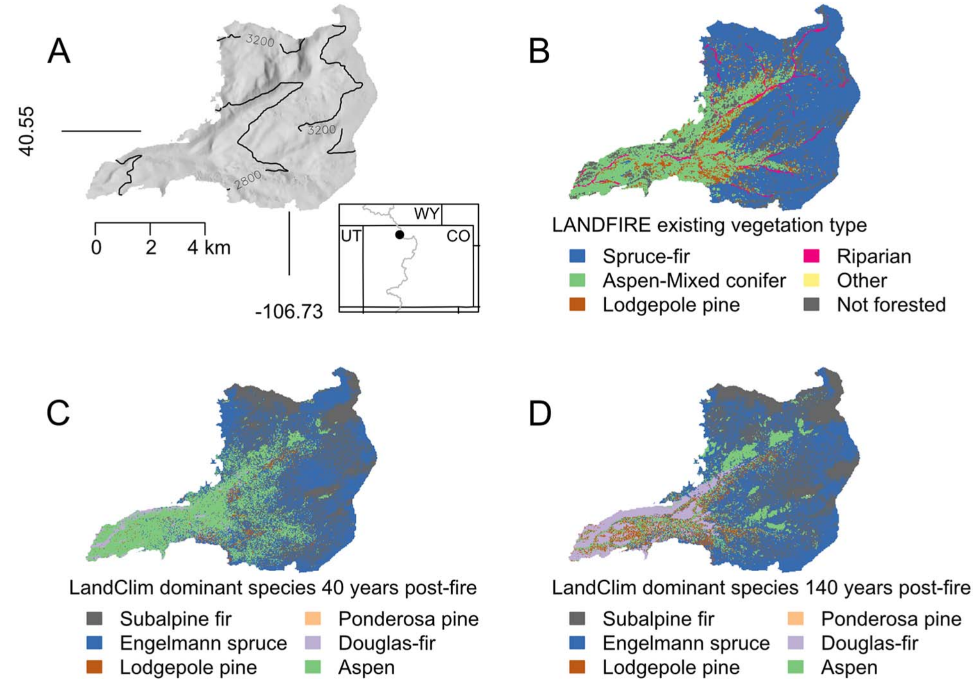

Fig. 1. Study area: (A) Topography, longitude and latitude of Buffalo Pass case study watershed. The inset map shows the location (black dot) of the case study watershed on the western slope of the continental divide (grey line) in northern Colorado (CO); (B) Existing vegetation types (EVT) per LANDFIRE. Spruce-fir refers to both dry-mesic and mesic original EVT, Aspen-Mixed conifer includes all aspen, aspen-mixed conifer and mixed conifer EVT, Lodgepole refers to the EVT "Rocky Mountain Lodgepole Pine Forest", and other refers to EVTs that occupied <20 cells and include limber, ponderosa and pinyon pine-juniper. Not forested refers to all grass, shrub and barren lands; (C) Dominant species (highest biomass share) simulated by LandClim 40 years after a simulated fire that burned most of the area below ca. 2900 m asl. This represents the data that were used to initialize scenario runs starting from year 1900; (D) LandClim simulated dominant species 140 years post-fire representing possible current forest vegetation. Note that ponderosa pine was included in the simulations but 140 years after fire is only dominant in two cells at the western, low-elevation tip of the case study area.

spruce-fir forests have no evidence of extensive fire in the past three centuries (Kulakowski and Veblen 2002). We used climate data that were gridded to 5 arc-minutes from PRISM (Daly et al. 2008, Coulson et al. 2010) for both the historical (1900–2009) and future (2010–2099) time series (Table 1) and calculated elevation lapse rates for monthly temperature and precipitation using the 1971–2000 climate normal data that were available from PRISM on a 30 arc-second grid. Elevation, aspect and slope were available from a digital elevation model with a resolution of 30 m (U.S. Geological Survey 2013). We derived cell-specific available soil water capacity (AWC) in the case study landscape by interpolating coarse-scale AWC estimates from the STATSGO database using elevation and the compound topographic index (Appendix A: Fig. A9; Gessler et al. 2000, Henne et al. 2013).

The importance of beetle pressure (P_{bd}) relative to forest susceptibility is determined by the scaling coefficient C_{pb} (Appendix A: Eq. A2). Because no direct empirical basis was available, we estimated C_{pb} using an inverse modelling approach (Hartig et al. 2012, Temperli et al. 2013). We ran LandClim with varying estimates of C_{pb}, compared simulated spruce beetle disturbance rotations with tree ring-derived spruce beetle disturbance rotations, and then inferred the C_{pb} value that best matched the simulated and empirical rotations. To this end, we ran LandClim under the historical (1900–2009) cli-

Table 1. Historical (1961–1990) annual and summer (Apr–Sept) mean temperature (T) and precipitation sums (P), and average (2070–2099) anomalies thereof based on output from three different global circulation models forced by the IPCC AR4 A2 emission scenario that were interpolated to a 5 arc-minute grid (Joyce et al. 2011). Data refer to a grid point within our case study area at 2754 m asl.

Climate scenario	Annual T	Summer T	Annual P	Summer P
Historic	2.1°C	8.9°C	1077 mm	402 mm
CGMC31 A2 (+4.4°AT/−9%SP)	+4.4°C	+3.3°C	+8%	−9%
CCSM3 A2 (+5.2°AT/+12%SP)	+5.2°C	+3.8°C	+10%	+12%
MIROC32 A2 (+7.0°AT/−29%SP)	+7.0°C	+6.0°C	−11%	−29%

mate using the above topographic and soil input. These model runs were initialized with simulated data that approximate conditions in 1900 (Fig. 1C), as we describe and evaluate below. Simulation results from the latter 110 years were used to calculate spruce beetle disturbance rotations as the ratio between the respective time period (110 years) and the proportion of infested area during that time. A value of 0.08 for C_{pb} resulted in a beetle rotation of 205 years, which best matched the empirically found "turnover time" of 259 years (Veblen et al. 1994) and "recurrence interval" of <100 years (Eisenhart and Veblen 2000) close-by and partly within our case study landscape, respectively.

In these and subsequent simulations we included both fire and wind disturbances. Fire was simulated as in Schumacher et al. (2006), which resulted in a fire rotation of 678 years under historical climate and is consistent with previous research on fire rotation in Colorado's spruce-fir zone (Veblen et al. 1994, Buechling and Baker 2004, Sibold et al. 2006). To account for relatively frequent small and rare large windthrow events in Colorado's subalpine forests (Veblen et al. 1991, Kulakowski and Bebi 2004), we parameterized stochastic wind disturbances in LandClim to a rotation of 489 years and a minimum, maximum and 95th-quantile wind throw patch size of <0.1, 322.2 and 9.6 ha, respectively.

Model evaluation

We were not able to formally validate LandClim simulations because independent data that have not been used for model parameterization were not available. Nevertheless, we scrutinized the model for its applicability for projecting the dynamics of Colorado's subalpine forests and spruce beetle disturbance regimes by evaluating several aspects of the model. First we tested whether LandClim adequately represents the interactions among climate, soil, spruce beetle, fire and wind disturbances, and forest dynamics such that the expected distribution of tree species in the case study landscape can be reproduced. To this end we ran LandClim with the previously described parameterization for 3000 years attaining a pseudo-equilibrium state using a climate time-series that we constructed from 3000 random samples of the years 1900–2009. In pseudo-equilibrium, fluctuations of forest characteristics such as forest biomass or species composition around a long-term equilibrium are driven by interannual climatic variations and disturbances. To approximate the vegetation that developed after the late 19th century fires at lower elevations of our case study, we first selected a decade when a series of large fires was simulated due to the simultaneous occurrence of conducive climate and fuel state. These simulated fires burned almost all forest below 2900 m asl. We then compared the simulated vegetation that developed 140 years after these simulated fires to the mapped distribution of the currently existing forest vegetation types from LANDFIRE.

A second test evaluated the sensitivity of the LandClim spruce beetle module to temporal variations in temperature and drought by comparing simulated with empirically documented temporal dynamics of spruce beetle disturbance in northwestern Colorado (Hart et al. 2014*a*). To this end, we simulated forest and disturbance dynamics on a generic 1 km^2, flat landscape with 1900–2009 PRISM climate data that were averaged over the northwestern Colorado spruce-fir zone, i.e., the same data set that Hart et al. (2014*a*) used in their analyses of spruce beetle-climate interactions. To account for uncertainties regarding initial forest state and wind and fire disturbance we conducted 20 simulations with the same climate input but started each replicate from a different initial forest state. The initial forest states were random picks from a spinup simulation. Thus, these initial forest states represented a range of possible forest states that may have emerged under the historical climate.

In a third test we evaluated whether LandClim adequately captures long-term, forest-mediated disturbance interactions, i.e., the observed pattern of decreased beetle infestation in young forests that developed following beetle, fire and wind disturbance (Schmid and Frye 1977, Veblen et al. 1994, Bebi et al. 2003, Kulakowski and Veblen 2006, Hart et al. 2015). To this end we analyzed the output data from the spinup simulations under the randomized historical climate that we used to initialize the above climate-sensitivity test. We assessed the probability that a cell experiences beetle infestation in the 100 time steps (decades) following wind, fire and beetle disturbance by calculating the percentage of beetle infested cells that have been disturbed by beetles, fire and wind in 1–100 previous time steps.

Model application

To test our hypothesis that climate change may reduce forest susceptibility to spruce beetle in the long-term and that this may reduce spruce beetle-induced tree mortality even if climate becomes more favorable for the beetles, we applied LandClim to the study watershed (Fig. 1A) under three widely different climate change scenarios (Table 1; Appendix B: Figs. B1–B3). The climate scenarios are projections of three Global Circulation Models (CGCM31, CCSM3 and MIROC32) that were forced by the medium-high IPCC AR4 A2 emission pathway and for which the data were interpolated to a 5 arc-minute grid (Joyce et al. 2011). While the CCSM3 GCM is being considered as particularly suitable for the western United States (Cayan et al. 2009, Westerling et al. 2011), the outputs of the two other GCMs were used to encompass the extreme ends of climate change projection uncertainty, irrespective of their suitability for the western United States. The models respectively project 4.4°C, 5.2°C and 7.0°C increases in annual mean temperature (AT) and −9%, +12% and −29% changes in summer precipitation (SP) for the end of the century (2070–2099; Table 1). Hence we here use the acronyms +4.4°AT/−9%SP, +5.2°AT/+12%SP and +7.0°AT/−29%SP to refer to the climate change projections. In addition to these climate change scenarios we used a baseline climate scenario that we constructed by sampling years from the historical (1900–2009) record. We started all simulations from the year 1900, simulated through 2009 using the historical climate and then used the climate change and baseline scenario data to simulate through 2099. To assess vegetation development under end-of-century conditions we extended the simulations through 2199 using random samples from 2070–2099 temperature and precipitation anomalies based on the zero-order approximation that climate will stabilize towards the end of this century.

To determine the effect of bark beetles, we ran all climate change scenarios with and without bark beetle disturbance, but included fire and wind disturbance in all simulations. Below we focus on this set of simulations. To control for the effect of fire on forest succession under climate change, we ran additional simulations with fire switched off but including all climate scenarios and beetle and wind disturbance. We initialized the scenarios with the simulation data that were generated to evaluate the simulated distribution of tree species. To represent conditions in 1900, we used the data simulated 40 years after the simulated large fires (Fig. 1C). To account for the stochasticity in climate scenarios, fire ignitions and wind events, we replicated all simulation runs 20 times.

We aggregated all simulation results to low (2200–2800 m asl) and high (2800–3340 m asl) elevation bands reflecting the current transition to spruce-fir forests. We depict forest dynamics as developments in tree species-specific biomass and stem numbers aggregated over all replicates. Spruce beetle disturbance dynamics are depicted by the development of beetle-killed Engelmann spruce biomass over time. To reveal the mechanisms of beetle disturbance dynamics, we show the developments in beetle voltinism (i.e., the average number of generations spruce beetles may realize per year; Appendix A), drought-induced susceptibility (S_{dr}), total susceptibility (S_{cell}) and total spruce biomass.

We isolated the effects of spruce beetle disturbance and climate change (i.e., the combined effect of a change in temperature and drought) to reveal their relative importance in determining the development of Engelmann spruce host biomass. Following Temperli et al. (2013), we calculated the effect of beetle disturbance and climate change as the spruce biomass difference of simulations that included beetle and climate change, respectively, to reference simulations that included neither beetles nor climate change. Accordingly, the combined effect of climate change and beetle disturbance was assessed by the spruce biomass difference between simulations that included both beetles and climate change and the reference simulations. To measure how beetle disturbance and climate change interact on spruce biomass, we subtracted the beetle and climate change effects individually from the combined beetle-climate change effect. Negative and positive values for this interaction effect mean that climate change enhances or dampens, respectively, bark beetle disturbance as compared to historical conditions. If, for example, climate change enhances beetle-induced spruce mortality due to higher temperatures and drought, spruce biomass is lower than would be expected from the additive effects of beetle disturbance and climate change. Vice versa, in a situation where climate change dampens beetle disturbance due to increased drought-induced spruce mortality that in turn deprives the beetles of breeding material, the remaining spruce biomass will be higher than expected from the additive beetle and climate change effects.

RESULTS

Model evaluation

Vegetation patterns simulated to represent 140 years of post-fire forest development support the use of LandClim to reconstruct and project vegetation dynamics in response to climate and disturbance drivers in subalpine forests of Colorado (cf. Schumacher et al. 2006). Consistent with the distribution of existing vegetation types in LANDFIRE (Fig. 1B, D), simulated forests were dominated by spruce and fir at higher elevations >2800 m asl. Lower elevations supported young post-fire aspen, lodgepole pine, and Douglas-fir forest with Douglas-firs becoming increasingly dominant as they grew larger.

Simulations driven by the averaged historical (1900–2009) climate of northwestern Colorado generally agree with documentary and tree ring-based evidence of northwestern Colorado's beetle outbreak history (Fig. 2A; Fig. 2 in Hart et al. 2014*a*). LandClim simulations reproduced the sharp increase in spruce beetle activity in the early 2000s and the increased spruce beetle activity in the 1930s and the 1950s. However, large outbreaks documented in the 1940s were not reproduced by LandClim. Possible explanations are that local climatic factors and factors other than climate, which have not been adequately represented by our generic simulations, were important in triggering the 1940s outbreaks. Schmid and Frye (1977), for example, noted that all past major outbreaks (including the 1940s outbreak) have been initiated by stand disturbances such as wind throw and logging and the ensuing increased abundances of susceptible coarse woody debris. Nevertheless, we concluded from this test that the LandClim beetle model adequately captured the general historical record of bark beetle outbreaks and its climate-driven trend, and can thus be used to assess beetle disturbance dynamics in response to climate variability.

In our assessment of LandClim's ability to represent expected patterns of long-term disturbance interactions we found that the probability of beetle infestation is reduced for respectively ca. 140, 100 and 120 years in previously beetle, fire and wind disturbed cells (Fig. 2B). In contrast to cells previously disturbed by fire and wind, the probability of re-disturbance in cells previously disturbed by beetles is elevated for one decade. This simulation result reflects the aggregation behavior of beetles (Byers 1989) and the fact that spruce beetles may take several years to attack and colonize a susceptible stand. Our assessment of beetle pressure accounts for this behavior by including the beetle killed biomass in the previous decade as a contributing factor (Eq. 3 in Temperli et al. 2013, Simard et al. 2011). The relatively low percentage of cells disturbed by beetles following fire reflects the relatively low area proportion disturbed by fire in each decade, which in turn results from the low fire spread probabilities and fuel flammability under the climate averaged over the northwestern

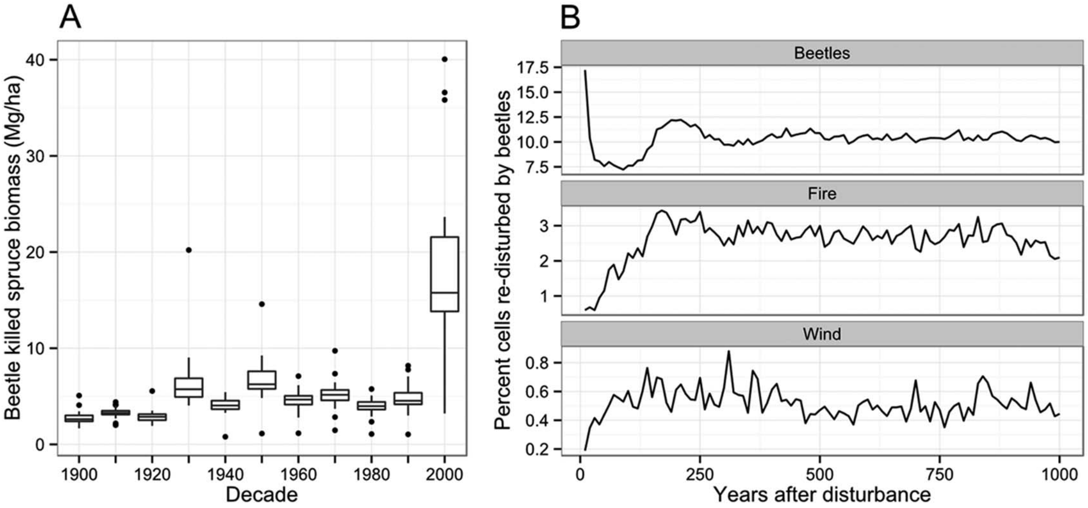

Fig. 2. Model evaluation. (A) Boxplots showing the distribution of 20 replicates of simulated beetle-killed Engelmann spruce biomass by decade. (B) Temporal development of the proportion of cells that have been re-disturbed by beetles after beetle (top), fire (middle) and wind (bottom) disturbance.

Colorado spruce-fir zone (Schumacher et al. 2006, Hart et al. 2014*a*). The 100–140 year time frame of reduced susceptibility to beetles following all disturbance types reflects the time required for spruce to grow to susceptible sizes (e.g., 0.9 S_{dbh} at 36 cm spruce DBH; Appendix A: Fig. A3). This simulated 100–140 year time-lag corresponds with previous findings from tree ring reconstructions that suggest the susceptibility to spruce beetle is reduced for at least 70 years following stand-replacing fire (Veblen et al. 1994, Kulakowski et al. 2003, Kulakowski and Veblen 2006). Re-disturbance percentages and time-lags are highly contingent on the severity of previous disturbance (also see the discussion below on the possible underestimation of fire-severity simulated by LandClim), the spatial scale under consideration (forest patch vs. stand vs. landscape) and the local climate that influences spruce regrowth, which complicates comparisons across case studies and between simulated and empirical data. However, the important result of this test is that the implemented short-term relationships between forest state and forest susceptibility to beetles play out as the expected pattern of reduced spruce beetle disturbance following previous disturbances. Hence, this test confirms the suitability of LandClim to assess patterns of long-term, forest-mediated disturbance interactions.

Vegetation dynamics and wildfire

Simulations under climate change project drastic shifts in species composition in comparison to simulations under historical climate (Fig. 3). The simulations under historical climate show Douglas-fir becoming increasingly dominant in the initially aspen and lodgepole pine dominated forests at lower elevation (<2800 m asl). This aspen-lodgepole pine forest was severely impacted by a simulated fire in the 1910s that reduced forest biomass to ca. 2/3 of the initialized biomass. The spruce-fir dominated forest at higher elevations (>2800 m asl) experienced only limited fire in the 1910s and remained approximately constant with respect to biomass and stem numbers. The total tree density at the end of the simulation period at high elevation was projected to be 2135 stems/ha with 6% of spruce and 2% of fir trees >25 cm DBH and with these larger trees contributing 53% and 27% to total spruce and fir biomass, respectively.

The lower elevation mixed aspen-conifer forest is projected to be replaced and dominated by the more drought-tolerant ponderosa pine and Douglas-fir by the year 2100 under all climate change scenarios. These species may realize faster growth rates with warmer temperatures and may out-compete similarly sized spruce and fir trees (Appendix A: Table A1). Aspen, spruce, fir, and lodgepole pine retain small portions of

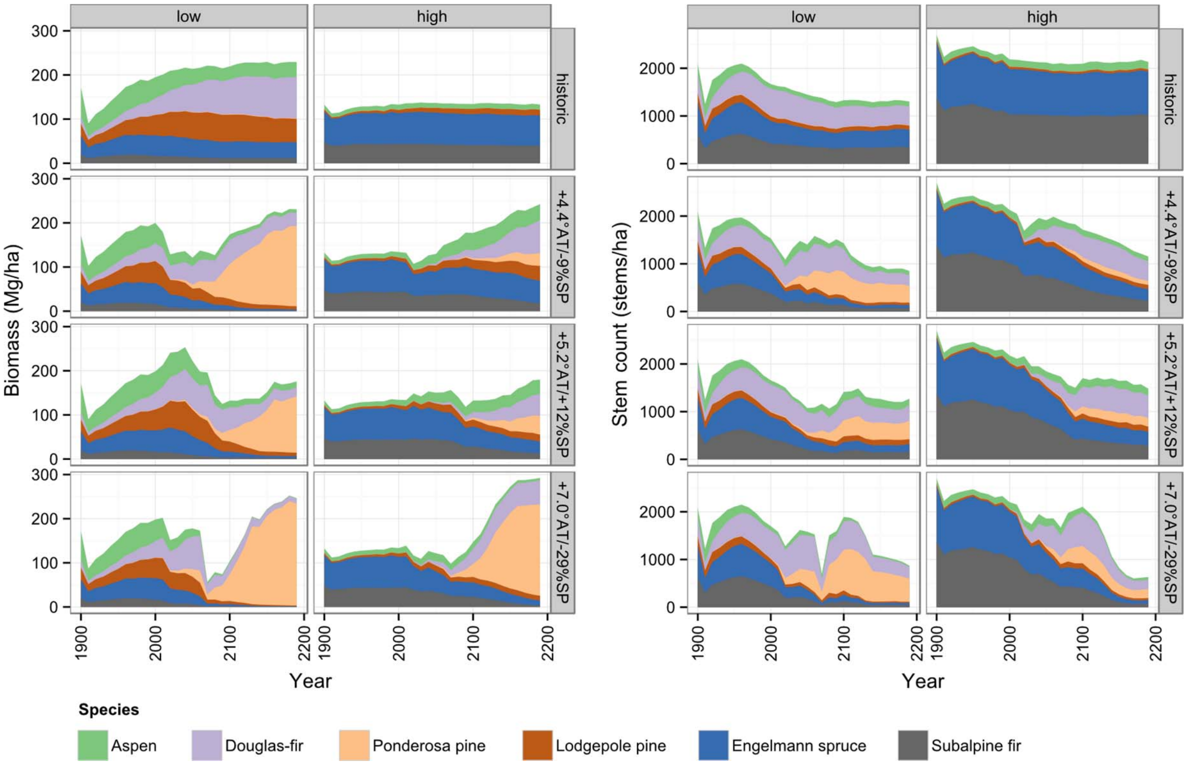

Fig. 3. Development of species-specific live biomass (left) and stem count (right) at low (≤2800 m asl) and high (>2800 m asl) elevation and under four climate scenarios that are labeled at the right side of panels (see also Table 1). Biomass and stem counts were averaged over 20 replicate simulations and refer to simulations including beetle, fire and wind disturbance.

forest biomass and stem count under the moderate +4.4°AT/−9%SP and intermediate +5.2°AT/+12%SP climate scenarios. However, if a drastic precipitation decrease is projected (+7.0°AT/−29%SP), aspen, spruce, fir and lodgepole pine are eliminated on shallow soils and at elevations <2800 m asl. Douglas-fir and ponderosa pine are projected to become part of the species mixture at elevations >2800 m asl towards the end of this century and by the end of the simulation (year 2199) these species start to replace spruce and fir. The magnitude of this projected species shift increases with projected temperature change. Ponderosa pine stem counts accrue to 30% (188 stems/ha) by 2199 at high elevations and under extreme climate change (+7.0°AT/−29%SP), while biomass shares rise up to 71% (207 Mg/ha). These simulated ponderosa pines grow to relatively large sizes with ponderosa pines >40 cm DBH comprising 66% of total forest biomass.

Fire activity increased under climate change (Appendix B: Fig. B4). The yearly percent area burned at lower elevations averaged across 20 replicates over the 2100–2199 period was 0.032% under the historical climate and increased to 1.6%, 4.7% and 1.8% under the moderate +4.4°AT/−9%SP, the intermediate +5.2°AT/+12%SP and the extreme +7.0°AT/−29%SP scenario, respectively. The yearly percent area burned in the 2100–2199 period at higher elevations >2800 m asl was 0.026% under the historical climate and 0.6%, 3.0% and 0.25% under the three climate scenarios, respectively. Biomass burned developed similarly, with the highest increase being at lower elevations and under the +5.2°AT/+12%SP scenario. Under this climate scenario inter-annual temperature and precipitation variability was highest resulting in the most extreme drought years (Appendix B Figs. B1–B3). Increased fire-related tree mortality favored tree regeneration due to decreasing competition for light. In comparison to simulations that did not include fire (Appendix B: Figs. B5 and B6), this resulted in higher stem densities and a ca. 20–30 year earlier establishment of Douglas-fir and ponderosa pine in formerly spruce and fir dominated areas.

Drivers of spruce beetle disturbance

Historical temperatures were high enough for beetles to realize a complete generation per year at elevations <2800 m asl in most decades (Fig. 4A). At elevations >2800 m asl between 0.60 and 0.72 generations were completed per year (voltinism) in the first half of the 20th century, indicating that a two-year life cycle was predominant. Thereafter, voltinism gradually increased to 0.81 in the 2000s and reached 1 in the first half of this century under all climate scenarios, meaning that beetles reproduced within one year. These seemingly high voltinism estimates are averages over the two elevation bands (mean elevation: 2571 and 3077 m asl, respectively) and thus represent the lower and warmer end of the historical spruce-fir zone and potential spruce beetle habitat in Colorado (2850–3500 m asl; Peet 1981). Drought-induced host susceptibility to bark beetle infestation increased under all climate scenarios with the highest increase under the extreme scenario +7.0°AT/−29%SP. The variation among replicates in estimates of drought-induced susceptibility was relatively large, which highlights the sensitivity of drought-induced susceptibility to random differences in the climate time series.

The increases in temperature- and drought-related drivers of beetle disturbance were counteracted by developments in forest composition and structure (Fig. 4A). Spruce biomass started to decrease early in the 21st century at low elevations under all climate change scenarios and at higher elevations under the two more severe scenarios (+5.2°AT/+12%SP and +7.0°AT/−29%SP). These decreases in spruce size- and spruce share-induced susceptibility overrode the outbreak-promoting effects of increased drought and caused total forest susceptibility to decrease in the long-term.

Development of spruce beetle disturbance

The simulated beetle-induced spruce mortality integrated the developments in the driving factors of beetle disturbance (Fig. 4B). Beetle-killed spruce biomass averaged over the 20 replicates fluctuated between 0.03 and 0.44 Mg ha^{-1} yr^{-1} at elevations <2800 m asl and under historical climate. The maximum simulated beetle-killed biomass realized by one of the 20 replicates under these conditions was 1.3 Mg ha^{-1} year^{-1}. Climate change decreased the abundance of susceptible spruce at these elevations, which reduced beetle disturbance to nearly zero by the end of this century. Beetle disturbance at elevations >2800 m asl gradually increased during the historical period and peaked at 0.85 Mg ha^{-1} year^{-1} between 2000 and 2009. Assuming a continuation of the historical climate, average beetle-killed biomass fluctuated around 0.30 Mg ha^{-1} year^{-1} for the remainder of the simulation period. Under moderate climate change (+4.4°AT/−9%SP) beetle-killed biomass remained at the level of the 2000–2009-decade for another two decades and then fluctuated between 0.25 and 0.50 Mg ha^{-1} year^{-1}, i.e., slightly higher than under historical climate, for the rest of the simulation period. If both increasing temperatures and precipitation were simulated (+5.2°AT/+12%SP), spruce biomass remained high (Fig. 4A) and supported high beetle disturbance until the middle of this century. Thereafter, beetle-induced spruce mortality decreased to 0.12 Mg ha^{-1} year^{-1}, i.e., to 36% of the average of the historical period (0.34 Mg ha^{-1} year^{-1}). Under extreme climate change (+7.0°AT/−29%SP) beetle-killed biomass peaked at >1.25 Mg ha^{-1} year^{-1} in the 2020s and then decreased below the historical period by 2070 reaching 6% of the historical average by the end of the simulation period. In sum, under all climate scenarios and elevations beetle-induced spruce mortality decreased compared to the historical period in the long term, except for the high elevations under moderate climate change (+4.4°AT/−9%SP), where beetle disturbance was slightly higher and more variable than under historical conditions.

Net effects of climate change on spruce beetle disturbance

Climate change dampened the effect of beetle disturbance on Engelmann spruce biomass under most conditions, because the combined effect of climate change and beetle disturbance decreased

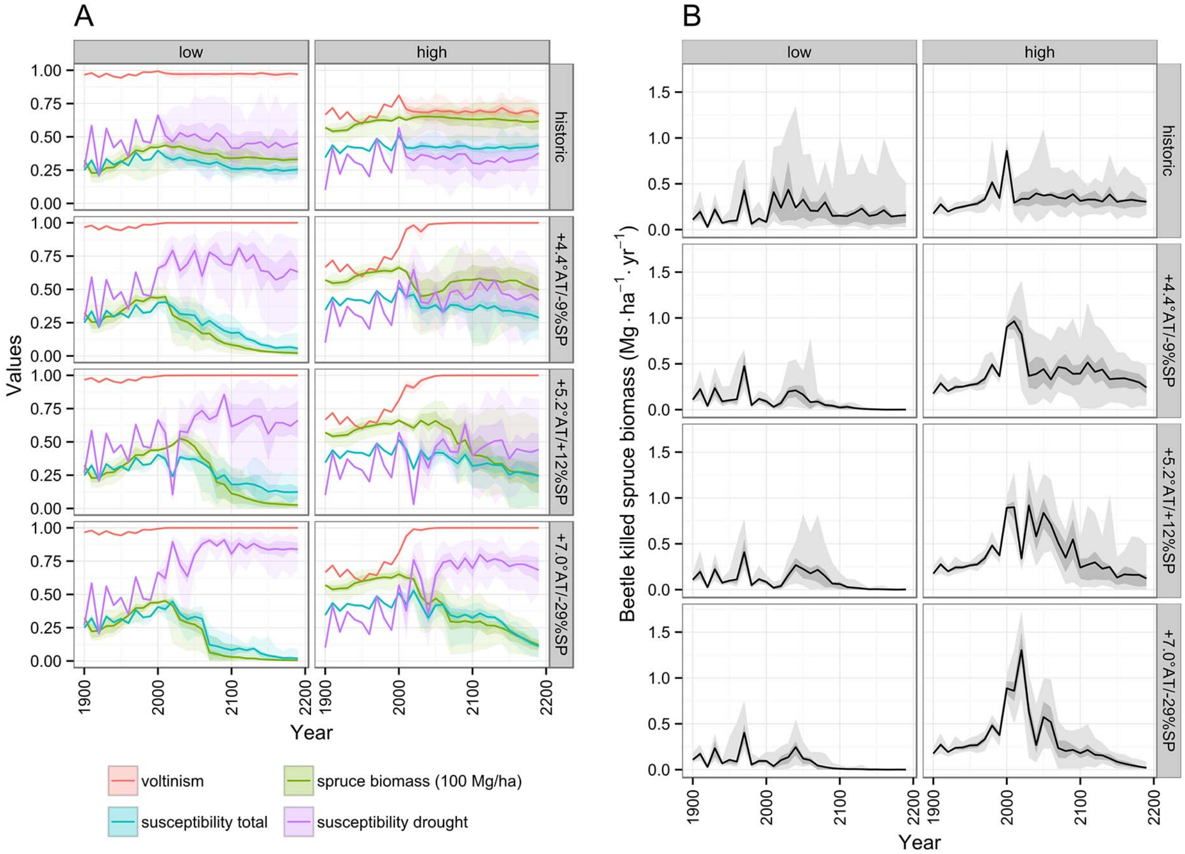

Fig. 4. Panel (A) shows the development of beetle model parameters by elevation (low: ≤2800, high: >2800 m asl) and climate scenario. Voltinism (range: 0.5–1) indicates the temperature-driven number of generations the spruce beetle population can realize per year. Spruce biomass is the live standing biomass of Engelmann spruce on the landscape in 100 Mg/ha. Total susceptibility is an index (range: 0–1) describing the susceptibility induced by the combined influence of spruce size, spruce abundance and drought-stress in spruce; susceptibility drought indicates the drought component of total susceptibility. Light shaded uncertainty ribbons indicate minima and maxima and darker shaded ribbons lower and upper quartiles of 20 replicate simulations. (B) Development of beetle-killed Engelmann spruce biomass by elevation (low: ≤2800, high: >2800 m asl) and climate scenario. The black line indicates the mean, light shaded uncertainty ribbons indicate minima and maxima and darker shaded ribbons lower and upper quartiles of 20 replicate simulations.

the availability of susceptible spruce in the long term (Fig. 5). Comparing spruce development without beetle disturbance between historical and climate change conditions isolated the effect of climate change (Appendix B: Fig. B7). Climate change resulted in a long-term decrease in spruce biomass <2800 m asl under all climate scenarios. However, this decrease did not start until year 2050 if summer precipitation was projected to increase under the +5.2°AT/+12%SP scenario. Above >2800 m asl climate change even enhanced spruce growth under this scenario until 2070. Thereafter spruce biomass started to decline and reached values below the baseline scenario by the end of the simulation period (60.5 vs. 128.5 Mg/ha, respectively). With a moderate (+4.4°AT/−9%SP) reduction in summer precipitation higher elevation spruce biomass remained approximately constant, whereas severe climate change (+7.0°AT/−29%SP) reduced spruce biomass at high elevations at the beginning of this century.

Including spruce beetle disturbance in simulations under historical climate reduced spruce

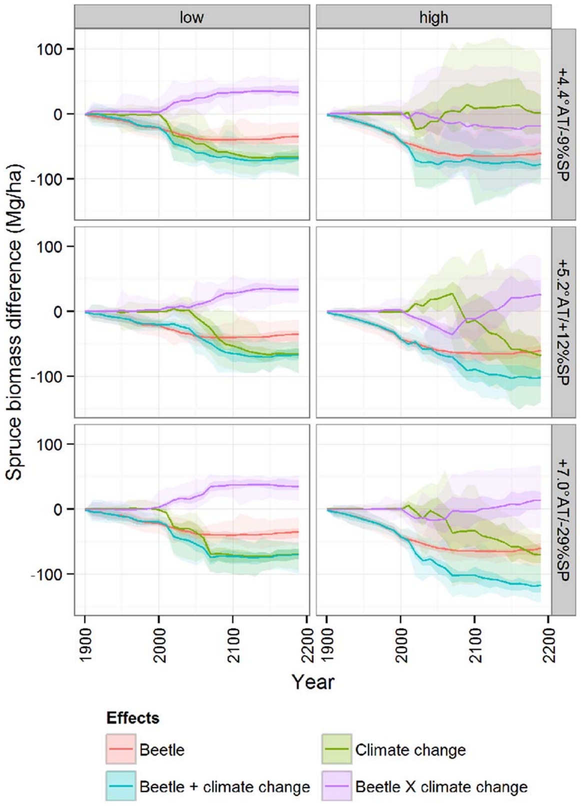

Fig. 5. Effect of beetles, climate change, the combined effect of beetles and climate change (Beetle + climate change) and the interaction effect of beetle and climate change (Beetle × climate change). Effects are expressed in differences in Engelmann spruce biomass to baseline simulations that do not include beetles and climate change. Light shaded uncertainty ribbons indicate minima and maxima and darker shaded ribbons lower and upper quartiles of 20 replicate simulations.

biomass at lower elevations by 35.0 Mg/ha (49.3%) by the end of the simulation period (Fig. 5). At higher elevations this beetle effect was even greater with a 60.0 Mg/ha (46.7%) spruce biomass reduction.

The combined effect of beetle disturbance and climate change on spruce biomass was stronger than the effects of either climate change or beetle disturbance individually under all climate scenarios and at all elevations (Fig. 5). However, beetle disturbance and climate change did not affect spruce biomass in a simple additive way. The interaction between climate change and beetle disturbance was negative at elevations <2800 m asl under all climate change scenarios, and thus had a positive, stabilizing effect on spruce biomass. This important finding illustrates that the combined effect of climate change and beetle disturbance on spruce biomass was less than the simple additive effect of climate change and beetle disturbance. The underlying mechanism for this negative effect of climate change on beetle-induced tree mortality is the depletion of spruce due to both climate change and beetle disturbance. In contrast, climate change and beetle disturbance interacted synergistically at higher elevations >2800 m asl, under the relatively moderate +4.4°AT/–9%SP scenario over the whole simulation period and under the more severe +5.2°AT/+12%SP and +7.0°AT/–29%SP scenarios until ca. 2070. Climate change intensified beetle disturbance under these conditions such that the climate change-beetle interaction effect led to a further reduction in spruce biomass. The dominant mechanism for this synergistic, reinforcing interaction is the positive effect of climate change on beetle brood development and drought-induced susceptibility of spruce to beetles. Beetles and climate change began to interact negatively also >2800 m asl. after ca. 2070 and under more severe climate change (+5.2°AT/+12%SP and +7.0°AT/–29%SP) when the depletion of susceptible spruce became increasingly important. While individual replicates of the beetle and climate change effects, i.e., spruce biomass differences, showed large departures from the mean, the interquartile ranges suggest robust trends in these effects (Fig. 5).

DISCUSSION

Assessment of future bark beetle disturbance dynamics requires integration of at least three mechanisms by which climate change acts upon bark beetles (Temperli et al. 2013): (1) changes in temperature directly affect beetle phenology and population development (Hansen et al. 2001, Bentz et al. 2010), (2) changes in drought affect the defense mechanisms of the host trees (McDowell et al. 2011, Hart et al. 2014*a*), and (3) long-term (decades to centuries) changes in climate and disturbance regimes affect forest species composition and stand structure (Rehfeldt et al. 2006, Turner 2010), thereby acting upon beetle disturbance dynamics indirectly through changes in the availability of spruce hosts (Økland and Berryman 2004, Temperli et al. 2013). We used a simulation modeling approach and integrated these three mechanisms to provide novel insights into their relative importance in driving the dynamics of spruce beetle disturbance under climate change in a case study watershed representative of Colorado's subalpine forests.

We found that with increasing magnitude and advancement of climate change, drought- and spruce beetle-induced spruce mortality and concomitant shifts in species composition decrease the availability of the beetles' breeding material. The reduction in spruce abundance is important enough that in the long term and under more severe climate scenarios spruce beetle disturbance decreases below historical values even though increasing temperatures favor beetle population growth and drought is projected to increase host tree susceptibility to beetles.

This finding is an important addition to previous studies that projected the potential for future spruce beetle disturbance over large regions based on climate and static forest habitat variables (Bentz et al. 2010, DeRose et al. 2013). These studies did not take into account shifts in the distribution and structure of spruce forests or the effects of future beetle or fire disturbance on forest structure and composition. While conducted at a much smaller scale (watershed vs. western U.S. and Canada) and using different realizations of the IPCC AR4 A2 emission scenario, our projections of spruce beetle voltinism are consistent with those of Bentz et al. (2010): by the end of this century we expect a high probability of univoltine rather than semivoltine life cycles in most of the spruce-fir zone. Also, our assessment confirms DeRose et al.'s (2013) predictions of the expansion of suitable spruce beetle habitat due to projected temperature increases.

The importance of forest composition and structure in determining spruce beetle disturbance in our simulations corroborates DeRose et al.'s (2013) finding that spruce beetle habitat variables such as spruce basal area are more important than temperature variables in modeling spruce beetle's realized environmental niche. This empirically-based finding is reflected in the design of our simulation model that gives high weight to habitat variables in assessing forest susceptibility to beetles, beetle population pressure and the resulting cell-specific infestation risk (Appendix A: Eq. A9; Eq. 4 in Temperli et al. 2013). Since beetle habitat variables are dynamically coupled with climate and beetle disturbance in our model, they shift with time, unlike the static niche model of DeRose et al. (2013). This dynamic coupling of climate, beetle phenology and beetle habitat variables, as well as negative feedbacks from future disturbance by fire and bark beetles are the key differences between our approach and most previous assessments (e.g., Bentz at al. 2010, DeRose et al. 2013). Our results suggest that these dynamic feedbacks are pivotal in understanding spruce beetle disturbance dynamics under climate change as their explicit consideration reverses the expectation of increased beetle disturbance.

Recent projections of shifts in forest composition and structure and therefore in the spruce beetle's habitat under climate change generally agree in direction. The shift from spruce-fir to mixed conifer forest that we simulated under end-of-century climate is consistent with climate envelope and process models that predict upward elevational shifts in the distribution ranges of ponderosa pine, Douglas fir and Engelmann spruce (Rehfeldt et al. 2006, Crookston et al. 2010, Notaro et al. 2012). These vegetation shifts suggest that climatic conditions for Engelmann spruce will become unsuitable in much of its current geographic range. Whether spruce-fir forests and spruce beetles may expand beyond current tree-lines and elevations that our study landscape covers is difficult to project and likely depends on geomorphic and non-climatic factors and whether higher precipitation at higher elevations may compensate for increased moisture stress due to warmer temperatures (Villalba et al. 1994, Hu et al. 2010, Macias-Fauria and Johnson 2013).

Our projected vegetation shifts should be interpreted cautiously given the study's limitations. The simulated increases of Douglas-fir and ponderosa pine result first from warmer projected temperatures and concomitant increases in fire and spruce beetle disturbance. Higher temperatures and increased light-availability at the forest floor promote Douglas-fir and ponderosa pine establishment and growth. Second, Douglas-fir and ponderosa pine were parameterized to attain larger maximum tree size (i.e., biomass) than Engelmann spruce or subalpine fir (Appendix A: Table A1). While the improved establishment and growth conditions for Douglas-fir and ponderosa pine at higher elevations under warming temperatures is well supported (Burns and Honkala 1990, Rehfeldt et al. 2006), we may have overestimated Douglas-fir and ponderosa pine tree-size. Notably, the present version of LandClim does not account for tree mortality due to mountain pine beetle and Douglas-fir beetle (*Dendroctonous pseudotsugae* Hopkins). Higher mortality rates due to beetles may prevent Douglas-fir and ponderosa pine from attaining the large sizes that we simulated under climate change.

Additionally, we may have underestimated increased fire-induced tree mortality. Even though our finding of increased fire activity agrees with other future projections (Appendix B: Fig. B4; Westerling et al. 2011), the ability of large numbers of Douglas-fir and ponderosa pine trees to reach large sizes under future fire regimes is difficult to validate. Two factors may have led us to overestimate their survival and growth. First, Douglas-fir and ponderosa pine were parameterized to be less fire-sensitive than smaller fir and spruce trees (Appendix A: Table A1; Schumacher et al. 2006) and thus experienced less fire-induced mortality. Second, the LandClim fire module does not consider increased fire spread rates under crown fire conditions that may occur with high fuel loads. Hence, we may have underestimated large, high-severity stand replacing fires and concomitant mortality of large trees (Schumacher et al. 2006, Cruz and Alexander 2010).

The underestimation of Douglas-fir and ponderosa pine mortality due to beetles and large stand-replacing fires may have two contrasting implications for the simulated spruce abundance under climate change. First, beetle-induced mortality of Douglas-fir and ponderosa pine may lead to reduced competition from these species and higher resource availability for Engelmann spruce. This in turn could result in a slower spruce decline then our simulations suggest under climate change. In contrast, increased crown-fire activity would lead to increased mortality in all tree species, which in turn would accelerate the decline of spruce. In sum, projections of future forest composition and structure are still afflicted with large uncertainties related to the choice of climate change scenarios and tree species and disturbance responses to climate change (e.g., Xu et al. 2009), but they largely agree in the decline of the area suitable for future Engelmann spruce growth and thus a decline in spruce beetle habitat.

Whether the declining abundance of large spruce due to climate change and beetle disturbance offsets the effects of warming on brood development and the increased drought-induced spruce susceptibility to beetles depends on drought severity. We demonstrated that climate change enhances or dampens beetle disturbance depending on whether or not drought surpasses a threshold. At this threshold, drought not only results in high susceptibility of Engelmann spruce to beetles but also leads to drought stress-induced mortality. In our model this threshold is reached locally, i.e., in a simulation cell, when drought-stress reduces the Engelmann spruce growth rate for at least 3 consecutive years to $<10\%$ of its potential maximum under optimal, stress-free environmental conditions (Schumacher et al. 2004). Such conditions are met by a LandClim drought index value of 0.347, which corresponds to a summer vapor pressure deficit of 8.567 mbar (Appendix A: Fig. A2).

Both this study in Colorado and Temperli et al. (2013) in Central Europe showed that the range of drought conditions where host-tree susceptibility to beetles is high but not yet lethal to the host trees is relatively narrow. In our model this narrow range is determined by the two relationships that describe drought-induced susceptibility to beetles and the drought-dependent growth response and thus mortality of the host tree species (Appendix A: Fig. A2). These two relationships implicitly account for a complex set of interdependent mechanisms that determine photosynthesis, tree growth, pools of non-structural carbon, water transport, mechanisms to defend against beetles and many other biotic pathogens and ultimately tree mortality (Bigler et al. 2006, McDowell et al. 2011). Further research on the nature and relative importance these mechanisms is critical to more accurately disentangle and model ecosystem-specific timing and severity of drought- and beetle-induced mortality under climate change (e.g., Jönsson et al. 2012). While our simulations showed that drought may mask the importance of blowdown under climate change conditions (cf. Temperli et al. 2013), a priority for further research is also to corroborate this finding empirically by more accurately quantifying the blowdown effect on forest susceptibility to spruce beetles (Jenkins et al. 2014).

We validated the sensitivity of the LandClim spruce beetle model to variations in the climate of the past century. To this end we compared the output of LandClim simulations on a generic, flat 1 km^2 landscape to Hart et al.'s (2014*a*) regional spruce beetle disturbance reconstructions. That procedure, of course, limits the validation to broad-scale and long-term climatic influences. A more spatially precise validation including the influences of local topography and climate, soil properties and disturbance history at the same spatial scale and resolution as the LandClim model would have been desirable. However, the necessary reconstructions of past local climate, forest succession and disturbance history for multiple watersheds in northwestern Colorado are currently not available. Such data would be extremely valuable, not only for model validation, but also to better understand the mechanisms that drive bark beetle disturbances.

The challenges to validate LandClim simulations are counterbalanced with LandClim's relatively generic approach to integrating climate drivers, forest succession and disturbances. This generality facilitates the identification of ecological mechanisms that operate over wide environmental gradients and across ecosystem boundaries. Hence, LandClim may be applied to other conceptually similar beetle-host systems to test, for example, whether host tree depletion may also be important in determining the long-term dynamics in mountain pine beetle and Douglas-fir beetle disturbance under climate change (Aukema et al. 2008, Raffa et al. 2008). These and further LandClim applications may inform anticipatory adaptive management that needs to account for projections and uncertainties of tree species-specific growth conditions and disturbance regimes (Millar et al. 2007, Temperli et al. 2012, Six et al. 2014).

CONCLUSIONS

We adapted the climate-sensitive forest landscape model LandClim and further developed the model's representation of spruce beetle (*Dendroctonus rufipennis*) disturbance dynamics in Colorado's subalpine forests. The resulting model advances previous work in that it explicitly accounts for changes in forest development due to climate change and feedbacks from fire and beetle disturbance (Bentz et al. 2010, DeRose et al. 2013). It integrates the climate and forest structural drivers of spruce beetle disturbance from tree to landscape scales and from years to centuries to identify emergent patterns in forest landscape and disturbance dynamics.

Our simulations under three climate change scenarios corroborate previous assessments that project future climate to become increasingly conducive to spruce beetle outbreaks. Concomitantly, we project an increase in Engelmann spruce mortality due to both drought and spruce beetle disturbance, which is likely to shift tree species dominance to more drought-adapted Douglas-fir and ponderosa pines. This decrease in host tree availability offsets the positive climate change effects on beetle population growth to the degree that beetle disturbance decreases in the long term at low elevations (<2800 m asl) and also at higher elevations under more severe climate change scenarios. Whether climate change enhances or dampens spruce beetle disturbance depends on whether drought surpasses a threshold, above which not only stress-induced susceptibility to beetles but also drought-induced host tree mortality is increased. Further research is necessary to disentangle the complex interactions among drought-stress, bark beetles and other pathogens that ultimately cause tree mortality. We suggest that host tree depletion due to drought- and beetle-induced tree mortality may also be important for disturbances by other climate-sensitive bark beetle species (e.g., mountain pine beetle and Douglas-fir beetle). Incorporating these beetle species into the scenarios investigated in this study is thus a high priority for future work. Further applications of climate-sensitive forest landscape models should focus on the role of wildfire and wind disturbances, test varying beetle and fire mitigation treatments and assess their impact on forest ecosystem service provision. Climate impact assessments such as the here depicted climate-driven shifts in forest and disturbance dynamics need to be considered in long-term adaptive management.

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LITERATURE CITED

Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. Dan Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: influences of spatiotemporal patterns and climate. Ecography 31:348–358.

Bebi, P., D. Kulakowski, and T. T. Veblen. 2003. Interactions between fire and spruce beetles in a subalpine rocky mountain forest landscape. Ecology 84:362–371.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. BioScience 60:602–613.

Bentz, B., J. Vandygriff, C. Jensen, T. Coleman, P. Maloney, S. Smith, A. Grady, and G. Schen-Langenheim. 2014. Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. Forest Science 60:434–449.

Bigler, C., O. U. Braker, H. Bugmann, M. Dobbertin, and A. Rigling. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9:330–343.

Bigler, C., D. Kulakowski, and T. T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. Ecology 86:3018–3029.

Buechling, A., and W. L. Baker. 2004. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. Canadian Journal of Forest Research 34:1259–1273.

Bugmann, H. 2001. A review of forest gap models. Climatic Change 51:259–305.

Bugmann, H., and W. Cramer. 1998. Improving the behaviour of forest gap models along drought gradients. Forest Ecology and Management 103:247–263.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. USDA Forest Service, Washington, D.C., USA.

Byers, J. A. 1989. Chemical ecology of bark beetles. Experientia 45:271–283.

Cayan, D., M. Tyree, M. Dettinger, H. Hidalgo, T. Das, E. Maurer, P. Bromirski, N. Graham, and Reinhard Flick. 2009. Climate change scenarios and sea level rise estimates for the California 2009 climate change scenarios assessment. PIER Research Report CEC-500- 2009-014. California Climate Change Center, Sacramento, California, USA.

Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93:2175–2185.

Colorado State Forest Service. 2014. 2013 Report on the health of Colorado's forests. Colorado State University, Fort Collins, Colorado, USA.

Coulson, D. P., L. A. Joyce, D. T. Price, D. W. McKenney, R. M. Siltanen, P. Papadopol, and K. Lawrence. 2010. Climate scenarios for the conterminous United States at the 5 arc minute grid spatial scale using SRES scenarios A1B and A2 and PRISM climatology. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Crookston, N. L., G. E. Rehfeldt, G. E. Dixon, and A. R. Weiskittel. 2010. Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. Forest Ecology and Management 260:1198–1211.

Cruz, M. G., and M. E. Alexander. 2010. Assessing crown fire potential in coniferous forests of western North America: a critique of current approaches and recent simulation studies. International Journal of Wildland Fire 19:377–398.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. International Journal of Climatology 28:2031–2064.

DeRose, R. J., B. J. Bentz, J. N. Long, and J. D. Shaw. 2013. Effect of increasing temperatures on the distribution of spruce beetle in Engelmann spruce forests of the Interior West, USA. Forest Ecology and Management 308:198–206.

Dyer, E. D. A., and D. W. Taylor. 1971. Spruce beetle brood production in logging slash and wind-thrown trees in British Columbia. Information Report BC-X-062. Canadian Forestry Service, Pacific Forest Research Centre, Victoria, British Columbia, Canada.

Eisenhart, K. S., and T. T. Veblen. 2000. Dendrochronological detection of spruce bark beetle outbreaks in northwestern Colorado. Canadian Journal of Forest Research 30:1788–98.

Gessler, P. E., O. A. Chadwick, F. Chamran, L. Althouse, and K. Holmes. 2000. Modeling soil–landscape and ecosystem properties using terrain attributes. Soil Science Society of America Journal 64:2046–2056.

Hansen, E. M. 2014. Forest development and carbon dynamics after mountain pine beetle outbreaks. Forest Science 60:476–488.

Hansen, E. M., and B. J. Bentz. 2003. Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). Canadian Entomologist 135:697–712.

Hansen, E. M., B. Bentz, and D. Turner. 2001. Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). Canadian Entomologist 133:827–841.

Hart, S. J., T. T. Veblen, K. S. Eisenhart, D. Jarvis, and D. Kulakowski. 2014*a*. Drought induces spruce beetle (Dendroctonus rufipennis) outbreaks across northwestern Colorado. Ecology 95:930–939.

Hart, S. J., T. T. Veblen, and D. Kulakowski. 2014*b*. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? Forest Ecology and Management 318:44–53.

Hart, S. J., T. T. Veblen, N. Mietiewicz, and D. Kulakowski. 2015. Negative feedbacks on bark beetle outbreaks: widespread and severe spruce beetle infestation restricts subsequent infestation. PLoS ONE 10:e0127975.

Hartig, F., J. Dyke, T. Hickler, S. I. Higgins, R. B. O'Hara, S. Scheiter, and A. Huth. 2012. Connecting dynamic vegetation models to data: an inverse perspective. Journal of Biogeography 39:2240–2252.

Henne, P. D., C. Elkin, D. Colombaroli, S. Samartin, H. Bugmann, O. Heiri, and W. Tinner. 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. Landscape Ecology 28:819–833.

Hu, J., D. J. P. Moore, S. P. Burns, and R. K. Monson. 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. Global Change Biology 16:771–783.

Jenkins, M., E. Hebertson, and A. Munson. 2014. Spruce beetle biology, ecology and management in the Rocky Mountains: an addendum to Spruce Beetle in the Rockies. Forests 5:21–71.

Jönsson, A. M., L. M. Schroeder, F. Lagergren, O. Anderbrant, and B. Smith. 2012. Guess the impact of *Ips typographus*: an ecosystem modelling approach for simulating spruce bark beetle outbreaks. Agricultural and Forest Meteorology 166–167:188–200.

Joyce, L. A., D. T. Price, D. W. McKenney, R. M. Siltanen, P. Papadopol, K. Lawrence, and D. P. Coulson. 2011. High resolution interpolation of climate scenarios for the conterminous USA and Alaska derived from general circulation model simulations. RMRS-GTR-263. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Kulakowski, D. W., and P. Bebi. 2004. Range of variability of unmanaged subalpine forests. Forum für Wissen, Eidg. Institut für Schnee- und Lawinenforschung SLF, Davos, Switzerland.

Kulakowski, D., D. Jarvis, T. T. Veblen, and J. Smith. 2012. Stand-replacing fires reduce susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. Journal of Biogeography 39:2052–2060.

Kulakowski, D., and T. T. Veblen. 2002. Influences of fire history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. Journal of Ecology 90:806–819.

Kulakowski, D., and T. T. Veblen. 2006. The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. Canadian Journal of Forest Research 36:2974–2982.

Kulakowski, D., T. T. Veblen, and P. Bebi. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. Journal of Biogeography 30:1445–1456.

Macias-Fauria, M., and E. A. Johnson. 2013. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. Proceedings of the National Academy of Sciences USA 110(2):8117–8122.

McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology and Evolution 26:523–532.

Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17:2145–2151.

Negrón, J. F., and C. J. Fettig. 2014. Mountain pine beetle, a major disturbance agent in US western coniferous forests: a synthesis of the state of knowledge. Forest Science 60:409–413.

Notaro, M., A. Mauss, and J. W. Williams. 2012. Projected vegetation changes for the American

Southwest: combined dynamic modeling and bioclimatic-envelope approach. Ecological Applications 22:1365–1388.

Økland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. Agricultural and Forest Entomology 6:141–146.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio 45:3–75.

Price, J. I., D. W. McCollum, and R. P. Berrens. 2010. Insect infestation and residential property values: a hedonic analysis of the mountain pine beetle epidemic. Forest Policy and Economics 12:415–422.

Raffa, K., B. Aukema, B. Bentz, A. Carroll, J. Hicke, M. Turner, and W. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501–517.

Rehfeldt, G. E., N. L. Crookston, Marcus V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.

Reynolds, K. M., and E. H. Holsten. 1994. Relative importance of risk factors for spruce beetle outbreaks. Canadian Journal of Forest Research 24:2089–2095.

Ryan, K. C., and T. S. Opperman. 2013. LANDFIRE: a national vegetation/fuels data base for use in fuels treatment, restoration, and suppression planning. Forest Ecology and Management 294:208–216.

Scheller, R., and D. Mladenoff. 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. Landscape Ecology 22:491–505.

Schmid, J. 1981. Spruce beetles in blowdown. Research Note RM-411. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Schmid, J., and R. Frye. 1977. Spruce beetle in the Rockies. GTR RM-49. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Schmid, J. M., and R. H. Frye. 1976. Stand ratings for spruce beetles. Research Note RM-309. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Schumacher, S. 2004. The role of large-scale disturbances and climate for the dynamics of forested landscapes in the European Alps. Dissertation. Swiss Federal Institute of Technology ETH Zürich, Switzerland.

Schumacher, S., H. Bugmann, and D. Mladenoff. 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecological Modelling 180:175–194.

Schumacher, S., B. Reineking, J. Sibold, and H. Bugmann. 2006. Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. Landscape Ecology 21:539–554.

Seidl, R., P. M. Fernandes, T. F. Fonseca, F. Gillet, A. M. Jönsson, K. Merganičová, S. Netherer, A. Arpaci, J.-D. Bontemps, and H. Bugmann. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecological Modelling 222:903–924.

Sherriff, R. L., E. E. Berg, and A. E. Miller. 2011. Climate variability and spruce beetle (*Dendroctonus rufipennis*) outbreaks in south-central and southwest Alaska. Ecology 92:1459–1470.

Shore, T. L., and L. Safranyik. 1992. Susceptibility and risk rating system for the mountain pine beetle in lodgepole pine stands. Information Report BC-X-336. Forestry Canada, Pacific Forestry Centre, Victoria, British Columbia, Canada.

Sibold, J. S., T. T. Veblen, and M. E. González. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography 33:631–647.

Simard, M., E. N. Powell, K. F. Raffa, and M. G. Turner. 2011. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone? Global Ecology and Biogeography 21:556–567.

Six, D. L., E. Biber, and E. Long. 2014. Management for mountain pine beetle outbreak suppression: Does relevant science support current policy? Forests 5:103–133.

Temperli, C., H. Bugmann, and C. Elkin. 2012. Adaptive management for competing forest goods and services under climate change. Ecological Applications 22:2065–2077.

Temperli, C., H. Bugmann, and C. Elkin. 2013. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. Ecological Monographs 83:383–402.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

U.S. Geological Survey. 2013. LANDFIRE.US_DEM. U.S. Geological Survey, USGS EROS, Sioux Falls, South Dakota, USA. http://landfire.cr.usgs.gov/viewer/

Veblen, T. T., K. S. Hadley, E. M. Nel, T. Kitzberger, Marion Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology 82:125–135.

Veblen, T. T., K. S. Hadley, and M. S. Reid. 1991. Disturbance and stand development of a Colorado subalpine forest. Journal of Biogeography 18:707–

716.

Villalba, R., T. T. Veblen, and J. Ogden. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology 75:1450–1462.

Wallin, K. F., and K. F. Raffa. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. Ecological Monographs 74:101–116.

Werner, R. A., and E. H. Holsten. 1997. Dispersal of the spruce beetle (*Dendroctonus rufipennis*) and the engraver beetle (*Ips perturbatus*) in Alaska. PNW-RP-501. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences USA 108(32):13165–13170.

Xu, C., G. Z. Gertner, and R. M. Scheller. 2009. Uncertainties in the response of a forest landscape to global climatic change. Global Change Biology 15:116–131.

SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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