

Exploring interactions among multiple disturbance agents in forest landscapes: simulating effects of fire, beetles, and disease under climate change

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Introduction

In light of the potential for climate change to have adverse effects on natural, political, social, and economic systems, ecologists have been called upon to investigate the consequences of anthropogenic climate change on the world's ecosystems (Bachelet et al. 2000). However, exploration of the numerous, complex, and multi-scale interactions among ecological processes, disturbance agents, and climate drivers present intractable challenges with respect to scientific exploration as traditional field methods used to explore ecosystem responses to environmental change are inadequate to capture complex interactions that occur across large areas and long time periods (Keane et al. 2015b). Multi-scale ecological interactions often result in non-linear feedbacks that produce novel and unanticipated landscape responses to changing climates (Temperli et al. 2013). These can be explored using simulation modeling, in which computer programs are used to quantitatively simulate complex ecological processes and their interactions over decades or centuries (McKenzie et al. 2014).

Most ecological responses to climate change are best evaluated and simulated at landscape scales using landscape models (LMs). Because of their limited spatial extent, finer-scale stand models cannot fully incorporate spatial aspects of disturbance regimes ([Bugmann 2001](#)), and coarser-scale Dynamic Global Vegetation Models (DGVMs) are not designed to simulate important species- and plant-level disturbance effects such as successional trajectories and disturbance survival (Flannigan et al. 2009). Spatially explicit simulations using LMs have greatly improved our ability to explore and understand complex interactions (Scheller and Mladenoff 2007; Perry and Millington 2008). Several sources provide details on landscape change modeling (Mladenoff and Baker 1999), ecosystem dynamics (Canham et al. 2004), and spatial fire spread and effects (Gardner et al. 1999). In various reviews, LMs are described based on their design, structure, detail, resolution, and geographical area (see Keane et al. 2004; He 2008; Baker 1989; Scheller and Mladenoff 2007, respectively). To realistically predict climate change effects, LMs must be structured to simulate disturbance processes, vegetation growth and mortality, and species composition and distribution as well as their interactions across multiple scales (Bachelet et al. 2000; Purves and Pacala 2008). However, the level of mechanistic detail

needed to realistically simulate important interactions among these processes and variables remains a central challenge in landscape modeling (Gustafson 2013).

In this presentation, we explore a unique subset of the many ecological interactions that occur at landscape scales—the interactions among disturbances. Disturbances influence vegetation distribution, structure, and composition, and may indirectly and directly interact with one another and with changing climate to create novel landscapes (Kitzberger et al. 2012). Warming climates have already altered interactions among disturbance regimes resulting in highly visible and rapidly occurring changes in landscape composition and structure, and the importance of these interactions have been shown in studies across the world (Green and Saladin 2005; Parker et al. 2006). To demonstrate the importance of effects of single and interacting disturbances on landscapes, we focused on a subset of disturbances that are common across many US Rocky Mountain landscapes: wildland fire (any fire that occurs in a non-developed or sparsely developed area), mountain pine beetle (*Dendroctonus ponderosae*), and white pine blister rust (*Cronartium ribicola*). We use a landscape simulation model to evaluate how single and interacting disturbances respond to changes in climate and influence landscapes. Because the magnitude, trend, and type of disturbance interactions differ across ecosystems, our simulation results cannot be wholly extrapolated to other landscapes; however, our goal in this chapter is to demonstrate the general importance of disturbance interactions in influencing future landscape composition and structure.

The Simulation Model and Application

FireBGCv2 (Fire BioGeoChemical model Version 2) is a bottom-up, mechanistic, individual tree, forest succession model containing stochastic properties implemented in a spatial domain (see Keane et al. 2011 for complete model documentation). It can be categorized as a landscape fire succession model (Keane et al. 2004), a forest landscape model (He 2008), or a landscape dynamics model (Mladenoff and Baker 1999). Versions of the model have been used to address a wide variety of research questions including climate change effects on stream temperatures (Holsinger et al. 2014), wildlife, and vegetation composition (Loehman et al. 2011); management effectiveness; grazing interactions with fire (Riggs et al. 2015); landscape structure; fuel-snag dynamics; and carbon emissions (Keane et al. 1997). FireBGCv2 simulates basic processes such as tree growth, organic matter decomposition, and litterfall using detailed physical and biogeochemical relationships (Keane et al. 2011). Long-term daily weather streams drive primary canopy processes (e.g., transpiration, photosynthesis, and respiration), vegetation phenology (e.g., curing, leaf fall), and fire dynamics (e.g., ignition, fuel moisture, spread, intensity) within the simulation landscape.

We simulated all combinations of wildland fire, mountain pine beetle, and white pine blister rust for two forested landscapes that comprise a range of climate, vegetation, and fire regime types common to the US Rocky Mountain region:

- **East Fork of the Bitterroot River (EFBR):** A 128,000 ha dry mixed-conifer ecosystem in western Montana, USA, with an historical low- to high-frequency, mixed-severity fire regime. Lower-elevation stands comprise primarily ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*), and higher elevation stands are dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) (Holsinger et al. 2014).

- **Yellowstone Central Plateau (YCP):** An 80,000 ha, high-elevation lodgepole pine ecosystem in Yellowstone National Park, USA, with an historical low-frequency, high-severity fire regime. Stands contain minor amounts of Douglas-fir, whitebark pine, subalpine fir, and Engelmann spruce (Clark et al. 2016[in press]).

We simulated disturbance interactions under two climate scenarios:

- **Current climate:** The recorded daily weather for the last 50+ years collected within or near each of the simulation landscapes, compiled by the National Climatic Data Center. Weather years were used in sequence, repeated for multiple cycles over a 250-year simulation period.
- **Warmer climate:** A climate change scenario in which temperatures increase by an average of 2.8 °C relative to historical weather. Climate offsets for each landscape represent an ensemble average of climate model projections for the A2 emissions scenario (IPCC 2007) downscaled to 12 km for the period 2070 to 2099 (Girvetz et al. 2009).

FireBGCv2 simulations are usually performed with multiple replicates to account for stochastic model elements (e.g., Loehman et al. 2011) but we did only one run per scenario for the purposes of illustration. For each 250-year simulation, disturbances were implemented beginning in the initial simulation year. We report two response variables sensitive to disturbance interaction effects: species composition (dominant species of each modeled stand) and tree basal area ($\text{m}^2 \text{ha}^{-1}$).

Results

Average basal area across each landscape at all three study locations is highest under no-disturbance scenarios and is subsequently reduced by WPBR, MPB, and fire (in order of increasing influence), and then by their interactions (Figure 1). For CCE, EFBR, and YCP under current climate, fire activity alone accounted for a substantial portion of the reduction in basal area as compared with the no-disturbance scenario (8.7, 11.0, and 19.7%, respectively) while WPBR alone accounted for the least change (1.2, 1.0, and 0.3%, respectively), presumably because of the low abundance of five-needle pines. However, fire interactions with MPB and WPBR significantly changed basal area the most (Keane et al. 2015a), but fire-MPB interactions further reduced basal area (11.5, 14.7, and 13.0%) and the interactions from all three disturbances resulted in the most change (15.0, 18.6, 20.1%), even with five-needle pines a relatively minor component of our simulation landscapes. While WPBR killed less than 1.0% of basal area per year, it killed over 20% of the whitebark pine basal area. And MPB killed around 2% of basal area per year but it killed around 15% of the total basal area of the pines. Fire killed from 4-6% of the basal area per year.

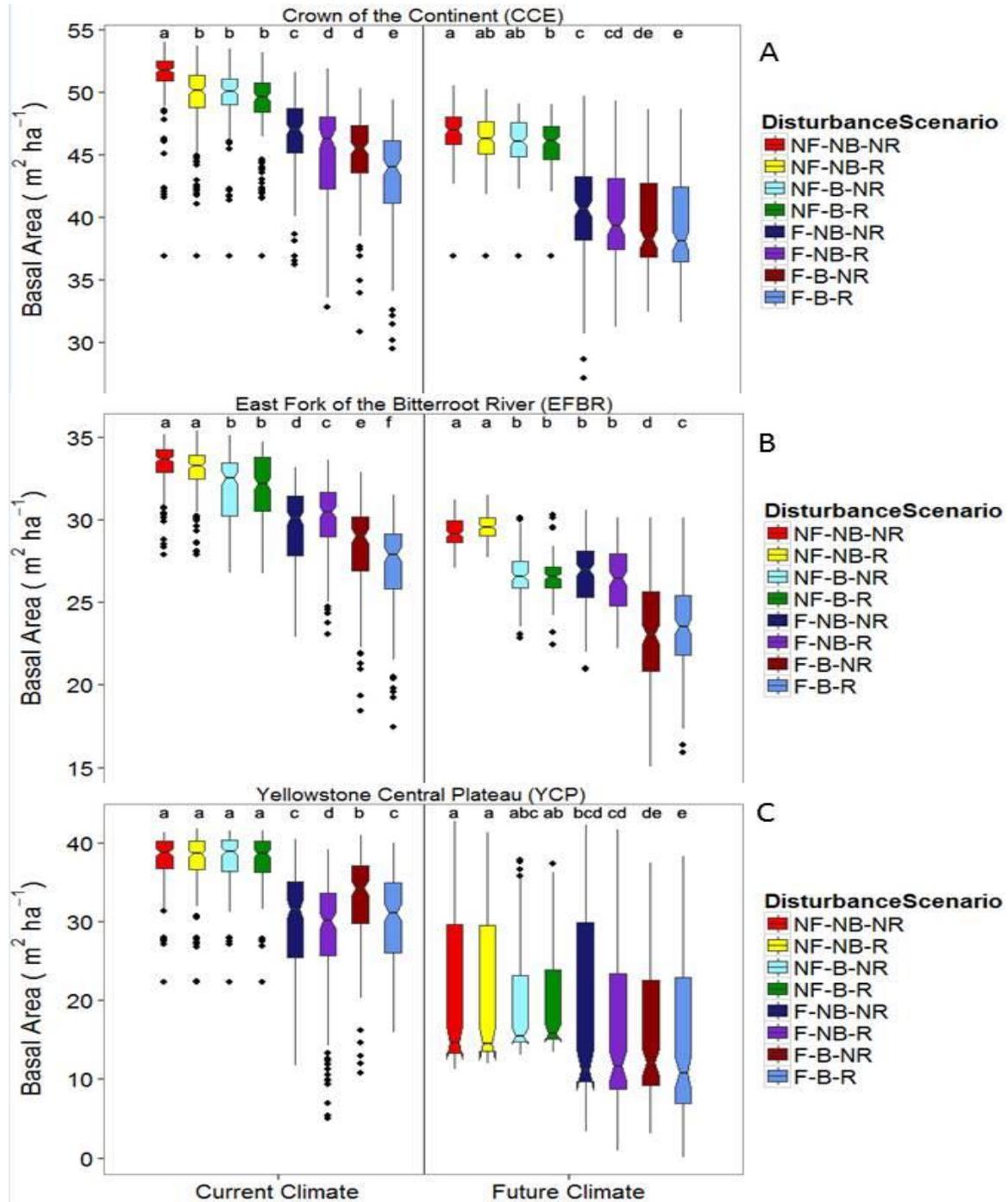


Figure 1. Boxplots showing the differences between non-disturbance scenarios with disturbance alone and disturbance combinations for both current and future climates for the three simulation landscapes: (A) Crown of the Continent (CCE), (B) East Fort of the Bitterroot River (EFBR), and (C) Yellowstone Central Plateau. Letters atop each boxplot indicate significance ($p < 0.05$) across scenarios. Letters indicate the following disturbances: Fire and no fire (F, NF), MPB and no MPB (B, NB), WPBR and no WPBR (R, NR).

Disturbance interactions modeled under future climate significantly altered landscape basal area as compared with no-disturbance and current climate scenarios. All three landscapes experienced lower productivity in basal area under the no disturbance scenario with future climate (10, 13, 46% reduction in basal area for CCE, EFBR, and YCP, respectively). Again, fire was the most influential disturbance accounting for 12, 9, and 16% reductions in basal area killing about 5-7% of the basal area per year, and WPBR was the least significant disturbance (>1% basal area reductions for all landscapes). The magnitude of the basal area reductions with disturbance interactions were significantly larger under warmer climates with >15% reductions in basal area when all disturbances were simulated.

Discussion

Several important results emerged from the simulation experiment. First, disturbance interactions caused easily detectable, direct, and immediate effects on landscape basal area and species composition (Figure 1). Second, in most cases, disturbance interaction effects outweighed direct climate impacts on forests, and in all cases, disturbances and their interactions modeled under future climate significantly altered basal area and species composition (Figure 1). Third, the disturbance interactions were rarely additive across disturbances; the impact of one disturbance alone is not the same as when other disturbances are included in the simulation. Last, we found that effects of climate changes and disturbances differed across study areas because they were mediated through species-specific sensitivity and susceptibility; landscape responses may be non-linear as the result of reciprocal interactions of climate, fire, MPB, and WPBR through several disturbance cycles. We conclude that climate changes acting in tandem with these disturbances have the potential to shift landscapes to novel configurations.

Many factors determine the frequency and magnitude of landscape responses to interacting disturbances (Keane et al. 2015a). The biophysical environment – and particularly landscape composition and climate - is perhaps the most important. Species composition and configuration (i.e., vegetation pattern) controls fire behavior and fire effects, and host availability for and susceptibility to MPB attacks and WPBR infections. For example, current MPB outbreaks in North America might have been less intense and more localized if wildland fires had not been excluded over the last century because fire exclusion increased the abundance of host species of sufficient size and abundance for insect and disease epidemics (Carroll et al. 2003). Predictions of warmer temperatures and increased drought stress suggest that the total area susceptible to or affected by beetle outbreaks and large or severe fires may increase in the coming decades (Williams et al. 2013). Although climate changes directly affect forests, our results suggest that indirect effects, mediated through disturbances and interactions, have greater impact.

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