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Cascading effects of feedbacks, disease, and climate change on alpine treeline dynamics

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) is important for tree island development in some alpine treeline ecosystems in western North America; therefore the effects of an exotic disease on whitebark pine may cascade to other species and affect how treeline responds to climate change. We developed an agent-based model to examine the interactive impacts of blister rust and climate change on treeline dynamics. Our model includes positive and negative feedback effects for population processes and infection in a neighborhood. We simulated a present-day-like whitebark pine treeline community in the northern U.S. Rocky Mountains under stable conditions, and then conditions of disease, climate amelioration, and their combination. The loss of pine to disease was only partly compensated by the effect of climate change, and resulted in less facilitation for other species—reversing the positive effects of climate amelioration. Spatially explicit simulation captured the cascading effects of neighborhood facilitation on treeline populations and patterns.

1. Introduction

Forest ecosystems worldwide are increasingly subject to the interacting effects of multiple disturbance processes, which include climate change and pathogen invasions (e.g., Millar et al., 2007, 2012). The significant decline of whitebark pine (*Pinus albicaulis*; nomenclature: www.itis.gov) due to white pine blister rust (*Cronartium ribicola* (Uredinales: Cronartiaceae) (hereafter referred to as blister rust) and its consequences for forest ecosystems provide a compelling illustration of this problem. In forest ecosystems dependent on keystone species, such as whitebark pine treeline communities, there is a pressing need to understand the complex interactions between vegetation, disease, and climate change—because the combined impacts of disturbance and increasing temperatures on these sensitive ecosystems are unknown (Tomback and Resler, 2007). Simulation modeling is one approach to understanding the potential impacts of such interactions. Here, we develop an agent-based simulation model to investigate a relatively underexplored area of research, the response of whitebark pine treeline communities to the combined effects of climate change and blister rust. These communities represent ecosystems driven by complex interactions of abiotic and biotic disturbances that can have measureable consequences in terms of ecosystem response to change (Hobbs et al., 2009). Our simulations focus on the cascading effects of disease on treeline dynamics.

1.1. Alpine treeline

The alpine treeline ecotone (ATE) is a transition zone between upper elevation subalpine forest and treeless alpine tundra (Holtmeier, 2009). At the ATE, trees approach their physiological limits in the stressful high elevation environments, where factors such as high evapotranspiration, cold temperatures, and wind abrasion limit establishment and growth (e.g., Holtmeier, 2009; Körner, 2012). In this environment, ecologically significant relations in the function of neighbors are revealed (i.e., positive feedback switches or competition—facilitation switches: Wilson and Agnew, 1992; Callaway et al., 2002). For neighboring conifer trees at the ATE the amelioration of abiotic stresses facilitates the establishment of additional surrounding trees. These interactions,

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coupled with the spatial availability of scarce resources necessary for growth (van der Valk and Warner, 2009) and sheltered sites (Resler et al., 2005), can create tree islands, often wind-shaped ‘hedges’, which result in a patchy vegetation pattern across the ATE landscape (Marr, 1977; Holtmeier, 1982; Malanson et al., 2007, 2011).

Research suggests whitebark pine plays a key role initiating tree islands because of its frequency in lead, windward positions relative to other tree species—where it shelters and facilitates conifers such as Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) (Resler and Tomback, 2008; Blakeslee, 2012; Tomback et al., 2014). Whitebark pine is both a foundation species in promoting forest structure (Ellison et al., 2005), and a keystone species by providing more ecosystem services than its abundance would suggest (Tomback et al., 2001). An important example of this is the mutual dependency between whitebark pine and Clark's nutcracker (*Nucifraga columbiana*) for seed dispersal and propagation (Tomback, 1982). Nutcrackers transport whitebark pine seeds from the subalpine and cache them near boulders or other natural landmarks (such as the base of trees or logs) in the ATE (Tomback and Linhart, 1990). Whitebark pine's tolerance for windy and exposed climates enable its growth and longevity in the ATE, where its facilitative role ameliorates abiotic stresses for adjacent conifers and promotes growth and development of tree islands (Blakeslee, 2012; Tomback et al., 2014).

Whitebark pine is suffering widespread mortality from multiple disturbances throughout its western North American range, including the invasive blister rust disease caused by the fungal pathogen *Cronartium ribicola* (Schwandt et al., 2010). Recently, blister rust has been observed in the dry and cold environments of whitebark pine treeline communities east of the Rocky Mountain Continental Divide (Tomback and Resler, 2007; Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna et al., 2013). Blister rust reduces vigor in whitebark pine by damaging the cambium via cankers, ultimately killing the tree (McDonald and Hoff, 2001; Geils et al., 2010). Disease-induced mortality of whitebark pine is a potentially important negative feedback occurring in treeline systems given that the decline of whitebark pine may also reduce tree island initiation in the upper ATE and thus other conifer species (Tomback and Resler, 2007). From research examining treeline positions as bioclimatic indicators of climate change (cf. Kupfer and Cairns, 1996; Smith et al., 2009; Harsch and Bader, 2011), and our current knowledge of whitebark pine's climatic niche in forest communities (Rehfeldt et al., 2006), current climate warming trends should advance whitebark pine above the current ATE. However, in blister rust-impacted treelines, the mortality of whitebark pine may confound interpretations of treeline positions—treelines that are responding to a changing climate and a disease-altered ecosystem (Tomback and Resler, 2007). Spatially explicit simulation models are useful tools for investigating possible alternative outcomes in such a system (e.g., Alftine and Malanson, 2004; Zeng and Malanson, 2006; Bader et al., 2008; Colombaroli et al., 2010).

1.2. Agent-based modeling

Simulation models are often used to understand the response of ecotones to climate change (e.g., Noble, 1993; Cairns and Malanson, 1998; Bader et al., 2008). Cellular models capture spatial processes by representing a system's geographic domain through a cell neighborhood (Tobler, 1979), and applying local neighborhood associations among cells to calculate dynamic response within the system (Malanson, 1999; Fonstad, 2006). Agent-based models (ABMs) (formerly ‘individual-based models’, cf. Railsback and Grimm, 2012), are a class of simulation models that use autonomous entities called ‘agents’ as the building blocks of complex systems (Bonabeau, 2002; Grimm and Railsback, 2005) and are effective in researching landscape dynamics in the context of ecosystem response to climate change, and human disturbance (Parker et al., 2003; Gibon et al., 2010). ABMs, where a lattice of cells represents the landscape and agents interact within this lattice based on neighborhood rules, are useful for analyzing the emerging dynamics at a landscape-scale (Travis et al., 2005; Malanson et al., 2006; Dunn and Majer, 2007). Some studies that have examined dynamics of ATE spatial patterns used cellular models to include dispersal limitations (Malanson, 1997; Wallentin et al., 2008) or to incorporate neighborhood rules based on feedback processes in alpine systems (Malanson, 1997; Malanson et al., 2001; Alftine and Malanson, 2004; Zeng and Malanson, 2006; Díaz-Varela et al., 2010). Our treeline ABM is similar in structure to that of Wallentin et al. (2008) in that it is focused on basic population dynamics, but it is the first of its kind to model ATE landscapes as a grid of cells on which neighbors affect how tree species establish, grow branches (which increases spatial association), build tree islands, and become infected. It elucidates feedbacks affecting the spatial patterns and processes of treeline populations through which disturbance cascades to multiple species.

1.3. Whitebark pine treeline model

To assess treeline response to the singular and combined effects of blister rust disease and climate change on whitebark pine treeline community dynamics, we examined changes to the populations and patterns of the treeline ABM and implemented five scenarios in our simulations: 1) ‘Untreated’ (no disease or climate amelioration), 2) ‘Disease’, 3) ‘Climate’, 4) ‘Climate and Disease’, and 5) ‘Accelerated Climate and Disease’ (a worst-case scenario). From these scenarios, we observed the impacts of disease on conifer populations and clustering patterns (the formation of tree islands). We examined the change in treeline dynamics due to the cascading effects of feedbacks, disease, and climate amelioration in a system dependent on a foundation and keystone species.

2. Methods and model description

We developed an ABM to simulate a whitebark pine treeline community in the upper limits of the ATE (e.g., Fig. 1), using our field data and observations in Rocky Mountain treelines (Resler and Tomback, 2008; Smith et al., 2011; Smith-McKenna, 2013; Smith-McKenna et al., 2013) and other findings from the literature to inform the model. In some northern Rocky Mountain treelines, sun and wind-tolerant whitebark pines (Arno and Hoff, 1989) facilitate relatively sun-intolerant subalpine fir and Engelmann spruce, promoting growth and development of tree islands under stressful conditions (Resler and Tomback, 2008; Resler and Fonstad, 2009). These three species dominated our sampled treeline populations and therefore served as agents in our model. To align with IPCC reports of increasing trends of warming temperatures and snow/ice melt, particularly for western North America (IPCC, 2007, 2013), we simulated climate change by ameliorating stress in the cold ATE environment—improving growing conditions for trees. We also assessed treeline response to the introduction of blister rust by incorporating spatial negative feedbacks to the model (as cellular rules), based on our findings that whitebark pine trees have slightly higher likelihoods of blister rust infection depending on proximity to tree islands, tree island size (Resler and Tomback, 2008), and proximity to moisture sources (Smith et al., 2011; Smith-McKenna et al., 2013).

We used Netlogo (v. 4.1.2) software (Wilensky, 1999) to develop a hypothetical landscape of the ATE and to simulate scenarios in an