The importance of within-patch heterogeneity for population dynamics of a high elevation pine

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Introduction

Mountainous regions across the globe are some of the habitats most strongly affected by climate change (Jump *et al.* 2009). They are experiencing climate change that is rapid relative to other regions, and organisms in montane habitats are sensitive to changes in temperature, particularly at upper elevation limits where temperature is generally a limiting factor (Pauli *et al.* 2007; Jump *et al.* 2009; Ettinger *et al.* 2011). In order to predict how these species will respond to climate change, it is important to develop reliable models for characterizing how mountain species are affected by environmental variation. These models will need to be capable of incorporating some of the unique aspects of mountain habitats, such as the steep climatic gradients experienced by organisms from the lower to upper bounds of their range and the natural habitat patches created by mountaintops. I aim to test whether within-population variation, such as elevation gradients, can change predictions for the persistence of a high elevation pine, using new and existing demographic data for whitebark pine (*Pinus albicaulis*) in the Elkhorn Mountains of Oregon.

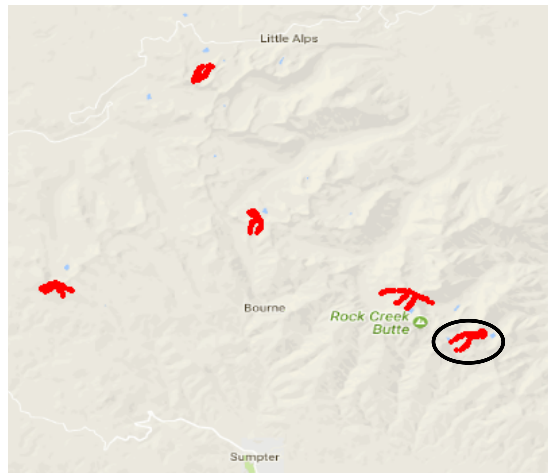

Figure 1. Regional map of the field sites in the Elkhorn Mountains of northeastern Oregon. The locations of trees that were sampled as part of this project are shown in red. The current work was done at Elkhorn Peak, circled in black in the lower right-hand corner.

The site:

The Elkhorn Mountains (Fig. 1), which form the highest subsection of the Blue Mountains, are a small mountain range in northeastern Oregon. The high elevations are dominated by whitebark pine and subalpine fir at high elevations, transitioning into lodgepole pine, Douglas fir, and white fir at lower elevations. Aside from the charismatic plant life, the Elkhorn Mountains are also home to an abundance of other notable characters, including mountain goats, elk, and a variety of birds and small mammals (Fig. 2).

Figure 2. Fauna, large and small, of the Elkhorn Mountains.

Meet the species:

Whitebark pine (Fig. 3) is a high elevation conifer that is found throughout western North America (Arno & Hoff 1989). It plays an important role in habitat formation in subalpine habitats (Ellison *et al.* 2005), as well as affecting hydrology via regulation of snow melt (Farnes 1990). Additionally, it produces energy-rich seeds which are an important food source for organisms from birds to rodents to grizzly bears (Kendall 1983; Mattson *et al.* 2001). Unfortunately, due to the combined effects of climate change, fire suppression, insect outbreaks and an invasive pathogen, whitebark pine is declining throughout its range and is listed as "Endangered" on the IUCN Red List ("The IUCN Red List of Threatened Species" 2016).

Figure 3. A small whitebark pine clings to a rock at the top of Elkhorn

Whitebark pine has a patchy distribution, with local populations existing on mountaintop "islands", and replaced by other species at lower elevations (Cottone & Ettl 2001). Local populations are susceptible to extinction due to fires and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*). Recolonization of populations, and any other movement between local populations, is due entirely to movement by an avian seed disperser, Clark's nutcracker (*Nucifraga columbiana*) (Hutchins & Lanner 1982) (Fig. 4), which occasionally carries seeds sufficiently far to transport seeds between local populations on nearby peaks and to recolonize extinct populations (Lorenz *et al.* 2011).

Figure 4. A Clark's nutcracker pulls seeds out of a whitebark

Environmental variables: I am interested in the responses of vital rates to environmental variation, so I measured two environmental drivers that are relevant for whitebark pine: aggregation and elevation.

Aggregation: Whitebark pine seedlings germinate almost exclusively from Clark's nutcracker caches (Hutchins & Lanner 1982), so they often grow in tight clusters, which could lead to either competition between the trees or beneficial facilitation if they shelter each other from harsh conditions (Callaway 1998; Alftine & Malanson 2004).

Elevation: Temperature is a major environmental factor limiting the growth of whitebark pine (Perkins & Swetnam 1996; Dolanc *et al.* 2013), so trees at higher, colder elevations will likely have slower growth than trees at lower elevations. However, lower elevation trees will be subject to stronger competition from other species, mostly subalpine fir (*Abies lasiocarpa*) (Larson & Kipfmueller 2010).

Furthermore, the mountain pine beetle, a major threat to whitebark pine, requires high temperatures to outbreak, so lower elevation trees are likely to face higher impacts from the mountain pine beetle (Amman 1973; Safranyik 1978).

Purpose

While doing fieldwork in the Elkhorn Mountains in August 2017, supported by the American Alpine Club, I planted seedlings at varying elevations and levels of aggregation which will be used to quantify seedling growth and survival rates for whitebark pine. In combination with previously collected demographic data, I will using the seedling data to build population models to test for the effects of within-population variation in elevation and aggregation on the population dynamics of whitebark pine. Specifically, I will address the following questions:

1) What are the individual demographic responses to aggregation and elevation for whitebark pine?
2) How does accounting for within-population variation change our predictions of whitebark pine persistence?

Methods

Demographic data collection: In previous years, my field assistants and I collected demographic data at 5 local populations within the Elkhorn Mountains to construct population models for whitebark pine. At each site, we collected data from trees along four transects running from the top of the mountain to the lower elevation limit of whitebark pine. For each tree sampled, we collected data on elevation, aggregation of trees, and demographic data, as follows: we collected cores from 20 trees, alive or dead, along each transect to estimate annual growth and adult survival. By coring dead trees and determining the year of death, we obtained survival rates for adult trees. We collected reproductive data from every reproductive tree that we cored to estimate total yearly cone production and average number of seeds produced per cone.

Figure 5. Greg Schultz and Emily Schultz plant seedlings at the top of Elkhorn Peak. Photo credit: Brian Schultz

Planting experiment: On this trip, we started an experiment to measure seedling survival in the field. We planted seed in a growth chamber to produce seedlings for planting. We planted the seedlings at 10 elevations along three transects at one site. At each elevation, we planted the seedlings at five levels of aggregation: 1, 2, 3, 4, and 5 seedlings per cluster, which covers the typical range of densities we observed in the field (Fig. 5). For the next two years, we will return to the site to monitor the elevation- and density-specific survival of the seedlings.

Population models: I will use the demographic data to construct two population models: a model using average values for each population, and a model that accounts for within-population heterogeneity. Each population will have a chance of experiencing a catastrophe, either a fire or a beetle outbreak, based on probabilities calculated from outbreak and fire records. I will incorporate dispersal by allowing a portion of the seeds produced move to another population. Dispersal rate between patches will be based on the literature on Clark's nutcracker, which provides dispersal distances of individual dispersal events by radio-tracked birds (Lorenz et al. 2011). For each set of models, I will predict time to extinction for whitebark pine. I will compare the output of the two models to determine if within-patch variation is important for characterizing the persistence of whitebark pine in the region.

Discussion

Preliminary results: Variation in elevation and aggregation affected the survival, growth, and reproduction of whitebark pine. Elevation had a negative effect on growth, but a weak positive effect on reproduction. The effect of aggregation was generally positive, suggesting that whitebark pine trees facilitate the growth and reproduction of other whitebark pines. Adult survival was generally high across elevation and levels of aggregation, and any effects were weak. At this point, because I do not yet have the results of my planting experiment, germination and seedling survival rates were based on literature values and do not incorporate the effects of elevation and aggregation. At the population level, accounting for the within-population variation in elevation and aggregation resulted in a higher population growth rate and longer persistence for whitebark pine populations (Fig. 6). This was mostly due to the effect of variation on growth of the trees. However, both models predicted that whitebark pine populations are declining.

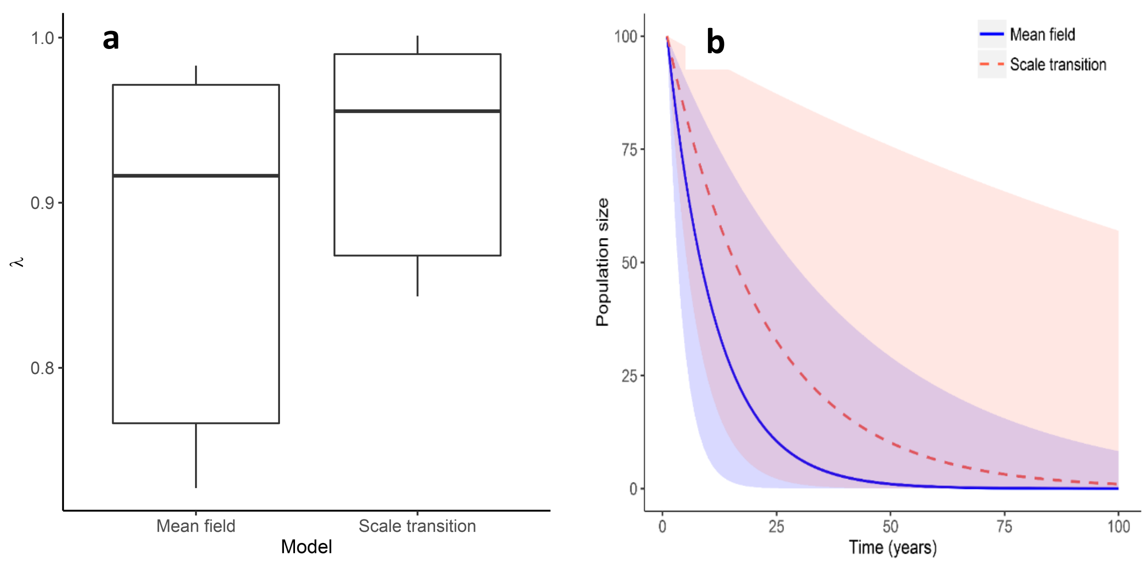

Figure 6. a) Population growth rates calculated from the mean field model, which uses average values for the populations and the scale transition model, which accounts for within-population variation. b) Population projections for the next 100 years using the mean field model and the scale transition model.

In the future, I hope to do additional seedling planting experiments to increase my sample size and plant at other sites. I would also like to plant seeds directly in the field to measure germination rates at different elevations. Analysis is still ongoing, and next, I will incorporate fires, beetle outbreaks, and dispersal to estimate the regional persistence of whitebark pine.

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