



Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution

Katherine M. Renwick, Monique E. Rocca & Thomas J. Stohlgren

Keywords

Climate change; Competition; Disturbance; Ecotone; Lodgepole pine; *Pinus contorta*; Range shift

Abbreviation

MPB = mountain pine beetle.

Nomenclature

USDA Plants Database
(<https://plants.usda.gov/java/>)

Received 31 March 2015

Accepted 7 March 2016

Co-ordinating Editor: Beverly Collins

Renwick, K.M. (corresponding author,
katie.renwick@gmail.com)^{1,2},

Rocca, M.E.
(Monique.Rocca@colostate.edu)^{1,2,3},

Stohlgren, T.J.
(thomas.stohlgren@colostate.edu)³

¹Graduate Degree Program in Ecology,
Colorado State University, Fort Collins, CO
80523, USA;

²Department of Ecosystem Science and
Sustainability, Colorado State University, Fort
Collins, CO 80523, USA;

³Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins, CO
80523, USA

Abstract

Aim: Climate change will alter the geographic distribution of many species, but in forest communities, long-lived trees often persist after the climate is no longer suitable for recruitment. Disturbance events may accelerate distribution shifts in forested ecosystems by removing persistent trees and creating new recruitment opportunities for species better adapted to the current climate. Here, we investigate how biological disturbances such as insect outbreaks may interact with climate change to initiate tree species range shifts.

Location: Southern Rocky Mountains, Colorado, USA.

Methods: We compared tree and seedling data from long-term monitoring transects established in 1992–1995 and re-sampled in 2012 following a widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak. Transects are located along elevational gradients at the altitudinal range margins of lodgepole pine (*Pinus contorta*).

Results: We found that recruitment had declined through time at the trailing edge of lodgepole pine's distribution (lower elevation range margin), where there are now many fewer seedlings compared to the leading edge (upper elevation range margin). At the trailing edge, mountain pine beetle increased mortality of mature lodgepole pines relative to background levels. This mortality was associated with an increase in recruitment of Douglas-fir (*Pseudotsuga menziesii*), a lower elevation tree species. At the leading edge of lodgepole pine's distribution, overstorey mortality was associated with only a modest increase in the density of lodgepole pine seedlings (mean increase of 362 seedlings·ha⁻¹), and instead favoured more shade-tolerant competitors (mean increase of 2182 seedlings·ha⁻¹).

Conclusion: While there is some evidence that climate change is beginning to alter the altitudinal range of lodgepole pine, mountain pine beetle disturbance will likely facilitate this process only at the trailing (lower elevation) range margin. At the leading (upper elevation) range margin, range expansion may be limited by competition with trees and seedlings of species not susceptible to mountain pine beetle. A physical disturbance such as fire that can eliminate competing species may be required for the upward expansion of lodgepole pine's leading range margin. For tree species such as lodgepole pine that are affected by periodic insect outbreaks, ranges may shrink in the near term if this disturbance–climate interaction continues to drive range retractions that outpace range expansions.

Introduction

Many species are expected to shift their geographic ranges in response to climate change. Much of the research aimed at documenting and forecasting these range shifts assumes that migrations will occur gradually and continuously, but this may not be true for all taxa (Chapin et al. 2004). Many tree species are not migrating at a rate consistent with climate change (Renwick & Rocca 2015), resulting in vegetation communities where species are not in equilibrium with the current climate (Svenning & Sandel 2013). Inertia is common in forests because trees are long-lived and can develop extensive root systems that allow them to tolerate rising temperatures and persist in environments that are no longer suitable for seedlings (Davis 1986). This creates a competitive environment that can delay the establishment of species better suited to the current climate (Urban et al. 2012). A closed canopy can also contribute to inertia in forest composition by moderating temperature in the understorey (Chen et al. 1993). Understanding what conditions are necessary to overcome migration lags and facilitate range shifts is a critical step in forecasting future tree distributions.

Disturbance events that cause widespread mortality of overstorey trees could potentially accelerate range shifts by killing persistent trees and reducing competition so that species better adapted to the current climate are able to establish (Overpeck et al. 1990; Turner 2010). Previous work on disturbance impacts at the leading edge of several boreal tree species distributions has demonstrated that fire may initiate northward migration (Landhäusser & Wein 1993; Johnstone & Chapin 2003). Relatively little research, however, has examined whether biological disturbances such as insects and pathogens can also facilitate migration. These are similar to physical disturbances such as fire, in that they often cause widespread mortality of mature trees, resulting in a pulse of new recruitment. When insect outbreaks kill host trees, the effective water supply, available N and understorey light penetration may all increase, creating more favourable conditions for trees and seedlings potentially better adapted to the current climate (Edburg et al. 2012). The increased light penetration associated with canopy loss can also increase the ground-level temperature (von Arx et al. 2012), which might be expected to amplify the effects of broad-scale temperature increases associated with climate change.

The impact of biological disturbances on range margins, however, may differ from that of physical disturbances. Because biological disturbance agents often target specific species, the boundary of the disturbance can be defined as the range of the target species. This means that, unlike a physical disturbance such as fire, biological disturbances are unlikely to enhance recruitment potential beyond the

leading edge of a target species' distribution in cases where other dominant tree species are not susceptible to the disturbance agent. Impacts to soils, nutrient availability and understorey vegetation are also typically more modest following biological disturbances compared to these impacts following physical disturbances such as fire.

Here, we investigate the potential for biological disturbances to facilitate altitudinal range shifts by examining the response of lodgepole pine ecotones to the combined effects of mountain pine beetle disturbance and a recent warm period. Insect outbreaks are expected to increase in frequency and severity as a consequence of climate change (Overpeck et al. 1990; Raffa et al. 2008), and could have a large impact on tree species range margins. Several recent studies have found that mountain pine beetle disturbance caused increases in seedling recruitment and shifts in forest composition throughout the core of *P. contorta's* range (Sibold et al. 2007; Collins et al. 2011; Dhar & Hawkins 2011; Diskin et al. 2011; Pelz & Smith 2012), but the impact of this disturbance on range margins is still largely unknown.

A shift in the trailing edge of lodgepole pine's distribution (i.e. a range retreat) would be driven by mortality, and thus characterized by the death of existing canopy trees in the absence of sufficient seedling recruitment to replace them. In contrast, a shift in the leading edge of lodgepole pine's distribution (i.e. a range expansion) would be driven by new recruitment, and thus characterized by an increase in seedling densities at and beyond the existing range margin.

We hypothesized that: (1) at the trailing edge (lower range margin) of lodgepole pine's distribution, mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) would initiate a range *retreat* by killing mature trees in areas no longer suitable for recruitment, whereas (2) at the leading edge (upper range margin) MPB would *not* initiate a range *expansion*, because the disturbance is confined to the existing range of lodgepole pine. While a range expansion at the leading edge could potentially be accelerated by MPB if the tree species located beyond lodgepole pine's range margin were also impacted by the beetle, we were unable to examine that potential in our study area. This work will enhance our understanding of how biological disturbances affect the timing of expected climate-driven distribution shifts.

Methods

Study area

Study sites are located in Rocky Mountain National Park, Colorado, USA (Fig. 1). Vegetation in this region varies with elevation in relation to temperature and precipitation gradients (Peet 1981). Lower elevations are dominated by

ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) woodlands, which transition into stands dominated by lodgepole pine (*Pinus contorta*) in the central elevations. Higher elevations that are cooler and wetter are typically dominated by spruce/fir forest (*Picea engelmannii* and *Abies lasiocarpa*), with stands of limber pine (*Pinus flexilis*) occupying the rockiest sites.

Like many mountain systems, the study area has experienced a higher than average rate of climate warming (Pepin 2000). This trend was particularly pronounced throughout the past 20 yr (Fig. 2). Precipitation data taken from the same station showed no significant trend. The observed increase in temperature will consequently result in greater water stress for trees. Three species of pine occurring in our study area (*P. ponderosa*, *P. contorta* and *P. flexilis*) also have been affected by recent MPB outbreaks that killed millions of trees throughout western North America (Wulder et al. 2010; Edburg et al. 2012).

Data collection

In 2012, we resampled nine ecotone transects (Table 1) originally established between 1992 and 1995 to monitor climate change impacts (Stohlgren & Bachand 1997; Stohlgren et al. 1998, 2000). These transects represent four ecotone types: two at lodgepole pine's trailing edge (lower range margin) (Ponderosa–Lodgepole and Douglas-fir–Lodgepole) and two at the leading edge (upper range margin) (Lodgepole–Spruce/Fir and Lodgepole–Limber). We sampled two to three replicate transects for each ecotone type. All transects span the transition zone between a forest stand dominated by lodgepole pine to forest dominated by a different species, and vary in length according to the distance covered by this ecotone.

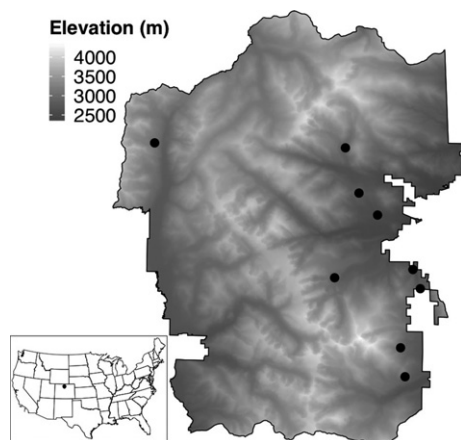


Fig. 1. Map of Rocky Mountain National Park with locations of ecotone transects shown. The inset maps shows the location of Rocky Mountain National Park in Colorado, USA.

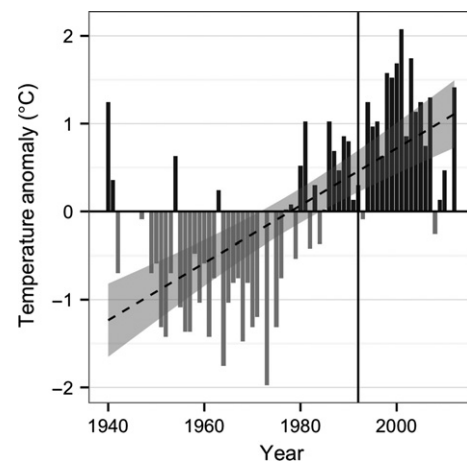


Fig. 2. Mean annual temperature anomaly (deviation from mean) for 1940–2012 at the Grand Lake weather station (053500). The vertical line represents when the ecotone transects were established (initial sampling). The 20-yr period before the initial sampling was cooler than the 20-yr period leading up to the 2012 re-sampling, but still above average for the past 70 yr. The dashed line represents a linear fit for temperature anomaly as a function of year ($P < 0.001$, $R^2 = 0.41$).

Each transect consists of contiguous 20×20 m plots with permanent corner markers. Slope is constant within each transect. Aspect is also constant within transects except at Bear Lake, where elevation is constant and the temperature gradient is due to changes in aspect. When the transects were established, the largest trees in each plot were cored and aged to ensure that the ecotones represent underlying abiotic gradients as opposed to old disturbance boundaries (Stohlgren & Bachand 1997). Stand age is constant within each transect, and varies only minimally between transects (Table 1).

We followed the original sampling protocol to ensure that data were comparable between sampling years. For each tree (≥ 2.5 -cm diameter), we recorded the DBH, species and whether the tree was alive or dead. For dead pine trees, we also determined if mortality was caused by MPB based on the presence of pitch tubes and beetle galleries. We estimated time since mortality using a scale based on the percentage of needles and fine twigs remaining (Keene 1955; Klutsch et al. 2009).

Lodgepole pine can have serotinous cones which are sealed closed by resin, but levels of serotiny often vary across the landscape (Tinker et al. 1994). Because high levels of serotiny could be associated with an abundant seed crop, we assessed serotiny of each lodgepole pine tree (live or dead) using binoculars to examine the cones. Trees were classified into one of four categories: no cones, serotinous ($>90\%$ of cones are serotinous), mixed serotinous ($10\text{--}90\%$ of cones are serotinous), or non-serotinous ($<10\%$ of cones are serotinous).

Table 1. Transects re-sampled in 2012. Total lodgepole pine basal area declined on all trailing edge transects, including one with no MPB disturbance (Aspen Brook). Basal area increased slightly on the undisturbed leading edge transects, but declined where disturbance intensity was high. Average lodgepole pine seedling density in 2012 (seedlings·ha⁻¹) was generally higher on the leading edge (higher elevation) transects.

Ecotone Type	Transect	Stand Age (yr)	Elevation Range (m)	No. Plots	% Change Lodgepole BA	2012 Lodgepole Seedling Density (ha ⁻¹)
Ponderosa–Lodgepole	Deer Ridge	150	2740–2800	14	–82	48
	Upper Beaver	150	2230–2250	9	–94	90
Douglas-fir–Lodgepole	Thunder Mountain	130	2620–2630	6	–39	42
	Aspen Brook	115	2727–2764	6	–4	29
Lodgepole–Spruce/Fir	Bear Lake	110	2922–2922	11	–18	136
	Hitchens's Gulch	130	2960–2990	7	–87	284
Lodgepole–Limber	Wild Basin	140	2980–3080	13	9	42
	Meeker Drainage	120	3000–3050	10	11	195
	Lawn Lake	150	3020–3080	11	20	111

The density of seedlings (<1.37 m in height) was tallied by species for each plot except on the Lodgepole–Spruce/Fir transects, where a subsampling procedure was used in keeping with the original surveys. For these transects, seedlings were sampled in four subplots with a 3-m radius located at the centre of each 10 × 10 m subplot, because seedlings were too dense to accurately measure all within the larger 20 × 20 m plot. Subplot centres were permanently marked, so we are confident that our subsampling procedure captured the same area as when the transects were originally established.

Because seedling mortality can be high in the first year of growth, current-year germinants were not counted in either survey. Transects were re-sampled during the same month as the initial sampling to minimize any potential impacts of variability in seedling mortality across a single growing season. Finally, we updated the original plot elevations using a new GPS unit with much higher accuracy.

Analysis

We analysed changes in tree and seedling density across ecotones separately for trailing edge (lower elevation) and leading edge (upper elevation) ecotones. We fitted linear regression models to assess whether changes in tree density and seedling density within each ecotone type reflect an upslope migration, a response to MPB disturbance or an interaction between the two. Separate models were fitted for trees and seedlings of each species. In all models, the response variable (2012 tree or seedling density) was log-transformed to meet model assumptions.

We were primarily interested in three potential predictor variables: elevation, MPB disturbance severity (total basal area killed, m²·ha⁻¹) and the interaction between elevation and MPB disturbance. A positive coefficient for elevation would indicate an upward shift within a given ecotone type consistent with warming climate. A significant interaction between elevation and disturbance would

indicate that the effect of disturbance depended on the effect of elevation, or *vice versa*. One caveat to this approach is that a strong climate effect might extend beyond the width of the ecotone, such that the entire ecotone transect reflects changes in density. In this case, an elevation effect would not be identified in the model, although qualitative comparisons of densities between the trailing and leading edge ecotones may prove helpful. A positive (or negative) effect for MPB would indicate that sites more heavily impacted by the beetle would have higher (or lower) tree or seedling densities than those less impacted.

Initial density, from the first survey in the 1990s, was included as a fourth predictor in each model. This parameter is not of interest in itself, but including it serves several important purposes. First, it focuses the regression on *changes* in tree and seedling density over time instead of on absolute density. Second, it accounts for variability generated by unmeasured abiotic factors that would not be expected to change rapidly with time, such as edaphic conditions. A further benefit of this model structure is that it allows change in density to vary both additively (based on the intercept) and as a ratio of the original density (based on the regression coefficient).

All predictor variables were standardized by subtracting the mean from each observation and dividing by the SD. Because differences in aspect among transects led to slight differences in the elevation range spanned by each, elevation was standardized separately for each transect. For the Bear Lake transect, we standardized the Beers-transformed aspect (Beers et al. 1966) and used this in place of elevation, which is constant across the transect. Our treatment of elevation means that a positive coefficient for this term is indicative of movement towards cooler areas along the gradient represented by any given ecotone.

The two trailing edge ecotone types were modelled together including a potential ecotone type effect, but the two leading edge ecotone types had to be modelled separately because the Lodgepole–Limber ecotone type did not

have any MPB activity, making type perfectly correlated with disturbance. Model selection was based on Akaike's information criterion corrected for small sample size (AICc; Hurvich & Tsai 1989). We calculated Moran's I statistic for the residuals of all final models and found no evidence of spatial autocorrelation. All analyses were conducted using the R software (R Foundation for Statistical Computing, Vienna, AT). Additional details on model formulation are included in Appendix S1.

Results

Changes in trailing edge ecotones

Lodgepole pine basal area declined across all four trailing edge ecotone transects, including one transect with no evidence of MPB activity (Aspen Brook; Table 1). The largest loss in basal area occurred in pure lodgepole pine plots along these transects, eliminating the steep gradient in lodgepole pine basal area that initially characterized these ecotone types (Stohlgren & Bachand 1997; Stohlgren et al. 1998). Background mortality rates of trees not killed by beetles averaged 8% on trailing edge ecotones (mean basal area $0.48 \text{ m}^2\text{-ha}^{-1}$), and contributed minimally to changes in basal area. Models indicate that shifts in the distribution of lodgepole pine trees across trailing edge ecotones were unrelated to elevation or ecotone type (Table 2). Few saplings were recruited into the tree class ($>1.37\text{-m}$ tall) in the 20 yr following initial sampling (mean 11 ± 3 saplings- ha^{-1}). Predictions from the best model suggest that in the absence of MPB disturbance, no significant decline in tree density would have been expected (Fig. 3).

No lodgepole pine seedlings were observed in the lowest elevation plots on any of these transects (Fig. 4), even where seedlings had been found in the original sampling. The best model for lodgepole pine seedling density reflects this change, suggesting that while seedling density is positively related to MPB disturbance, the effect of

elevation is several times stronger, regardless of ecotone type (Table 2).

Other species present on these ecotones also experienced changes in density and distribution. In the Douglas-fir–Lodgepole ecotone type, the decline in lodgepole pine basal area was partially offset by increases in Douglas-fir basal area across all elevations (25% increase). Douglas-fir seedling densities also increased by 25%; this increase was associated with areas of high MPB disturbance intensity (Appendix S1).

On the Ponderosa–Lodgepole ecotone transects, Ponderosa pine basal area also declined as a result of MPB disturbance, resulting in a large decline in total basal area across the entire ecotone. The distribution of ponderosa seedlings might be expected to shift upward into areas previously dominated by lodgepole pine, but seedlings were actually too rare to model. Douglas-fir was also present on the Ponderosa–Lodgepole ecotone, and this instead became the dominant species in terms of both tree basal area and seedling density. The number of Douglas-fir seedlings responded strongly to MPB disturbance (Appendix S1), more than doubling in this ecotone type.

Changes in leading edge ecotones

Patterns of change at the leading edge lodgepole pine ecotones were more variable and depended on ecotone type. Lodgepole pine basal area declined on the Lodgepole–Spruce/Fir transects where many trees were killed by MPB, but the decline was primarily concentrated at lower end of the ecotone where lodgepole pine dominates the overstorey. The Spruce/Fir ecotone type experienced some of the highest mortality observed, with up to 98% of lodgepole pine basal area killed in some plots. Unlike the trailing edge ecotones, the model for lodgepole pine tree density did not include a term for elevation, and changes in tree density were attributed solely to MPB disturbance (Table 2).

Table 2. Models relating the density of lodgepole pine trees and seedlings to elevation (Elev) and disturbance intensity (MPB) on trailing edge ecotones (modelled together) and the two leading edge ecotone types. Initial density of trees or seedlings (Init) was included in all models to isolate changes over time.

Ecotone	Best Model		Model-Averaged Parameter Estimates (SE)				
	Adj. R^2	P-Value	Intercept	Init	MPB	Elev	Elev x MPB
Trailing Edge							
Trees	0.89	<0.001	4.4 (0.1)	1.8 (0.2)	−0.8 (0.1)	−0.1 (0.2)	0.4 (0.1)
Seedlings	0.49	<0.001	−1.9 (0.8)	2.5 (0.9)	0.5 (0.8)	2.2 (0.9)	–
Lodgepole - Spruce/Fir							
Trees	0.91	<0.001	5.3 (0.1)	1.4 (0.1)	−0.6 (0.1)	–	–
Seedlings	0.5	0.002	−2.0 (1.1)	2.3 (1.1)	3.7 (1.1)	–	–
Lodgepole - Limber							
Trees	0.96	<0.001	6.4 (0.0)	0.9 (0.0)	–	0.0 (0.0)	–
Seedlings	NULL		3.1 (0.7)	0.1 (0.4)	–	–	–

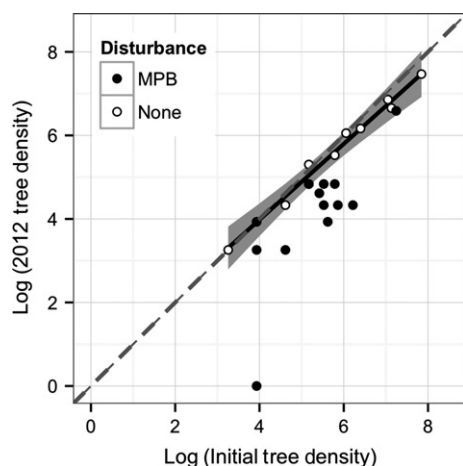


Fig. 3. The 2012 density of lodgepole pine trees on the trailing edge ecotones as a function of initial tree density. The grey dashed line shows a 1:1 relationship (no change). Points represent density measured in plots, with open circles indicating no disturbance while solid circles show plots affected by mountain pine beetle. The solid black line represents the modelled density (95% confidence interval) holding disturbance constant at zero. Little change in lodgepole pine tree density would be expected in the absence of disturbance.

The seedling model for the Lodgepole–Spruce/Fir ecotone type suggests that disturbance was associated with an increase in lodgepole pine seedling recruitment (positive coefficient for disturbance intensity), but patterns of new recruitment showed no relationship to elevation once the effect of disturbance was accounted for (Table 2). The

highest elevation with a lodgepole pine seedling present actually declined slightly on both Lodgepole–Spruce/Fir transects. Lodgepole pine sapling recruitment was low on the Lodgepole–Spruce/Fir ecotone (mean 26 ± 11 saplings·ha⁻¹) compared to the Lodgepole–Limber ecotone (mean 62 ± 9 saplings·ha⁻¹).

The large decline in lodgepole pine basal area on the Lodgepole–Spruce/Fir ecotone resulted in a shift in dominance towards spruce and fir at lower elevations that were previously dominated by lodgepole pine. Disturbance was also associated with increases in the density of spruce and fir seedlings, which are far more abundant than lodgepole pine and together comprise 98.5% of the seedlings in this ecotone type.

On the Lodgepole–Limber ecotone where there was no beetle activity, lodgepole pine basal area increased slightly across the entire elevation gradient. This change was primarily driven by growth of existing trees, although recruitment of new saplings also contributed to the change. Lodgepole pine seedling recruitment was extremely variable and did not change significantly (Fig. 4). The best model for both tree and seedling density included just initial density, suggesting that patterns of change were unrelated to elevation.

Differences between the trailing and leading edge

Demographic trends over the past 20 yr differ somewhat between the trailing and leading edge of lodgepole pine's distribution. The background mortality rate, or percentage

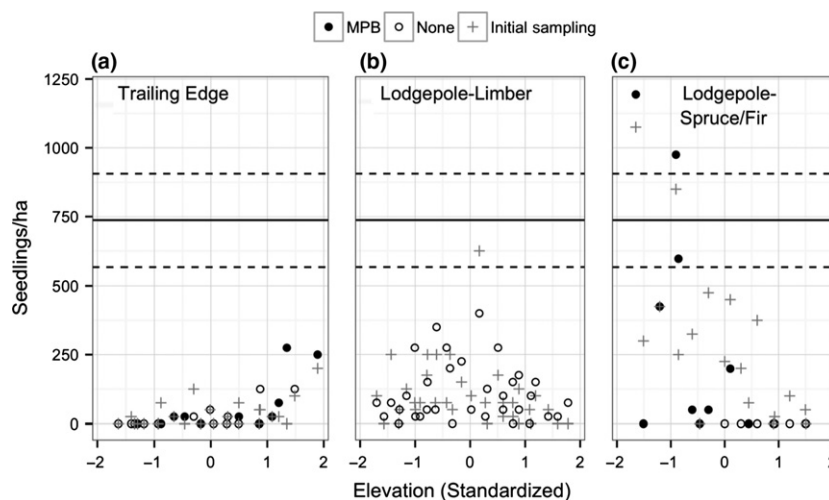


Fig. 4. The relationship between elevation and density of lodgepole pine seedlings in 1992 (crosses) and 2012 (circles). The solid horizontal line indicates the average range-wide density of lodgepole seedlings (\pm SE, dashed lines) from plots throughout Rocky Mountain National Park (Diskin et al. 2011). On the trailing edge ecotone (a), no seedling recruitment was found at the lowest elevations. Despite a positive MPB disturbance effect (Table 2), recruitment was below the range-wide average (Diskin et al. 2011) across the entire trailing edge ecotone. On the Lodgepole–Limber Pine ecotone type (b), changes in seedling density were not related to elevation and do not indicate an upward expansion at the leading edge of lodgepole pine's range. Similarly, on the Lodgepole–Spruce/Fir ecotone type (c), there is no evidence of increased recruitment at higher elevations.

of trees that died due to something other than MPB, was 8% at the trailing edge and 3% at the leading edge, although this difference is not significant (Wilcoxon rank sum test, $P = 0.27$). Sapling recruitment, or the number of new trees >2.5-cm diameter, was significantly lower at the trailing edge (mean 11 saplings·ha⁻¹) compared to the leading edge (mean 47 saplings·ha⁻¹, Wilcoxon rank sum test, $P = 0.0001$). Lodgepole pine seedling densities in 2012 were also much lower at the trailing edge (mean 42 seedlings·ha⁻¹) compared to the leading edge (mean 139 seedlings·ha⁻¹, Wilcoxon rank sum test, $P = 0.01$). Even on the three leading edge transects that were undisturbed, seedling densities (mean 91 seedlings·ha⁻¹) were more than twice those found on transects at lodgepole pine's trailing range margin.

Besides climate, none of the underlying factors that might affect these observed differences in lodgepole pine demographic patterns differed greatly between trailing vs leading edge ecotones. The average stand age was 136 yr for trailing edge ecotones, compared to 130 yr for leading edge ecotones. Both range margins were attacked by MPB during a similar time frame; mean time since mortality for trees was 4 yr at both range margins. Serotiny was somewhat higher on the trailing edge ecotones (38% compared to 22%), but this difference was not statistically significant (Wilcoxon rank sum test, $P = 0.82$). Differences in percentage serotiny at the plot level showed no relationship to differences in seedling density; a linear model fitted to the full set of plot data ($n = 86$) with percentage serotiny predicting log-transformed seedling density was not significant ($P = 0.399$, $R^2 = -0.004$).

Discussion

The differences in lodgepole pine seedling and sapling recruitment at the trailing vs leading edge of lodgepole pine's distribution are consistent with a modest climate warming effect, even on undisturbed transects. Both trailing edge ecotone types exhibited low lodgepole pine recruitment and growth, as would be expected in a warming climate and in the absence of fire. This was true even for the one undisturbed transect (Aspen Brook). Seedling densities were well below the range-wide average (Diskin et al. 2011) across all trailing edge ecotones. The leading edge ecotone types had nearly twice as many seedlings and saplings as trailing edge ecotones, suggesting that conditions are more favourable for recruitment at these cooler sites.

Differences in stand age and serotiny levels represent two potentially confounding factors, but likely did not contribute to the observed differences in mortality and recruitment at trailing vs leading edge ecotones. Stand age was constant within each transect, and differences in age

between transects were minor relative to the temporal scale of post-fire forest dynamics. Serotiny levels did not vary significantly between trailing vs. leading edge ecotones, and did not affect patterns of seedling recruitment at the local (plot) level where one would expect it to have the most impact. Perhaps seed availability does not limit seedling recruitment because most plots had at least some trees that were non-serotinous and could provide a continuous seed source. Furthermore, previous work in our study area found that by 4 yr post-MPB mortality, 36% of trees with serotinous cones show evidence of cones opening and seeds being released (Rocca, unpubl data). Seeds from serotinous cones have been shown to be viable for at least 3 yr and possibly longer after beetle attack (Aoki et al. 2011). Dead serotinous trees would therefore provide a massive source of seeds accumulated during the tree's lifetime, resulting in a potentially larger lodgepole pine seed bank at the lower range margin. Non-serotinous trees, which were more common at the leading edge range margin, represent a single year of seed production. The fact that we saw more lodgepole pine seedlings at the leading edge range margin, where serotiny was lower, suggests that climate is likely more limiting than propagule pressure.

Changes within individual ecotones help elucidate the interaction between disturbance and climate in driving tree species range shifts. We expected that MPB disturbance would play an important role in initiating a range shift at the trailing edge of lodgepole pine's distribution by killing mature trees in areas no longer suitable for recruitment, and the data support our hypothesis. On transects where MPB damage was minimal, the persistence of many lodgepole pine trees suggests that the trailing edge is experiencing inertia and will change more slowly in the absence of disturbance. In contrast, the large decline in basal area across ecotones affected by the beetle outbreak is consistent with the gradual erosion of trailing range margins expected for tree species (Jump et al. 2009). The low rate of lodgepole pine sapling recruitment on these ecotones and lack of low-elevation seedling recruitment suggest that recent climatic conditions were unsuitable for regeneration.

The data also support our hypothesis that because MPB is host-specific, this disturbance type will not be sufficient to overcome inertia and facilitate a range expansion at the leading edge of lodgepole pine's distribution. We found no evidence of climate-induced expansion on either the disturbed or undisturbed transects. On the Lodgepole–Limber ecotone transects where disturbance was lacking, basal area and seedling density did not change significantly, and there was no evidence of upward migration despite the recent warming trend. Similarly, the elevational pattern of seedlings on the Lodgepole–Spruce/Fir ecotone type did not change, despite high levels of disturbance. On this

ecotone type, the presence of two strong competitors that were not affected by the MPB outbreak (Engelmann spruce and subalpine fir) likely hindered establishment of shade-intolerant lodgepole seedlings at higher elevations. This is consistent with results from a similar study in the Swiss Alps, where competition rather than climate was found to limit upward expansion of the *Pinus sylvestris* range margin (Hättenschwiler & Körner 1995).

Seedlings of both spruce and fir increased in density as a consequence of the MPB outbreak, and will continue to compete with lodgepole pine seedlings in the absence of a physical disturbance such as fire. Lodgepole pine can be successional to spruce and fir, and the current patterns of seedling recruitment suggest that species composition will change substantially on these sites, potentially resulting in a contraction of the area where lodgepole is currently dominant. Furthermore, the reduction in future seed production where mature lodgepole pines were killed by MPB may slow or delay range expansion even if a future fire reduces competition and creates physical conditions more favourable for lodgepole recruitment.

A similar pattern was observed at the leading edge of ponderosa pine's distribution, even where disturbance occurred above its current distribution in areas dominated by lodgepole pine. Seedling recruitment was extremely low, and did not show any signs of an upward shift in distribution as might be expected due to the recent rise in temperatures. For species such as lodgepole and ponderosa pine that are targeted by biological disturbance agents, the difference in impact between trailing vs leading edges could mean an overall range retraction in the absence of fire.

In contrast, physical disturbances such as fire have been shown to initiate periods of rapid range expansion for disturbance-dependent species such as lodgepole pine and quaking aspen (Landhäusser & Wein 1993; Johnstone & Chapin 2003; Landhäusser et al. 2010). This is likely due in part to the recruitment requirements of these species, which often require both soil disturbance and abundant light for successful seedling establishment (Astrup et al. 2008; Landhäusser et al. 2010). In contrast, Douglas-fir, Engelmann spruce and subalpine fir all responded to the MPB outbreak with increased recruitment in previously lodgepole-dominated stands. Biological disturbances may be more likely to initiate range expansion for species such as these that do not require soil disturbance and are more shade tolerant.

Our results suggest that the rate and timing of range expansion is likely to depend on complex patterns of both biological and physical disturbances and vary in relation to the life-history traits of individual species. Inertia is evident in the slow rate of change across lodgepole pine ecotones, but the long-term vegetation trajectory of our sample sites

remains uncertain. Subsequent disturbances such as fire coupled with the potential for non-linear responses to both regional climate change and altered microclimate may drive more dramatic changes in the future.

Conclusions

Mountain pine beetle disturbance killed many mature lodgepole pine trees across both of its range margins. This disturbance initiated an upward shift in the trailing edge of lodgepole pine's distribution and a subsequent shift towards dominance by Douglas-fir, which is a non-target species. The impact of disturbance was different at the leading edge of lodgepole pine's distribution, which did not advance in elevation as would be expected with a warming climate. For target species like lodgepole pine, biological disturbance can accelerate range retreat, but may actually slow range expansion, resulting in an overall decrease in the area dominated by that species. This is particularly true of species such as lodgepole and ponderosa pine, which experience episodic recruitment often requiring a physical disturbance such as fire, and are consequently unlikely to see an immediate boost in recruitment.

Acknowledgements

N.T. Hobbs and J. Sibold provided helpful comments during the development of this manuscript. We thank the Rocky Mountain National Park staff, especially J. Visty, J. Connor and P. McLaughlin, for helping to facilitate this research. This project was financially supported by the National Park Service, Rocky Mountain Nature Association and a McIntire–Stennis award to Colorado State University.

References

- Aoki, C.F., Romme, W.H. & Rocca, M.E. 2011. Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. *The American Midland Naturalist* 165: 446–451.
- von Arx, G., Dobbertin, M. & Rebetez, M. 2012. Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agricultural and Forest Meteorology* 166–167: 144–155.
- Astrup, R., Coates, K. & Hall, E. 2008. Recruitment limitation in forests: lessons from an unprecedented mountain pine beetle epidemic. *Forest Ecology and Management* 256: 1743–1750.
- Beers, T.W., Dress, P.E. & Wensel, L.C. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64: 691–692.
- Chapin, F., Callaghan, T., Bergeron, Y., Fukuda, M., Johnstone, J., Juday, G. & Zimov, S. 2004. Global change and the boreal forest: thresholds, shifting states or gradual change? *Ambio* 33: 361–365.

- Chen, J., Franklin, J.F. & Spies, T.A. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63: 219–237.
- Collins, B.J., Rhoades, C.C., Hubbard, R.M. & Battaglia, M.A. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *Forest Ecology and Management* 261: 2168–2175.
- Davis, M. 1986. Climatic instability, time lags, and community disequilibrium. In: Diamond, J. & Case, T.J. (eds.) *Community ecology*, pp. 269–284. Harper & Row, New York, NY, US.
- Dhar, A. & Hawkins, C.D.B. 2011. Regeneration and growth following mountain pine beetle attack: a synthesis of knowledge. *BC Journal of Ecosystems and Management* 12: 1–16.
- Diskin, M., Rocca, M.E., Nelson, K.N., Aoki, C.F. & Romme, W.H. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 41: 782–792.
- Edburg, S.L., Hicke, J.A., Brooks, P.D., Pendall, E.G., Ewers, B.E., Norton, U., Gochis, D., Gutmann, E.D. & Meddens, A.J. 2012. Cascading impacts of bark beetle-caused tree mortality on coupled biogeophysical and biogeochemical processes. *Frontiers in Ecology and the Environment* 10: 416–424.
- Hättenschwiler, S. & Körner, C. 1995. Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. *Journal of Vegetation Science* 6: 357–368.
- Hurvich, C.M. & Tsai, C.L. 1989. Regression and time series model selection in small samples. *Biometrika* 76: 297–307.
- Johnstone, J.F. & Chapin, F.S. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. *Global Change Biology* 9: 1401–1409.
- Jump, A.S., Mátyás, C. & Peñuelas, J. 2009. The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution* 24: 694–701.
- Keene, F. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. *Journal of Forestry* 53: 720.
- Klutsch, J., Negron, J.F., Costello, S.L., Rhoades, C.C., West, D.R., Popp, J. & Caissie, R. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management* 258: 641–649.
- Landhäusser, S. & Wein, R.W. 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: climate-change-vegetation-response hypotheses. *Journal of Ecology* 81: 665–672.
- Landhäusser, S.M., Deshaies, D. & Liefers, V.J. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. *Journal of Biogeography* 37: 68–76.
- Overpeck, J., Rind, D. & Goldberg, R. 1990. Climate-induced changes in forest disturbance and vegetation. *Nature* 343: 51–53.
- Peet, R. 1981. Forest vegetation of the Colorado front range. *Vegetatio* 45: 3–75.
- Pelz, K.A. & Smith, F.W. 2012. Thirty year change in lodgepole and lodgepole/mixed conifer forest structure following 1980s mountain pine beetle outbreak in western Colorado, USA. *Forest Ecology and Management* 280: 93–102.
- Pepin, N. 2000. Twentieth-century change in the climate record for the Front Range, Colorado, USA. *Arctic, Antarctic, and Alpine Research* 32: 135–146.
- Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G. & Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58: 501.
- Renwick, K.M. & Rocca, M.E. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. *Global Ecology and Biogeography* 24: 44–51.
- Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E. & Scott, J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. *Ecological Applications* 17: 1638–1655.
- Stohlgren, T. & Bachand, R. 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology* 78: 632–641.
- Stohlgren, T., Bachand, R., Onami, Y. & Binkley, D. 1998. Species–environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology* 135: 215–228.
- Stohlgren, T., Owen, A. & Lee, M. 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. *Biodiversity and Conservation* 9: 65–86.
- Svenning, J.-C. & Sandel, B. 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* 100: 1266–1286.
- Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H. & Turner, M.G. 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. *Canadian Journal of Forest Research* 24: 897–903.
- Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849.
- Urban, M.C., Tewksbury, J.J. & Sheldon, K.S. 2012. On a collision course: competition and dispersal differences create non-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society of London, Series B* 279: 2072–2080.
- Wulder, M., Ortlepp, S., White, J., Coops, N. & Nelson, T. 2010. A provincial and regional assessment of the mountain pine beetle epidemic in British Columbia: 1999–2008. *Journal of Environmental Informatics* 15: 1–13.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details on model selection.