DISSERTATION

THE INTERACTIVE EFFECTS OF CLIMATE AND DISTURBANCE ON TREE SPECIES DISTRIBUTIONS

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ABSTRACT

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Climate change is expected to alter species distributions as ranges shift to track favorable temperature and precipitation regimes. Range shifts are already being observed across a wide range of taxa, but many species are not keeping pace with the rate of recent climate warming. This is particularly true for tree species, which often experience significant migration lags due to a variety of non-climatic factors that can hinder range expansion or delay range retreats. Because many other species depend on trees for food or habitat, migration lags in tree species may have cascading impacts on a wide range of taxa that would otherwise face few barriers to migration.

The importance of understanding how climate change will affect tree species distributions prompted several related research questions: 1) What factors contribute to the observed lags in tree species distributions? 2) Can biotic disturbances accelerate climate-driven shifts at the range margins of trees species? 3) How important is climate in determining landscape-scale vegetation patterns? My dissertation research addresses these questions using an integrated approach that draws on exiting literature, field sampling, and statistical models to inform our understanding of potential climate change impacts on tree species distributions.

Observations of contemporary tree species migrations occurring throughout the world suggest that migration lags are pervasive and can be caused by a wide variety of abiotic factors and biotic processes. Tree migrations are likely to occur episodically when migration constrains

are overcome, resulting in temporal variability in the migration rate. Physical disturbances such as fire can reduce competition and initiate periods of rapid change, but the effects of biological disturbances such as insect outbreaks are more nuanced. A case study examining the impacts of climate change and mountain pine beetle (*Dendroctonus ponderosae*) disturbance at lodgepole pine (*Pinus contorta*) range margins suggests that while biological disturbances may accelerate a range retreat by killing mature trees, they do not initiate range expansion for the target species. The impact of non-climatic constraints on current tree species distributions was also evident at the landscape scale, and climatic variables alone proved insufficient to explain patterns of co-occurrence among tree species. Together, these findings suggest that Rocky Mountain tree species will not uniformly shift upward in elevation as the climate continues to warm. Range shifts will likely be episodic and idiosyncratic, and forecasts based solely on climate data may over-estimate the rate and under-estimate the landscape-scale heterogeneity of potential distribution changes.

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1 Introduction

The ongoing impacts of climate change have been noted with alarm by many scientists (Parmesan & Yohe, 2003), and are likely to intensify throughout the coming century (IPCC, 2007). Understanding how ecological communities will respond is of critical importance if we are to mitigate negative impacts on biodiversity and adapt management practices to better suit a changing world. One common expectation is that species distributions will shift towards cooler latitudes and altitudes as the location of their climate envelope shifts. Bioclimatic niche models are commonly used to forecast how distributions are likely to shift in the future and aid in conservation planning (Iverson & Prasad, 2002).

Empirical research quantifying ongoing range shifts, however, suggest that many species are migrating more slowly than expected based on the rate of climate change, causing distribution shifts to differ from model predictions (Zhu *et al.*, 2011). This is particularly true for tree species distributions, which often experience inertia as a result of their longevity and sedentary nature (Lenoir & Svenning, 2014). A better understanding of how non-climatic factors shape the realized niche and constrain migrations is required if we are to accurately predict how tree ranges may shift as a consequence of climate change.

Like many high-elevation ecosystems, Rocky Mountain forests have experienced particularly high rates of warming throughout the past century (Pepin, 2000). Changes in temperature and precipitation regimes have been coupled with widespread outbreaks of bark beetles, which have killed millions of trees and affected a large percentage of the forested

landscape (Bentz *et al.*, 2010). Insect outbreaks are expected to become more common and severe as a result of climate change (Raffa *et al.*, 2008), and the interaction between this disturbance and the direct effects of climate is likely to have a profound impact on tree communities. Other abiotic and biotic factors may also be important in shaping future tree communities in this region, but the relative importance of these non-climatic factors in controlling range dynamics is still poorly understood.

This work explores how non-climatic factors can complicate the impacts of climate change on tree species distributions. Chapter one takes a global perspective and reviews evidence of migration lag in contemporary tree migrations, with a particular emphasis on migration constrains and the role of disturbance in facilitating migration. Chapter two is a case study that uses field data to examine how climate change may interact with mountain pine beetle disturbance to accelerate range shifts in Rocky Mountain tree species. Chapter three expands on this study by modelling the landscape-scale impacts of climate on tree species distributions using a joint species distribution modeling framework, which also tests for unmeasured climactic or biological factors that contribute to heterogeneity in vegetation patterns. Together, these different components make an important contribution to our understanding of the factors that control tree species distributions and affect their ability to track climatic changes.

2 Temporal context affects the observed rate of climate-driven range shifts in tree species

2.1 Introduction

Species are expected to shift their geographic ranges in response to a rapidly changing global climate (Pearson & Dawson, 2003; VanDerWal *et al.*, 2012). Monitoring of ongoing range shifts, however, suggests that migration rates often lag behind the rate of climate change (Bertrand *et al.*, 2011a; Bedford *et al.*, 2012; Devictor *et al.*, 2012). Tree species may be particularly vulnerable to migration lags because they are sessile, long-lived, and often slow to mature (Davis, 1986; Lenoir & Svenning, 2013). They are also relatively well-studied, and examples of contemporary tree migrations provide important insight into spatiotemporal controls on migration rate.

Trees are critical components of many ecosystems, and lags in the migration response can lead to changes in the composition and structure of forests that may have far-reaching implications for associated species and ecosystem processes (Solomon & Kirilenko, 1997; Johnstone & Chapin, 2003; Bonan, 2008). Paleoecological evidence suggests that many past tree migrations occurred more slowly than climatic changes, resulting in time lags before species were able to fully occupy newly suitable areas (Davis, 1989). Given the high rate of anthropogenic climate change (Jackson *et al.*, 2009a) coupled with widespread habitat fragmentation (Schwartz, 1993), migration lags are expected to be even more prevalent in the future and could ultimately lead to the extirpation of some species (Davis, 1989; Aitken *et al.*, 2008).

In this review, we synthesize evidence of contemporary tree migrations and examine why so few range shifts appear to track climatic changes. Several factors are commonly thought to constrain migration rates; we highlight examples of these but emphasize temporal controls that drive episodic migration patterns and create variability in migration rates. The importance of temporal context in understanding tree migrations suggests new research priorities and has important implications for forecasting and facilitating future range shifts.

2.2 Rate of contemporary tree migrations lags temperature change

Recent range shifts linked to anthropogenic climate change have been observed for tree species, but in contrast to many other taxa (Chen *et al.*, 2011), few tree species seem to be keeping pace with the rate of climate change (Appendix S1 in Supporting Information). Among studies that quantified altitudinal shifts in tree species distributions, only about half of the species studied show evidence of range shifts (43% of species shifted at the trailing edge, 45% at the leading edge, and 53% at the distribution center) (Appendix S1). Fewer than 22% of species have shifted far enough to keep pace with climatic changes, however (Appendix S1). In a study comparing adult and seedling distributions of tree species in France, the average shift in optimum elevation (69 m) was only half that expected based on temperature trends (Lenoir *et al.*, 2009). Bodin et al. (2013) found that the average migration rate of forest plants (12.6m/decade) was seven times slower than the rate of climate change, and only 2 out of 31 tree species studied were migrating fast enough to keep pace with temperature changes.

Latitudinal tree migrations have also been documented, though less research has been devoted to changes in this dimension of species distributions (Jump *et al.*, 2009). Studies

quantifying altitudinal range shifts found that on average, 23% of species showed evidence of advancing towards cooler latitudes (leading-edge shift), while shifts in the distribution center were observed 29% of the time (Appendix S1). A greater number of species (84%) showed evidence of trailing-edge range shifts, suggesting a high potential for overall range contractions (Zhu *et al.*, 2011). The greater distance required for latitudinal vs. altitudinal range shifts creates a higher potential for migration lags in dispersal-limited species such as many trees (Jump *et al.*, 2009), and the lower number of range shifts observed at the center (29% vs. 53%) and leading edge (23% vs. 45%, Appendix S1) supports this expectation.

Modern tree ranges are largely shifting more slowly than the ranges of herbaceous species with shorter generation times. In a study calculating changes in plant distributions over an 80-year period in the Caledonian Mountains, neither of the tree species considered shifted significantly up, in contrast to a general trend of upward migration averaging 41.3 m for all plant species (Felde *et al.*, 2012). Research documenting range shifts of Arizona plants over a nearly 50-year period found that 56% of all plants shifted their lower boundary up, but only 25% of tree species (Brusca *et al.*, 2013). A similar pattern was observed by Lenoir *et al.* (2008), who found that herbaceous species exhibiting faster population turnover shifted upward significantly farther than woody species, for which there was no consistent trend of upward migration.

2.3 Possible explanations for low migration rates

2.3.1 Spatial constraints

Dispersal limitation is perhaps the best-studied migration constraint, and is often evoked to explain migration lags (Svenning & Skov, 2004; Normand *et al.*, 2011). Leading-edge migrations

are driven by new recruitment that occurs beyond the established range margin, and so depend on successful seed production, dispersal, establishment, and survival. Trees are slow to reach reproductive maturity (Petit & Hampe, 2006), and seeds of many species are typically dispersed close to the parent plant (Clark *et al.*, 2001). Sparse populations at the leading edge of a species' range can limit migration potential as a result of reduced propagule pressure (Clark *et al.*, 2001; Iverson *et al.*, 2004).

Geographic barriers exacerbate dispersal limitation for species that lack mechanisms for long-distance dispersal (Davis *et al.*, 1986). Lake Michigan, for example, caused a 1000-year lag in the migration of *Fagus grandifolia* before it eventually reached the far shore via long-distance dispersal (Davis *et al.*, 1986). Simulation models used to investigate how the Brooks Range in Alaska may impact northward tree migrations in response to anthropogenic climate change indicate that a time lag greater than 1000 years is likely before forests reach the northern slope (Rupp *et al.*, 2001). Migrations can also be halted by a lack of suitable habitat, as was observed in the Montseny Mountains of Spain where *Fagus sylvatica* migrated upward until it reached the peak and could go no farther (Peñuelas & Boada, 2003). Habitat availability is increasingly limited by land conversion, and human-modified landscapes create new, artificial barriers that will further constrain modern tree migrations (Honnay *et al.*, 2002).

2.3.2 Climatic niche constraints

The climatic niche can be defined via a complex combination of variables that may change in different directions or at different rates (VanDerWal *et al.*, 2012). This can cause migration rates to differ from the rate of change in average temperature, which is frequently used as a

benchmark. A large study of California plants, for example, suggests that many species distributions track water balance more closely than temperature or precipitation alone (Crimmins *et al.*, 2011). For some high-altitude plants, changes in the duration or spatial patterns of snowpack may explain observed range shifts (Felde *et al.*, 2012). Seasonal means may also be important for some species, with both summer and winter temperatures influencing growth and survival of trees at their upper range margin (Kullman & Öberg, 2009).

The focus on averages of climate variables is also problematic because the processes of mortality and recruitment that drive tree migrations are often more sensitive to climatic extremes (van Mantgem & Stephenson, 2007; Jackson *et al.*, 2009a). Long-lived trees can persist despite rising temperatures, but extremes of temperature or precipitation may cause periods of high mortality that drive rapid range retreats (Allen *et al.*, 2010). A 1950s drought in northern New Mexico, for example, killed many *Pinus ponderosa* near its lower range margin and caused the woodland-forest ecotone to shift two kilometers in under five years (Allen & Breshears, 1998).

Trailing-edge migration lags can also arise where spatial variability in climate creates microrefugia that allow small populations of trees to persist in areas beyond the core of their range (Dobrowski, 2011). Estimates of climate change velocity based on coarse-resolution climate data can miss such refugia, particularly in mountainous terrain where the high degree of topographic complexity creates fine-scale variability in climatic conditions (Lenoir *et al.*, 2013). A further mismatch in estimates of climate change velocity and actual changes can occur in forest ecosystems where canopy cover moderates ground-level temperature, buffering species from climatic extremes (Chen *et al.*, 1993).

2.3.3 Non-climatic niche constraints

While climate is an important component of the fundamental niche for plants, non-climatic factors such as edaphic constraints and biotic interactions impose additional filters that may prevent a species from occupying all areas that are suitable climatically (Pearson & Dawson, 2003). Some apparent migration lags may consequently reflect range limits that are not associated with climate or where the effect of climate is mediated by other factors (Bertrand *et al.*, 2012; Corlett & Westcott, 2013). Many treelines, for example, are controlled by topography or soil conditions and are therefore unlikely to advance as a consequence of rising temperatures (Holtmeier & Broll, 2005, 2007). The 500-1500 year time lag in *Betula* migration following deglaciation has similarly been attributed to inadequate soil development that delayed establishment (Pennington, 1986).

Biotic interactions can also affect the geographic distribution of a species (Stanton-Geddes *et al.*, 2012; HilleRisLambers *et al.*, 2013), and their potential to slow or inhibit the range expansion of plant species has been the subject of several recent reviews (Van der Putten, 2012; Corlett & Westcott, 2013; HilleRisLambers *et al.*, 2013; Svenning *et al.*, 2014). At the leading edge of species migrations, positive interactions with mutualist pollinators and dispersers may be required for reproduction and dispersal, while negative interactions such as competition and herbivory can reduce establishment and population growth rates (Svenning & Sandel, 2013; Svenning *et al.*, 2014). The trailing (lower elevation/latitude) edge of species distributions can also depend on non-climatic factors, and climate-mediated shifts in competitive interactions may even drive downward shifts for some plant species (Lenoir *et al.*, 2010). Climate change will likely have divergent impacts on different species or trophic levels,

which may disrupt biotic interactions in ways that alter community composition and affect migration potential (Van der Putten *et al.*, 2010; Van der Putten, 2012).

Evidence of recent tree migrations further supports the importance of biotic interactions in controlling the range limits of plant species. Competition for light appears to be the primary limiting factor at the upper range margin of *Pinus sylvestris*, which has not changed despite planting experiments that indicate recruitment is possible at higher elevations (Hättenschwiler & Körner, 1995). In the temperate-boreal forest ecotone, the northward migration of shade-intolerant temperate species occurs primarily in treefall gaps that reduce competition for light and space (Leithead *et al.*, 2010, 2012). Competition with grass and shrubs can inhibit treeline expansion into alpine meadows that are otherwise suitable climatically (Holtmeier & Broll, 2007).

Herbivory can also cause migration lags by reducing the growth and survival of new seedlings (Van der Putten *et al.*, 2010). Moose herbivory prevents range expansion of *Populus tremula* in Sweden, where the leading edge remained stable over a 30-year period despite high levels of growth and recruitment within the current range boundary (Van Bogaert *et al.*, 2009). The upper range margin of *Betula pubescens* in northern Sweden is similarly constrained by a combination of insect defoliators and reindeer herbivory (Van Bogaert *et al.*, 2011). Because climate change can alter biotic interactions through differential impacts on trees and their consumers, future impacts of herbivory on migration potential are difficult to predict (Van der Putten *et al.*, 2010).

For tree species, factors contributing to the realized niche can vary with life stage (Stohlgren *et al.*, 1998; Bertrand *et al.*, 2011b). The regeneration niche, which represents the

environmental conditions within which a species can successfully reproduce (Grubb, 1977), is important in determining the rate and timing of range expansion. Species that depend on disturbances to create conditions suitable for recruitment, for example, will experience migration lags between disturbance events (Brubaker, 1986). This explains patterns of range expansion at the northern range limit of *Pinus contorta*, where high post-fire seedling densities indicate that climate is not limiting and migration is instead slowed by disturbance-dependent recruitment (Johnstone & Chapin, 2003). A similar pattern was observed in the Canadian arctic, where *Populus balsamifera* and *Betula papyrifera* migrated northward into previously treeless tundra following a severe fire that created more suitable seedbeds (Landhäusser & Wein, 1993).

2.3.4 Temporal variability in migration rates

While the migration constraints discussed above can delay tree migrations, this delay is often temporary. Some of the most rapid range shifts reported have followed periods of relative range stability (Allen & Breshears, 1998; Landhäusser *et al.*, 2010); these demonstrate a high potential for episodic distribution shifts that occur abruptly once barriers are removed. Spatial migration constraints can be overcome when a rare instance of long-distance dispersal establishes an outlier population that provides a seed source for further range expansion (Neilson *et al.*, 2005). Disturbances such as fire and insect outbreaks can facilitate migration by reducing competition or creating soil conditions that favor recruitment of a given species beyond its upper range margin (Landhäusser & Wein, 1993; Landhäusser *et al.*, 2010). A crash in herbivore populations that allows a period of increased seedling recruitment may similarly

allow range expansion for tree species constrained by intensive browsing (Van Bogaert *et al.*, 2011).

Climate variability can also cause an episodic migration pattern for species where seedling establishment occurs infrequently in response to rare climatic conditions. Cyclical precipitation anomalies driven by the El Niño–Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), for example, are commonly linked to temporal patterns of tree mortality and recruitment (Swetnam & Betancourt, 1998; Brown & Wu, 2005). Climatic fluctuations such as these can have a bigger effect at range edges where species are at the margin of their climatic tolerance (Villalba & Veblen, 1998). *Pinus edulis* migration patterns over the past millennium demonstrate the importance of climatic variability; range expansion occurred episodically during particularly wet decades but was delayed by an extended drought (Gray *et al.*, 2006). At the forest-steppe ecotone in northern Patagonia, decadal-scale wet periods facilitated establishment of *Austrocedrus chilensis* seedlings (Villalba & Veblen, 1998) and may be necessary for range expansion.

Range retractions can also occur episodically. Time lags at the trailing edge of tree distributions can occur where long-lived trees that have developed deep root systems survive despite rising temperatures that prevent establishment of more drought-sensitive seedlings (Brubaker, 1986). A severe drought or disturbance that causes high mortality of mature trees can initiate a rapid range retraction (Allen & Breshears, 1998). Climatic extremes are expected to become more common as a result of climate change (Easterling *et al.*, 2000), as are disturbances such as fire and insect outbreaks that can cause widespread tree mortality

(Overpeck *et al.*, 1990). This suggests an increased likelihood of episodic tree migrations at both range margins.

Because range shifts will occur episodically for many tree species, the migration *rate* will not be constant through time. Calculations of short-term migration rate consequently depend on the time period considered and whether or not this captures an episodic shift (Fig. 1). This complicates attempts to determine if a given species is experiencing a migration lag or if an observed lag is likely to persist in the future.

2.4 Priorities for Future Research

Most of the research on contemporary tree migrations has focused on detecting and quantifying range shifts. To better understand and forecast how species distributions will change in the future, new research should instead emphasize constraints on tree migrations and conditions that enable species to overcome these constraints. We still know little about

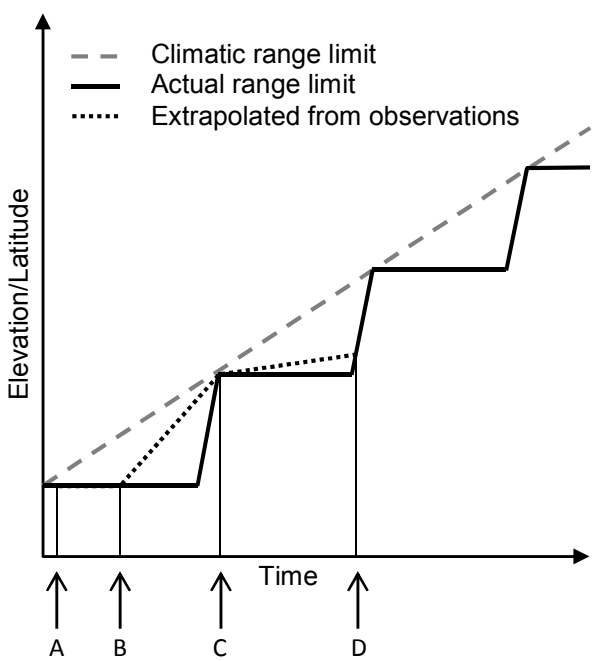

Figure 2-1 Schematic diagram of the temporal relationships between climate and range shifts for a typical pattern in which a species' range moves episodically. The slope of the dashed line represents the rate of change in the location of a species' climate envelope. The slope of the solid line represents actual migration rate (change in elevation/time). The slope of the dotted line represents observed migration rate. Observed migration rate is zero (no migration) if measurements are taken at time points A and B. Observed migration rate is faster than climate change if measurements taken at B and C, but is slower than climate change if measurements are taken at time points C and D. Calculated migration rate consequently depends on the time period of observation.

which climatic variables are important for

different species, how climate extremes may impact range margins, and how fine-scale topoclimatic variability may facilitate persistence. And while many researchers acknowledge that biotic interactions can influence species distributions, few studies have attempted to quantify their relative importance in relation to climate or edaphic variables (Wisz *et al.*, 2013). The high potential for episodic range shifts also suggests that migration rates will vary over time and cannot be fully understood without considering the temporal context.

To help disentangle the controls on tree species migrations, we recommend a combination of different approaches. Field studies of ongoing tree migrations will continue to provide valuable information on how species are responding to climate change, but these should be coupled with experiments that isolate climatic or niche-related controls to determine their relative influence. Simulation models of forest change should also be employed to examine interactions among migration constraints at large spatial and temporal scales. Until we understand the mechanisms that drive observed range shifts for individual species, it will be difficult to assess vulnerability and forecast change.

Studies with a greater temporal resolution are particularly important in enhancing our understanding of demographic processes that drive tree species migrations (van Mantgem & Stephenson, 2007). Most of the work documenting modern range shifts relies on just two time points, often several decades apart. This is problematic because episodic range shifts can appear as trends if sampling periods are too far apart to note a sudden change (Fig. 2-1). Short-duration studies may miss episodic shifts entirely. More continuous and long-term monitoring of tree species distributions would better capture distribution shifts that do not occur linearly

with respect to time, and could help to identify migration constraints and establish a more direct link between specific climate variables and tree migrations.

New research and monitoring programs would benefit from a comprehensive approach assessing changes across the entire range of each species. Because recent work has often focused on demonstrating change, many authors have studied shifts in the distribution center (Table 2-S1), which is responsive to changes in demographic rates throughout the entire range and consequently provides a robust measure of change. Measures of central tendency may be inadequate to determine migration constraints, however, because they cannot distinguish between shifts at one range margin, both margins, or an upward skew in the distribution with both margins remaining constant (Woodall *et al.*, 2013). Focusing on the distribution center can therefore mask the more nuanced patterns of change expected for most species. Additional monitoring of range margins (Stohlgren *et al.*, 2000) and across entire distributions (Urli *et al.*, 2014) is necessary to adequately characterize changes and determine how other factors mediate the migration response. Recent work focused on modelling species distributions using flexible response forms (Lenoir *et al.*, 2009; Urli *et al.*, 2014) and monitoring range margin locations based on the 10th and 90th percentile of modeled distributions (Lenoir *et al.*, 2009; Woodall *et al.*, 2009; Zhu *et al.*, 2011) avoid many of the statistical challenges inherent in studies of species distributions.

2.5 Facilitating migrations through management

If research and monitoring indicate that a species is vulnerable due to one or more migration constraints, management intervention may be necessary to facilitate range shifts. Understanding which barriers contribute to migration lags can aid in determining appropriate

and cost-effective actions. Geographic and anthropogenic barriers to migration likely pose the greatest threats to future biodiversity (Meier *et al.*, 2012); these may necessitate a broad-scale and multi-species approach. One possible method involves protecting a network of natural areas that can provide a pathway to more favorable climatic regions, though increasing habitat connectivity may not be sufficient to ensure migration of species with limited dispersal (Honnay *et al.*, 2002). Replacing plantation forestry with methods that increase diversity presents another opportunity to provide pathways for migration by allowing natural infilling by species better adapted to the current climate (Pitelka, 1997). Where land development has left little or no suitable habitat, a more targeted approach may be necessary. Assisted migrations, where seedlings are transplanted into sometimes distant areas as they become climatically suitable, can mitigate dispersal limitation in cases where long-distance dispersal appears insufficient to overcome geographic barriers (McLachlan *et al.*, 2007).

The importance of disturbance in facilitating range shifts suggests opportunities to manipulate forest ecosystems in ways that would expedite migrations for a suite of tree species. For many disturbance-dependent species, prescribed fires could allow more rapid range expansion. Harvesting practices can also be used to reduce competition where it is thought to delay migration of ecologically or economically valuable species. A modeling study found that forest harvesting disturbance reduced migration lags for certain forest types, though the effect was greater for early-successional species that are constrained by competition for light (Vanderwel & Purves, 2014). Utilizing multiple approaches such as prescribed fires coupled with plantings may be necessary to enable migration of tree species constrained by multiple

interacting factors, or to maintain diversity in forests where some species are disturbance-sensitive.

Where browse damage or grazing by domestic animals prevents range expansion, reducing the herbivore population might be a key step in allowing natural migration. Recent treeline rise in Switzerland, for example, was primarily attributed to pasture abandonment that allowed trees to expand into climatically-suitable areas where regeneration was previously constrained by grazing (Gehrig-Fasel *et al.*, 2007).

Understanding which species are likely to need management intervention, and which may be experience a temporary migration lag that will eventually be overcome through natural processes, will allow resources to be allocated more effectively. Continued monitoring of any migration interventions can also provide a valuable source of data to enhance understanding of migration constraints and inform future work. The best management strategies will be adaptive and flexible enough to change as our understanding of migration dynamics is improved (Millar *et al.*, 2007).

2.6 Conclusions

Anthropogenic climate change is already beginning to alter tree species distributions, and research suggests that migration lags are common. Tree migrations are slowed by a suite of spatial and niche-related constraints, but these are often temporary. There is a high potential for episodic range shifts when migration constraints are overcome. As a result, migration rates will not be constant through time. This complicates calculations of migration lags and hinders attempts to predict the rate and timing of future range shifts. Management focused on preserving biodiversity must consequently utilize flexible approaches that account for the high

degree of uncertainty surrounding migration dynamics. Additional research focused on quantifying range constraints and identifying triggers that facilitate rapid shifts would enhance our understanding of migration lags and advance attempts to forecast and manage future range shifts.

2.7 Acknowledgements

We thank J. Lenoir and two anonymous reviewers for comments that greatly improved this manuscript.

2.8 Supplementary Material

Table 2-S1: Studies reporting species-level changes in the altitudinal or latitudinal range of tree species. Treeline studies are not included because they are well-covered elsewhere (Harsch *et al.*, 2009). While many species are experiencing range shifts, most are not shifting as fast as climate. O.P. = observation period; % keeping pace = percent of all species migrating as fast as the climate is changing; NA = unable to calculate based on published results.

Range Metric	Range Dimension	O.P. (yrs)	# tree species	% shifting	% keeping pace	Citation
center	altitude	4	38	87	18	Feeley *et al.*, 2011
center	altitude	10	31	29	6	Bodin *et al.*, 2012
center	altitude	10	5	20	NA	Urli *et al.*, 2014
center	altitude	20	17	76	21	Lenoir *et al.*, 2009
center	altitude	22	31	29	NA	Lenoir *et al.*, 2008
center	altitude	30	3	100	33	Kelly & Goulden, 2008
center	altitude	75	22	55	55	Crimmins *et al.*, 2011
center	altitude	80	2	0	0	Felde *et al.*, 2012
center	altitude	NA	5	20	NA	Rabasa *et al.*, 2013
center	latitude	NA	65	20	NA	Zhu *et al.*, 2013
center	latitude	39	2	1	NA	Hernández *et al.*, 2014
center	latitude	NA	40	43	NA	Woodall *et al.*, 2009
Total/Mean (altitudinal shifts)			**154**	**53%**	**22%**	
Total/Mean (latitudinal shifts)			**107**	**29%**	**NA**	
trailing edge	altitude	40	3	67	NA	Beckage *et al.*, 2008
trailing edge	altitude	49	8	25	25	Brusca *et al.*, 2013
trailing edge	altitude	10	1	0	0	Hättenschwiler & Körner, 1995

trailing edge	altitude	20	17	65	0	Lenoir *et al.*, 2009
trailing edge	altitude	NA	7	0	NA	Rabasa *et al.*, 2013
trailing edge	altitude	55	1	100	100	Peñuelas & Boada, 2003
trailing edge	latitude	NA	92	79	NA	Zhu *et al.*, 2011
trailing edge	latitude	NA	6	38	NA	Bell *et al.*, 2013
Total/Mean (altitudinal shifts)			**37**	**43%**	**11%**	
Total/Mean (latitudinal shifts)			**98**	**84%**	**NA**	
leading edge	altitude	40	3	100	NA	Beckage *et al.*, 2008
leading edge	altitude	49	8	0	0	Brusca *et al.*, 2013
leading edge	altitude	80	2	0	0	Felde *et al.*, 2012
leading edge	altitude	10	1	0	0	Felde *et al.*, 2012
leading edge	altitude	20	17	59	0	Lenoir *et al.*, 2009
leading edge	altitude	NA	7	14	NA	Rabasa *et al.*, 2013
leading edge	altitude	NA	8	75	NA	Vitasse *et al.*, 2012
leading edge	altitude	55	2	100	NA	Peñuelas & Boada, 2003
leading edge	latitude	NA	20	5	NA	Woodall *et al.*, 2013
leading edge	latitude	NA	92	35	NA	Zhu *et al.*, 2011
leading edge	latitude	28	1	100	NA	Cavanaugh *et al.*, 2014
leading edge	latitude	NA	6	8	NA	Bell *et al.*, 2013
Total/Mean (altitudinal shifts)			**48**	**45%**	**0%**	
Total/Mean (latitudinal shifts)			**119**	**23%**	**NA**	

3 Disturbance accelerates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution

3.1 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). Research suggests that 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 understory (Chen *et al.*, 1993). Understanding what conditions are necessary to overcome migration lags and facilitate range shifts is a critical first step in forecasting future tree distributions.

Disturbance events that cause widespread mortality of overstory 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). Recent 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 higher understory temperature and a pulse of new recruitment. When insect outbreaks kill host trees, the effective water supply, available nitrogen, and understory light penetration may all increase, creating better conditions for trees and seedlings 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 heighten the effects of broad-scale temperature increases in a way that mirrors the effects of physical disturbances. The impact of biological disturbances on range margins, however, may differ because biological disturbance agents often target specific species, and so the boundary of the disturbance can be defined by the range the target species. This means 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.

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. 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), mountain pine beetle disturbance would initiate range *expansion* by allowing increased seedling recruitment at higher elevations, but only where the disturbance extends beyond the current range margin. Where the extent of a biological disturbance is defined by the range of the target species, it is unlikely to facilitate range expansion for that species. The work will enhance our understanding of how biological disturbances affect the timing of expected climate-driven distribution shifts.

3.2 Materials and methods

3.2.1 Study area

Study sites are located in Rocky Mountain National Park, Colorado, USA. Vegetation in this region varies with elevation in relation to temperature and precipitation gradients (Peet, 1981). Lower elevations are dominated by ponderosa pine (*Pinus ponderosae*) and Douglas-fir (*Pseudotsuga mensiesii*) 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 40 years (Fig. 3-1). Three species of pine occurring in our study area (*P. ponderosae*, *P. contorta*,

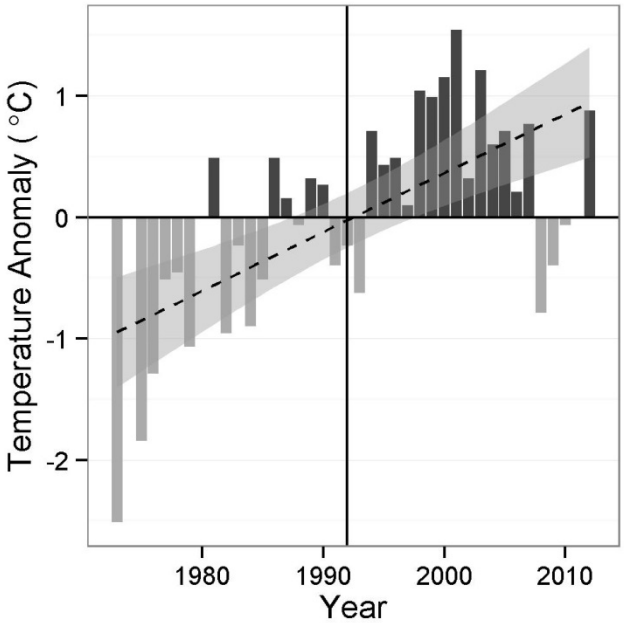

Figure 3-1 Temperature anomaly (deviation from the mean) for the 40-year period spanning 1973-2012 at the Grand Lake weather station ((053500). The vertical line represents when the ecotone transects were established (initial sampling). The 20-year period before the initial sampling was cooler than the 20-year period leading up to the 2012 re-sampling. The dashed line represents a linear fit for temperature anomaly as a function of year ($p < .001$, $R^2 = .38$).

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). In Rocky Mountain National Park, the combined effects of disturbance and climate are likely to have an immediate and lasting impact on forest ecosystems.

3.2.2 Data collection

In 2012, we resampled nine ecotone transects (Table 3-1) originally established between 1992 and 1995 to monitor climate change impacts (Stohlgren & Bachand, 1997; Stohlgren *et al.*, 1998, 2000). The transects represent four ecotone types: two at lodgepole pine's lower range margin (Ponderosa – Lodgepole and Douglas-fir – Lodgepole) and two at the upper range margin (Lodgepole – Spruce/Fir and Lodgepole – Limber). We sampled 2-3 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. Each transect consists of contiguous 20x20m plots with permanent corner markers. The largest trees in each plot were cored and aged to ensure that the ecotones represent underlying abiotic gradients as opposed to disturbance history (Stohlgren & Bachand, 1997).

We followed the original sampling protocol to ensure that data was comparable between sampling years. For each tree (>=2.5 cm diameter), we recorded the diameter at breast height (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. 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. We updated the original plot elevations using a new GPS unit with much higher accuracy.

3.2.3 Analysis

We analyzed changes in tree and seedling density across ecotone separately for trailing edge (lower elevation) and leading edge (upper elevation) ecotones. To assess whether changes in tree and seedling density within each ecotone type reflect an upslope migration, response to mountain pine beetle disturbance, or an interaction between the two, we fit linear regression models. Separate models were fit for trees and seedlings of each species.

All predictor variables were standardized by subtracting the mean from each observation and dividing by the standard deviation. With elevation, this was done separately for each

transect because differences in aspect among transects led to slight differences in the elevation range spanned by each. 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. Models were fit in R (R Core Team, 2014) and selection was based on AICc. Additional details on model formulation are included in Appendix A.

We were primarily interested in three potential predictor variables: elevation, MPB disturbance severity (total basal area killed), 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 varied at different elevations.

3.3 Results

3.3.1 Mountain pine beetle disturbance

The degree of mountain pine beetle mortality varied widely among both ecotone types and transects (Table 3-1). Among the transects spanning the trailing edge of lodgepole pine's distribution, the Ponderosa – Lodgepole ecotone experienced the largest decline in total basal area, while Douglas-fir – Lodgepole ecotone was less severely affected. At the leading edge, the Lodgepole – Spruce/Fir ecotone experienced high lodgepole pine mortality, while the Lodgepole – Limber transects were largely unaffected. Within transects affected by the outbreak, total basal area (BA) killed in any given plot ranged from 0-35 m^2/ha (mean 6.2 m^2/ha). Background mortality rates of trees not killed by beetles averaged 8% on trailing-edge

ecotones and 3% on leading-edge ecotones, and contributed minimally to changes in basal area.

Table 3-1 Transects re-sampled in 2012. Disturbance intensity, calculated as the total BA killed by mountain pine beetle, varied widely both within and across ecotone types. Total lodgepole pine basal area declined on all lower-elevation transects, including one with no MPB disturbance (Aspen Brook). Basal area increased slightly on the relatively undisturbed upper-elevation transects, but declined where disturbance intensity was high.

Ecotone Type	Transect	Elevation Range	Transect Length (m)	Disturbance Intensity	% change lodgepole BA
Ponderosa - Lodgepole	Deer Ridge	2740 - 2800	280	0.47	-0.82
	Upper Beaver	2230 - 2250	180	0.63	-0.94
Douglas-fir - Lodgepole	Thunder Mountain	2620 - 2630	120	0.20	-0.39
	Aspen Brook	2727 - 2764	120	0.00	-0.04
Lodgepole - Spruce/Fir	Bear Lake	2922 - 2922	220	0.17	-0.18
	Hitchens's Gulch	2960 - 2990	140	0.43	-0.87
Lodgepole - Limber	Wild Basin	2980 - 3080	260	0.01	0.09
	Meeker Drainage	3000 - 3050	200	0.00	0.11
	Lawn Lake	3020 - 3080	220	0.02	0.20

3.3.2 Changes in trailing-edge ecotones

Lodgepole pine basal area declined across all four lower ecotone transects, including one transect with no evidence of MPB activity (Aspen Brook, Table 3-1). The greatest loss in BA occurred in pure lodgepole pine plots along these transects, eliminating the steep gradient in lodgepole pine BA that initially characterized these ecotone types. Models indicate that shifts in the distribution of lodgepole pine trees across lower-elevation ecotones were unrelated to elevation or ecotone type (Table 3-2). Few saplings were recruited into the tree class (> 1.37m tall) in the 20 years following initial sampling (mean 11 +/- 3 saplings/ha). Predictions from the best model suggest that in the absence of MPB disturbance, no significant decline in tree density would have been expected (Fig. 3-2).

Table 3-2. Models relating the density of lodgepole pine trees and seedlings to elevation and disturbance intensity on trailing edge ecotones (modeled together) and the two leading edge ecotone types. Init = initial density, MPB = BA killed by mountain pine beetle, Elev = elevation.

	Best model		Model-Averaged Parameter Estimates (SE)					
Ecotone	adj. R^2	P-value	Intercept	Init	MPB	Init x MPB	Elev	Init x Elev
Trailing Edge								
Trees	0.93	<.001	4.4 (.1)	2.0 (.1)	- 0.9 (.1)	.64 (.12)	-	-
Seedlings	0.49	<.001	- 1.9 (.8)	2.5 (.9)	0.5 (.8)	-	2.2 (.9)	-
Lodgepole - Spruce/Fir								
Trees	0.91	<.001	5.3 (.1)	1.4 (.1)	- 0.6 (.1)	-	-	-
Seedlings	0..50	.002	-2.0 (1.1)	2.3 (1.1)	3.7 (1.1)	-	-	-
Lodgepole - Limber								
Trees	0.96	<.001	6.4 (.04)	0.9 (.04)	-	-	0.0 (.03)	0.0 (.05)
Seedlings	NULL		3.1 (.7)	0.1 (.4)	-	-	-	-

No lodgepole pine seedlings were observed in the lowest-elevation plots on any of these transects (Fig. 3-3), even where seedlings had been found in the original sampling. The best model for 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 3-2).

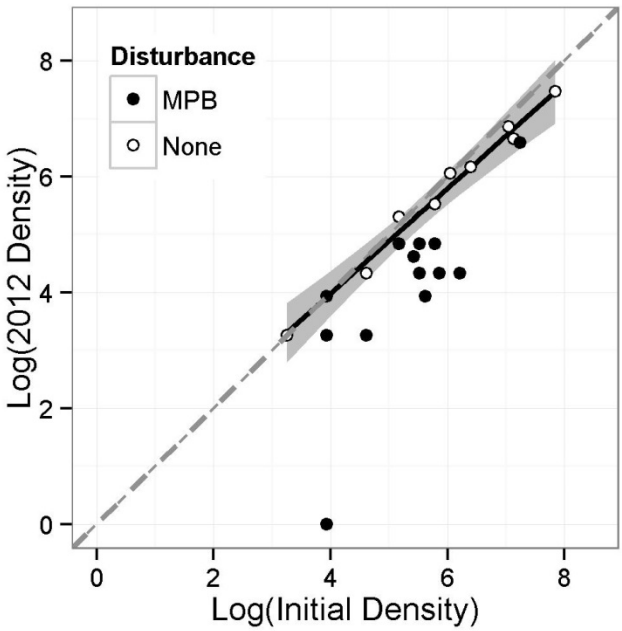

Figure 3-2 The 2012 density of lodgepole pine trees on the trailing-edge ecotones as a function of initial density. The gray dashed line shows a 1:1 relationship (no change). Points represent plots, with open circles indicating no disturbance while solid circles show plots affected by mountain pine beetle. The solid black line represents the modeled density (95% confidence interval) holding disturbance constant at zero. Little change in lodgepole pine tree density would be expected in the absence of disturbance.

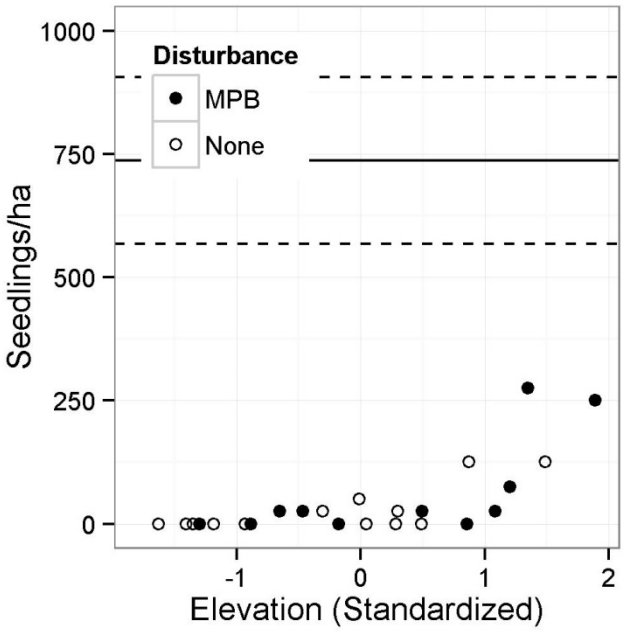

Figure 3-3 The relationship between elevation and 2012 density of lodgepole pine seedlings along trailing edge ecotones. The solid horizontal line indicates the average density of pre-disturbance lodgepole seedlings (+/- SE, dashed lines) from throughout its range in Rocky Mountain National Park (Diskin *et al.*, 2011). No seedling recruitment was found at the lowest elevations, and seedling densities were below the range-wide average across the entire trailing-edge ecotone, regardless of MPB disturbance.

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 BA was partially offset by increases in Douglas-fir BA across all elevations (25% increase). Douglas-fir seedling densities also increased by 25%; this increase was associated with areas of high disturbance intensity (Table 3-S1).

On the Ponderosa – Lodgepole ecotone transects, Ponderosa pine BA also declined as a result of MPB disturbance, resulting in a large decline in total BA 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 BA and seedling density. The number of Douglas-fir seedlings responded strongly to MPB disturbance (Table 3-S1), more than doubling in this ecotone type.

3.3.3 Changes in leading-edge ecotones

Patterns of change at the upper-elevation 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 transects where lodgepole pine dominates the overstory. 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. As with the lower ecotones, the model for lodgepole pine tree density included a term for MPB disturbance, but not elevation (Table 3-2).

The seedling model suggests that disturbance was associated with an increase in seedling recruitment (positive coefficient for disturbance intensity), but patterns of new recruitment showed no relationship to elevation once disturbance was controlled for (Fig. 3-4). The highest elevation with a lodgepole pine seedling present actually declined slightly on both Lodgepole – Spruce/Fir transects. Sapling recruitment was low on the Lodgepole – Spruce/Fir ecotone (mean 26 +/- 11 saplings per ha) compared to the Lodgepole-Limber ecotone (mean 62 +/- 9 saplings/ha).

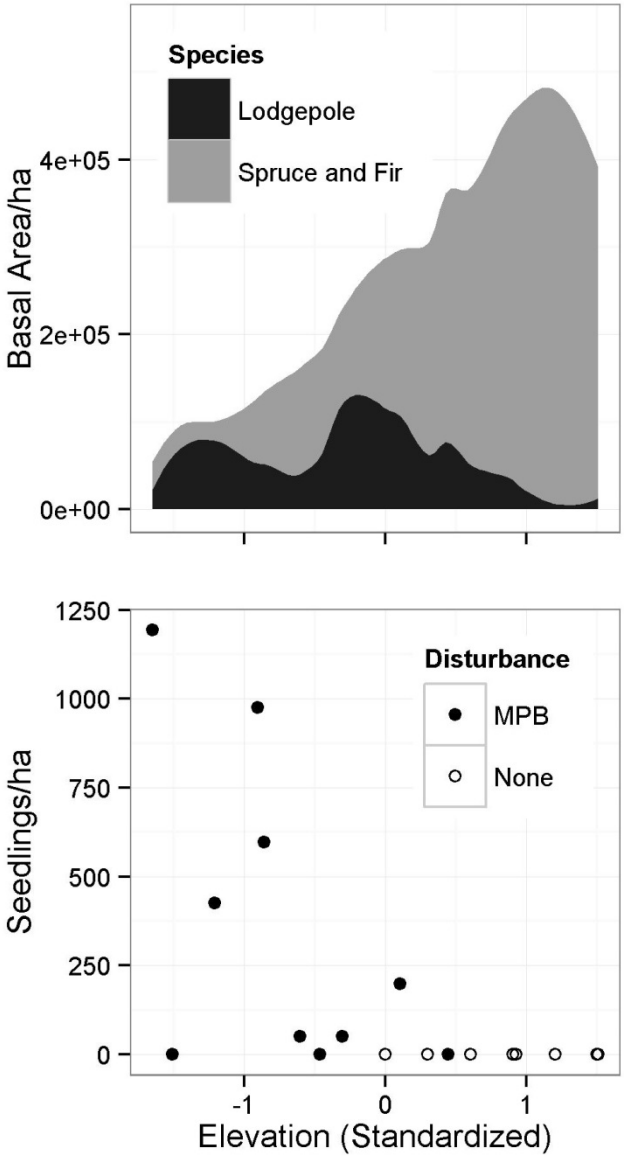

Figure 3-4 Lodgepole – Spruce/Fir ecotone type. 2012 basal area (smoothed) of lodgepole pine, Englemann spruce, and subalpine fir as a function of elevation (top panel). Spruce and fir basal area increase with elevation, driving an increase in total basal area across the ecotone. 2012 lodgepole seedling density as a function of elevation (bottom panel). No seedlings were found at the highest elevations, where competition with overstory trees may limit upward expansion.

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, though recruitment of new saplings also contributed to the change. Seedling recruitment was extremely variable and did not change significantly (Fig 3-5). The best model for both tree and seedling density included just initial density, suggesting that patterns of change were unrelated to elevation.

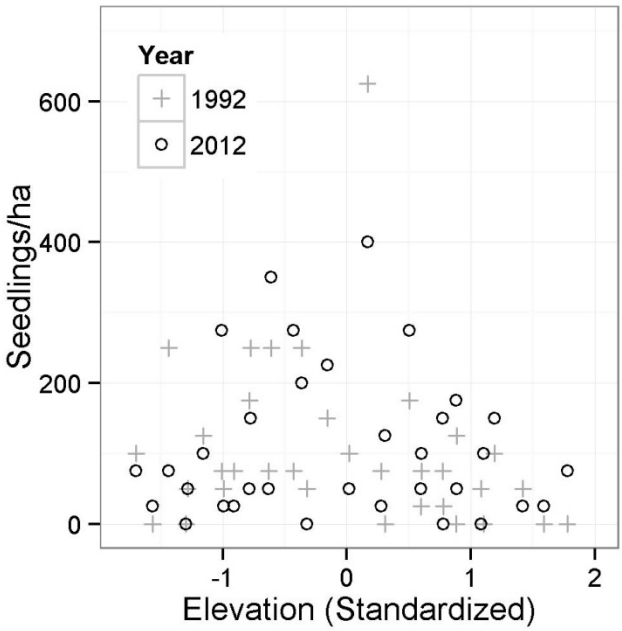

Figure 3-5 Lodgepole – Limber ecotone type. Density of lodgepole seedlings in 1992 and 2012 as a function of elevation. Changes in seedling density were not related to elevation and do not indicate an upward expansion on lodgepole pine's range.

3.4 Discussion

The differences in 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. The background (non-MPB) mortality rate at the trailing edge was also nearly twice that at the leading edge, where an increase in BA on undisturbed transects points to higher growth as well. The leading edge ecotone types had nearly twice as many seedlings and saplings as trailing edge ecotones, suggesting that conditions are more favorable for modest recruitment at these cooler sites.

Changes within individual ecotones help elucidate the interaction between disturbance and climate in driving tree species range shifts. We expected that mountain pine beetle disturbance would play an important role in initiating a range shift at the trailing edge of lodgepole pine's distribution, 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 BA 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 indicate that while disturbance may be required to kill mature trees, recent climatic conditions were unsuitable for regeneration.

The upper range margin of lodgepole pine remained relatively stable, and we found no evidence that the MPB outbreak accelerated range expansion. On the Lodgepole – Spruce/Fir ecotone type, the presence of two strong competitors that were not affected by the MPB outbreak likely hindered establishment of shade-intolerant lodgepole seedlings at higher elevations. Seedlings of both spruce and fir increased in density as a consequence of the mountain pine beetle outbreak, and will continue to compete with lodgepole pine seedlings in the absence of a physical disturbance such as fire. Furthermore, the reduction in propagule pressure where mature lodgepole pine were killed by MPB may slow or delay range expansion even if a future fire reduces competition and creates physical conditions more favorable for lodgepole recruitment.

A similar pattern was observed at the upper range margin of ponderosa pine, 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 can tolerate a higher level of understory competition.

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.

3.5 Conclusion

Mountain Pine Beetle disturbance killed many mature lodgepole pine trees across both its upper and lower 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 upper range margin of lodgepole pine, 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 occupied 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.

3.6 Supplementary material

3.6.1 Additional methods

To isolate changes in density and account for variability generated by unmeasured abiotic factors, initial density, from the first survey in the 1990s, was included as a predictor in each model. This parameter is not of interest in itself, but allows us to focus on how the additional predictor variables (elevation and disturbance) affect change over time. 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).

The two trailing edge ecotone types were modeled together including a potential type effect, but the two leading edge ecotone types had to be modeled separately because the Lodgepole – Limber type did not have any MPB activity, making type perfectly correlated with disturbance. In all models, the response variable (2012 tree or seedling density) was log-transformed to meet model assumptions.

All two-way interactions were included as potential predictor variables, but the number of possible predictors in any given model was restricted to roughly 1/10 the number of data points, resulting in slight differences in the set of candidate models for ecotone types with different numbers of plots (Table 3-S1). A random transect effect was initially included, but was dropped from final models because it did not affect parameter estimates or standard errors and the variance estimates were close to zero. Semi-variograms fit to model residuals showed no evidence of spatial autocorrelation and values of Moran's I were not significant, so we did

not include a spatial term in any of the models. To incorporate uncertainty in model selection, we used model-averaged parameter estimates if more than one model had ΔAICc values < 2. Model averaging was done using the MuMIn package (Barton, 2014) , including zero for parameters when they were absent from a model .

Table 3-S1 Complete set of models tested. Bold models were averaged to account for uncertainty in model selection. Init = initial density, MPB = BA killed by mountain pine beetle, Elev = elevation.

Candidate Model	AICc	Δ AICc
Lower Ecotone- Lodgepole Trees		
Init x MPB	**42.17**	**0**
Init + MPB	59.73	17.56
Init + MPB + type	60.84	18.67
Init + MPB + Elev	62.63	20.46
Init + type	66.53	24.36
Init + Elev + type	69.56	27.39
Init x type	69.62	27.45
Init	72.42	30.25
Init + Elev	74.98	32.81
NULL	10.653	64.36
Lower Ecotone- Lodgepole Seedlings		
Init + Elev	**152.77**	**0**
Init + Elev + MPB	**153.48**	**0.71**
Init + MPB	155.48	2.71
Init x Elev	155.68	2.91
Init + Elev + type	155.86	3.09
Init	157.35	4.58
Init + MPB + type	157.43	4.66
Init x MPB	158	5.23
Init + type	160.15	7.38
Init x type	160.72	7.95
NULL	166.83	14.06
Spruce/Fir Ecotone- Lodgepole Trees		
Init + MPB	**23.22**	**0**
Init	38.21	14.98
Init + Elev	39.14	15.92
NULL	62.45	39.23
Spruce/Fir Ecotone- Lodgepole Seedlings		
Init + MPB	**112.76**	**0**

Init + Elev	115.81	3.06
Init	119.65	6.9
NULL	121.37	8.62
Limber Ecotone- Lodgepole Trees		
Init	**-15.99**	**0**
Init x Elev	**-15.43**	**0.56**
Init + Elev	**-14.29**	**1.7**
NULL	95.99	111.97
Limber Ecotone- Lodgepole Seedlings		
NULL	**190.83**	**0**
Init	**192.65**	**1.82**
Init x Elev	193.25	2.42
Init + Elev	195.23	4.4
Douglas-fir seedlings		
Init + MPB	**128.24**	**0**
Init + MPB + type	**128.31**	**0.07**
Init	**129.02**	**0.78**
Init + Elev	130.75	2.51
Init x MPB	130.84	2.6
Init + MPB + Elev	131.2	2.96
Init + type	131.4	3.16
Init x type	133.02	4.79
Init x Elev	133.08	4.84
Init + Elev + type	133.23	4.99
NULL	150.12	21.89

4 The importance of non-climatic constraints on the landscape-scale distribution of Rocky Mountain trees species

4.1 Introduction

While climate exerts the dominant influence on species distributions at large (regional to continental) spatial scales, biotic processes and additional abiotic variables often constrain landscape-scale species distributions (Pearson & Dawson, 2003). Despite the acknowledged influence of such variables, including land-use and disturbance history, competition, and dispersal, bioclimatic niche models rarely include them (Guisan & Thuiller, 2005). By omitting important predictors, these models may fail to accurately characterize a species' climatic niche (Davis *et al.*, 1998). Furthermore, bioclimatic niche models often implicitly assume that climate alone is sufficient to predict how species distributions may shift as a consequence of climate change. This assumption has rarely been tested (Araújo & Luoto, 2007), and the impact of non-climatic factors in determining the distribution of different taxa remains a fundamental and largely unanswered question in ecology. Understanding the importance of additional biotic and abiotic factors relative to climate is of critical importance given the interest in forecasting how species distributions may change in the future.

Biotic interactions are perhaps the most frequently omitted, but several recent studies have made important strides towards quantifying their impact on tree species distributions. By including the abundance of *Nothofagus* trees as a covariate in models predicting the distribution of other tree species, Leathwick & Austin (2001) were able to demonstrate that

competition has a negative impact on the abundance of different genera and can alter the distribution of species along a temperature gradient. A similar study of tree species in Switzerland also found that including co-occurring species as predictor variables improved model performance (Meier *et al.*, 2010). While these studies demonstrate the potential importance of accounting for heterospecific trees in distribution models, the modelling technique used has several important drawbacks. Including other taxa as covariates may result in unstable parameter estimates because the presence of other species tends to be highly correlated with environmental predictor variables. The model structure also implicitly assumes a causal relationship, whereas the distribution of both the predictor and response species may instead be responding in divergent ways to an un-modeled environmental gradient.

Regardless of the underlying cause of relationships between species, both biotic interactions and un-modeled abiotic variables can contribute to patterns of residual covariance; i.e. the covariance that remains after accounting for the influence of broad-scale climatic drivers. Recently, several authors have proposed a different modelling approach that takes advantage of this residual covariance among species to incorporate the impacts of non-climatic variables (Ovaskainen *et al.*, 2010; Golding, 2013; Pollock *et al.*, 2014). These so called "joint distribution models" are a type of multivariate regression that incorporates residual correlations among species into the error structure in the form of a variance-covariance matrix. This approach has been shown to offer several advantages over modeling species individually. Joint distribution models can improve the accuracy of model predictions for rare species by "borrowing strength" from more common species (Ovaskainen & Soininen, 2011), and the residual correlations themselves may provide new ecological insights regarding the interactions

among species (Ovaskainen *et al.*, 2010; Pollock *et al.*, 2014). The technique has successfully been applied to model the joint distribution of several different community types, including both aquatic (Ovaskainen & Soininen, 2011; Golding, 2013) and terrestrial (Ovaskainen *et al.*, 2010; Pollock *et al.*, 2014) systems.

Forest communities in the Rocky Mountains present an interesting opportunity for utilizing a joint distribution model to examine the influence of non-climatic factors in shaping patterns of co-occurrence among tree species. Previous studies have found that competition can limit recruitment at lower elevations (Peet, 1981), whereas facilitation is important for seedling establishment at high-elevation sites with harsh climatic conditions (Rebertus *et al.*, 1991). Studies of biotic interactions have primarily focused on seedlings, however, and little is known about how the cumulative effects of competition or facilitation in the time leading up to canopy recruitment may influence the distribution of mature trees.

In addition to the potential impact of biotic interactions, other non-climatic factors likely affect landscape-scale tree species distributions. Disturbances such as fire and insect outbreaks are common in Rocky Mountain forests, and can lead to heterogeneity in forest composition. Several common tree species are largely dependent on disturbance for regeneration, and the recruitment niche is often narrower than that of mature trees (Jackson *et al.*, 2009b). Estimating the relationship between climate and species distributions is consequently challenging in this ecosystem, particularly when we lack data for important covariates such as disturbance history or ground-level climate, which can differ from regional climate (Chen *et al.*, 1993) and may exert a stronger influence on recruitment patterns (Dingman *et al.*, 2013).

Here, we utilize a joint distribution model to investigate two related hypotheses: 1) non-climatic factors are important in shaping the landscape-scale distribution of Rocky Mountain tree species, and 2) as a result, modelling the distribution of species jointly will improve parameter estimates and predictive accuracy relative to the traditional method of modelling each species separately. Alternatively, if the distribution of each species is entirely controlled by climate variables included in the model, we would expect to see no significant residual correlations because the model would perfectly account for the niche of each species. The joint model would then offer no improvement over a collection of single-species distribution models. By modelling species jointly and comparing the results to single-species models, we hope to contribute new insights about the relative importance of climatic controls on tree species distributions and generate new hypotheses about the factors influencing patterns of co-occurrence.

4.2 Methods

4.2.1 Study area

Rocky Mountain National Park is located in the Colorado Front Range of the Rocky Mountains. Elevation in the park ranges from 2300 to 4300 A. S. L., with tree species occurring between 2370m and 3600m elevation. The high degree of topographic relief within the park creates compressed climatic gradients, resulting in rapid species turnover with increasing elevation (Allen & Peet, 1990). Natural disturbances such as fire, insect outbreaks, and blowdowns contribute to heterogeneity in vegetation patterns within elevation zones, and can have a lasting impact on forest composition (Sibold *et al.*, 2007).

Our study focused on seven tree species common throughout the Rocky Mountains: ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) (Table 4-1). Five of these species are confined to relatively distinct climate zones, with ponderosa pine and Douglas-fir occurring on warmer, drier sites at lower elevations, lodgepole pine forming monospecific stands in the central elevations, and Engelmann spruce and subalpine fir more typical on cooler, wetter sites found at higher elevations (Peet, 1981). Quaking aspen and limber pine both have wide climatic niches, and their landscape-scale distribution is more strongly constrained by other factors. Aspen is more common in areas that experience stand-replacing fires, and regeneration may be further constrained by elk herbivory and competition with conifers (Kaye *et al.*, 2003, 2005). Limber pine typically occurs on rocky sites with shallow soil and ridgelines where wind precludes establishment of less-hardy species (Rebertus *et al.*, 1991).

Table 4-1 The seven focal species, with the observed elevation range of each in our dataset (5th percentile, median, and 95th percentile) and the number of occurrences for trees and seedlings of each species.

		Observed Elevation Range			Occurrences	
Species	Abbreviation	5th %	median	95th %	Trees	Seedlings
Pinus ponderosa	PIPO	2568	2568	2818	96	31
Pseudotsuga menziessii	PSME	2637	2637	3011	105	76
Populus tremuloides	POTR	2758	2758	3040	78	86
Pinus flexilis	PIFL	3011	3011	3202	70	48
Pinus contorta	PICO	2915	2915	3111	172	89
Abies lasiocarpa	ABLA	3039	3039	3295	129	91
Pices engelmannii	PIEN	3069	3069	3406	166	110

Dispersal syndrome also varies among our study species, and may contribute to differences in the relationship between seedling dispersion and the distribution of mature trees

among different species. Ponderosa pine and limber pine both produce large, heavy seeds that are primarily dispersed by animals. Douglas-fir, subalpine fir, and Engelmann spruce are all wind-dispersed. Lodgepole pine can form serotinous cones, and so the timing of dispersal is often linked to fire. Recruitment from seeds is rare for aspen, for which vegetative reproduction via root sprouts is more common.

4.2.2 Data sources

Presence-absence data for both trees and seedlings of our seven focal species were obtained from two complementary sources. Plot data from the National Park Service Vegetation Inventory Program (VIP) were used to characterize the broad-scale spatial distribution of tree species. The 294 forest plots from this program were located using a distributed random gradsect sampling scheme (Salas *et al.*, 2005), and provide good spatial coverage of our study region .

To better inform estimates of tree species range margins, we also utilized plot data from ecotone transects that span the boundary zone between forest stands dominated by different species (Stohlgren *et al.*, 2000). Sampling across the range margins of species can better characterize the environmental limits to seedling establishment and canopy recruitment (Stohlgren *et al.*, 1998). Including ecotone plots is particularly important here because it provides a more complete representation of co-occurrence patterns for species that may only be found together at their range margins, which can aid in the estimation of residual correlation. Sampling methods for the ecotone plots are described by Stohlgren & Bachand (1997). The study design and sampling methods for the VIP plots can be found in Salas *et al.*

(2005). Plots from both studies were the same size (.04 ha), and were all sampled between 2003 and 2012 (Renwick *et al.*, 2014).

The climate data used represent 30-year monthly normals for the period from 1971-2000. To better represent fine-scale climatic gradients controlled by topography, we used downscaled PRISM data derived from the program ClimateWNA (Wang *et al.*, 2012). ClimateWNA is a statistical downscaling program that provides scale-independent estimates of common climate variables by adjusting PRISM data based on latitude, longitude, and elevation. Climate variables for each plot were extracted using the coordinates of the plot center. In addition to climatic variables, we also included topographic wetness index (TWI) to account for the impact of slope position and drainage area on soil moisture. TWI was derived from a 10-meter digital elevation model (DEM) using ArcGIS version 10.1.

4.2.3 Analysis

We modeled the joint distribution of trees and seedlings for our seven focal species using a latent-variable formulation of the multivariate probit model. The response variable Y_{ij} represents an i x j matrix of presence-absence data for tree species j at plot i. We included both trees and seedlings of each species for a total of J = 14 species by life-stage combinations sampled at n = 409 plots.

In the latent-variable formulation of the probit model, the link function is replaced by an indicator variable, such that

$$P(Y_{ij} = 1) = P(Z_{ij} > 0), \quad \text{for sites } i...n \text{ and species } j...J \qquad (1)$$

where Z_{ij} is a latent variable drawn from a multivariate normal distribution with mean μ_{ij} and variance defined by a J x J covariance matrix. The process model is then defined as

$$\mu_{ij} = \beta_{j1} + \beta_{j2}X_i + \ldots + \beta_{jk}X_{ik} \quad (2)$$

where k is the number of predictor variables included in the model. The covariance matrix can then be re-scaled into a correlation matrix for greater ease of interpretation. A positive residual correlation can be interpreted as evidence that two species co-occur more frequently than expected based on their modeled environmental niche, whereas a negative residual correlation indicates that the species co-occur less frequently than expected.

For the sake of simplicity, both the response and predictor variables were assumed to be observed without error. This assumption is probably valid for the presence of trees and seedlings, which are relatively easy to spot and identify. It is more problematic for the climate data, which originated at a coarse resolution and might not adequately represent the plot-level microclimate. As we were primarily interested in comparing the influence of commonly-available climate variables to un-modeled factors (possibly including microclimate), the omission of observation error should not affect our conclusions.

Models were implemented in R (R Core Team, 2014), with posterior distributions sampled using the Monte Carlo Markov Chain (MCMC) software JAGS (Plummer, 2003) via the rjags package (Plummer, 2014). We used a modified version of code developed by Pollock *et al.* (2014), and an excellent discussion of the implementation of multivariate probit models can be found in their paper. We ran three chains with a burn-in of 210000 iterations and sampled the posterior distributions from a further 40000 iterations thinned by a factor of 40, resulting in

1000 iterations per chain. Model convergence was evaluated via visual inspection of trace and density plots as well as the Gelman-Rubin (Gelman & Rubin, 1992) and Heidelberger-Welch (Heidelberger & Welch, 1983) diagnostics, which were both calculate using the coda package (Plummer *et al.*, 2010).

We used uninformative priors for all parameters. For the regression coefficients, we used vague normal priors with mean 0 and variance 10000. For the covariance matrix, we used an inverse Wishart prior with the scale matrix set to a J x J identity matrix and J + 1 degrees of freedom. This results in a marginally uniform distribution on each off-diagonal element of the covariance matrix, and consequently exerts little influence on the estimates of covariance (Gelman & Hill, 2007)

We compared a small set of candidate models (Table 4-2) with sets of predictor variables chosen because of their ecological relevance and widespread availability. For climatic variables, we focused on mean annual temperature (MAT) and its quadratic, mean annual precipitation (MAP) and its quadratic, the interaction between MAT and MAP, and temperature differential (TD), or the difference between mean warmest month temperature and mean coldest month temperature. Mean annual temperature and precipitation were highly correlated with seasonal variables in our study area, and so were thought to provide an adequate representation of broad-scale climatic

Table 4-2 Predictor variables included in each of the six candidate models, and mean AUC for all species. AUC was not estimated for two models because they failed to converge. TWI = topographic wetness index, TD = temperature differential, MAT = mean annual temperature, MAP = mean annual precipitation, CMD = climatic moisture deficit.

Predictors	Mean AUC
TWI, TD, MAT, MAP	0.77
TWI, TD, MAT, MAT^2, MAP	0.83
TWI, TD, MAT, MAT^2, MAP, MAP^2	-
TWI, TD, MAT, MAP, MAT x MAP	-
TWI, TD, CMD, CMD2	0.81
TWI, PC 1-5	0.84

controls. All of the candidate models included TD and topographic wetness index (TWI), which were included because neither was strongly correlated with other climatic variables and so could add new information to the model without interfering with convergence.

In addition to the various combinations of MAT and MAP, we also tested a model that instead used climatic moisture deficit (CMD), which incorporates both temperature and precipitation and has been shown to be an important driver of tree species distributions (Crimmins *et al.*, 2011). Finally, we tested a model that included 26 of the annual and seasonal climate variables available from ClimateWNA transformed into principle components using the stats package (R Core Team, 2014). The first five principle components together explained 99% of the variance in climate space, and were included as predictors along with TWI. This was compared to the former models to test the ability of mean annual temperature and precipitation to effectively represent a broader set of correlated climate variables. The in-sample predictive accuracy of each model was measured using area under the receiver operating characteristic curve (AUC). AUC was calculated for each species individually using the pROC package (Robin *et al.*, 2011).

To determine how the inclusion of species correlations affects parameter estimates and predictive power, we also fit a more traditional univariate probit regression model for trees and seedlings of each species. The model formulation, covariates, and priors for these were identical to the joint model, but with the error term estimated separately for each species instead of as a covariance matrix. For the single-species models, we used a vague uniform distribution for the prior on variance in place of the inverse-Wishart prior used in the joint model.

4.3 Results

4.3.1 Model selection and evaluation

Achieving convergence in the joint model proved difficult, and we were unable to generate stable parameter estimates for the models including MAP^2 or the interaction between MAT and MAP. Of the models that converged, the simplest model (no quadratics or interaction terms) performed the worst at in-sample prediction, but results from the other three models were similar (Table 4-2). The model that used principle components to represent a broader suite of climate variables did not offer any appreciable gains in predictive ability over models that only included measures of temperature and precipitation. We chose to base all further analysis on the model that included TWI, TD, MAT, MAT^2, and MAP. This model was selected because of the greater ease of interpretation.

4.3.2 Comparison to single-species models

We observed several differences in the mean and precision of parameter estimates from the joint versus the single-species models types. Parameter estimates from the single – species models were generally less precise, with the joint model producing narrower credible intervals for 82 out of the 84 species- by life-stage- by parameter-combinations. The mean credible interval width was significantly smaller for the joint model (paired t-test, $p < .0001$, df = 83).

For most species, parameter estimates generated by the two model types were similar. For ponderosa pine and limber pine, however, the single-species models tended to over-estimate the effect size of climatic variables relative to the joint model (Fig. 4-1). This same pattern was evident and even more striking for seedlings of these species. The differences were

not significant (overlapping 95% credible intervals), but they *were* systematic, with the absolute value of parameter estimates from the single-species model tending to be larger than those from the joint model.

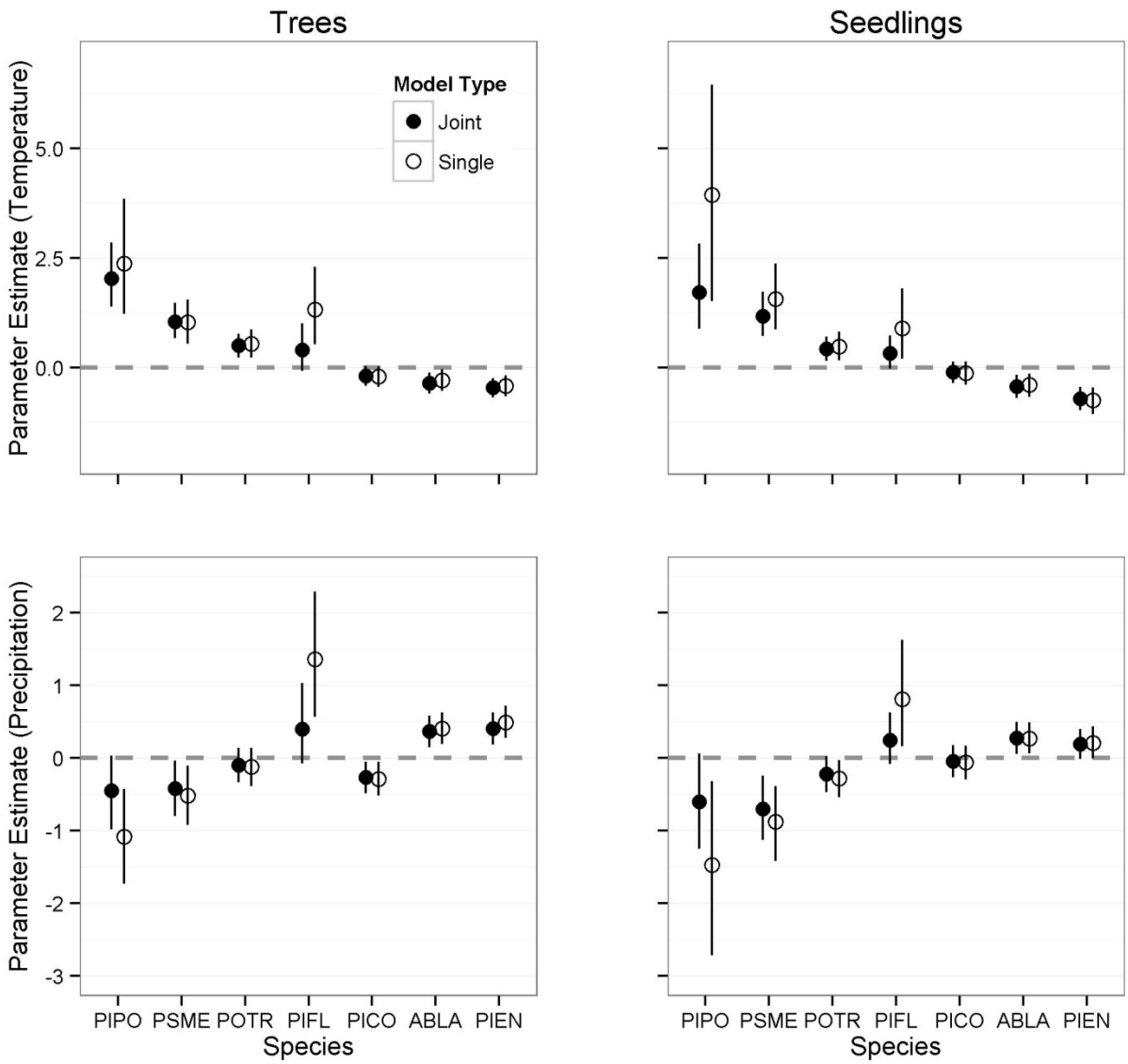

Figure 4-1 Estimated coefficients for temperature (top panels) and precipitation (bottom panels) for each species from the joint vs. single-species model with 95% credible intervals. The left panels are for trees, whereas the right panels show seedlings. Species abbreviations are listed in Table 4-1.

Despite these differences in parameter estimates for some species, predictive accuracy of the two model types did not differ (Fig. 4-2). An AUC value of .5 indicates model predictions are no better than random, whereas a value of 1 corresponds to a perfect ability to distinguish between presences and absences. All of the AUC values generated by both model types were well above 0.7, which is the cut-off frequently used to indicate utility of the model (Swets, 1988). AUC varied among species, but was relatively consistent for trees and seedlings of the same species (Fig. 4-2).

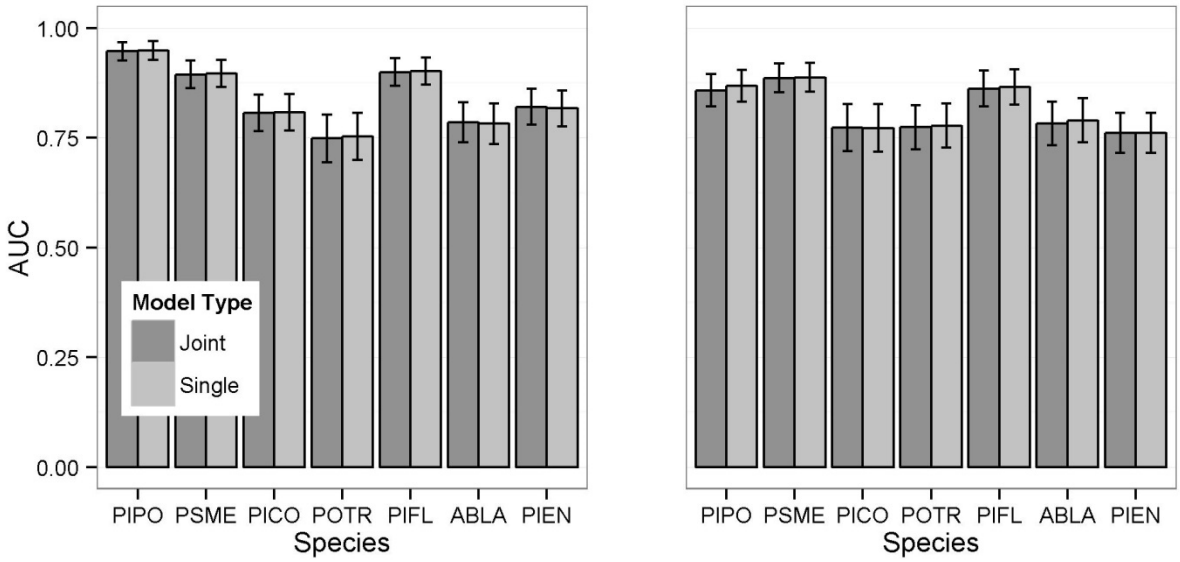

Figure 4-2 Comparison of area under the receiver operating characteristic curve (AUC) from the joint vs. single-species distribution models, for trees (left panel) and seedlings (right panel) of each species.

4.3.3 Comparison of climate niche among species and life stages

Parameter estimates can provide an indication of how each species responds to different climatic predictor variables. Response to temperature and precipitation varied

strongly among species (Fig. 4-1). Ponderosa pine and Douglas-fir were associated with high temperatures and low precipitation. At the opposite end of the spectrum, subalpine fir and Engelmann spruce were associated with cooler, wetter sites. Parameter estimates for environmental predictors included in the model did not differ significantly between trees and seedlings of any given species.

Correlations due to shared environmental response can complement examination of individual parameters by providing an aggregate measure of the similarity between the modeled environmental niche of two species. Estimates of correlation due to environment were significant for 78 out of the 91 species by life-stage combinations (Table 4-3), of which 69% were positive. Patterns of correlation between trees and conspecific seedlings due to the modeled environmental niche were strong (> 0.9 for all species), which is not surprising given the similarity in parameter estimates. Similarly, for any given species, the amount of correlation with heterospecific trees or seedlings attributed to the modeled environment did not differ between conspecific trees and seedlings (Fig. 4-3). For lodgepole pine, a broadly-distributed species occupying a central position on the temperature gradient, correlations with other species due to the environment were generally positive or insignificant (Fig. 4-4). Other species all showed a mix of positive and negative environmental correlations. Engelmann spruce, for example, exhibited a strong positive correlation due to environment with subalpine fir, but insignificant or negative environmental correlations with all other species (Fig. 4-4).

Table 4-3 Correlation due to the modeled environmental niche for each pair of species. Stars denote estimates with credible intervals that do not overlap zero. Bold numbers highlight the correlation due to environment between trees and conspecific seedlings. Correlation due to environment was calculated using the method described by Pollock et al. 2014.

		Ponderosa Pine		Douglas-fir		Lodgepole Pine		Quaking Aspen		Limber Pine		Subalpine Fir		Engelmann Spruce	
		T	S	T	S	T	S	T	S	T	S	T	S	T	S
Ponderosa Pine	T	1													
	S	***0.98****	1												
Douglas-fir	T	0.96*	0.96*	1											
	S	0.97*	0.98*	***0.98****	1										
Lodgepole Pine	T	0.41*	0.50*	0.51*	0.51*	1									
	S	0.27	0.38*	0.37*	0.36*	***0.93****	1								
Quaking Aspen	T	0.87*	0.91*	0.88*	0.89*	0.74*	0.66*	1							
	S	0.86*	0.91*	0.87*	0.9*	0.73*	0.65*	***0.97****	1						
Limber Pine	T	0.41*	0.45*	0.58*	0.49*	0.64*	0.65*	0.58*	0.54*	1					
	S	0.50*	0.56*	0.63*	0.58*	0.8*	0.79*	0.73*	0.7*	***0.92****	1				
Subalpine Fir	T	-0.65*	-0.57*	-0.6*	-0.61*	0.27*	0.45*	-0.24*	-0.26*	0.07	0.13	1			
	S	-0.67*	-0.59*	-0.58*	-0.61*	0.31*	0.47*	-0.26*	-0.28*	0.14	0.17	***0.97****	1		
Engelmann Spruce	T	-0.78*	-0.71*	-0.74*	-0.75*	0.07	0.27	-0.43*	-0.43*	-0.07	-0.05	0.96*	0.94*	1	
	S	-0.83*	-0.76*	-0.74*	-0.77*	0.09	0.26	-0.5*	-0.50*	-0.01	-0.03	0.91*	0.94*	***0.95****	1

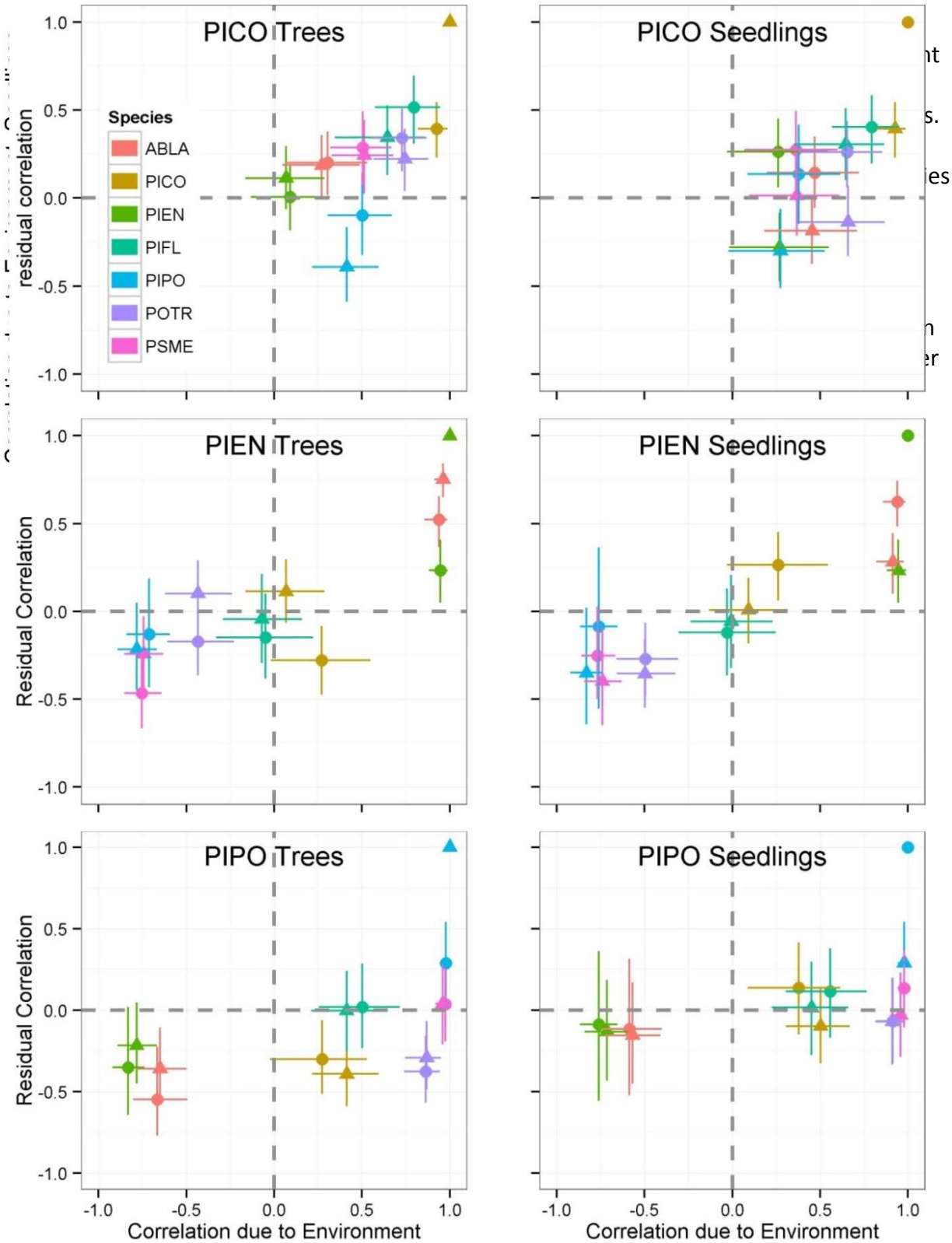

Figure 4-4 Correlations due the environment compared to residual correlations for lodgepole pine (top panels), Engelmann spruce (middle panels), and ponderosa pine (bottom panels). Triangles represent trees of other species while circles represent seedlings of other species.

4.3.4 Patterns of Residual Correlation

Estimates of the residual correlation were significant for 45 out of the 91 pairs examined (Table 4-4). Of these, the majority (62%) were positive. The residual correlations between trees and conspecific seedlings were significant and positive for all seven focal species (Fig. 4-5). Trees and seedlings of all species showed significant residual correlation with trees and seedlings of at least one other species, with one exception: ponderosa pine seedlings did not have residual correlation with trees or seedlings of any other species (Fig. 4-4).

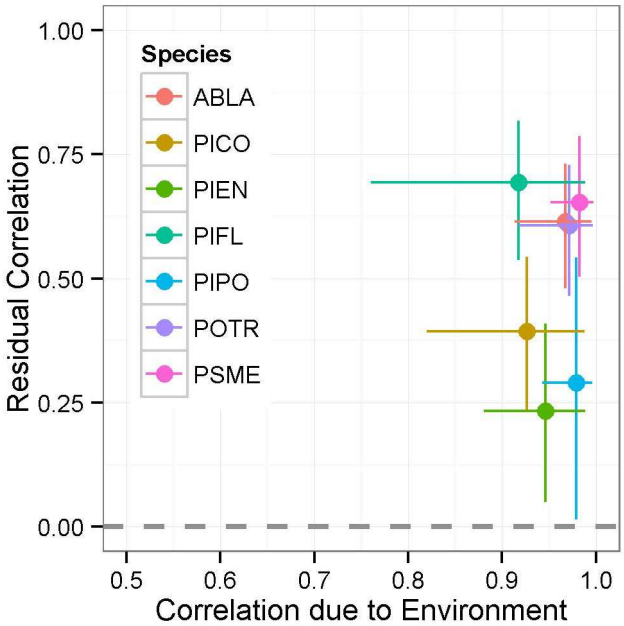

Figure 4-5 Correlation due to the environment compared to residual correlation for trees and conspecific seedlings of each species.

When comparing trees of different species, 10 out of the 21 residual correlations were significant, of which the majority (6) were positive (Fig. 4-6a). The pattern of residual correlations between seedlings of different species was similar, with 7 positive correlations and only 2 negative (Fig. 4-6b). When comparing seedlings to heterospecific trees, however, we found the opposite pattern: the majority of significant residual correlations were *negative* (Fig. 4-6c).

This prompted a comparison of the differences between the residual correlations associated with trees vs. seedlings of each species. For ponderosa pine, Douglas-fir, aspen, and limber pine, none of the residual correlations differed between trees and seedlings. The differences that did occur tended to be due to the fact that seedlings showed a more

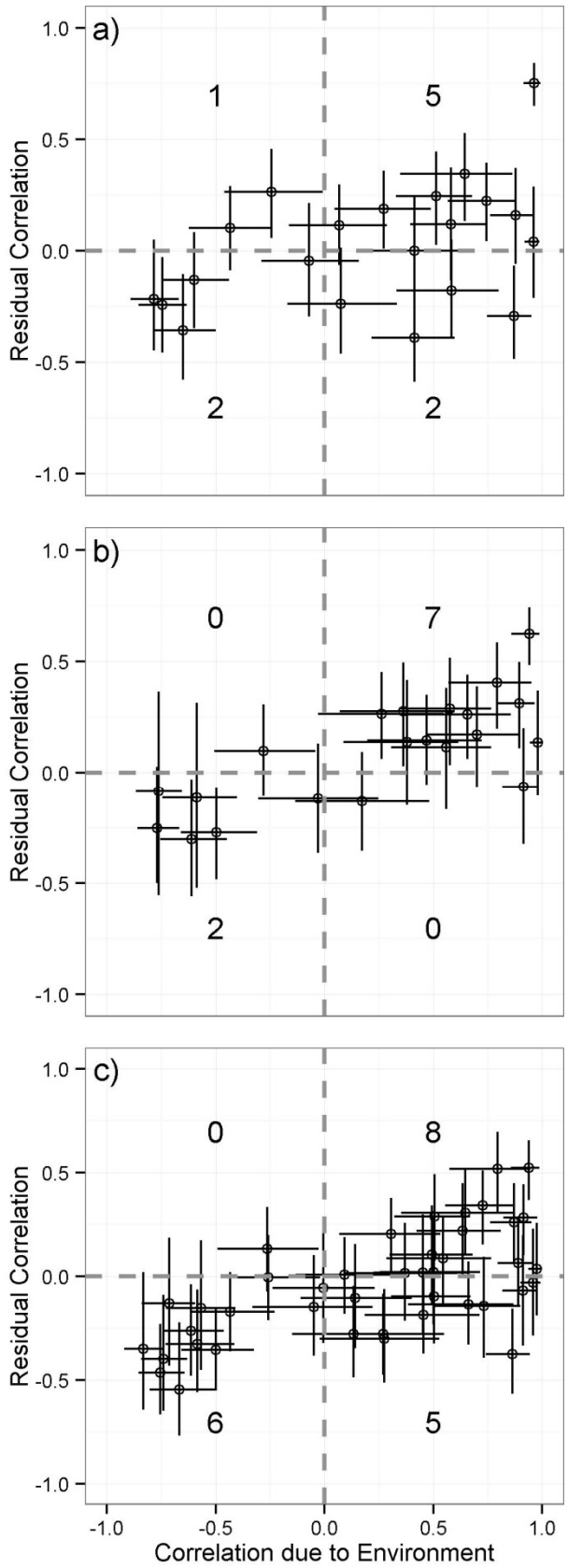

Figure 4-6 Correlation due to the environment compared to residual correlation for each pair of heterospecific a) trees, b) seedlings, and c) trees with heterospecifc seedlings. Numbers represent the number of significant correlations in each quadrant.

negative residual correlation with heterospecific trees. This is most evident for lodgepole pine seedlings, which showed significant negative residual correlations with Engelmann spruce and subalpine fir trees despite a positive residual association between these species and lodgepole pine trees (Fig. 4-7). Ponderosa pine is the exception; trees exhibited negative residual correlations with many other species, whereas seedlings show no significant residual correlations (Fig. 4-4).

Table 4-4 Residual correlations for each pair of species. Stars denote estimates with credible intervals that do not overlap zero. Bold numbers highlight the residual correlation between trees and conspecific seedlings.

		Ponderosa Pine		Douglas-fir		Lodgepole Pine		Quaking Aspen		Limber Pine		Subalpine Fir		Engelmann Spruce	
		T	S	T	S	T	S	T	S	T	S	T	S	T	S
Ponderosa Pine	T	1													
	S	***0.29****	1												
Douglas-fir	T	0.04	0	1											
	S	0.04	0.13	***0.65****	1										
Lodgepole Pine	T	-0.39*	-0.1	0.24*	0.29*	1									
	S	-0.30*	0.14	0.02	0.27*	***0.39****	1								
Quaking Aspen	T	-0.29*	-0.1	0.16	0.06	0.22*	-0.14	1							
	S	-0.38*	-0.1	0.26*	0.31*	0.34*	0.26*	***0.61****	1						
Limber Pine	T	0.00	0.02	0.12	0.1	0.34*	0.31*	-0.18	0.09	1					
	S	0.02	0.11	0.22	0.29*	0.52*	0.4*	-0.14	0.17	***0.69****	1				
Subalpine Fir	T	-0.36*	-0.2	-0.13	-0.26*	0.19*	-0.19*	0.26*	-0.01	-0.24	-0.28*	1			
	S	-0.55*	-0.1	-0.33*	-0.3*	0.20*	0.14	0.13	0.1	-0.11	-0.13	***0.62****	1		
Engelmann Spruce	T	-0.22	-0.1	-0.24*	-0.47*	0.11	-0.28*	0.10	-0.17	-0.04	-0.15	0.75*	0.52*	1	
	S	-0.35	-0.1	-0.4*	-0.25	0.01	0.26*	-0.36*	-0.27*	-0.06	-0.12	0.28*	0.62*	***0.23****	1

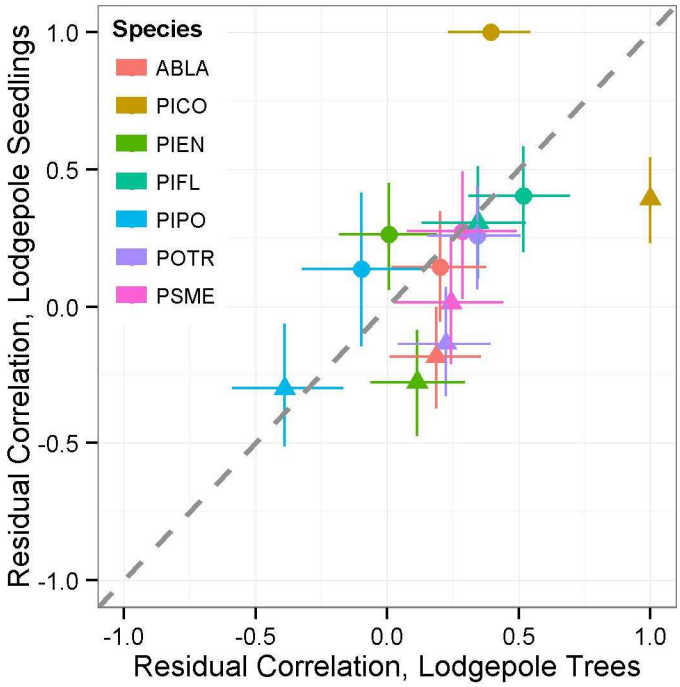

Figure 4-7 Residual correlation of lodgepole pine trees with other species compared to that of lodgepole pine seedlings with other species. Triangles represent trees, circles represent seedlings. Species abbreviations are listed in Table 4-1.

4.4 Discussion

The presence of significant residual correlations in the joint distribution model supports our hypothesis that the distribution of rocky mountain tree species is poorly explained by climatic factors alone. Similarly, the increased precision of parameter estimates from the joint model relative to the single-species models fit our expectation that modelling species jointly would improve parameter estimates by "borrowing strength" based on the parameters of correlated species (Ovaskainen & Soininen, 2011). The species with the most noticeable differences in precision tended to be less prevalent. Ovaskainen & Soininen (2011) observed a similar pattern, noting that joint distribution models can improve parameter estimates for rare species. The parameter estimates for aspen, however, did not differ noticeably between the joint and single models, despite the fact that the prevalence of aspen trees was lower than that of ponderosa pine (Table 4-1). This suggests that the differences are not merely an artefact of sample size, and may instead have an ecological explanation.

One possible explanation is that the landscape-scale ranges of limber pine and ponderosa pine are more closely controlled by un-measured environmental factors that happen to be correlated with the climate variables included in our model. This would help explain the puzzling positive bias in effect size of parameters from the single models relative to the joint model. Single models overestimate the importance of variables such as temperature and precipitation because they can serve as proxies for un-modeled variables such as fire history and competition. Ponderosa pine, for instance, is adapted to frequent surface fires and recruitment typically depends on precipitation immediately following a fire, rather than the long-term average used in our model. Average precipitation is correlated with fire frequency,

however, and the negative residual correlation between ponderosa and other species that are not fire-adapted but do respond to precipitation may allow the joint model to determine a more accurate parameter estimate for this variable.

While the precise cause of residual correlations between species is impossible to determine from a correlative study, observed patterns suggest several interesting hypotheses regarding factors that influence species distributions. Knowledge of the ecology of each species may aid in the interpretation of residual correlations (Latimer *et al.*, 2009), as can comparison to the correlation explained by the modeled environmental niche (Pollock *et al.*, 2014). Finally, differences in the residual correlations of trees vs. conspecific seedlings can also contribute to our understanding of covariance patterns between species.

If two species with strong positive correlation in the modeled environmental niche also exhibit positive residual correlation, this may suggest a shared response to additional climatic or environmental variables, though it is impossible to rule out the possibility of a facilitative interaction between the species. Engelmann spruce and subalpine fir are biologically similar and frequently co-occur, which is reflected by the high degree of correlation in their modelled environmental niche (.96 for trees). The two species also exhibit significant residual correlation (.75 for trees). Given the similar biology of these species, it is likely that this residual correlation represents a similar response to un-modeled abiotic factors. In contrast, ponderosa pine and Douglas-fir also share a similar environmental niche (correlation due to environment of .96 for trees), yet do not have a significant residual correlation. Here, the environmental and climatic predictor variables included in the model may be sufficient to characterize patterns of co-occurrence between these species.

The negative residual correlations between ponderosa pine and several other species suggest that its landscape-scale distribution may still depend on other un-modeled factors such as disturbance history. If the only negative residual correlations were between ponderosa and species with overlapping climatic niches, such as lodgepole pine and Douglas-fir, we might suspect competition. However the negative residual correlation with Engelmann spruce and subalpine fir, two high-elevation species rarely found with ponderosa, suggests that other underlying abiotic factors are more likely the cause.

Where the sign of the environmental vs. residual correlation differs, interpretation becomes more complicated. Lodgepole pine seedlings had a positive environmental correlation with trees of both Engelmann spruce and subalpine fir, yet a negative residual correlation. Lodgepole pine seedlings are shade-intolerant and may be unlikely to co-occur with spruce and fir trees because their dense canopies do not allow sufficient light to reach the forest floor. The residual correlations between lodgepole pine *trees* and trees of both spruce and fir were either positive or insignificant, as were the residual correlations between lodgepole pine seedlings and seedlings of spruce and fir. This lends further support to our hypothesis that the negative residual correlations described above are driven by competitive exclusion.

In contrast, both seedlings and trees of lodgepole pine had negative residual correlations with ponderosa pine trees. Here, the similarity in response of trees and seedlings may suggest a divergent response to un-modeled abiotic factors between the species. Ponderosa pine trees exhibited a similar pattern in its correlations with aspen, which closely resembles lodgepole pine in that recruitment of both species is typically associated with stand-replacing fires. The positive residual correlation between aspen trees and lodgepole pine trees

also suggests that these species have a similar response to unmeasured covariates, and it is plausible to assume that their negative residual correlation with ponderosa pine may be due to the same factor. Fires in ponderosa pine stands within our study area are rarely stand-replacing (Kaufmann *et al.*, 2006), resulting in an intact canopy that can preclude establishment of aspen and lodgepole pine.

The positive residual correlations observed for trees and conspecific seedlings of each species were expected, and may stem from dispersal limitation, important but un-modeled environmental factors, or likely some combination of both. The residual correlation between trees and seedlings of Engelmann spruce was notably lower than several other species, which could be explained by the superior dispersal distance of its seeds but may also indicate that annual temperature and precipitation do a better job of capturing its environmental niche than for other species.

4.5 Conclusion

While broad-scale climatic drivers may shape the fundamental niche of species, we found evidence that the realized niche of rocky mountain trees is also influenced by other factors. Residual correlations between species suggest either biotic interactions or a shared response to unmeasured abiotic factors, and can be both positive and negative for the species included in our study. In some species, patterns of residual correlation differed between life stages, suggesting that the regeneration niche may be influenced by factors that exert a lesser impact on the distribution of mature trees.

Failing to account for residual correlation between species can result in biased parameter estimates, and may over-estimate the significance of parameters that are not

biologically relevant, yet are correlated with important unmeasured covariates. If the sole goal is prediction, parameter estimates are of little interest in themselves, and the predictive accuracy was not significantly improved by modelling species jointly. For predicting how climate change may impact future distributions, however, generating precise and accurate parameter estimates for climatic variables is more critical because climate my become decoupled from any underlying factors that influence the regression coefficients in the single-species model. While joint distribution models are no substitution for experiments that can isolate the true effect of climatic variables on different species, they may provide a more cost-effective way estimate how species respond to climate using existing data.

5 Conclusions

My dissertation research examined the controls on tree species distributions and range limits in mountain landscapes. Throughout, I have highlighted the importance of non-climatic factors that affect species distributions and shown the importance of considering these when examining patterns of climate-driven range shifts. Tree species distributions will not uniformly shift upslope as the climate warms, and non-climatic factors such as biotic processes and disturbance legacies should be incorporated into models that seek to forecast future tree species distributions.

The global review of range shift studies demonstrated that many different factors can constrain tree migrations and result in observed migration rates that are slower than expected based on the rate of temperature change. The case study of lodgepole pine ecotones was entirely consistent with these findings; I found that lodgepole pine range margins have shifted very little in Rocky Mountain National Park, despite a warming climate and a widespread disturbance event that reduced competition. I had expected that mountain pine beetle disturbance would facilitate recruitment of species better adapted to the current climate, but the impact on patterns of seedling dispersion turned out to be minimal. Individual species may vary in their ability to take advantage of new recruitment opportunities presented by the interaction between insect outbreaks and a warming climate, and fire-adapted species may not respond as strongly to biological disturbances. By extending my investigation of non-climatic controls on tree species distributions to the landscape scale, I demonstrated that the patterns of co-occurrence among tree species cannot be explained by climate alone. Patterns of residual

correlations between species suggest that unmeasured factors, likely competition in many cases, are important in determining the seedling distributions of some species, while fire history may explain the residual covariance in tree distributions.

Together, this body of work suggests a new framework for understanding migration lags by considering both non-climatic range constraint and the temporal context of range shifts. My research demonstrates the importance of considering a broader suite of variables when forecasting how forest communities may change in the future. I expect that future tree distributions will not uniformly shift upslope, as disturbance patterns, landscape context, and species-specific migration constraints complicate range dynamics. Failure to account for these additional factors when forecasting change will likely compromise the accuracy of predictions. Future research should focus on quantifying the effects of non-climatic range constraints and refining modelling techniques capable of incorporating a broader suite of variables.

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