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Scale-dependent Contributions of Abiotic and Biotic Factors to Tree Species Composition Patterns in the US Rocky Mountains

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composition patterns in the US Rocky Mountains, Ph.D., Program in Ecology, May 2016.

Scale-dependence is recognized as a ubiquitous feature of ecological systems. Ecologists have traditionally hypothesized a hierarchy of factors affecting the composition of ecological communities, with biotic interactions exerting a dominant influence at fine spatial scales, and abiotic factors such as climate driving patterns at broad spatial scales. However, the role of biotic interactions at macroecological scales has been increasingly questioned, with many ecologists hypothesizing that biotic interactions may have discernable effects on species distributions. Here, I evaluate the relative effects of climate and species interactions on composition patterns of tree species in the US Rocky Mountains. At fine spatial scales, I model the radial growth of trees along montane ecotones and evaluate sensitivity to temperature, precipitation, and interspecific competition. Climate has an overwhelming influence on radial growth of all species, and interactions among co-occurring tree species appear to be weak. Scaling the effects of biotic interactions to macroecological scales presents a complex statistical challenge, and I demonstrate that commonly used community-level models are an inappropriate technique, as they average species responses and fail to accurately reproduce co-occurrence patterns. As an alternative to community-level models, I use a novel Joint Species Distribution Modeling approach to demonstrate that the co-occurrence patterns of Rocky Mountain trees are overwhelmingly explained by climate, with little influence of interactions among tree species. I review evidence for the factors shaping North American tree species distributions and argue that species interactions may fail to affect macroecological patterns among Rocky Mountain tree species due to a historical legacy that has promoted strong responses to climate. Current tree distributions predominantly reflect the influences of climate with a likely influence of human land use.

SCALE-DEPENDENT CONTRIBUTIONS OF ABIOTIC AND BIOTIC FACTORS TO TREE
SPECIES COMPOSITION PATTERNS IN THE US ROCKY MOUNTAINS

by

Paige Elise Parry

A dissertation submitted to the University of Wyoming in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY

Laramie, Wyoming

May 2016

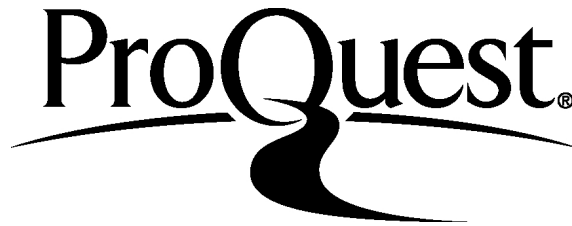
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INTRODUCTION

“The problem of pattern and scale is the central problem in ecology, unifying population biology and ecosystem science, and marrying basic and applied ecology.” –Richard Levins 1992, pp 1943

The field of ecology has often been characterized by a lack of generalities and unifying principles, a feature that distinguishes ecology from many other scientific fields such as physics. Many, if not all ecological phenomena appear to be context-dependent, varying across species, systems, space, and time, with differential explanatory value in different contexts (Whittaker et al. 2001). The lack of unifying principles in ecology has often been seen as an impediment to progress, yet it has been argued that context-dependence itself may unite ecological phenomena and provide some level of theoretical congruence and unification to the field of ecology (Schneider 2001). Spatial scale is one particular ecological context across which the importance and effects of ecological factors vary. Spatial scale-dependence is now recognized as a ubiquitous characteristic of ecological systems (Pearson & Dawson 2003; Sandel 2015), but did not become a major consideration among ecologists until the late 1970s and early 1980s. At this time, impressive advances in computation and analytical capacity allowed ecologists to explore patterns and processes in new ways, leading to a heightened recognition of spatial scale-dependence (Schneider 2001; McGill 2010). Scale-dependence is now well engrained into the field of ecology, and ecologists are increasingly taking up the task of quantifying precisely how patterns and processes vary across spatial scales (Sandel 2015). This effort holds tremendous

potential to bring unification and congruence to ecology, but for many ecological factors we are still lacking a general understanding of when scale-dependence will and will not operate.

Understanding the scale-dependence of biotic interactions, in particular, has been central to this effort. Substantial investigation and debate has focused on the scale-dependence of biotic interactions, with little consensus emerging. While some ecologists argue that biotic interactions matter primarily for patterns observed at local spatial scales, others contend that, within the appropriate context, biotic interactions can generate effects that influence species distributions observed at macroecological scales. This debate centers on several important characteristics of biotic interactions. Chief among these is the fact that biotic interactions themselves are inherently local as they occur between individual organisms (McGill 2010; Clark et al. 2014; Sandel 2015). Another argument for the local nature of biotic interactions emphasizes the coarse resolution at which species distributions are observed and the consequences of this resolution for observing any effects of biotic interactions. Specifically, biotic interactions may contribute to local species patterns, such as growth, productivity and abundance, but the fine-scale variation in these effects is averaged out when occurrence is evaluated across large grid cells, as when assessing macroecological species composition patterns. Thus, it has been proposed that biotic interactions and their effects may only be observable with fine-grained spatial characterization, specifically at scales less than 1km^2 (Pearson & Dawson 2003; Soberón & Nakamura 2009). This line of thinking has led some authors to propose a hierarchy of ecological factors affecting species composition patterns across spatial scales (**Fig 1.**), with climate operating as the dominant factor at broad spatial scales. As spatial scale decreases, topography and land cover may increasingly contribute to species composition patterns, and biotic interactions will be most significant at very local scales (Pearson & Dawson 2003; Cazalles et al. 2015).

Still, other ecologists have argued that biotic interactions may exert impacts that affect species distribution patterns observed at macroecological scales. While biotic interactions themselves occur between individuals existing at local scales, the sum of those interactions may occur across a large enough spatial extent to produce effects that observably impact species distributions (Sandel 2015). Particularly when species respond to the same underlying environmental gradients, pairwise interactions are likely to generate consistent effects across species distributions (Clark et al. 2014).

Despite considerable research effort, empirical evidence regarding the scale-dependence of biotic interactions is still lacking. Nonetheless, substantial theoretical advances have provided a general outline of the contexts in which we may expect the effects of biotic interactions to be scale-dependent, and in which contexts biotic interactions may be expected to act consistently across spatial scales. In particular, mathematical models have demonstrated that both the interaction under consideration and the strength of the interaction will determine the scale-dependence of biotic interactions (Araújo & Rozenfeld 2014; Godsoe et al. 2015). Positive biotic interactions, such as mutualism and commensalism, can be expected to generate effects that are observable across spatial scales, while the spatial signature of negative biotic interactions, including competition and amensalism, declines with increasing scale (Araújo & Rozenfeld 2014). This occurs because negative biotic interactions are rarely strong enough to exclude species from sufficiently large patches of habitat to be detectable at the coarse spatial resolutions that characterize species distributions (Whittaker et al. 2001). However, where sufficiently strong negative interactions exist to prevent species from co-existing across large patches of habitat, biotic interactions may have a notable effect on species distributions (**Fig. 2**; Godsoe et al. 2015).

Although these hypotheses provide useful guidance for empirical studies, it is still unclear to what degree they hold true in natural settings. It should also be noted that most theoretical work on this subject has evaluated the effects of biotic interactions only in terms of patterns of species co-occurrence. However, at local scales, biotic interactions may be an important determinant of other species composition patterns such as growth and abundance. The ability of these effects to impact patterns at broader spatial scales is generally unknown.

In reality, representing the impacts of biotic interactions at broad spatial scales is a difficult task, and this difficulty often impedes progress towards understanding the scale-dependencies of biotic interactions. Complications arise from the fact that interactions are unlikely to be static over the full distribution of a species and thus may not be amenable to characterization in species distribution models, which infer a general relationship across a species' distribution (Soberón & Nakamura 2009). Additionally, appropriately aggregating interactions that occur between individuals to a measurement relevant to macroecological scales is difficult to achieve without losing critical information or distorting relationships (Clark et al. 2014). Finally, biotic interactions may be closely correlated with climate or other broad-scale variables used to define species distributions, and evaluating these factors in tandem may mask true relationships (Soberón & Nakamura 2009; Pollock et al. 2014). Despite these difficulties, understanding scale-dependencies in the factors generating ecological patterns has been identified as a critical challenge in ecology, particularly as accurate predictions of species across broad spatial scales become increasingly necessary (Araújo & Rozenfeld 2014).

Clarity on the scale-dependencies of biotic interactions can be provided by studies that evaluate the importance of multiple ecological factors across various spatial scales and species composition patterns (Whittaker et al. 2001; McGill 2010; Sandel 2015). In this dissertation, I

take up this challenge by evaluating the relative importance of climate and interspecific interactions across spatial scales and species composition patterns. Empirical studies of the effects of biotic interactions on species distributions have historically focused on competition due to its perceived ubiquity, and I extend that focus by evaluating scale-dependencies in the impacts of interactions occurring within the same trophic level (i.e. competition and facilitation). Rather than attempting to explicitly model competition, which, as noted, is a function of individual interactions that are not easily represented at the macroecological scale (Clark et al. 2014), I focus on evaluating the outcomes of biotic interactions on species composition patterns across spatial scales to infer the importance of underlying biotic interactions.

In Chapter 1, I explore the relative impacts of climate and competition at a local scale. At fine spatial scales, the patterns that may be impacted most strongly by species interactions may differ from those patterns observed across broad spatial scales. In particular, biotic interactions have been demonstrated in many systems to influence various aspects of species performance and demography, including individual growth. In this chapter, I quantify the impacts of competition and climate on the radial growth of three tree species along ecotones in the US Rocky Mountains. These ecotones represent local distribution edges and, as such, performance along ecotones is likely to be an important determinant of overall distribution patterns. I demonstrate that climate has greater relative importance for tree radial growth than competition at both upper and lower distribution edges. This finding clarifies the role of biotic interactions at local scales in this particular species context and indicates a dominant role for climate even at local scales.

In Chapter 2, I extend the search for an appropriate method to represent the impacts of species interactions at macroecological scales by evaluating the utility of community-level modeling approaches relative to species distribution models (SDMs). Community-level models (CLMs) simultaneously consider the distributions of multiple species and have been proposed as a method to account for the effects of interspecific interactions on species distributions. I demonstrate that CLMs perform very similarly to SDMs, yet predict a higher degree of spatial overlap (i.e. co-occurrence between species). CLMs average environmental responses across multiple species, effectively expanding the observed climate envelope of individual species and producing inaccurate predictions. I conclude that CLMs are an inappropriate tool for assessing the impacts of biotic interactions at macroecological scales.

As an alternative to the CLM approach, in Chapter 3 I apply a Joint Species Distribution Model (JSDM) to evaluate and predict the co-occurrence of multiple species. This approach is unique in its ability to ascribe co-occurrence to either shared environmental responses or to biotic interactions, and provides a powerful assessment of the contexts in which biotic interactions impact species distributions. I utilize this approach with co-occurrence data of ten dominant tree species occurring across the U.S. Rocky Mountains, and demonstrate that biotic interactions among these species have little influence on distributions relative to climate.

In Chapter 4, I outline a conceptual framework for North American tree species distributions that synthesizes relevant literature in a comprehensive review. This framework rests on an exploration of historical context, which provides consistency and parsimony for the variety of findings regarding the factors shaping tree species distributions across North America. In general, this review demonstrates that biotic interactions have seldom been shown to matter for species distributions in this particular ecological context. The conceptual consistencies outlined

in this chapter demonstrate that the concept of scale-dependency can provide unification across ecological phenomena.

Cumulatively, the work represented in this dissertation represents a significant advancement in understanding the scale-dependencies of an important ecological process. I conclude by returning to the issue of scale-dependency of biotic interactions and rely on the information provided throughout this dissertation to propose an improved hierarchy of the factors affecting species composition patterns, specifically as they pertain to North American, and in particular Rocky Mountain trees.

References

- Araújo, MB, Rozenfeld, A. 2014. The geographic scaling of biotic interactions. *Ecography* 37: 406-415.
- Cazalles, K, Mouquet, N, Mouillot, D, Gravel, D. 2015. On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography* DOI: 10.1111/ecog.01714
- Clark, JS, Gelfand, AE, Woodall, CW, Zhu, K. 2014. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications* 24: 990-999.
- Godsoe, W, Murray, R, Plank, MJ. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38: 001-009.
- Levins, SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- McGill, BJ. 2010. Matters of scale. *Science* 328: 575-576.
- Pearson, RG, Dawson, TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.
- Pollock, LJ, Tingley, R, Morris, WK, Golding, n, O'Hara, RB, Parris, KM, Vesk, PA, McCarthy, MA. 2014. Understanding co-occurrence by modeling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5: 397-406.
- Sandel, B. 2015. Towards a taxonomy of spatial scale-dependence. *Ecography* 38: 358-369.
- Schneider, DC. 2001. The rise of the concept of scale in ecology. *BioScience* 51: 545-553.

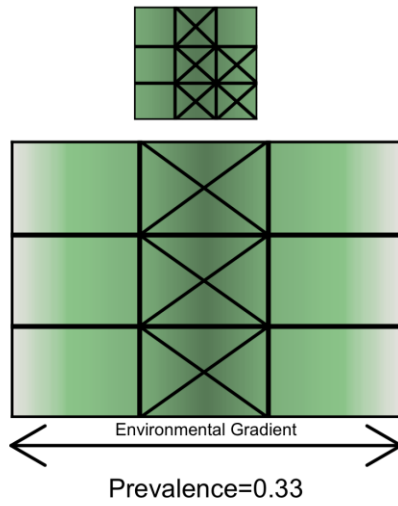
- Soberón, J, Nakamura, M. 2009. Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences* 106: 19644-19650.
- Whittaker, RJ, Willis, KJ, Field, R. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28: 453-470.

FIGURES

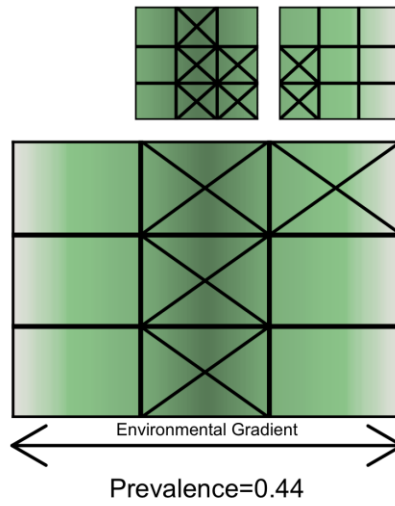
Figure 1. Hierarchical schematic of the spatial scales at which multiple ecological factors are hypothesized to be influential. This hierarchy represents traditional thinking on scale dependencies and hypothesizes that biotic interactions will only influence species composition patterns at fine spatial scales, ranging from the micro to the local extent. Reproduced with permission from Pearson & Dawson (2003).

Figure 2. The theoretical effects of species interactions across an environmental gradient. In the absence of biotic interactions (a), a species can be hypothesized to occupy all suitable habitat, as is demonstrated by occurrence (X) across both fine (upper panel) and coarse (lower panel) spatial resolutions. Where biotic interactions result in facilitation (b), a species may extend its distribution into formerly unsuitable habitat. In this instance, facilitation is strong enough to allow a species to extend into two neighboring fine resolution grid cells, which expands its distribution into one neighboring coarse resolution cell, thereby affecting its distribution (prevalence=0.44). If competition occurs with the same strength (c), a species may be restricted from occurring in suitable habitat, though this effect is unlikely to be large enough to be observed at a coarse spatial resolution. However, if competition is strong enough to exclude a species from a large patch of habitat (d), the effects may be detectable at a coarse spatial resolution, thereby constraining the species distribution (prevalence=0.22).

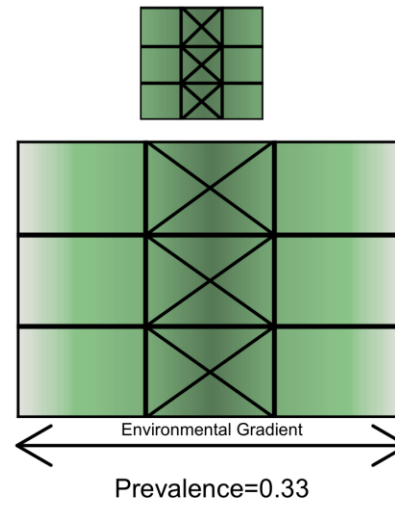
a) no interactions



b) facilitation



c) competition



d) competitive exclusion

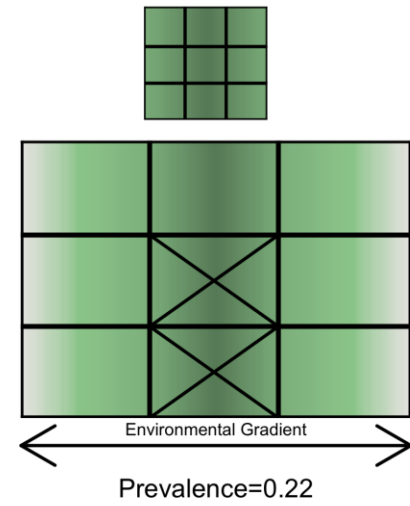


Figure 2

CHAPTER 1: THE RELATIVE INFLUENCES OF CLIMATE AND COMPETITION ON TREE GROWTH ALONG MONTANE ECOTONES IN THE ROCKY MOUNTAINS

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1.1 ABSTRACT

Distribution shifts of tree species are likely to be highly dependent upon population performance at distribution edges. Understanding the drivers of aspects of performance, such as growth, at distribution edges is thus crucial to accurately predicting responses of tree species to climate change. Here, we use a Bayesian model and sensitivity analysis to partition the effects of climate and crowding, as a metric of competition, on radial growth of three dominant conifer species along montane ecotones in the Rocky Mountains. These ecotones represent upper and lower distribution edges of two species, and span the distribution interior of the third species. Our results indicate a greater influence of climate (i.e. temperature and precipitation) than crowding on radial growth. Competition importance appears to increase towards regions of more favorable growing conditions, and precise responses to crowding and climate vary across species. Overall, our results suggest that climate will likely be the most important determinant of changes in tree growth at distribution edges of these montane conifers under future climate.

1.2 INTRODUCTION

Rapid changes in temperature and precipitation over the next century are predicted to drive notable shifts in plant distributions (Parmesan 2006; McKenney et al. 2007; Kelly & Goulden 2008). Understanding the factors driving population performance at distribution edges will help to clarify expected species responses to future climatic conditions, as these edges likely represent either climatically-induced physiological limitations or competition-related limitations on population growth that may vary under future climate (Stohlgren & Bachand 1997). While a number of studies have identified factors controlling species occurrence at distribution edges (e.g. Case et al. 2005; Morin et al. 2007; Barbeito et al. 2012; Schurr et al. 2012; Hargreaves et al. 2014), growth rates of individuals, which may be a better indicator of overall population performance, have received less attention (Lasky et al. 2013; Bin et al. 2015). Distribution shifts ultimately result from spatial and temporal variation in demographic rates (establishment, growth, mortality, dispersal) resulting from both abiotic and biotic influences (Pulliam 2000; Knutson & Pyke 2008; Clark et al. 2011; Schurr et al. 2012; HilleRisLambers et al. 2013; Normand et al. 2014). While establishment and mortality events at distribution edges directly underlie species persistence and migration (Serra-Diaz et al. 2015), these demographic responses are often difficult to observe across broad regions without large-scale longitudinal studies (e.g. Clark et al. 2011). Growth, however, is more easily observed than alternative demographic rates and is strongly related to both fecundity and mortality risk through individual nutritional status (Kobe et al. 1995; van Mantgem et al. 2003; Wyckoff & Clark 2005; Clark et al. 2011). Growth can thus act as an integrative indicator of population performance that reflects sensitivity to both broad-scale abiotic drivers and local resource dynamics (McMahon et al. 2010; Clark et al. 2011). Additionally, growth responds rapidly to climate change, allowing growth rates to act as a

particularly useful indicator of population sensitivity to climate change (McMahon et al. 2010; Renwick et al. 2015).

Both climate and competition have been recognized as important controls on plant growth, though their relative importance at distribution edges remains uncertain (Normand et al. 2014). Climate has been consistently shown to limit growth of temperate trees at range and distribution edges (e.g. Grabherr et al. 1994; Cannone et al. 2007; Morin et al. 2007; Barbeito et al. 2012; Case & Duncan 2014), though its influence has rarely been evaluated relative to that of competition (but see Ettinger et al. 2011; Ettinger et al. 2013). Where relative effects have been evaluated, the focus has been primarily on edges occurring at treeline (Case & Duncan 2014), and rarely for distribution edges that occur within closed-canopy forests (but see Ettinger et al. 2011, 2013). The importance of climate relative to competition is generally expected to increase in regions of high abiotic stress (Tilman 1982; Keddy 1989; Gaudet & Keddy 1995), and several empirical studies have corroborated this theory (Coomes & Allen 2007; Meier et al. 2010; Kunstler et al. 2011; Gómez-Aparicio et al. 2011; Hargreaves et al. 2014). Within closed-canopy forests, competition is expected to be greater than at forest edges owing to dense tree cover, and dense canopies may buffer climate effects (Holman & Peterson 2006; Ettinger et al. 2011; HilleRisLambers et al. 2013; Dobrowski et al. 2015). Distribution edges within closed canopies are encountered by many species in mountain environments, and resolving drivers of growth variation at such edges is crucial to understanding population and distribution responses to climate change.

In this study, we use a Bayesian model to directly quantify the contributions of climate (i.e. temperature and precipitation) and a metric of competition (i.e. crowding) to tree radial growth for three abundant conifer species (*Pinus contorta* var. *latifolia* [Engelm.], *Pinus*

ponderosa var. *scopulorum* [Engelm.], *Pseudotsuga menziesii* var. *menziesii* [Mirb.]), across closed-canopy ecotones in the Central and Northern U.S. Rocky Mountains. These ecotones represent upper distribution edges of *Pinus ponderosa* and lower distribution edges of *Pinus contorta*. *Pseudotsuga menziesii* co-occurs with both *Pinus* species at mid-elevations, and thus has its distribution interior in these ecotone regions (Peet 1981; Sherriff & Veblen 2006; Schoennagel et al. 2011). The focal species have been studied extensively across our study region, and previous studies have identified distinct life-history traits that may influence each species' sensitivity to climate and competition. In the Central and Northern Rocky Mountains, *Pinus contorta* and *Pinus ponderosa*, both relatively shade-intolerant species, regenerate rapidly following disturbance (Peet 1981; Burns & Honkala 1990; Hood et al. 2012). Growth of *Pinus contorta* is thought to be regulated by high intraspecific competition in dense, regenerating stands (Day 1972; Peet 1981; Knowles & Grant 1983; Burns & Honkala 1990; Copenhaver & Tinker 2014). *Pinus ponderosa* growth has been found to be highly correlated with temperature (Carnwath et al. 2012), as it can withstand a broad range of precipitation conditions due to deep tap roots (Burns & Honkala 1990; Nystrom Mast et al. 1998). *Pseudotsuga menziesii* is a moderately shade-tolerant species that generally establishes in canopy gaps (Burns & Honkala 1990; Schoennagel et al. 2004; Keeling et al. 2006; Devine & Harrington 2008; LeMay et al. 2009; Briggs et al. 2012) and prefers mid-elevation habitats characterized by moderate temperature and precipitation (Sterba & Monserud 1995; LeMay et al. 2009). *Pseudotsuga menziesii* tends to act as a later-seral species in mid-elevation forests in this region, replacing both *Pinus ponderosa* and *Pinus contorta* with sufficient time between stand-replacing fire events (Peet 1981; Burns & Honkala 1990; Scott et al. 1998; Baker et al. 2007).

Our objectives were to 1) quantify the relative influences of climate and crowding on tree radial growth along closed-canopy ecotones for our focal species and; 2) assess variation in the relative importance of competition among species and across climate gradients that are relevant in the context of climate change. We hypothesize that climate effects will be greater than the effects of crowding at distribution edges. Further, we hypothesize that the importance of competition among individuals of each species will increase towards more favorable climatic conditions.

1.3 MATERIALS AND METHODS

Field Data

Tree radial growth data were collected from a series of plots nested within 3 sites in the Central and Northern U.S. Rocky Mountains during June and July of 2014. Sampling sites were selected to capture the range of conditions across which the focal species co-occur, and were located in the montane zones of the Bighorn National Forest, WY, Bitterroot National Forest, MT, and Ashley National Forest, UT. All sites are characterized by elevational zonation of dominant tree species with mixed stands occurring in regions of overlap. Detailed site descriptions may be found in **Appendix 1**.

At each study site, 5-6 sampling transects were established to encompass the shift in dominant vegetation from upper-elevation *Pinus contorta* stands to lower-elevation *Pinus ponderosa* stands. While our approach of sampling across only one ecotone type does not allow us to evaluate factors controlling growth at upper and lower distribution edges of each individual species, it does enable us to draw general inference as to the relative influences of climate and crowding on growth at closed-canopy distribution edges without magnifying the influence of

unmeasured factors that may be included by sampling across a broader elevational range (e.g. additional species, edaphic factors, radiation, microclimate). This asymmetric sampling design is consistent with similar studies (Ettinger et al. 2011; Ettinger et al. 2013). Transect number was limited by availability of *Pinus contorta* – *Pseudotsuga menziesii* – *Pinus ponderosa* ecotones in each site. Each transect consisted of three 20x20m (0.04 ha) sampling plots spaced equidistantly. Transect length varied according to the length of the transition zone between dominant overstory species.

To estimate the impact of neighborhood basal area on tree radial growth, we collected neighborhood data for a three mature trees of each represented focal species in each plot. Each focal tree was measured at DBH (diameter at breast height, 1.37m) and cored to the pith. Within an 11m radius of each focal tree, DBH was recorded for all neighboring trees belonging to one of the three focal species. An 11m neighborhood radius is consistent with recommendations from other neighborhood studies conducted within montane forests of the Rocky Mountains (Woodall et al. 2003; Contreras et al. 2011), and corresponds with roughly 3.5 times the average crown radius, or the estimated zone of competitive influence (Lorimer et al. 1983). Other species such as *Populus tremuloides* and *Abies lasiocarpa* were present in several plots, but made up only a negligible portion of neighborhood basal area and were thus ignored during data collection.

Cores extracted from focal trees were processed according to standard procedures, and ring widths were measured using an ACU-RITE Velmex tree-ring measurement system (HEIDENHAIN Corporation, Schaumburg, IL). Cores were visually cross-dated (Stokes & Smiley 1986), and increments from the most recent 10 years of growth (2004 through 2013) were averaged to relate mean annual growth increment to climate and neighborhood competition (i.e. crowding). Only the most recent 10 years were retained because neighborhood data was not

deemed to be reliable beyond this range; unknown growth, regeneration and mortality events occurring within each neighborhood could have resulted in substantial temporal variation in neighborhood basal area beyond the temporal range included in this study. In total, 172 tree cores and corresponding neighborhoods were retained for analysis: 63 of *Pinus contorta*, 49 of *Pinus ponderosa*, and 60 of *Pseudotsuga menziesii*.

Climate Data

Climate data for each plot was extracted from the ClimateWNA database. ClimateWNA provides high-resolution climate estimates suitable for integration with our plot-level data by downscaling monthly PRISM data from Western North America to specific point estimates using bilinear interpretation (Wang et al. 2012). As a major aim of this study was to quantify changes in growth across environmental gradients that are relevant in the context of climate change, we selected climate variables that have, in some cases, already changed substantially from long-term mean values, and are forecast to continue to change in the future (Dobrowski et al. 2013; IPCC 2013). Initial variables selected were mean annual temperature (*MAT*), mean warmest month temperature (*MWMT*), mean annual precipitation (*MAP*), mean annual summer (May to September) precipitation (*MSP*), summer heat-moisture index ($SHM=((MWMT)/(MSP/1000))$), degree-days above 5°C (growing degree-days; *DD5*), frost-free period (*FFP*), and precipitation as snow (*PAS*). Climate variables were averaged across the last 10 years of tree growth to remain consistent with mean radial increment data. All selected temperature variables were found to be highly correlated with one another (Pearson's $r > 0.7$), as were all precipitation variables, necessitating that only one variable from each group be included in the radial growth models. We evaluated each pair of uncorrelated temperature and precipitation variables separately and

retained the best-fitting models (see **Radial Growth Model**). While climate may have an indirect effect on crowding by influencing competitor density, neighborhood basal area in this study was not significantly correlated with any climate variable (Pearson's $r < [0.5]$). Using averaged values likely contributed to the decoupling of climate and crowding in our data. Due to this lack of correlation as well as model limitations associated with sample size (see section 3.3), the effects of crowding and climate were evaluated independently.

Radial Growth Model

Mean radial growth of individual trees over the past ten years was modeled as a function of climate and basal area of competitors using a Bayesian regression model adapted from Kunstler et al. (2011). Tree size and age were initially included as model covariates, but showed insignificant effects for all species and were thus removed from the final models. A separate model was fitted for each of the focal species. Models with both linear and nonlinear climate effects were evaluated for convergence and fit and models with linear climate effects (**Eqn. 1.1**) were retained for all subsequent evaluation and analysis. While plant species have been shown to respond in a Gaussian-like fashion to gradients of temperature and precipitation (Boucher-Lalonde et al. 2012), our data span only a portion of each species' climatic tolerance. As such, only a localized region of each Gaussian-like response is captured, which may be adequately represented by a linear function. Interaction terms were evaluated in initial model formulations (temperature x precipitation, climate x competition), but inclusion of additional terms prevented convergence with the limited sample size of this data set, thus necessitating a simpler model form. The final models regress mean radial growth (G ; $\text{mm}\cdot\text{yr}^{-1}$) for focal tree i in plot p and

transect t against focal tree size measured as DBH or age measured in years (X), climate (T and P), and an index of neighborhood crowding (NI):

Equation 1.1
$$G_{i,p,t} = \frac{\alpha_t + \beta_1 T_p + \beta_2 P_p}{(1 + \frac{NI_i}{\beta_3})^{\beta_4}}$$

α , β_1 , β_2 , β_3 , and β_4 are parameters to be estimated. α is a random effects term that accounts for transect-level variability in abiotic conditions left unexplained by other model parameters. β_1 and β_2 describe the effects of temperature (T_p) and precipitation (P_p), respectively, at each plot. Crowding is represented by a semi-distance-independent neighborhood index (Ledermann 2010), NI_i (**Eqn. 1.2**). Neighborhood indices have a rich history of use for evaluating the effects of competition on tree growth (e.g. Bella 1971; Hegyi 1974; Lorimer 1983; Weigelt & Jolliffe 2003; Canham et al. 2004; Contreras et al. 2011; Baribault & Kobe 2011; Aakala et al. 2013). These indices relate neighbor tree size and proximity to focal tree growth, with the assumption that neighboring trees could be affecting one another through both below- and aboveground mechanisms of competition (Larocque 2002; Woodall et al. 2003; Canham et al. 2004). While resource heterogeneity can contribute to considerable variation in precise competition outcomes, neighborhood indices reflect the general relationship between resource consumption and plant size (Weiner 1985; Weiner & Thomas 1986; Casper & Jackson 1997; Tilman 1982; Weigelt & Jolliffe 2003). The neighborhood index used in this study is a function of the summed basal area (BA ; m^2) of all trees within an 11m radius of the focal tree:

Equation 1.2
$$NI_i = \sum_{j=1}^n BA_{1,j} + BA_{2,j} + BA_{3,j}$$

where 1, 2 and 3 represent the focal species *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii*, respectively. An 11m neighborhood radius is consistent with the estimated zone of competitive influence, or roughly 3.5 times the average crown radius (Lorimer et al 1983; Contreras et al. 2011). We selected BA as our metric of competitor size because it has been demonstrated to scale more directly with the competitive effect of a neighbor than DBH (Canham et al. 2004). A pooled neighborhood index that includes all species of neighbors was necessary to reduce model dimensionality and allow for convergence. This approach does not allow us to directly evaluate the effect of interspecific versus intraspecific crowding, but does enable us to compare the overall effect of crowding to climate effects.

The growth model assumes a logistic relationship between neighborhood basal area (NI) and tree radial growth. In this specification, β_3 adjusts the intercept of the logistic relationship and β_4 represents the slope, which can be used to understand the strength of the neighborhood effect relative to climate effects. A positive value for β_4 represents a negative relationship between tree radial growth and neighborhood basal area, while a negative value represents a positive relationship.

All explanatory variables were re-scaled by dividing by their ranges prior to parameter estimation to aid parameter interpretation and improve model convergence. Radial growth ($G_{i,p,t}$) was modeled as normally distributed, with mean equal to the regression equation and a variance of ε , an estimated parameter that represents the process error. ε was characterized by an inverse gamma distribution, $\sim IG(0.1, 10)$, selected because of its conjugacy with the normal distribution. The transect effect parameter, α , was distributed normally with a prior mean of zero and variance

τ . τ was modeled with a gamma distribution and informative priors. All β parameters were distributed normally with uninformative priors centered on zero with large variance, $\sim N(0,100)$.

Posterior parameter distributions were estimated using Markov Chain Monte Carlo (MCMC) methods within the JAGS 3.13 interface for R (Plummer 2014). Each model was run for 50,000 iterations with a burn-in period of 2,000 iterations to achieve convergence. Iterations were thinned to every 100th value for post-processing. Each model was run with four chains, and convergence was assessed visually.

Separate models were fitted with different pairs of temperature and precipitation variables. The evidence for variable selection was evaluated using posterior predictive loss (PPL), a model fit criterion. This criterion accounts for goodness-of-fit and penalizes for complexity while avoiding specification of the number of parameters, which is often difficult for hierarchical models (Gelfand & Ghosh 1998). The model with the lowest PPL score for each species was selected for subsequent analysis. Model bias was assessed by calculating the slope of the relationship between observed and fitted values; a value of 1 indicates no bias.

Additional Analyses

We performed a sensitivity analysis to determine how model parameters vary in their effects on tree radial growth. Sensitivity analyses are aimed to demonstrate how model output varies across a range of plausible parameter values corresponding with uncertainty in parameter estimates (Saltelli 2005; Larocque et al. 2008; Crosetto & Tarantola 2001). Parameter uncertainty arises from variability in data, and in this way, the sensitivity analysis propagates data variability and parameter uncertainty through to model output. This approach allows for more meaningful interpretation of the influences of individual parameters than relying on a

comparison of parameter point estimates, which may be misleading for poorly-constrained parameters (Larocque et al. 2008; LeBauer et al. 2013). Following the methods for Bayesian sensitivity analysis outlined by LeBauer et al. (2013), we calculated sensitivity as the derivative of the model output with respect to each individual parameter. Parameters were evaluated at seven quantiles from each parameter's posterior distribution corresponding with the posterior mean, the 2.5% quantile, the 97.5% quantile, and quantiles corresponding with 1, 2, and 3 standard deviations on the standard normal distribution. This range was selected to represent the range of plausible values for a given parameter. All other parameters were held constant at their posterior mean while a single parameter was perturbed. The derivative of each relationship between parameter values and model output was used to approximate the model sensitivity to a given parameter. Because parameters were fitted based on re-scaled variables, sensitivity can be compared across parameters (Saltelli 2005). High parameter sensitivity is interpreted as representing a larger influence of that parameter on variation radial growth, and low sensitivity as a smaller influence (Larocque et al. 2008). High sensitivity may arise either as a result of true variability in parameter effects or from poor characterization of a parameter by insufficient or inadequate data.

Model output from the best models for each species was used to evaluate relationships between tree growth and competition importance across the climate gradients encountered in the study region. Fitted radial growth models were used to estimate competition importance for each focal tree. A standard index of competition importance was used, which calculates competition importance as a function of the relative difference of tree growth in the absence and presence of neighbors (**Eqn. 1.3**; Welden & Slauson 1986; Brooker et al. 2005; Kunstler et al. 2011):

Equation 1.3 $C_{imp} = \frac{G_0 - G_c}{\max(G_0) - \min(G_c)}$

where G_0 represents the predicted growth in the absence of competitors (i.e. NI was set at zero to predict G_0) and G_c represents the predicted growth with competitor basal area equal to that observed for each focal tree. Both G_0 and G_c are calculated with temperature and precipitation equal to observed values, allowing G_0 and G_c to vary across climate gradients. It should be noted that our data set included a number of individuals with low crowding, but no individuals for which neighbors were absent. Our G_0 values are thus predicted from the radial growth model and represent an extrapolation from our data. G_c values are also predicted from the model, but fall within the range of sampled values. Our use of modeled G_0 and G_c is consistent with standard applications of these metrics (e.g. Canham et al. 2004; Kunstler et al. 2011). Competition importance for each species was regressed across climate gradients using linear models. Predicted growth in the absence of competition (optimal growth) and modeled growth with observed neighborhood indices (realized growth) were also regressed against climate variables using linear models to assess growth rankings and the effect of crowding on growth across climate gradients.

1.4 RESULTS

Model Fit and Sensitivity

For all species, including *MSP* and *DD5* improved model fit for all species over all other combinations of uncorrelated precipitation and temperature variables (**Table 1.1**). Predicted versus observed growth relationships showed little bias in the models, though *Pseudotsuga*

menziesii growth was predicted with substantially more bias than either *Pinus contorta* or *Pinus ponderosa*.

For all species, mean parameter values showed a positive relationship between growing season temperature (β_1) and growth ($G_{i,p,t}$), and a negative relationship between summer precipitation (β_2) and growth (**Table 1.2**). When mean climate effects were evaluated independently with all other parameters and variables held constant at their mean values, growth varied more with temperature than with precipitation (**Fig. 1.1b,c**). *Pinus contorta* responded most strongly to both temperature and precipitation gradients, followed by *Pinus ponderosa* and *Pseudotsuga menziesii* (**Table 1.2; Fig. 1.1b,c**). In all cases, the competition parameter, β_4 , was positive, indicating a crowding effect of neighboring trees and a reduction in focal tree growth as neighborhood basal area increased. Both crowding parameters together (β_3, β_4) predict substantial decreases in growth with increasing *NI* for all species (**Fig. 1.1a**). The mean transect effects term, α , was characterized by a broad posterior distribution and high variance (τ). Random effects for individual transects varied between positive, negative and insignificant values with no discernable trend. Overall, parameter values showed similar trends for all three species.

The sensitivity analysis revealed a higher sensitivity of modeled radial growth variation of all species to the climate parameters (β_1, β_2) and a lower sensitivity to crowding parameters (β_3, β_4 ; **Table 1.3**). Sensitivity to α , which represents transect effects not accounted for by other parameters, was also greater than sensitivity to either crowding parameter. Sensitivity to crowding parameters was notable for all species, yet substantially lower than sensitivity to climate parameters. Because variance in covariates differs for each species, sensitivity values cannot be compared across species.

Competition Importance

Across all climate gradients, competition importance was generally low (<50%) and invariant for both *Pinus contorta* and *Pinus ponderosa* (**Fig. 1.2a,b**). *Pinus contorta* competition importance showed no significant linear relationship with any climate gradient (linear model $p>0.05$), while *Pinus ponderosa* competition importance declined slightly with increasing *MAP* and *PAS*. In contrast, *Pseudotsuga menziesii* competition importance varied significantly across all climate gradients analyzed (linear model $p<0.05$), increasing with temperature (*DD5*, *MAT*) and decreasing with increasing precipitation (*MSP*, *MAP*, *PAS*; **Fig. 1.2c**). Overall, competition importance was highest for *Pseudotsuga menziesii* in warmer, drier regions, while competition importance for *Pinus ponderosa* was slightly higher in drier regions.

Potential versus Realized Growth

Across all species and climate gradients, predicted optimal growth (growth in the absence of crowding) was generally higher than modeled realized growth in the presence of observed crowding, providing evidence for the role of neighboring trees in limiting focal tree growth (**Fig. 1.3**). For all three species, both realized and optimal growth generally increased with temperature and declined with precipitation. For *Pinus contorta* (**Fig 1.3a**), both optimal and realized growth were greatest in warmer, drier regions. Optimal growth was significantly greater than realized growth across the range of climate conditions, except for under very low *MSP*. On average, *Pinus contorta* realized growth was reduced by 45% from optimal growth.

Pinus ponderosa growth varied across gradients of *DD5*, *MAT*, *MAP* and *PAS*, but both optimal and realized growth were invariant to *MSP* (linear model $P>0.05$) and did not differ

significantly across the *MSP* gradient (**Fig. 1.3b**). Differences between optimal and realized growth were greatest in warmer and drier regions, and no difference was found under cooler, wetter conditions. *Pinus ponderosa* realized growth was reduced by an average of 21% from optimal growth, a lower average reduction than either *Pinus contorta* or *Pseudotsuga menziesii*.

Pseudotsuga menziesii realized growth was also invariant across an *MSP* gradient (linear model $P > 0.05$), yet optimal growth declined significantly with increasing *MSP*. Differences between *Pseudotsuga menziesii* optimal and realized growth were greatest in warmer, drier regions, with no difference in cooler, wetter regions. On average, *Pseudotsuga menziesii* realized growth was reduced by 39% from optimal growth (**Fig. 1.3c**).

1.5 DISCUSSION

The primary aim of this study was to quantify the relative influences of climate and competition on tree radial growth along montane ecotones. By constructing species-specific Bayesian models for tree radial growth, we were able to partition the effects of temperature, precipitation, and crowding. Our results show a greater relative influence of climate effects than crowding effects on radial growth, and relatively low competition importance at distribution edges within closed-canopy forests. In the context of climate change, these findings suggest that climate plays an important role in regulating tree growth at local distribution edges, and is likely to be a strong determinant of future distribution dynamics of these montane trees. However, the effects of crowding were also significant, indicating that crowding may mediate tree responses to future climate along ecotones.

Drivers of Growth Variation

Our findings show generally low competition importance across the range of climate conditions over which we sampled (**Fig. 1.2**) along with lower sensitivity of growth to variation in crowding effects than to variation in climate effects (**Table 1.3**). Together, these findings indicate that climate is a stronger driver of growth variation than crowding at these distribution edges and that trees at distribution edges may exhibit highly variable responses to climate. These findings suggest that the drivers of growth variation within closed-canopy distribution edges in our study region differ from those across distribution interiors. Studies conducted across distribution interiors have consistently found a greater impact of competition than climate on tree growth (e.g. Clark et al. 2011; Gómez-Aparicio et al. 2011). Within closed-canopy forest interiors, high productivity and strong local abiotic effects generally override the effects of climate (Holman & Peterson 2006). While few other studies have evaluated growth responses at closed-canopy distribution edges, Ettinger et al. (2011, 2013) quantified relationships between climate, tree growth and crowding across the altitudinal ranges of a suite of conifer species in the Pacific Northwest, capturing treeline, closed-canopy distribution edges and distribution interiors. The authors found strong relationships between growth, snowpack and temperature only at the upper range limits of the highest elevation species. Conversely, relationships between crowding and growth were found to be significant across species altitudinal ranges. These findings were interpreted as suggesting that climate regulates growth at upper limits of physiological tolerance, but within closed-canopy forests (i.e. interior populations and lower distributional limits), crowding drives growth variation. Our contrasting results may be due to the lower productivity and harsher climate in our study region, which may reduce resource competition while simultaneously increasing climatic stress relative to more temperate forests. Additionally, the tree species in this study show relatively narrow and distinct temperature envelopes (Bell et al.

2014a), indicating that they may easily meet abrupt physiological temperature limitations well below treeline.

Our models predicted growth of all species to increase with growing season temperature and to decline weakly with summer precipitation, which is consistent with strong temperature limitation on growth (**Table 1.2; Fig. 1.1**). Because we did not include an interaction between temperature and precipitation in the model formulation, it is possible that the contribution of each of these variables traded off in the model fitting process, making it difficult to draw inference from a comparison of the model's greater sensitivity to precipitation than to temperature. Further, the precipitation parameter was estimated with a broad credible interval (**Table 1.2**), indicating that the precipitation response is not well constrained by the data. This could either be due to poor data characterization, or it could reflect variable growth responses to precipitation at the observed scale. Variable and unpredictable relationships between growth and precipitation have been commonly identified in these species, with both positive and negative trends identified (Stohlgren & Bachand 1997; Lo et al. 2010; Miyamoto et al. 2010). Variation in precipitation-growth relationships is commonly related to the precise timing of precipitation (Chhin et al. 2008; Soulé & Knapp 2011), stand elevation (Lo et al. 2010), edaphic factors (Ogle et al. 2000; Pinto et al. 2007) or crown status (Carnwath et al. 2012), all of which may influence the amount of precipitation that is actually available for uptake by trees. Thus, our 10-year-averages of seasonal precipitation and growth trends characterized across a broad geographic range may not provide the temporal or spatial resolution needed to characterize strong directional relationships between precipitation and growth. The strong positive relationship between temperature and precipitation was better constrained by the data used in our analysis (**Table 1.2**)

and, consistent with other studies, suggests that temperature may be the most limiting factor on the growth of montane trees (Miyamoto et al. 2010; Klein et al. 2015).

Competition had the greatest effects on growth in warmer and drier regions, where all species showed the highest optimal growth (**Fig. 1.2; Fig. 1.3**). Trends of competition importance for all species were consistent with trends of realized and potential growth across climate gradients; differences between potential and realized growth were greatest where competition importance was highest, demonstrating that crowding has a greater impact on growth in regions of lower climatic stress. A trend of increasing competition importance with decreasing climatic stress has been frequently demonstrated in herbaceous plant communities (e.g. Brooker et al. 2005; Gaucherand et al. 2006), but has been only rarely evaluated in tree communities. In one such study, Kunstler et al. (2011) analyzed competition importance and abiotic stress across gradients of soil water availability and growing degree-days for European montane trees. Similar to our findings, this study found competition importance to be greatest in regions of highest tree growth. In our study, competition importance varied considerably across temperature and precipitation only for *Pseudotsuga menziesii*. This likely reflects greater competition for moisture in drier, productive habitats along with variation in species' physiological responses to moisture stress. Both *Pinus contorta* and *Pinus ponderosa* employ stress-avoiding strategies under conditions of moisture stress by adjusting leaf area to sapwood area ratios, thus minimizing the effect of moisture stress on cambium production (Delucia et al. 2000; Carnwath et al. 2012). *Pseudotsuga menziesii*, however, withstands moisture stress by tolerating low water potentials, yet its inability to avoid moisture stress results in dramatic effects on physiological processes, ultimately reducing growth under conditions of moisture stress (Niinemets & Valladeres 2006; Carnwath et al. 2012). Consequentially, *Pseudotsuga menziessii*

growth appears more sensitive to moisture stress, likely resulting from greater competition for moisture in productive, warm habitats, than *Pinus contorta* and *Pinus ponderosa*, which show relatively invariant competition importance across climate gradients.

We recognize that our quantification of competition via crowding is incomplete, as it does not recognize the processes of competition, the influence of potential non-tree competitors, or fine-scale heterogeneity in resource availability. Nevertheless, our neighborhood index does represent the well-documented outcomes of competition in forests, and similar indices have been successfully applied in a multitude of tree competition studies (e.g. Bella 1971; Hegyi 1974; Weigelt & Jolliffe 2003; Canham et al. 2004; Baribault & Kobe 2011; Contreras et al. 2011; Gomez-Aparicio et al. 2011; Kunstler et al. 2011; Aakala et al. 2013). Manipulation of neighborhood basal area via mechanical thinning or deliberate variation in spacing has been shown to result in consistent trends of increased radial growth in these and other species of conifer trees (Barrett 1961; Scott et al. 1998; Wonn & O'Hara 2001; Ferguson et al. 2011; Hood et al. 2012), which can be correlated with changes in soil resource availability following basal area reduction (Gundale et al. 2005). Strong competitive release following stand thinning has been demonstrated for single species stands of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii* in the Northern and Central Rockies (Scott et al. 1998; Ferguson et al. 2011; Hood et al. 2012), although ecotonal stands, which typically occur on steep and inaccessible slopes, have rarely received such experimental treatments (Scott et al. 1998). Thus, while our study does not directly measure resource availability, uptake, or use, the clear relationship identified between neighborhood basal area and tree growth, corroborated by thinning studies demonstrating increased resource availability and competitive growth release, reasonably suggest that changes in neighborhood basal area may influence focal tree growth via

competitive mechanisms. Further, within these closed-canopy, dry forests, competition from non-tree vegetation is unlikely to affect growth rates of mature trees (LeMay et al. 2009). Nevertheless, fine-scale resource heterogeneity may interact with radial growth at spatial and temporal resolutions not captured by our 10-year average growth trends and broad sampling gradients. Thus, competition may exert substantial finer-scale effects on tree growth that cannot be addressed by our approach, and our findings are best interpreted as representing the effects of crowding and climate.

Climate Change Implications

Climate is changing rapidly in the Rocky Mountain region and is predicted to drastically influence distributions of species (Luckman & Kavanagh 2000; Dobrowski et al. 2013; Bell et al. 2014b). Warming temperatures are predicted to drive upslope range shifts of tree species, with significant habitat loss for high-elevation species and increased dominance of lower-elevation species such as *Pinus ponderosa* (Bell et al. 2014b). The importance of competition in regulating distribution shifts has been postulated for tree communities (Case et al. 2005; Lenoir et al. 2010; Meier et al. 2010), and has been demonstrated to be an important determinant of performance at distribution edges among other temperate conifer tree species (Ettinger et al. 2011; Ettinger et al. 2013). Our findings demonstrate that climate is the dominant factor controlling growth at ecotonal distribution edges of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii*, with the importance of competition appearing to increase towards regions of lower climatic stress. While distribution shifts will be directly dependent upon establishment and mortality events (Pulliam 2000; Shurr et al. 2012; Bell et al. 2014b; Normand et al. 2014), growth is highly correlated with these demographic processes, is easier to observe, and responds more

immediately to environmental changes (Kobe et al. 1995; van Mantgem et al. 2003; Wyckoff & Clark 2005; McMahon et al. 2010; Clark et al. 2011; Renwick et al. 2015), thus acting as a useful proxy for population sensitivity to climate change. This suggests that climate may be a strong driver of shifts in distribution edges of montane trees. Overall, our results strengthen the findings of studies that have predicted distribution shifts in Rocky Mountain forests by assuming strong associations between climate and habitat suitability (Bartlein et al. 1997; Rehfeldt et al. 2006; Bell et al. 2014a). However, our results also demonstrate that competition does contribute measurably, albeit less than climate, to radial growth variation, and we thus caution against complete dismissal of the influences of crowding/competition.

The methods employed in this study make use of a relatively novel approach to reveal the drivers of growth variation along montane ecotones. Our Bayesian modeling approach and sensitivity analysis allow us to more precisely quantify the relative contributions of crowding and climate to growth variation and our data focus specifically within closed-canopy ecotones, allowing us to assess growth responses among populations that are particularly important in the context of distribution shifts, yet have received little attention. Overall, our findings indicate that climate is the dominant driver of variation in tree growth at closed-canopy distribution edges.

1.6 REFERENCES

- Aakala, T, Fraver, S, D'Amato, AW, Palik, BJ (2013) Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. *Forest Ecology and Management* 308: 128-135
- Baker, WL, Veblen, TT, Sherriff, RL (2007) Fire, fuels and restoration of ponderosa pine-Douglas fir forests in the Rocky Mountains, USA. *Journal of Biogeography* 34: 251-269
- Barbeito I, Dawes MA, Rixen C, Senn J, Bebi P (2012) Factors driving mortality and growth at treeline: a 30-year experiment of 92000 conifers. *Ecology* 93: 389-401
- Baribault, TW, Kobe, RK (2011) Neighbour interactions strengthen with increased soil resources in a northern hardwood forest. *Journal of Ecology* 99: 1358-1372
- Bartlein PJ, Whitlock C, Shafer SL (1997) Future climate in Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11: 782-792
- Barrett, JW (1961) Response of 55-year-old lodgepole pine to thinning. USDA Forest Service Research Note Number 206: Pacific Northwest Forest and Range Experiment Station
- Bell DM, Bradford JB, Lauenroth WK (2014a) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23: 168-180
- Bell DM, Bradford JB, Lauenroth, WK (2014b) Mountain landscapes offer few opportunities for high-elevation tree species migration. *Global Change Biology* 20: 1441-1451
- Bella, IE (1971) A new competition model for individual trees. *Forest Science* 17: 364-372
- Bin Y, Spence J, Wu L, Li B, Hao Z, Ye W, He F (2015) Species-habitat associations and demographic rates of forest trees. *Ecography* 38: 001-008

- Boucher-Lalonde B, Morin A, Currie DJ (2012) How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography* 21: 1157-1166
- Briggs, NA, Kuehne, C, Kohnle, U, Bauhus, J (2012) Root system response of naturally regenerated Douglas-fir (*Pseudotsuga menziesii*) after complete overstory removal. *Canadian Journal of Forest Research* 42: 1858-1864
- Brooker R, Kikvidze Z, Pugnaire FI, Callaway RM, Choler P, Lortie CJ, Michalet R (2005) The importance of importance. *Oikos* 109: 63-70
- Burns, RM, Honkala, BH, eds (1990) *Silvics of North America: Volume I, conifers*. USDA Forest Service Agriculture Handbook 654: Washington DC
- Canham, CD, LePage, PT, Coates, KD (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778-787
- Cannone N, Sgorbati S, Guglielman M (2007) Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment* 5: 360-364
- Carnwath GC, Peterson DW, Nelson CR (2012) Effect of crown class and habitat type on climate-growth relationships of ponderosa pine and Douglas-fir. *Forest Ecology and Management* 285: 44-52
- Case TJ, Holt RD, McPeck MA, Keitt TH (2005) The community context of species' borders: Ecological and evolutionary perspectives. *Oikos* 108: 28-46
- Case BS, Duncan RP (2014) A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position. *Ecography* 37: 838-851
- Casper, BB, Jackson, RB (1997) Plant competition underground. *Ann. Rev. Ecol. Syst.* 28: 545-570

- Chhin, S, Hogg, EHT, Lieffers, VJ, Huang, S (2008) Potential effects of climate change on the growth of lodgepole pine across diameter size classes and ecological regions. *Forest Ecology and Management* 256: 1692-1703
- Clark JS, Bell DM, Hersh MH, Nichols L (2011) Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology* 17: 1834-1849
- Contreras MA, Affleck D, Chung W (2011) Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *Forest Ecology and Management* 262: 1939-1949
- Coomes DA, Allen RB (2007) Effects of size, competition and altitude on tree growth. *Journal of Ecology* 95: 1084-1097
- Copenhaver PE, Tinker DB (2014) Stand density and age affect tree-level structural and functional characteristics of young, postfire lodgepole pine in Yellowstone National Park. *Forest Ecology and Management* 320: 138-148
- Day RJ (1972) Stand structure, succession, and use of Southern Alberta's Rocky Mountain Forest. *Ecology* 53: 472-478
- Delucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation in pines. *Global Change Biology* 6: 587-593.
- Devine, WD, Harrington, TB (2008) Belowground competition influences growth of natural regeneration in thinned Douglas-fir stands. *Canadian journal of Forest research* 38: 3085-3097

- Dobrowski SZ, Abatzoglou J, Swanson AK, Greenberg JA, Mynsberge AR, Holden ZA, Schwartz MK (2013) The climate velocity of the contiguous United States during the 20th century. *Global Change Biology* 19: 241-251
- Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin DG (2015) Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography* DOI: 10.1111/geb.12302
- Ettinger AK, Ford KR, HilleRisLambers J (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92: 1323-1331
- Ettinger AK, HilleRisLambers J (2013) Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100: 1344-1355
- Ferguson, DE, Byrne, JC, Wykoff, WR, Kummer, B, Hensold, T (2011) Response of ponderosa pine stands to pre-commercial thinning on Nez Perce and Spokane Tribal forests in the Inland northwest, USA. USDA Forest Service Research Paper RMRS-RP-88: Rocky Mountain Research Station
- Gaucherand S, Liancourt P, Lavorel S (2006) Importance and intensity of competition along a fertility gradient and across species. *Journal of Vegetation Science* 17: 455-464
- Gaudet CL, Keddy PA (1995) Competitive performance and species distribution in shoreline plant communities: A comparative approach. *Ecology* 76: 280-291
- Gelfand AE, Ghosh SK (1998) Model choice: A minimum posterior predictive loss approach. *Biometrika* 85: 1-11
- Gómez-Aparicio L, García-Valdéz R, Ruíz-Benito P, Zavala MA (2011) Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests:

- Implications for forest management under global change. *Global Change Biology* 17: 2400-2414
- Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature* 369: 448
- Gundale, MJ, DeLuca, TH, Fiedler, CE, Ramsey, PW, Harrington, MG, Gannon, JE (2005) Restoration treatments in a Montana ponderosa pine forest: Effects on soil physical, chemical and biological properties. *Forest Ecology and Management* 215: 25-38
- Hargreaves AL, Samis KE, Eckert CG (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist* 183: 157-173
- Hegyi, F (1974) A simulation model for managing jack-pine stands. In J Fries, ed, *Growth models for tree and stand simulation*, Royal College of Forestry: Stockholm, Sweden
- HilleRisLambers J, Harsch MA, Ettinger AK, Ford KR, Theobald EJ (2013) How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences* 1297: 112-125
- Holman, ML, Peterson, DL (2006) Spatial and temporal variability in forest growth in the Olympic Mountains, WA: sensitivity to climatic variability. *Canadian Journal of Forest Research* 36: 92-104
- Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659-19665
- Hood, SM, Smith, HY, Wright, DK, Glasgow, LS (2012) Management guide to ecosystem restoration treatments: Two-aged lodgepole pine forests of Central Montana, USA.

USDA Forest Service General Technical Report RMRS-GTR-294: Rocky Mountain
Research Station

IPCC (2013) Climate change 2013: The physical science basis. Contribution of Working Group I
to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change
[Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A.,
Xia, Y., Bex, V. & Midgley, P.M. (eds.)]. Cambridge University Press, Cambridge,
United Kingdom and New York, NY, USA, 1535 pp. DOI:
10.1017/CBO0781107415324.

Keddy PA (1989) Competition. Chapman & Hall, New York, NY.

Keeling EG, Sala A, DeLuca TH (2006) Effects of fire exclusion on forest structure and
composition in unlogged ponderosa pine/Douglas-fir forests. *Forest Ecology and
Management* 237: 418-428

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change.
Proceedings of the National Academy of Sciences 105: 11823-11826

Klein, T, Randin, C, Körner, C (2015) Water availability predicts forest canopy height at the
global scale. *Ecology Letters* doi: 10.1111/ele.12525

Knowles, P & Grant, MC (1983) Age and size structure analyses of Engelmann spruce,
ponderosa pine, lodgepole pine and limber pine in Colorado. *Ecology* 64: 1-9

Knutson KC, Pyke DA (2008) Western juniper and ponderosa pine ecotonal climate-growth
relationships across landscape gradients in southern Oregon. *Canadian Journal of Forest
Research* **38**: 3021-3032

Kobe, RK, Pacala, SW, Silander, JA Jr, Canham, CD (1995) Juvenile tree survivorship as a
component of shade tolerance. *Ecological Applications* 5: 517-532.

- Kunstler G, Albert CH, Courbaud B, Lavergne S, Thuiller W, Vieilledent G, Zimmermann NE, Coomes DA (2011) Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *Journal of Ecology* 99: 300-312
- Larocque, GR (2002) Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. *Forest Science* 48: 24-34
- Larocque GR, Bhatti JS, Boutin R, Chertov O (2008) Uncertainty analysis in carbon cycle models of forest ecosystems: Research needs and development of a theoretical framework to estimate error propagation. *Ecological Modelling* **219**: 400-412.
- Laskey JR, Sun IF, Su SH, Chen ZS, Keitt TH (2013) Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology* 101: 722-733
- LeBauer DS, Wang D, Richter KT, Davidson CC, Dietze MC (2013) Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs* **83**: 133-154
- Ledermann T (2010) Evaluating the performance of semi-distance-independent competition indices in predicting the basal area growth of individual trees. *Canadian Journal of Forest Research* 40: 796-805
- LeMay, V, Pommerening, A, Marshall, P (2009) Spatio-temporal structure of multi-storied, multi-aged interior Douglas fir (*Pseudotsuga menziesii* var. *glauca*) stands. *Journal of Ecology* 97: 1062-1074
- Lenoir J, Gégout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning JC (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33: 295-303

- Lo, YH, Blanco, JA, Seely, B, Welham, C, Kimmins, JPH (2010) Relationships between climate and tree radial growth in interior British Columbia, Canada. *Forest Ecology and Management* 259: 932-942
- Lorimer CG (1983) Tests of age-independent competition indices for individual trees in natural hardwood stands. *Forest Ecology and Management* 6: 343-360
- Luckman B, Kavanagh T (2000) Impact of climate fluctuations on mountain environments in the Canadian Rockies. *AMBIO* 29: 371-380
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience* 57: 939-948
- McMahon, SM, Parker, GG, Miller, DR (2010) Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences* 107: 3611-3615
- Meier ES, Kienast F, Pearman PB, Svenning JC, Thuiller W, Araújo MB, Guisan A, Zimmermann NE (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038-1048
- Meyer CB, Knight DH, Dillon GK (2003) Historic variability for the upland vegetation of the Bighorn National Forest, Wyoming. USFS Report No. 1102-0003-98-942. Bighorn National Forest: Sheridan, WY. U.S. Department of Agriculture, Forest Service.
- Miyamoto, Y, Griesbauer, HP, Green, DS (2010) Growth responses of three coexisting conifer species to climate across wide geographic and climate ranges in Yukon and British Columbia. *Forest Ecology and Management* 259: 514-523
- Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology* 88: 2280-2291

- Niinements U, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76: 521-547
- Normand S, Zimmerman NE, Schurr FM, Lischke H (2014) Demography as the basis for understanding and predicting range dynamics. *Ecography* 37: 1149-1154
- Nystrom Mast, J, Veblen, TT, Linhart, YB (1998) Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *Journal of Biogeography* 25: 743-755
- Ogle K, Whitham TG, Cobb NS (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81: 3237-3243.
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* 37: 637-669
- Peet, RK (1981) Forest vegetation of the Colorado Front Range: composition and dynamics. *Vetetatio* 45: 3-75
- Pinto PE, Gegout JC, Herve JC, Dhote JF (2007) Changes in environmental controls on the growth of *Abies alba* Mill. In the Vosges mountains, north-eastern France, during the 20th century. *Global Ecology and Biogeography* 16: 472-484.
- Plummer M (2014) rjags: Bayesian graphical models using MCMC. R package version 3-13. <http://CRAN.R-project.org/package=rjags>
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters* 3: 349-361
- Rehfeldt GE, Crookston NL, Warwell MV, Evans JS (2006) Empirical analyses of plant-climate relationships for the Western United States. *International Journal of Plant Sciences* 167: 1123-1150

- Renwick, KM, Rocca, ME (2015) Temporal context affects the observed rate of climate-driven range shifts in tree species. *Global Ecology and Biogeography* 24: 44-51
- Saltelli A (2005) Global sensitivity analysis: An introduction. Kenneth M. Hanson & Francois M. Hemez, eds. *Proceedings of the 4th International Conference on Sensitivity Analysis of Model Output*. Los Alamos National Laboratory.
- Schoennagel TT, Veblen TT, Romme WH (2004) The interaction of fire, fuels and climate across the Rocky Mountain landscapes. *Bioscience* 54: 661-676
- Schoennagel, T, Sherriff, RL, Veblen, TT (2011) Fire history and tree recruitment in the Colorado Front Range upper montane zone: implications for forest restoration. *Ecological Applications* 21: 2210-2222
- Schurr FM, Pagel J, Cabral S, Groeneveld J, Bykova O, O'Hara RB, Hartig F, Kissling WD, Linder HP, Midgley GF, Schröder B, Singer A, Zimmermann NE (2012) How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography* 39: 2146-2162
- Scott, JH (1998) Fuel reduction in residential and scenic forests: a comparison of three treatments in a Western Montana ponderosa pine stand. USDA Forest Service Research Paper RMRS-RP-5: Rocky Mountain Research Station
- Serra-Diaz JM, Franklin J, Dillon WW, Syphard AD, Davis FW, Meentemeyer RK (2015) California forests show early indications of both range shifts and local persistence under climate change. *Global Ecology and Biogeography* DOI: 10.1111/geb.12396
- Shaw JD, Long JN (2007) Forest ecology and biogeography of the Uinta Mountains, U.S.A. *Arctic, Antarctic and Alpine Research* 39: 614-628

- Sherriff, RL, Veblen, TT (2006) Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in Colorado. *Journal of Vegetation Science* 17: 705-718
- Smith HY, ed. (2000) The Bitterroot Ecosystem Management Research Project: What we have learned: symposium proceedings; 1999 May 18-20; Missoula, MT. General Technical Report RMRS-GTR-17. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Soulé, PT, Knapp, PA (2011) Radial growth and increased water-use efficiency for ponderosa pine trees in three regions in the Western United States. *The Professional Geographer* 63: 379-391
- Sterba, H, Monserud, RA (1995) Potential volume yield for mixed-species Douglas-fir stands in the Northern Rocky Mountains. *Forest Science* 41: 531-545
- Stohlgren TJ, Bachand RR (1997) Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology* 78: 632-641
- Stokes, MA, Smiley, TL (1968) An introduction to tree-ring dating. University of Chicago Press
- Tilman D (1982) Resource competition and community structure. *Monographs in Population Biology* 17: 1-296
- van Mantgem, PJ, Stephenson, NI, Mutch, LS, Johnston, VG, Esperanza, AM, Parsons, DJ (2003) Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. *Canadian Journal of Forest Research* 33: 1029-1038
- Wang T, Hamann A, Spittlehouse DL, Murdock TQ (2012) ClimateWNA- High-resolution spatial climate data for Western North America. *Journal of Applied Meteorology and Climatology* 51: 16-29
- Weigelt, A, Jolliffe, P (2003) Indices of plant competition. *Journal of Ecology* 91: 707-720

- Weiner, J (1985) Size hierarchies in experimental populations of annual plants. *Ecology* 66: 743-752
- Weiner, J, Thomas, SC (1986) Size variability and competition in plant monocultures. *Oikos* 47: 211-222
- Welden CW, Slauson WL (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Quarterly Review of Biology* 61: 23-44
- Witt C (2008) Forest resources of the Bighorn National Forest. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station
- Wonn, HT, O'Hara, KL (2001) Height:diameter ratios and stability relationships for four Northern Rocky Mountain tree species. *Western Journal of Applied Forestry* 16: 87-94
- Woodall CW, Fiedler CE, Milner KS (2003) Intertree competition in uneven-aged ponderosa pine stands. *Canadian Journal of Forest Research* 33: 1719-1726
- Wyckoff, P, Clark, JS (2005) Comparing predictors of tree growth: the case for exposed canopy area. *Canadian Journal of Forest Research* 35: 13-20

1.7 TABLES

Table 1.1. Posterior predictive loss (*PPL*) and bias values evaluating all pairs of uncorrelated temperature and precipitation variables in the linear climate effects model (**Eqn. 1.1**). PPL and bias are shown for the reduced model form, which eliminated size and age effects due to their insignificance.

Species	<i>MSP, FFP</i>		<i>MSP, MAT</i>		<i>MSP, MWMT</i>		<i>MAP, DD5</i>		<i>MSP, DD5</i>	
	PPL	Bias	PPL	Bias	PPL	Bias	PPL	Bias	PPL	Bias
<i>Pinus contorta</i>	222.17	0.871	215.29	0.875	213.27	0.863	213.11	0.866	209.59 ^a	0.865 ^a
<i>Pinus ponderosa</i>	- ^b	- ^b	156.53	0.893	159.49	0.893	159.58	0.900	153.45 ^a	0.890 ^a
<i>Pseudotsuga menziesii</i>	254.74	0.711	256.74	0.710	256.2	0.727	263.33	0.718	254.01 ^a	0.712 ^a

^a Values for selected models (lowest PPL)

^b Models that failed to converge

Table 2.1. Parameter values for the selected model for each species, showing both posterior mean values and 95% credible interval (CI) boundaries. β_1 represents the temperature effect, β_2 the precipitation effect, β_3 adjusts the intercept of the logistic crowding relationship, β_4 represents the strength of the crowding effect, α is a random effect for transect that accounts for unexplained abiotic dependence among trees within the same transect, τ characterizes the variance in the random effect, and ε represents the overall model error.

		<i>Pinus contorta</i>	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>
β_1	mean	0.726	0.676	0.510
	2.5% CI	0.504	0.391	0.330
	97.5% CI	0.964	1.118	0.804
β_2	mean	-0.058	-0.046	-0.033
	2.5% CI	-0.168	-0.144	-0.122
	97.5% CI	-0.001	-0.001	-0.001
β_3	mean	1.013	0.978	1.039
	2.5% CI	0.856	0.793	0.840
	97.5% CI	1.231	1.225	1.256
β_4	mean	1.218	1.681	0.442
	2.5% CI	0.640	0.134	0.036
	97.5% CI	2.262	6.291	1.055
α	mean	0.055	0.087	0.084
	2.5% CI	-1.401	-1.914	-1.138
	97.5% CI	1.735	2.404	1.717
ε	mean	0.343	0.368	0.257
	2.5% CI	0.218	0.227	0.165
	97.5% CI	0.524	0.576	0.385
τ	mean	0.798	1.517	0.551
	2.5% CI	0.223	0.405	0.074
	97.5% CI	1.962	4.449	1.847

Table 3.1. Sensitivity of model output (mean radial growth) to uncertainty in parameters, as estimated by perturbing each parameter within the range of its posterior distribution. Model sensitivity is the derivative of the relationship between perturbed parameter values and model output. β_1 and β_2 represent temperature and precipitation effects, respectively, and β_3 and β_4 account for the effect of neighborhood basal area; α is the random effect for transect.

	<i>Pinus contorta</i>	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>
β_1	1.741	2.681	1.815
β_2	3.857	7.587	5.755
β_3	0.427	0.433	0.110
β_4	0.019	0.108	0.058
α	0.502	0.769	0.633

1.8 FIGURES

Figure 1.1 Individual effects of crowding (*a*), temperature (*b*) and precipitation (*c*) on radial growth of *Pinus contorta*, *Pinus ponderosa* and *Pseudotsuga menziesii*. Crowding and precipitation show mean negative effects on growth, while temperature shows a mean positive effect. Individual effects are calculated by holding all other parameters and variables at their mean values

Figure 2.1 Competition importance across gradients of growing degree days (*a*), mean summer precipitation (*b*), mean annual temperature (*c*), mean annual precipitation (*d*) and precipitation as snow (*e*) was generally the highest and most variable for *Pseudotsuga menziesii*, while *Pinus contorta* and *Pinus ponderosa* competition importance varied little with climate. Mean competition importance predicted from linear models is presented with 95% CIs.

Figure 3.1 Modeled realized and predicted optimum growth of *Pinus contorta* (*a-e*), *Pinus ponderosa* (*f-j*) and *Pseudotsuga menziesii* (*k-o*) across climate gradients. In general, optimum growth was higher than realized growth, and growth increased towards warm and dry regions. Mean growth and 95% CIs from linear models are shown.

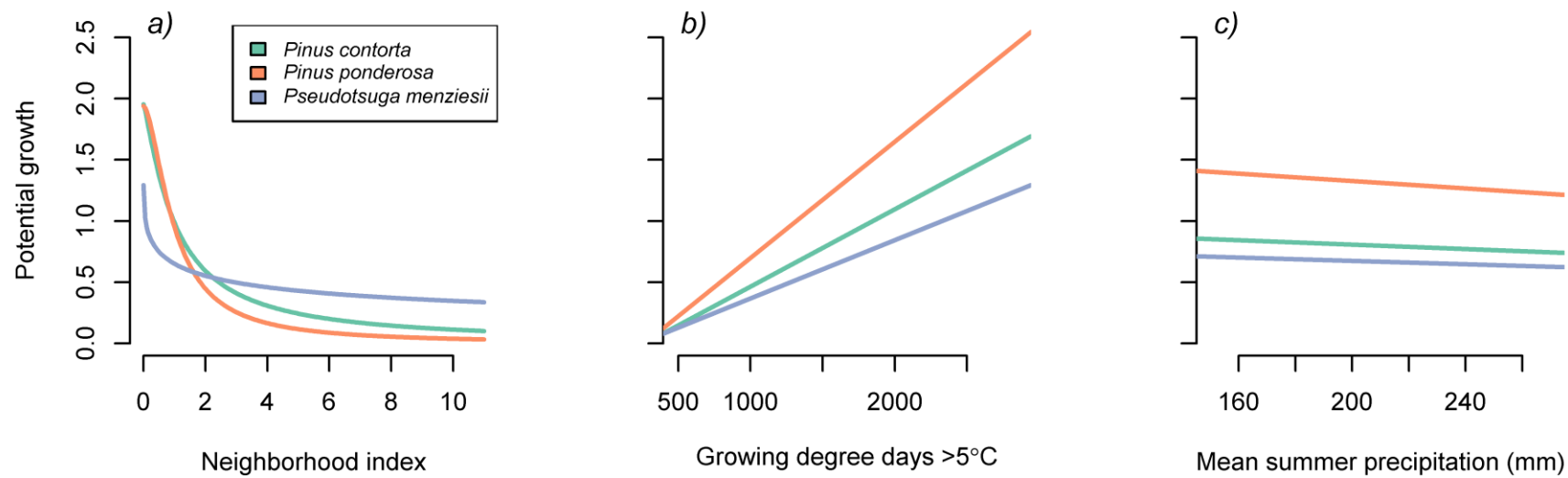


Figure 1.1

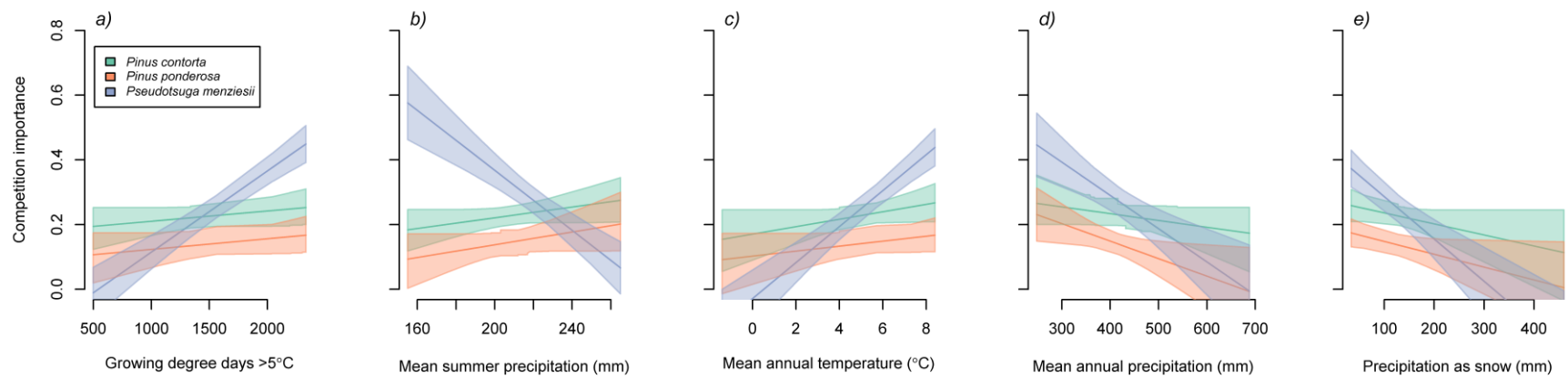


Figure 1.2

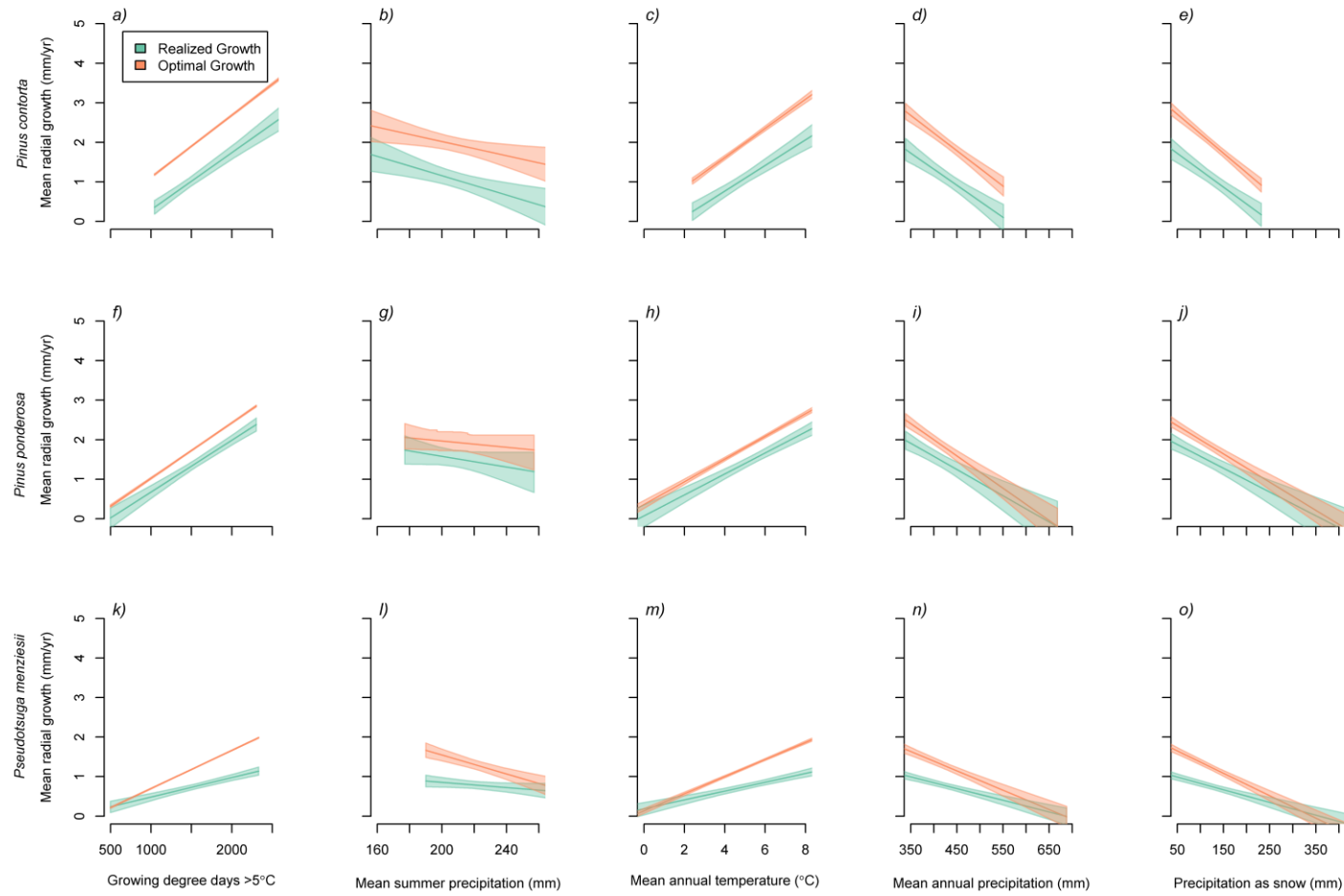


Figure 1.3

APPENDIX 1: STUDY SITE DESCRIPTIONS

A1.1 Bighorn National Forest, WY

The Bighorn National Forest (BNF) extends over most of the Bighorn Mountain Range in north-central Wyoming. The forest spans 447,500 ha at elevations ranging from 900-4000 m.a.s.l. (Meyer et al. 2003). Roughly 66% of the land is forested (Witt 2008). Forested land is characterized by two primary forest types: high-elevation forests (49% of forested area) consisting of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), and low-elevation forests (12% of forested area) comprised of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*) and limber pine (*Pinus flexilis*). Our focal species occur in three elevation zones, with overlapping elevation distributions resulting in mixed-species forests. *Pinus ponderosa* occurs primarily on the eastern foothills of the range at elevations ranging from 1500-2100m. *Pseudotsuga menziesii* dominates north-facing slopes on sedimentary substrates from 1500-2700m. *Pinus contorta*, the most abundant species on the BNF, occurs from 1800-3000m on granitic substrates (Meyer et al. 2003). *Pinus contorta* comprises an estimated 40% of all trees occurring on the forest, while *Pseudotsuga menziesii* accounts for 10% and *Pinus ponderosa* for less than 1% (Witt 2008).

Our sampling sites were located on the sub-summit plateau in the south-central portion of the Bighorn Mountains at elevations ranging from 2400-2800m. At these elevations, precipitation averages 63cm per year, and temperature ranges from -40°C to 43°C. Mean annual temperature at Burgess Junction on the sub-summit plateau is 1°C (Meyer et al. 2003). Across the plots measured in this study, *Pinus contorta* was the most abundant species, accounting for 50.4% of mature trees *Pinus ponderosa* comprised 12.6% and *Pseudotsuga menziesii*, 37.1%.

Sampling plots ranged from 1982 to 2451m (**Table A1.1**). Over the ten years included in this study, mean temperatures ranged from -2.5 to 10.4°C with an overall mean temperature of 3.9°C and mean precipitation of 44cm·yr⁻¹.

A1.2 Bitterroot National Forest, Montana

The Bitterroot National Forest (BRNF) is located in west-central Montana and north-eastern Idaho, extending over 642,300 ha. Elevations range from 975-3100m, with the highest elevations occurring in the Bitterroot Mountains on the west side of the Bitterroot Valley. Low-elevation forests are dominated by *Pinus ponderosa*, transitioning into a *Pseudotsuga menziesii* series, an *Abies grandis* series, and an *Abies lasiocarpa* series in the highest elevation zone. *Pseudotsuga menziesii* is the most common tree species, spanning elevations from 1100-1700m (Smith 2000).

Our sampling sites were located on the Bitterroot Front. The front comprises the eastern slopes of the Bitterroot Mountains, rising directly above the Bitterroot Valley. The lower slopes of the front are dominated by *Pinus ponderosa* (26% of basal area). In the mid-elevation zone, *Pinus contorta* (27% of total basal area) is co-dominant with *Pseudotsuga menziesii* (24% of total basal area). In high elevation forests, *Pinus contorta* is the most abundant of our focal species (44% of total basal area), and shares dominance with *Picea engelmannii*, *Abies lasiocarpa*, and *Pinus albicaulus* (Smith 2000).

Our plots were primarily located at low- to mid-elevations (917-1018m; **Table A1.2**) with a high proportion of *Pseudotsuga menziesii*. *Pseudotsuga menziesii* comprised 69.1% of all mature trees measured in our sampling plots. *Pinus contorta* represented 22.0%, and *Pinus*

ponderosa only 8.89%. Over the ten years included in this study, mean temperatures ranged from 0-16°C with an overall mean of 8.4°C and a mean precipitation of 38.7cm·yr⁻¹.

A1.3 Ashley National Forest, Utah

The Ashley National Forest (ANF) is located in northeastern Utah and Wyoming and includes portions of the Uinta mountain range. The forest spans 560,000 ha at elevations ranging from 1800 to over 4100 m. Forested land on the ANF is characterized by very distinct elevation zonation of tree species. The lowest elevation zones are dominated by *Pinus edulis* and *Juniperus* spp., transitioning into a *Pinus ponderosa* zone, a *Populus tremuloides*/*Pseudotsuga menziesii* zone, and a *Pinus contorta* zone. The highest elevation regions are dominated by *Picea engelmannii* and *Abies lasiocarpa*. Distributions of our three focal species overlap in canyons and drainages on the southern and northern slopes of the Uinta range. The ANF represents the southern limit of *Pinus contorta* in the western Rocky Mountains and the northern limit of *Pinus ponderosa* in the western-central Rocky Mountains (Shaw & Long 2007).

In general, forest type in this region is not significantly correlated with geologic formation, though *Pseudotsuga menziesii* consistently achieves its highest dominance on limestone formations. Tree distributions on the ANF have been found to be most strongly correlated with precipitation and temperature patterns. The region is characterized by wet summers and dry winters, driven by a monsoonal climate system (Shaw & Long 2007). Our sampling plots were located on both the northern and southern slopes of the Uinta Mountains in the eastern portion of the range. Minimum temperatures over the range of years included in this study averaged -2.4°C with a mean maximum of 12.2°C. Precipitation averaged 40.4cm·yr⁻¹, with an overall mean temperature of 4.9°C.

Our study sites spanned a relatively narrow elevation band ranging from 2293m to 3253m (**Table A1.3**). *Pinus contorta* was the most abundant species in our plots, comprising 63.5% of all mature trees. *Pseudotsuga menziesii* accounted for 24.5%, and *Pinus ponderosa* for 11.9%.

A1.4 REFERENCES

- Meyer CB, Knight DH, Dillon GK (2003) Historic variability for the upland vegetation of the Bighorn National Forest, Wyoming. USFS report no. 1102-0003-98-942. Department of Agriculture, Forest Service, Bighorn National Forest, Sheridan, WY.
- Shaw JD, Long JN (2007) Forest ecology and biogeography of the Uinta Mountains, U.S.A. *Arct Antarct Alp Res* 39:614-628.
- Smith HY (ed) (2000) The Bitterroot Ecosystem Management Research Project: what we have learned: symposium proceedings; 1999 May 18-20; Missoula, MT. General technical report RMRS-GTR-17. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT
- Witt C (2008) Forest resources of the Bighorn National Forest. US Department of Agriculture, Forest Service, Rocky Mountain Research Station

Table A1.1. Site details for the 25 plots sampled on the Bighorn National Forest, Wyoming.

Easting and Northing correspond with UTM coordinates.

Easting	Northing	Slope (°)	Aspect (°)	Elevation (m)
349784	4893958	35	134	2066
349954	4894132	38	139	2048
350255	4894357	25	102	2053
350494	4894538	42	75	2032
350777	4894641	12	100	1982
349245	4886290	20	58	2451
349437	4886316	14	28	2425
349595	4886437	13	20	2404
349845	4886556	21	40	2365
349907	4886794	17	71	2338
330223	4943985	32	2	2281
330249	4944051	31	335	2263
330265	4944126	28	6	2240
330297	4944215	34	284	2235
330273	4944270	34	297	2206
347777	4890275	8	16	2410
349644	4890628	20	318	2366
350522	4890574	16	33	2373
350587	4890433	8	0	2376
351261	4890715	23	165	2386
310498	4898319	13	313	2340
310589	4898025	10	226	2353
310590	4897918	8	250	2345
310605	4897701	33	182	2306
310617	4897533	12	184	2327

Table A1.2. Site details for the 25 plots sampled on the Bitterroot National Forest, Montana.

Easting and Northing correspond with UTM coordinates.

Easting	Northing	Slope (°)	Aspect (°)	Elevation (m)
718217	5162751	25	87	948
718125	5162980	31	70	944
718050	5163251	19	282	946
717815	5163315	34	290	948
717648	5163388	31	64	950
711031	5134617	37	38	1171
711175	5134594	28	74	1162
711276	5134533	35	63	1155
711350	5134451	31	109	1152
711363	5134363	38	128	1167
713353	5079440	24	88	1022
713174	5079940	26	85	1037
713216	5080416	33	116	1034
713334	5080999	48	22	1007
713048	5081412	29	146	1011
716130	5178143	43	153	941
716130	5178143	37	170	941
716106	5178241	31	152	939
716086	5178359	24	144	939
716132	5178435	22	133	937
713907	5077823	3	155	917
713905	5077744	9	130	1045
713883	5077639	27	29	1039
713907	5077545	34	84	1050
713905	5077469	34	160	1037

Table A1.3. Site details for the 30 plots sampled on the Ashley National Forest, Utah. Easting and Northing correspond with UTM coordinates.

Easting	Northing	Slope (°)	Aspect (°)	Elevation (m)
601695	4527439	0	334	2585
601808	4527589	33	36	2507
601937	4527785	32	24	2419
602024	4527902	36	38	2353
602144	4528073	66	332	3253
612687	4521643	7	33	2444
612700	4521739	8	321	2435
612622	4521897	5	116	2430
612622	4522009	21	60	2424
612678	4522066	14	72	2408
625125	4524096	39	330	2493
625138	452313	39	355	2613
625111	4524515	19	344	2353
625171	4524719	6	345	2305
625124	4524903	9	330	2293
601974	4497197	56	20	2485
602012	4497282	44	46	2446
602038	4497382	37	324	2400
602018	4497528	4	158	2388
602062	4497576	4	40	2383
551655	4487357	26	203	2824
551594	4487208	25	162	2781
551483	4487019	13	180	2756
551413	4486863	20	192	2708
551340	4486725	14	173	2676
636957	4518238	4	61	2401
636611	4518152	16	16	2427
636345	4518295	25	45	2475
636079	4518366	14	22	2518
635779	4518552	3	18	2527

CHAPTER 2: DO COMMUNITY-LEVEL MODELS ACCOUNT FOR THE EFFECTS OF BIOTIC INTERACTIONS? A COMPARISON OF COMMUNITY-LEVEL AND SPECIES DISTRIBUTION MODELING OF ROCKY MOUNTAIN CONIFERS

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2.1 ABSTRACT

Community-level models (CLMs) aim to improve species distribution modeling (SDM) methods by attempting to explicitly incorporate the influences of interacting species. However, the ability of CLMs to appropriately account for biotic interactions is unclear. We applied CLM and SDM methods to predict the distributions of three dominant conifer tree species in the U.S Rocky Mountains and compared CLM and SDM predictive accuracy as well as the ability of each approach to accurately reproduce species co-occurrence patterns. We specifically evaluated the performance of two statistical algorithms, *MARS* and *CForest*, within both CLM and SDM frameworks. Across all species, differences in SDM and CLM predictive accuracy were slight and can be attributed to differences in model structure rather than accounting for the effects of biotic interactions. In addition, CLMs generally over-predicted species co-occurrence, while

SDMs under-predicted co-occurrence. Our results demonstrate no real improvement in the ability of CLMs to account for biotic interactions relative to SDMs. We conclude that alternative modeling approaches are needed in order to accurately account for the effects of biotic interactions on species distributions.

2.2 INTRODUCTION

There is increasing evidence that species rarely occur in complete equilibrium with climate (e.g. Araújo et al. 2005a; Worth et al. 2014; Blois et al. 2014). Historical factors, dispersal, and biotic interactions have all been found to exert substantial constraints on species distributions and range movement of a variety of species (Araújo and Luoto 2007; Leathwick 2009; Meier et al. 2010; Boulangeat et al. 2012; Meineri et al. 2012; HilleRisLambers et al. 2013; Blois et al. 2014). Consequently, many recent developments in species distribution modeling have focused on incorporating non-climatic factors and community- and population-level processes into distribution predictions (e.g. Meier et al. 2010; Boulangeat et al. 2012; Kissling et al. 2012; Clark et al. 2014; Normand et al. 2014). These efforts are particularly important when the intended application of a model is to project to new environments or future climate scenarios where climate equilibrium assumptions are likely to break down (Klanderud and Totland 2005; Suttle et al. 2007; Araújo and Luoto 2007; Swab et al. 2015).

Biotic interactions among species, in particular, have been the subject of significant focus. Both positive and negative interactions may affect species distributions by either inhibiting or facilitating establishment, individual growth and population growth (Holt 2009; HilleRisLambers et al. 2013; Svenning et al. 2014). At a macroecological scale, the effects of such interactions may be manifest as non-random species co-occurrence patterns (Araújo et al. 2011; Blois et al. 2014; Clark et al. 2014). The information from such co-occurrence patterns may be formally incorporated into models and modeling frameworks that predict the distributions of multiple species. One such group of models, referred to as community-level models (CLMs), are intended to improve the performance of species distribution models (SDMs) by using co-occurrence as a proxy for biotic interactions (Ferrier & Guisan 2006). CLM

strategies may first combine distributions into community types, which are then predicted by the model ('assemble first, predict later'), or they may predict species independently and use a variety of ad hoc methods to combine SDM predictions ('predict first, assemble later'). Alternatively, the influences of interacting species can be accounted for directly within the modeling framework by predicting species distributions simultaneously ('assemble and predict together') (Ferrier & Guisan 2006; Baselga and Araújo 2010).

An obvious shortcoming of CLMs is their inability to explicitly account for the underlying processes driving species co-occurrence patterns (Baselga and Araújo 2010). This shortcoming is shared by many community ecology approaches, which regularly attribute non-random co-occurrence patterns to biotic interactions (Webb et al. 2002; Hardy 2008). Co-occurrence patterns can, however, be generated by a variety of alternative processes, including shared environmental responses of sympatric species, opposing environmental responses of parapatric species, or dispersal limitation (Boulangeat et al. 2012; Pollock et al. 2014; Morueta-Holme et al. 2015). When environmental responses are the primary driver of species co-occurrence patterns, simple SDMs may be sufficient modeling tools as they quantify only species-environment correlations. Nevertheless, where biotic interactions act as an important constraint on species distributions, their effects will be implicitly represented in the data sets used to fit distribution models (Olden et al. 2006; Baselga and Araújo 2009; Godsoe and Harmon, 2012). In such a case, an SDM will likely suffer from poor predictive accuracy when applied to new environments where fitted climate equilibrium relationships may break down (Araújo et al. 2005b; Godsoe & Harmon 2012; Wisz et al. 2013). Additionally, combined SDM predictions will likely fail to accurately reproduce co-occurrence patterns due to their reliance on simple climate-occurrence relationships (Guisan & Rahbek 2011; Pellissier et al. 2012). By more

explicitly accounting for the influence of interacting species in the model fitting process, CLMs may have the potential to address the shortcomings of SDMs. In particular, ‘assemble and predict together’ approaches, which model species simultaneously, may capture additional influences on species distributions. Specifically, if CLMs are able to account for effects of biotic interactions undetected by SDMs, we may expect systematic differences in model predictions that result in two primary outcomes: 1) if interspecific competition acts to constrain species distributions, CLMs should predict a lesser degree of spatial overlap among species (i.e. co-occurrence) than SDMs and 2) if facilitation among species acts to expand distributions beyond environmental tolerances, CLMs should predict a greater degree of spatial overlap than SDMs. In either instance, a model that accounts for biotic interactions should predict different co-occurrence patterns than SDMs, and these co-occurrence patterns should more accurately represent observed co-occurrence patterns (i.e. greater model performance and predictive accuracy). In this way, CLMs may have the potential to improve understanding of biotic constraints on species distributions despite their inability to explicitly address processes underlying co-occurrence patterns.

While CLMs and SDMs have been compared in previous studies, the combined results are inconclusive and thus appropriate applications for CLMs remain unclear (Baselga & Araújo 2009). CLMs have been shown to outperform SDMs in some cases (Elith et al. 2006; Olden et al. 2006), perform worse in other cases (Baselga and Araújo 2009), and to perform similarly (Leathwick et al. 2006). Differences in performance of the two modeling approaches have been largely attributed to differences in species prevalence and range size (Elith et al. 2006; Leathwick et al. 2006; Chatfield 2008; Baselga and Araújo 2009), or major statistical differences in the SDM and CLM models being compared (Elith et al. 2006; Baselga and Araújo 2010). In

light of these inconsistencies, there is a need to assess these two approaches using consistent statistical methods and species data with similar prevalence. Further, the comparative approaches used thus far have relied primarily on measures of model performance (e.g. classification accuracy, correlation between observed and fitted values), and have not compared differences in predicted co-occurrence patterns among the two approaches, which may provide greater insight into the underlying relationships captured by SDMs and CLMs (Guisan & Rahbek 2011).

Here, we compare the abilities of CLMs and SDMs to accurately predict the individual occurrence patterns and co-occurrence patterns of species of relatively similar prevalence by using two ‘assemble and predict together’ CLM methods and their SDM counterparts:

Multivariate Adaptive Regression Splines (*MARS*) and Conditional Random Forests (*CForest*).

We apply these models to predict current and future distributions of three dominant Rocky Mountain conifer tree species: *Pinus contorta* var. *latifolia* [(Engelm.), lodgepole pine], *Pinus ponderosa* var. *scopulorum* [(Engelm.), ponderosa pine] and *Pseudotsuga menziesii* var. *menziesii* [(Mirb.), Douglas-fir]. These canopy species form primarily parapatric distributions with distinct elevational zonation in the montane zone of the Rocky Mountains and co-occur with few other tree species (**Fig. 2.1**). Specifically, ponderosa pine dominates on dry, low elevation sites (>1700m), while Douglas-fir tends to occupy more xeric sites at mid-elevations (~2000m). Lodgepole pine forms primarily monospecific stands on more mesic and higher elevation slopes ranging in elevation from 2400-3000m, interacting with subalpine fir and Engelmann spruce at its upper elevational edge (Peet 1981). Lodgepole pine’s distribution is constrained to more northern latitudes than either ponderosa pine or Douglas-fir, yet focal interact along mid-elevation ecotonal bands in the Northern and Central Rockies and form mixed-species stands in portions of their ranges (Bartlein et al. 1997). These species exhibit

somewhat divergent climate envelopes, particularly with regards to precipitation (Bell et al. 2014). It is unclear what role interactions between these species play in shaping current distributions, but differences in competitive ability (Copenhaver-Parry and Cannon 2016) and dispersal (McCaughey et al. 1985) suggest that current distributions may differ substantially from climatic equilibrium. To evaluate the ability of each approach to account for the effects of biotic interactions, we first compare the predictive accuracy of CLMs and SDMs from the same families of models fit to current distribution data. We then assess accuracy of predicted co-occurrence patterns with particular emphasis on regions of known species overlap. We predict that: 1) CLMs should exhibit improved predictive accuracy over SDMs by explicitly accounting for the effects of biotic interactions, and 2) CLMs and SDMs should demonstrate systematic differences in predictions of species co-occurrence patterns, diverging most strongly in regions of known species overlap.

2.3 MATERIALS AND METHODS

Occurrence Data

Occurrence data for lodgepole pine, ponderosa pine and Douglas-fir were extracted from the U.S. Forest Service's Forest Inventory and Analysis (FIA) database. The FIA database consists of plot-level forest data from a comprehensive survey of forest conditions across the United States. Forests are surveyed every 5-10 years and data is provided at several spatial resolutions, based either on remote sensing (Phase 1), or field-level observations (Phase 2 and 3). The FIA has established 125,000 phase 2 plots per 6000 acres of forested land and 8000 phase 3 plots, or one for every 95,000 acres of forested land (Smith et al. 2002). Plots are stratified based on landscape homogeneity in an attempt to represent the full range of forest conditions and to

reduce spatial autocorrelation (Woudenberg et al. 2010). FIA data provides the most comprehensive source of presence/absence data on tree species available in the United States. FIA data does introduce a limitation to the spatial resolution of predictive models: coordinates of most plot locations are perturbed slightly within a 0.8km radius of actual plot locations (Woodall et al. 2010). However, perturbed coordinates used in SDMs have resulted in similar performance to SDMs using precise coordinates (Gibson et al. 2014), and the uncertainty in resolution is deemed acceptable for integration with 1km resolution climate data (C. Woodall, personal communication).

In this study, we made use of all available field-observation (Phase 2 and 3) FIA plots within the U.S. states of Montana, Idaho, Utah, Wyoming, Colorado, New Mexico and Arizona (**Fig. 2.1**). This study area was selected in order to capture the U.S. distributions of inland varieties of the focal species. For each plot, we extracted presence/absence data for lodgepole pine, ponderosa pine and Douglas-fir from the most recent plot surveys. Only live, mature trees were considered due to greater uncertainty in identification of seedlings and the possibility of sink (non-equilibrium) populations at plots with only seedlings of a given species. In total, 21,950 presence/absence observations were retained for analysis. Prevalence (proportion of plots where species occurs) was relatively similar for all species: 16% for lodgepole pine, 18% for ponderosa pine, and 28% for Douglas-fir.

Climate Data

Current climate estimates were extracted from the U.S. Forest Service's Moscow Forestry Sciences Laboratory (MFSL) down-scaled climate data set. MFSL data is provided at a 30 arc second (~1km) resolution as 30-year normals (1961-1990) with coverage spanning

Western North America. The MFSL data set provides plant-relevant climate variables for integration with ecological data (Rehfeldt 2006). We utilized only a subset of available climate variables to reduce model dimensionality and minimize overfitting, a problem common to both modeling methods used here (Hothorn et al. 2006; Leathwick et al. 2006). While model complexity may also contribute to overfitting, we evaluated possible overfitting of each method by validating models on geographically stratified data (see section 2.3). Climate variables were selected to represent seasonality of temperature and precipitation, which are known controls on Rocky Mountain tree distributions (Bell et al. 2014). To capture topographic relationships that may not be well represented by climate data, we extracted elevation (m.a.s.l.) from a USGS 30m digital elevation model (DEM), re-sampled to a 1km grid using bilinear interpolation to remain consistent with the resolution of the MFSL climate data. From this DEM, we derived an index of topographic radiation based on a continuous transformation of circular aspect (TRASP; Roberts & Cooper 1989; Evans et al. 2014). The ability of both modeling methods used here to accommodate collinearity has been questioned (Leathwick et al. 2006; Murphy et al. 2010), and thus we omitted highly correlated variables ($r > 0.7$) to ensure independence among covariates (Dormann et al. 2013). Final variables included growing degree days $> 5^{\circ}\text{C}$ (dd5), TRASP, growing season precipitation (gsp), and summer precipitation balance (smpbrb).

MARS model

Both single-species (SDM) and multiple-species (CLM) implementations of the *MARS* (Multivariate Adaptive Regression Spline) algorithm were used to fit climate and topography metrics to a subset of the occurrence data. Utilizing the same algorithm for both SDM and CLM implementations ensured that the only major differences between the two approaches were

related to the number of species being modeled, leaving inclusion of co-occurrence information as the most parsimonious explanation for substantial differences in SDM and CLM predictive performance. *MARS* uses piecewise parametric fitting of basis functions based on recursive partitioning regression with a back-fitting algorithm to maintain model parsimony (Friedman 1991). This back-fitting approach removes basis functions that no longer contribute substantially to model fit, thus minimizing overfitting problems that are common to many other recursive partitioning approaches. The *MARS* algorithm is designed to reduce computational complexity and increase analytical speed and greatly reduces the computational costs associated with alternative recursive partitioning methods (Friedman 1993). In the multiple-species implementation of *MARS*, basis functions are optimized simultaneously across all species (Friedman 1991). Because *MARS* is designed to accommodate continuous responses, we adopted the approach of Leathwick et al. (2006) to model probability of presence based on binary occurrence data. Basis functions generated by the *MARS* algorithm were used to fit a GLM with a logit link function. For the multiple-species implementation, GLM coefficients were fit separately for each species.

Because we lacked a large independent data set for model validation, we partitioned our data into calibration and validation datasets using a spatially-segregated splitting approach (Bahn & McGill 2013). This approach ensures greater independence between calibration and validation data and provides more realistic assessments of model predictive ability (Peterson et al. 2007). Following Bahn & McGill (2013) we quadrisected our data longitudinally. Quarters one and three were combined and used as calibration data, and quarters 2 and 4 were used as validation data. It should be noted that we found no spatial autocorrelation among our species occurrence data or our model covariates (Moran's $I=0$, effective spatial range $\phi=0$), likely due to the

stratified sampling approach used for FIA data and the complex, heterogeneous topography of our study region. However, the spatially-segregated splitting approach ensured that our models were validated on climatic and geographic conditions that were not fully represented in the calibration data, thus improving our ability to evaluate predictive accuracy (Araújo et al. 2005b; Bahn & McGill 2013). Single-species *MARS* models were developed for each species (SDMs), and a multiple-species *MARS* model was fit to all species simultaneously (CLM). Both additive models and two-way interaction models were fit and compared. Models were evaluated for fit and parsimony based on the Generalized Cross Validation (GCV) criterion (Craven and Wahba 1979), and the model with the lowest GCV in each pair was retained for subsequent analysis. In all cases, two-way interaction models were retained. All *MARS* models were fit with the ‘earth’ package (version 4.2.0; Milborrow 2015) in R (R Core Team 2014). Fitted models were then predicted back to climate and topography grids to spatially display probability of occurrence across the entire study region. Probability of occurrence was converted to predicted presence/absence using a prevalence-based threshold (Liu et al. 2005). Prevalence-based thresholds have been shown to outperform other threshold approaches, including approaches that maximize model performance criterion, and provide consistency when comparing predictions across species with similar prevalence (Liu et al. 2005). Maintaining consistency among species and models was a primary goal in our selection of methods, as our evaluation relies on the relative differences between modeling approaches and algorithms, rather than on the predictive accuracy of each approach on its own.

CForest Model

The *CForest* algorithm generates an ensemble of conditional classification trees using recursive partitioning and is designed to overcome some of the biases associated with the more commonly used Random Forest algorithm. Conditional trees differ from the standard classification trees in that the variable selection process is separated from the splitting value selection, thus minimizing bias towards variables with many splits. Both variable selection and split determination are accomplished by permutation tests that measure the association between covariates and responses based on a *P*-value. Stopping criteria based on statistical significance are incorporated into the *CForest* algorithm to halt recursion when additional splits do not contribute significantly to model fit. This approach maintains model parsimony and reduces overfitting. In the multiple species (CLM) implementation, all response variables are transformed to log-rank scores for use in the permutation test, and the association between covariates and the log-ranked responses is tested (Hothorn et al. 2006a).

We fit *CForest* models to individual species occurrence data (SDM) and to co-occurrence data for all species simultaneously (CLM). For each model, 128 trees were grown with 4 variables evaluated at each split. Models were fit to the same calibration data that the *MARS* models were constructed with, and evaluated on the same remaining validation data. All *CForest* models were fitted using the ‘party’ package (Hothorn et al. 2006b) in R (R Core Team 2014). As with the *MARS* models, probability of presence across the study region was modeled by predicting the fitted *CForest* models back to climate and topography grids, and predicted presence/absence was evaluated using a prevalence-based threshold.

Model Comparison

SDM and CLM predictions were compared using non-spatial metrics based on validation data and comparisons of mapped model predictions. The ability of models to discriminate between presences and absences was assessed with AUC, a threshold-independent metric that indicates both the sensitivity (correctly classified presences) and specificity (correctly classified absences) of the model (Manel et al. 2001). AUC is calculated as the area under the receiver-operating characteristic curve, which is generated by plotting sensitivity against the false positive rate for all possible threshold values. We also evaluate discriminatory and predictive ability using the true skill statistic (TSS), a prevalence-dependent criterion based on sensitivity and specificity as determined by the prevalence-based threshold (Allouche et al. 2006). TSS is used to indicate improvement of a model from random prediction, which is assessed at a TSS value of 0. Sensitivity and specificity, again estimated using a prevalence-based threshold, were also evaluated independently to pinpoint underlying differences in model discrimination. To assess geographic overlap of mapped predictions for both current and future conditions, we used Schoener's D statistic (D). D represents the proportional geographic overlap of two distribution predictions as an index ranging from 0-1 (Renkonen 1938; Warren et al. 2008; Rödder & Engler 2011). Differences in mapped predictions between CLMs and SDMs were also assessed by comparing the percent difference in total area predicted to be occupied by a given species ($Adiff$) based on a prevalence-based threshold. $Adiff$ was calculated as the percent difference in CLM predicted occurrence relative to SDM predicted occurrence; thus, a positive value indicates a greater area of occurrence under the CLM. We emphasize that these criterion are utilized as a comparative tool to assess differences between SDM and CLM approaches, rather than individual model performance, in an attempt to evaluate whether CLMs capture the effects of biotic interactions.

Species co-occurrence based on SDM and CLM predictions was evaluated by assessing the number of species predicted to be present at each site. For the SDM approach, we stacked SDM predictions for our three focal and calculated the sum of predicted presences at each site, ranging from zero to three. For the CLM predictions, we simply summed the number of species predicted present at each site from the simultaneous CLM prediction of all focal species. Similarities between predicted species occurrence and underlying data were evaluated by comparing the overall classification accuracy, sensitivity and specificity for each species richness classification (0-3), and Cohen's Kappa (κ ; Cohen 1960). κ was used because of its ability to evaluate classification accuracy on more than two categories.

For additional illustrative purposes, we introduced a small independent data set of species co-occurrence to further validate predicted species co-occurrence. These data classify the number of focal species present at sampling plots across four ecotones in the Northern and Central U.S. Rocky Mountains and were collected independently from FIA data (Copenhaver & Cannon 2016). These ecotones represent regions of known species overlap, and provide additional insight into the ability of SDMs and CLMs to capture true co-occurrence patterns. For this small data set, we visually compared the predicted number of species present at each site to measured values.

2.4 RESULTS

MARS

The predictive accuracy of SDMs and CLMs predicted to spatially-segregated validation data varied across species and discrimination metrics (**Table 2.1**). While the CLM approach slightly outperformed the SDM approach for lodgepole pine, predictive accuracy was higher for

ponderosa pine and Douglas-fir under the SDM. Overall, Douglas-fir, the most prevalent species, was predicted with the lowest accuracy. Nevertheless, differences between SDM and CLM predictive accuracy are slight across all species.

The SDMs and CLMs both predicted very similar geographic distributions for Douglas-fir and ponderosa pine, while geographic distributions for lodgepole pine differed more substantially, despite similar predictive accuracy across species (**Table 2.1**). This suggests that incorrectly classified locations for lodgepole pine were counterbalanced by the two modeling approaches; i.e. many locations predicted inaccurately by the SDM were predicted more accurately by the CLM and vice versa. This points to a difference in the underlying relationship captured by the two modeling approaches for lodgepole pine. This is consistent with the *Adiff* statistic, which identifies a larger difference in the area of predicted presence for lodgepole pine by the SDM versus the CLM relative to other species (26.8% increase in predicted area of occurrence by the CLM). Also consistent with *D*, *Adiff* was substantially smaller and negative for ponderosa pine (-1.71%) and Douglas-fir (-3.32%), indicating that both modeling approaches classified sites similarly for these two species. The CLM predicted a slightly smaller area of occurrence for ponderosa pine and Douglas-fir than the SDM.

In general, the SDM approach under-predicted species co-occurrence, while the CLM over-predicted co-occurrence (**Table 2.2; Fig. 2.2**). These differences are mostly due to differences in the predicted geographical extent of lodgepole pine, which was under-predicted by the SDM and over-predicted by the CLM. Classification accuracy for number of species present was similar and poor for both approaches, indicating that neither modeling approach appropriately captures co-occurrence. Consistent with our hypothesis, co-occurrence predictions diverge most strongly in mid-elevation zones in the Northern and Central Rockies, where species

are most likely to interact (**Fig. 2.2**). When compared to independent field data along ecotones of known species overlap (Copenhaver-Parry & Cannon 2016), SDMs generally under-predict the number of species present along ecotones(**Fig. 2.2 b-e**), particularly for the two southernmost ecotones (**Fig. 2.2 d,e**). The CLM, however, also fails to predict many sites of three-species co-occurrence in ecotones (**Fig. 2.2 g-j**).

CForest

Similar to the *MARS* results, predictive accuracy for the *CForest* algorithm differed only slightly between SDM and CLM models, and varied across species (**Table 2.1**). Predictive accuracy was slightly higher for CLM models for all species, though TSS values indicate that predictions were often only slightly better than random. Conversely, AUC values indicate fair to good predictive accuracy, suggesting that an alternative threshold approach may have produced improved classification accuracy. Douglas-fir was predicted with the lowest accuracy under both SDM and CLM approaches. In general, lodgepole pine was predicted with the greatest accuracy, though ponderosa pine data generated a higher AUC and specificity in the SDM.

Geographic predictions from SDMs and CLMs were relatively similar across all species, with ponderosa pine showing the greatest difference (lowest *D*; **Table 2.1**). Sensitivity and specificity between SDMs and CLMs also show the greatest difference for ponderosa pine, indicating that both modeling approaches classified many locations differently for this species. This is reflected by the *Adiff* statistic, which demonstrates a large difference in the area of predicted presence locations for ponderosa pine between the SDM and the CLM, and a smaller difference for lodgepole pine and Douglas-fir. Across all species, the CLM approach resulted in a greater area of predicted occurrence than the SDM approach.

Differences in co-occurrence prediction accuracy were slight between the two modeling approaches, and both demonstrated relatively poor agreement with observed co-occurrence (**Table 2.2**). Across the study region, SDMs under-predicted species co-occurrence, while the CLM over-predicted co-occurrence. Both approaches indicate substantial overlap of all three focal species in the Northern and Central Rockies and absence of lodgepole pine in the Southern Rockies, which is consistent with data (**Fig. 2.3a,f**). When predictions are evaluated against independent data from ecotonal regions, differences in species overlap between SDMs and the CLM appear to be slight. In general, both approaches reasonably agree with data in the two northernmost ecotones (**Fig. 2.3b,c,g,h**), while the CLM more accurately captures co-occurrence in the two southernmost ecotones (**Fig. 2.3d,e,i,j**). The SDM approach does not accurately capture the southern limit of lodgepole pine's distribution in the Rocky Mountains, and inaccurately limits the distribution of this species to a more northern extent.

MARS and CForest comparison

Differences in predictive accuracy between *MARS* and *CForest* models are similar in magnitude to differences between SDMs and CLMs within the same modeling approach (**Table 2.1**). In general, the SDM implementation of the *MARS* model demonstrated improved predictive accuracy over the *CForest* SDMs, while the *CForest* CLM generally predicted data more accurately than the *MARS* CLM. However, we note several important exceptions. First, when comparing CLMs, lodgepole pine was predicted more accurately by the *MARS* algorithm. Additionally, the *CForest* SDM model showed a higher AUC for ponderosa pine relative to the *MARS* SDM, yet all threshold-based statistics demonstrated improved classification for the

MARS model. However, we emphasize that differences in predictive accuracy between approaches are slight.

Neither modeling approach was able to reproduce species co-occurrence with good accuracy, yet *CForest* models demonstrated slightly improved classification agreement over *MARS* models (**Table 2.2**). In general, CLM predictions from the two modeling approaches were more similar than were SDM predictions (**Table 2.3**). Predicted area of occurrence was most similar for Douglas-fir across the two modeling approaches, and most dissimilar for lodgepole pine under the SDM and ponderosa pine under the CLM. We evaluated the *Adiff* of these two approaches as *CForest* relative to *MARS*; thus, a negative value indicates a larger predicted area of occurrence by the *MARS* model than the *CForest* model. Across all species, *MARS* predicted greater regions of occurrence than *CForest*, with the notable exception of the lodgepole pine SDM, where *CForest* predicted a larger area of occurrence than *MARS*. Differences were most pronounced for ponderosa pine when comparing SDM predictions, and lodgepole pine when comparing CLM predictions.

2.5 DISCUSSION

A species' distribution not only reflects its climate-induced physiological tolerances, but may also be shaped by interactions with other species (Case et al. 2015). At broad scales, biotic interactions are expected to generate non-random co-occurrence patterns and to alter species-environment relationships from those occurring in isolation (Wisz et al. 2013). Both of these expectations are fundamental assumptions of the CLM approaches evaluated in this study. CLMs are intended to more accurately model species-environment relationships by explicitly accounting for other species when assigning statistical correlations (Ferrier & Guisan 2006).

However, the ability of CLMs to appropriately account for the effects of biotic interactions has remained uncertain, and thus their utility as a modeling tool has been questioned (Baselga & Araújo 2009). We predicted that CLMs should predict systematically different species distributions than SDMs by incorporating biotic information. In particular, CLMs and SDMs should differ in the spatial overlap, or co-occurrence predicted for multiple species. We further predicted that if CLMs do in fact account for biotic interactions, the distributions and co-occurrence patterns predicted by CLMs should more accurately reproduce observed patterns than SDMs, indicated by an improvement in predictive accuracy.

Our results do demonstrate some systematic differences between CLM and SDM predictions, although trends are not entirely consistent across species. In general, CLMs predict larger areas of occurrence than SDMs (**Table 2.1**), and a greater degree of co-occurrence (**Table 2.2**). However, we note several important exceptions: in the case of the *MARS* algorithm, the SDM approach predicted slightly larger areas of occurrence for both ponderosa pine and Douglas-fir, although differences were small. The general trends observed suggest that inclusion of biotic information generally acts to alter the extent of the climatic niche of modeled species. This finding is consistent with the model fitting approaches used by both the *MARS* algorithm and the *CForest* algorithm, and may reflect model structure more than biological phenomena.

In the *MARS* algorithm, multispecies predictions are generated by optimizing basis functions simultaneously across all species (Friedman 1991; Leathwick et al. 2006). This essentially amounts to averaging environmental responses across all species. In the *CForest* CLM fitting process, a permutation test based on log-rank scores allows each species to have varying amounts of influence at each split, yet the model is still fit across all species simultaneously (Hothorn et al. 2006). Thus, in both algorithms, an averaging effect is imposed.

For species that exhibit opposing environmental responses or parapatric distributions, this averaging effect may alter the predicted climatic niche and geographical extent of each species, specifically by broadening the niche/extent of narrowly distributed or climatically constrained species, and constraining the niche/extent of more broadly distributed species (Madon et al. 2013). Our findings reflect the effects of this averaging process. For example, lodgepole pine is the most narrowly distributed species in our data set, with a distribution that is constrained to a more northern extent of the study region (**Fig. 2.1**). Additionally, lodgepole pine has a smaller climatic niche than either ponderosa pine or Douglas-fir, particularly with regards to summer precipitation (Bell et al. 2014). When modeled with the *MARS* CLM, the distribution of lodgepole pine is expanded relative to SDM predictions, while the distributions of ponderosa pine and Douglas-fir are constrained (**Table 2.2; Adiff**). Additionally, ponderosa pine and Douglas-fir distributions are more similar between SDM and CLM predictions, while lodgepole pine differs more substantially (**Table 2.2; D**). This may reflect differences in species prevalence, with more prevalent species (i.e. ponderosa pine and Douglas-fir) exerting greater influence in the averaging process. The *CForest* algorithm may overcome some of the limitations of a pure averaging process by allowing species to have varying degrees of influence at each split (Hothorn et al. 2006). In our *CForest* analysis, all species distributions were expanded in the CLM relative to the SDMs (**Table 2.2**). The greater consistency across species indicates that the *CForest* algorithm may minimize the influence of species prevalence and geographic extent on fitted environmental responses.

Despite systematic differences in model predictions related to the inclusion of biotic information, we found no consistent improvement in CLM predictive accuracy relative to that of SDMs. Differences in predictive accuracy between CLMs and SDMs were similar in magnitude

to differences between *MARS* and *CForest* models (**Table 2.3**), again indicating that model structure, rather than the effects of biotic interactions, explains much of the variation in model output. Additionally, both approaches failed to accurately reproduce patterns of species co-occurrence. CLMs generally predicted too great an area of three-species co-occurrence, while SDMs failed to predict many regions of three-species co-occurrence (**Table 2.2**). Further, neither approach sufficiently captured species co-occurrence along ecotones, particularly in the more southern portions of lodgepole pine's distribution (**Fig. 2.2; Fig. 2.3**). We do note that the *CForest* algorithm demonstrated higher classification accuracy for species co-occurrence than *MARS*, again indicating that the *CForest* algorithm overcomes some of the limitations associated with *MARS*'s pure averaging approach (Hothorn et al. 2006).

It is possible that our findings also indicate a limited role for biotic interactions in defining the distributions of our focal species. While mounting evidence from other plant systems has demonstrated improved predictions of tree distributions after accounting for biotic interactions (Rouget et al. 2001; Meier et al. 2010; Boulangeat et al. 2012; Clark et al. 2014), the strong elevational zonation in our study system may simply be a function of sharp physiological limitations that interact with climate to determine local distribution edges. This is consistent with the findings of Copenhaver-Parry & Cannon (2016), which identify climate as the primary driver of growth trends at distribution edges of our focal species. However, our SDM models generally failed to predict the distributional limit of lodgepole pine, and under-predicted co-occurrence, suggesting that factors in addition to the climatic factors evaluated here contribute to these species' distribution patterns. Our results indicate that it will require improved modeling approaches to determine the precise role of biotic interactions in structuring these species' distributions.

Both CLMs and SDMs have a variety of additional limitations related to their ability to account for biotic interactions that were not directly highlighted in our analyses. For example, both CLMs and SDMs are unable to account for changes in species interactions over time. The magnitude and direction of plant interactions have been shown to be altered by past environmental change, suggesting that changes in interactions will also be observed under future conditions (Tylianakis et al. 2008; Blois et al. 2013). Climatic changes may drive reversals in competitive hierarchies, or even result in novel species assemblages (Jackson et al. 2009). Specifically, large environmental changes may reduce the competitive advantage of more specialized species and favor generalist species (Schubert & Bottier 1995; Sahney & Benton 2008). Additionally, changes in interactions with other taxa across a variety of trophic levels may also have large impacts on future distributions. Of particular relevance in our study region, bark beetle outbreaks associated with climate warming have had a comparatively larger impact on *Pinus ponderosa* and *Pinus contorta* in the Rocky Mountains than on *Pseudotsuga menziesii* (Meddens et al. 2012). This competitive advantage is independent of climatic tolerance, and may result in range expansion of Douglas-fir and contraction of lodgepole pine and ponderosa pine that cannot be predicted by static CLMs or SDMs (Wisz et al. 2013). Neither CLMs nor SDMs can differentiate between the contributions of environmental tolerances and biotic interactions to co-occurrence patterns, making direct quantifications of the factors underlying species distributions impossible (Wisz et al. 2013; Pollock et al. 2014).

Our results suggest that CLMs offer no real improvement over SDMs in accounting for the effects of biotic interactions. Therefore, CLMs are unlikely to generate accurate predictions of species whose distributions are influenced by biotic interactions. This is highlighted in our results by similar predictive accuracy of SDMs and CLMs, poor classification accuracy for co-

occurrence patterns across both SDMs and CLMs, and over-prediction of species co-occurrence by CLMs. Further, CLMs cannot be used to identify the causes of climate-distribution disequilibria, which may be due to true biotic interactions or simply due to environmental factors that remain unaccounted for in the model. However, CLMs may find utility in modeling assemblages of regularly co-occurring and strongly overlapping species that demonstrate shared environmental responses and similar climatic niches (see Chatfield 2008; Baselga & Araujo 2009; Madon et al. 2013 for a more complete discussion of CLMs in this context). While our results do not directly evaluate the utility of CLMs in such contexts, we do demonstrate a slight improvement in classification accuracy for the *CForest* CLM over the *MARS* CLM, and note improvement in the species averaging process in the *CForest* algorithm. Thus, in contexts where a CLM may be appropriate, *CForest* is likely to produce more accurate predictions than *MARS*. Overall, we conclude that alternative methods to CLMs may provide more useful approaches to account for the effects of biotic interactions and, consequently, provide more reliable predictions of species distributions.

2.6 REFERENCES

- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology* 43: 1223-1232.
- Araújo MB, Pearson RG, Rahbek C. (2005a) Equilibrium of species' distributions with climate. *Ecography* 28: 693-695.
- Araújo MB, Pearson RG, Thuiller W, Erhard M (2005b) Validation of species-climate impact models under climate change. *Global Change Biology* 11: 1504-1513.
- Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743-753.
- Araújo MB, Rozenfeld A, Rahbek C, Marquet PA (2011) Using species co-occurrence networks to assess the impacts of climate change. *Ecography* 34: 897-908.
- Bahn V, McGill BJ (2013) Testing the predictive performance of distribution models. *Oikos* 122: 321-331.
- Bartlein PJ, Whitlock C, Shafer SL (1997) Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11: 782-792.
- Baselga A, Araújo MB (2009) Individualistic vs community modelling of species distributions under climate change. *Ecography* 32: 55-65.
- Baselga A, Araújo MB (2010) Do community-level models describe community variation effectively? *Journal of Biogeography* 37: 1842-1850.
- Bell DM, Bradford JB, Lauenroth WK (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23: 168-180.

- Blois JL, Gotelli NJ, Behrensmeyer AK, Faith JT, Lyons SK, Williams JW, Amatangelo KL, Bercovici A, Du A, Eronen DJ, Graves GR, Jud N, Labandeira C, Looy CV, McGill B, Patterson D, Potts R, Riddle B, Terry R, Tóth A, Villaseñor A, Wing S. (2014) A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. *Ecography* 37: 1095-1108.
- Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15 584-593.
- Case TJ, Holt RD, McPeck MA, Keitt H (2005) The community context of species' borders: Ecological and evolutionary perspectives. *Oikos* 108: 28-46.
- Chatfield BS (2008) How to find the one that got away. Predicting the distribution of temperate demersal fish from environmental variables. PhD Thesis, School of Earth and Geographical Sciences, University of Western Australia, Perth.
- Clark JS, Gelfand AE, Woodall CW, Zhu K (2014) More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications* 24: 990-999.
- Cohen J (1960) A coefficient of agreement for nominal scales. *Education and Psychological Measurement* 20: 37-46.
- Copenhaver-Parry PE, Cannon E (2016) The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* DOI 10.1007/s00442-016-3565-x

- Craven P, Wahba G (1979) Smoothing noisy data with spline functions. Estimating the correct degree of smoothing by the method of generalized cross-validation. *Numerical Mathematics* 31: 317-403.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 027-046.
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129-151.
- Evans JS, Oakleaf J, Cushman SA, Theobald D (2014) An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0. Available: <http://evansmurphy.wix.com/evansspatial>. Accessed: 2015.
- Ferrier S, Guisan A (2006) Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology* 43: 393-404.
- Friedman JH (1991) Multivariate adaptive regression splines. *The Annals of Statistics* 19: 1-67.
- Friedman JH (1993) Fast MARS. Technical Report No. 110: Department of Statistics, Stanford University.

- Gibson J, Moisen G, Frescino T, Edwards Jr TC (2014) Using publicly available forest inventory data in climate-based models of tree species distribution: Examining effects of true versus altered location coordinates. *Ecosystems* 17: 43-53.
- Godsoe W, Harmon, LJ (2012) How do species interactions affect species distribution models? *Ecography* 35: 811-820.
- Guisan A, Rahbek C (2011) SESAM- a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography* 38: 1433-1444.
- Hardy OJ (2008) Testing the spatial phylogenetic structure of local communities: statistical performances of different null models and test statistics on a locally neutral community. *Journal of Ecology* 96: 914-926.
- HilleRisLambers J, Harsch MA, Ettinger AK, Ford KR, Theobald EJ (2013) How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences* 1297: 112-125.
- Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659-19665.
- Hothorn T, Buehlmann P, Dudoit S, Molinaro A, Van Der Laan M (2006) Survival ensembles. *Biostatistics* 7: 355-373.
- Hothorn, T, Hornik K, Zeileis A (2006a) Unbiased recursive partitioning: A conditional inference framework. *Journal of Computational and Graphical Statistics* 15: 651-674.
- Hutchinson MF (1991) Continent wide data assimilation using thin plate smoothing splines. *BMRC Research Report 27*, Bureau of Meteorology, Melbourne, Australia.

- Hutchinson MF (2000) ANUSPLIN Version 4.1 User's Guide. Australian National University, Centre for Resource and Environmental Studies, Canberra.
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106: 19685-19692.
- Kissling WD, Dormann CF, Groenvelde J, Hickler T, Kühn I, McNemy GJ, Montoya JM, Römermann C, Schiffrers K, Schurr FM, Singer A, Svenning JC, Zimmermann NE, O'Hara RB (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography* 39: 2163-2178.
- Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology* 86: 2047-2054.
- Leathwick J (2009) Are New Zealand's Nothofagus species in equilibrium with their environment? *Journal of Vegetation Science* 9: 719-732.
- Leathwick JR, Elith J, Hastie T (2006) Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling* 199: 188-196.
- Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385-393.
- Madon B, Warton DI, Araújo MB (2013) Community-level vs species-specific approaches to model selection. *Ecography* 36: 1291-1298.
- Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38: 921-931.

- Mark DM, Smith B (2004) A science of topography: from qualitative ontology to digital representations. In: Bishop, M.P. & Shroder, J.F. (Eds.). Geographic Information Science and Mountain Geomorphology. Springer-Praxis, Chichester, England, pp. 75-97.
- McCaughey WW, Schmidt WC, Shearer RC (1985) Seed dispersal characteristics of conifers of the inland Mountain West. In: Shearer RC. Proceedings: Conifer Tree Seed in the Inland Mountain West Symposium. April 1985, Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service Intermountain Research Station: 50-62.
- Meddens AJH, Hicke JA, Ferguson CA (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22: 1876-1891.
- Meier ES, Kienast F, Pearman PB, Svenning JC, Thuiller W, Araújo MB, Guisan A, Zimmermann NE (2010) Biotic and abiotic variables show little redundancy in explaining tree species distributions. Ecography 33: 1038-1048.
- Meineri E, Skarpaas O, Vandvik V (2012) Modeling alpine plant distributions at the landscape scale: Do biotic interactions matter? Ecological Modelling 231: 1-10.
- Milborrow S. Derived from mda:mars by T. Hastie and R. Tibshirani. Uses A. Miller's Fortran utilities with T. Lumley's leaps wrapper. (2015) earth: Multivariate Adaptive Regression Splines. R package version 4.2.0. <http://CRAN.R-project.org/package=earth>
- Morueta-Holme N, Blonder B, Sandel B, McGill B, Peet RK, Ott JE, Violle C, Enquist BJ, Jorgensen PM, Svenning JC (2015). A network approach for inferring species association from co-occurrence data. Ecography DOI 10.1111/ecog.01892
- Murphy MA, Evans JS, Storfer A (2010) Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91: 252-261.

- Normand S, Zimmermann NE, Schurr FM, Lischke H (2014) Demography as the basis for understanding and predicting range dynamics. *Ecography* 37: 1149-1154.
- Olden JD, Joy MK, Death RG (2006) Rediscovering the species in community-wide predictive modeling. *Ecological Applications* 16: 1449-1460.
- Peet RK (1981) Forest vegetation of the Colorado Front Range: Composition and Dynamics. *Vegetatio* 45: 3-75.
- Pellissier L, Pradervand JN, Pottier J, Dubuis A, Maiorano L, Guisan A. 2012. Climate-based empirical models show biased predictions of butterfly communities along environmental gradients. *Ecography* 35: 684-692.
- Peterson TA, Papes M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* 30 550-560.
- Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, Vesik PA, McCarthy MA (2014) Understanding co-occurrence by modeling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5: 397-406.
- R Core Team. (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rehfeldt GL (2006) A spline model of climate for the Western United States. General Technical Report RMRS-GTR-165. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Renkonen O (1938) Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Annales Zoologici Societatis Zoologicae-Botanicæ Fennicæ* 'Vanamo' 6: 1-231.

- Roberts DW, Cooper SV (1989) Concepts and techniques of vegetation mapping. In Land Classifications Based on Vegetation: Applications for Resource Management. USDA Forest Service GTR INT-257, Ogden, Utah: 90-96.
- Rödger D, Engler JO (2011) Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography* 20: 915-927.
- Rouget M, Richardson DM, Lavorel S, Vayreda J, Gracia C, Milton SJ (2001) Determinants of distribution of six *Pinus* species in Catalonia, Spain. *Journal of Vegetation Science* 12: 491-502.
- Sahney S, Benton MJ (2008) Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society B* 275: 759-765.
- Samadi SZ, Sagareswar G, Tajiki M (2010) Comparison of General Circulation Models: methodology for selecting the best GCM in Kermanshah Synoptic Station, Iran. *International Journal of Global Warming* 2: 347-365.
- Schubert JK & Bottjer DJ (1995) Aftermath of the Permian-Triassic mass extinction event: Paleocology of Lower Triassic carbonates in the western USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 116: 1-39.
- Smith WB (2002) Forest inventory and analysis: a national inventory and monitoring program. *Environmental Pollution* 116: S233-S242.
- Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science* 315: 640-642.
- Svenning JC, Gravel D, Holt RD, Schurr FM, Thuiller W, Münkemüller T, Schiffrers KH, Dullinger S, Edwards TC Jr, Hickler T, Higgins SI, Nabel JEMS, Pagel J, Normand S

- (2014) The influence of interspecific interactions on species range expansion rates. *Ecography* 37: 1198-1209.
- Swab RM, Regan HM, Matthies D, Becker U, Bruun HH (2015) The role of demography, intra-species variation, and species distribution models in species' projections under climate change. *Ecography* 38: 221-230.
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351-1363.
- VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C (2014) SDMTTools: Species Distribution Modelling Tools: Tools for processing data associated with species distribution modeling exercises. R package version 1.1-221. <http://CRAN.R-project.org/package=SDMTTools>
- Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: Quantitative approaches to niche evolution. *Evolution* 62: 2868-2883.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Reviews of Ecology and Systematics* 33: 475-505.
- Wisn MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, Damgaard CF, Dormann CF, Forchhammer MC, Grytnes JA, Guisan A, Heikkinen RK, Høye TT, Kühn I, Luoto M, Maiorano L, Nilsson MC, Normand S, Öckinger E, Schmidt NM, Termansen M, Timmermann A, Wardle DA, Aastrup P, Svenning JC (2013) The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15-30.

- Woodall CW, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2010) Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology and Management* 259: 778-785.
- Worth JRP, Williamson GJ, Sakaguchi S, Nevill PG, Jorden GJ (2014) Environmental niche modelling fails to predict Last Glacial Maximum refugia: niche shifts, microrefugia or incorrect palaeoclimate estimates? *Global Ecology and Biogeography* 23: 1186-1197.
- Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL (2010) The forest inventory and analysis database: database description and user manual version 4.0 for phase 2. Gen. Tech. Rep. RMRS-GTR-245. USDA Forest Service Rocky Mountain Research Station, Fort Collins, Colorado, USA.

2.7 TABLES

Table 2.1. Predictive accuracy of CLM and SDM models fit under both the *MARS* and *CForest* algorithms along with geographic similarity in mapped predictions (*D*), and differences in area of predicted occurrence (*Adiff*).

		AUC		TSS		Sens.		Spof.		<i>D</i>	<i>Adiff</i> (%)
		<i>SDM</i>	<i>CLM</i>	<i>SDM</i>	<i>CLM</i>	<i>SDM</i>	<i>CLM</i>	<i>SDM</i>	<i>CLM</i>		
<i>MARS</i>	Lodgepole pine	0.862	0.876	0.574	0.630	0.852	0.884	0.759	0.746	0.742	26.8
	Ponderosa pine	0.833	0.833	0.507	0.488	0.696	0.680	0.811	0.808	0.866	-1.71
	Douglas-fir	0.803	0.790	0.451	0.399	0.809	0.773	0.642	0.627	0.943	-3.32
<i>CForest</i>	Lodgepole pine	0.812	0.861	0.571	0.629	0.767	0.853	0.804	0.776	0.814	10.2
	Ponderosa pine	0.836	0.850	0.481	0.558	0.639	0.814	0.842	0.744	0.749	29.9
	Douglas-fir	0.796	0.800	0.401	0.415	0.757	0.824	0.644	0.591	0.886	17.9

Table 2.2. Classification accuracy for predicted species co-occurrence patterns.

		Accuracy ^a	Kappa ^b	Percent Area ^c			
				0	1	2	3
CForest MARS	SDM	0.524	0.293	51.9	16.4	28.3	3.36
	CLM	0.505	0.272	54.6	16.1	23.2	6.00
	SDM	0.585	0.369	57.1	18.6	20.1	4.26
	CLM	0.544	0.331	49.9	16.1	27.4	6.66

^a the proportion of co-occurrences that were correctly predicted by the model.

^b a measure of agreement between true classified values and predicted classified values;

1=perfect agreement; 0=agreement equivalent to chance.

^c the percentage of the study area predicted to be occupied by the specified number of species.

Table 2.3. Comparison of *CForest* and *MARS* predictions.

	<i>D</i>		<i>Adiff (%)</i>	
	<i>SDM</i>	<i>CLM</i>	<i>SDM</i>	<i>CLM</i>
Lodgepole pine	0.705	0.804	2.80	-19.30
Ponderosa pine	0.746	0.759	-67.40	-15.40
Douglas-fir	0.820	0.860	-45.40	-15.60

D represents the geographic similarity of *MARS* and *CForest* predictions, and *Adiff* represents the percent difference in predicted area of occurrence (a positive value indicates a greater area of occurrence under the *CForest* model).

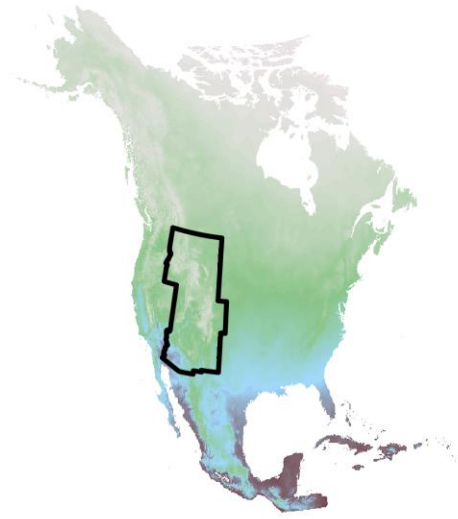
2.8 FIGURES

Figure 2.1. The study area (a) encompassed the U.S. states of Idaho, Montana, Utah, Wyoming, Colorado, Arizona and New Mexico. FIA data used to model species occurrence demonstrate the general distribution of lodgepole pine (b), ponderosa pine (c) and Douglas-fir (d) across the study region. Presence locations for each species are shown in *black*, while absence locations are shown in *gray*. Points are superimposed on a gradient of growing degree days $>5^{\circ}\text{C}$, which is a covariate that was consistently selected for in the models developed in this study.

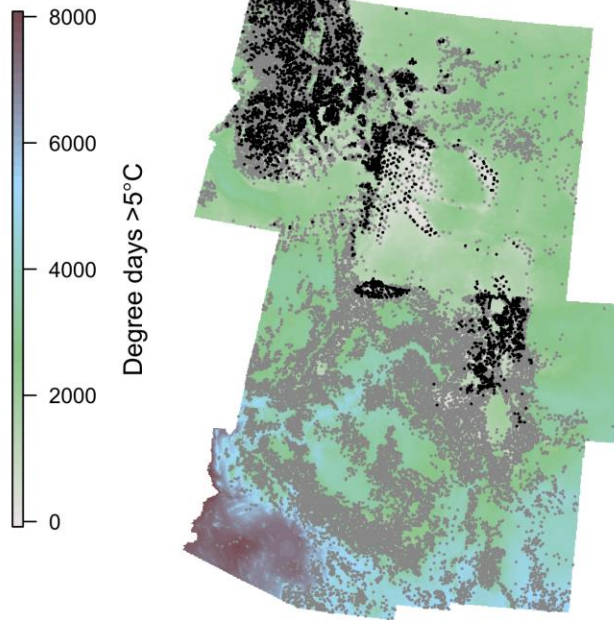
Figure 2.2. Co-occurrence predictions from the *MARS* SDMs (a-e) and the *MARS* CLM (f-j). Across ecotones where all species are known to interact, both the SDM models (b-e) and the CLM model (g-j) generally failed to accurately reproduce observed species co-occurrence patterns (*colored points*).

Figure 2.3. Co-occurrence predictions from the *CForest* SDMs (a-e) more accurately classify species occurrence in more northern ecotonal regions (b,c), but fail to model known regions of three species occurrence (*red points*) in more southern ecotones (d-e). Co-occurrence predictions from the *CForest* CLM (f-j) show a greater area of species overlap than SDM predictions, particularly for regions of three-species overlap (*red*), and show slightly improved classification of species overlap along ecotones (g-j) when compared to independent observation data (*colored points*).

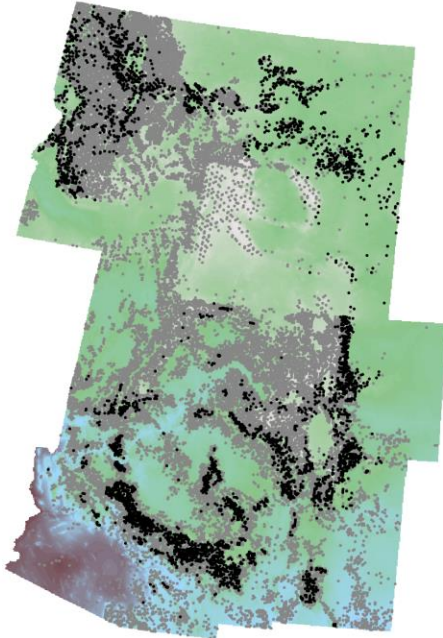
a) Study area



b) Lodgepole pine



c) Ponderosa pine



d) Douglas-fir

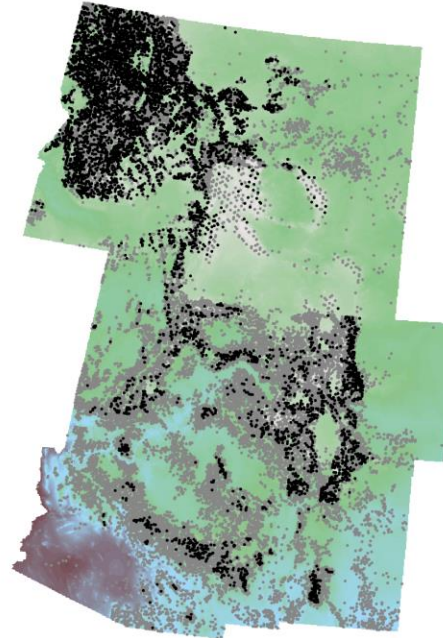


Figure 2.1

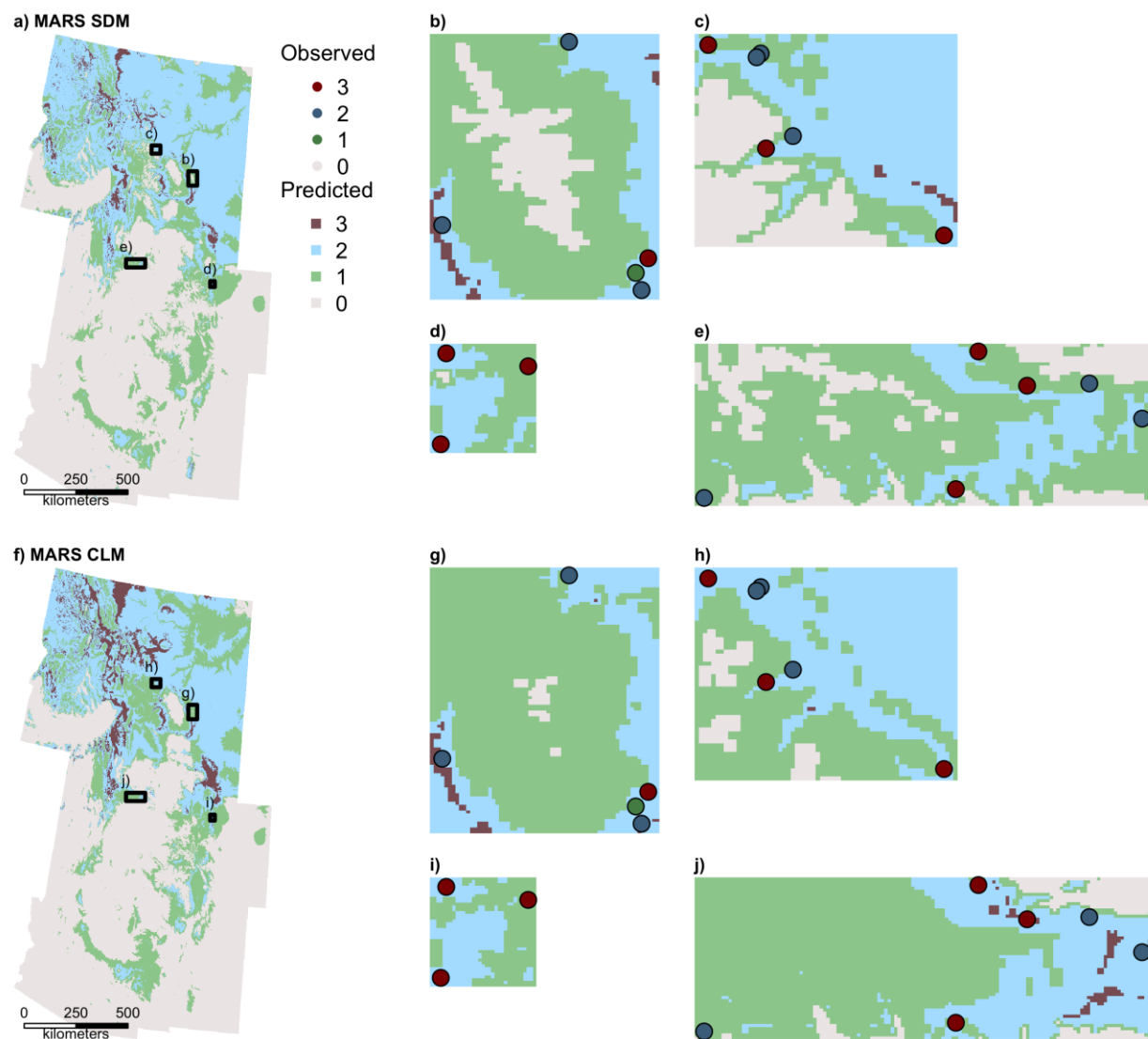


Figure 2.2

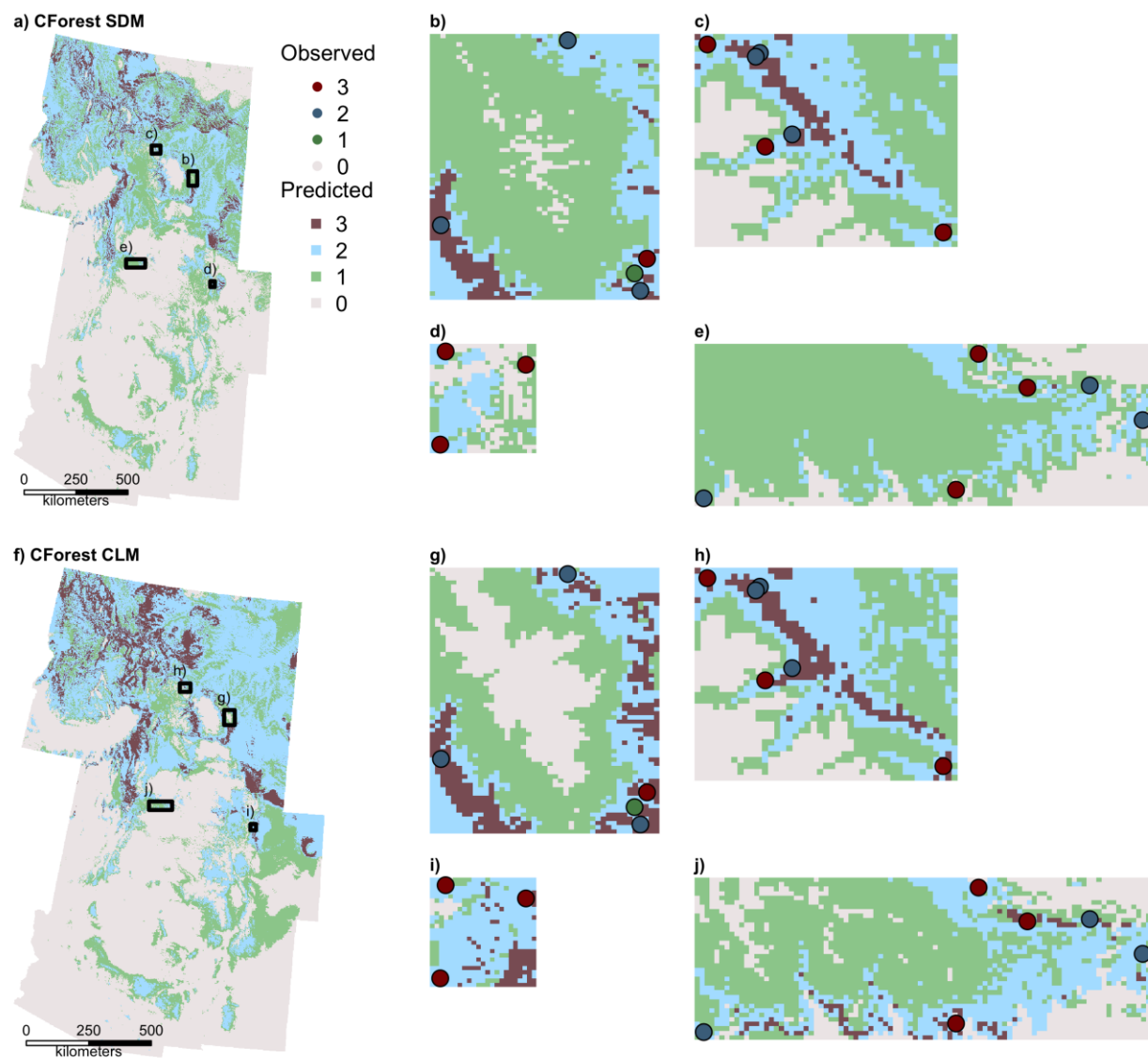


Figure 2.3

CHAPTER 3: CLIMATE, NOT BIOTIC INTERACTIONS, EXPLAINS TREE CO-OCCURRENCE PATTERNS IN THE US ROCKY MOUNTAINS

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3.1 ABSTRACT

Species distributions are hypothesized to be shaped by a variety of factors acting across multiple spatial scales. The role of biotic interactions has been particularly emphasized, but scale-dependencies in ecological factors have hampered comparisons of the relative effects of biotic interactions and climate on species distributions. Here, we use a Joint Species Distribution Model (JSDM) to simultaneously model the co-occurrence patterns of ten dominant tree species across the US Rocky Mountains. The JSDM approach allows us to attribute species co-occurrence patterns to either environmental responses or potential interspecific biotic interactions. Our results demonstrate that shared environmental responses can largely explain the co-occurrence patterns of Rocky Mountain tree species, with little to no importance of biotic interactions evident from our analysis. However, variation in model performance across species indicates that alternative factors not considered in the JSDM may contribute to species distribution patterns, particularly among lower elevation tree species. We conclude that the distributions of Rocky Mountain tree species predominantly reflect the influence of broad-scale climatic factors.

3.2 INTRODUCTION

While much research effort has recently been focused on resolving the drivers of species distribution patterns, considerable uncertainties remain for many species and systems. Species distributions are shaped by a variety of factors acting across multiple spatial scales (Pulliam 2000; Araújo et al. 2011; Schurr et al. 2012; Normand et al. 2014), and disentangling the relative influences of these factors is not always a straightforward process. Species distributions are underlain by a complex association of local and regional processes including biotic interactions, dispersal limitation, population dynamics, fine-scale variation in resource availability and broad-scale climatic gradients (Cazelles et al. 2015; Morueta-Holme et al. 2015; Serra-Diaz et al. 2015). However, scale-dependencies in these processes and their effects often complicate comparative investigations of the relative importance of individual factors to species distribution patterns (Sandel 2015; Kissling et al. 2012). Scaling hypothesized drivers to comparable scales may enable relative comparisons, yet often results in the loss of potentially important variation in underlying processes, thereby complicating inference (Holt 2009; Kissling et al. 2012). These challenges have been recently highlighted by investigations seeking to integrate species interactions and climate in models of regional species occurrence.

Climate, a regional factor with coarse spatial resolution, has traditionally been understood to be the dominant factor shaping species distributions (Woodward 1987), as it correlates particularly well with species occurrence patterns observed at a comparable spatial resolution (Austin 1999; Morin et al. 2007; Boucher-LaLonde et al. 2012). Species interactions, which are a function of resource-consumer dynamics operating at a very fine spatial resolution (Soberón & Nakamura 2009), have been traditionally dismissed as increasingly undetectable as spatial scale broadens (Pearson & Dawson 2003). However, when interactions are sufficiently and uniformly

strong to alter local species dynamics over a large enough region, their effects may be detectable at macroecological scales (Pulliam 2000; Schurr et al. 2012; Normand et al. 2014; Thuiller et al. 2014; Sandel 2015). This spatial signature of species interactions may be highly dependent upon environmental conditions, with negative interactions (e.g. competition) impacting occurrence patterns more strongly under favorable environmental conditions, and positive interactions (e.g. facilitation) increasing in relative importance in regions of environmental stress (Brown et al. 1996; Zimmerman et al. 2015).

A number of recent studies have demonstrated improvements in species distribution models by incorporating potentially interacting species as model covariates (Leathwick & Austin 2001; Araújo & Luoto 2007; Meier et al. 2010; Pellissier et al. 2010), lending support for the hypothesis that species interactions may exert a substantial influence on species distribution patterns. However, the investigative approach used in these studies inappropriately assumes unidirectional relationships between pairs of interacting species (Clark et al. 2014). As an alternative, community-level approaches (CLMs) attempt to account for species interactions by modeling species simultaneously (Ferrier & Guisan 2006; Baselga & Araujo 2010). However, CLMs appear to involve many statistical limitations, the most prominent being their inability to appropriately capture individual species' environmental responses (Copenhaver-Parry et al. 2016). Further, both SDM and CLM approaches are unable to disentangle true species interactions from alternative factors that could underlie species associations, such as shared environmental constraints and dispersal limitations (Guisan & Thuiller 2005; Meineri et al. 2012; Morueta-Holme et al. 2015; Kissling et al. 2012; Wisz et al. 2013). These issues complicate valid inference and preclude general conclusions regarding the relative influences of species interactions and abiotic environmental factors on species distributions.

Analyzing species co-occurrence patterns presents a promising way forward, as co-occurrence patterns may represent the effects of both species interactions and environmental responses, thereby integrating local and regional processes, and are observed at a scale that is consistent with inference on distributions. Analysis of non-random co-occurrence patterns has a rich history of use pertaining to understanding the drivers of species composition patterns at local scales (Connor et al. 2013), yet has only recently been extended to macroecological scales (Wisz et al. 2013; Clark et al. 2014; Pollock et al. 2014; Morueta-Holme et al. 2015; Royan et al. 2015). Species interactions may scale up to influence co-occurrence patterns by causing species to occur together either more or less frequently than expected due to chance (Wisz et al. 2013). In the former case, facilitation between species may allow species to occur beyond their range of climatic tolerance (LeRoux et al. 2012; Thuiller et al. 2013), or species may exhibit shared responses to environmental conditions (Ovaskainen et al. 2010; Royan et al. 2015). In the latter case, competitive exclusion may restrict species co-occurrence (Case et al. 2005; Godsoe & Harmon 2012), or species may exhibit opposing responses to environmental conditions (i.e. species sorting; Ricklefs & Jenkins 2011; Boulangeat et al. 2012). Disentangling the factors underlying species co-occurrence patterns allows for quantification of the relative influences of the abiotic environment and species interactions on species distributions, and can be accomplished within a Joint Species Distribution Modeling (JSDM) framework.

The JSDM approach exploits residual correlation in species co-occurrence patterns to infer the strength of positive and negative interspecific interactions. Species co-occurrence can be partitioned to represent that explained by species responses to climate, and co-occurrence left unexplained. When climatic and other influences that may give rise to non-random co-occurrence patterns are adequately described, this residual correlation is likely to indicate the

influence of species interactions (Ovaskainen et al. 2010; Clark et al. 2014; Pollock et al. 2014).

In practice, accounting for all potential drivers of co-occurrence patterns is a difficult task, and the JSDM approach relies on substantial interpretation regarding the residual correlation. As with all correlative approaches, interpretation is best made by relying on both model output and ecological context. When interpreted carefully, JSDM may offer an improved approach to partitioning the effects of the abiotic environment from those of potential species interactions. Such measures are crucial to understanding the integrated impacts of local and regional processes on biogeographical patterns, which will enable more accurate predictions of biodiversity changes (Cazelles et al. 2015).

In this study, we evaluate co-occurrence patterns of 10 commonly-occurring canopy tree species in the U.S. Rocky Mountains using a JSDM (Pollock et al. 2014) to disentangle co-occurrence patterns arising from environmental responses and those indicative of species interactions. While strong elevational zonation in tree distributions in this region have been traditionally explained by climate (Bartlein et al. 1997; Rehfeldt et al. 2006; Shrag et al. 2008), species interactions may give rise to similar patterns and have not been sufficiently evaluated (Wiens 2011; Graham et al. 2014). Additionally, climate envelopes of many of our focal species show substantial overlap (Bell et al. 2014a), suggesting that climatic gradients are likely not the sole driver of tree distribution patterns in this region. Quantifying the relative influences of climate and species interactions on co-occurrence patterns of these species will help to clarify expected species responses to climate change and provide more detailed insight in to the factors underlying species distributions. To address these goals, our specific objectives were to: 1) evaluate the relative influences of climate and potential species interactions on co-occurrence

patterns, and 2) develop predictions of species distributions that account for potential positive and negative interspecific interactions.

3.3 MATERIALS AND METHODS

Tree co-occurrence data

Occurrence data, detailing presence and absence locations, were extracted from the U.S. Forest Service's Forest Inventory and Analysis (FIA) database. The FIA database consists of plot-level forest data from a comprehensive survey of forest conditions across the United States. The FIA program uses remote sensing methods to aggregate landscapes into relatively homogenous regions, which are then represented by a common plot on which detailed field observations are made (Woudenberg et al. 2010). Across the conterminous United States, one field observation plot has been established for approximately every 25 km² of forested land. These plots span all forest ownership types and provide the most comprehensive source of presence/absence data on forest species available in the United States (Smith 2002). To protect plot integrity and private ownership, all publicly available FIA plot coordinates are perturbed within a 0.8km radius of actual plot locations (Woodall et al. 2010). Perturbed coordinates do not appear to reduce the performance of species distribution models relative to precise coordinates (Gibson et al. 2014), and the uncertainty in resolution is deemed acceptable for integration with 1km resolution climate data (C. Woodall, personal communication).

This study made use of the most recent survey data (2003-2012) for all FIA field observation plots within the U.S. states of Montana, Idaho, Utah, Wyoming, Colorado, New Mexico and Arizona (**Fig. 3.1**). Presence and absence locations were extracted for ten commonly occurring tree species (**Table 3.1**): subalpine fir, Engelmann spruce, whitebark pine, two-needle

pinyon, lodgepole pine, limber pine, ponderosa pine, Douglas-fir, quaking aspen and gambel oak. These species were selected for their dominance in the study region and for commonalities in life history traits that suggest the potential for interspecific interactions. Specifically, we selected species that represent a range of shade tolerance, drought tolerance and habitat preferences and are adapted to a variety of disturbance regimes in order to capture variability across our study region, yet maintained representation of species sharing strong similarities for each of these traits. In the initial model testing phase, an additional 19 tree species that also occur in the study region were included, yet their low prevalence skewed model correlations. Only species whose prevalence exceeded 3.3%, or 500 occurrence records, were included in the final formulation of the model. Seedling records were excluded from the data due to greater uncertainty in species identification and potentially lower sampling intensity (Woodall et al. 2010; Woudenberg et al. 2010); only individuals exceeding 2.5 cm diameter at breast height (DBH) were included. In total, 15,365 FIA plots were used to detail recorded presence and absence locations.

Because all FIA data is collected on forested land, an additional 5000 pseudo-absence points were selected from non-forested land using an environmental filter to properly constrain species occurrence predictions. Non-forested pseudo-absence locations were randomly drawn from a multivariate characterization of environmental space, corresponding with the environmental covariates used in the JSMD. Samples were constrained within a 5% buffer beyond the multivariate environmental distribution of the FIA data in order to prevent artificial inflation of model parameters caused by unconstrained sampling (Van der Wal & Shoo 2009). Specifically, including additional absence data beyond forested regions enables the model to more accurately distinguish between presence and absence locations (Mateo et al. 2012), and

sampling within a defined range of environmental conditions allows the environmental correlations among species only occurring in forested regions to become disentangled (Senay et al. 2013). An environmental filter was selected due to its demonstrated ability to improve the discriminatory power of occurrence models over random sampling or geographic filtering (Varela et al. 2014; Iturbide et al. 2015).

Climate data

Climate variables were selected to represent seasonal and annual precipitation, which have a strong demonstrated influence on tree species within our study region (Rehfeldt et al. 2006; Bell et al. 2014a). We evaluated a suite of annual and seasonal climate variables for use in the co-occurrence model (**Table 3.2**). Only a subset of environmental variables were selected to minimize overfitting and to prevent collinearity. Specifically, only variables with a correlation <0.7 were included within the same model formulation (Dormann et al. 2013). The model selection methods used are detailed in the modeling procedure.

All climate data were extracted from the U.S. Forest Service Moscow Forestry Sciences Laboratory downscaled climate dataset (MFSL; Rehfeldt 2006). These data represent climate normals (1961-1990) downscaled to a 30 arc second resolution ($\sim 1 \text{ km}^2$) using thin-plate spline methods. The extent of MFSL data spans North America, with increased testing and application of data covering Western North America (Rehfeldt 2006; Rehfeldt et al. 2006). Both the temporal and spatial resolution of these data were deemed consistent with the spatial resolution of FIA plot-level data and the temporal influence of climate on long-lived trees. Topographic data used to calculate *TRASP* (**Table 3.2**) were derived from a 30m USGS digital elevation

model, resampled to a 1km grid using bilinear interpolation to remain consistent with the spatial resolution of climate and occurrence data.

Modeling procedure

Species co-occurrence was modeled using the Joint Species Distribution Model (JSDM) approach of Pollock et al. (2014); a more comprehensive model description is provided in the original publication. This approach uses a latent variable formulation of a Bayesian hierarchical multivariate probit regression to predict multiple species distributions simultaneously and to disentangle the ecological processes underlying co-occurrence patterns. In the JSDM formulation, continuous environmental covariates are related to discrete, binary presence/absence outcomes through a latent variable, which acts in place of a probit link function. The mean of this latent variable determines the probability of occurrence of a given species at a given location, and presence or absence can be inferred by invoking a threshold probability. We set occurrence thresholds individually for each species by calculating the probability that maximized the true skill statistic (TSS), a measure of model discrimination and performance that ranges from -1 to 1, with values >0 indicating better-than-chance discrimination (Allouche et al. 2006). Species in the JSDM are correlated through a multivariate normal distribution, each dimension of which is characterized by independent latent variable distributions related through a variance/covariance matrix. As in standard probit regression, the standard deviation of each latent variable distribution is set to one so that the variance/covariance matrix is directly interpretable as a correlation matrix. Regression coefficients are re-scaled by dividing by the standard deviation of the correlation matrix in order to be interpretable as regular probit regression coefficients.

The JSDM structure allows for the correlation among species occurrence patterns to be decomposed to quantify correlation attributable to environmental covariates, and residual correlation, which, if all influential environmental variables have been appropriately accounted for, may represent correlation due to species interactions. We attempted to adequately account for all probable climatic influences by using a comprehensive variable and model selection approach, yet the possible influence of unmeasured environmental factors must still be considered in interpretation of model output (Wisz et al. 2013; Pollock et al. 2014; Royan et al. 2015). In particular, residual correlation unrelated to biotic interactions may arise from omission of relevant climate variables (Royan et al. 2015), underlying topographic variation (Serra-Diaz et al. 2015), dispersal limitation (Morueta-Holme et al. 2015), or disturbance (Foster et al. 2016). In each of these cases, species associations detectable at the scale of inference may be explained by similarly broad gradients of alternative factors. For example, a large geographic dispersal barrier is likely to affect the dispersal of multiple species simultaneously, causing species associations detectable in broad-scale occurrence patterns that are unexplained by climatic gradients. While we cannot account for every alternative explanation for residual correlation in our model specification, we do attempt to interpret residual correlation with consideration of these alternative factors. With careful interpretation and model specification, the JSDM approach can be used to identify cases where species interactions are the most parsimonious explanation for residual correlation (Wisz et al. 2013; Pollock et al. 2014; Royan et al. 2015).

The JSDM was fit using Markov Chain Monte Carlo (MCMC) sampling within the R2Jags interface (Su & Yajima 2015) in Program R Version 3.2.1 (R Core Team 2015). Two chains were run for 50,000 iterations, with the first 20,000 iterations discarded as burn-in. Chains were thinned to every 150th value, and convergence was assessed visually using trace plots. The

model was initiated using uninformative priors to characterize both the latent variable mean and variance, and an uninformative prior was also placed on the inverse Wishart prior for the variance/covariance matrix (Pollock et al. 2014).

Because the JSDM approach cannot directly account for biotic interactions, variable selection is a crucial step in making strong inference on modeled correlation. We achieved model selection by comparing posterior predictive loss (PPL) estimates for a) model formulations using different combinations of environmental covariates, and b) nested models with different levels of covariate interactions. PPL is a model fit criterion that accounts for goodness-of-fit and penalizes for model complexity. PPL is particularly suitable for use with hierarchical models as it calculates model complexity in a manner that avoids specification of the number of model parameters. We fit the JSDM with multiple uncorrelated sets of seasonal and annual temperature and precipitation variables in addition to *TRASP*, a topographic variable, and selected the set that minimized the PPL criterion. Within this selected model, we then evaluated a series of possible interaction structures (**Table 3.3**), and selected the formulation with the lowest mean PPL for inference and prediction. The relative influences of climate and potential species interactions were evaluated by comparing the strength of environmental versus residual correlation for each species. We also compared predictions made using the JSDM to those made without accounting for covariance among species to determine whether the information contained in co-occurrence patterns can improve predictions of species distributions.

3.4 RESULTS

Final covariates selected for modeling species co-occurrence were mean annual temperature, growing season precipitation, winter precipitation, temperature differential, and

TRASP (**Table 3.3**). The full model, which included all possible quadratic terms and interactions, minimized the PPL relative to all nested models and was chosen as the best fitting model (**Table 3.3**). The full model always showed better-than-chance discrimination ($TSS > 0$), and generally performed well for all species ($0.46 \leq TSS \leq 0.69$; **Table 3.4**). The Kappa statistic indicates lower discrimination accuracy than TSS, though Kappa is known to be biased by species prevalence (Allouche et al. 2006). High-elevation species (subalpine fir, Engelmann spruce, whitebark pine, lodgepole pine) were predicted more accurately than lower elevation species (two-needle pinyon, ponderosa pine, Douglas-fir, gambel oak; **Table 3.4**). Imperfect discrimination was generally due to low specificity, corresponding with overprediction of occurrence; the JSDM generally predicted a broader geographic distribution than is represented by species observations (data not shown).

Environmental and residual correlations from the fitted model imply little to no influence of species interactions on co-occurrence patterns. For all species, correlation due to environmental covariates far exceeded residual correlation (**Fig. 3.2**). In most cases, environmental correlations were positive, indicating shared environmental responses (**Fig. 3.2a**). Strong negative environmental correlations were only observed between two-needle pinyon, a low elevation species, and subalpine fir, Engelmann spruce, whitebark pine, and lodgepole pine, all high elevation species. Species with weaker environmental correlation (e.g. gambel oak, two-needle pinyon, ponderosa pine) were also predicted less accurately (**Table 3.4**), indicating that unaccounted for environmental covariates may be important in defining the distributions of these lower elevation species.

Residual correlation only exceeded an absolute value of 0.5 in the case of subalpine fir and Engelmann spruce, two high elevation species that regularly co-occur and were well

predicted by the model (**Fig. 3.2b**; **Fig. 3.3**). Positive residual correlation and high predicted overlap of distributions suggests that facilitation may influence the co-occurrence patterns of these two species (**Fig. 3.4**).

Overall, predictions made by the JSDM do not differ substantially from predictions made without accounting for species covariance. Even when the most extreme example of residual correlation is evaluated, the effect of covariance on the probability of co-occurrence is minimal (**Fig. 3.3**). Predictions of species distributions generated from the JSDM (**Fig. 3.4**) reflect model discrimination statistics; high elevation species (**Fig. 3.4a-c,e,f**) show more constrained and accurate distributions than lower elevation species (**Fig. 3.4d,g-j**). Combined with lower environmental correlation for low-elevation species, these results indicate that the factors defining the distributions of Rocky Mountain trees may differ between low and high elevation species.

3.5 DISCUSSION

Our primary goals in this study were to evaluate the relative influences of climate and potential species interactions on the co-occurrence patterns of Rocky Mountain trees, and to develop predictions of species distributions that account for these factors. The results from the fitted JSDM demonstrate that species co-occurrence patterns can be largely explained by shared responses to climate, with little to no importance of biotic interactions evident in our results. Our findings thus support the predominant role of climate in shaping species occurrence patterns across broad spatial scales (Woodward 1987; Pearson & Dawson 2003; Soberón & Nakamura 2009)

Attribution of co-occurrence patterns

Environmental correlation and residual correlation represent the proportion of species co-occurrence that is explained by climate covariates and the proportion left unexplained, respectively. Residual correlation reflects non-random species co-occurrence that is unrelated to climate covariates; thus, if all relevant climate variables are included in the model, parsimony dictates that residual correlation may imply the influence of biotic interactions such as interspecific competition or facilitation (Pollock et al. 2014). However, topographic variation (Serra-Diaz et al. 2015), dispersal limitation (Morueta-Holme et al. 2015) and disturbance (Foster et al. 2016) can also generate non-random co-occurrence patterns that are independent of climate. Hence, attributing residual correlation to underlying drivers requires careful interpretation and consideration of ecological context, species life history and model structure (Royan et al. 2015).

We found that the co-occurrence patterns of Rocky Mountain tree species can be primarily attributed to shared environmental responses, with little evidence of an influence of alternative factors (**Fig. 3.2; Fig. 3.3**). Environmental correlation was positive for all species except one, indicating that many Rocky Mountain tree species respond similarly to environmental gradients. This agrees with climate envelope estimates for these species, which show a large degree of overlap across temperature and precipitation gradients (Bell et al. 2014a). Only one species, two-needle pinyon, demonstrates opposing environmental responses to many of the other modeled species, as represented by negative environmental correlations (**Fig. 3.2**). Two-needle pinyon occurs in woodlands of the Great Basin physiographic province along with gambel oak and Utah juniper (*Juniperus osteosperma*). Precipitation regimes in these lower elevation woodlands differ dramatically from those characterizing Rocky Mountain forests

(Brown et al. 1998), and may generate distinct environmental responses of species occupying these two physiographic provinces (Rehfeldt et al. 2006). In this study, gambel oak was characterized by somewhat weak environmental correlation, particularly with high elevation forest species, which can similarly be explained by the unique physiographic features of its occupied habitat (Brown et al. 1998).

While the factors underlying residual correlation cannot be precisely determined using the JSDM approach, consistently weak residual correlation relative to environmental correlation rules out any substantial influence of biotic interactions on regional co-occurrence patterns of Rocky Mountain tree species (**Fig. 3.2**). Biotic interactions have been repeatedly hypothesized to influence species distribution patterns (Austin 2002; Wiens 2011; Wisz et al. 2013; Svenning et al. 2014), though direct empirical analyses of such influences are scarce. In several studies, potentially interacting species have been included as covariates used to predict distributions and abundance of tree species (Leathwick & Austin 2001; Rouget et al. 2001; Meier et al. 2012). These studies generally found that interacting species were necessary to accurately estimate tree community structure (abundance, basal area), but were of little significance relative to climate when predicting species occurrence. Boulangeat et al. (2012) found a similar result when modeling the abundance and occurrence of alpine plant species, suggesting that this general pattern may hold across plant taxa. Process-based models, which can directly account for the influence of competitors and model occurrence as a function of physiological limitations rather than climatic correlation, have also found that biotic interactions generally fail to explain tree occurrence at broad spatial scales, specifically among North American tree species (Morin et al. 2007; Gutiérrez et al. 2016).

Our results clearly demonstrate that accounting for covariance between tree species does not appear to substantially alter predicted probabilities of co-occurrence, even for the species pair with the strongest residual correlation (**Fig. 3.3**). These results should not be taken to imply that interspecific biotic interactions do not occur among the species evaluated in this study. On the contrary, a number of plot- and stand-level studies have demonstrated decreases in growth and abundance of trees associated with increases in the growth and abundance of neighbors (e.g. Perry 1985; Canham et al. 2004; Contreras et al. 2011; Gómez-Aparicio et al. 2011; Kunstler et al. 2011; Foster et al. 2016), and facilitation of high-elevation and late-successional seedlings is a well-documented phenomenon (e.g. Chapin et al. 1994; Saccone et al. 2010; Fajardo & McIntire 2011; McIntire & Fajardo 2014). However, these local interactions may not be sufficiently strong or uniform to impact species occurrence patterns observed over broad spatial scales. In the case of Rocky Mountain tree species, previous research has demonstrated that weak competitive interactions between species exert little influence on growth at local distribution edges relative to climate (Copenhaver-Parry & Cannon 2016). Disturbance, which is a ubiquitous feature of Rocky Mountain forests, may further mediate the effects of interactions on long-lived trees by initiating secondary succession before competitive exclusion can occur (Connell 1961; Grime 1973; Roxburgh et al. 2004). Thus, the impact of interspecific interactions on population growth among these species may not be strong enough to either exclude species from otherwise suitable habitat, or to allow species to expand into climatically unsuitable habitat (Soberón & Nakamura 2009; Svenning et al. 2014). Weak interactions and relative ease of co-occurrence at local scales leads to scale-dependencies in biotic interactions, whereby interactions that occur at local scales do not impact broad scale occurrence patterns (Araújo & Rozenfeld 2014; Godsoe et al. 2015).

Weak residual correlation among species and the small effect of covariance on species co-occurrence may also be attributable to the large spatial extent over which these species were modeled. Rocky Mountain tree species exhibit a high degree of local adaptation across their ranges, generating heterogeneous community dynamics and environmental responses (Aitken et al. 2008; Gray & Hamann 2013; Montwé et al. 2016). For example, lodgepole pine, which consists of four subspecies, spans 4000 km in latitude and occupies environments with mean annual temperatures ranging from -5°C to 12°C. Local adaptation among lodgepole pine populations generates a broad range of environmental responses (Rehfeldt et al. 1999). However, individual lodgepole pine populations generally exhibit low genetic diversity and narrow realized niches that are strongly impacted by the identity of co-occurring species, which varies across their range (Peet et al. 1981; Rehfeldt et al. 1999; Aitken et al. 2008). Heterogeneous community dynamics and environmental responses in lodgepole pine and other tree species may drive variation in co-occurrence patterns among populations that is lost when species responses and co-occurrence relationships are averaged across a broad scale and large spatial extent.

The strong positive environmental correlation identified for most species pairs in this study implies that species share many climatic requirements and occupy climatically similar locations. These findings agree with climate envelope models for many of these species, which show substantial envelope and distribution overlap across temperature and precipitation gradients (Rehfeldt et al. 2006; Bell et al. 2014a). Because trees share many resource requirements (Silvertown 2004), it may at first seem contradictory that these species co-occur without interacting strongly. The shared environmental responses and lack of strong interactions identified in this study may result from the complex topography of the habitats that these species occupy, along with rapid and frequent species migration and community re-shuffling. Strong

interactions often arise as a result of coevolution (Case et al. 2005; Thompson 2005), yet a prominent legacy of coevolution is unlikely across much of North America where glacial cycles have prevented sufficiently long periods of climatic stability (Araújo et al. 2011). Rocky Mountain tree species have responded to past climatic instability by repeated instances of migration, causing range contraction and expansion and re-shuffling of biotic communities (Jackson & Overpeck 2000; Williams et al. 2004; Jackson et al. 2009). This process is ongoing under contemporary climate change, and even small differences in environmental responses of Rocky Mountain tree species have been predicted to drive substantial differences in migration rates and climate change responses (Gray & Hamann 2013; Bell et al. 2014b). Additionally, complex terrain influences in mountain landscapes including cold air drainages, strong elevation gradients, and fine-scale slope and aspect effects may decouple regional climate from climate experienced *in situ*, generating extreme heterogeneity in local habitat (Dobrowski et al. 2011). Such heterogeneity coupled with slight differences in species environmental responses may drive fine-scale segregation in species distributions that are not detectable at the scale at which we evaluated co-occurrence patterns. For example, fine-scale topoclimatic variation in the Colorado Front Range has been shown to generate variable soil moisture conditions that mediate the effects of regional climate on lodgepole pine and ponderosa pine, driving differing responses of these species to moisture availability (Adams et al. 2014). In fact, community-level studies have long documented fine-scale variation in Rocky Mountain tree species spatial patterns with topographic position, most notably related to ridgelines and drainages (Peet 1981). The existence of weak residual correlation among most species pairs in our study (**Fig. 3.2**), along with the small effect of covariance on the probability of co-occurrence (**Fig. 3.3**) may indicate that habitat

features play an important role in defining the fine-scale co-occurrence patterns of Rocky Mountain tree species, but these effects are lost at broad scales of analysis.

Only two of the species evaluated in this study exhibited noteworthy residual correlation: subalpine fir and Engelmann spruce (residual correlation=0.59; **Fig. 3.2**). Environmental correlation for this species pair still exceeded residual correlation, but our results indicate that facilitation might contribute to co-occurrence patterns of these species. Subalpine fir and Engelmann spruce are both high-elevation species that almost exclusively co-occur (Peet 1981; Rehfeldt et al. 2006). Both species establish late in seral stands of aspen (Calder & St. Clair 2012; Buck & St. Clair 2014), limber pine (Donnegan & Rebertus 1999) and lodgepole pine (Kayes & Tinker 2012). These successional patterns may mask the true facilitative relationships characterizing co-occurrence among these species. Establishment of spruce and fir seedlings requires soil resource and light conditions that are generally only found under closed canopies (Buck & St. Clair 2014). Early seral species such as limber pine, lodgepole pine and aspen have all been shown to facilitate the establishment of spruce and fir seedlings simultaneously by providing favorable microclimate and through nurse plant effects (Donnegan & Rebertus 1999; Calder & St. Clair 2012; Buck & St. Clair 2014). However, co-occurrence of facilitators and spruce and fir only occurs early in spruce-fir stand development, as increasing spruce-fir dominance eventually leads to high mortality of early seral species (Calder & St. Clair 2012). Our models did not include seedling data, and were thus unable to capture a facilitative relationship between subalpine fir-Engelmann spruce, and limber pine, lodgepole pine, and aspen. However, the positive residual correlation between Engelmann spruce and subalpine fir likely reflects these other facilitative relationships, which affect seedlings of both species simultaneously. These results indicate that biotic interactions may be stronger and more

influential for the co-occurrence patterns of late seral species, yet temporal variation in distribution patterns due to succession may mask many of these relationships.

JSDM performance, strengths and limitations

The JSDM model performed well for all species modeled in this study (**Table 3.4**), yet showed consistently higher performance for high elevation species than low elevation species. This is consistent with the findings of Bell et al. (2014a) who fitted individual climate envelope models to predict the distributions of a similar suite of Rocky Mountain tree species. As in our study, a shared group of covariates was used to predict each species. The lower performance of the JSDM for low elevation species in our study is generally due to low specificity, or over-prediction of species occurrence. Ultimately, the JSDM was unable to properly constrain the climate envelopes of these low elevation species. We suspect that this is due to the necessity of fitting the model with a shared group of covariates for all species. It is likely that low elevation species may respond more strongly to different climate covariates, or a more complex suite of covariates, than those that explain the co-occurrence patterns of high elevation species well. For example, several studies have demonstrated a greater importance of precipitation, particularly growing season precipitation, for predicting the distributions of lower elevation western North American tree species, while higher elevation species appear to respond most strongly to temperature, in particular growing degree days (Bartlein et al. 1997; Rehfeldt et al. 2006; Morin et al. 2007). However, Gray & Hamann (2013) found that temperature variables were more important in predicting the distributions of both low and high elevation species in the Rocky Mountains, with both groups of species predicted well by their model. In our study, we included both temperature and precipitation effects (**Table 3.2**), and also considered various combinations

of covariates in our model fitting approach. While the chosen suite of covariates showed the best fit overall, tradeoffs may exist for individual species.

An alternative explanation may be that low elevation species tend to occupy larger ranges (**Fig. 3.4**). Wide ranging species may occupy a broader range of environmental conditions, generally leading to noisy occurrence-environment relationships (Brotons et al. 2004; McPherson & Jetz 2007). This often decreases the ability of a model to discriminate suitable habitat, even when prevalence is controlled for (Brotons et al. 2004; Segurado & Araujo 2004; McPherson & Jetz 2007; Morin et al. 2007). If this is the case, a more complex suite of environmental covariates may be needed to explain the distributions of low elevation species. However, many of the climate covariates considered in this study exhibited high collinearity. Like most statistical approaches, the JSDM cannot accommodate collinearity without compromising interpretation of model parameters, thus limiting the number of covariates that can be included (Dormann et al. 2013).

It is also possible that lower elevation species distributions reflect the influences of alternative factors, such as human impacts, more strongly than the distributions of higher elevation species. In North America, human activities are mostly concentrated at low elevations (Van der Putten 2012). Road development, agricultural practices, logging activities, human alteration of fire regimes, and exurban development may all contribute to distribution limits that do not occur in equilibrium with climate (Ramankutty & Folley 1999; Coops et al. 2005; Rhemtulla et al. 2009; Foster & D'Amato 2015; Nowacki & Abrams 2015; Lembrechts et al. 2016). In particular, clearcut logging and fire suppression have led to dramatic changes in spatial patterning of species across the Rocky Mountains, with the most prominent changes observed for low and mid elevation tree species (Gallant et al. 2003). Because these effects impact individual

species independently, they would not be captured in the residual correlation of the JSDM, which represents unexplained covariance in species distributions.

While the JSDM performed well for all species, the main limitation of this approach as detected in this study is the necessity of modeling all species with a shared suite of covariates. For many species groups that respond discordantly to the environment, this statistical requirement may hinder accurate prediction and subsequent interpretation of correlations. However, we emphasize that the performance of the JSDM across all species included in this study was adequate, and the gains in ecological understanding achieved by directly quantifying environmental and residual correlation were substantial.

Conclusions

Interspecific biotic interactions have frequently been hypothesized to influence species distributions (Austin 2002; Wiens 2011; Wisz et al. 2013; Svenning et al. 2014; Sandel 2015; Cazelles et al. 2015), though theoretical work suggests that these impacts will only be realized in specific ecological contexts (Godsoe & Harmon 2012; Araújo & Rozenfeld 2014; Godsoe et al. 2015). Although the JSDM approach employed here cannot directly quantify the impact of biotic interactions, our results indicate that shared environmental responses explain much of the covariance in distribution patterns of Rocky Mountain tree species. Alternative factors, including biotic interactions, do not appear to contribute meaningfully to species co-occurrence. Our findings emphasize the importance of ecological context for understanding the factors that control species distributions. However, variation in model performance across species also indicates that species distributions may be influenced by additional factors not evaluated here, such as dispersal limitation (Svenning & Skov 2007), human land use (Foster & D'Amato 2015),

disturbance (Le Roux et al. 2013), or other environmental covariates (Pollock et al. 2014; Royan et al. 2015). In order to generate reliable predictions of species distributions, future modeling efforts must continue to extend beyond climate envelope approaches to consider additional unresolved influences on species distributions.

3.6 References

- Adams, HR, Barnard, HR, Loomis, AK. 2014. Topography alters tree growth-climate relationships in a semi-arid forested catchment. *Ecosphere* 5: 148.
- Aitken, SN, Yeaman, S, Holliday, JA, Wang, T, Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1: 95-111.
- Allouche, O, Tsoar, A, Kadmon, R. 2006. Assessing the accuracy of species distribution models: Prevalence, Kappa and the True Skill Statistic (TSS). *Journal of Applied Ecology* 43:1223-1232.
- Araújo, MB, Luoto, M. 2007. The importance of biotic interactions modeling species distributions under climate change. *Global Ecology and Biogeography* 16: 743-753.
- Araújo, MB, Rozenfeld, A. 2014. The geographic scaling of biotic interactions. *Ecography* 37: 406-415.
- Araújo, MB, Rozenfeld, A, Rahbek, C, Marquet, PA. 2011. Using species co-occurrence networks to assess the impacts of climate change. *Ecography* 34: 897-908.
- Austin, MP. 1999. A silent clash of paradigms: Some inconsistencies in community ecology. *Oikos* 86: 170-178.
- Austin, MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modelling* 157: 101-118.
- Bartlein, PJ, Whitlock, C, Shafer, SL. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* 11: 782-792.
- Baselga, A, Araújo, MB. 2010. Do community-level models describe community variation effectively? *Journal of Biogeography* 37: 1842-1850.

- Bell, DM, Bradford, JB, Lauenroth, WK. 2014a. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23: 168-180.
- Bell, DM, Bradford, JB, Lauenroth, WK. 2014b. Mountain landscapes offer few opportunities for high-elevation tree species migration. *Global Change Biology* 20: 1441-1451.
- Boucher-Lalonde, V, Morin, A, Currie, DJ. 2012. How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography* 21: 1157-1166.
- Boulangeat, I, Gravel, D, Thuiller, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15: 584-593.
- Brotons, L, Thuiller, W, Araújo, MB, Hirzel, AH. 2004. Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. *Ecography* 27: 437-448.
- Brown, JH, Stevens, GC, Kaufman, DM. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Annual Reviews of Ecology and Systematics* 27: 597-623.
- Brown, DE, Reichenbacher, F, Franson, SE. 1998. A classification of North American biotic communities. The University of Utah Press: salt Lake City, UT.
- Buck, JR, St. Clair, SB. 2014. Stand composition, proximity to overstory trees and gradients of soil moisture influence patterns of subalpine fir seedling emergence and survival. *Plant Soil* 381: 61-70.
- Calder, WJ, St. Clair, SB. 2012. Facilitation drives mortality patterns along succession gradients of aspen-conifer forests. *Ecosphere* 3: 57.

- Canham, CD, LePage, PT, Coates, KD. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778-787.
- Case, TJ, Holt, RD, McPeck, MA, Keitt, TH. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108: 28-46.
- Cazelles, K, Mouquet, N, Mouillot, D, Gravel, D. 2015. On the integration of biotic interaction and environmental constraints at the biogeographical scale. *Ecography* 38: 001-011.
- Chapin, FS, Walker, LR, Fastie, CL, Sharman, LC. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64: 149-175.
- Clark, JS, Gelfand, AE, Woodall, CW, Zhu, K. 2014. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications* 24: 990-999.
- Connell, JH. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723.
- Connor, EF, Collins, MD, Simberloff, D. 2013. The checkered history of checkerboard distributions. *Ecology* 94: 2403-2414.
- Contreras, MA, Affleck, D, Chung, W. 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *Forest Ecology and Management* 262: 1939-1949.
- Coops, NC, Waring, RH, Law, BE. 2005. Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model: 3-PG. *Ecological Modelling* 183: 107-124.

- Copenhaver-Parry, PE, Cannon, E. 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* DOI 10.1007/s00442-016-3565-x
- Copenhaver-Parry, PE, Albeke, SE, Tinker, DB. 2016. Do community-level models account for the effects of biotic interactions? A comparison of community-level and species distribution modeling of Rocky Mountain conifers. *Plant Ecology* DOI: 10.1007/s11258-016-0598-5
- Dobrowski, SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* 17: 1022-1035.
- Donnegan, JA, Rebertus, AJ. 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* 81: 1370.
- Dormann, CF, Elith, J, Bacher, S, Buchmann, C, Carl, G, Carré, G, García Márquez, JR, Gruber, B, Lafourcade, B, Leitão, PJ, Münkemüller, T, McClean, C, Osborne, PE, Reineking, B, Schröder, B, Skidmore, AK, Zurell, D, Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 027-046.
- Fajardo, A, McIntire, EJB. 2011. Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology* 99: 642-650.
- Ferrier, S, Guisan, A. 2006. Spatial modeling of biodiversity at the community level. *Journal of Applied Ecology* 43: 393-404.
- Foster, JR, D'Amato, AW. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. *Global Change Biology* 21: 4497-4507.

- Foster, JR, Finley, AO, D'Amato, AW, Bradford, JB, Banerjee, S. 2016. Predicting tree biomass growth in the temperate-boreal ecotone: is tree size, age, competition or climate response most important? *Global Change Biology*. DOI: 10.1111/gcb.13208
- Gallant, AL, Hansen, AJ, Coucnilman, JS, Monte, DK, Betz, DW. 2003. Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed. *Ecological Applications* 13: 385-403.
- Gibson, J, Moisen, G, Frescino, T, Edwards Jr, TC. 2014. Using publicly available forest inventory data in climate-based models of tree species distribution: examining effects of true versus altered location coordinates. *Ecosystems* 17: 43-53.
- Godsoe, W, Harmon, LJ. 2012. How do species interactions affect species distribution models? *Ecography* 35: 811-820.
- Godsoe, W, Murray, R, Plank, MJ. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38: 001-009.
- Gómez-Aparicio, L, García-Valdés, R, Ruíz-Benito, P, Zavala, MA. 2011. Disentangling the relative importance of climate, size and competition in tree growth in Iberian forests: implications for forest management under global change. *Global Change Biology* 17: 2400-2414.
- Graham, CH, Carnaval, AC, Cadena, CD, Zamudio, KR, Roberts, TE, Parra, JL, McCain, CM, Bowie, RCK, Moritz, C, Baines, SB, Schneider, CJ, VanDerWal, J, Rahbek, C, Kozak, KH, Sanders, NJ. 2014. The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography* 37: 711-719.
- Gray, LK, Hamann, A. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change* 117: 289-303.

- Grime, JP. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Guisan, A, Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993-1009.
- Gutiérrez, AG, Snell, RS, Bugmann, H. 2016. Using a dynamic forest model to predict tree species distributions. *Global Ecology and Biogeography* 25: 347-358.
- Holt, RD. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659-19665.
- Iturbide, M, Bedia, J, Herrera, S, del Hierro, O, Pinto, M, Gutiérrez, JM. 2015. A framework for species distribution modeling with improved pseudo-absence generation. *Ecological Modelling* 312: 166-174.
- Jackson, ST, Overpeck, JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26: 194-220.
- Jackson, ST, Betancourt, JL, Booth, RK, Gray, ST. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106: 19658-19692.
- Kayes, LJ, Tinker, DB. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management* 263: 57-66.
- Kissling, WD, Dormann, CF, Groenvelde, J, Hickler, T, Kühn, I, McNerny, GJ, Montoya, JM, Römermann, C, Schiffers, K, Schurr, FM, Singer, A, Svenning, S-C, Zimmermann, NE, O'Hara, RB. 2012. Towards novel approaches to modeling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography* 39: 2163-2178.

- Kunstler, G, Albert, CH, Courbaud, B, Lavergne, S, Thuiller, W, Vieilledent, G, Zimmermann, NE, Coomes, DA. 2011. Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients. *Journal of Ecology* 99: 300-312.
- Leathwick, JR, Austin, MP. 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* 82: 2560-2573.
- Lembrechts, JJ, Alexander, JM, Cavieres, LA, Haider, S, Lenoir, J, Keuffer, C, McDougall, K, Naylor, BJ, Nuñez, MA, Pauchard, A, Rew, LJ Nijs, I, Milbau, A. 2016. Mountain roads shift native and non-native plant species ranges. *Ecography* DOI: 10.1111/ecog.02200
- Le Roux, PC, Virtanen, R, Heikkinen, RK, Luoto, M. 2012. Biotic interactions affect the elevational ranges of high-latitude plant species. *Ecography* 35: 1048-1056.
- Le Roux, PC, Virtanen, R, Luoto, M. 2013. Geomorphological disturbance is necessary for predicting fine-scale species distributions. *Ecography* 36: 800-808.
- Mateo, RG, Croat, TB, Felicísimo, AM, Muñoz, J. 2010. Profile or group discriminative techniques? Generating reliable species distribution models using pseudo-absences and target-group absences from natural history collections. *Diversity and Distributions* 16: 84-94.
- McIntire, EJB, Fajardo, A. 2014. Facilitation as a ubiquitous driver of biodiversity. *New Phytologist* 201: 403-416.
- McPherson, JM, Jetz, W. 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography* 30: 135-151.
- Meier, ES, Kienast, F, Pearman, PB, Svenning, J-C, Thuiller, W, Araújo, MB, Guisan, A, Zimmerman, NE. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. *Ecography* 33: 1038-1048.

- Meier, ES, Lischke, H, Schmatz, DR, Zimmermann, NE. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* 21: 164-178.
- Meineri, E, Skarpaas, O, Vandvik, V. 2012. Modeling alpine plant distributions at the landscape scale: Do biotic interactions matter? *Ecological modeling* 231: 1-10.
- Montwé, D, Isaac-Renton, M, Hamann, A, Spiecker, H. 2016. Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north. *Global Change Biology* 22: 806-815.
- Morin, X, Augspurger, C, Chuine, I. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology* 88: 2280-2291.
- Morueta-Holme, N, Blonder, B, Sandel, B, McGill, BJ, Peet, RK, Ott, JE, Viole, C, Enquist, BJ, Jørgensen, PM, Svenning, J-C. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography* DOI: 10.1111/ecog.01892
- Normand, S, Zimmermann, NE, Schurr, FM, Lischke, H. 2014. Demography as the basis for understanding and predicting range dynamics. *Ecography* 37: 1149-1154.
- Nowacki, GJ, Abrams, MD. 2015. Is climate an important driver of post-European vegetation change in the eastern United States? *Global Change Biology* 21: 314-334.
- Ovaskainen, O, Hottola, J, Siitonen, J. 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 91: 2514-2521.
- Pearson, RG, Dawson, TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

- Pellissier, L, Pradervand, J-N, Pottier, J, Dubuis, A, Maiorano, L, Guisan, A. 2012. Climate-based empirical models show biased predictions of butterfly communities along environmental gradients. *Ecography* 35: 684-692.
- Peet, RK. 1981. Forest vegetation of the Colorado Front Range: Composition and dynamics. *Vegetatio* 4: 3-75.
- Perry, DA. 1985. The competition process in forest stands. In: Attributes of trees as crop plants. MGR Cannell & JE Jackson, eds. Institute of Terrestrial Ecology, Abbots Ripton, Hunts, England.
- Pollock, LJ, Tingley, R, Morris, WK, Golding, N, O'Hara, RB, Parris, KM, Veski, PA, McCarthy, MA. 2014. Understanding co-occurrence by modeling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution* 5: 397-406.
- Pulliam, HR. 2003. On the relationship between niche and distribution. *Ecology Letters* 3: 349-361.
- Ramankutty, N, Foley, JA. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13: 997-1027.
- Rehfeldt, GE, Ying, CC, Spittlehouse, DL, Hamilton, DA. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs* 69: 375-407.
- Rehfeldt, GE. 2006. A spline model of climate for the Western United States. USDA Forest Service General Technical Report RMRS-GTR-165, Rocky Mountain Research Station, Fort Collins, CO.
- Rehfeldt, GE, Crookston, NL, Warwell, MV, Evans, J. 2006. Empirical analyses of plant-

- climate relationships for the western United States. *International Journal of Plant Sciences* 167: 1123-1150.
- Rhemtulla, JM, Mladenoff, DJ, Clayton, MK. 2009. Historical forest baselines reveal potential for continued carbon sequestration. *Proceedings of the national Academy of Sciences* 106: 6082-6087.
- Ricklefs, RE, Jenkins, DG. 2011. Biogeography and ecology: towards the integration of two disciplines. *Philosophical Transactions of the Royal Society B* 366: 2438-2448.
- Rouget, M, Richardson, DM, Lavorel, S, Vayreda, J, Gracia, C, Milton, SJ. 2001. Determinants of distribution of six *Pinus* species in Catalonia, Spain. *Journal of Vegetation Science* 12: 491-502.
- Roxburgh, SH, Shea, K, Wilson, JB. 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology* 85: 359-371.
- Royan, A, Reynolds, SJ, Hannah, DM, Prudhomme, C, Noble, DG, Sadler, JP. 2015. Shared environmental responses drive co-occurrence patterns in river bird communities. *Ecography* DOI: 10.1111/ecog.01703
- Saccone, P, Pagès, J-P, Girel, J, Brun, J-J, Michalet, R. 2010. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. *The New phytologist* 187: 831-842.
- Sandel, B. 2015. Towards a taxonomy of spatial scale-dependence. *Ecography* 38: 358-369.
- Schurr, FM, Pagel, J, Sarmiento Cabral, J, Groeneveld, J, Bykova, O, O'Hara, RB, Hartig, F, Kissling, WD, Linder, HP, Midgley, GF, Schröder, B, Singer, A, Zimmermann, NE. 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. *Journal of Biogeography* 39: 2146-2162.

- Segurado, P, Araújo, MB. 2004. An evaluation of methods for modeling species distributions. *Journal of Biogeography* 31: 1555-1568.
- Senay, SD, Worner, SP, Ikeda, T. 2013. Novel three-step pseudo-absence selection technique for improved species distribution modeling. *PLOS One* 8: e71218.
- Serra-Diaz, JM, Franklin, J, Sweet, LC, McCullough, IM, Syphard, AD, Regan, HM, Flint, LE, Flint, AL, Dingman, JR, Moritz, M, Redmond, K, Hannah, L, Davis, FW. 2015. Averaged 30 year climate change projections mask opportunities for species to establish. *Ecography* DOI: 10.1111/ecog.02074
- Schrag, AM, Bunn, AG, Graumlich, LJ. 2008. Influence of bioclimatic variables on treeline conifer distribution in the Greater Yellowstone Ecosystem: Implications for species of conservation concern. *Journal of Biogeography* 35: 698-710.
- Silvertown, J. 2004. Plant coexistence and the niche. *TRENDS in Ecology and Evolution* 19: 605-611.
- Smith, WB. 2002. Forest inventory and analysis: a national inventory and monitoring program. *Environmental Pollution* 116: S233-S242.
- Soberón, J, Nakamura, M. 2009. Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Science* 106: 19644-1950.
- Su, Y-S, Yajima, M. 2015. R2jags: Using R to run 'JAGS'. R package version 0.5-7. <https://CRAN.R-project.org/package=R2jags>
- Svenning, J-C, Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* 10: 453-460.
- Svenning, J-C, Gravel, D, Holt, RD, Schurr, FM, Thuiller, W, Münkemüller, T, Schiffrers, KH, Dullinger, S, Edwards, TC, Hickler, T, Higgins, SI, Nabel, JEMS, Pagel, J, Normand, S.

2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37: 001-012.
- Thompson, JN. 2005. The geographic mosaic of coevolution. The university of Chicago Press: Chicago, IL.
- Thuiller, W, Münkemüller, T, Lavergne, S, Mouillot, D, Mouquet, N, Schiffrers, K, Gravel, D. 2013. A road map for integrating eco-evolutionary processes into biodiversity models. *Ecology Letters* 16: 94-105.
- Thuiller, W, Münkemüller, T, Schiffrers, KH, Georges, D, Dullinger, S, Eckhart, VM, Edwards, TC, Gravel, D, Kunstler, G, Merow, C, Moore, K, Piedallu, C, Vissault, S, Zimmermann, NE, Zurell, D, Schurr, FM. 2014. Does probability of occurrence relate to population dynamics? *Ecography* 37: 1155-1166.
- Van der Putten, WH. 2012. Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Reviews of Ecology, Evolution and Systematics* 43: 365-383.
- Van der Wal, J, Shoo, LP. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecological Modelling* 4: 589-594.
- Varela, S, Anderson, RP, García-Valdés, R, Fernández-Conzález, F. 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. *Ecography* 37: 1084-1091.
- Wiens, JJ. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366: 2336-2350.

- Williams, JW, Shuman, BN, Webb III, T, Bartlein, PJ, Leduc, PL. 2004. Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs* 74: 309-334.
- Wisz, MS, Potter, J, Kissing, WD, Pellissier, L, Lenoir, J, Damgaard, CF, Dormann, CF, Forchhammer, MC, Grytnes, J-A, Guisan, A, Heikkinen, RK, Høye, TT, Kuhn, I, Luoto, M, Maiorano, L, Nilsson, M-C, Normand, S, Ockinger, E, Schmidt, NM, Termansen, M, Timmermann, A, Wardle, DA, Aastrup, P, Svenning, J-C. 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biological Reviews* 88: 15-30.
- Woodall, CW, Oswalt, CM, Westfall, JA, Perry, CH, Nelson, ME, Finley, AO. 2010. Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology and Management* 259: 778-785.
- Woodward, FI. 1987. *Climate and plant distribution*. Cambridge University Press: Cambridge, UK.
- Woudenberg, SW, Conkling, BL, O'Connell, BM, LaPoint, EB, Turner, JA, Waddell, KL. 2010. *The Forest Inventory and Analysis database: database description and users manual version 4.0 for phase 2*. USDA Forest Service General Technical Report RMRS-GTR-245. Southern Research Station, Blacksburg, VA.

3.7 Tables

Table 3.1 Ten dominant Rocky Mountain tree species were selected for this study due to their prevalence and life-history traits.

Selected species display strong elevational zonation, and most species span much of the latitudinal range of the study area.

Species	Common name	<i>n</i> (prevalence)	Latitude (decimal degrees)	Elevation (m)
<i>Abies lasiocarpa</i>	subalpine fir	2622(0.17)	33.6-48.9	624-3718
<i>Picea engelmannii</i>	Engelmann spruce	2567(0.17)	32.7-48.9	670-3804
<i>Pinus albicaulus</i>	whitebark pine	511(0.03)	42.1-48.9	1531-3166
<i>Pinus edulis</i>	two-needle pinyon	3362 (0.22)	32.1-41.6	1157-3196
<i>Pinus contorta</i>	lodgepole pine	2411 (0.16)	37.3-48.9	613-3709
<i>Pinus flexilis</i>	limber pine	513 (0.03)	35.2-48.9	1186-3709
<i>Pinus ponderosa</i>	ponderosa pine	2816 (0.18)	32.0-48.9	426-3147
<i>Pseudotsuga menziesii</i>	Douglas-fir	4290 (0.28)	31.4-48.9	426-3521
<i>Populus tremuloides</i>	quaking aspen	1587 (0.10)	32.4-48.9	638-3718
<i>Quercus gambelii</i>	gambel oak	1630 (0.11)	31.4-41.4	1333-2987

Prevalence = number of occupied sites / total number of sites

Table 3.2 A suite of climate and topography variables were extracted from the Moscow Forestry Sciences Laboratory downscaled climate estimates data set (charcoal.cnre.vt.edu/climate/) and evaluated for inclusion in this analysis. Selected variables are denoted with an asterisk (*).

Covariate	Description	Calculation
<i>Temperature</i>		
<i>DD0</i>	degree-days less than 0°C	
<i>DD5</i>	degree-days greater than 5°C	
<i>FFP</i>	length of frost-free period	
<i>MAT*</i>	mean annual temperature	
<i>MMax</i>	mean maximum temperature in warmest month	
<i>MMin</i>	mean minimum temperature in coldest month	
<i>TDiff*</i>	temperature differential	<i>MMax-MMin</i>
<i>Precipitation</i>		
<i>GSP*</i>	growing season precipitation	Apr+May+Jun+July+Aug+Sep
<i>MAP</i>	mean annual precipitation	
<i>SMRPB</i>	summer precipitation balance	(July+Aug+Sep)/(Apr+May+June)
<i>WINP*</i>	winter precipitation	<i>MAP-GSP</i>
<i>Topography</i>		
<i>TRASP*</i>	topographic radiation index based on a continuous transformation of circular aspect	See Roberts & Cooper 1989; Evans et al. 2014

Evans, JS, Oakleaf, J, Cushman, SA, Theobald, D. 2014. *An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0*. Available: <http://evansmurphy.wix.com/evansspatial>. Accessed: 2015.

Roberts, DW, Cooper, SV. 1989. *Concepts and techniques of vegetation mapping*. In *Land Classifications Based on Vegetation: Applications for Resource Management*. USDA Forest Service GTR INT-257, Ogden, Utah: 90-96.

Table 3.3 Five nested model structures were evaluated for fit. The full model, which accounted for all possible quadratic terms and interactions between covariates, minimized the posterior predictive loss (PPL) and was selected as the best model [denoted by an asterisk (*)].

	Main effects	Quadratic terms	Interaction terms	PPL (mean and 95% CI)
(1)*	<i>MAT</i>	<i>MAT</i> ²	<i>GSP</i> × <i>MAT</i>	63843 (63131-64662)
	<i>GSP</i>	<i>GSP</i> ²	<i>MAT</i> × <i>WINP</i>	
	<i>WINP</i>	<i>WINP</i> ²	<i>MAT</i> × <i>TDiff</i>	
	<i>TDiff</i>	<i>TDiff</i> ²	<i>MAT</i> × <i>TRASP</i>	
	<i>TRASP</i>	<i>TRASP</i> ²	<i>GSP</i> × <i>WINP</i>	
			<i>GSP</i> × <i>TDiff</i>	
			<i>GSP</i> × <i>TRASP</i>	
			<i>TDiff</i> × <i>WINP</i>	
			<i>TRASP</i> × <i>WINP</i>	
			<i>TDiff</i> × <i>TRASP</i>	
(2)	<i>MAT</i>	<i>MAT</i> ²	<i>GSP</i> × <i>MAT</i>	74220 (72280-76464)
	<i>GSP</i>	<i>GSP</i> ²	<i>MAT</i> × <i>WINP</i>	
	<i>WINP</i>	<i>TDiff</i> ²	<i>MAT</i> × <i>TDiff</i>	
	<i>TDiff</i>		<i>GSP</i> × <i>WINP</i>	
			<i>GSP</i> × <i>TDiff</i>	
			<i>TDiff</i> × <i>WINP</i>	
(3)	<i>MAT</i>	<i>MAT</i> ²		
	<i>GSP</i>	<i>GSP</i> ²		
	<i>WINP</i>	<i>WINP</i> ²		
	<i>TDiff</i>	<i>TDiff</i> ²		
	<i>TRASP</i>	<i>TRASP</i> ²		
(4)	<i>MAT</i>	<i>MAT</i> ²	<i>MAT</i> × <i>TDiff</i>	67722 (66962-68256)

	<i>GSP</i>	<i>GSP</i> ²	<i>MAT</i> × <i>TRASP</i>	
	<i>WINP</i>	<i>WINP</i> ²	<i>TDiff</i> × <i>TRASP</i>	
	<i>TDiff</i>	<i>TDiff</i> ²		
	<i>TRASP</i>	<i>TRASP</i> ²		
(5)	<i>MAT</i>	<i>MAT</i> ²	<i>GSP</i> × <i>WINP</i>	74612 (73016-76611)
	<i>GSP</i>	<i>GSP</i> ²	<i>GSP</i> × <i>TRASP</i>	
	<i>WINP</i>	<i>WINP</i> ²	<i>TRASP</i> × <i>WINP</i>	
	<i>TDiff</i>	<i>TDiff</i> ²		
	<i>TRASP</i>	<i>TRASP</i> ²		

Table 3.4 The full model performed well for all species, as indicated by measures of model discrimination (Kappa, TSS). TSS values, which, in contrast to Kappa, are not biased by species prevalence, show better-than-chance discrimination for all species (TSS>0). High elevation species were generally estimated with greater accuracy than low elevation species.

Species	Kappa	TSS
Subalpine fir ^a	0.43	0.69
Engelmann spruce ^a	0.39	0.67
Whitebark pine ^a	0.13	0.64
Two-needle pinyon ^b	0.26	0.46
Lodgepole pine ^a	0.30	0.60
Limber pine ^a	0.06	0.48
Ponderosa pine ^b	0.25	0.46
Douglas-fir ^b	0.32	0.46
Quaking aspen ^b	0.18	0.52
Gambel oak ^b	0.17	0.46

^a high elevation species

^b low elevation species

3.8 Figures

Figure 3.1 The study area spans the US portion of the Rocky Mountain range and encompasses the states of Idaho, Montana, Wyoming, Utah, Colorado, Arizona and New Mexico. 15,365 FIA survey plots were used in this analysis; only locations where study species are present are shown.

Figure 3.2 In all cases, environmental correlation (**a**) was stronger than residual correlation (**b**), demonstrating that species co-occurrence patterns can be largely explained by environmental responses.

Figure 3.3 The effect of covariance on the probability of co-occurrence of the species pairs with the largest residual correlation (0.59; subalpine fir and Engelmann spruce). The black dashed line illustrates no difference between predicted probabilities of co-occurrence with and without covariance, while the solid gray line characterizes the trend in the effect of covariance. For this species pairs, which demonstrates positive residual correlation, accounting for covariance among species slightly increases the probability that both species occur at a site (**a**) and that neither occur at a site (**b**), and slightly decreases the probability that one species will be present at a site while the other is absent (**c-d**).

Figure 3.4 Predicted species distributions generated from the fitted JSDM. Species shown are subalpine fir (**a**), Engelmann spruce (**b**), whitebark pine (**c**), two-needle pinyon (**d**), lodgepole pine (**e**), limber pine (**f**), ponderosa pine (**g**), Douglas-fir (**h**), quaking aspen (**i**), and gambel oak (**j**).

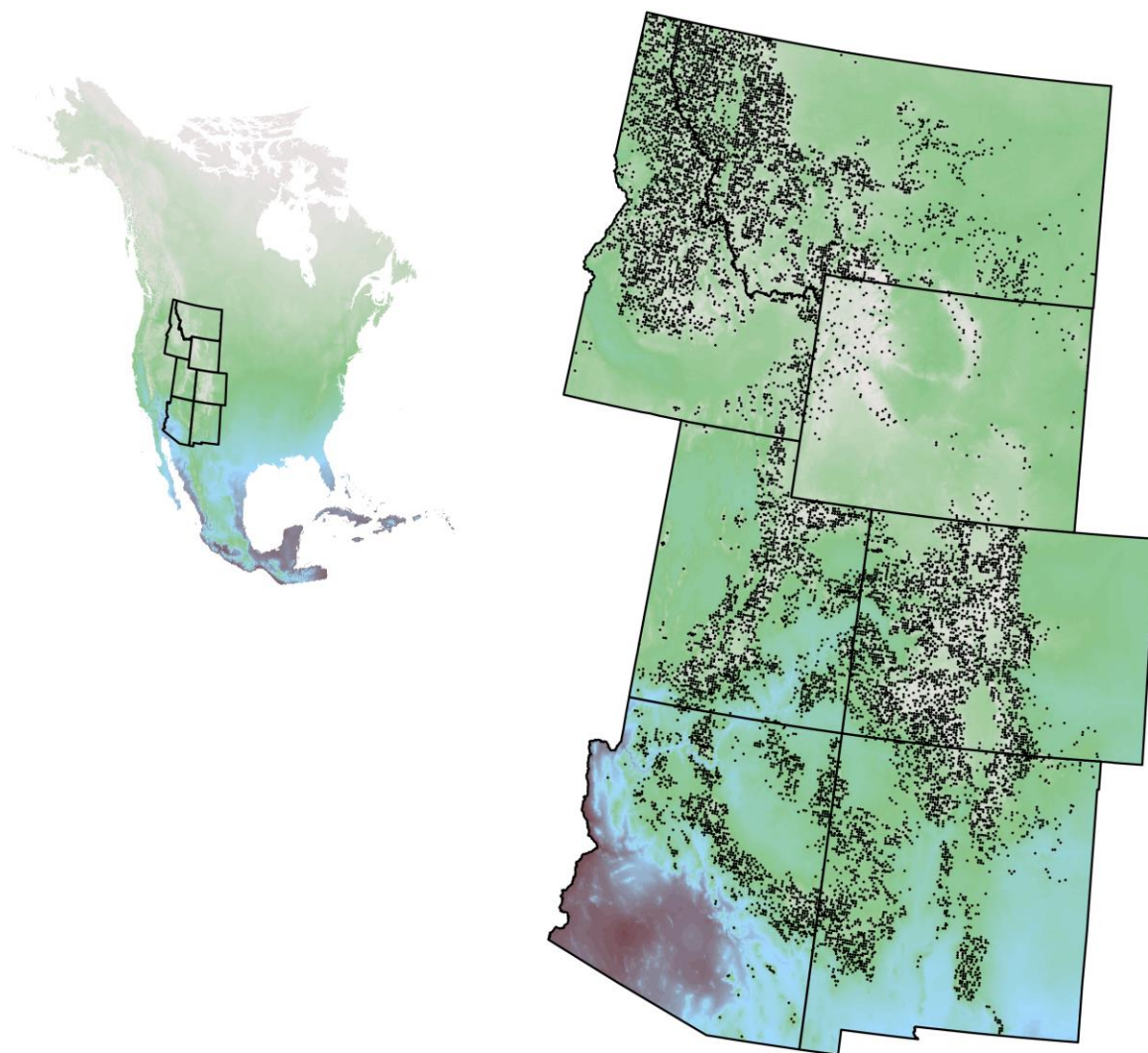


Figure 3.1

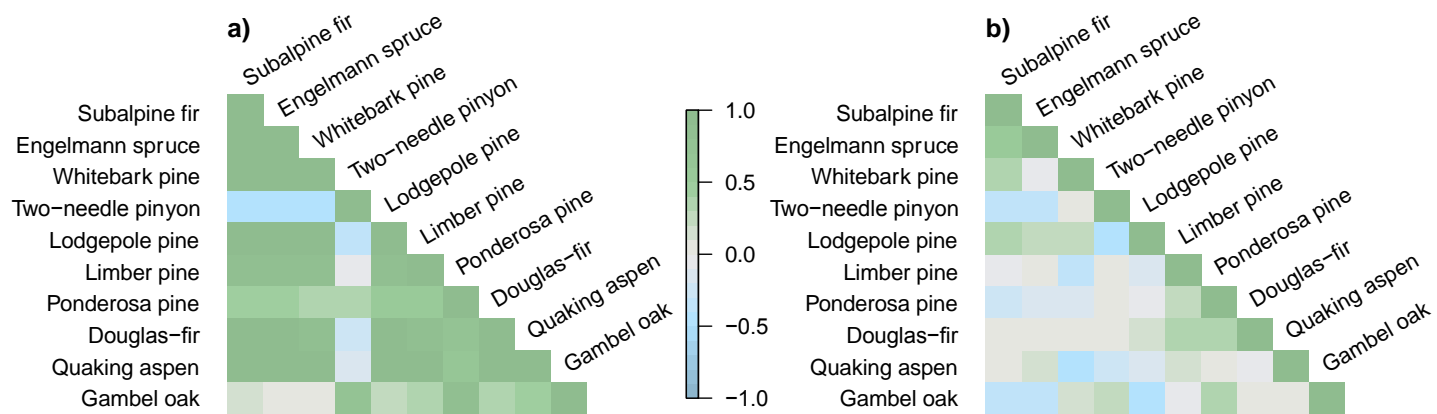


Figure 3.2

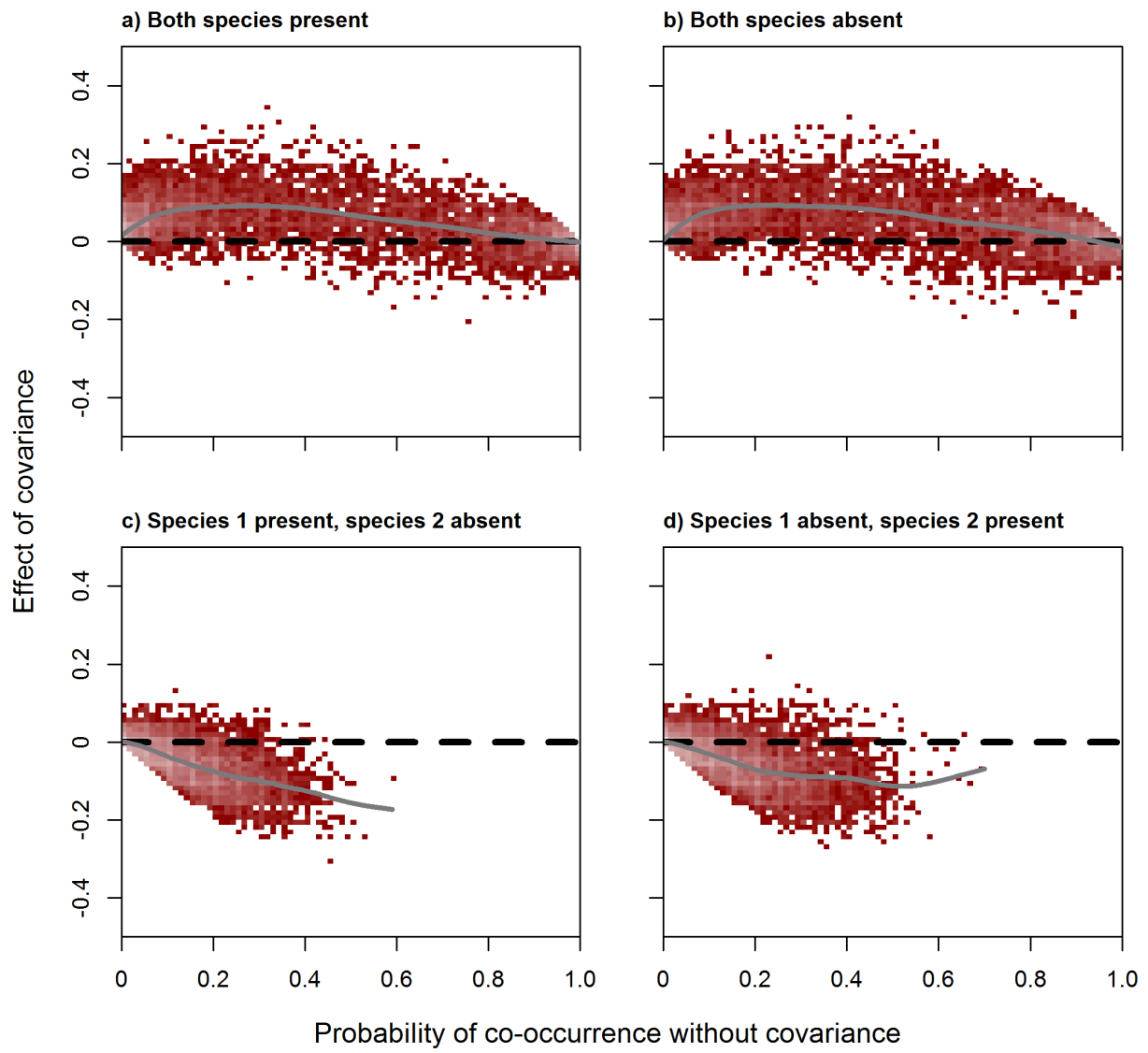


Figure 3.3

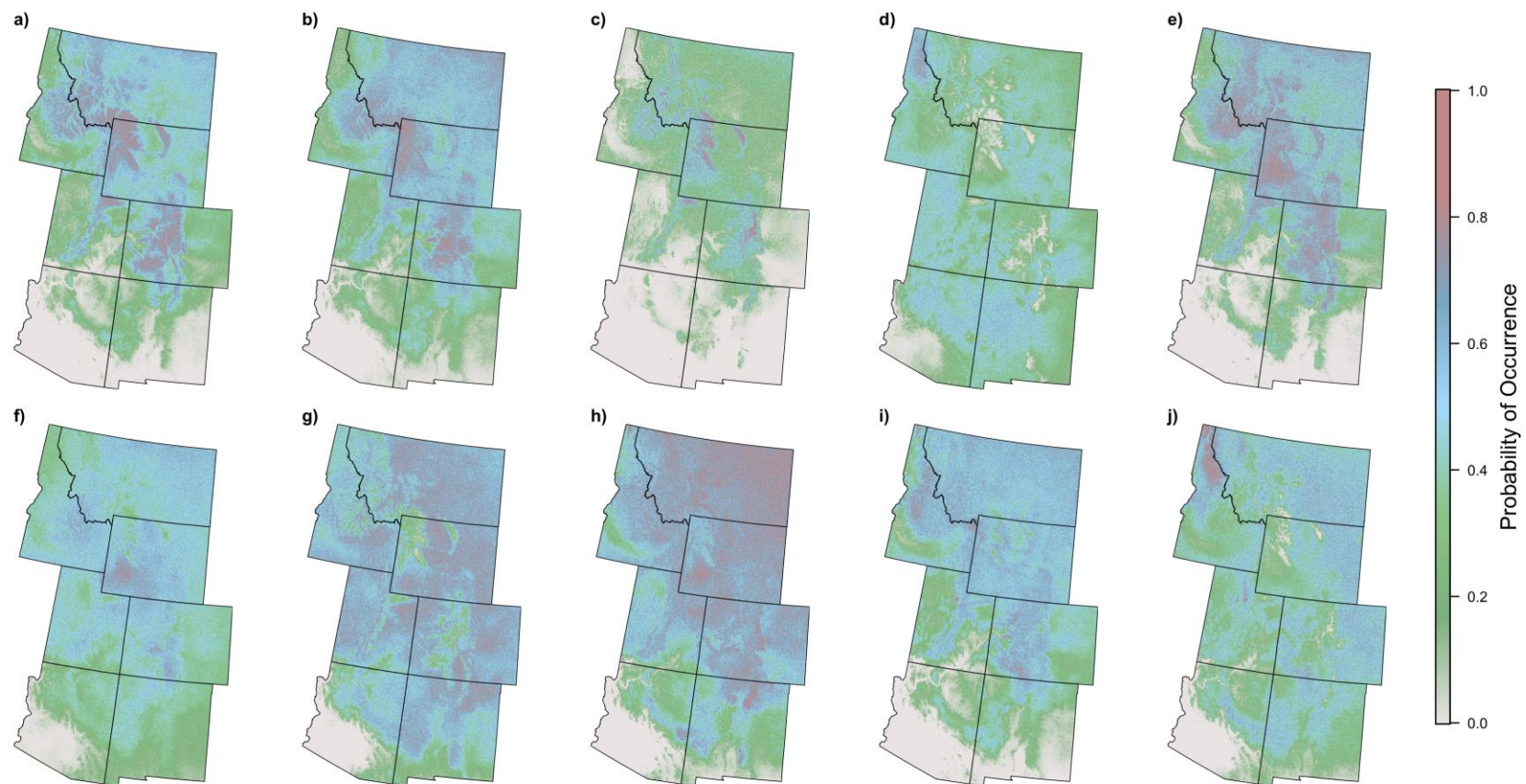


Figure 3.4

CHAPTER 4: TOWARDS AN IMPROVED CONCEPTUAL UNDERSTANDING OF NORTH AMERICAN TREE SPECIES DISTRIBUTIONS

Paige E. Copenhaver-Parry & Daniel B. Tinker

4.1 ABSTRACT

Species distributions have often been assumed to represent climatic limitations, yet recent evidence has challenged these assumptions and emphasized the potential importance of biotic interactions, dispersal limitation, and disturbance. Despite significant investigation into these factors, a synthetic understanding of where and when these factors may be important is lacking. Here, we review evidence for the factors shaping the historical and contemporary distributions of North American tree species and argue that a cohesive conceptual framework must be informed by an understanding of species ecological and evolutionary history. We further demonstrate that available evidence offers little indication for a significant influence of biotic interactions or dispersal limitation on species distributions. Disturbance may provide important constraints on distributions in limited contexts. Overall, historic and contemporary evidence suggests that species distributions are strongly influenced by climate, yet examples of disequilibrium with climate abound. We propose that differences among life stages and the impacts of human land use may contribute to explaining these inconsistencies and are deserving of greater research attention.

4.2 INTRODUCTION

The patterns and processes of species distributions form a major research theme in ecology. Understanding the factors underlying observed distribution patterns has important implications for species conservation and climate change predictions, yet efforts to quantify these factors are often complicated by inconsistencies in species' relationships with their occupied environment. Specifically, species distributions have often been shown to be well explained by a combination of broad-scale climatic factors, indicating strong climatic control on species distribution patterns (Woodward 1987; Brown et al. 1996; Soberón & Nakamura 2009). Strong correlations between bioclimatic factors and tree species distributions have been observed across North America (Rehfeldt et al. 2006; Morin et al. 2007; Boucher-Lalonde et al. 2012; Bell et al. 2014; Morueta-Holme et al. 2015). However, among ecologists it is still broadly maintained that species distributions rarely occur in equilibrium with climate. Evidence in support of this hypothesis comes in the form of range shift studies, which often document failure of many species to track contemporary climate change (Lenoir et al. 2010; Corlett & Westcott 2013). Across North America, limited climate tracking has been recorded among tree species in California (Serra-Diaz et al. 2015), at the Alaska treeline (Dial et al. 2015), in western North American forests (Gray & Hamann 2013), and among eastern North American tree species (Woodall et al. 2009; Murphy et al. 2010; Zhu et al. 2012). In response to evidence for failure of species distributions to maintain equilibrium with contemporary climate, alternative factors including biotic interactions, dispersal limitation and disturbance have been proposed as prominent underlying drivers of species distribution patterns (e.g. Austin 2002; HilleRisLambers et al. 2013; Siefert et al. 2015).

Despite strong theoretical evidence of the potential influences of these alternative factors on species distributions (e.g. Case et al. 2005; Godsoe & Harmon 2012; Araújo & Rozenfeld 2014; Godsoe et al. 2015), few consistencies have emerged in empirical studies and the precise contexts in which these factors influence distributions remain unclear. As a result, ecologists lack a cohesive framework to guide investigations of species distributions (Cassini et al. 2011). Without a better conceptual understanding of the factors underlying species distribution patterns, progress on models that can ascribe processes to patterns will be hampered, and predictions of species distributions across time and space will continue to be uncertain and inconsistent.

Global generalizations of the factors underlying distributions may be impossible to arrive at due to large variation in species environmental tolerances, dispersal ability, and ecological and evolutionary history, yet regional trends may emerge among species with shared life history characteristics. We focus here on North American tree species in an attempt to provide an improved understanding of when and where certain factors may contribute to distribution patterns. Specifically, we review evidence regarding the historical and contemporary distributions of North American tree species (**Fig. 4.1**) and emphasize the importance of historical context for understanding species distributions. Biogeographers and ecologists have often argued for greater integration of historical biogeography and macroecology on the basis that species' ecological and evolutionary history provides a great deal of context for determining current distribution patterns (e.g. Brown et al. 1996; Ricklefs 2004; Jackson et al. 2009; Lavergne et al. 2010). The historical environment of a species exerts selective pressures that shape the traits that underlie species responses to current environmental conditions; these responses determine the environments in which a species can and cannot persist (i.e. the species distribution; Brown et al. 1996).

North American tree species have a unique historical legacy characterized by strong climate variability and repeated periods of glaciation (Williams et al. 2004). This legacy has undoubtedly influenced how species currently respond to climate, dispersal barriers, natural disturbance regimes, and co-occurring species. We provide a comprehensive review of the history of North American tree species distributions and propose that species are generally well adapted to respond predominantly to climate. We then review the contemporary evidence for the roles of biotic interactions, dispersal limitation, and disturbance in shaping species distributions. Finally, we suggest avenues for further research that may fill knowledge gaps and contribute to an improved conceptual understanding of the distributions of North American tree species.

We limit our review to examples involving North American trees precisely because of the distinct ecological and evolutionary history of these species that allow us to infer some level of shared historical legacy. While North America, Europe and Asia all share many tree taxa and have a joint history of glaciation (Manchester 1999; Mucina & Wardell-Johnson 2011), North American flora exhibits several key distinctions. First, North America is characterized by fewer large topographic barriers, and as a result, exhibits lower species diversity than similar floristic regions (Xiang et al. 2004; Jaramillo-Correa et al. 2009). Additionally, Europe and Asia have much longer histories of human influence and habitat modification, with profound implications for species distributions. Precisely because of the strong influence of historical legacies on contemporary distribution patterns, distributions of European and Asian tree species may be expected to respond more strongly to different underlying factors than those that are deemed to be particularly important for North American trees.

4.3 HISTORICAL CONTEXT

Historical contingencies are likely to have left persistent imprints on the contemporary distributions of North American tree species (Jackson et al. 2009; Jaramillo-Correa et al. 2009), yet have often been overlooked in attempts to explain the factors driving contemporary species distributions. North American trees have persisted through periods of dramatic climatic fluctuations, involving rapid range shifts, contractions, expansions, and frequent shuffling of species assemblages (**Fig. 4.2**). Persistence through these periods of extreme environmental variability provides evidence for traits that confer broad climatic tolerance and rapid climate tracking such as high fecundity, prominent dispersal mechanisms, rapid colonization ability, and high levels of local adaptation and phenotypic plasticity (Jaramillo-Correa et al. 2009). Overall, there is little evidence or context to suggest substantial coevolution among tree species (Thompson 2005), thus bringing into question the historical or contemporary importance of biotic interactions on the distributions of North American tree species. Plentiful evidence suggests that climate has historically been the dominant factor driving North American tree species distributions, and that past environmental pressures have selected for species and traits that continue to respond strongly to climate (Ricklefs et al. 2004).

The history of North American tree species is marked by unstable, rapidly changing climate characterized by numerous periods of no-analog conditions.

North American tree species have evolved in the context of a rapidly changing climate marked by repeated glacial cycles. Despite the cyclic nature of such changes, each interglacial, glacial, stadial and interstadial period has featured unique climatic condition from other periods, resulting in the occurrence of repeated periods of no-analog climates (Jackson & Overpeck 2000; Williams and Jackson 2007). These past climate changes occurred rapidly, and at times drove

glacial and interglacial cycles within one to several human generations (Harrison et al. 2010). In fact, past climatic changes have been so rapid and variable that they could not have been driven by orbital forcing alone, and much variation is attributed to North Atlantic Heinrich events, the Northeast Pacific subtropical high pressure system, and accompanying climatic cycles including the El Niño Southern Oscillation, Pacific Decadal Oscillation, and the Atlantic Multidecadal Oscillation (Clark & Bartlein 2005; Jackson et al. 2009; Krause & Whitlock 2013). These cycles drove punctuated changes in climate that were superimposed on the glacial-interglacial trend and accelerated glacial advance and retreat to cycles of only tens to hundreds of years (Clark & Bartlein 1995; Krause & Whitlock 2013). Ice cores preserve a record of the dramatic climatic changes that drove glacial cycles, and record decadal temperature oscillations of 4°C or more over the past millennium (Willis et al. 2000). In addition to variation on annual to decadal scales, past climates featured higher-than-present temperature seasonality on an annual scale and spatially varying wet and dry cycles (Williams et al. 2006; Williams & Jackson 2007; Jackson et al. 2009). Throughout this period of extremely variable climate, temperate tree taxa dominated the vegetation landscape and persisted throughout dramatic environmental changes (Williams et al. 2004; Williams & Jackson 2007; Jaramillo-Correa et al. 2009).

North American tree species appear to have conserved broad climatic niches over time.

The climatic niche boundaries of many plant species appear to be conserved over evolutionary time (Jackson & Overpeck 2000), and phylogenetic analyses have identified niche conservatism as a strong driver of richness patterns specifically among North American trees (Qian et al. 2015). Multiple lines of evidence suggest that North American trees have maintained particularly broad fundamental niches, likely as the result of rapid and frequent climatic changes

(Willis et al. 2000; Jiménez-Moreno et al. 2010). Strong environmental fluctuations select for generalist strategies (Jackson & Overpeck 2000), or generate a high degree of local climatic adaptation among individual populations (Lavergne et al. 2010). Low rates of diversification in North American plants relative to similar floristic regions implies a prominent strategy of ecological generalization (Xiang et al. 2004). Indeed, generalist species have a demonstrated ability to persist in the face of extreme climatic fluctuations and to spread rapidly in periods of favorable climate (Jackson et al. 2009). North American tree species display direct evidence of broad climatic niches and generalist strategies in the face of fluctuating climate, either by enduring unfavorable periods in isolated refugial populations (Fastie 1995; Jackson & Overpeck 2000; Jaramillo-Correa et al. 2009), tracking climatic changes rapidly (**Fig. 4.2**; Williams et al. 2004), or persisting in relatively stable ranges through strong climatic changes (Jackson & Overpeck 2000).

Strong dispersal and colonization mechanisms have facilitated rapid species range shifts in response to climatic changes.

The fossil pollen record consistently demonstrates rapid movement of North American vegetation in response to millennial-scale climate variability, with little to no discernable lag between tree distributions and climate despite long generation times (Prentice et al. 1991; Jackson & Overpeck 2000; Jiménez-Moreno et al. 2010). Pollen data suggest that the distributions of North American tree species have not lagged climate within the temporal limits of the sampling and dating resolution (50-100 yr; Prentice et al. 1991; Williams et al. 2004; Harrison et al. 2010). These rapid responses are likely a combination of persistence within glacial refugia and subsequent dispersal from refugia, along with dispersal from southern

populations (Bennett et al. 1991; Clark et al. 2001; Williams et al. 2004). Periods of unfavorable climate and glaciation drove repeated contractions of tree distributions to southern regions. Dispersal from southern populations, including infrequent yet important long-distance dispersal events, enabled rapid range expansion during periods of deglaciation (Jackson & Overpeck 2000). Rapid movement of tree species was facilitated by the north-south orientation of North American mountain ranges (Perlman & Adelson 1997; Bonicksen 2000). However, tree species migration rates are best estimated at $<100\text{m}\cdot\text{yr}^{-1}$, sometimes as slow as $<10\text{m}\cdot\text{yr}^{-1}$ (Clark et al. 2001), and rates of several hundred $\text{m}\cdot\text{yr}^{-1}$ would be necessary to explain rapid post-glacial colonization from southern populations alone (Ricklefs et al. 2004). This indicates the persistence of Pleistocene tree populations in northern glacial refugia (Clark et al. 2001). Refugial populations of *Picea* and *Pinus* taxa have been recorded at the edges of ice sheets in Alaska and western North America, and dispersal from these populations appears to match the rate of glacial retreat (**Fig. 4.2**; Fastie 1995; Jackson & Overpeck 2000; Williams et al. 2004). Complex, mountainous topography appears to have played an important role in maintaining refugial populations of tree species throughout much of North America (Jaramillo-Correa et al. 2009).

All records of post-glacial range expansion suggest well-developed mechanisms of dispersal and colonization among North American tree species. Strong dispersal mechanisms can evolve in response to rapid climate changes and enable species to track climate rapidly, as appears to be the case for many North American species (Thomas et al. 2001; Massot et al. 2008; Lavergne et al. 2010). Alternatively or in conjunction with rapid climate tracking, dispersal capacity can evolve to maintain disjunct metapopulations at regional scales, which is consistent with the occurrence of rapid dispersal from glacial refugial populations, and the maintenance of

genetic diversity within isolated refugial populations (Jaramillo-Correa et al. 2009; Lavergne et al. 2010; Kubisch et al. 2013). Evolution of dispersal in response to fluctuating climate appears to be a likely process in North American tree species, whose histories have been marked by numerous periods of range contractions, expansions and shifts occurring across altitudinal gradients, latitudinal gradients, and both in northerly-southerly and easterly-westerly directions (Williams et al. 2004; Jiménez-Moreno et al. 2010; Willis et al. 2000).

Repeated shuffling of species assemblages were driven by individualistic responses of species to climate, and limited evidence for a historical role of biotic interactions exists.

Biotic interactions, particularly interspecific competition, have often been hypothesized as underlying drivers of contemporary tree distributions. Historical context indicates little to no evidence for a role of interspecific interactions among tree species in shaping past tree distributions, bringing into question the potential for such factors to contribute to contemporary distributions. Due to rapid glacial cycles, formation of no-analog climates, and repeated instances of range expansion, contraction and shuffling, North American tree species have rarely co-existed for substantial enough periods of time to drive evolution of niche partitioning or any form of adaptation to co-occurring species (Case et al. 2005; Thompson 2005; Araújo et al. 2011), and contemporary communities bear the imprint of historical mechanisms of species sorting (Ricklefs et al. 2004; Wiens 2011; Copenhaver-Parry & Bell *in prep*). North American tree species have undergone repeated periods of community shuffling in response to past climate change, underscoring the individualistic responses to climate exhibited by tree species at millennial timescales (Williams et al. 2004). Variable dispersal rates, fundamental niches, and response times drove the repeated disaggregation of existing communities as species responded

to different dimensions of changing climate, resulting in repeated formation of no-analog communities (Jackson & Overpeck 2000; Williams & Jackson 2007). Such communities persisted for short periods of time before again disaggregating in response to the next major climate fluctuation, resulting in a lack of opportunity for coevolution among North American tree species (Lavergne et al. 2010; Blois et al. 2013). This reshuffling and limited biotic pressure for diversification is consistent with relatively constant rates of diversification over time, and the lack of contemporary evidence for niche filling (Ricklefs et al. 2004; Wiens 2011). This suggests that competition was not an important force structuring historic species distributions (Williams et al. 2004; Blois et al. 2014). Blois et al. (2014) evaluated the relative contributions of climate, dispersal and species interactions to historic species associations for 106 fossil pollen taxa from eastern North America, and found that species associations were overwhelmingly attributable to climatic limitations with little evidence for the influence of biotic interactions. Similarly, numerous studies have found fossil pollen assemblages to be tightly associated with climate (Grimm et al. 1993; Jackson & Overpeck 2000 Williams et al. 2002; Shuman et al. 2004; Yu 2007). Ultimately, North American tree species appear to have responded strongly to climate, preventing stable associations from forming, which likely prevented evolution of competitive or facilitative relationships among co-occurring species. This evidence, combined with the historical context of rapidly fluctuating and variable climate, broad climatic niches, and strong dispersal and colonization mechanisms, indicate that North American tree species have experienced conditions that would likely select for strong climatic responses, resulting in climatic control on species distributions.

4.4 CONTEMPORARY EVIDENCE

Contemporary distributions of North American tree species are typically well predicted by climate (Morin et al. 2007; Boucher-Lalonde et al. 2012; Morueta-Holmes et al. 2015). However, species typically fail to occupy all climatically suitable space, indicating that alternative factors may also have important influences on species distributions. Most hypotheses regarding the factors driving disequilibrium of contemporary species distributions with climate emphasize the potential importance of biotic interactions, dispersal limitation and natural disturbances (e.g. Austin 2002; Case et al. 2005; Wiens 2011; Godsoe & Harmon 2012; Wisz et al. 2013; Araújo & Rozenfeld 2014; Svenning et al. 2014). All of these factors may exclude species from climatically suitable space, yet their tendency to do so over a large enough region to noticeably impact species distributions has been questioned (Soberón & Nakamura 2009; Wiens 2011).

Increasing empirical evidence addressing each of these hypothesized factors suggests that the direct effects of such factors on North American tree species distributions may be limited. Consideration of biotic interactions in species distribution models and range models has generally failed to improve predictions beyond those made using bioclimatic factors alone, indicating that interactions may be too weak to scale up to the level of the distribution (**Table 4.1**). Similarly, dispersal limitation, in most instances, fails to explain failure of species to migrate in concert with climate change, though few studies have tested dispersal limitation directly. Disturbance appears to drive temporal instability in species distributions and may influence distributions at forest-grassland ecotones, yet most of the effects of disturbance are not independent of climate. Overall, available empirical evidence indicates that climate may be the dominant driver of contemporary North American tree species distributions and, where species

occur in disequilibrium with climate, alternative factors beyond those reviewed in this section should be considered (see section 4.5: *Priorities for future research*).

Empirical evaluations of the contemporary distributions of North American trees offer little evidence for the influence of biotic interactions.

Ecologists have long investigated the role of biotic interactions among communities at local extents, yet it is only recently that theory, data and tools have become available to address biotic interactions at broader spatial scales. Biotic interactions may include a variety of species relationships (i.e. predator-prey, herbivory, competition, facilitation, parasitism, etc.; see Van der Putten et al. 2010), yet most theory development and empirical work related to species distributions has focused on interspecific interactions occurring within the same trophic level, such as competition and facilitation. Hence, we will hereafter use the broader terminology of “biotic interactions” to refer specifically to competition and facilitation. Biotic interactions result from resource-consumer dynamics operating between individuals (Soberón & Nakamura 2009; Clark et al. 2014), and are theorized to scale up to the level of the species distribution by altering population growth and demographic rates sufficiently to determine the spatial location of entire populations (Svenning et al. 2014). Such effects are likely to result only from particularly strong interactions (Araújo & Rozenfeld 2014; Godsoe et al. 2015). Sufficiently strong interactions are most likely to arise through coevolution of interacting species, which is in turn dependent upon protracted periods of stable climate and co-occurrence (Case et al. 2005; Araújo et al. 2011). Because North American tree species have been exposed to repeated periods of glaciation and climatic instability, they lack evidence of a coevolved history. Hence, the biotic interactions that

occur at local scales among North American tree species are unlikely to be strong enough to affect broad-scale distribution patterns (Thompson 2005; Araújo et al. 2011).

While few empirical studies have evaluated the importance of biotic interactions on the distributions of North American tree species, those that exist do, in fact, indicate that biotic interactions may not discernably affect distribution patterns (**Table 4.1**). For example, Morin et al. (2007) modeled the distributions of 17 boreal and temperate North American tree species using a process-based model to determine whether realized species distributions differed from those predicted based on physiological limitations. Tree species in their study appeared to occur largely in equilibrium with their potential distributions, indicating that factors that may vary independently of climate, such as interactions and/or dispersal, do not appear to constrain distributions. Additionally, both northern and southern distributional limits were well-explained by the impact of climate on phenology, which is consistent with other studies on these species (Pither 2003) and implicates climate as the predominant driver of North American tree species distributions.

Additional studies have attempted to directly incorporate biotic interactions into models to evaluate their role relative to climate. For example, Clark et al. (2014) simultaneously predicted the joint distribution and abundance patterns of eastern North American tree species and found that models that accounted for co-occurring species reproduced distributions more accurately than models predicting species distributions independently. These results indicate that species distributions co-vary, yet patterns of co-occurrence could be attributable to either biotic interactions or shared environmental responses. Copenhaver-Parry & Bell (Chapter 3) applied a similar modeling approach to a suite of tree species occurring in the US Rocky Mountains and extended the approach to evaluate the relative contributions of environment and species

interactions to co-occurrence patterns. Species co-occurrence in this study was primarily attributable to environmental responses, and biotic interactions appeared to play little to no role in the joint distributions of Rocky Mountain tree species. These combined findings indicate that North American trees respond to similar underlying climatic gradients (Clark et al. 2014), again illustrating the overwhelming influence of climate in determining the distributions of these species, yet distributions do not appear to be influenced by interspecific biotic interactions.

Even when the mechanisms of competition are included in models, competition only appears to affect local composition patterns and stand dynamics, while distribution patterns are overwhelmingly explained by broad-scale bioclimatic factors (Gutiérrez et al. 2016). Biotic interactions have been shown to influence abundance patterns far more strongly than distributions in a variety of other plant systems and regions (Rouget et al. 2001; Meier et al. 2011; Boulangeat et al. 2012), and this may be a general pattern indicative of the averaging of weak, local interactions across broad spatial scales (Soberón & Nakamura 2009; Araújo & Rozenfeld 2014).

Studies of species performance at distribution edges have also contributed to greater understanding of the influence of biotic interactions on North American tree species distributions. If biotic interactions do, in fact, contribute to distributional limits, individuals at distribution edges would be expected to exhibit performance declines in association with increased strength of biotic interactions. A series of studies conducted at the upper and lower elevational distribution edges of tree species in the Pacific Northwest have evaluated the contributions of climate and competition to tree growth and concluded that climate (i.e. cold temperatures and high snowpack) determine growth at upper distribution edges, while competition fails to explain either distribution edge (Ettinger et al. 2011; Ettinger et al. 2013).

Copenhaver-Parry & Cannon (2016) evaluated growth responses at lower and upper distributional edges of montane trees in the Rocky Mountains, and found that climate overwhelmingly influenced growth patterns at both edges. In either case, interactions do not appear to contribute substantially to species performance at distribution edges, again providing evidence for relatively weak interactions among North American tree species. However, it should be noted that Ettinger et al. (2013) identified a high sensitivity of seedlings to competition at lower distribution edges (HilleRisLambers et al. 2013), which is consistent with evidence indicating that regeneration patterns of western US trees may be strongly influenced by biotic interactions (Dobrowski et al. 2015). Regeneration dynamics of North American trees across broad scales have been little evaluated (but see Bell et al. 2014), and these findings indicate a need for further investigation into the links between biotic interactions, regeneration dynamics and distribution patterns (see section 4.1: *Life Stage*).

Direct evidence for the influence of dispersal limitation on distributions of North American tree species is generally inconclusive, yet range shift studies indicate that tree distributions are not moving in equilibrium with climate.

Dispersal limitation has been accepted as a general constraint on plant distributions, particularly in the Northern hemisphere (Gaston 2009; Hargreaves et al. 2014; Svenning & Skov 2007), yet surprisingly few direct empirical evaluations of its influence on North American tree distributions exist. Many North American tree species have relatively high fecundity, high seed release height, and dispersal syndromes that allow for long distance dispersal (Clark 1998; Fenner & Thompson 2004; Aitken et al. 2008), and all of these characteristics are related to strong dispersal ability (Fenner & Thompson 2004). However, the extent to which these traits

influence species distributions is difficult to directly determine. Additionally, the rate of current climate change drastically exceeds past climate change events, and dispersal traits evolved in response to past climatic pressures may not be sufficient to maintain equilibrium with current climate (Aitken et al. 2008). Range shift studies of species in response to contemporary climate change have been used to infer the role of dispersal, as dispersal distances have been assumed to represent a dominant control on rates of plant movement (Corlett & Westcott 2013).

In general, range shifts of North American tree species are occurring at a pace that is far slower than that of climate velocity. This is broadly indicated by a failure of seedling distributions to extend beyond adult distributions, demonstrating regeneration failure beyond current distribution edges. For example, the mean latitude of seedlings for a number of eastern North American tree species has been shown to occur only slightly further north than the mean latitude of biomass for tree species with more northerly distributions (Woodall et al. 2009), with limited colonization beyond the range margin (Murphy et al. 2010). At the same time, many eastern North American species show strong signs of range contraction at both northern and southern boundaries (Woodall et al. 2009; Murphy et al. 2010; Zhu et al. 2012), which is inconsistent with the movement of suitable habitat under climate change.

Similarly, regeneration patterns in western US forests indicate range contraction, particularly along southern and western range margins, though regeneration failure has also been demonstrated in core areas (Bell et al. 2014). Individual populations of western North American tree species have been shown to lag their 1961-1990 climatic niches by ~130km in latitude or 60m in elevation with particularly pronounced lags in the Rocky Mountains and boreal forests, indicating regeneration failure at both latitudinal and elevational distribution limits (Gray & Hamann 2013). While slow migration rates have often been interpreted as evidence of dispersal

limitation, migration may be limited by alternative factors unrelated to dispersal (Clark et al. 1998). In fact, regeneration failure at range boundaries of eastern North American tree distributions were found to be unrelated to seed size and dispersal characteristics (Zhu et al. 2012), and dispersal ability has also failed to explain the range sizes of North American tree species (Morin & Chuine 2006).

Zhu et al. (2012) proposed that patterns among eastern North American tree species are likely related to human-caused habitat fragmentation. Habitat fragmentation has been shown to reduce species migration in both simulation (Kubisch et al. 2013) and empirical (Higgins et al. 2003) studies and is predicted to drastically reduce the rate of plant migration in response to contemporary climate change (Corlett & Westcott 2013; see section 4.2: *Human land use*). While fragmented landscapes may present significant barriers to dispersal, North American tree species have historically demonstrated an ability to overcome even large dispersal barriers when given enough time (Jackson & Overpeck 2000; Gugger et al. 2008; Lesser & Jackson 2012). Another strong hypothesis for migration lags suggests that trees, which have particularly long generation times, are likely to exhibit episodic range shifts, with particularly long time lags in between migration episodes (Renwick et al. 2015). These episodes may be related to disturbances or periods of particularly suitable climatic conditions (Renwick et al. 2015), and may involve establishment of disjunct colonization populations, as has been observed for ponderosa pine in the western United States (Lesser & Jackson 2012). Thus, if species can achieve climatic equilibrium following episodic migration events, observation time, rather than dispersal limitation, may explain slow migration rates of tree species.

Direct evidence of the influence of dispersal limitation on North American tree distributions is limited, yet several studies have attempted to infer its role by studying species

distributions relative to climatic suitability. For example, Morin et al. (2007) used a process-based model (PHENOFIT) to predict the distributions of 17 North American boreal and temperate species, and found no indication that dispersal limitation influenced species distributions at the continental scale. Similarly, Boucher-Lalonde et al. (2012) found that the majority of eastern North American tree species occupy distributions that are completely ringed by unoccupied but climatically suitable areas. The presence of suitable unoccupied habitat both north and south of current range margins indicates that failure to disperse northward (in the direction of the current climate velocity) cannot fully explain disequilibrium of distributions with climate. To explain this pattern, Boucher-Lalonde et al. (2012) propose that the edges of species distributions are populated with sink populations. While these populations would technically be outside of the species climatic niche (i.e. the climatic space in which population growth is positive; Hutchinson 1957; Holt 2009), they are erroneously included in models used to predict species' suitable habitat, thus generating somewhat spurious correlations between species occurrence and climate. This may lead to predictions of suitable habitat in regions that cannot in reality support persistent populations.

This hypothesis is corroborated by transplant studies beyond species' ranges, which offer more direct evidence of whether distributions are limited by climatic tolerance or dispersal limitation (Gaston 2009; Hargreaves et al. 2014). Such studies are relatively rare, particularly for long-lived tree species. In the few available examples involving North American trees, jack pine (*Pinus banksiana*; Asselin et al. 2001), sugar maple (*Acer saccharum*; Kellman 2004) and gambel oak (*Quercus gambelii*; Neilson & Wullstein 1983) have all shown limited success when transplanted beyond their distributional limits, as evidenced by low germination success, low seedling survival, or failure to produce viable seed. These findings are consistent with the

observation that low germination and establishment success often limit the establishment of new populations more strongly than dispersal mechanisms (Fenner & Thompson 2004).

Nevertheless, other studies offer evidence for a more prominent role of dispersal limitation in shaping North American tree species distributions. For example, Iverson et al. (2004) paired a distribution model with a dispersal/migration model to predict the probability of colonization for five eastern North American tree species over the next 100 years and found that species are unlikely to establish further than 10-20km beyond their current distribution boundaries. The structure of the model dictates that low colonization probability is due to limited dispersal, and the authors suggest that this may be explained by low abundance of species near range edges, thus reducing the number of dispersed propagules. However, Murphy et al. (2010) found high abundance of these same species at their northern distributional limits, demonstrating inconsistencies among these two studies. In perhaps the strongest demonstration of dispersal limitation of North American tree distributions, Siefert et al. (2015) found a strong mismatch in the latitudinal and elevational limits of eastern tree species, with species often occupying broader climatic niches across elevational than latitudinal gradients. These findings suggest a failure to reach potential latitudinal limits. Further, they found that latitude/elevation were correlated with dispersal mode and maximum height. However, this study did not evaluate mismatches in southern latitudinal and low elevation limits, which allows for the possibility of high elevation sink populations occurring beyond species' true climatic limits (Boucher-LaLonde et al. 2012), or a stronger influence of human land use at high latitudes relative to high elevations (see section 4.5 *Priorities for future research*).

Overall, the direct evidence for the influence of dispersal limitation on North American tree species distributions is scarce, yet many studies demonstrate failure of species to occupy all

climatically suitable regions. Studies of tree regeneration following disturbance also demonstrate the ability of seeds to rapidly disperse long distances into disturbed sites, often covering distances >200m in a single regeneration event (Wirth et al. 2008; Turner et al. 1997; Romme et al. 2005). Rapid long-distance colonization following disturbance may reflect enhanced abiotic conditions for germination on post-disturbance sites, or reduced competition during establishment (Wirth et al. 2008). Taken together, these studies suggest that alternative factors that control species establishment may provide a more parsimonious explanation of observed disequilibrium of species distributions with climate than failure of propagules to reach suitable sites (i.e. dispersal limitation).

Disturbance may generate temporal instability in tree species distributions, but is unlikely to override the effects of climate on distribution patterns with the exception of species at the forest-grassland ecotone.

Natural disturbance regimes are an important characteristic of North American forests and have undoubtedly played an important role in the evolutionary history of tree species (Hopper 2009; Mucina & Wardell-Johnson 2011; He et al. 2015). Disturbances such as fire, drought, insect outbreaks and extreme weather events have large effects on North American forests (Dale et al. 2001), yet the impacts of such disturbances on species distributions remain unclear (Austin 2002; le Roux et al. 2013). This may be because few disturbances have sufficiently homogenous effects across a large enough spatial extent to be detectable at the spatial resolution of species distributions. For example, bark beetle outbreaks have decimated large areas of North American forests, but their effects are heterogeneous within a stand, with both live and dead trees remaining in affected areas (Meddens et al. 2012). Thus, while the

impacts of such catastrophic outbreaks are large, they may only be detectable as changes in abundance, rather than changes in occurrence at the scale of the species distribution. In fact, many disturbances generate patchy landscape dynamics that are not detectable at the level of the distribution (Lienard & Strigul 2016), with the notable exception of fire, which can affect large, continuous areas. Nevertheless, while the immediate effects of disturbance may not always be large enough to impact species distributions, natural disturbances may leave legacies that provide opportunities for gradual changes in distribution patterns over time.

Specifically, disturbances have been proposed to act as an important mechanism in distribution shifts by reducing competition and providing favorable environmental conditions for previously excluded species to establish (Dale et al. 2001; Leithead et al. 2010). Abundant examples exist of species composition shifts on disturbed sites, yet the implications of altered establishment patterns for species distributions do not appear to be persistent. For example, the 1988 fires in Yellowstone National Park provided an opportunity for broad-scale establishment of aspen seedlings and an increase in aspen occurrence relative to pre-fire conditions (Turner et al. 2003; Romme et al. 2005). At the time, high aspen seedling densities were suggested to be indicative of a potential range expansion event, yet re-measurement of burned areas in subsequent years has shown that many aspen have been outcompeted by recovering lodgepole pine (Hansen et al. 2015), which has resumed its historical distribution in Yellowstone. Similarly, Franklin et al. (2004) observed distributions of a suite southern Californian plant species, including trees, in response to variable fire rotation intervals, and found that *Pinus coulteri* maintained a stable regeneration niche under all rotation intervals, but was capable of transient expansion during longer fire-free periods. Thus, disturbance may drive temporal

disequilibrium in species distributions, particularly in the context of forest succession, but on longer temporal scales these effects may be diluted by the overriding impacts of climate.

However, long-term stability may be disrupted when climate changes, and in such instances disturbance may offer opportunities for pulsed distribution shifts. For example, in the Sierra Nevada Mountains in California, low regeneration of subalpine and montane tree species following fire was attributed to a 2°C shift in temperature that made previously occupied locations unsuitable for germinating individuals (Loudermilk et al. 2013). Distribution shifts associated with disturbance have also been observed at the boreal-temperate forest ecotone in Canada, where treefall gaps in boreal species-dominated forests have provided opportunities for temperate tree species to establish and shift their distributions northward (Leithead et al. 2010). Nevertheless, in both of these cases regeneration was still dependent on climatic conditions. Disturbance may affect the timing of regeneration events, thereby shaping transient distribution dynamics, but the composition and long-term persistence of regenerating species will still ultimately depend upon climatic suitability.

In fact, studies that have directly evaluated the impacts of both disturbance and climate on species distributions have found little evidence that disturbance exerts any independent effects on distributions (Woodall et al. 2013; Crimmins et al. 2014). Disturbances such as fire and insect outbreaks are highly correlated with and often controlled by climate, particularly when observed at a broad scale (Coops et al. 2005; Whitman et al. 2015). Fire in particular is synchronized across broad geographical regions by climate, and alternative drivers including topography and fuels only appear to drive variation at finer spatial scales (Westerling et al. 2006; Falk et al. 2007; Littell et al. 2010; Ireland et al. 2012).

However, there may be instances in which disturbance frequency becomes extreme enough to override the long-term effects of climate on tree species distributions. Modeling studies have shown that climatic suitability of many North American angiosperm tree species extends into North American prairies, which are currently maintained as grasslands by frequent fires that exclude long-lived tree species (Bond et al. 2005). In the Black Hills of South Dakota, USA, fire maintains grasslands in regions that are climatically suitable for ponderosa pine, thus truncating the pine distribution relative to climatic equilibrium (King et al. 2013). Historic fire suppression by humans also appears to involve a threshold of nonclimatic environmental change beyond which species distributions may shift in disequilibrium with climate. Fire suppression has been shown to drive expansion of closed-canopy forests into previously open grasslands in the eastern US (Nowacki & Abrams 2008; Rhemtulla et al. 2009), and to result in encroachment of less fire-tolerant species, such as Douglas-fir (*Pseudotsuga menziesii*), hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*) and white fir (*Abies concolor*) into historically pure ponderosa pine stands in the western US (Coops et al. 2005). Fire suppression involves a drastic departure from natural disturbance regimes, and such strong human impacts may decouple climate from other environmental factors influencing species distributions (see section 4.2: *Human land use*).

Taken together, these results indicate that most disturbance regimes are insufficient to override climatic controls on distributions of North American trees, but may drive temporal instability in species distributions by providing opportunities for establishment and initiating forest succession. However, a threshold in disturbance frequency may exist beyond which species distributions are maintained in long-term disequilibrium with climate. The effects of

disturbance on distributions may be most important at forest-grassland ecotones and in regions where disturbance regimes have been drastically impacted by human activities.

4.5 PRIORITIES FOR FUTURE RESEARCH

The available evidence regarding the distributions of North American tree species suggests that historical species distributions have responded primarily to climate, and that contemporary distributions cannot be explained by significant influences of interspecific biotic interactions, dispersal limitation, or disturbance. This may be seen to confirm the long-held assumption that North American tree species distributions are driven primarily by climate (Woodward 1987), yet considerable evidence demonstrates that many species are failing to track contemporary climate change (Woodall et al. 2009; Murphy et al. 2010; Zhu et al. 2012; Gray & Hamann 2013; Dial et al. 2015; Serra-Diaz et al. 2015). Apparently, factors beyond those reviewed above must contribute to the observed climate disequilibrium. Below, we highlight two proposed factors that we believe deserve increased research attention with regards to species distributions, and particularly the distributions of North American trees. Specifically, we emphasize the unique niches of tree seedlings and their importance for determining distribution limits, along with the influence of human land use on both species distributions and distribution shifts. At the same time, we recognize that evidence for the roles of the factors reviewed above (biotic interactions, dispersal limitation, disturbance) is far from complete, and these factors, too, deserve continued research attention.

Life Stage

While the majority of investigations seeking to understand the factors controlling species distributions of trees have considered primarily mature individuals, a growing body of evidence indicates that seedling characteristics may be more strongly related to distributional limits than adult characteristics (Jackson et al. 2009). The persistence and migration of tree species in a particular location depends upon successful regeneration (Clark et al. 2011; Bell et al. 2014; Máliš et al. 2016), which is likely to depend more on seedling establishment than on adult reproductive success. Seedlings generally show a greater sensitivity to climate and biotic factors than adult conspecifics, thus occupying much narrower niches (Cavender-Bares & Bazzaz 2000; Maher & Germino 2006; Jackson et al. 2009; Lenoir et al. 2009). In particular, seedlings are highly susceptible to periods of drought, owing to their poorly developed and shallow root systems (Fenner & Thompson 2004), and to competition, which is one of the most significant causes of tree seedling mortality (Lorimer et al. 1994; Fenner & Thompson 2004).

Several studies have documented a restricted climatic niche of western US tree seedlings relative to adult conspecific niches, with the greatest differences occurring near distributional limits (Stohlgren et al. 1998; Bell et al. 2014; Dobrowski et al. 2015). In particular, seedlings distributions have been found to be restricted to lower elevations (Stohlgren et al. 1998), and are constrained to sites beneath existing forest canopies, where climate may be buffered (Dobrowski et al. 2015). Water availability appears to be the primary climatic constraint limiting the distributions of seedlings of these species, but biotic factors may also play an important role (Dobrowski et al. 2015). Specifically, aggregated regeneration patterns indicate that seedlings may rely on facilitation from parent plants and other adult conspecifics to escape exposure to unfavorable climate and competition (Fenner & Thompson 2004; Dobrowski et al. 2015). However, these static spatial patterns of seedling and adult distributions mask long-term

fluctuations in spatial patterns of seedling establishment that may contribute to current distribution limits.

Due to broader niches and greater environmental tolerance, mature trees are capable of persisting under conditions that prevent continual establishment of seedlings (Johnstone et al. 2010). However, short periods of favorable climate or reduced biotic pressure following disturbance may provide opportunities for regeneration pulses, during which seedlings are capable of establishing in otherwise sub-optimal habitats. Such patterns of episodic recruitment appear to be the normal pattern of establishment for most tree species (Jackson et al. 2009). In tree species occurring in the Rocky Mountains, episodic recruitment events have been shown to maintain long-term distribution limits for high elevation species (Stohlgren et al. 1998), to expand distributions to new, unoccupied locations (Lesser & Jackson 2012), and to alter species composition, shifting adjacent species distributions towards climatic equilibrium (Johnstone et al. 2010).

Most often, episodic recruitment events are more strongly associated with short periods of particularly favorable climate than with disturbance, particularly at the broad scales that characterize species distributions. For example, recruitment pulses of fire-adapted ponderosa pine in the southwestern United States over broad spatial and temporal scales are strongly correlated with pluvial periods, which not only reduce climatic stresses on seedlings, but also reduce fire frequency, allowing sufficient time for successful establishment (Brown & Wu 2005). Serra-Diaz et al. (2015) identified a similar pattern of regeneration pulses in Californian forests, and suggest that such patterns may typically go undetected when analyzing species distributions against long-term average climate trends. The species in their study responded strongly to climatic fluctuations, and were able to take advantage of very short windows of climatic

suitability to establish. These studies caution that while adult tree species distributions may not appear to occur in equilibrium with contemporary climate, climate may still be the dominant control on species distributions by determining when and where seedlings can establish. However, due to the episodic nature of seedling establishment, static evaluations of seedling distributions relative to adult distributions may not reflect long-term climatic controls on tree species distributions.

Seedlings, however, are also particularly sensitive to biotic interactions, which may also contribute to distribution limits of North American tree species. In a study to determine the factors controlling elevational distribution limits of trees on Mount Rainier in Washington, USA, HilleRisLambers et al. (2013) found that competition cannot explain adult tree and sapling growth at range limits, yet seedlings showed a much greater sensitivity to competition at their lower distribution limits. These findings suggest that competition with seedlings may play a role in determining the lower distribution limits of these species. This study also demonstrated, in agreement with other studies, that the critical transition in environmental requirements and sensitivities in trees occurs between the seedling and sapling stages, thus implicating seedlings as particularly sensitive indicators of environmental controls on species distributions (HilleRisLambers et al. 2013; Máliš et al. 2016). Similarly, Godoy et al. (2015) found that eastern North American tree seedlings show a strong negative density dependence towards their southern distributional limits that is strongly correlated with recruitment potential. These authors also identified a trend of strong positive density dependence at northern distributional limits, indicating that facilitation may be an important mechanism promoting seedling establishment in more stressful climates. Density-dependence in recruitment of these species does not appear to depend on the identity of co-occurring individuals (Johnson et al. 2012), which is consistent with

the hypothesis that North American tree species lack a coevolved history and thus are not particularly sensitive to interspecific interactions. While biotic interactions certainly appear to contribute to the distribution patterns of eastern North American tree seedlings, climate sensitivity, particularly to seasonal freezing temperatures, still appears to be the dominant factor explaining seedling recruitment patterns (Godoy et al. 2015).

These studies suggest that climate may be the overriding control on seedling establishment, and thus distribution limits in North American tree species, yet a notable exception exists. In a study of the distribution of regenerating trees in California forests, Serra-Diaz et al. (2015) found no evidence for a strong relationship between regeneration and climate. Management activities associated with human land use appeared to be a more important driver of regeneration patterns in this region, though this hypothesis has not been fully explored. In general, the available evidence indicates that the climatic sensitivity of seedlings may play a particularly important role in defining tree distributions, yet few studies have directly evaluated their specific role, likely owing to the difficulty of capturing recruitment trends that occur over long temporal scales. However, we posit that by devoting a greater amount of research focus to the role of seedlings, many apparent and unexplained inconsistencies regarding current distribution patterns of North American trees may be resolved.

Human land use

Human land use has been suggested as a factor underlying disequilibrium of North American tree distributions with climate (e.g. Zhu et al. 2012; Corlett & Westcott 2012; Van der Putten 2012), but few analyses have tested this influence explicitly. Clearly, forest clear cutting, agricultural conversion, or exurban expansion will remove trees from climatically suitable

regions and truncate their distributions, yet the extent to which such practices have impacted distributions has seldom been explicitly quantified, making it difficult to generalize on the relative importance of human land use for contemporary tree distributions. Nevertheless, observations of range shifts under climate change are providing increasing opportunities to document the effects of human activities on range limits.

For example, the slow migration rates of many tree species relative to the rate of climate change have been attributed to human-caused habitat fragmentation in several studies (Honnay et al. 2002; Scheller & Mladenoff 2008; Zhu et al. 2012; Serra-Diaz et al. 2015). Habitat fragmentation directly reduces seed dispersal distance and increases the probability that dispersed seeds land in unfavorable sites, thus preventing species from spreading into all climatically suitable regions (Honnay et al. 2002; Higgins et al. 2003; Van der Putten 2012). This effect has been modeled directly for North American tree species: in a simulation of migration patterns of 22 tree species in northern Wisconsin, USA, landscape fragmentation caused by human activities was shown to limit effective seed dispersal and to prevent species from moving in equilibrium with climate (Scheller & Mladenoff 2008). Reduced migration and range expansion in this simulation were primarily attributable to limited seedling establishment in human-impacted regions and resultant tree distributions showed truncated distributions, particularly at northern extents, relative to climatic suitability. Human-caused habitat fragmentation may also promote upslope range shifts by providing microrefugial habitats that allow species to establish above natural distribution limits, such as has been observed along mountain roads (Lembrechts et al. 2016).

In other cases, cessation of human activities has allowed species with historically truncated distributions to slowly equilibrate with climate. These distribution expansions are often

associated with less intensive forest harvesting and reforestation of agricultural land, which represents the dominant land cover change in the United States throughout the 19th and 20th centuries (Ramankutty & Foley 1999). Forest expansion onto former agricultural sites has been documented across the United States, from western North America (Loudermilk et al. 2013), to the central United States (Rhemtulla et al. 2009), to eastern North America (Thompson et al. 2011).

In fact, abandonment of old fields in eastern North America may provide one of the most direct examples of the effects of human land use on tree distributions. In particular, conifer distributions throughout the eastern United States were dramatically truncated by historical agricultural expansion, yet large-scale land abandonment throughout the 20th century has allowed conifer distributions to expand onto old fields (Raup 1966; Cavallin & Vasseur 2009). Colonization onto these heavily modified sites is limited by low germination success, resulting in relatively slow expansion (Cavallin & Vasseur 2009). Thus, many species whose distributions were historically affected by extensive agricultural practices in the eastern United States are probably still not in equilibrium with climate, despite substantial land abandonment.

Patterns of forest expansion following human land abandonment may occur more rapidly in mountainous regions, where short dispersal distances allow for rapid movement. Examples of this are more abundant in European mountain ranges, where a long history of high elevation grazing has historically constrained treeline downslope of its climatic limit. Recent cessation of human activities has allowed the treeline to expand upslope in many regions, and changes in treeline associated with land use have occurred far more rapidly than those associated with climate (Gehrig-Fasel et al. 2007; Palombo et al. 2013; Ameztegui et al. 2015). In North America, human activities are often concentrated at lower elevations (Van der Putten 2012), and

downslope movement of North American tree species has been observed in association with changes in land use. In the northeast United States, patterns of downslope shifts in boreal forests could reflect recovery of historic distributions following the cessation of decades of selective harvesting of red spruce at lower elevation edges (Foster & D'Amato 2015).

Human alteration of natural disturbance regimes may also, in some cases, have drastic impacts on tree distributions. Recent evidence suggests that most eastern North American tree distributions may be in disequilibrium with climate due to human fire management throughout the 19th century. Specifically, prescribed burning drove a contraction in the distribution of conifers and a large expansion in oak distributions until fire suppression was introduced. These altered forests have responded to fire suppression by exhibiting a shift towards dominance of species that prefer more mesic conditions. Neither of these historical distribution patterns appears to be representative of climatic control, and the impacts of human management on these systems may be much larger than the impact of climate (Nowacki & Abrams 2015). As reviewed in section 4.4, fire suppression may also allow for encroachment of forest species into grasslands, thus expanding tree distributions (Coops et al. 2005; Nowacki & Abrams 2008; Rhemtulla et al. 2009)

Aside from these few examples, the impacts of human land use on broad-scale species distributions have been little investigated, and land use is almost never incorporated into species distribution models. However, the available studies demonstrate that human land use may be an important factor limiting the distributions of North American tree distributions relative to climatic suitability. Further, while limited, the evidence for human impacts on distributions is more consistent than evidence for dispersal limitation, natural disturbances, or biotic interactions. Additional research is needed to determine the precise contexts in which human land use may

play a particularly important role in constraining species distributions, and which distributions reflect these influences most strongly. Ultimately, this should lead to improved efforts to incorporate metrics of human land use into species distribution models and range models, which will help to clarify the factors controlling species distribution patterns.

4.6 CONCLUSIONS

In this review, we demonstrate how ecological and evolutionary history provides powerful context for understanding contemporary distribution patterns. The history of North American tree species distributions indicates that species traits have been shaped within an environment of extreme climate variability and rapidly shifting distributions. Species have had limited opportunities for coevolution or specialization, and instead demonstrate traits that allow for rapid responses to changes in climate. This historical legacy would be expected to contribute to contemporary distribution patterns that are shaped predominantly by climate, with little importance of biotic interactions and dispersal limitation. Our review of contemporary distribution patterns indicates that North American tree distributions largely reflect this historical legacy. Overall, little empirical evidence exists for any significant influence of biotic interactions and dispersal limitation, although we acknowledge that evidence regarding these two factors is incomplete and further research may reveal previously unidentified relationships. Specifically, few studies have evaluated the role of interactions across trophic levels (but see Moorcroft et al. 2006; Van der Putten et al. 2012) or have attempted to distinguish between dispersal limitation and failure to establish. The role of disturbance has received little attention at spatial scales relevant to species distributions, but available evidence suggests that climate may override the effects of disturbance with the exception of specific contexts where thresholds in disturbance

frequencies are crossed, beyond which trees can no longer maintain persistent populations. Human modification of habitat and disturbance regimes may contribute to the apparent disequilibrium of tree distributions with contemporary climate and generate new responses that cannot be predicted from species' ecological and evolutionary history. These findings are summarized in **Figure 4.3**, which offers a schematic representation of the factors influencing North American tree species distributions.

We conclude by arguing that a consistent conceptual framework of North American tree species distributions must not only consider historical legacy, but must also address the influences of differences in life stage along with the impacts of human land use. Future species distributions may well be shaped by the ability of tree seedlings to establish in human-modified habitat, which may drive marked disequilibrium of species distributions with climate. Such considerations are crucial, as our understanding of the factors and mechanisms underlying species distributions will determine our ability to accurately predict future changes in species distributions, and to recommend management and conservation strategies that will effectively protect biodiversity.

4.7 REFERENCES

- Aitken, SN, Yeaman, S, Holliday, JA, Wang, T, Curtis-McLane, S. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications* 1:95-111.
- Ameztegui, A, Coll, L, Brotons, L, Ninot, JM. 2015. Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecology and Biogeography* 25: 263-273.
- Araújo, MB, Rozenfeld, A. 2014. The geographic scaling of biotic interactions. *Ecography* 37: 406-415.
- Araújo, MB, Rozenfeld, A, Rahbek, C, Marquet, PA. 2011. Using species co-occurrence networks to assess the impacts of climate change. *Ecography* 34: 897-908.
- Asselin, H, Fortin, M-J, Bergeron, Y. 2001. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. *Forest Ecology and Management* 140: 29-37.
- Austin, MP. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecological Modelling* 157: 101-118.
- Bell, DM, Bradford, JB, Lauenroth, WK. 2013. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* 23: 168-180.
- Bennett, KD, Tzedakis, PC, Willis, KJ. 1991. Quaternary refugia of north European trees. *Journal of Biogeography* 18: 103-115.
- Blois, JL, Zarnetske, PL, Fitzpatrick, MC, Finnegan, S. 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341: 499-504.

- Blois, JL, Gotelli, NJ, Behrensmeyer, AK, Faith, JT, Lyons, SK, Williams, JW, Amatangelo, KL, Bercovici, A, Du, A, Eronen, JT, Graves, GR, Jud, N, Labandeira, C, Looy, CV, McGill, B, Patterson, D, Potts, R, Riddle, B, Terry, R, Tóth, A, Villaseñor, A, Wing, S. 2014. A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary. *Ecography* 37: 1095-1108.
- Bond, WJ, Woodward, FI, Migley, GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist* 165: 525-538.
- Bonnicksen, TM. 2000. America's ancient forests: From the ice age to the age of discovery. John Wiley & Sons: New York, NY, USA.
- Boucher-Lalonde, V, Morin, A, Currie, DJ. 2012. How are tree species distributed in climatic space? A simple and general pattern. *Global Ecology and Biogeography* 21: 1157-1166.
- Boulangeat, I, Gravel, D, Thuiller, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15: 584-593.
- Brown, PM, Wu, R. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86: 3030-3038.
- Brown, JH, Stevens, GC, Kaufman, DM. 1996. The geographic range: Size, shape, boundaries, and internal structure. *Annual Reviews of Ecology and Systematics* 27: 597-623.
- Case, TJ, Holt, RD, McPeck, MA, Keitt, TH. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108: 28-46.
- Cassini, MH. 2011. Ecological principles of species distribution models: the habitat matching rule. *Journal of Ecology and Biogeography* 38: 2057-2065.

- Cavallin, N, Vasseur, L. 2009. Red spruce forest regeneration dynamics across a gradient from Acadian forest to old field in Greenwich, Prince Edward Island National Park, Canada. *Plant Ecology* 201: 169-180.
- Cavender-Bares, J, Bazzaz, FA. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 124: 8-18.
- Clark, PU, Bartlein, PJ. 1995. Correlation of late Pleistocene glaciation in the western United States with North Atlantic Heinrich events. *Geology* 23: 483-486.
- Clark, JS. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *The American Naturalist* 152: 204-224.
- Clark, JS, Lewis, M, Horvath, L. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. *The American Naturalist* 157: 537-554.
- Clark, JS, Bell, DM, Hersh, MH, Nichols, L. 2011. Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. *Global Change Biology* 17: 1834-1849.
- Clark, JS, Gelfand, AE, Woodall, CW, Zhu, K. 2014. More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications* 24: 990-999.
- Coops, NC, Waring, RH, Law, BE. 2005. Assessing the past and future distribution and productivity of ponderosa pine in the Pacific Northwest using a process model: 3-PG. *Ecological Modelling* 183: 107-124.

- Copenhaver-Parry, PE, Cannon, E. 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* DOI 10.1007/s00442-016-3565-x
- Corlett, RT, Westcott, DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology and Evolution* 28: 482-488.
- Crimmins, SM, Dobrowski, SZ, Mynsberge, AR, Safford, HD. 2014. Can fire atlas data improve species distribution model projections? *Ecological Applications* 24: 1057-1069.
- Dale, VH, Joyce, LA, McNulty, S, Neilson, RP, Ayres, MP, Flannigan, MD, Hanson, PJ, Irland, LC, Lugo, AE, Peterson, CJ, Simberloff, D, Swanson, FJ, Stocks, BJ, Wotton, BM. 2001. Climate change and forest disturbances. *BioScience* 51: 723-734.
- Dial, RJ, Smeltz, TS, Sullivan PJ, Rinas, CL, Timm, K, Ceck, JE, Tobin, SC, Golden, TS, Berg, EC. 2015. Shrub-line but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. *Global Change Biology* DOI: 10.1111/gcb.13207
- Dobrowski, SZ, Swanson, AK, Abatzoglou, JT, Holden, ZA, Safford, HD, Schwartz, MK, Gavin, DG. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography* 24: 917-927.
- Ettinger, AK, Ford, KR, HilleRisLambers, J. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology* 92: 1323-1331.
- Ettinger, AK, HilleRisLambers, J. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. *American Journal of Botany* 100: 134-1355.
- Falk, DA, Miller, C, McKenzie, D, Black, AE. 2007. Cross-scale analysis of fire regimes. *Ecosystems* 10: 809-823.

- Fastie, CL. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* 76: 1899-1916.
- Fenner, M, Thompson, K. 2004. *The Ecology of Seeds*. Cambridge University Press: Cambridge, UK.
- Foster, JR, D'Amato, AW. 2015. Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. *Global Change Biology* 21: 4497-4507.
- Franklin, J, Syphard, AD, He, HS, Mladenoff, DJ. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8: 885-898.
- Gaston, KJ. 2009. Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B* 276: 1395-1406.
- Gehrig-Fasel, J, Guisan, A, Zimmermann, NE. 2007. Tree line shifts in the Swiss Alps: Climate change or land abandonment? *Journal of Vegetation Science* 18: 571-582.
- Godoy, O, Rueda, M, Hawkins, BA. 2015. Functional determinants of forest recruitment over broad scales. *Global Ecology and Biogeography* 24: 192-202.
- Godsoe, W, Harmon, LJ. 2012. How do species interactions affect species distribution models? *Ecography* 35: 811-820.
- Godsoe, W, Murray, R, Plank, MJ. 2015. The effect of competition on species' distributions depends on coexistence, rather than scale alone. *Ecography* 38: 001-009.
- Gray, LK, Hamann, A. 2013. Tracking suitable habitat for tree populations under climate change in western North America. *Climatic Change* 117: 289-303.

- Grimm, EC, Jacobson, GL, Watts, WA, Hansen, BCS, Maasch, KA. 1993. A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich events. *Science* 261: 189-211.
- Gugger, PF, McLachlan, JS, Manos, PS, Clark, JS. 2008. Inferring long-distance dispersal and topographic barriers during post-glacial colonization from the genetic structure of red maple (*Acer rubrum* L.) in New England. *Journal of Biogeography* 35: 1665-1673.
- Gutiérrez, AG, Snell, RS, Bugmann, H. 2016. Using a dynamic forest model to predict tree species distributions. *Global Ecology and Biogeography* 25: 347-358.
- Hansen, WD, Romme, WH, Ba, A, Turner, MG. 2016. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. *Forest Ecology and Management* 362: 218-230.
- Hargreaves, AL, Samis, KE, Eckert, CG. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist* 183: 157-173.
- Harrison, SP, Goñi, MFS. 2010. Global patterns of vegetation response to millennial-scale variability and climate change during the last glacial period. *Quaternary Science Reviews* 29: 2957-2980.
- He, T, Belcher, CM, Lamont, BB, Lim, SL. 2016. A 350-million-year-legacy of fire adaptation among conifers. *Journal of Ecology* 104: 352-363.
- Higgins, SI, Lavorel, S, Revilla, E. 2003. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101: 354-366.

- HilleRisLambers, J, Harsch, MA, Ettinger, AK, Ford, KR, Theobald, EJ. 2013. How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences* 1297: 112-125.
- Holt, RD. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106: 19659-19665.
- Honnay, O, Verheyen, K, Butay, J, Jacquemyn, H, Bossuyt, B, Hermy, M. 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters* 5: 525-530.
- Hopper, SD. 2009. OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant Soil* 322: 49-86.
- Hutchinson, GE. 1957. Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22: 415-427.
- Ireland, KB, Stan, AB, Fulé, PZ. 2012. Bottom-up control of a northern Arizona ponderosa pine forest regime in a fragmented landscape. *Landscape Ecology* 27: 983-997.
- Iverson, LR, Schwartz, MW, Prasad, AM. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Biogeography* 13: 209-219.
- Jackson, ST, Overpeck, JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26: 194-220.

- Jackson, ST, Betancourt, JL, Booth, RK, Gray, ST. 2009. Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106: 19658-19692.
- Jaramillo-Correa, JP, Beaulieu, J, Khasa, DP, Bousquet, J. 2009. Inferring the past from the present phylogeographic structure of North American forest trees: seeing the forest for the genes. *Canadian Journal of Forest Research* 39: 286-307.
- Jiménez-Moreno, G, Anderson, RS, Desprat, S, Grigg, LD, Grimm, eC, Heusser, LE, Jacobs, BF, López-Martínez, C, Whitlock, CL, Willard, DA. 2010. Millennial-scale variability during the last glacial in vegetation records from North America. *Quaternary Science Reviews* 29: 2865-2881.
- Johnson, DJ, Beaulieu, WT, Bever, JD, Clay, K. 2012. Conspecific negative density dependence and forest diversity. *Science* 336: 904-907.
- Johnstone, JF, McIntire, EJB, Pederson, EJ, King, G, Pisaric, MJ. 2010. A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. *Ecosphere* 1: 1-21.
- Kellman, M. 2004. Sugar maple (*Acer saccharum* Marsh.) establishment in boreal forest: results of a transplantation experiment. *Journal of Biogeography* 31: 1515-1522.
- King, DA, Bachelet, DM, Symstad, AJ. 2013. Climate change and fire effects on a prairie-woodland ecotone: projecting species range shifts with a dynamic global vegetation model. *Ecology and Evolution* 3: 5076-5097.
- Krause, TR, Whitlock, C. 2013. Climate and vegetation change during the late-glacial/early-Holocene transition inferred from multiple proxy records from Blacktail Pond, Yellowstone National Park, USA. *Quaternary Research* 79: 391-402.

- Kubisch, A, Degan, T, Hovestadt, T, Poethke, HJ. 2013. Predicting range shifts under global change: the balance between local adaptation and dispersal. *Ecography* 36: 873-882.
- Lavergne, S, Mouquet, N, Thuiller, W, Ronce, O. 2010. Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Reviews of Ecology, Evolution and Systematics* 41: 321-350.
- Leithead, MD, Anand, M, Silva, LCR. 2010. Northward migrating trees establish in treefall gaps at the northern limit of the temperate-boreal ecotone, Ontario, Canada. *Oecologia* 164: 1095-1106.
- Lembrechts, JJ, Alexander, JM, Cavieres, LA, Haider, S, Lenoir, J, Keuffer, C, McDougall, K, Naylor, BJ, Nuñez, MA, Pauchard, A, Rew, LJ Nijs, I, Milbau, A. 2016. Mountain roads shift native and non-native plant species ranges. *Ecography* DOI: 10.1111/ecog.02200
- Lenoir, J, Gégout, J-C, Pierrat, J-C, Bontemps, J-D, Dhôte, J-F. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986-2006). *Ecography* 32: 765-777.
- Lenoir, J, Gégout, J-C, Guisan, A, Vittoz, P, Wohlgemuth, T, Zimmermann, NE, Dullinger, S, Pauli, H, Willner, W, Svenning, J-C. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33: 295-303.
- Le Roux, PC, Virtanen, R, Luoto, M. 2013. Geomorphological disturbance is necessary for predicting fine-scale species distributions. *Ecography* 36: 800-808.
- Lesser, MR, Jackson, ST. 2012. Making a stand: five centuries of population growth in colonizing populations of *Pinus ponderosa*. *Ecology* 93: 1071-1081.

- Liénard, JF, Strigul, NS. 2016. Modeling of hardwood forest in Quebec under dynamic disturbance regimes: a time-inhomogeneous Markov chain approach. *Journal of Ecology* DOI: 10.1111/1365-2745.12540
- Littell, JS, Oneil, EE, McKenzie, D, Hicke, JA, Lutz, JA, Norheim, RA, Elsner, MM. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change* DOI 10.1007/s10584-010-9858-x
- Lorimer, CG, Chapman, JW, Lambert, WD. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82: 227-237.
- Loudermilk, EL, Scheller, RM, Weisberg, PJ, Yang, J, Dilts, TE, Karam, SL, Skinner, C. 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interactions. *Global Change Biology* 19: 3502-3515.
- Maher, EL, Germino, MJ. 2006. Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience* 13: 334-341.
- Máliš, F, Kopecký, M, Petřík, P, Vladovič, j, Merganič, J, Vida, T. 2016. Life-stage, not climate change, explains observed tree range shifts. *Global Change Biology* DOI: 10.1111/gcb.13210
- Manchester, SR. 1999. Biogeographical relationships of North American Tertiary floras. *Annals of the Missouri Botanical Garden* 86: 472-522.
- Massot, M, Clobert, J, Ferrier, R. 2008. Climate warming, dispersal inhibition and extinction risk. *Global Change Biology* 14: 461-469.

- Meddens, AJH, Hicke, JA, Ferguson, CA. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22: 1876-1891.
- Meier, ES, Lischke, H, Schmatz, DR, Zimmermann, NE. 2012. Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography* 21: 164-178.
- Moorcroft, PR, Pacala, SW, Lewis, MA. 2006. Potential role of natural enemies during tree range expansions following climate change. *Journal of Theoretical Biology* 241: 601-616.
- Morin, X, Chuine, I. 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters* 9: 185-195.
- Morin, X, Augspurger, C, Chuine, I. 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? *Ecology* 88: 2280-2291.
- Morueta-Holme, N, Blonder, B, Sandel, B, McGill, BJ, Peet, RK, Ott, JE, Viole, C, Enquist, BJ, Jørgensen, PM, Svenning, J-C. 2016. A network approach for inferring species associations from co-occurrence data. *Ecography* DOI: 10.1111/ecog.01892
- Mucina, L, Wardell-Johnson, GW. 2011. Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant Soil* 341: 1-23.
- Murphy, HT, VanDerWal, J, Lovett-Doust, J. 2010. Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters* 13: 1233-1244.
- Neilson, RP, Wullstein, LH. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. *Journal of Biogeography* 10: 275-297.

- Nowacki, GJ, Abrams, MD. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58: 123-138.
- Nowacki, GJ, Abrams, MD. 2015. Is climate an important driver of post-European vegetation change in the eastern United States? *Global Change Biology* 21: 314-334.
- Palombo, C, Chirici, G, Marchetti, M, Tognetti, R. 2013. Is land abandonment affecting forest dynamics at high elevation in Mediterranean mountains more than climate change? *Plant Biosystems* 147: 1-11.
- Perlman, DL, Adelson, G. 1997. *Biodiversity: Exploring values and priorities in conservation*. Blackwell Science: Malden, MA, USA.
- Pither, J. 2003. Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society of London B* 270: 475-481.
- Prentice, IC, Bartlein, PJ, Webb III, T. 1991. Vegetation and climate change in eastern North America since the Last Glacial Maximum. *Ecology* 72: 2038-2056.
- Qian, H, Wiens, JJ, Zhang, J, Zhang, Y. 2015. Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* 38: 241-250.
- Ramankutty, N, Foley, JA. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13: 997-1027.
- Raup, HM 1966. The view from John Sanderson’s farm: a perspective for the use of the land. *Forest History* 10: 2-11.
- Rehfeldt, GE, Crookston, NL, Warwell, MV, Evans, J. 2006. Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences* 167: 1123-1150.

- Renwick, KM, Rocca, ME. 2015. Temporal context affects the observed rate of climate-driven range shifts in tree species. *Global Ecology and Biogeography* 24: 44-51.
- Rhemtulla, JM, Mladenoff, DJ, Clayton, MK. 2009. Historical forest baselines reveal potential for continued carbon sequestration. *Proceedings of the national Academy of Sciences* 106: 6082-6087.
- Ricklefs, RE. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167.
- Ricklefs, RE. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7: 1-5.
- Romme, WH, Turner, MG, Tuskan, GA, Reed, RA. 2005. Establishment, persistence, and growth of aspen (*Populus tremuloides*) seedlings in Yellowstone National Park. *Ecology* 86: 404-418.
- Rouget, M, Richardson, DM, Lavorel, S, Vayreda, J, Gracia, C, Milton, SJ. 2001. Determinants of distribution of six *Pinus* species in Catalonia, Spain. *Journal of Vegetation Science* 12: 491-502.
- Scheller, RM, Mladenoff, DJ. 2008. Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. *Climate Research* 36: 191-202.
- Serra-Diaz, JM, Franklin, J, Sweet, LC, McCullough, IM, Syphard, AD, Regan, HM, Flint, LE, Flint, AL, Dingman, JR, Moritz, M, Redmond, K, Hannah, L, Davis, FW. 2015. Averaged 30 year climate change projections mask opportunities for species to establish. *Ecography* DOI: 10.1111/ecog.02074

- Shuman, B, Newby, P, Huang, Y, Webb III, T. 2004. Evidence for the close climatic control of New England vegetation history. *Ecology* 85: 1297-1310.
- Siefert, A, Lesser, MR, Fridley, JD. 2015. How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients. *Global Ecology and Biogeography* 24: 581-593.
- Soberón, J, Nakamura, M. 2009. Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Science* 106: 19644-1950.
- Stohlgren, TJ, Bachand, RR, Onami, Y, Binkley, D. 1998. Species-environment relationships and vegetation patterns: effects of spatial scale and tree life-stage. *Plant Ecology* 135: 215-228.
- Svenning, J-C, Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters* 10: 453-460.
- Svenning, J-C, Gravel, D, Holt, RD, Schurr, FM, Thuiller, W, Münkemüller, T, Schiffers, KH, Dullinger, S, Edwards, TC, Hickler, T, Higgins, SI, Nabel, JEMS, Pagel, J, Normand, S. 2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37: 001-012.
- Thomas, CD, Bodsworth, EJ, Wilson, RJ, Simmons, AD, Davies, ZG. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411: 577-581.
- Thompson, JN. 2005. *The geographic mosaic of coevolution*. The university of Chicago Press: Chicago, IL.
- Thompson, JR, Foster, DR, Scheller, R, Kittredge, D. 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. *Ecological Applications* 21: 2425-2444.

- Turner, MG, Romme, WH, Gardner, RH, Hargrove, WW. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecological Monographs* 67: 411-433.
- Turner, MG, Romme, WH, Reed, RA, Tuskan, GA. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecology* 18: 127-140.
- Van der Putten, WH, Macel, M, Visser, ME. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the royal Society B* 365: 2025-2034.
- Van der Putten, WH. 2012. Climate change, aboveground-belowground interactions, and species' range shifts. *Annual Reviews of Ecology, Evolution and Systematics* 43: 365-383.
- Westerling, AL, Hidalgo, HG, Cayan, DR, Swetnam, TW. 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313: 940-943.
- Whitman, E, Batllori, E, Parisien, M-A, Miller, C, Coop, JD, Krawchuk, MA, Chong, GW, Haire, SL. 2015. The climate space of fire regimes in north-western North America. *Journal of Biogeography* 42: 1736-1749.
- Wiens, JJ. 2011. The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society B* 366: 2336-2350.
- Williams, JW, Jackson, ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5: 475-482.
- Williams, JW, Shuman, BN, Webb III, T, Bartlein, PJ, Leduc, PL. 2004. Late-Quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs* 74: 309-334.

- Williams, JW, Shuman, B, Barlein, PJ, Whitmore, J, Gajewski, K, Sawada, M, Minckley, T, Shafer, S, Viau, AE, Webb III, T, Anderson, PM, Brubaker, LB, Whitlock, C, Davis, OK. 2006. An atlas of pollen-vegetation-climate relationships for the United States and Canada. Dallas, TX: American Association of Stratigraphic Palynologists foundation.
- Willis, KJ, Bailey, RM, Bhagwat, SA, Birks, HJB. 2000. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using paleoecological data. *Trends in Ecology and Evolution* 25: 583-591.
- Wirth, C, Lichstein, JW, Dushoff, J, Chen, A, Chapin, FS. 2008. White spruce meets black spruce: Dispersal, postfire establishment, and growth in a warming climate. *Ecological Monographs* 78: 489-505.
- Wisz, MS, Potter, J, Kissing, WD, Pellissier, L, Lenoir, J, Damgaard, CF, Dormann, CF, Forchhammer, MC, Grytnes, J-A, Guisan, A, Heikkinen, RK, Høye, TT, Kuhn, I, Luoto, M, Maiorano, L, Nilsson, M-C, Normand, S, Ockinger, E, Schmidt, NM, Termansen, M, Timmermann, A, Wardle, DA, Aastrup, P, Svenning, J-C. 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biological Reviews* 88: 15-30.
- Woodall, CW, Oswalt, CM, Westfall, JA, Perry, CH, Nelson, MD, Finley, AO. 2009. An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management* 257: 1434-1444.
- Woodall, CW, Zhu, K, Westfall, JA, Oswalt, CM, D'Amato, AW, Walters, BJ, Lintz, HE. 2013. Assessing the stability of tree ranges and influence of disturbance in eastern US forests. *Forest Ecology and Management* 291: 172-180.

- Woodward, FI. 1987. Climate and plant distribution. Cambridge University Press: Cambridge, UK.
- Xiang, Q-Y, Zhang, WH, Ricklefs, RE, Qian, H, Chen, ZD, Wen, J, Li, JH. 2004. Regional differences in rates of plant speciation and molecular evolution: A comparison between eastern Asia and eastern North America. *Evolution* 58: 2175-2184.
- Yu, Z. 2007. Rapid response of forested vegetation to multiple climatic oscillations during the last deglaciation in the northeastern United States. *Quaternary Research* 67: 297-303.
- Zhu, K, Woodall, CW, Clark, JS. 2012. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* 18: 1042-1052.

4.8 TABLES

Table 4.1. Studies that have evaluated the impacts of biotic interactions on North American tree species distributions have used a variety of approaches, and have generally concluded that the interspecific interactions evaluated (competition, facilitation) do not strongly impact species distributions.

Citation	Location	Representation of biotic interactions	Findings/Conclusions
Morin et al. 2007	North America	Process-based model used to identify if species distributions differ from those predicted based on physiological limitations	Continental scale distribution can be largely explained by the impact of climate on phenology, with no evidence for a significant impact of competition
Ettinger et al. 2013	Mount Rainier, Washington, USA	Growth responses of trees to climate and competition at elevational distribution edges	Competition does not influence distribution limits of adult and sapling trees, but may contribute to lower distribution edge of seedlings
Clark et al. 2014	Eastern US	Species co-occurrence in a Joint Species Distribution Model	Tree distributions co-vary, but it is unclear if this is due to biotic interactions or shared environmental responses

Gutiérrez et al. 2016	Pacific Northwest	Neighborhood competition introduced at stand level in forest GAP model	Regional patterns are best explained by bioclimatic parameters alone
Copenhaver-Parry & Cannon 2016	US Rocky Mountains	Growth responses of trees to climate and competition at elevational distribution edges	Climate has a greater relative impact on tree growth than competition at both upper and lower distribution edges
Copenhaver-Parry & Bell <i>in prep</i>	US Rocky Mountains	Species co-occurrence in a Joint Species Distribution Model	Climate explains much more variance in species co-occurrence patterns than interspecific interactions

4.9 FIGURES

Figure 4.1. The distribution of major forest types across North America. Data are taken from 2010 land cover estimates from MODIS satellite imagery (<http://modis.gsfc.nasa.gov/>).

Figure 4.2. Historic distribution of *Pinus* across North America, from the Last Glacial Maximum to the present. Blue regions represent ice cover. Reconstructions are based on fossil pollen evidence, and regions with too little data for reliable reconstruction are left blank. All images were extracted from the Pollen Viewer (<http://www.ncdc.noaa.gov/paleo/pollen/viewer/webviewer.html>) and are based on data presented in Williams et al. (2004).

Figure 4.3. Schematic representation of the hypothesized impacts of ecological factors on North American tree species distributions based upon the evidence reviewed here. Important factors span a variety of spatial scales and may impact species distributions strongly (solid lines) or weakly (dashed line).

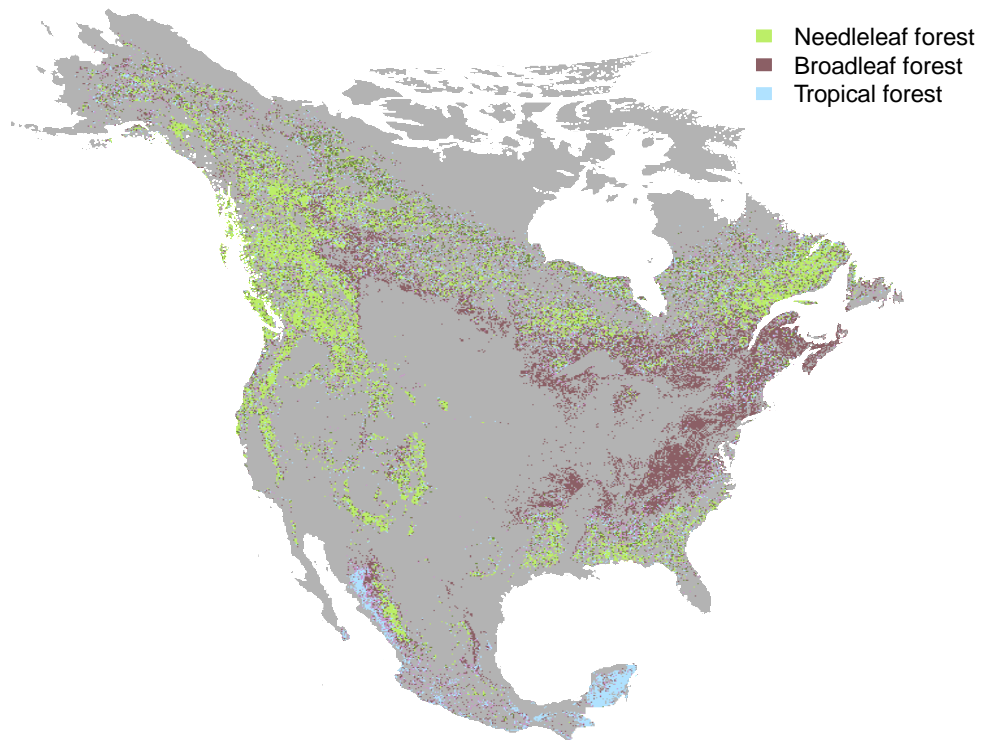


Figure 4.1

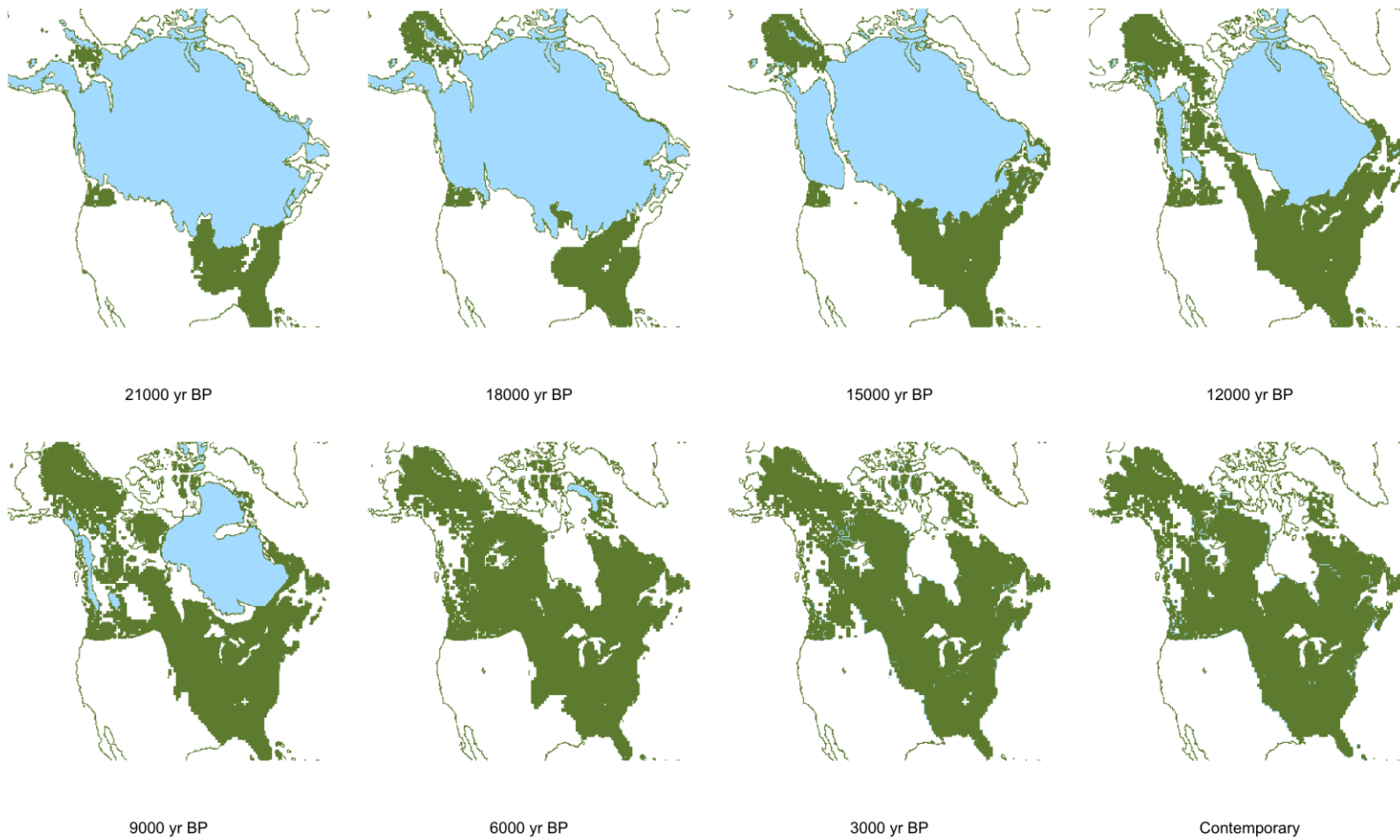


Figure 4.2

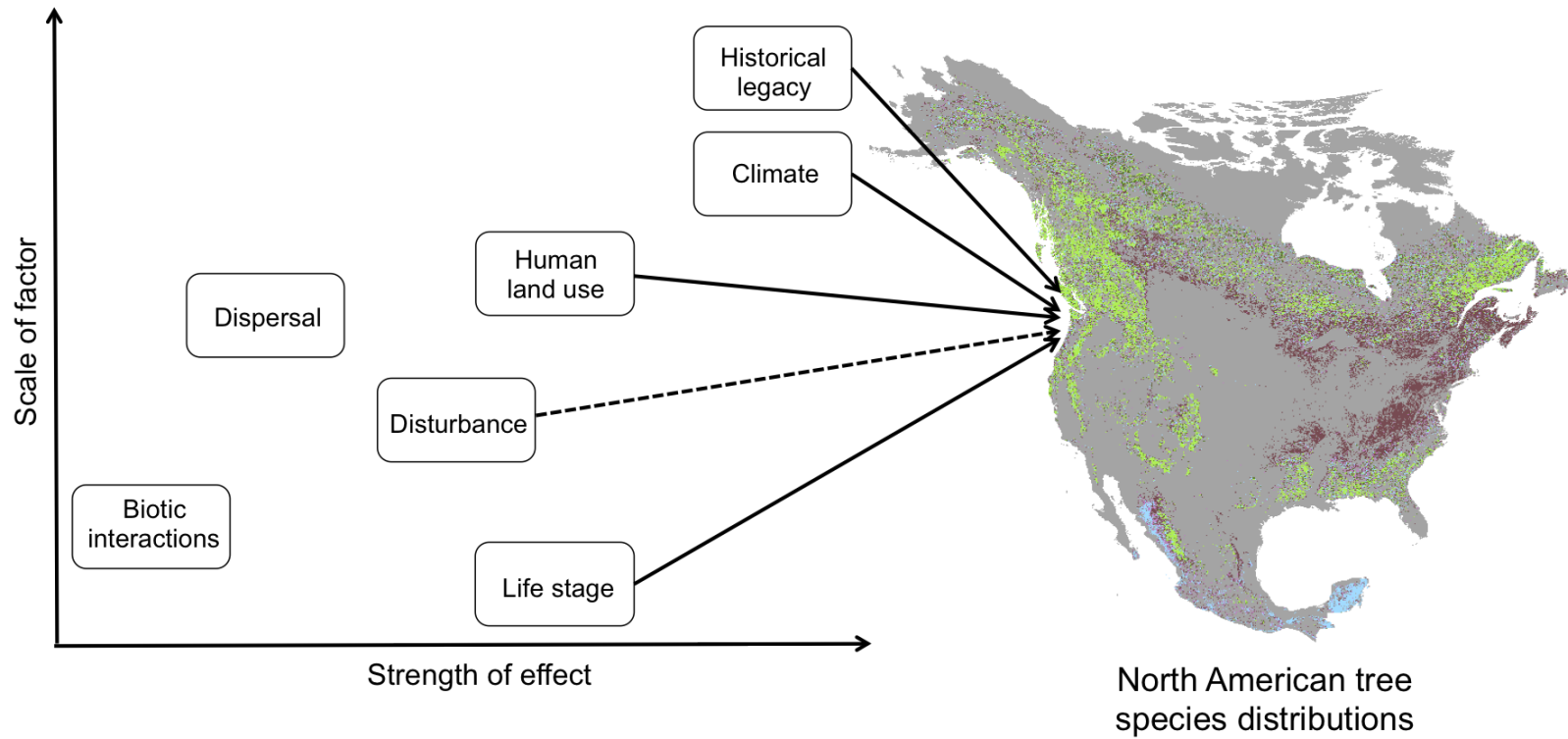


Figure 4.3

CONCLUSIONS

The field of ecology has long recognized the importance of both biotic and abiotic factors to species composition patterns. Efforts to understand variation in the relative effects of these factors across spatial scales have recently benefited from the availability of large data sets and the development and application of increasingly sophisticated modeling techniques. Still, the scale-dependencies of ecological factors have remained unclear for many species and systems. In this research, I have utilized modern statistical modeling techniques to analyze the relative contributions of climate and interactions among tree species to both species growth variation at the local scale and species occurrence patterns at the regional scale. In Chapter one, I showed that climate has an overwhelming influence on patterns of species growth variation along montane ecotones, indicating that interspecific interactions among some co-occurring species may be weak, even at local scales. In Chapter two, I established the importance of carefully scrutinizing and testing modeling approaches, and the necessity of ensuring that models are fit for their intended purpose. Specifically, I demonstrated that community-level models, which have been put forth as a method to account for species interactions, are unable to appropriately capture co-occurrence patterns of Rocky Mountain tree species due to important statistical limitations. As an alternative to the community-level modeling approach, I used a Joint Species Distribution model in Chapter three to evaluate the relative contributions of environmental responses and species interactions to co-occurrence patterns of Rocky Mountain tree species. This analysis revealed the overriding influence of climate and shared environmental responses of species on co-occurrence patterns and the relatively small role of interactions among tree species. Taken together, these findings indicate that Rocky Mountain tree species respond predominantly

to climate, both at local and regional scales, and that interactions among tree species may not be an important structuring force of species composition patterns in Rocky Mountain forests.

In Chapter four, I review the available literature to propose a coherent conceptual framework that explains the factors controlling the distributions of North American tree species. Here, I argue that historical context is necessary to understand contemporary distribution patterns. North American tree species, including the Rocky Mountain species that are the subjects of Chapters one through three, have evolved within a context of strong climatic fluctuations. The overwhelming influence of climate on past distributions has left an imprint on contemporary distributions, which do not appear to be consistently or strongly constrained by biotic interactions or dispersal limitation. I propose that human land use and life stage are likely factors explaining the disequilibrium of some species with climate.

Figure 1 represents a revision to the proposed hierarchy of Pearson & Dawson (2003), presented in the Introduction, and summarizes the scales at which particular ecological factors have a discernable impact. This figure has been revised to reflect the insight gained from the research presented in this dissertation. This figure is presented with the recognition that many ecological factors and scales have not been directly analyzed in this work, and the effects in such contexts are a continual research frontier that is being pursued by many ecologists working across a wide range of ecological systems. This dissertation in particular suggests that the effects of biotic interactions among Rocky Mountain tree species are weak and have little influence at both the local and regional scale (bold dashed arrow). Conversely, climate has an overwhelming influence across these spatial scales (bold solid arrow). Other factors that have not been empirically evaluated here include topography, land use, disturbance and habitat. Based upon other empirical studies presented in the review, I include the hypotheses that disturbance has

discernable impacts at the regional scale in limited contexts, and human land use may have important and large effects at the regional scale (dashed arrows). Greater understanding of the factors underlying species composition patterns will be achieved through additional empirical studies, continued development of novel modeling methods, and insight from multiple taxa and ecological systems. Such work is currently underway, and, along with this research, represents an important contribution to scientific understanding and to the management and protection of biodiversity.

References

Pearson, RG, Dawson, TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12: 361-371.

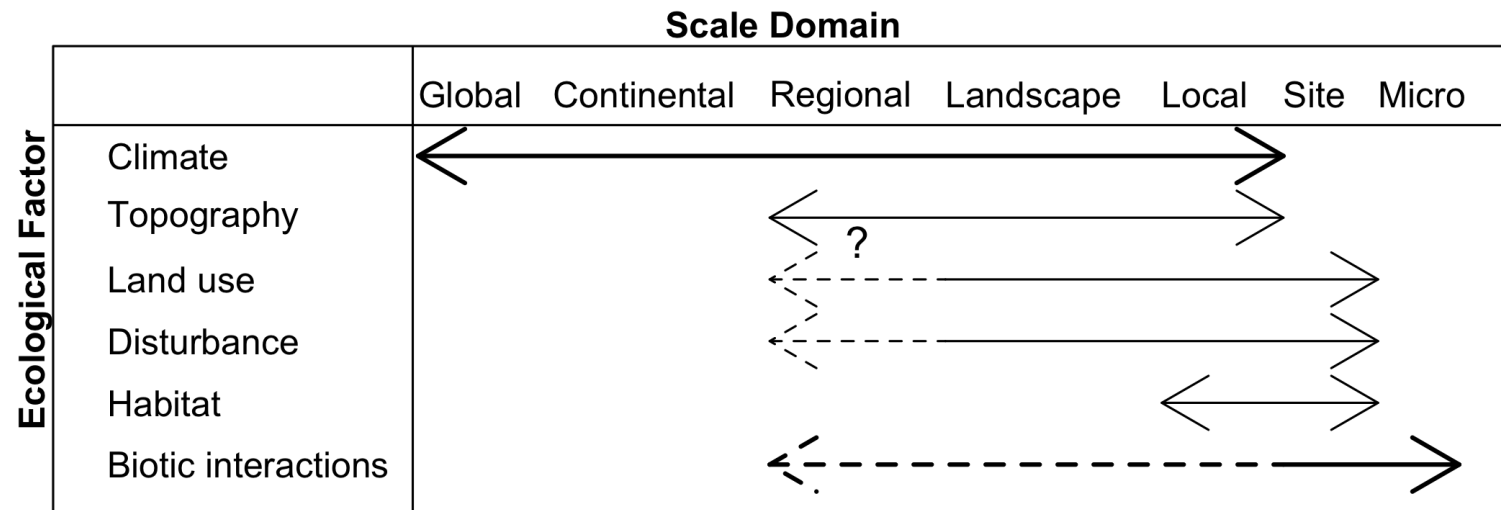


Figure 1