DISSERTATION

FROM GENES TO LANDSCAPES:
THE DISTRIBUTION OF WESTERN CONIFERS

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2013

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ABSTRACT

FROM GENES TO LANDSCAPES: THE DISTRIBUTION OF WESTERN CONIFERS

Managing and conserving forest ecosystems under a rapidly changing climate will require an understanding of the drivers of species distributions across a gradient of temporal and spatial scales. My dissertation research evaluated the relationship between distributional patterns of tree species and the processes driving these patterns from local to continental scales. I addressed three questions: 1) Which local abiotic and biotic processes are most important in determining the distribution of tree species along a hydrologic gradient in southeast Alaska? 2) How is genetic variation partitioned across the range of *Pinus contorta*, and is this variation explained by geographic or landscape variables? 3) How will *Pinus contorta* respond to predicted climate change?

At the local scale, I assessed the role of abiotic and biotic constraints in limiting three tree species (*Pinus contorta, Picea sitchensis,* and *Tsuga heterophylla*) along a hydrologic gradient in southeast Alaska. I used a Bayesian hierarchical model to identify the strongest predictors of species' occurrence and biomass. Model predictions identified abiotic variables, including soil nitrogen, pH, and depth to water, as the primary factors limiting species' success in anaerobic wetland ecosystems. Competition was identified as the limiting factor in aerobic forest ecosystems. At the continental scale, I quantified the impact of historic evolutionary processes in shaping patterns of genetic diversity across the range of *Pinus contorta,* a widespread and morphologically variable species. I estimated gene flow and assessed the effect of the landscape on population structure. Gene flow is high across the range of the species, and patterns of variation are most strongly influenced by landscape barriers to gene flow and the environmental variation associated with its heterogeneous range. This suggests that, despite widespread gene flow, subspecies are adapted to local conditions. I then used correlative and mechanistic species distribution models to evaluate potential, future habitat suitability at the species and subspecies levels of *Pinus contorta*. Model results predict that *P. contorta* will maintain a large portion of its current habitat, but two of the more geographically constrained subspecies will lose a significant portion of suitable habitat.

My work provides an understanding of the ecological and evolutionary processes shaping tree species distributions across a gradient of temporal and spatial scales, from historic to current timeframes and local to range-wide extents. Results from my research show that different processes determine patterns of distribution across this gradient of scales. Linking these patterns and processes will be essential for forest management and conservation in light of a rapidly changing climate.

ACKNOWLEDGEMENTS

This process has been one of the most rewarding and most challenging experiences of my life. Many wonderful people were instrumental in my success. David gave me the opportunity of a lifetime in selecting me for his southeast Alaska project. Over the last four years, he has shown continual support and faith in me - allowing me to pursue the research I was most passionate about, supporting me in my decision to teach each semester, and encouraging me to aim high. I know we will be friends and colleagues for many years to come. Amy took under her wing as I ventured into the world of population genetics and species distribution modeling. I owe her a mountain of gratitude for the many hours she spent talking me through things and challenging me to be the best scientist that I could be. Dan provided countless hours of scientific discourse, mentoring, and sound advice. He facilitated my growth as an instructor by giving me freedom, support, and opportunities to find my voice and my style. I am especially grateful for the last-minute meetings that gave me the confidence to succeed in my interview and my dissertation. Jason reminded and inspired me to be passionate about forest ecosystems. Our multi-hour conversations infused me with desire to explore, ponder, and question the incredible complexity of these natural systems. I also need to thank Skip Smith for believing in me and hiring me to teach many of his courses. These opportunities were essential to my development as an instructor.

A few very special mentors cannot go unmentioned. Paul Alaback inspired and encouraged me to be a forest ecologist. I strive to emulate his passion for the natural world and hope that I too have a twinkle in my eye when I teach about forest ecosystems. Paul has so selflessly offered time, advice, mentorship, and friendship over the last 11 years. He has watched me grow into an ecologist, scientist, teacher, and now professor. Words cannot express how

grateful I am. Tom DeLuca believed in me, funded me, and rooted me from bachelor's to PhD. Dave D'Amore welcomed me into his lab, his home, and his family without batting an eye. Thank you for keeping me out of the rain, well fed, and well loved. Our many conversations these last four years have inspired me and also guaranteed that you are stuck with me for a while.

In the process of collecting data for this work, there were many latitudes crossed, states driven, trees sampled, wells installed, samples processed, and PCRs run. These tasks would have been impossible without the help of many people, including: Kelly Chesus, Kristen Pelz, Michael McInenly, Amber Shanklin, Helen Bothwell, Seema Sheth, John Paul, Becky Chong, Ed Gage, Reid Dihle, and Wes Swaffar. Kristin Marshall was instrumental in running the Bayesian model for chapter 2, providing both brilliance and friendship in the process. John Shaw and Valerie Hipkins of the USFS provided samples, advice, and manpower to my landscape genetics work. Robert Lichvar of the Army Corps of Engineers (CREEL) provided financial support for my southeast Alaska research and education.

Thank you to my dear friends for putting up with me and still loving me these last four years: Kate Cueno, Toni De Santo, Ann Erickson, Michael McInenly, Natalie Meyer, Kristen Pelz, Covey Potter, and Amber Shanklin.

I am especially grateful for my family – Mom, Dad, Danny, and Chickie. Thank you for the unconditional love, the push to find my passion, the freedom to pursue these dreams, the financial and emotional support, and your brilliance. You have truly shaped me, and I am so happy to be yours. Finally, I am thankful for my biggest fan and greatest love, Dan. Words cannot express how grateful I am for your love, patience, tolerance, bike maintenance, and delicious cooking. You are the key to my health and happiness. I am so looking forward to a dissertation-free lifetime together.

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1 Introduction

"*Predicting the fate of forest tree populations in a rapidly changing climate requires the integration of knowledge across biological scales from genes to ecosystems, across spatial scales from seed and pollen dispersal distances to the breadth of species' ranges, and across temporal scales from the phenology of annual developmental cycle traits to glacial and interglacial cycles*."

~ Aitken et al. 2008 ~

Understanding the processes governing the distribution and arrangement of species is a fundamental task of ecological research. Yet despite centuries of research on species distributions, the task of identifying the causes, mechanisms, and consequences of distributional patterns remains a major scientific challenge (Johnstone and Chapin 2003). This task is confounded by species-specific life and evolutionary histories that influence the balance between ecological and evolutionary forces (Wiens and Donoghue 2004, MacDonald et al. 2008). Ecological theory suggests that species' occurrence is determined by abiotic and biotic constraints on dispersal, germination, and success (Hutchinson 1957, Whittaker et al. 1973, Wiens and Donoghue 2004). These factors limit species to a specific set of environmental conditions and determine local landscape patterns. Evolutionary theory states that natural selection and gene flow are the primary factors controlling a species' response to ecological constraints and determine distributional patterns over large spatial scales (Mayr 1963, Slatkin 1987, Holt 2003). The interplay of these ecological and evolutionary processes creates a complex pattern of geographic variation in species' occurrence, distribution, and population connectivity (Slatkin 1987).

Tree species are some of the most widely distributed and highly valued species worldwide, playing foundational roles in ecosystem function and providing countless services (Aitken et al. 2008). Over the last 150 years, forests have been subjected to considerable anthropogenic disturbance, fragmentation, and loss. Simultaneously, climate change has altered local and regional habitat conditions, and there is substantial evidence that recent changes have already affected the distribution of many forest species (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006). During the 21st Century, warming is anticipated to occur at a faster rate than during any recent ice-free era (Huntley 1991, Walther et al. 2002, Field 2007). Further changes in climate may leave tree species especially vulnerable, as the rate of change may be too rapid for the long generation times of these species (Davis and Shaw 2001, Hamrick 2004). In order to properly manage and conserve forested ecosystems under a rapidly changing climate, we must first gain a better understanding of the drivers of species distributions across a gradient of spatial and temporal scales (Millar et al. 2007, Aitken et al. 2008).

My dissertation research investigated the ecological, biogeographic, and evolutionary processes that drive tree species' distributions across a gradient of temporal and spatial scales. My work provides an understanding of the ecological and evolutionary processes shaping distributions from historic to current timeframes and across local to range-wide extents. I addressed the following questions: 1) Which local abiotic and biotic processes are most important in determining the distribution of tree species along a hydrologic gradient in southeast Alaska? 2) How is genetic variation partitioned across the range of *Pinus contorta*, and is this variation explained by geographic or landscape variables? 3) How will *Pinus contorta* respond to predicted climate change?

Chapter 2 evaluates patterns of tree species distributions along a hydrologic gradient in southeast Alaska. Across an ecological gradient, biotic interactions may limit a species' distribution under more favorable conditions, while its physiological tolerance of abiotic conditions may determine its distribution under more stressful conditions (Weiher and Keddy 1999, Wilson 1999, Rand 2000, Sanderson et al. 2008). Species respond to local abiotic and biotic stressors in different ways, and explaining how some species can occupy wide environmental gradients while others cannot is central to describing species' distributions and identifying environmental niches (Jackson et al. 2009). In southeast Alaska, three tree species (*Pinus contorta* ssp. *contorta, Picea sitchensis,* and *Tsuga heterophylla*) vary in occurrence and abundance across a distinct hydrologic gradient. I used this hydrologic gradient to test the theory that abiotic constraints limit species at the more stressful end of an ecological gradient, while biotic constraints limit distributions under more favorable conditions.

Chapter 3 is a landscape analysis of population structure across the range of *Pinus contorta*, one western North America's most widely distributed conifers. Many tree species have extensive ranges that occur over a broad range of environments. Heterogeneity in landscape and environmental conditions can create sharp boundaries between populations, shaping gene flow and patterns of population structure. Widespread, morphologically-variable species provide a natural experiment for evaluating the role of ecological and evolutionary processes in shaping the distribution of a species, particularly the role of gene flow in determining variation among populations and across environmental gradients (Latta 2004). *Pinus contorta* is divided into four morphologically and geographically distinct subspecies (ssp. *latifolia, contorta, murrayana*, and *bolanderi*) (Critchfield 1957). Each subspecies grows in a discrete portion of the species' range and is hypothesized to be adapted to local environmental and climatic conditions (Ying and

Liang 1994, Rehfeldt et al. 1999, 2001). We have little knowledge on the effect of the landscape on variation within the species and among subspecies. In this chapter, I used landscape genetics to quantify population structure across the range of *Pinus contorta.* I hypothesized that populations are connected by long-distance gene flow, possessing high within- but low among-population genetic variation, and that the landscape influences patterns of genetic differentiation.

Chapter 4 is an analysis of potential habitat suitability for *Pinus contorta* under both current and future climate conditions. Climate change has the potential to alter the composition and distribution of western forests (Aitken *et al.* 2008). Species may be forced to adapt or migrate to track suitable habitat, with long-lived, immobile tree species left especially vulnerable to habitat loss. All tree species are expected to experience lags in their response to changing climate (Clark 1998, Davis and Shaw 2001, Malcolm et al. 2002, Aitken et al. 2008). Identifying the habitats under which tree species may persist will be essential for forest conservation and management (Wang et al. 2010, Mimura and Aitken 2010). The goal of this research was to evaluate how ongoing climatic change might alter the distribution of *Pinus contorta*. I used correlative and mechanistic models to evaluate potential, future habitat suitability at the species and subspecies levels. My main objectives were to 1) make predictions of habitat suitability across this widespread tree species and 2) examine whether incorporation of the distribution and physiological tolerance of each subspecies altered predictions of suitability.

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2 The role of abiotic and biotic factors in determining patterns of tree species' distributions across a distinct hydrologic gradient in southeast Alaska

2.1 Introduction

Describing species' environmental niches requires an understanding of the influence of abiotic and biotic factors in determining a species' local distribution, but the relative importance of abiotic versus biotic constraints remains highly disputed (Simberloff et al. 1999, Martin 2001, Laughlin and Abella 2007). Failure to physiologically cope with abiotic conditions can lead to a species' absence from an ecosystem (Cooper 1982, Tilman 1982, Vince and Snow 1984, Chase and Leibold 2003, Sanderson et al. 2008). Competition, on the other hand, may better explain a species' presence or absence from an ecosystem (Hardin 1960, Keddy 1989, Grime 2002, Callaway et al. 2011). Strong competitors may dominate in less stressful habitats and displace poorer competitors to less favorable habitats (Hardin 1960, Keddy 1989, Sanderson et al. 2008). It is unlikely, however, that species experience landscapes as a binary mosaic of suitable and unsuitable habitat but instead as complex gradients of abiotic and biotic stressors (McIntyre and Barrett 1992, Manning et al. 2004, McGarigal and Cushman 2005).

Across an ecological gradient, biotic interactions may limit a species' distribution under more favorable conditions, while its physiological tolerance of abiotic conditions may determine its distribution under more stressful conditions (Weiher and Keddy 1999, Wilson 1999, Rand 2000, Sanderson et al. 2008). While some species are constrained to a narrow range of conditions, others may tolerate a broader range of conditions and have little habitat specificity (Baltzer et al. 2007). Species respond to local abiotic and biotic stressors in different ways, and explaining how some species can occupy wide environmental gradients while others cannot is central to describing species' distributions and identifying environmental niches (Jackson et al. 2009).

In southeast Alaska, plant communities vary across distinct hydrologic gradients that develop from geologic history, topography, and a recent history of glaciation. The region is dominated by coastal, temperate rainforest with an abundance of peat-forming ecosystems. Four ecosystem types represent the vegetation and appear closely tied to topographic position and depth to groundwater (D'Amore et al. 2012). These four types are distinguishable by vegetative structure and are classified as (Cowardin et al. 1979): palustrine emergent wetland (PEM), palustrine scrub-shrub wetland (PSS), palustrine forested wetland (PFO), and upland (U). Three tree species (*Pinus contorta* ssp. *contorta, Picea sitchensis,* and *Tsuga heterophylla*) vary in their occurrence and abundance along this hydrologic gradient. *Pinus contorta* (Douglas Ex. Louden) ssp. *contorta* (shore pine) grows only in PEM and PSS sites, whereas *Picea sitchensis* (Bong. (Carr.)) (Sitka spruce) occurs only on steeper forested wetland and upland sites. *Tsuga heterophylla* (Raf. (Sarg)) (western hemlock) grows in all ecosystem types along this gradient. Hydrologic regime is thought to be a driving force behind tree species distributions in this region (Zoltai and Vitt 1995, Asada et al. 2003), but it is unlikely that plant community distributions are simply reflections of differences in water table depth and dynamics. Distinctive environmental conditions and biotic interactions strongly influence the distribution of *P. contorta, P. sitchensis,* and *T. heterophylla,* but the relative contribution of each in determining species' occurrence and abundance is unknown for specific ecosystems types and likely varies across different spatial scales.

I used this hydrologic gradient in southeast Alaska to test the theory that abiotic constraints limit species at the more stressful end of an ecological gradient, while biotic constraints limit distributions under more favorable conditions. I hypothesized that abiotic constraints, specifically depth to groundwater and soil nutrients, limit *P. sitchensis* and *T. heterophylla* growth in more stressful PEM and PSS wetlands, while competition excludes *P. contorta* from PFO and U sites. This hypothesis would be rejected if I found that perennially saturated, nutrient-poor conditions of PEM and PSS sites do not limit the occurrence and abundance of *P. sitchensis* and *T. heterophylla*; that *P. sitchensis* and *T. heterophylla* do not competitively exclude *P. contorta* from forested and upland sites; and that all species respond to the same driving factors.

2.2 Methods

Study Region

This study was conducted in the vicinity of Juneau, Alaska, USA, in the north-central portion of the Alexander Archipelago (58°26’40”N, 134°13’47”W). This region is bounded by the Juneau Icefield to the east and the Lynn Canal to the west (Kelly et al. 2007). Oceanic climate, glacier runoff, and a recent history of glacial recession strongly influence local climate and environmental conditions. Regional climate is hypermaritime, consisting of mild, wet winters and cool, wet summers (Carrara et al. 2007). Juneau’s mean annual precipitation is 150 cm but can exceed 225 cm, with rain falling an average of 230 days a year (Carrara et al. 2007, Kelly et al. 2007).

The study area landscape transitions from the Pacific Ocean into steep glaciated mountain ranges. This ocean to mountain gradient includes glacier-fed rivers, *Sphagnum* species-dominated peatlands, and conifer forests (Alaback 1982, DellaSala et al. 2011). Palustrine (PEM, PSS, PFO) and upland (U) sites are the most commonly mapped wetland communities within the region, occurring along a distinct hydrologic gradient and characterizing valley bottoms within southeast Alaska (U.S. Department of Agriculture (USDA) 1997, Fellman and D'Amore 2007). Palustrine sites include all non-tidal wetlands that are dominated by trees, shrubs, herbaceous plants, or emergent mosses and are bounded by uplands (Cowardin et al. 1979). The terms emergent, scrub-shrub, and forest denote the dominant plant life form's influence on habitat structure. Soils of PEM, PSS, and PFO sites are highly developed peatlands (1 – 4 m peat depth) and Spodosols (D'Amore et al. 2012); glacial till is common within the top meter of the soil profile on upland sites and greatly influences drainage conditions (Swanston 1969, Collins 1974, Alaback 1982).

Site Selection and Installation

I used the National Wetland Inventory (NWI) classification system (Cowardin et al. 1979) to stratify the Juneau region into commonly mapped ecosystem types. Sites were preliminarily distinguished in ArcGIS 9.2 (ESRI, Redlands, CA) and classified as PEM, PSS, PFO, or U. Study sites were randomly selected for each ecosystem type using the Generalized Random-Tessellation Stratified (GRTS) selection process. This spatially balanced, probability-based survey was implemented in R 2.9.2 (R Core Team 2008) using the *spsurvey* package, the GRTS function, and equal probability selection (Stevens and Olsen 2004, Detenbeck et al. 2005; Kincaid 2008). It allowed for variable inclusion probabilities, sample frame inaccuracies, a temporal sampling design, and uneven spatial densities for variables of interest (Stevens and Olsen 2004). The GRTS selection process produced a list of randomly dispersed sampling sites for each ecosystem type, while minimizing sampling efforts and retaining the ability to make inferences at the landscape scale.

To verify ecosystem type classification, sites were visited in the order of GRTS selection and excluded if they did not match their mapped NWI classification. Twelve field sites were selected from this list and established across mainland Juneau and adjacent Douglas Island (Figure 2.1), with three replicate sites selected for each of the four ecosystem types (PEM, PSS, PFO, U) (Figure 2.2). This represents a statistical population of inference of about 1200 km^2, but I expect the factors driving species distributions in this population would be similar across a larger spatial extent of similar ecosystems in the region.

To capture within-site variation in the potential driving factors, each site was stratified by differences in topography, and four sampling units were selected in each site. One groundwater-monitoring well was installed at each sampling unit and used as a plot-center for data collection. The following data were measured in each plot: elevation, aspect, slope, landform position, and presence/absence of each tree species (Table 2.1). The relevé sampling method was used to collect percent cover data on all vascular plant and moss species occurring on each site (Knapp 1984). Additional data collection and analysis was conducted within a nested, hierarchical sampling design, which encompassed three spatial scales: ecosystem type ($n_{types} = 4$), site (n_{sites} = 4 ecosystem type x 3 replicates = 12), and groundwater monitoring well plots (n_{wells} = 12 sites x 4 wells per site = 48). These scales were chosen to capture variability in the effects of abiotic and biotic factors on tree species occurrence and abundance. To address my hypotheses, I collected the following data over a four-year study period: occurrence and abundance of each tree species, depth to groundwater, pH, soil nitrogen, and light availability.

Tree Occurrence and Abundance

Tree occurrence and abundance were measured using a modified version of the USFS Forest Inventory and Analysis (FIA) protocol (USDA Forest Service, 2007; Bechtold &

Patterson, 2005). One 0.1 ha plot was established at each well location, with species and bole diameter measured for each live tree. Trees < 10 cm in diameter were tallied by mid-point diameter class (0 – 2.5, 2.5 – 5, 5 – 10), while trees greater than 10 cm were sampled for diameter at breast height (DBH). Tree abundance was derived from diameters and defined as the total aboveground tree biomass per unit area. The biomass regression equation used was as follows (Jenkins et al., 2003):

$$\mathrm{bm} = \mathrm{Exp}\,(\beta_0 + \beta_1 \ln \mathrm{dbh}) \tag{2.1}$$

where bm is total overstory biomass (kg dry weight), dbh is diameter-at-breast-height (cm), and $\beta_0 + \beta_1$ are species-specific parameters. Plot-level biomass was calculated for each species by summing individual tree biomass values and estimating values at the site-level (Jenkins et al. 2003). Biomass values were then converted to per unit area values (expressed in Mg/ha).

Groundwater Monitoring

Depth to groundwater was assessed using four monitoring wells per site to quantify temporal and spatial variation in water table levels and identify differences within and among sites. Wells were constructed from 3.8-centimeter (cm) diameter, fully-slotted, schedule-40 PVC pipe and installed to a maximum of one meter below the soil surface using a hand auger. From May through August, depth to the water table was manually measured bi-weekly. The distance from the top of the well casing to the water table was recorded using a measuring tape and confirmed with an electronic tape. Pressure transducers were installed in select wells to record hourly water table depth and monitor fine-scale variation in groundwater fluctutation, using *In Situ* level troll 100 loggers (Fort Collins, CO). Logger data was corrected for barometric pressure by using barometric pressure logger data and adjusting for elevation. Values for depth to water table were summarized into annual and growing season values of maximum water table depth, minimum water table depth, mean depth to water, and number of growing season days when the water table was within the rooting zone (>-20 cm, Coutts and Philipson 1978, Wang et al. 2002). The growing season was defined as the 138-day period between May 15th and September 30th (NOAA/NWS Juneau, Alaska). Groundwater pH was measured in each well using an Orion 3 star pH meter; growing season pH was measured multiple times during this four-year study, and mean values were used for analysis.

Soil Nitrogen

Extractable soil nitrogen (N) was quantified as the sum of ammonium and nitrate in 0-15 cm depth cores (Fellman and D'Amore 2007). Samples were collected three meters north of each monitoring well, with replicate samples extracted to capture intra-site variation in N availability. A 10-cm diameter PVC pipe was inserted into the soil surface to a depth of 15 cm from the top of the O horizon. All plant roots were cut away from the core, leaving an intact core of known depth, diameter, and volume (for detailed methods, see Hart et al. 1994). Cores were immediately placed in a gallon zip seal plastic bag, kept cool on ice, and returned to the lab for analysis. One bulk density sample was also collected per site. Large blocks were cut from the soil and taken back to the lab. Subsamples of 1.25 mL were extracted from each block and dried to a constant weight. Bulk density was calculated based on this dry weight and expressed in Mg/m^3. All samples were processed and analyzed within 48 hours of collection.

Samples were extracted following the procedure described in Robertson et al (1999). Duplicate 15 g portions of each sample were mixed with 100 mL of 1.0M KCl in 120 mL Falcon specimen cups. Samples were shaken for 1 minute on a shaker table, left to sit overnight, and shaken again for 1 minute the following morning. After settling for at least 45 minutes, the supernatant in each specimen cup was drawn into a large syringe through a Whatman GF/D filter. Three laboratory replicates were split among 20 mL scintillation vials and kept on ice until analyzed. All extracted sub-samples were analyzed for dissolved NO_3-N (nitrate) and NH_4-N (ammonium) by flow-through colorimetry at the University of Georgia analytical laboratory.

Light

Light available for germination under the forest canopy was measured using hemispherical photographs. Canopy photographs were taken at each monitoring well using a Nikon Coolpix 3000 digital camera equipped with a FC-E8 21x fisheye lens. Photographs were taken over a two day period using the following protocol: under overcast conditions, 1 m above ground surface, top of lens oriented to true North, and with tripod legs adjusted to draw lens parallel to canopy. Images were processed using Gap Light Analyzer (GLA) version 2.0 (Frazer et al. 1999). GLA settings were adjusted to account for image orientation, geographic location (latitude and longitude), elevation, and time of year. Images were first transformed to black-and-white. Image pixels were then separated into sky versus foliage using the threshold procedure. Each photograph was analyzed twice to reduce error associated with threshold distinctions. Total light transmission, the fraction of light reaching the ground relative to the light above the canopy, was derived in GLA according to Frazer et al (1999).

Statistical Analysis

I used a Bayesian hierarchical modeling approach to assess the relative importance of local abiotic and biotic variables in determining the occurrence and abundance of *Pinus contorta,* *Picea sitchensis,* and *Tsuga heterophylla* across different spatial scales. Prior to modeling, I ran preliminary analyses to examine the relationship between tree abundance and each abiotic variable. All analyses were implemented using R 2.15.2 (R Core Team 2012). First, I examined the dataset for well- and site-level spatial autocorrelation and for correlations among predictor variables. To test for spatial autocorrelation in tree species occurrence and abundance, I used the *spdep* package to compute *Moran's I* and *Geary's C.* Canonical correspondence analysis (CCA) was employed to test the effects of abiotic variables on the composition and structure of the vegetation (understory and overstory) and to identify any environmental gradients within the dataset. I ran principal components analysis (PCA) on all potential predictors to reduce model parameters to a set of minimally correlated variables (correlation < 0.65). Initial assessments of covariance suggested that the relationship between tree abundance and depth to groundwater was quadratic for *P. sitchensis* and *T. heterophylla*. Values were transformed into quadratic terms, and both linear and quadratic terms were used in the abundance model. Incorporation of this quadratic term suggests that biomass is highest at an optimal range of depth to groundwater, with a decline in biomass above or below this range. The final set of predictors included: depth to groundwater (linear and quadratic terms), pH, light, soil N, and biomass of other species.

Descriptive statistics and one-way Analysis of Variance (ANOVAs) were used to examine significant differences in potential predictors across ecosystem types. Separate generalized linear models (GLM) were run for species occurrence and abundance to preliminarily identify the variables potentially explaining patterns of distribution. Model selection and Akaike Information Criterion Scores (AIC) were used to evaluate the strength of the models. The model with the lowest AIC score was identified as the model best explaining the data (Burnham and Anderson 2002). The significance of selected predictors were considered and compared against Bayesian model results.

A Bayesian hierarchical generalized linear mixed model (GLMM) was used to assess the relative importance of abiotic and biotic factors in determining tree species' occurrence and abundance (Diez and Pulliam 2007). The model specifically detected any effects of depth to groundwater, pH, nitrate-N, ammonium-N, light, and competition on forest composition and structure. The hierarchical structure of this model allowed for predictions across the three spatial scales (well, site, and ecosystem type) and explicitly accounted for uncertainty associated with any random effects. Separate models were developed for predicting occurrence and abundance of the region's three tree species (*P. contorta, P. sitchensis, a*nd *T. heterophylla*).

The occurrence of each species was modeled under a binary Bernoulli process, $Y_{ij} \sim$ Bernoulli (ϕ_{ij}), where Y_{ij} represents species occurrence at each well *i* in each site *j*, and ϕ_{ij} is the estimated probability of occurrence at each well. For each species, estimated probabilities of occurrence at each well location were related to abiotic and biotic linear predictors as

$$\log\left(\frac{\phi_{ij}}{1-\phi_{ij}}\right) = \alpha_j + \sum_{m=1}^{M} \beta_m \mathrm{X}_{mi} \tag{2.2}$$

where α_j is a site level random intercept term, β_m are *M* regression coefficients, and X_{mi} are well-level abiotic and biotic data. Maximum depth to groundwater (cm), nitrate-N, ammonium-N, and transmitted light (%) were included as potential abiotic predictors. Light was used as a surrogate variable for the biotic effects of competition on species' occurrence.

The abundance of each species was modeled under a Normal distribution, Y_{ij}, where Y_{ij} represents species abundance at each well *i* in each site *j.* For each species, estimated probabilities of abundance were related to abiotic and biotic linear predictors as

$$\mu_{ij} = \alpha_j + \sum_{m=1}^{M} \beta_m \mathrm{X}_{mi} + \rho_i + \sigma_r^2 \tag{2.3}$$

with variables defined as in Equation 2.2. In this model, random effects for site and ecosystem type, ρ_i, were included as normal random variables, such that $\rho_i \sim Normal(0, {\sigma_t}^2)$ where $\sigma_t$represents the variance among ecosystem types. Nitrate-N, ammonium-N, pH, and both linear and quadratic terms for depth to groundwater (cm) were included in the model as potential abiotic predictors. Maximum depth to groundwater (cm) was used in the *P. contorta* and *P. sitchensis* models; minimum depth to water (cm) was used as the water table predictor variable in the *T. heterophylla* abundance model. Biomass of other tree species (Mg/ha) was used as a surrogate variable for the biotic effects of competition on species' abundance (Waring and Running 2010). Inclusion of biomass was assumed to be a reasonable substitute for the effects of competition (e.g. *P. sitchensis* and *T. heterophylla* biomass was included in the *P. contorta* abundance model).

To allow the data to drive predictions, all models were fit using flat, non-informative priors (Gamma (0.01,0.01) for inverse residual variance, Normal (0,100) for regression coefficients, and uniform (0, 10) for random effects) (Gelman 2006). All continuous covariates were standardized and modeled at the plot level. Random intercepts at the site and ecosystem type levels represent higher levels of the hierarchical model. Model parameters were estimated in R 2.15.2 using Jags (Plummer 2011). Markov Chain Monte Carlo (MCMC) runs used a Gibbs sampler to generate posterior prediction means of model parameters. I ran 80,000 iterations with a burn-in of 70,000 on three chains, which allowed autocorrelation in each chain to drop below 0.1 after 10 iterations and the Gelman-Rubin statistic to drop below 0.1. I used posterior estimates from the MCMC model runs to identify the abiotic and biotic variables driving the occurrence and abundance of each tree species (*P. contorta, P. sitchensis,* and *T. heterophylla*). I estimated a Bayesian R^2 at each level of the model in order to quantify the proportion of variance explained across this hierarchical scale. Both marginal and conditional R^2 were calculated using the medians of the parameter posteriors; marginal R^2 includes the variance explained by fixed effects, while conditional R^2 includes the proportion of variation explained by both fixed and random effects (Nakagawa and Schielzeth 2013). I also calculated variance partition coefficients (Goldstein et al. 2002) to identify the partitioning of unexplained variation across this hierarchical sampling schema.

2.3 Results

Spatial correlation was minimal across the levels of inference, with *Moran's I* falling close to 0 and *Geary's* C close to 1 at the well ($I = 0.03$, $p = 0.07$; $C = 0.94$, $p = 0.08$) and site ($I = -0.12$, $p = 0.10$; $C = 1.05$, $p = 0.10$) levels. Incorporation of spatial analysis into the predictive model was unnecessary. Canonical correspondence analysis (CCA) identified pH (eigenvalue = 0.974, $p<0.005$), nitrate-N (0.935, $p<0.005$), and light (0.993, $p<0.001$) as the main correlates of plant community composition and the local environmental gradient (Appendix 2.1, Figures A.2.1 & A.2.2). The relationships between plant communities and environmental variables drove clustering of the PFO and U sites. The first canonical correspondence axis arranged the PEM and PSS sites opposite the PFO and U sites, but the PEM and PSS sites did not cluster together along the second axis. Distinct community composition and differences in environmental variables separate these sites across the second canonical axis. The first and second canonical axes explained 75% of the total variation, and a global permutation of the data was highly significant ($p<0.001$).

Descriptive statistics revealed differences in mean values of abiotic and biotic variables across sites and ecosystem types (Table 2.2 and Figure 2.4). Mean annual depth to water was highly variable and significantly different among ecosystem types (Figure 2.3, $p < 0.001$). Over the four-year sampling period, the water table of PEM and PSS sites rarely dropped below the plant rooting zone (top 20 cm, Coutts and Philipson 1978, Wang et al. 2002), while the water table in the U sites never reached the rooting zone (Table 2.2). The water table was within the rooting zone in PEM and PSS sites for an average of 121 (±10) and 102 (±30) days of the 140 day Juneau growing season A water table near the soil surface, low pH, and minimal overstory biomass accumulation were identified as distinctive characteristics of PEM and PSS sites (Table 2.2 and Figure 2.4). Minimal forest canopy cover develops on these ecosystem types. Plants grow under high light conditions and in the absence of competition from dominant overstory trees. *Pinus contorta* is the dominant tree, and *T. heterophylla* occurs as a minor component. *Picea sitchensis* is absent from all emergent and scrub-shrub wetlands, with the exception of one PSS site (Eagle PSS, Table 2.2). Conversely, a greater depth to groundwater ($p<0.001$), higher pH ($p<0.01$), and greater abundance of overstory biomass ($p< 0.001$) characterize the PFO and U ecosystem types. These sites do, however, differ in depth to water over the course of the growing season. The water table was within the rooting zone in PFO sites for an average of 74 days (±46) during the growing season, but the water table was absent from the rooting zone in the U site (0 of 138 days). *Pinus contorta* is absent from all PFO and U sites. *Tsuga heterophylla* has the highest abundance on all PFO and U sites, but *P. sitchensis* is a dominant overstory tree in both ecosystem types (Table 2.2). ANOVAs detected significant differences in all abiotic variables across ecosystem types (Figure 2.4).

Results from GLM runs were in agreement with results from Bayesian model analysis and are not presented here (See Appendix Tables A.2.1 and A.2.2). In Bayesian modeling, the distributions of *P. contorta*, *P. sitchensis,* and *T. heterophylla* were explained by a distinct set of local abiotic and biotic variables for each species (Figure 2.5). Model runs produced probability estimates for each parameter. If the estimated probability of an abiotic or biotic parameter did not cross zero, it was considered significantly different than zero at the 95% level (Figure 2.5, Appendix Tables A.2.3 and A.2.4). Both the occurrence and abundance of *P. contorta* were explained by variables related to the biotic effects of competition. High light availability was the strongest predictor of *P. contorta* occurrence, while *P. sitchensis* biomass was the strongest predictor of abundance. *Pinus contorta* was positively correlated with percent of transmitted light and negatively correlated with *P. sitchensis* abundance (Figure 2.5; 95% credible interval, CI).

Maximum depth to groundwater was the most influential variable in determining *P. sitchensis* occurrence. The estimation of this parameter does not cross zero (95% CI), and its negative value indicates that *P. sitchensis* occurrence declines when the water table is closer to the soil surface (Figure 2.5). The best predictor of *P. sitchensis* abundance was pH, with a 95% probability that pH is most important in driving abundance of this species across the gradient. For *T. heterophylla*, ammonium-N availability was the strongest predictor of occurrence, with species presence negatively associated with light (95% CI). The importance of ammonium-N in predicting occurrence is more likely an indicator that this species requires greater nutrient availability for establishment rather than it being dependent on the availability of this specific nutrient. Abundance of *T. heterophylla* was best explained by the quadratic transformation of minimum depth to water and pH (Figure 2.5). The significance of this quadratic depth to water term reveals that the abundance of this species' is highest under an optimal range of hydrologic conditions, with abundance declining above and below this optimum range. Positive parameter estimates (Figure 2.5, 95% CI) indicate that this optimal range is associated with a lower water table and a higher pH.

Both the abundance and occurrence models performed well in explaining the distribution of each tree species (Table 2.3). Based on estimates of conditional R^2, the abundance models explained 68, 43, and 45 percent of the variation across all levels of hierarchy for *P. contorta*, *P. sitchensis*, and *T. heterophylla*. The occurrence models were a better fit to the data, with 95, 96, and 95 percent of the variation explained by the full model for *P. contorta*, *P. sitchensis*, and *T. heterophylla* presence (marginal R^2, Table 2.3). Posterior predictions nearly always correctly assigned species' presence and absence (Table 2.3). Overall, these results suggest that the abiotic and biotic parameters modeled explain most of the variation in abundance and almost perfectly explain variation in occurrence of these three species.

The incorporation of site and ecosystem type as random effects allowed for modeling of additional variation within the dataset. Site and ecosystem type estimates varied across these different spatial scales (Figure 2.6). The parameters identified in the Bayesian model analysis (Figure 2.5) were the strongest predictors of tree species' occurrence and abundance at the well level. Model performance at each spatial scale varied across species (Table 2.4). Predictions of *P. contorta* abundance were best explained at the site (12 percent) and well levels (34 percent). Abundance differed within each site as a function of well-level variation in abiotic and biotic variables. The inclusion of random terms indicated that additional factors contribute to the distribution of *P. contorta* at greater spatial scales, as variance was higher between the PEM and PSS ecosystem types (54 percent.) The highest variation in predicted *P. sitchensis* abundance occurred at the well level (64 percent), with abundance better predicted and more comparable at the levels of site and ecosystem type (20 and 16 percent). *Tsuga heterophylla* abundance was consistent across sites (0 percent variance at site level) but highly variable between wells (65 percent) and between ecosystem types (35 percent). These results suggest the importance of abiotic and biotic factors varies across different spatial scales.

2.4 Discussion

A fundamental part of ecological research lies in describing patterns of species' distributions and identifying the processes shaping these distributions. This research is essential for defining a species' niche and understanding a species' response to abiotic and biotic factors. I hypothesized that abiotic constraints, specifically depth to groundwater and soil nutrients, limit growth in more stressful wetlands ecosystems, while competition constrains species in more favorable forested sites. Along a hydrologic gradient in southeast Alaska, abiotic factors are more important in explaining *P. sitchensis* and *T. heterophylla* distributions. A higher water table, lower nutrient availability, and low pH limit the occurrence and abundance of *P. sitchensis* and *T. heterophylla* in wetland ecosystems. Conversely, *P. contorta* is absent from forested sites because of light limitations that are likely driven by competition from other tree species. The probability of a species' occurrence and abundance is functionally related to local environmental variables and its interactions with other organisms. I demonstrated that the distribution of tree species across an ecological gradient is driven by species- and location-specific responses to abiotic and biotic stressors. These results support the theory that abiotic constraints limit some species at the more stressful end of an ecological gradient, while biotic constraints limit the distribution of other species under more favorable conditions.

Ecology of the Hydrologic Gradient

The four ecosystem types (PEM, PSS, PFO, and U) occurring along this gradient were distinctive both in plant community composition and in their environment. Most notably, each site was characterized by a different hydrologic regime (Figure 2.3) that appears to be predominantly driven by topographic position on the landscape (Table 2.1). Emergent and scrub-shrub sites are peatlands that lie at valley toe slopes or occur as raised terraces (D'Amore et al. 2010). Saturated conditions in the rooting zone and low pH are stressful and limiting for many tree species, and these conditions limited the abundance of *P. sitchensis* and *T. heterophylla* in PEM and PSS sites (Lieffers and Rothwell 1986, Conlin and Lieffers 1993a). Forested wetlands and uplands occur on the steeper end of this topographic gradient. The absence of water within the root zone over portions of the growing season appears to allow for the success of *P. sitchensis* and *T. heterophylla* along the steeper portions of this gradient.

Site hydrologic regime plays an integral role, but it acts in concert with other abiotic and biotic variables factors to determine the success and distribution of each tree species (Yu and Ehrenfeld 2010). Nutrient availability and site pH are also a function of a site's topographic position on the landscape and are controlled largely by hydrologic inputs (Rochefort et al. 2012). Sites receiving groundwater that has interacted with mineral soil have higher mineral concentrations and are less acidic than those isolated from groundwater (Bedford and Godwin 2003). Differences in hydrologic regime and nutrient availability are driving variation in plant community composition and overstory biomass across the four ecosystem types.

Species Distributions

Across the hydrologic gradient, *Pinus contorta* ssp. *contorta* occurs only in the saturated, nutrient-poor conditions of PEM and PSS wetlands. I hypothesized that its absence from PFO and U sites was due to competitive exclusion. This subspecies of *Pinus contorta* is understudied, while research on subspecies *latifolia* has been extensive (Critchfield 1957, Chen et al. 1996, Schoettle and Smith 1999, Rehfeldt et al. 2001). *Pinus contorta* ssp. *latifolia*, the most-widely distributed subspecies of *Pinus contorta* (Critchfield 1957), is documented to be both shade intolerant and a poor competitor (Burns and Honkala 1990). This species is often outcompeted by shade-tolerant species, such as spruce and fir but is documented to tolerate a wide variety of environmental conditions (Lotan and Perry 1983, Muir and Lotan 1985, Lotan and Critchfield 1990). Previous research has also shown that *P. contorta* ssp. *latifolia* is more tolerant of anaerobic conditions and potentially has structures that allow for internal oxygen transport under such conditions (Coutts and Philipson 1978, Conlin and Lieffers 1993a, Wolken et al. 2011). My results conclude that these life history traits are also true for the understudied coastal *P. contorta* ssp. *contorta*, where it grows under the anaerobic conditions of PEM and PSS wetlands but not in the aerobic PFO and U sites. Model results predict *P. contorta* growth across a wide range of local, environmental conditions (Figure 2.5) but only under high light conditions and in the absence of a *P. sitchensis* canopy. My results support the hypothesis that this species is excluded from PFO and U sites by low light conditions and competition, not from a failure to cope with the conditions occurring across this gradient (Lotan and Critchfield 1990, Rehfeldt et al. 1999).

The occurrence and abundance of *P. sitchensis* is greatest on the upper end of this hydrologic gradient, with its abundance explaining the exclusion of *P. contorta* from PFO and U sites (Figure 2.5). *Picea sitchensis* co-occurs with *T. heterophylla* on PFO and U ecosystem types. This species is shade-tolerant but is considered less competitive than *T. heterophylla* (Taylor 1990, Mason et al. 2004). I hypothesized that abiotic stressors limit the occurrence and abundance of this species in PEM and PSS sites. My results suggest that establishment is constrained by anaerobic soil conditions that limit oxygen transport and nutrient availability, supporting prior research on rooting tolerance of *P. sitchensis* and other boreal *Picea* species

(Coutts and Philipson 1978, Lieffers and Rothwell 1986, Conlin and Lieffers 1993b). The species' physiological intolerance of anaerobic conditions explains its absence from the emergent and scrub-shrub wetlands, while response to competition from *T. heterophylla* explains its lower abundance on co-occurring PFO and U sites. The gentle slopes and landscape position of PEM and PSS sites create anaerobic conditions, low pH, and minimal nutrient flow (Chapin et al. 2004, D'Amore et al. 2010); these factors interact to create an inhospitable environment for the establishment and growth of *P. sitchensis.*

Tsuga heterophylla occurs at all sites and in all ecosystem types along this gradient, supporting its broad tolerance of abiotic and biotic conditions. I hypothesized that abiotic stressors, specifically depth to groundwater and nutrient availability, limit the abundance of *T. heterophylla* at the lower end of this hydrologic gradient. Across this hydrologic gradient, *T. heterophylla* presence is best explained by soil nitrogen, and abundance is determined by depth to groundwater and pH. These drivers suggest that *T. heterophylla* is able to establish on sites once its minimum nutrient requirements are met but that its abundance is governed by the interplay between groundwater flow and nutrient availability. To some degree, *T. heterophylla* is able to tolerate the wetland sites, but the anaerobic conditions associated with this landscape position limit nutrient flow, pH, and the subsequent growth of this species. *Tsuga heterophylla* is not limited by biotic interactions along this gradient, but its occurrence and abundance are constrained by the physiological stress associated with a high water table and low nutrient availability.

Plant community composition and abundance often vary as a function of nutrient availability and pH (Bedford and Walbridge 1999, Chapin et al. 2004), and studies have shown that plant community composition is highly correlated to pH (Vitt and Chee 1990, Chapin et al.

2004). Prior wetland research has also identified depth to groundwater and water chemistry as the most important drivers of plant distributions across hydrologic gradients (Vitt et al. 1990, Asada et al. 2003). In southeast Alaska, the occurrence and abundance of *P. sitchensis* and *T. heterophylla* are determined by these same factors – nutrient limitations, pH, and depth to groundwater. One potential explanation for *P. sitchensis* and *T. heterophylla* occurrence on wetland sites, despite sensitivity to a high water table and low pH, is that germination is closely tied to specific environmental and climatic conditions that allow for aerobic conditions in wetland sites. For instance, it is possible that dry summers, as occurred in 2009, result in a water table low enough to allow the germination and establishment of *P. sitchensis* and *T heterophylla* in typically inhospitable PEM and PSS wetlands.

The occurrence and abundance of forest tree species in southeast Alaska is both species- and location-specific. Abiotic factors limit *P. sitchensis* and *T. heterophylla* occurrence in the saturated, nutrient-poor wetlands, while the biotic effects of competition exclude *P. contorta* from the more favorable forested and upland conditions. My models showed that species' occurrence and abundance vary across different scales of analysis but that the factors limiting the distribution of each species' are consistent across increasing spatial scales. This research is one of the first to quantify the drivers of tree species' distributions across a hydrologic gradient and to specifically test the relative importance of abiotic versus biotic factors in determining the growth of these tree species. Collectively, these results highlight the importance of ecological and hydrologic interactions. The feedbacks between abiotic and biotic processes directly shape tree species distributions across different spatial scales and along hydrologic gradients. Understanding the role of each factor and the interactions among processes are essential to describing a species' niche and in determining drivers of its distribution.

Table 2.1: Descriptions of each site in Juneau, Alaska, including ecosystem type, location, landscape features, and tree species' occurrence (0/1). PICO = *Pinus contorta* ssp. *contorta,* PISI = *Picea sitchensis,* and TSHE = *Tsuga heterophylla.*

Site Name	Ecosystem Type*	Latitude	Longitude	Elevation (m)	Aspect	Slope	Landform Position	PICO Presence (0/1)	PISI Presence (0/1)	TSHE Presence (0/1)
FAA	PEM	58.33578	-134.56222	52	North	0	flat lowland	1	0	1
Water Tower PEM	PEM	58.27284	-134.42079	211	North	5	sloping lowland	1	0	1
Ski Area Fen	PEM	58.28849	-134.53043	278	West	10	sloping lowland	1	0	1
Eagle River PSS	PSS	58.52952	-134.81861	11	Southeast	0	flat lowland	1	1	1
Water Tower PSS	PSS	58.27801	-134.41075	130	South	0	sloping lowland	1	0	1
Mt Jumbo	PSS	58.26144	-134.38673	203	North	0-5	sloping lowland	1	0	1
Tee Harbor	PFO	58.42273	-134.75595	48	West	5-10	smooth hillslope	0	1	1
Fish Creek	PFO	58.32709	-134.56751	61	South	5	sloping lowland	0	1	1
Ski Area PFO	PFO	58.28835	-134.52925	306	West	15	smooth hillslope	0	1	1
Eagle River U	U	58.41010	-134.61721	52	South	20	smooth hillslope	0	1	1
Peterson	U	58.48095	-134.77828	77	North	20	smooth hillslope	0	1	1
Sheep Creek	U	58.26595	-134.32890	122	Southeast	20	mountain	0	1	1

* PEM = Palustrine Emergent Wetland, PSS = Palustrine Scrub Shrub, PFO = Paulstrine Forested Wetland, U = Upland

Table 2.2: Mean and standard error **(± SE) of** abiotic and biotic characteristics of each study site, including species abundance, depth to groundwater, pH, soil nitrogen, and percent transmitted light. PICO = *Pinus contorta* ssp. *contorta,* PISI = *Picea sitchensis,* and TSHE = *Tsuga heterophylla.*

Site Name	Ecosystem Type*	PICO Abundance (Mg/ha)	PISI Abundance (Mg/ha)	TSHE Abundance (Mg/ha)	Mean Annual Depth to Water (cm below surface)	Mean Growing Season Depth to Water (cm below surface)	Mean Growing Season Days Depth to Water >-20 (cm)	Groundwater pH	NH_4 (ug/g)	NO_3 (ug/g)	Transmitted Light (%)
FAA	PEM	17.67 (± 0.62)	0	0.53 (± 0.14)	6.25 (± 3.70)	12.76 (± 2.79)	123 (± 7)	4.12 (± 0.05)	14.71 (± 1.2)	10.87 (± 1.28)	96.19 (± 0.33)
Water Tower PEM	PEM	27.86 (± 2.40)	0	3.37 (± 2.24)	5.32 (± 1.73)	5.61 (± 1.12)	123 (± 15)	4.92 (± 0.12)	28.81 (± 10.76)	12.99 (± 7.00)	83.85 (± 6.57)
Ski Area Fen	PEM	6.97 (± 2.52)	0	1.29 (± 0.44)	7.22 (± 4.30)	16.04 (± 1.27)	117 (± 8)	4.81 (± 0.03)	16.53 (± 2.31)	15.14 (± 3.61)	80.01 (± 5.06)
Eagle River PSS	PSS	2.71 (± 1.42)	4.27 (± 0.96)	3.97 (± 1.41)	14.64 (± 3.65)	20.98 (± 2.14)	64 (± 13)	4.35 (± 0.07)	17.84 (± 6.53)	24.04 (± 6.03)	86.94 (± 1.40)
Water Tower PSS	PSS	48.41 (± 0.84)	0	2.52 (± 0.62)	11.07 (± 5.4)	21.61 (± 1.98)	109 (± 3)	4.57 (± 0.06)	10.58 (± 2.73)	13.05 (± 3.86)	57.49 (± 7.44)
Mt Jumbo	PSS	37.35 (± 2.80)	0	4.48 (± 0.81)	4.66 (± 3.10)	5.47 (± 2.53)	132 (± 8)	4.38 (± 0.15)	42.19 (± 2.51)	10.47 (± 1.80)	85.91 (± 4.14)
Tee Harbor	PFO	0	68.07 (± 16.43)	267.61 (± 22.63)	16.51 (± 2.30)	20.03 (± 5.73)	108 (± 5)	5.41 (± 0.08)	72.42 (± 29.11)	5.20 (± 0.32)	13.33 (± 1.10)
Fish Creek	PFO	0	91.35 (± 28.48)	267.58 (± 10.71)	15.49 (± 3.70)	21.37 (± 3.23)	105 (± 5)	5.84 (± 0.13)	95.53 (± 26.59)	5.05 (± 0.90)	19.02 (± 2.52)
Ski Area PFO	PFO	0	75.27 (± 10.61)	335.95 (± 12.91)	62.10 (± 13.50)	79.8 (± 9.6)	9 (± 2)	4.96 (± 0.08)	12.48 (± 3.82)	3.22 (± 0.46)	15.16 (± 1.13)
Eagle River U	U	0	96.42 (± 9.02)	307.33 (± 5.83)	84.05 (± 12.03)	94.76 (± 7.93)	0	5.86 (± 0.18)	23.49 (± 8.40)	4.04 (± 0.95)	18.53 (± 2.60)
Peterson	U	0	31.18 (± 13.30)	585.50 (± 93.85)	95.69 (± 7.20)	101 (± 1.00)	0	5.88 (± 0.17)	8.04 (± 1.15)	4.55 (± 0.73)	11.87 (± 0.45)
Sheep Creek	U	0	213.62 (± 38.85)	451.36 (± 63.43)	79.04 (± 13.47)	93.06 (± 3.67)	0	5.95 (± 0.14)	38.42 (± 26.21)	9.39 (± 3.22)	15.88 (± 0.47)

* PEM = Palustrine Emergent Wetland, PSS = Palustrine Scrub Shrub, PFO = Paulstrine Forested Wetland, U = Upland

Table 2.3: Model summaries of occurrence and abundance for each species. Marginal R^2 is the proportion of variance explained by fixed effects. Conditional R^2 is the proportion of variance explained by fixed and random effects. Assignment statistics assess the proportion of the time the model correctly assigns the presence/absence data. Results assess model performance across all levels of the hierarchy: well, site, and ecosystem type. PICO = *Pinus contorta* ssp. *contorta,* PISI = *Picea sitchensis,* and TSHE = *Tsuga heterophylla.*

	Occurrence Models			**Abundance Models**	
	Marginal R^2	Correctly Assigned Presence	Correctly Assigned Absence	Marginal R^2	Conditional R^2
PICO	0.95	0.98	0.96	0.07	0.68
PISI	0.96	0.84	0.82	0.10	0.43
TSHE	0.95	0.95	0.51	0.14	0.45

Table 2.4: Variance partition coefficients (VPCs) for each species at each level of hierarchy (well, site, and ecosystem type). VPCs explain how variance is partitioned for each model. Values represent the amount of unexplained variation at each spatial scale. PICO = *Pinus contorta* ssp. *contorta,* PISI = *Picea sitchensis,* and TSHE = *Tsuga heterophylla.*

	PICO	PISI	TSHE
Well	0.34	0.64	0.65
Site	0.12	0.20	0.00
Ecosystem Type	0.54	0.16	0.35

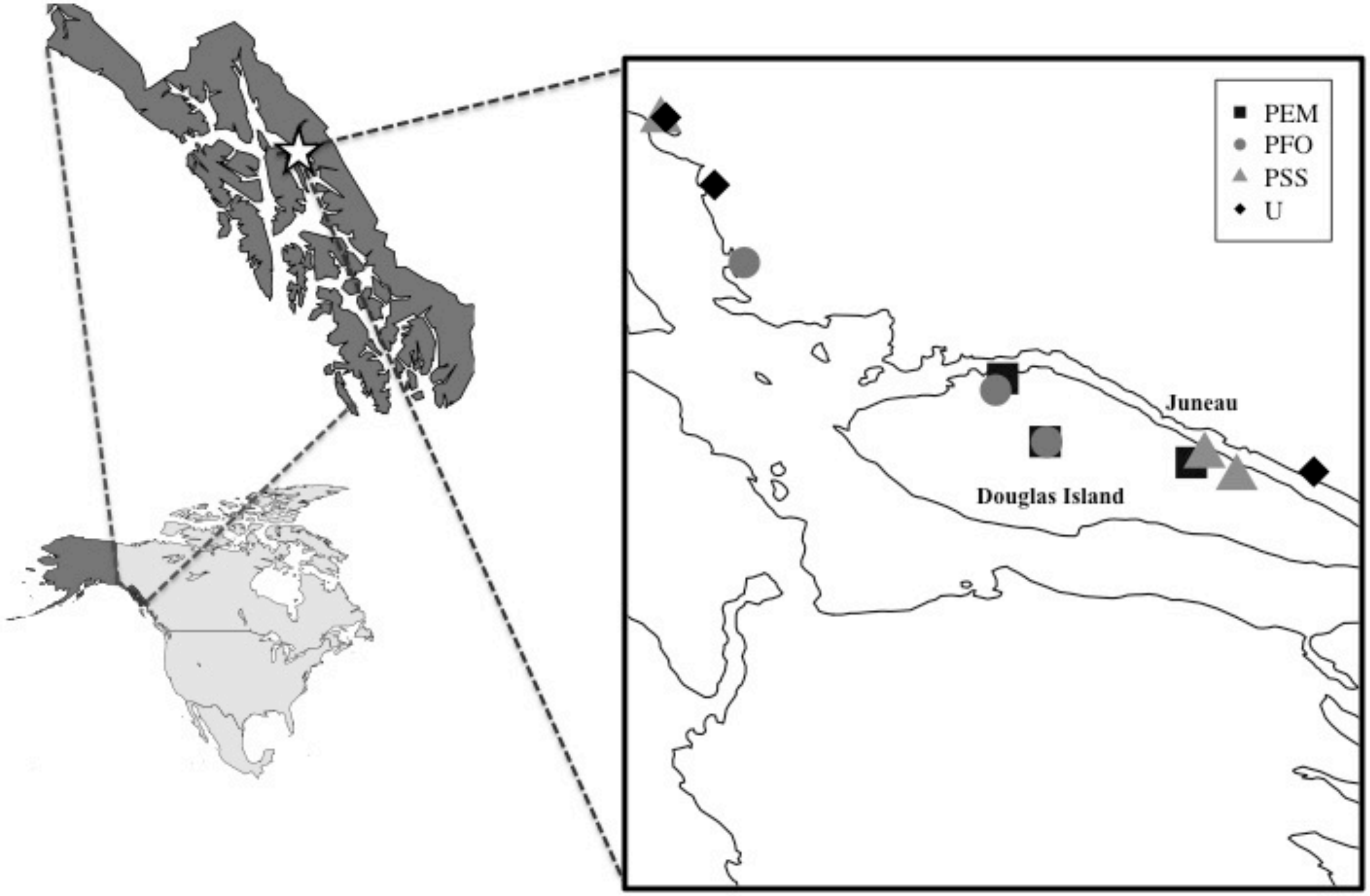

Figure 2.1: Study site locations on Mainland Juneau and adjacent Douglas Island in southeast Alaska. Site symbols represents one of four ecosystem types. PEM = Palustrine emergent wetland, PSS = Palustrine scrub-shrub wetland, PFO = Palustrine forested wetland, and U = upland.

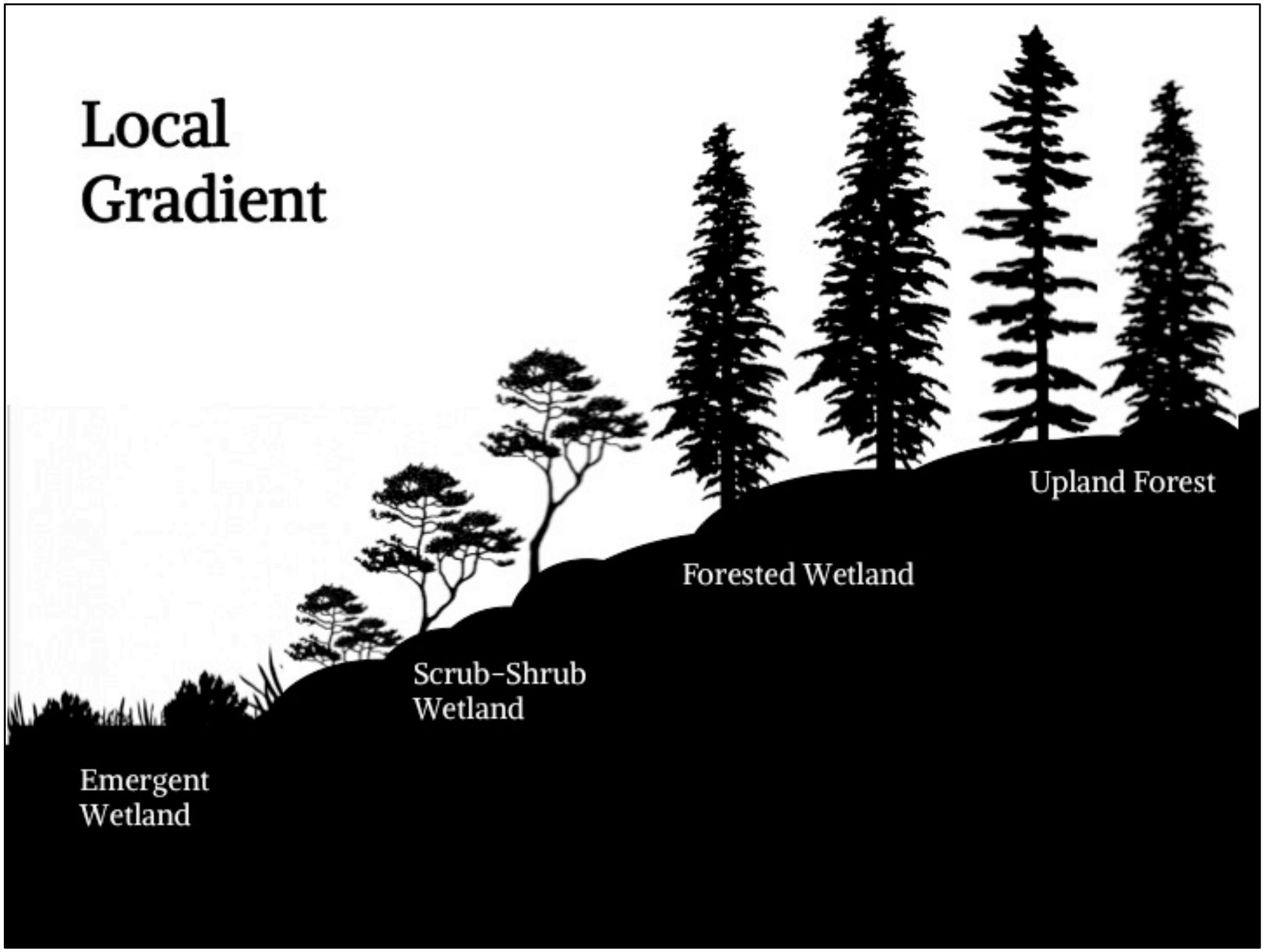

Figure 2.2: Distribution of ecosystem types across a distinct hydrologic gradient in southeast Alaska. Ecosystem types are classified, based on Cowardin et al. (1979), as: Palustrine emergent wetlands, Palustrine scrub-shrub wetlands, Palustrine forested wetlands, and upland forests.

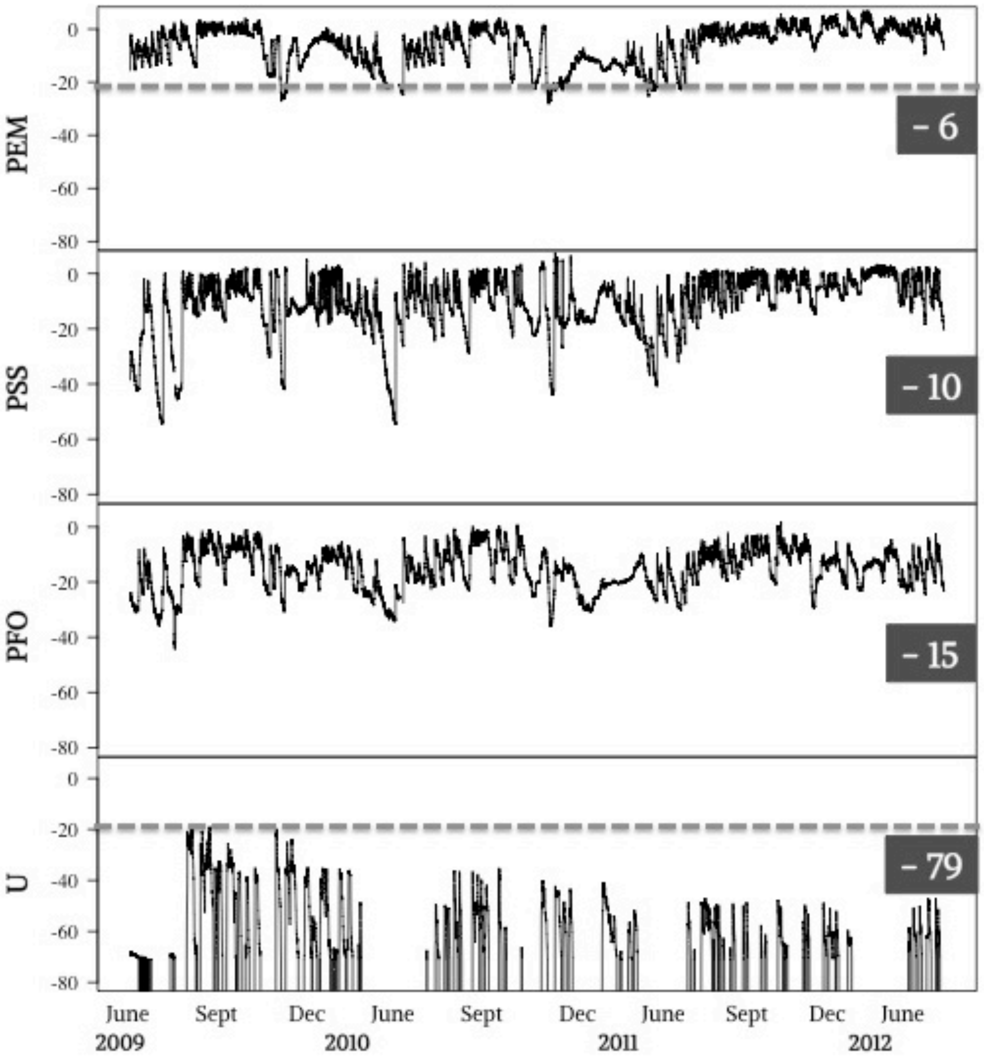

Figure 2.3: Hydrographs of mean hourly depth to water for each ecosystem type over the four-year study period (2009 - 2012). Mean annual depth to water is displayed in the grey box. The gray, hashed line marks the plant-rooting zone (Wang et al. 2002), showing the contrasting water table influence on plants growing in PEM versus U sites. Differences in depth to water we significant at $p < 0.001$. PEM = Palustrine emergent wetland, PSS = Palustrine scrub-shrub wetland, PFO = Palustrine forested wetland, and U = upland.

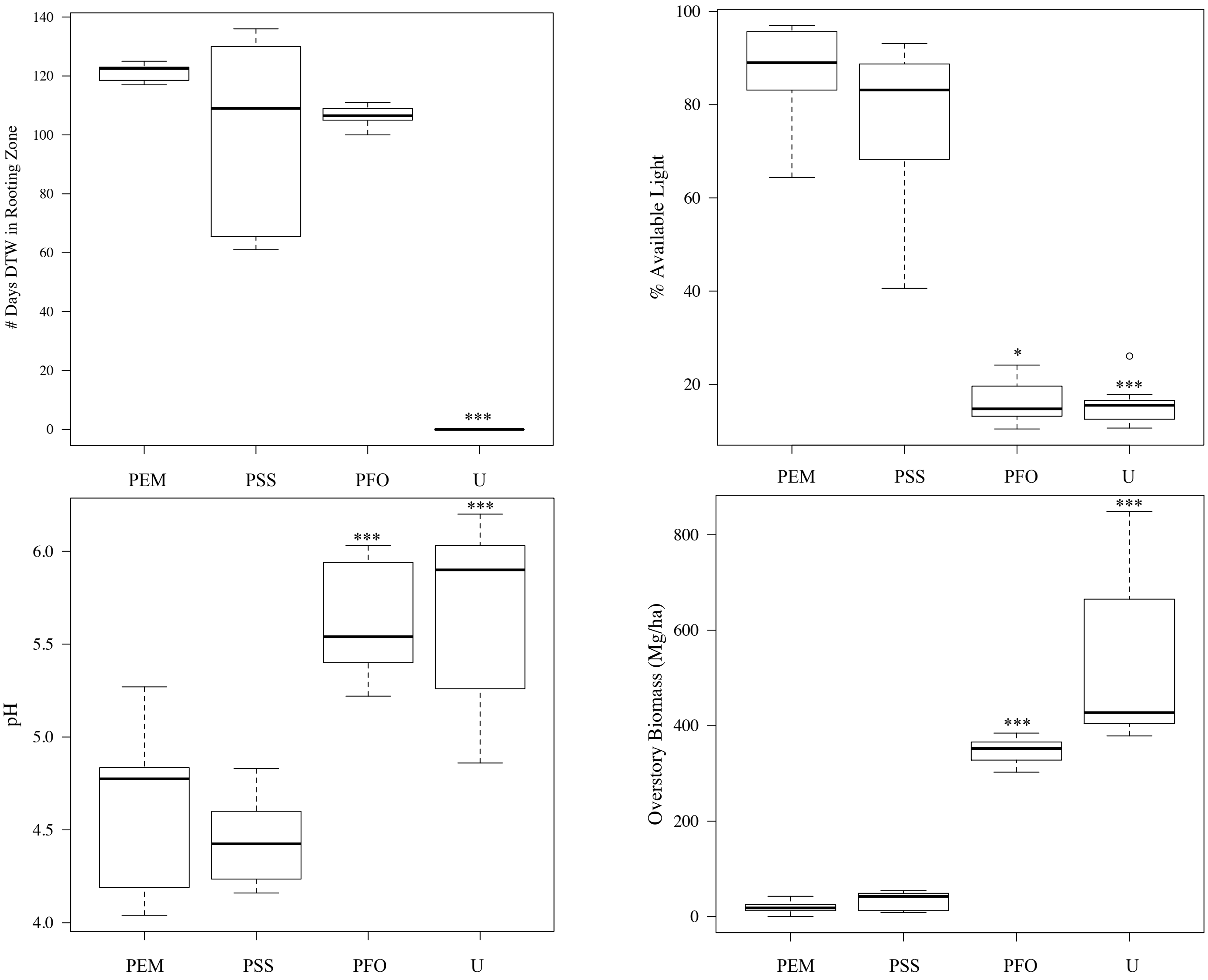

Figure 2.4: Variation in abiotic and biotic variables by ecosystem type, including: days where depth to water is in rooting zone (>-20 cm, Wang et al. 2002), available light (%), pH, and Overstory biomass. PEM = Palustrine emergent wetland, PSS = Palustrine scrub-shrub, PFO – Palustrine forested wetland, and U = Upland forest.

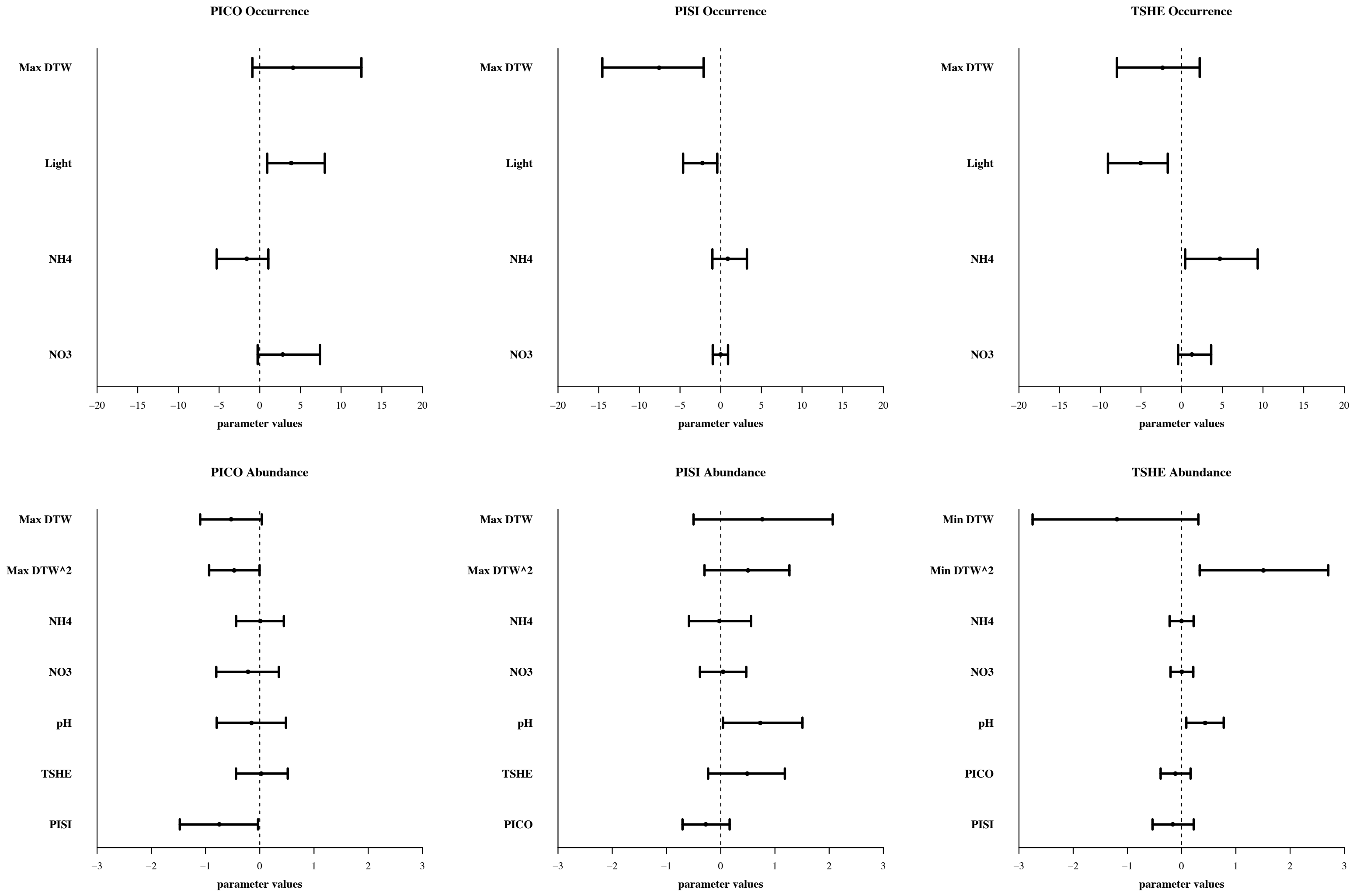

Figure 2.5: Parameter estimates from the Bayesian hierarchical model. The top row shows model output from the abundance models, and the bottom row shows output from the occurrence models. Points represent the mean values, and lines display the 95% credible interval. Those variables with intervals that do not cross the vertical zero line may be considered significantly difference from zero at the 95% level. PICO = *Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla*.

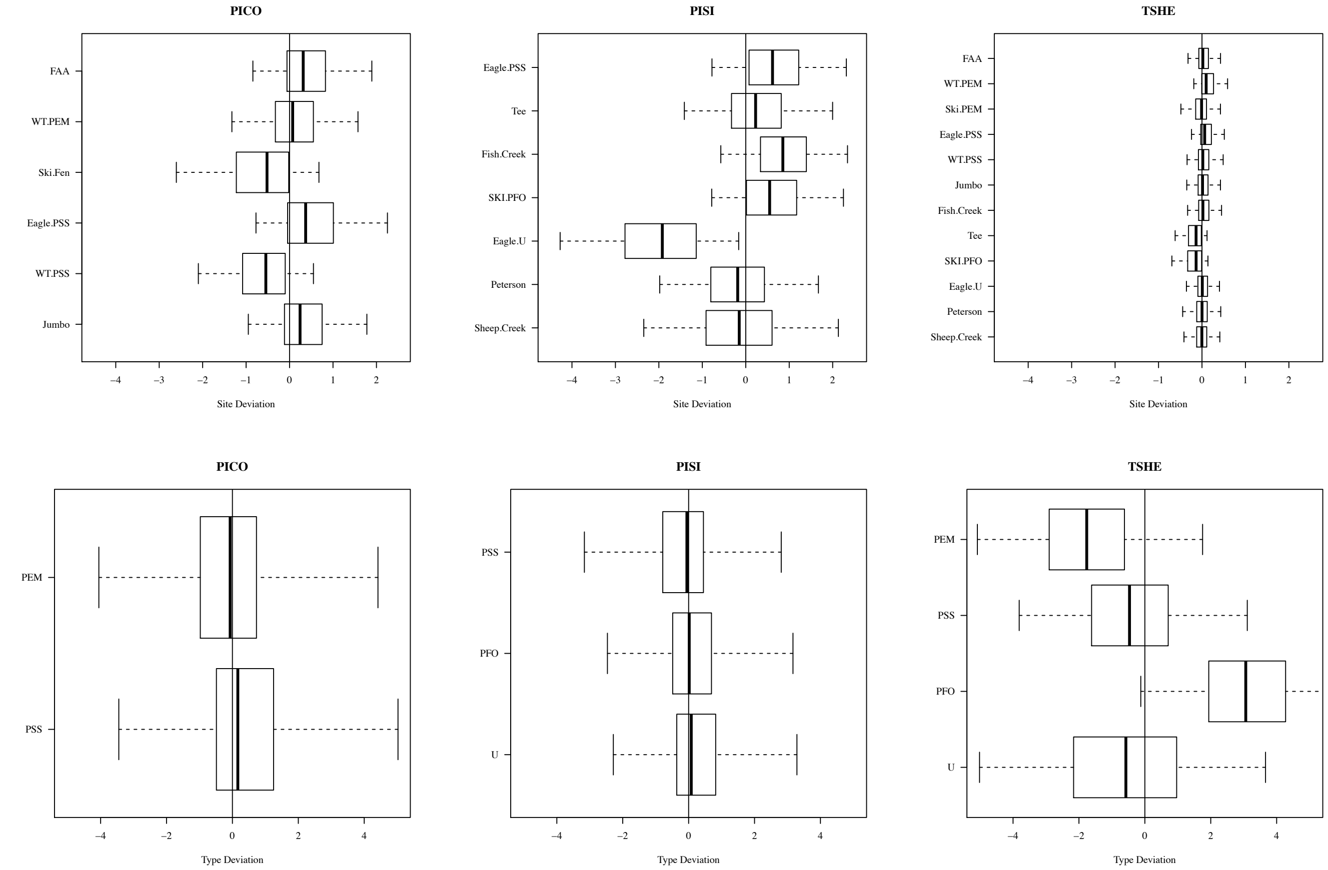

Figure 2.6: Parameter estimates of site and ecosystem type random effects for the species' abundance model. Black bars represent predicted means; boxes display the 25th and 75th percentiles; whiskers show the 90% credible interval. Those variables with intervals that do not cross the vertical zero line are considered significantly different from zero at the 90% level. Site effects are presented in the top row, and ecosystem type effects are displayed in the bottom row. PICO = *Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, and TSHE = *Tsuga heterophylla*. PEM = Palustrine emergent wetland, PSS = Palustrine scrub-shrub wetland, PFO = Palustrine forested wetland, and U = Upland.

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Appendix 2.1

Table A.2.1: Generalized linear model results for the species' occurrence models. Model selection used Akaike Information Criterion (AIC) scores. **Bolding** indicates model best explaining the data. PICO =*Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla*.

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Model	AIC Score	Deviance
PICO ~ Light + NO_3 + NH_4 + Max_DTW	21.09	11.09
PICO ~ Light + NO_3 + Max_DTW	19.51	11.51
PICO ~ Light + Max_DTW	19.18	13.18
PICO ~ Light	18.61	14.61
PICO ~ Light + NO_3	**18.57**	**12.57**
TSHE ~ Light + NO_3 + NH_4 + Max_DTW	28.27	18.28
TSHE ~ Light + NO_3 + NH_4	26.77	18.77
TSHE ~ Light + NH_4	**26.09**	**20.09**
PISI ~ Light + NO_3 + NH_4 + Max_DTW	36.52	26.52
PISI ~ Light + NH_4 + Max_DTW	34.52	26.52
PISI ~ Light + Max_DTW	**32.77**	**26.77**

Table A.2.2: Generalized linear model results for the species' abundance models. Model selection used Akaike Information Criterion (AIC) scores. **Bolding** indicates model best explaining the data. PICO =*Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla.*

Model	**AIC Score**	**Deviance**
PICO_Mass ~ pH +NO3 + NH4 + Max_DTW + PISI_mass + TSHE_mass	394.48	7468
PICO_Mass ~ pH +NO3 + Max_DTW + PISI_mass + TSHE_mass	392.59	7484
PICO_Mass ~ pH +NO3 + PISI_mass + TSHE_mass	390.85	7526
PICO_Mass ~ NO3 + PISI_mass + TSHE_mass	389.51	7630
PICO_Mass ~ PISI_mass + TSHE_mass	**388.21**	**7741**
TSHE_Mass ~ pH + NO3 + NH4 + Min_DTW + PISI_mass + PICO_mass	584.13	388235
TSHE_Mass ~ pH + NO3 + Min_DTW + PISI_mass + PICO_mass	582.16	388492
TSHE_Mass ~ pH + NO3 + Min_DTW + PICO_mass	580.35	389996
TSHE_Mass ~ pH + NO3 + Min_DTW	580.00	403679
TSHE_Mass ~ pH + Min_DTW	**579.62**	**417500**
PISI_Mass ~ pH + NO3 + NH4 + Max_DTW + PICO_mass + TSHE_mass	521.64	105607
PISI_Mass ~ pH + NO3 + NH4 + PICO_mass + TSHE_mass	519.64	105710
PISI_Mass ~ pH + NH4 + PICO_mass + TSHE_mass	517.69	105710
PISI_Mass ~ pH + PICO_mass + TSHE_mass	516.28	107023
PISI_Mass ~ pH + PICO_mass	514.80	108201
PISI_Mass ~ pH	**514.46**	**112000**

Table A.2.3: Bayesian parameter estimates, mean and 95% credible intervals, for the occurrence model. **Bolding** indicates strongest predictors of abundance. PICO =*Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla.*

Species	Parameter	Mean	CI 2.5%	CI 97.5%
PICO	Max_DTW	4.11	-0.91	12.50
	Light	**3.86**	**0.92**	**7.99**
	NH_4	-1.59	-5.30	1.05
	NO_3	2.83	-0.26	7.41
PISI	Max_DTW	**-7.57**	**-14.55**	**-2.10**
	Light	**-2.24**	**-4.62**	**-0.42**
	NH_4	0.87	-1.02	3.22
	NO_3	-0.01	-0.98	0.91
TSHE	Max_DTW	-2.34	-7.96	2.22
	Light	**-5.02**	**-9.06**	**-1.71**
	NH_4	**4.17**	**0.44**	**9.35**
	NO_3	1.26	-0.43	3.63

Table A.2.4: Bayesian parameter estimates, mean and 95% credible intervals, for the abundance model. Bolding indicates strongest predictors of abundance. PICO =*Pinus contorta* ssp. *contorta*, PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla.*

Species	Parameter	Mean	CI 2.5%	CI 97.5%
PICO	Max_DTW	-0.53	-1.10	0.04
	Max_DTW^2	**-0.47**	**-0.93**	**0.00**
	NH_4	0.01	-0.43	0.44
	NO_3	-0.21	-0.80	0.35
	pH	-0.15	-0.79	0.48
	TSHE	0.03	-0.44	0.52
	PISI	**-0.75**	**-1.47**	**-0.03**
PISI	Max_DTW	0.77	-0.50	2.07
	Max_DTW^2	0.51	-0.30	1.27
	NH_4	-0.02	-0.59	0.56
	NO_3	0.04	-0.38	0.47
	pH	**0.73**	**0.04**	**1.51**
	TSHE	0.49	-0.23	1.18
	PICO	-0.27	-0.70	0.16
TSHE	Min_DTW	-1.19	-2.75	0.31
	Min_DTW^2	**1.51**	**0.33**	**2.70**
	NH_4	0.00	-0.22	0.22
	NO_3	0.00	-0.20	0.21
	pH	**0.43**	**0.09**	**0.78**
	PISI	-0.11	-0.39	0.16
	PICO	-0.16	-0.54	0.22

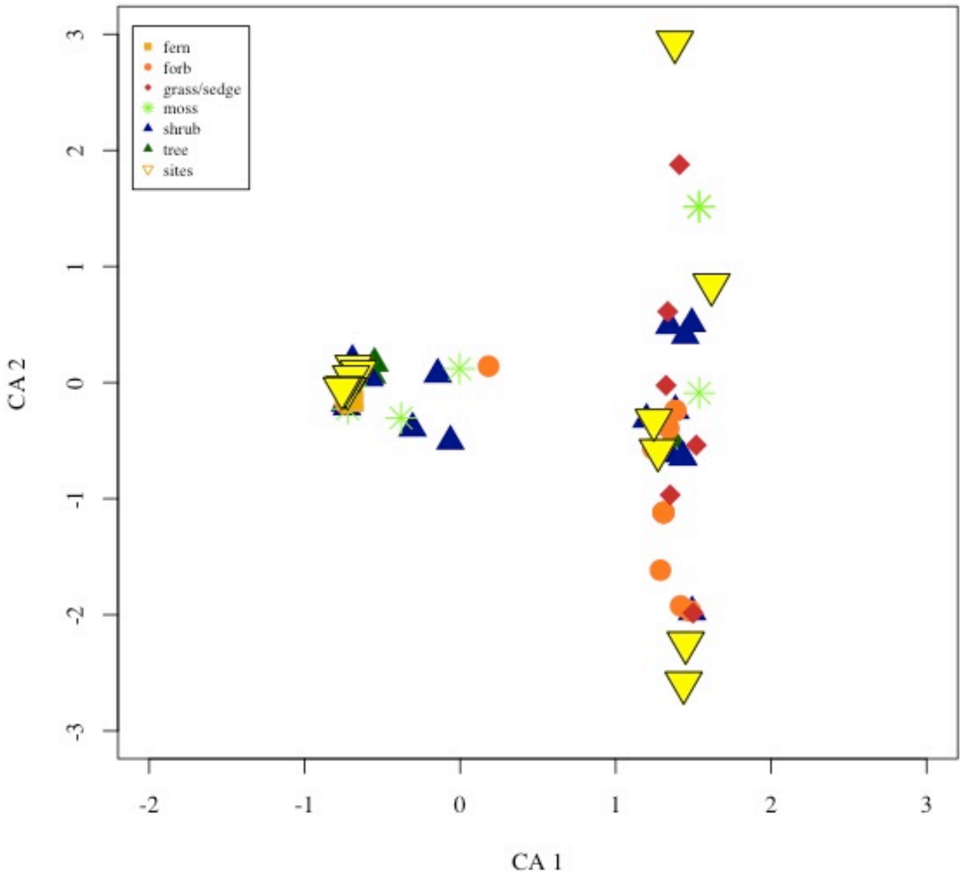

Figure A.2.1: Canonical correspondence analysis figure displaying plant community and sites, based on environmental gradient. The first and second axes explain 75% of the variation in the dataset ($p<0.001$).

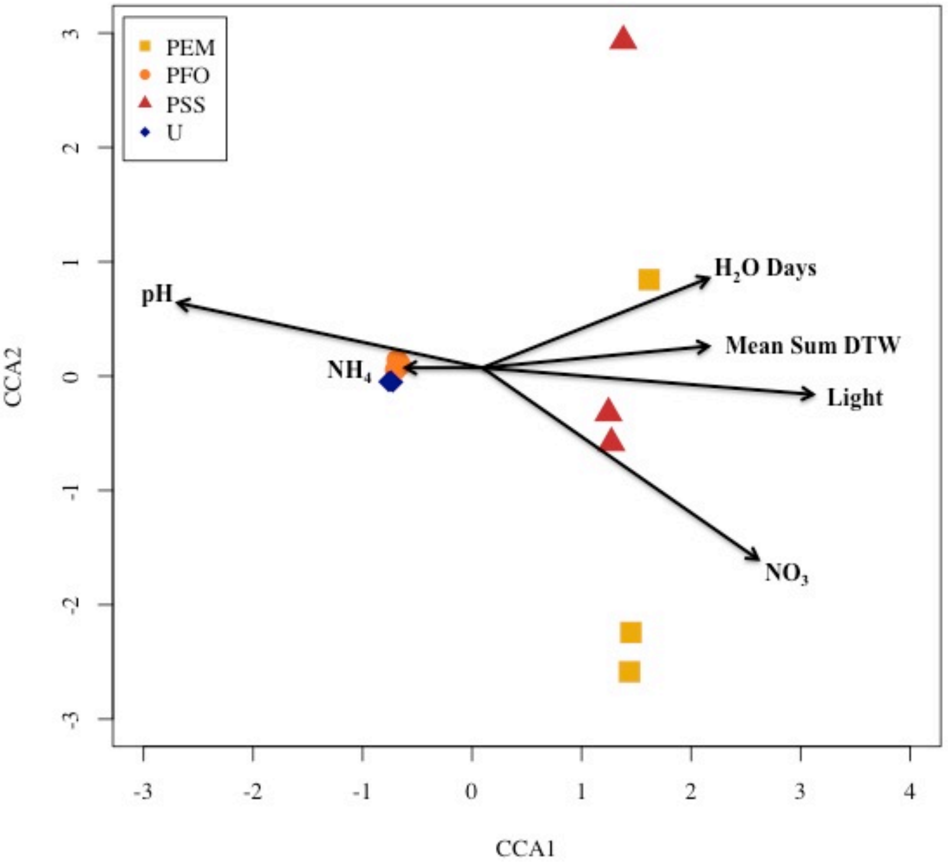

Figure A.2.2: Canonical correspondence analysis figure displaying sites and the environmental variables driving the axes. Sites are classified by ecosystem type. The first and second axes explain 75% of the variation in the dataset ($p<0.001$). PEM = Palustrine emergent wetland, PSS = Palustrine scrub-shrub, PFO = Palustrine forested wetland, and U = upland forest.

3 Shaping a species: landscape influence on range-wide patterns of genetic structure across *Pinus contorta*

3.1 Introduction

Identifying the ecological and evolutionary processes driving morphological variation within a species range is a central task in ecological research. Trait variation is the expression of a species' ability to occupy a diversified niche and persist under a range of conditions (Mayr 1963, Van Valen 1965). Species occurring across heterogeneous landscapes are subject to different selection pressures, which can have consequences for the distribution and maintenance of genetic diversity (Eckert et al. 2012). Heterogeneity in landscape and environmental conditions can create sharp boundaries between populations, shaping gene flow and patterns of population genetic structure. Widespread, morphologically-variable species provide a natural experiment for evaluating the role of ecological and evolutionary processes in shaping the distribution of a species, particularly the role of gene flow in determining variation among populations and across environmental gradients (Latta 2004). Understanding the processes shaping gene flow and determining patterns of genetic diversity requires knowledge on the influence of the landscape in structuring populations (Manel et al. 2003, Storfer et al. 2007).

Many tree species have extensive ranges that occur over a broad range of environments. Some have been documented to effectively disperse and remain connected through gene flow among distant populations and across heterogeneous landscapes (Hamrick 2004, Savolainen et al. 2007, Kremer et al. 2012). These widely-dispersed, wind pollinated species appear to overcome the substantial landscape barriers known to limit gene flow among other plant populations, but the effect of the landscape on dispersal and connectivity has rarely been tested in tree species. Members of the *Pinus* genus prove to be especially intriguing study organisms for research on gene flow and connectivity of widespread, morphologically-variable plant species. Our understanding of the life history and population structure of these species is complicated by long-distance pollen dispersal, lengthy generation times, slow migration rates, and competing hypotheses of post-glacial histories (Clark 1998, Hamrick 2004, Aitken et al. 2008).

Pinus contorta (Douglas Ex. Louden) occurs across western North America; its success across environmentally and climatically heterogeneous landscapes provides a strong example for testing the relationship between gene flow and landscape characteristics. *Pinus contorta* is one of the most widely distributed trees in North America, playing an ecologically, economically, and historically important role in western forests from Baja California to the Yukon Territory (Critchfield and Little 1966, Wheeler and Guries 1982a, Wheeler and Critchfield 1985). It grows across a broad range of elevations, extending from sea level along the Pacific coast to over 3500 m in the Sierra Nevada Mountains of California and occurring as a dominant species from coastal to subalpine forests (Critchfield and Little 1966, Wheeler and Critchfield 1985, Rehfeldt et al. 1999).

Pinus contorta is divided into four morphologically and geographically distinct subspecies (ssp. *latifolia, contorta, murrayana*, and *bolanderi*; Figure 3.1) (Critchfield 1957). All four subspecies have two-needle fascicles and scaly bark, with variations in crown shape and tree form. Each subspecies grows in a discrete portion of the species' range and is hypothesized to be adapted to local climate and environmental conditions (Ying and Liang 1994, Rehfeldt et al. 1999, 2001). The geographic distributions of the subspecies do not overlap and occur under different combinations of local conditions, except for the occurrence of subspecies c*ontorta* and *bolanderi* in Mendocino, California. Subspecies appear to be isolated from one another by ice fields, deserts, mountain ranges, and coastal waters.

Population genetics research on *P. contorta* (Wheeler and Guries 1982b, Yang and Yeh 1995, Fazekas and Yeh 2006) has shown high gene flow among subspecies and various divisions of population structure. We have little knowledge on the effects of landscape barriers and heterogeneity on variation within the species and among subspecies. In this research, I explored two questions: 1) how is genetic variation partitioned within *P. contorta*, a species that is geographically widespread but has potential for long-distance gene flow? and 2) do subspecies represent genetic clusters, or is genetic variation better explained by landscape barriers to gene flow? I hypothesized that populations across the range of the species are connected by long-distance gene flow, possessing high within- but low among-population genetic variation, and that the landscape influences patterns of genetic differentiation. My objectives were to 1) quantify the distribution of genetic variation within *P. contorta*, 2) determine whether distinct genetic clusters contribute to population genetic structure, and, if so, whether these breaks align with specific landscape characteristics, and 3) examine how genetic differentiation among populations relates to geographic or landscape variables.

3.2 Methods

Study Design and Sampling

Potential sampling locations were identified using occurrence data from U.S. Forest Service Forest Inventory & Analysis (FIA) (FIA, *accessed July 2010;* John Chase, Glenn Christensen, and John D. Shaw, *personal communication*) and British Columbia Ministry of Forests Biogeoclimatic Ecosystem Classification (BEC) (Will MacKenzie, *personal communication*) survey records. Regardless of subspecies designation, sampling locations were clustered into six ecologically and geographically distinct regions: 1) Sierra Nevada, 2) Coastal California and Oregon, 3) Southeast Alaska, 4) Yukon Territory to central British Columbia, 5)

Rocky Mountains (Jasper National Park, AB through Colorado), and 6) Black Hills (Figure 3.1; Table 3.1). These regions represent major physiographic divisions of western North America, which are based on landform and conspicuous landscape features (Fenneman 1917). Regional delineation presumed the potential for population connectivity within and isolation across these boundaries.

Ten sampling locations were randomly selected from within five of the six stratified regions (regions one through five). In region four, we targeted a portion of sampling toward inclusion of variety *yukonensis*, with two locations ultimately selected for analysis. We also avoided sampling across a large portion of central British Columbia to prevent unintentional sampling of commonly occurring commercial plantations. In region six (Black Hills), the two known populations were sampled. The U.S. Forest Service Rocky Mountain Research Station's FIA program provided samples for subspecies *latifolia* in areas not sampled under this study design, including from Colorado, Idaho, Montana, and Utah. Subspecies *latifolia* occupies the greatest portion of the species' range, and this was reflected in our design. Sampling locations per subspecies were distributed in the following manner ($n = 51$, Figure 3.2): ssp. *latifolia* = 24 (47%), ssp. *contorta* = 13 (25%), ssp. *murrayana* = 11 (22%), and ssp. *bolanderi* = 3 (6%).

A total of one gram of fresh, current-year needles was collected from ten individuals at each sampling location. To reduce the likelihood of sampling related individuals, trees selected for sampling were a minimum of 50 m apart. Needles were placed in manila coin envelopes and dried in silica gel desiccant. Basic morphological data was collected on each tree, including tree form and the presence or absence of serotinous cones (0 or 1). Tree form data was classified into four categories: 1) short stature, twisted bole, 2) short stature, straight bole, 3) tall tree, large diameter (>50 cm), or 4) tall tree, small diameter (<50 cm).

I chose to prioritize sampling a greater number of locations given the geographic scope of the *P. contorta* distribution even though sampling more individuals per location would increase the reliability of population-level estimates. This schema provides the statistical power necessary to detect geographic patterns in genetic structure (Eckert et al. 2008).

DNA Extraction and Microsatellite Amplification

Total genomic DNA was extracted from silica gel-dried needles at the U.S. Department of Agriculture National Forest Genetics Laboratory (Placerville, CA) using DNeasy plant kits (Qiagen, Valencia, CA). After screening twenty-two previously developed markers (Hicks et al. 1998, Stoehr and Newton 2002, Parchman et al. 2010, Lesser et al. 2011) for amplification and polymorphism in a subset of populations from each subspecies, I selected one polymorphic cpDNA marker and nine, highly polymorphic SSR markers for further analysis across all samples (69FR, PICO1, PICO4, PICO7, PICO77, PICO104, PICO109, PICO138, PICO154, PICO179; Table A.3.1) (Stoehr and Newton 2002, Parchman et al. 2010, Lesser et al. 2011).

Microsatellite loci were amplified in multiplex under identical conditions. Locus-specific primers were 5’-tailed with universal primer sequences (as described by Missiaggia & Grattapaglia 2006), including: D8S1132f-FAM (5’-[6FAM]GGCTAGGAAAGGTTAGTGGC-3’), D12S1090f-TAMRA (5’-[TAMRA]ACCAACCTAGGAAACACAG-3’), and DYS437f-HEX (5’-[5HEX]GACTATGGGCGTGAGTGCAT-3’). PCR amplification reactions were prepared in 4 uL volumes and consisted of: 0.01 U/uL Phusion HotStart II Polymerase (Thermo Scientific, Rockford, IL), 1X Phusion HF Buffer (Thermo Scientific), 3.0 mM $MgCl_2$, 200 nM dNTPs, 200 nM universal and reverse locus-specific primers, 20 nM forward tailed locus-specific primer, 1X KAPA Enhancer 1 (KAPA Biosystems, Woburn, MA), 6% glycerol, and approximately 5 ng template DNA. Thermal cycling was performed under the following conditions: 1 cycle of 90 C for 2 min; 40 cycles of 90 C for 30 sec, 63 C for 2 min, and 72 C for 15 sec; 1 cycle of 72 C for 10 min. PCR products were separated on a 3730xl Genetic Analyzer (Life Technologies, Carlsbad, CA), and peak sizes were determined using GeneMarker v2.2 (SoftGenetics LLC, State College, PA). All samples were scored three times to verify peaks and resolve any conflicts in scoring.

Descriptive Statistics and Genetic Diversity

Statistical analyses tested the importance of sampling location (*n* = 51), region (*n* = 6), and subspecies (*n* = 4) in explaining genetic variation. Prior to analysis, MICROCHECKER 2.2.3 was used to test for evidence of null alleles and screen for genotyping errors, including allelic dropout and stuttering (Van Oosterhout *et al.* 2004). No evidence for allelic dropout or stuttering was detected, but the presence of null alleles occurred at two loci, so we used MICROCHECKER to adjust homozygote genotypes to more accurately reflect estimated null allele frequency (Van Oosterhout *et al.* 2004) and used adjusted allele frequencies in all subsequent analyses. Genetic diversity statistics were calculated in GENALEX 6.5 (Peakall and Smouse 2006, 2012). Analysis of molecular variance (AMOVA) was also performed in GENALEX to quantify the distribution of molecular variation within and among sampling locations, regions, and subspecies.

Population Clustering

STRUCTURE 2.3.2 (Pritchard et al. 2000, Falush et al. 2007) was run without spatial information to estimate the number of discrete population genetic clusters (*K*) and assign individuals to these genetic clusters without grouping them *a priori* based on geographic location. Values of $K = 1 – 10$ were tested under a correlated allele frequency model by running replicate simulations ($n = 5$) with a burn-in of 200,000 iterations and a run length of 1,000,000 Markov Chain Monte Carlo (MCMC) repetitions. Model runs assumed admixture among sampling locations, with the admixture parameter (α) set to vary and inferred separately for each. Preliminary model runs, testing an independent allele frequency model and K = 1-51, did not differ from the more biologically realistic correlated allele frequency model and a smaller *K*.

The most likely value of *K* was determined using STRUCTURE HARVESTER (Earl and VonHoldt 2012), which plots the log probability [$L(K)$] of the data over multiple runs and compares it to the ΔK using the Evanno method (Evanno *et al.* 2005). Results from the five replicate STRUCTURE runs with the highest likelihood scores were merged in CLUMPP 1.1.2 (Jakobsson and Rosenberg 2007) and visualized with DISTRUCT 1.1(Rosenberg 2004).

Assignment testing was also implemented in GENELAND 4.0.3 (Guillot, *et al.* 2005, 2005, 2012) to assess the role of geographic location in determining population structure and morphological variation among populations. This analysis incorporated both geographic location and the phenotypic data derived from field assessment of tree morphology. Phenotypes were differentiated by two variables: tree form (n = 1-4) and the presence or absence of serotinous cones (0 or 1). The value of *K* was allowed to vary among replicate ($n = 10$) simulations from 1 – 51, and model runs consisted of the following: 2,000 burn-in iterations; 1,000,000 MCMC repetitions with a thinning of 1000; spatial uncertainty (Δ) of 0.02 (~ 1.4 km) to account for measurement error; a maximum rate of Poisson process equal to 100 (default); and a maximum number of nuclei set to 1016. These analyses assigned each individual to one genetic cluster, with clustering a function of genetic, geographic, and phenotypic information. The most likely number of genetic clusters was inferred from convergence of the MCMC chain and through comparison of the log-likelihood posterior distribution across multiple runs (n = 10).

Landscape Genetics

Landscape genetics analyses were used to quantify the effect of geographic distance and landscape features on population genetic structure (Manel *et al.* 2003). First, pairwise genetic distances was calculated in GENODIVE (Meirmans and Van Tienderen 2004). Mantel tests of isolation by distance (IBD), isolation by resistance (IBR), and isolation by barrier (IBB) were performed in GENODIVE under 999 permutations. Analyses correlated genetic differentiation with ecologic distances to infer the effect of the landscape on population genetic structuring (Cushman et al. 2006, Balkenhol et al. 2009). I also ran partial Mantel tests on all combinations of genetic, geographic, and ecological distance matrices (e.g. Genetic ~ Resistance | Geographic) to assess the degree of association between genetic and ecological distance after accounting for the influence of geographic distance.

Tests of IBD used pairwise genetic distance (untransformed F_{ST} and $F_{ST}/(1 - F_{ST})$) with respective pairwise geographic distance (log km) (Mantel 1967, Rousset 1997). The Mantel test of IBD was performed in a hierarchical manner, examining the isolation by distance relationship across all sampling locations, within regions, and within subspecies (excluding ssp. *bolanderi* due to small sample size).

The Mantel test of IBR used a resistance map derived from modeling in MAXENT 3.3.3k (Phillips *et al.* 2006), assuming that habitat suitability is a valid approximation for landscape resistance to dispersal (Wang et al. 2008, Hagerty et al. 2010). I assessed suitability using 20,505 FIA and BEC *P. contorta* occurrence records and layers of current (1950-2000), 1 km^2 resolution

WORLDCLIM climate data (Hijmans *et al.* 2005). A Principal Components Analysis (PCA) was run in R 2.15.2 (R Core Team 2012) on WORLDCLIM variables for 20,505 randomly-selected points from across the range of *P. contorta* to identify and remove highly correlated climate variables. Of the 19 downscaled bioclimatic variables, five minimally correlated variables (correlation < 0.65) were selected, including mean annual temperature (°C), mean minimum coldest month temperature (°C), mean annual precipitation (mm), precipitation of wettest month (mm), and precipitation of driest month (mm). Layers were processed in ArcGIS 10.1 and used in MAXENT for predictive habitat modeling.

MAXENT was run at the species-level under the following settings: minimum training presence threshold, logistic output, 0.5 probability of presence, and 25% of the data used as random testing points. The resultant model was evaluated using receiver-operating characteristics (ROC) and had a test score (area under the curve - AUC) of 0.98 ($p < 0.001$). A threshold of 60% probability of suitability (0 = lowest suitability, 100 = highest suitability) was set for identifying suitable versus unsuitable habitat. Any predictions falling under the 60% probability mark were classified as unsuitable (Angert et al. 2011). MAXENT output was transformed into a binary matrix and used to define landscape resistance. I scaled resistance from 0 to 1, assigning suitable habitat cells a value of 0 and unsuitable a value of 1. I then used the COSTDISTANCE function in ArcGIS to calculate least-cost path and pairwise landscape resistance between all sampling locations. Pairwise resistance values were evaluated against pairwise genetic distance (F_{st}) in a Mantel test of IBR.

A Mantel test of IBB was used to assess the role of landscape barriers in governing population genetic structure. Hypothesized barriers were defined prior to analysis and delineated based on likelihood of limiting gene flow across this widespread, wind-pollinated species. Four significant barriers were identified: Central Valley of California, coastal waters of the Pacific Ocean, Juneau Icefield and Coast Mountain Range, and Great Basin-Intermountain West (Figure 3.3). The landscape features identified as barriers represent combinations of geographic distances and ecological conditions likely to hinder gene flow. Under the IBB model, I assumed panmixia on either side of identified barriers with minimal to no gene flow between. Pairs located on the same side of a barrier were coded as 0, while those separated by the barrier were coded as 1. Pairwise distances were used to create a barrier matrix for analysis in a Mantel test of IBB.

Canonical correspondence analysis (CCA) was employed using the '*vegan*' package in R 2.15.2 to test the effects of environmental variables on genetic differentiation (F_{st}) and population clustering. Sampling location environmental variables were derived for the period from 1981 – 2010 using ClimateWNA 4.72 (Wang et al. 2006). A PCA was utilized to reduce the full set of environmental variables to a set of minimally correlated variables (correlation < 0.65), including mean warmest and coldest mean temperature (°C), mean summer precipitation (mm), annual heat to moisture index (AHM), and climatic moisture deficit (difference between evaporation and precipitation). Environmental variables were regressed on pairwise genetic differentiation to identify patterns in the dataset (Angers et al. 1999). Global permutation tests (999 permutations) were used to identify significant environmental drivers of population structure and statistical associations between canonical axes.

3.3 Results

Descriptive Statistics

Tests of Hardy-Weinberg Equilibrium across sampling locations indicated that nearly 28% (144 of 510 tests) of locus-by-sampling-location comparisons deviate from expectations ($p < 0.05$). All loci selected for analysis were highly polymorphic, and the minimum percentage of polymorphic loci by site was 70 (Table 3.2). A total of 252 alleles were identified across the ten markers, with the number of alleles per locus ranging from 10 (locus PICO4) to 56 (locus PICO104). The mean number of alleles (N_A) ranged from 2.50 (± 0.401 SE) in Dundas Bay (ssp. *contorta*, southeast Alaska) to 5.70 (± 1.248 SE) in Lemhi (ssp. *latifolia*, Idaho). Mean heterozygosity (H_E) was 0.505 (± 0.011 SE) among sites, 0.373 among regions, and 0.375 among subspecies.

The proportion of variation (F_{ST}) residing among sites was 0.167 ($p < 0.001$; Table 3.2). Among regions and subspecies, F_{ST} was lower (0.049 and 0.054; $p < 0.001$). Pairwise F_{ST} ranged from 0.025 to 0.376 (not presented here), with the southeast Alaska Jumbo Bog sampling location and three California sampling locations (Russian Gulch, Spring Ranch, and Tuolumne Meadows) having the highest F_{ST} scores. Larger pairwise values were detected for sites with both landscape barriers and larger geographic distance between them. Site-specific F_{IS} values (Table 3.2) ranged from -0.106 at Idaho (ssp. *latifolia*, Idaho), a heterozygote excess consistent with outbreeding, to 0.427 at Dawson Saddle (ssp. *murrayana*, California), a heterozygote deficiency consistent with inbreeding. Estimates of inbreeding rates were also high at FAA Bog (0.357, ssp. *contorta*, southeast Alaska) and at Eagle (0.359, ssp. *latifolia*, Colorado).

AMOVA analyses among sampling locations revealed that most of the genetic diversity (87 percent) is attributable to variation within sampling locations (Table 3.3). A small, but significant ($p < 0.001$), portion of population structure resides among sampling locations (13 percent). Analyses across larger sampling extents indicated that more variation resides among sampling locations than among regions (6 percent) or subspecies (5 percent) (Table 3.3).

Population Clustering

Evanno method plots of ΔK (Supplementary Material, Figure A.3.1, Evanno *et al.* 2005) from STRUCTURE output identifed three ($K = 3$) as the most likely number of genetic clusters (Figures 3.4 & 3.5). Despite a lack of geographic information in the model, STRUCTURE clearly distinguished major clusters that coincide well with three subspecies and their spatial arrangement in relation to distinct landscape features (Figure 3.4). Individuals east of the Rocky Mountains cluster together and show high levels of genetic similarity across these subspecies *latifolia* individuals. Subspecies c*ontorta* individuals from southeast Alaska cluster predominantly into a second group. Finally, individuals from subspecies *murrayana* of the Sierra Nevada Mountains cluster into a third group. Subspecies *bolanderi* individuals have a high probability of membership to the same cluster as *latifolia* individuals, but all coastal individuals do show high levels of admixture and membership to all three genetic clusters. Across all subspecies, no one individual is exclusive to a single genetic cluster (Figures 3.4 & 3.5).

The same pattern of range-wide structuring ($K = 3$) was detected under the spatial model implemented in GENELAND (Figure 3.6). The incorporation of geographic location also allowed for identification of potential landscape barriers to dispersal. Boundaries between GENELAND clusters visually correlate with distinct landscape features and potential barriers to gene flow when overlaid onto landscape maps. One boundary corresponds to the genetic discontinuity between subspecies *murrayana* of the Sierra Nevada Mountains and subspecies *contorta* along the coast of California and Oregon, indicating that the Central Valley of California might act as a barrier to gene flow (Figure 3.6a). A second barrier is apparent in the Intermountain West, which is potentially acting as a barrier to gene flow between subspecies *murrayana* of the Sierra Nevada Mountains and subspecies *latifolia* of the Rocky Mountains (Figure 3.6b). Finally, a third boundary between clusters correlates to the Juneau Icefield and Coast Mountain Range as barriers to gene flow between subspecies *contorta* of southeast Alaska and subspecies *latifolia* (Figure 3.6c). The Pacific Ocean was not identified as a barrier to gene flow, which suggests that subspecies c*ontorta* is connected across its coastal range from southeast Alaska to central California.

Landscape Genetics

The Mantel test of IBD identify a weak signature of isolation by distance ($r^2 < 0.06$, $p < 0.001$, Figure A.3.2), indicating that pairwise geographic distance does not explain population structuring. Mantel tests of landscape features included comparisons to pairwise resistance (IBR) and the presence of barriers (IBB). Each of these tests revealed some signature of isolation by landscape features (Table 3.4) at 12 and 11 percent, respectively ($p < 0.001$). Mantel r-values calculated in these analyses suggest positive correlation between these landscape factors and pairwise genetic distance (Table 3.4). Pairwise Mantel r-values were not significant (Table 3.4), indicating that there is no additional influence of the landscape after correcting for geographic distance.

The CCA revealed a strong influence of mean summer precipitation ($p < 0.001$), climate moisture deficit ($p <0.001$), and annual heat to moisture index ($p < 0.01$) on genetic differentiation and population clustering (Figure 3.7). The first and second canonical axes explained 31 percent of the variation in the dataset ($p < 0.001$).

3.4 Discussion

Determining the importance of landscapes in controlling species' dispersal and migration is essential to understanding patterns of distribution and connectivity (Storfer *et al.* 2007).

Landscapes have the potential to shape gene flow and determine population structure by constraining the germination and success of individuals. In *Pinus contorta*, there is low genetic differentiation across the range of the species, and patterns of differentiation are most strongly influenced by potential landscape barriers to gene flow and the environmental variation associated with its heterogeneous range.

Pinus contorta showed moderate population differentiation ($F_{ST} = 0.167$) at the continental scale, consistent with previous *P. contorta* population genetics research in concluding high gene flow and low differentiation among populations (Table 3.5). Genetic differentiation (F_{ST}) calculated in this study was slightly higher than that quantified in previous research (Wheeler and Guries 1982b, Fazekas and Yeh 2006), which is likely due to the inclusion of extensive sampling of subspecies *murrayana*. Inbreeding estimates (F_{IS}) correlated well with each site's degree of connectivity to adjacent *P. contorta.* For example, the Idaho sampling location had an F_{IS} of -0.106, which indicates high outbreeding. This population occurs in the Rocky Mountain region of the subspecies *latifolia* distribution, an area dominated by *P. contorta* forest cover and with high levels of connectivity across forest stands. Conversely, the Dawson Saddle site had an F_{IS} of 0.427, which suggests a high level of inbreeding. This population is located at the southern extent of the species range in the Angeles National Forest, with individuals growing in low densities within a mixed-conifer stand and isolated from other *P. contorta* stands. The other sites with the highest inbreeding coefficients, the FAA Bog (0.357) and Eagle sites (0.359), occur at the northwestern and southeastern range margins of the species, respectively. The populations with the highest coefficients were those occurring at the edges of the species' range. Overall, *P. contorta* is highly connected ($F_{ST} = 0.167$) across its range.

Although F_{ST} values were consistent with widespread gene flow among populations, there is structuring across the species' range. Incorporating the landscape into an assessment of population genetics allowed me to identify *P. contorta* population structure that was not previously apparent. The patterns observed within this species cannot be explained by simple isolation by distance (Figure A.3.2). Results from Mantel tests (Table 3.4) indicate that landscape elements are limiting gene flow by acting as barriers gene flow. Landscape barriers (Figures 3.3 & 3.6) and environmental conditions (Figure 3.7) better explained population differentiation than isolation from gene flow.

The three genetic clusters identified in this analysis (Figures 3.4 & 3.5) correspond with North American physiographic regions (Fenneman 1917) that are separated by conspicuous geographic barriers and characterized by distinct environmental conditions. The genetic clusters identified here coincide with three of the four subspecies (*contorta, latifolia,* and *murrayana*), and the geographic distribution of genetic clustering supports the taxonomic treatment of these three subspecies (Critchfield 1957). Subspecies *bolanderi* populations were assigned to the subspecies *latifolia* cluster despite the geographic distance between the two subspecies and their distinct morphological traits. The affiliation of subspecies *bolanderi* with *latifolia* does not correspond with our assumptions of landscape and geographic influence, but my results do indicate that connectivity and gene flow is high among all populations. Cluster analysis by Wheeler and Guries (1982) identified two genetic clusters – one representing southern British Columbia and the United States and another including northern British Columbia and the Yukon. Their analysis did not include samples from the southern extent of the species' range, where I identified a third genetic cluster. In this study, subspecies *murrayana* populations are separated into a distinct genetic cluster that corresponds with the Sierra Nevada region.

Three of my four hypothesized barriers, including the Central Valley of California, the Juneau Icefield and Coast Mountain Range complex, and the Intermountain West, were identified as potential drivers of population structure. Admixture was present in all populations (Figure 3.5), however, indicating gene flow across these boundaries. Pines are prolific producers of pollen and have the capacity for long distance dispersal (MacDonald and Cwynar 1985, Kremer et al. 2012), which has the potential to impact genetic differentiation following even one reproductive event (Kremer *et al.* 2012). Dispersal events have been documented to reach distances of up to 3,000 km for pine species (Campbell *et al.* 1999), so rare long-distance dispersal events may be enough to maintain connectivity across the geographic extent of *P. contorta*. The potential barriers identified in this study were likely penetrable at one time or another.

A strong relationship exists between genetic differentiation (F_{ST}) and environmental conditions ($p < 0.001$; Figure 3.7). Differentiation was significantly related to mean summer precipitation, climate moisture deficit, and annual heat to moisture index (Figure 3.7). The CCA clearly indicated a strong influence of these local environmental factors on genetic structure. Clustering in the CCA is significantly associated ($p < 0.001$) with environmental variables, and plant morphology is distinct within each cluster. This indicates that the balance between growing season precipitation and temperature may control the success of individuals and their phenotypic expression of traits. The morphological variation coincides with landscape heterogeneity and can be related to specific environmental factors. This suggests that, despite widespread gene flow, subspecies are adapted to local conditions. The strength of selection based upon morphological variation has yet to be quantified, but my results provide a basis for testing local adaptation across the three genetic groups. Tests of local adaptation across all four subspecies are likely to reveal fitness differences and support the distinction between each.

Identifying the factors and processes shaping species' distributions has long been a central task in ecology (Holt 2003). The landscape and environmental heterogeneity of western North America shapes variation and the geographic distribution of genetic information in *Pinus contorta*. Landscape elements, including topographic barriers and local environmental factors, drive differentiation despite gene flow. Testing local adaptation of the three subspecies identified here (c*ontorta, latifolia,* and *murrayana*) is the next step needed in linking differentiation to local fitness and would provide a much better understanding of the drivers of variation among subspecies.

Table 3.1: Geographic descriptions of each *Pinus contorta* sampling location by subspecies and region.

Subspecies	Region	Site	Site Ownership	Location	*N* (*total* = 508)	Latitude	Longitude	Average Elevation (m)
ssp. *murrayana*	Sierra Nevadas	Wellman's Divide	San Jacinto State Park	California	10	33.7991	-116.6746	2956
		Hidden Lake Drive	San Jacinto State Park	California	10	33.8019	-116.6422	2651
		Onyx Peak	San Bernardino National Forest	California	10	34.1953	-116.7126	2743
		Champion	San Bernardino National Forest	California	10	34.2190	-116.9732	2307
		Dawson Saddle	Angeles National Forest	California	10	34.3678	-117.8034	2415
		Big Meadow	Sequoia National Forest	California	10	35.8872	-118.3429	2372
		Horeshoe Meadows	Inyo National Forest	California	10	36.4486	-118.1700	3049
		Crooked Meadows	Inyo National Forest	California	10	37.8424	-118.8626	2656
		Tuolumne Meadows	Yosemite National Park	California	10	37.8715	-119.3731	2600
		Levitt Meadows	Humboldt-Toiyabe National Forest	California	10	38.3088	-119.5870	2523
		Luther Pass	Tahoe National Forest	California	10	38.7870	-120.0019	2212
ssp. *bolanderi*	Coastal California and Oregon	Russian Gulch	California SP	California	10	39.3111	-123.7600	132
		Van Damme Pygmy	California SP	California	10	39.2631	-123.7376	183
		Van Damme	California SP	California	10	39.2658	-123.7500	160
ssp. *contorta*		Spring Ranch	California SP	California	10	39.2857	-123.7959	44
		Patrick's Point	California SP	California	10	41.1397	-124.1606	52
		Towala Dunes	California SP	California	10	41.7964	-124.2232	28
		Port Oxford	Oregon SP	Oregon	10	42.7392	-124.5107	151
		Sand Dunes	Siuslaw NF	Oregon	10	44.0633	-124.1198	7
	Southeast Alaska	Old Sitka	Tongass NF	Alaska	10	57.1286	-135.3687	45
		Blanket Bog	Tongass NF	Alaska	10	56.6387	-132.6610	66
		Bay Bog	Tongass NF	Alaska	10	58.0588	-135.0962	21
		Jumbo Bog	City and Borough of Juneau	Alaska	10	58.2615	-134.3864	203
		Sundown Bog	City and Borough of Juneau	Alaska	15	58.3340	-134.5941	23
		FAA Bog	State of Alaska	Alaska	10	58.3358	-134.5622	50
		Dundas Bay	Glacier Bay National Park	Alaska	5	58.3253	-136.2032	0
		Dick's Arm	Glacier Bay National Park	Alaska	10	58.2301	-136.6287	0
ssp. *latifolia*	Yukon to Central Britsh Columbia	Alcan Highway	Yukon Forest Management	Yukon Territory	15	60.8528	-135.7060	670
		Mt McIntyre$^{\delta}$	Yukon Forest Management	Yukon Territory	10	60.6561	-135.2151	1213
		Canol Road$^{\delta}$	Yukon Forest Management	Yukon Territory	20	60.5669	-133.0992	1351
		Pine Flats	Yukon Forest Management	Yukon Territory	10	60.1398	-130.2309	866
		Edziza	Ministry of Forests	British Columbia	10	57.2055	-130.2252	789
		Smithers Community Forest	Ministry of Forests	British Columbia	10	54.7370	-127.2562	865
	Rocky Mountains	Columbia Icefields	Jasper National Park	Alberta	10	52.3569	-117.3489	1569
		Glacier Lake	Banff National Park	Alberta	10	51.9731	-116.7596	1456
		Windermere Kootenay	Kootenay National Park	Alberta	10	50.8809	-116.0481	1182
		Flathead*	Flathead National Forest	Montana	11	48.4572	-113.6403	1620
		Judith Basin*	Helena National Forest	Montana	10	46.3211	-111.8512	2215
		Lewis & Clark*	Lewis and Clark National Forest	Montana	6	46.8209	-110.4757	1982
		Lemhi*	Bitterroot National Forest	Montana	11	45.4771	-113.8847	2040
		Idaho*	Nez Perce National Forest	Idaho	3	45.2690	-115.0195	1993
		Custer*	Salmon-Challis National Forest	Idaho	8	44.4960	-114.5536	2640
		Valley*	Payette National Forest	Idaho	11	44.6545	-115.8714	1925
		Fremont*	Targhee National Forest	Idaho	6	44.3423	-111.6920	2056
		Bunsen Peak	Yellowstone National Park	Wyoming	12	44.9218	-110.7195	2194
		Summit*	Wasatch National Forest	Utah	11	40.9192	-110.6473	3090
		Eagle*	White River National Forest	Colorado	7	39.6099	-106.4021	2868
		Gunnison*	Gunnison National Forest	Colorado	5	38.6162	-106.5003	3109
		Larimer*	Arapaho-Roosevelt National Forest	Colorado	12	40.3772	-105.3533	2720
	Black Hills	Tillson Creek	Black Hills National Forest	South Dakota	10	44.1859	-103.8353	1965
		Nahant School	Black Hills National Forest	South Dakota	10	44.1989	-103.7740	1786

δ Subepcies further classifed as var. *yukonensis* (Strong 2010)

* Samples collected via the USFS Forest Inventory & Analysis Program

Table 3.2: Descriptive statistics for all sampling locations sampled in this *Pinus contorta* population genetics study.

Subspecies	Site	N	*PPL*	N_A	N_E	H_E	uH_E	*F Index*
ssp. *murrayana*	Wellman's Divide	10	100	4.200	2.734	0.452	0.476	0.320
	Hidden Lake Drive	10	90	4.100	2.805	0.472	0.497	0.243
	Onyx Peak	10	100	4.800	3.146	0.543	0.571	0.239
	Champion	10	90	4.900	3.064	0.516	0.543	0.267
	Dawson Saddle	10	100	5.500	3.179	0.647	0.692	0.427
	Big Meadow	10	100	4.000	2.238	0.468	0.495	0.299
	Horeshoe Meadows	10	100	5.100	2.851	0.570	0.600	0.194
	Crooked Meadows	10	100	6.000	3.418	0.560	0.589	0.061
	Tuolumne Meadows	10	100	4.800	3.148	0.449	0.472	0.149
	Levitt Meadows	10	100	4.800	2.887	0.500	0.527	0.220
	Luther Pass	10	100	4.600	3.163	0.563	0.594	0.224
Among sites		*110*	*98*	*4.800*	*2.967*	*0.522*	*0.550*	*0.323*
ssp. *bolanderi*	Russian Gulch	10	80	4.100	2.637	0.420	0.442	0.064
	Van Damme Pygmy	10	90	4.400	2.844	0.451	0.474	0.272
	Van Damme	10	90	4.200	2.804	0.480	0.505	0.021
Among sites		30	*87*	*4.233*	*2.762*	*0.450*	*0.474*	*0.193*
ssp. *contorta*	Spring Ranch	10	80	3.400	2.311	0.389	0.409	0.120
	Patrick's Point	10	90	4.300	3.012	0.539	0.568	0.272
	Towala Dunes	10	100	4.800	2.798	0.486	0.509	0.125
	Port Oxford	10	90	4.100	2.696	0.527	0.558	0.189
	Sand Dunes	10	90	4.800	2.887	0.473	0.498	0.142
	Old Sitka	10	100	5.100	3.086	0.573	0.603	0.177
	Blanket Bog	10	100	4.100	2.491	0.522	0.549	0.030
	Bay Bog	10	100	4.300	2.781	0.528	0.556	0.196
	Jumbo Bog	10	70	4.500	2.642	0.459	0.483	0.198
	Sundown Bog	15	100	4.600	2.481	0.489	0.508	0.180
	FAA Bog	10	100	4.200	2.433	0.507	0.533	0.357
	Dundas Bay	5	80	2.500	1.940	0.390	0.433	0.143
	Dick's Arm	10	90	4.200	2.898	0.534	0.567	0.239
Among sites		*130*	*92*	*4.223*	*2.650*	*0.493*	*0.521*	*0.279*
ssp. *latifolia*	Alcan Highway	15	90	4.500	2.696	0.522	0.545	0.278
	Mt McIntyre	10	100	4.800	2.976	0.573	0.606	0.276
	Canol Road	20	100	4.400	2.423	0.494	0.511	0.329
	Pine Flats	10	90	5.200	3.689	0.589	0.621	0.303
	Edziza	10	100	4.700	3.084	0.562	0.595	0.104
	Smithers Community Forest	10	100	4.900	3.437	0.571	0.601	0.213
	Columbia Icefields	10	100	3.800	2.078	0.455	0.489	0.145
	Glacier Lake	10	100	5.300	2.903	0.522	0.551	0.085
	Windermere Kootenay	10	100	5.100	3.349	0.565	0.596	0.115
	Flathead	11	90	4.800	3.106	0.528	0.557	0.318
	Judith Basin	10	100	4.700	2.872	0.554	0.584	0.219
	Lewis & Clark	6	70	3.400	2.575	0.393	0.429	0.286
	Lemhi	11	100	5.700	4.244	0.602	0.631	0.290
	Idaho	3	70	2.300	1.874	0.350	0.420	-0.106
	Custer	8	90	3.900	2.582	0.493	0.549	0.184
	Valley	11	100	4.700	3.142	0.511	0.535	0.252
	Fremont	6	90	3.500	2.605	0.473	0.534	0.285
	Bunsen Peak	12	100	5.600	3.278	0.520	0.544	0.273
	Summit	11	100	5.000	2.907	0.572	0.600	0.268
	Eagle	7	90	3.800	2.797	0.511	0.551	0.359
	Gunnison	5	80	3.100	2.455	0.426	0.473	0.101
	Larimer	12	100	4.400	3.154	0.541	0.564	0.307
	Tillson Creek	10	100	4.700	2.604	0.502	0.530	0.181
	Nahant School	10	100	4.200	2.470	0.443	0.467	0.235
Among sites		*238*	*94*	*4.438*	*2.887*	*0.511*	*0.545*	*0.323*
Among subspecies		508	*100*	*13.825*	*4.217*	*0.375*	*0.560*	*0.054*
Among regions		*508*	*100*	*11.717*	*4.034*	*0.373*	*0.566*	*0.049*
Among all sites		***508***	***94***	***4.449***	***2.837***	***0.505***	***0.536***	***0.167***

PPL, percent polymorphic loci; N_A, mean number of different alleles; N_E, mean number of effective alleles; H_E, expected heterozygosity; uH_E, unbiased expected heterozygosity; *F Index*, *Fis* within populations and *Fst* among populations

Table 3.3: Results of Analysis of Molecular Variance (AMOVA) among *Pinus contorta* subspecies (*n* = 4), regions (*n* = 6), and sampling locations (*n* = 51). AMOVA results show that most of the genetic variation is partitioned within subspecies, regions, and sampling locations. A small, but statistically significant, portion is partitioned among these levels of analysis. The Fixation indices (F_{ST}, R_{ST}, *and* Φ_{ST}) estimate the level of genetic differentiation at each level. A value of 0 indicates panmixia, while a value of 1 indicates complete isolation.

N	Source of genetic variation	d.f.	SS	MS	%	F_{ST}^*	R_{ST}^*	ϕ_{ST}^*
4	Among subspecies	3	118.38	39.46	5	0.045	0.068	0.051
	Within subspecies	1012	3101.63	3.06	95			
6	Among regions	5	167.73	33.55	6	0.049	0.072	0.054
	Within regions	1010	3052.28	3.02	94			
51	Among sampling locations	50	597.44	11.95	13	0.133	0.442	0.089
	Within sampling locations	965	2622.58	2.72	87			

d.f., degrees of freedom; SS, sum of squares; MS, mean square

* P-value ≤ 0.001

Table 3.4: Results from Mantel and partial Mantel tests of the effect of geographic and ecological distance on genetic differentiation in *Pinus contorta*. The r^2 value shows that 12% of genetic variation is attributable to landscape resistance and 11% is attributable to landscape barriers.

Mantel or Partial Mantel Test	r^2	Mantel's r
Genetic ~ Geographic	0.029	0.170*
Genetic ~ Resistance	0.124	0.352*
Genetic ~ Barrier	0.106	0.326*
Genetic ~ Geographic | Resistance	-	-0.038
Genetic ~ Geographic | Barrier	-	0.011
Genetic ~ Resistance | Geographic	-	0.337
Genetic ~ Resistance | Barrier	-	0.145
Genetic ~ Barrier | Geographic	-	0.307
Genetic ~ Barrier | Resistance	-	0.037

In the partial Mantel tests, a vertical bar separates the main matrices (on the left) from the covariate matrix (on the right), which is partialed out in analysis.

* $p < 0.001$

Table 3.5: Comparisons of genetic differentiation among population genetics studies of *Pinus contorta*.

Subspecies	Region	Pop No.	H_e	F_{ST}	G_{ST}	R_{ST}	% Among Pop	% Within Pop	Marker Type	Reference
ssp. *murrayana*										
	CA and OR	4	0.1163	-	0.036	-	-	-	RAPDs	Fazekas and Yeh, 2006
	Sierra Nevadas, CA	11	0.522	0.079	-	0.363	8	92	EST SSRs	This study
ssp. *bolanderi*										
	Mendocino, CA	11	0.119 - 0.129	0.039 - 0.065	-	-	3 - 6	-	allozymes	Aitken and Libby, 1994
	Mendocino, CA	3	0.45	0.031	-	0.028	3	97	EST SSRs	Thus study
ssp. *contorta*										
	Coastal CA to BC	7	0.1131	-	0.079	-	-	-	RAPDs	Fazekas and Yeh, 2006
	Coastal CA to SE AK	13	0.493	0.142	-	0.605	14	86	EST SSRs	This study
ssp. *latifolia*										
	BC to Montana	19	0.151	-	0.067	-	-	-	RAPDs	Fazekas and Yeh, 2006
	Wyoming	22	0.543 - 0.708	0.01-0.02	0.111	-	-	-	EST SSRs	Parchman et al, 2011
	Yukon to CO	24	0.511	0.114	-	0.390	11	89	EST SSRs	This study
ssp. *latifolia* & *contorta*										
	Coastal PNW and BC	91	0.878	0.356	0.365	0.568	-	-	mtDNA	Godbout et al., 2008
All subspecies	Large portion of range	28	0.116	-	0.061	-	6	91	allozymes	Wheeler and Guries, 1982
	Large portion of range	31	0.1357	-	0.09	-	9	91	RAPDs	Fazekas and Yeh, 2006
	Entire range of species	51	0.373	0.167	-	0.442	13	87	EST SSRs	This study

H_E, expected heterozygosity; F_{ST}, Wright's inbreeding coefficient; G_{ST}, Nei's coefficient of genetic variation; R_{ST}, Slatkin's measure of genetic diversity under stepwise mutation model

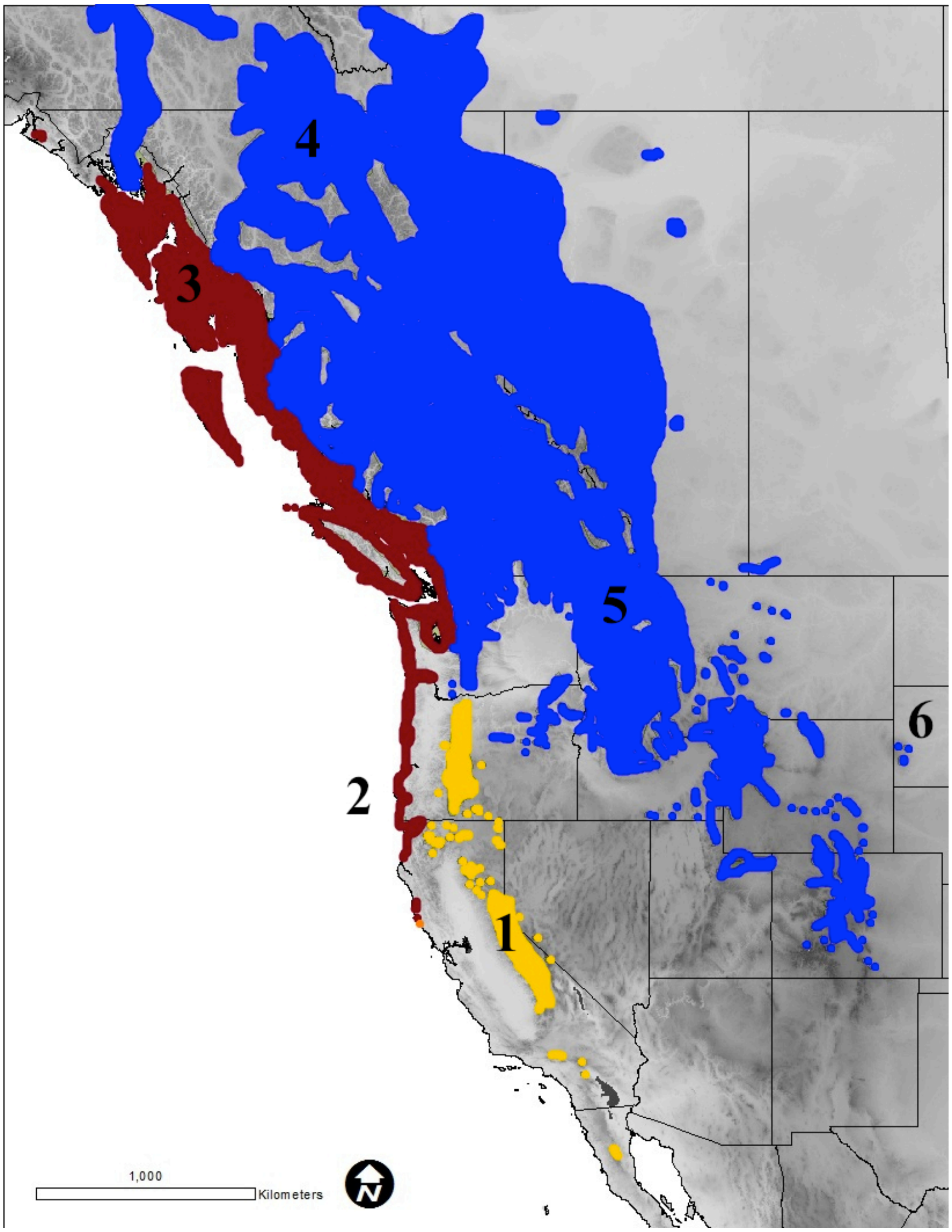

Figure 3.1: Distribution of the subspecies of *Pinus contorta*. Numbers represent regional delineation (Fenneman 1917). Blue = ssp. *latifolia*, red = ssp. *contorta*, yellow = ssp. *murrayana*, orange = ssp. *bolanderi*. Subspecies *bolanderi* is endemic to Mendocino county, California, and barely visible on this range-wide map.

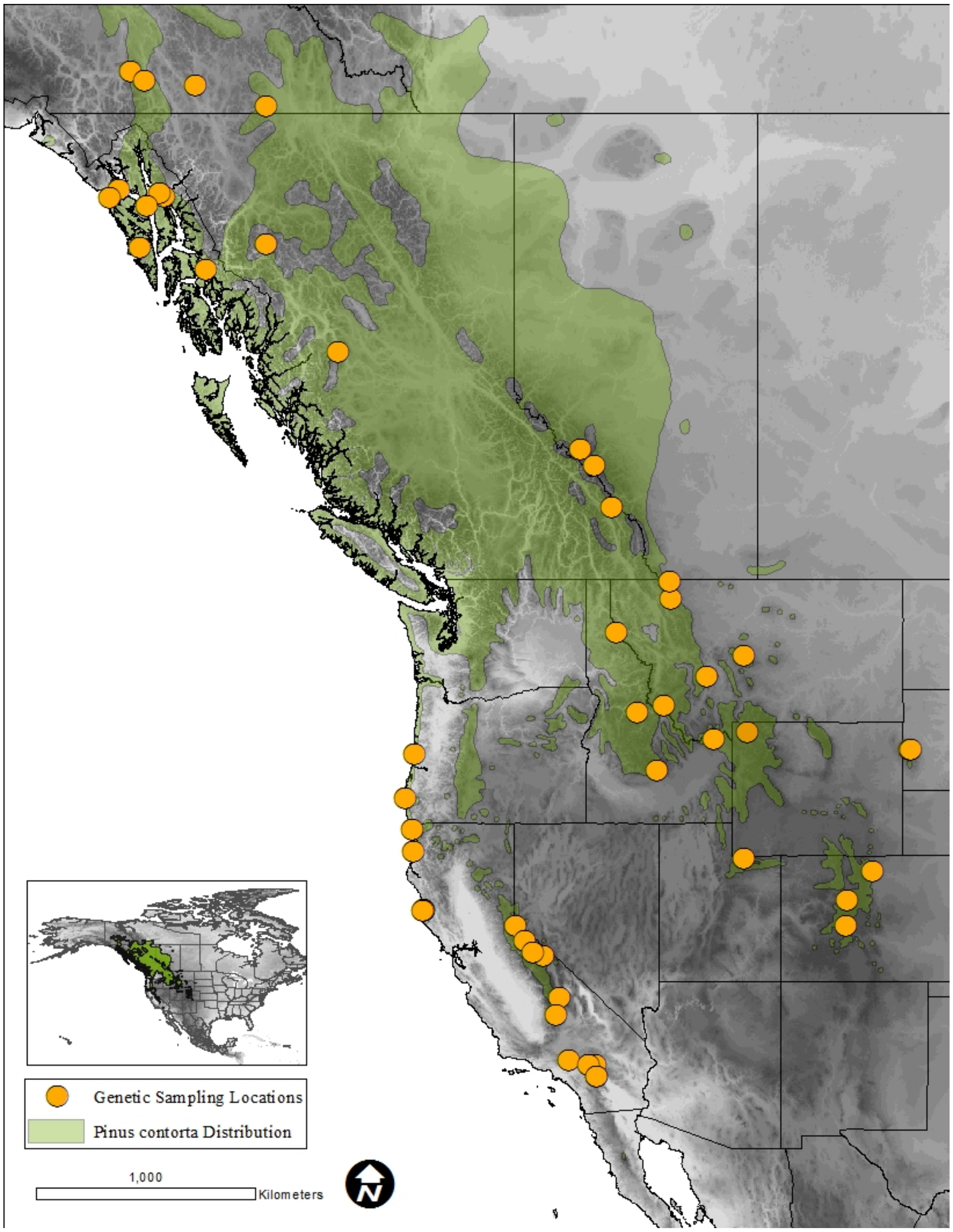

Figure 3.2: Sampling locations across the range of *Pinus contorta* in western North America.

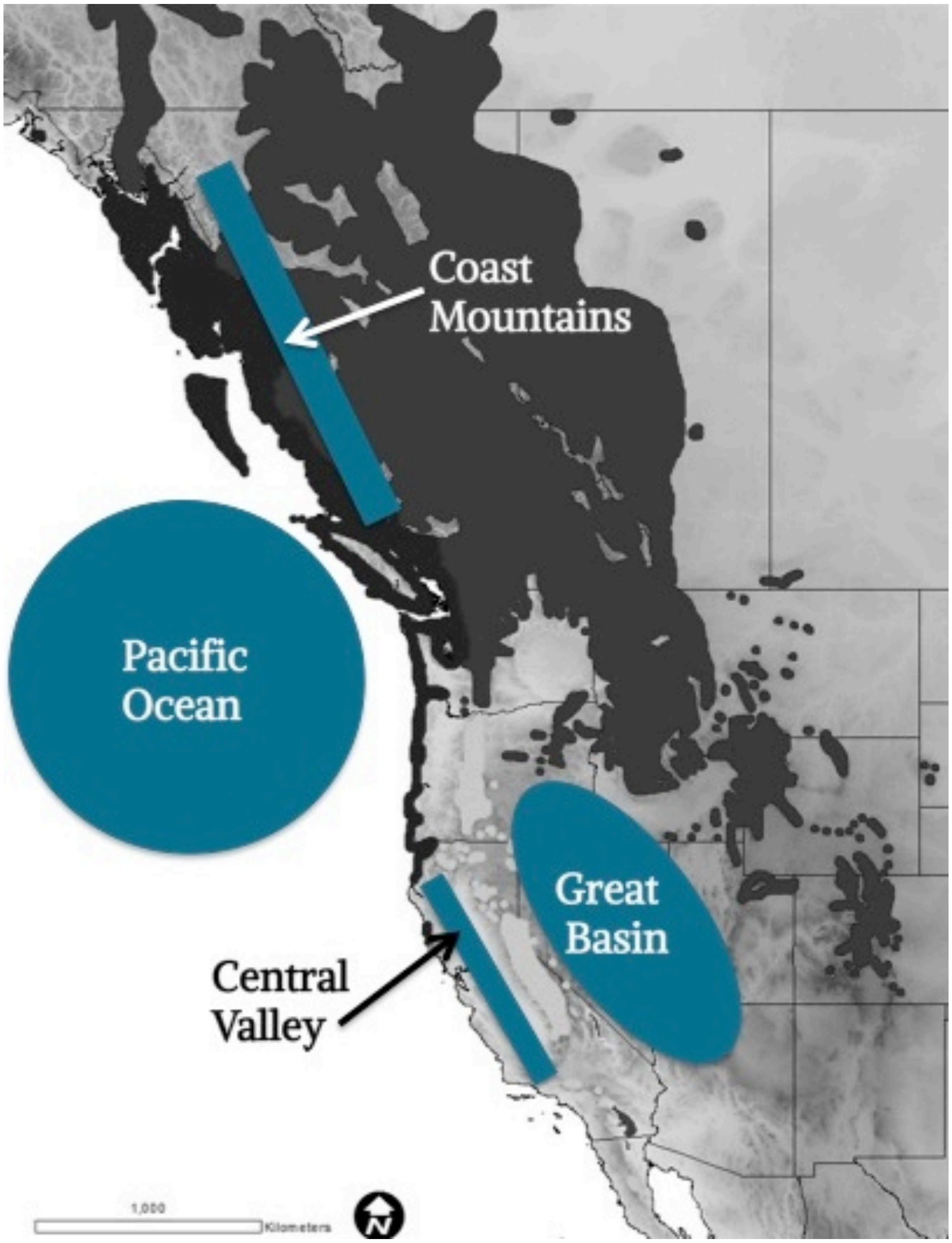

Figure 3.3: Potential barriers (*n* = 4) to gene flow across the range of *Pinus contorta*, including the Coast Mountains, the Great Basin and Intermountain West region, the Central Valley of California, and the Pacific Ocean.

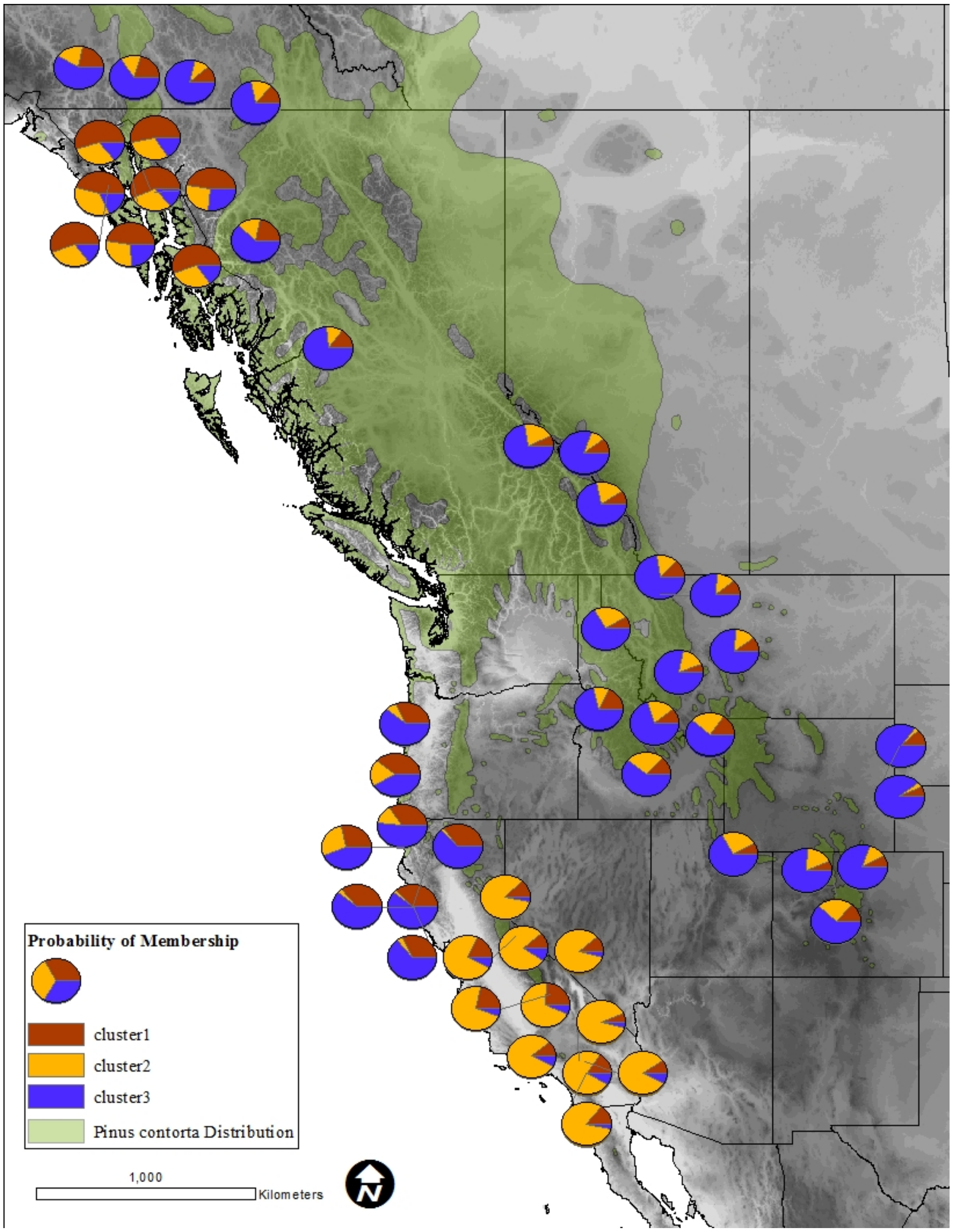

Figure 3.4: Population structure of *Pinus contorta*, as identified by replicated STRUCTURE analysis and merged using CLUMPP. Probability of membership to each genetic cluster (*n* = 3) is represented by a population-level pie chart, indicating three genetic clusters with admixture across all populations.

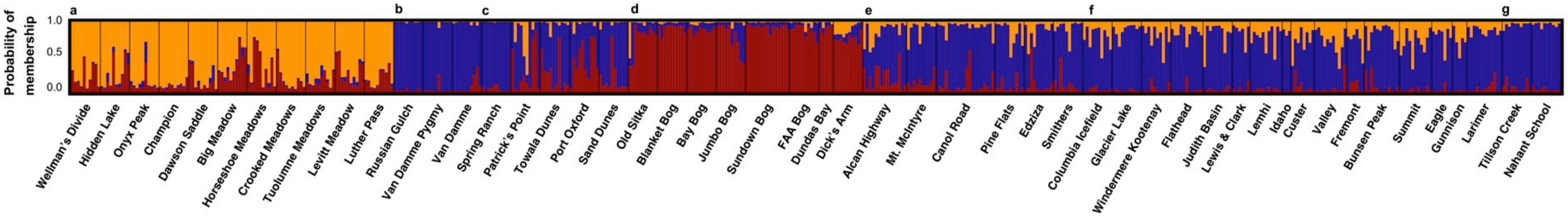

Figure 3.5: *Pinus contorta* population structure across western North America. Bars show the average probability of membership (*y*-axis) to each genetic cluster (*n* = 3) of individuals (*n* = 508) at each sampling location (*n* = 51) as identified by STRUCTURE. Populations are ordered from the southern Sierra Nevadas (California, USA) north to the Yukon Territory (Canada) and then south through the Rocky Mountains, allowing for visualization of each population in reference to adjacent populations and identified as: a) Sierras, ssp. *murrayana*, b) Coastal California, ssp. *bolanderi*, c) Coastal California to Oregon, ssp. *contorta*, d) Southeast Alaska, ssp. c*ontorta*, e) Yukon Territory to central British Columbia, ssp. *latifolia*, f) Rocky Mountains, ssp. *latifolia*, and g) South Dakota*,* ssp. *latifolia*

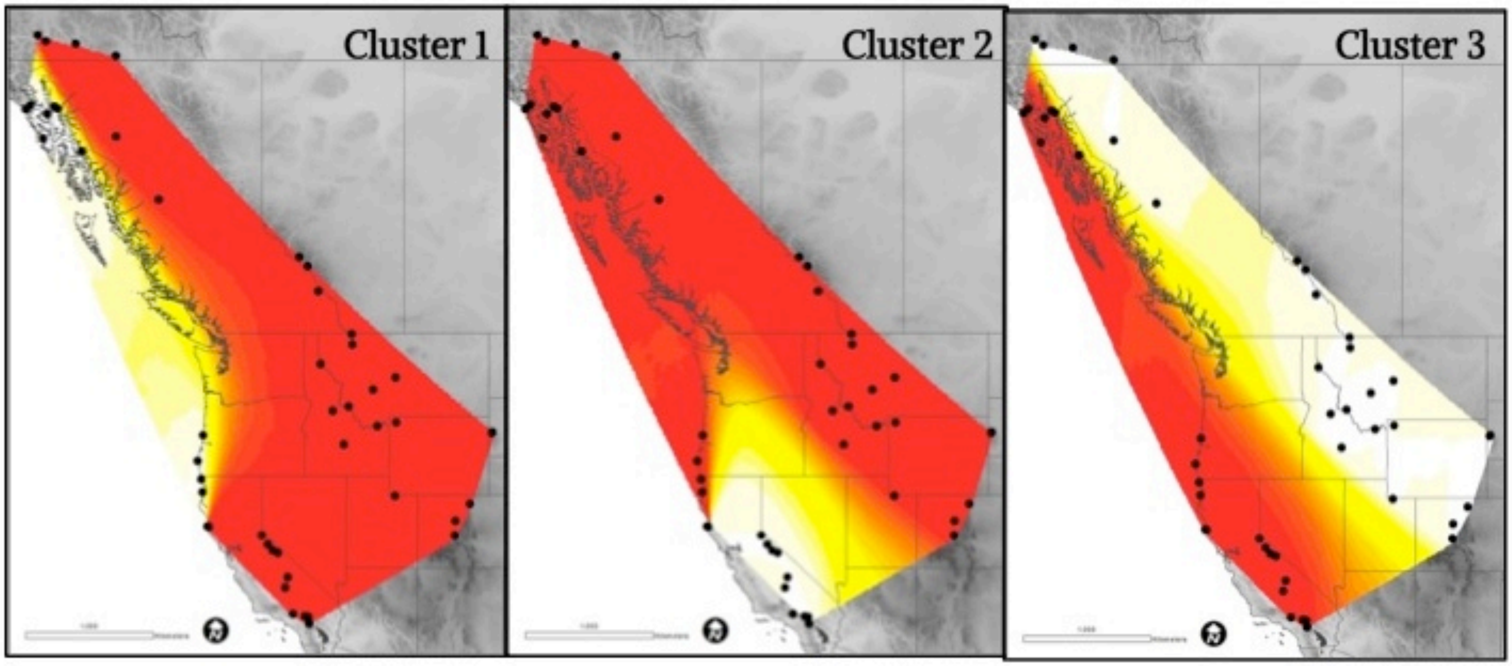

Figure 3.6: *Pinus contorta* genetic clusters (*K* = 3) as identified in GENELAND. Maps show posterior probabilities of cluster membership for each of the three inferred clusters. Color scaling indicates probability of membership to each cluster, with lighter shading (white to yellow) indicating the highest probability of cluster membership and a decreasing probability of membership as color darkens (orange to red). Black

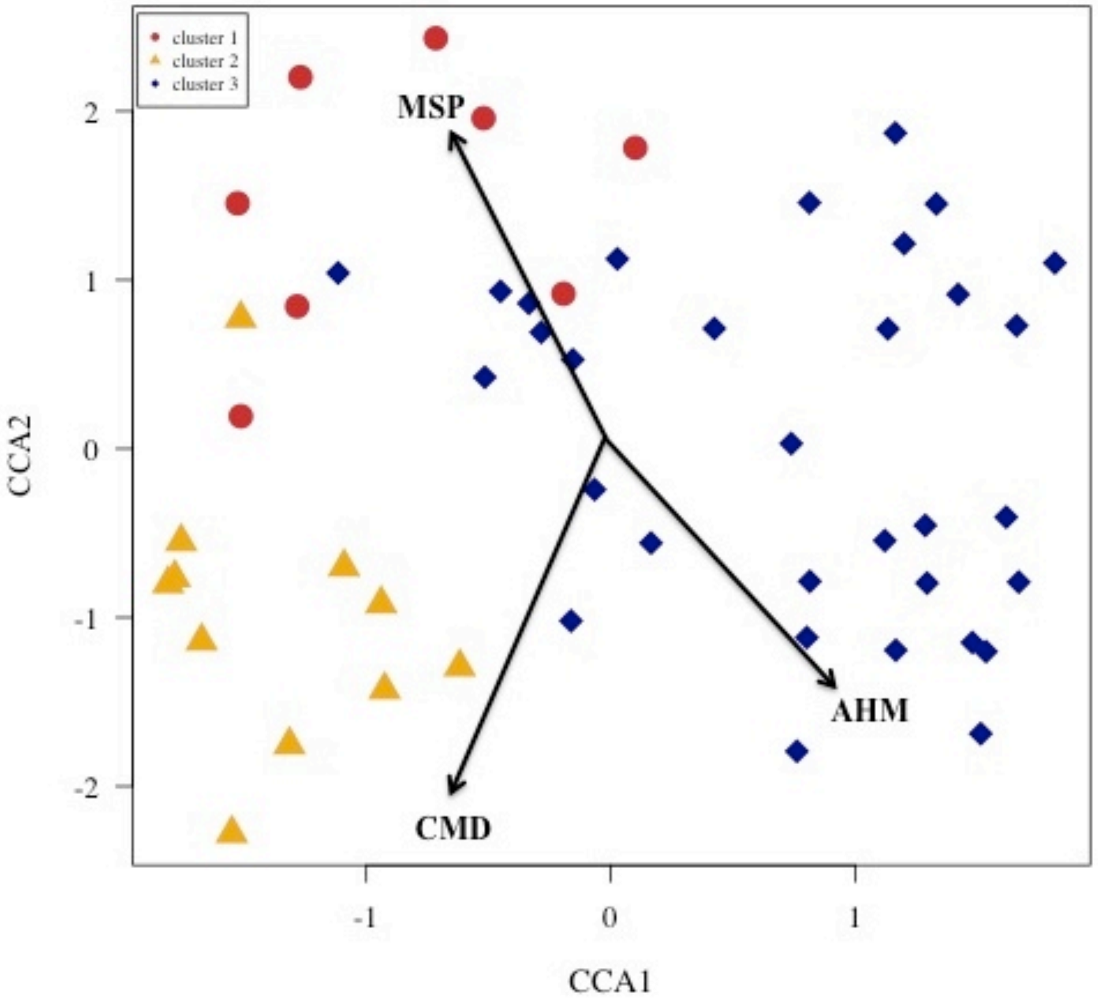

Figure 3.7: Canonical correspondence analysis of local environmental variables regressed on population differentiation (F_{ST}) of *Pinus contorta* sampling locations. Populations are coded by majority cluster membership (*n* = 3). MSP = mean summer precipitation (mm), CMD = climate moisture deficit, AHM = annual heat to moisture index. The first and second canonical axes explain 35% of the variation in population differentiation ($p < 0.001$).

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Appendix 3.1

Table A.3.1: Microsatellite (SSR) and chloroplast (cpDNA) markers used in this population genetics analysis of *Pinus contorta*.

Marker Name*	Marker Type	Primer Sequence - F	Primer Sequence - R	Repeat	Size (bp)	Annealing Temp (C)
69FR	cpDNA	TTTCGGGCTCCACTGTTATC	CGTACTCAATTTGTTACTAC	A_{10}	-	55
PICO1	SSR	ATGCGGTTTAACAAGCACTAC	GGATTGTCACCTGGACTAGAG	CTT	18	57
PICO4	SSR	ACACTGGGCTACAAAATTCAC	TTCCTTGCTCTTTTTATCAGC	CAT	21	57
PICO7	SSR	TCGCAAACCCTAATCAGAAC	CTGATATTGAGGCTGCTGTG	GCA	15	58
PICO77	SSR	GTGCTTGTGGTTGGATATTTG	AAGGAAGTTGGAAGACCGTAG	TGA	18	58
PICO104	SSR	CCTGATCAAGCCTTCAAATAC	GATGTTGAAAGATATCCCATTG	ATT	42	56
PICO109	SSR	AAAAGGGTTCCTTATGCACAC	AAAACCAACCACGTATGTGTC	TG	34	58
PICO138	SSR	GAAGTGGTGCCTCTATGTTTG	ATGCAAATGGAAGAACTTGTG	TG	34	57
PICO154	SSR	AGTCTCAAAATGGACAAGTCG	ACCTAACATAACCGCAATCAC	TG	40	57
PICO179	SSR	TCACGAAAGACCTTGAAAGAC	CCAAGAAAGACAAGGAGTCAC	ATG	33	57

* All markers from Lesser *et al.* 2011 (Supplementary Material) with the excpetion of 69FR (Stoehr & Newton 2002).

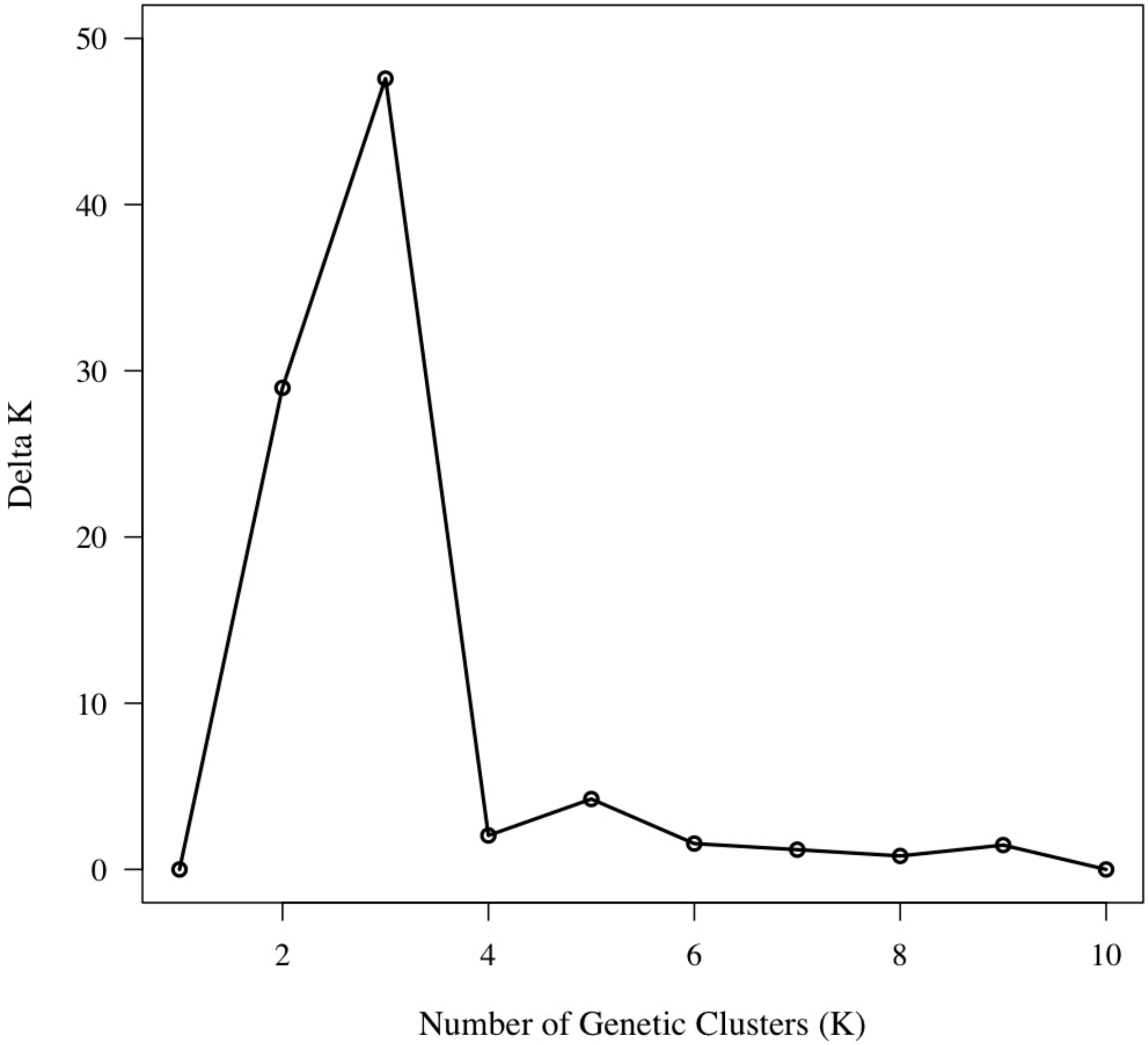

Figure A.3.1: Evanno et al. (2005) plot for detecting the most likely value of *K* (number of genetic clusters) from the STRUCTURE output of *Pinus contorta* assignment testing.

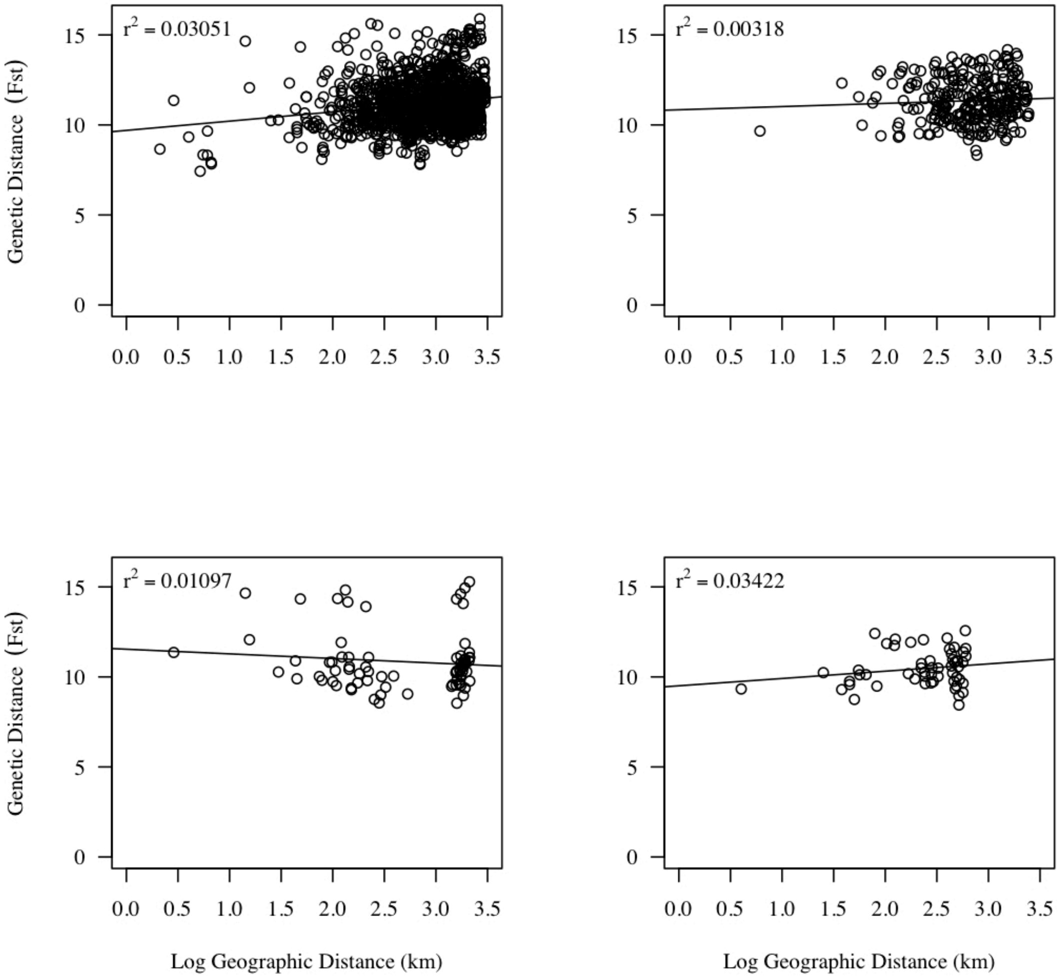

Figure A.3.2: Isolation by Distance (IBD) patterns across (clockwise, from top left) a) *Pinus contorta* (all subspecies), b) subspecies *latifolia*, c) subspecies c*ontorta*, and d) subspecies *murrayana*. Geographical distance only explains between 1% and 6% ($p < 0.001$) of the variation in genetic distance across the species.

4 Adapting to novel climates: predicting response of the subspecies of *Pinus contorta* to climate change

4.1 Introduction

Climate change is a primary threat to the health, productivity, and sustainability of forests across western North America (Field et al. 2007, Millar et al. 2007, Aitken et al. 2008). Over the next century, warming is anticipated to occur at a faster rate than during any recent ice-free era (Huntley 1991, Walther et al. 2002, IPCC 2007), and there is substantial evidence that changing climate has already significantly altered the distribution and abundance of many species (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan 2006). Trees are long-lived, sessile organisms with limited seed dispersal and slow migration rates. Researchers have documented a decline in local regeneration and the migration of subalpine tree species to higher elevations (Millar et al. 2004, Danby and Hik 2007a, 2007b). Continued shifts in climate are likely to expose additional tree species to unsuitable, or even novel, habitat within their current range of distribution. These species will then be forced to adapt or migrate in order to persist under future conditions.

Climate is credited as a main driver of species distributions, because it asserts strong selective pressure on natural populations (Clausen et al. 1940, Jump and Penuelas 2005). Local adaptation allows species to thrive under native conditions, and species often decline in fitness when subjected to foreign environments (Clausen et al. 1940, 1941). Many tree species, despite high gene flow, are hypothesized to be locally adapted to current habitat conditions (Hamrick et al. 1992). Adaptation to future climates may require rapid evolution of a suite of traits; the long lifespan and lengthy time to reproductive maturity may hinder this adaptive response for many tree species (Jump and Penuelas 2005). With climate change anticipated to continue at a rapid rate, tree species may be especially vulnerable to habitat loss if populations are unable to adapt to changes in local climate and environmental conditions (Hamrick 2004, Chuine et al. 2006).

A predicted consequence of maladaptation is the migration of plant species to higher elevations and latitudes, as the conditions to which they are adapted move outside of their current range (Jump and Penuelas 2005, Aitken et al. 2008). Migration requires successful dispersal and establishment in previously unoccupied portions of a species' range. This response may be the best option for long-lived, geographically-constrained tree species that have specific ecological niche requirements (Davis and Shaw 2001, Pfenninger et al. 2007, Sexton et al. 2009). Migratory rates, however, will need to not only exceed maximum post-glacial rates but also disperse across highly fragmented, human-dominated landscapes (Hamrick 2004, Millar et al. 2007). Consequently, all tree species are expected to experience lags in their response to changing climate (Clark 1998, Davis and Shaw 2001, Malcolm et al. 2002, Aitken et al. 2008). Identifying the habitats under which tree species may persist will be essential for forest conservation and management (Wang et al. 2010, Mimura and Aitken 2010).

Pinus contorta (Douglas Ex. Louden) is one of the most widely distributed trees in North America, playing an ecologically and economically important role in western forests from Baja California to the Yukon Territory (Critchfield and Little 1966, Wheeler and Guries 1982, Wheeler and Critchfield 1985). Its distribution encompasses an extensive geographic and climatically heterogeneous range, making it an appropriate species for examining the role of climate in determining tree species' occurrence. *Pinus contorta* has been divided into four geographically and morphologically distinct subspecies (ssp. *latifolia, contorta, murrayana,* and *bolanderi*) (Critchfield 1957). Each subspecies inhabits a discrete portion of the species' range, growing under and hypothesized to be adapted to local climate and environmental conditions (Ying and Liang 1994, Rehfeldt et al. 1999, 2001). It is unclear how the subspecies of *P. contorta* will respond to changing climate and if subspecies will respond concordantly to novel conditions. Tree species are expected to experience reduced ranges under rapid climate change (Clark 1998, Hamrick 2004), but, given its range of environmental tolerance, *P. contorta* may be able to adapt or migrate to suitable habitat under these changing conditions.

I used correlative and mechanistic models to evaluate potential, future habitat suitability at the species and subspecies levels of *Pinus contorta*. Correlative models assume that climate is the primary determinant of a species' realized niche, whereas mechanistic models represent the fundamental niche (Pearson and Dawson 2003). Correlative models were used to predict suitability based on occurrence records and local climate, while mechanistic models incorporated data on physiological tolerance into predictions (Buckley et al. 2010). Subspecies correspond to the genetic clusters I identified in Chapter 3 and are defined as subspecies c*ontorta, latifolia*, and *murrayana*. In this study, I asked two questions: 1) will *P. contorta* maintain its distribution over a large portion of western North America under predicted climate change? and 2) will subspecies (*contorta, latifolia,* and *murrayana*) respond differently to climate change? My main objectives were to 1) make predictions of habitat suitability across this widespread tree species and 2) examine whether incorporation of the distribution and physiological tolerance of each subspecies altered predictions of suitability.

4.2 Methods

Occurrence and Climate Data

Occurrence data was obtained from U.S. Forest Service Forest Inventory & Analysis (FIA, *accessed July 2010;* John Chase, Glenn Christensen, and John D. Shaw, *personal communication*) and British Columbia Ministry of Forests Biogeoclimatic Ecosystem Classification (BEC) (Will MacKenzie, *personal communication*) survey records. Presence records totaled 20,505 locations across western North America, with the extent of the species' distribution ranging from 30 to 65 degrees North latitude and -145 to -100 degrees West longitude. Modeling extent for predictions of future suitable habitat was expanded to 70 degrees latitude and -170 degrees longitude to encompass a greater area for potential distribution shifts. These occurrence records and this extent were used for species-level assessment. Clusters identified in population genetics analyses (Chapter 3) were used to subdivide the species' occurrence records into three locally adapted groups for modeling at the subspecies-level.

Current (1950-2000, WORLDCLIM, Hijmans et al. 2005) and future (A2, 2080, Canadian Global Climate Model 3) 1 km^2 resolution climate data were downloaded and prepared in ARCGIS 10.1 (ESRI, Redlands, CA). A Principal Components Analysis (PCA) was run in R 2.15.2 (R Core Team 2012) on WORLDCLIM variables for 20,505 randomly-selected points from across the range of *P. contorta* to identify and remove highly correlated climate variables. Of the 19 downscaled bioclimatic variables, five minimally correlated variables (correlation < 0.65) were selected, including mean annual temperature (°C), mean minimum coldest month temperature (°C), mean annual precipitation (mm), precipitation of wettest month (mm), and precipitation of driest month (mm). Distribution and environmental layers were clipped to match the study area. Processed layers were then used in MAXENT (Phillips et al. 2006) and ECOCROP (Hijmans and Graham 2006) for predictive habitat modeling.

Correlative Modeling

MAXENT v 3.3.3e (Phillips et al. 2006) was run at both the species- and subspecies-levels under the following settings: minimum training presence threshold, logistic output, 0.5 probability of presence, 25% of the data used as random testing points, and 50 replicates. Models used the 20,505 *P. contorta* occurrence records and processed climate layers to predict habitat suitability under both current and future distributions. This simulation estimated the probability of presence conditional on the environment, generating percent probabilities of a grid cell being suitable habitat (Elith et al. 2011).

Mechanistic Modeling

I used the ECOCROP model in DIVA-GIS 7.5 to run a mechanistic model of habitat suitability (Hijmans et al. 2005, Hijmans 2012). Prior to modeling, growth estimates and response curves were developed at the species- and subspecies-levels. Growth data was obtained from the British Columbia Illingworth provenance trial tests (Illingworth 1978; Nick Ukrainetz, *personal communication*). In 1974, provenance field trials were developed across 60 sites in British Columbia to evaluate genotype by environment interactions for 142 *Pinus contorta* populations (Figure 4.1). I calculated biomass accumulation rates for each population over the 32-year sampling period by using the following equation (Jenkins et al., 2003):

$$bm = \mathrm{Exp}\,(\beta_0 + \beta_1 \ln dbh) \tag{4.1}$$

where bm is total overstory biomass (kg dry weight), dbh is diameter at breast height (cm), and $\beta_0 + \beta_1$ are species-specific parameters. Plot-level biomass was calculated for each subspecies by summing individual tree biomass values and estimating values at the provenance-level (Jenkins et al. 2003). I averaged population-level biomass at each provenance location for each subspecies.

CLIMATEWNA (Wang et al. 2006a, 2012) was then used to extract local, growing-season climate data (1971 – 2010) for each population and each Illingworth Provenance location (Table 4.1). Population-level growth over the 32-year timeframe was used to develop temperature and precipitation response curves for each subspecies, which were assumed to be reasonable surrogates for subspecies' physiological response to local climate. The data were normally distributed, so I fit a Gaussian curve to the data for each subspecies using the *'nls'* function in R 2.15.2 (Angilletta 2006, Angert et al. 2011). Curves were used to identify the following threshold values for ECOCROP input: killing temperature (KT), minimum temperature for growth (T_{min}), maximum temperature for growth (T_{max}), minimum temperature for optimal growth (T_{optmin}), maximum temperature for optimal growth (T_{optmax}), minimum rainfall for growth (R_{min}), maximum rainfall for growth (R_{max}), minimum rainfall for optimal growth (R_{optmin}), and maximum rainfall for optimal growth (R_{optmax}). Minimum and maximum growing periods (G_{min} and G_{max}) were extracted from CLIMATEWNA output and averaged for each subspecies. Thresholds were developed from population-level data for both the species and subspecies models (Table 4.2).

Model Evaluation

A threshold of 60% probability of suitability (0 = lowest suitability, 100 = highest suitability) was set for identifying suitable versus unsuitable habitat. Any predictions falling under the 60% probability mark were classified as unsuitable under future conditions (Angert et al. 2011). Suitability values were extracted and converted to binary presence/absence (0/1) values using the '*raster*' package in R 2.15.2. Range maps were created for all model runs using the new binary layers.

Model performance was evaluated using receiver-operating characteristics (ROC) and area under the curve (AUC). Estimates of the relative contribution of each environmental layer to predictions were also produced in MAXENT model output. These estimates allowed for identification of the environmental variable most important in driving model predictions. The higher the value for variable contribution, the better a variable was in predicting species' occurrence.

I calculated a number of metrics to compare predictions from correlative versus mechanistic models and under current versus future climate scenarios (Hijmans and Graham 2006, Angert et al. 2011). Percent of habitat lost was calculated from the total number of grid cells predicted to be classified as unsuitable over the 80-year timeframe (2000 – 2080). To evaluate correlative models against mechanistic models, I calculated relative range size (RRS) using the following equation (Hijmans and Graham 2006):

$$\mathrm{RRS} = -1 * (m/c - 1) \tag{4.2}$$

where m is the area the mechanistic model predicts as suitable, and c is the area the correlative model predicts as suitable. This metric was also calculated to assess the effects of climate change on predictions made under each model, where, in this case, m and c are the predictions for current and future conditions. The RRS score identifies the variance in range predicted by the two models (e.g. a score of 3 implies range size predicted by the correlative model is four times as large as that predicted by the mechanistic model). Finally, I ran a Wilcoxon test on RRS scores in R 2.15.2 to determine the statistical significance of differences between the correlative and mechanistic models under both current and future climates.

4.3 Results

Model predictions for current *P. contorta* habitat suitability were significantly different ($p < 0.05$) using MAXENT versus ECOCROP (Table 4.3). Both correlative and mechanistic model predictions recognized differences in local climate, and predictions at the subspecies- level were a more realistic portrayal of the physiological tolerance of local populations and the distribution of each subspecies. Suitability modeling in MAXENT was a better match ($p < 0.05$) to the current range of the species, while the EcoCrop model predicted suitable habitat outside of the species' current distribution (Figures A.4.1 & A.4.2).

Under future climate scenarios, both MaxEnt and EcoCrop predicted a loss of suitable habitat (30 and 36%) and shifts in the distribution of *Pinus contorta* (Figure 4.2). The extent of loss was greater under the MaxEnt model for all subspecies' runs, but loss of suitable habitat at the species-level was higher in EcoCrop (Table 4.3). MaxEnt predicted a nearly complete loss of habitat for subspecies *murrayana* (67%), but EcoCrop predicted that it would maintain more than half of its current habitat (Figure 4.6). MaxEnt also predicted a 64% loss in suitable habitat for subspecies c*ontorta*, with this loss much smaller (26%) in EcoCrop predictions (Table 4.3, Figure 4.4). Predictions of future *latifolia* habitat were more consistent in percent suitable habitat (Table 4.3, Figure 4.5). Although models predict some loss of habitat, suitable *P. contorta* habitat is maintained across much of its current distribution.

All MaxEnt models had high values for goodness of fit (AUC values >0.93; Table 4.4). The importance of climate variables to model predictions varied across models and subspecies (Table 4.4). Mean annual precipitation was the most important predictor of ssp. *contorta* occurrence (AUC = 0.98), but mean annual temperature was the best predictor of ssp. *latifolia* and *murrayana* occurrence as well as species-wide predictions (AUC = 0.94, 0.99, and 0.98; Table 4.4). Mean precipitation of the driest month was also a strong predictor in both *latifolia* and species-wide models.

The negative RRS values (Table 4.3) suggest that the change in range size as predicted using the correlative model were consistently smaller than those predicted in the mechanistic model. Values closest to zero included predictions for ssp. *latifolia* (current, 0.09) and at the species-level (future, -0.04), indicating that predictions between correlative and mechanistic models were not that different for these levels of analysis (Table 4.3). Conversely, the high negative RRS value for future subspecies *murrayana* (-49) showed that model predictions were very different between the correlative and mechanistic model runs. In most instances, MAXENT predicted much greater habitat loss under future climate conditions.

4.4 Discussion

Pinus contorta is one of the most widely distributed tree species in western North America. It is reported to have the widest range of environmental tolerance of any North American conifer (Lotan and Critchfield 1990), allowing it to grow and survive under a wide range of habitat conditions. The subspecies of *P. contorta* already grow in sites known to limit the growth of other conifers, including peatlands, sand dunes, coastal rocky cliffs, and at treeline (Lotan and Critchfield 1990). I used correlative and mechanistic species distribution models to make predictions of future habitat suitability for this widespread tree species. I discovered three things in this analysis. First, species- and subspecies-level model predictions were not in agreement. This support the hypothesis that subspecies are adapted to local conditions and will respond individualistically to a changing climate (Ying and Liang 1994, Rehfeldt et al. 1999, 2001; Chapter 3). Second, incorporating physiological tolerance into predictions of current suitable habitat indicated that *P. contorta* could grow over a greater geographic extent than its current distribution. The predictions from mechanistic modeling suggest that *P. contorta* is excluded from some suitable, and potentially optimal, habitat, including lower elevations and in coastal habitats of California. My model predictions support conclusions from previous *latifolia* common garden research, which showed that the subspecies of *P. contorta* tend to grow outside of their optimum and are limited in occurrence by the effects of competition with other species (Rehfeldt et al. 1999, 2001). Third, mechanistic models predicted that each subspecies would maintain a portion of its habitat, while correlative models predicted a nearly complete loss of subspecies c*ontorta* and *murrayana*. The contrasting predictions suggest that the distribution of *P. contorta* could be limited by the effects of competition and disturbance rather than by an inability to grow under altered conditions.

Under species-wide correlative and mechanistic modeling, *Pinus contorta* was able to maintain a large portion of its range under both correlative and mechanistic model predictions. Some current habitat along the Pacific Northwest coast and in the southwestern United States was predicted to become unsuitable (Figure 4.2), but, overall, the species maintains its presence across the mountainous regions of western North America it currently occupies. Modeling at the species-level was biased toward the most widely distributed subspecies, *latifolia*. These models assumed that all subspecies would be able to tolerate the conditions under which this subspecies grows. These assumptions are, however, unrealistic given the distinct climate and environmental conditions each subspecies grows in. Subspecies-level predictions removed this bias and made predictions based on the physiological tolerances of each subspecies.

Plant populations are likely to be adapted to the local climate and environmental conditions from which they originated (Clausen et al. 1940, 1941), and the subspecies of *P. contorta* occur in geographically and climatically distinct regions (Critchfield 1957). My geographic analysis of genetic structure (Chapter 3) showed a strong association of population structure with climate variables and indicated local adaptation of the subspecies of *P. contorta*. Each subspecies is unlikely to respond in the same manner to the effects of climate change. The species-level models were dominated by ssp. *latifolia* records and assumed that subspecies would respond in a similar manner. Given the more narrow distributions of the other subspecies, subspecies-level modeling was more appropriate. Incorporation of physiological and subspecies-level data produced models that did not align with species-level predictions and altered model predictions of suitable habitat (Figures 4.3 – 4.6). Predictions at the subspecies-level indicated substantial niche segregation among subspecies and identified distinct drivers of occurrence for each subspecies. These drivers corresponded with local climate and support the hypothesis that each subspecies is locally adapted (Chapter 3). Given the distribution of each subspecies, the importance of these variables (Table 4.4) makes biological sense.

Pinus contorta may be able to grow over a greater geographic extent than it currently does. The mechanistic modeling predictions can be interpreted as representing the fundamental niche of the species, or the area within which existence is possible (Hutchinson 1957). By adding physiological tolerance into model predictions, current suitable habitat is predicted as greater than the species' range would suggest. For example, mechanistic models predicted lower elevations in the Sierra Nevada Mountains as suitable habitat for subspecies *murrayana* (Figure A.4.8), but this subspecies only grows at high elevations (1900 to 3200 m) in this region. These predictions support the results from common garden research in concluding that populations do not grow under their physiological optimum (Rehfeldt et al. 1999, 2001). *Pinus contorta* is a light-demanding species and thought to be most limited by competition from other tree species (Lotan and Critchfield 1990). Each subspecies may be able to tolerate a wide range of conditions but is constrained to its current to distribution by biotic interactions. For this species, correlative model predictions made at the subspecies-level may be a better estimation of future suitable habitat, because these models indirectly incorporate the biotic influence of competition and are representative of the realized niche of each subspecies.

Pinus contorta ssp. *latifolia* is one of the most important timber species in British Columbia, and numerous studies have focused on this subspecies and its potential response to climate change (Rehfeldt et al. 1999, 2001, Wang et al. 2006b, Coops and Waring 2010). My results support the common garden research of Rehfeldt and colleagues (2001) in concluding that *P. contorta* is physiologically able to grow over a greater extent than its current range. Prior work focused on subspecies *latifolia*, but model results indicate that this physiological response is true across all subspecies. My results also demonstrate that incorporation of subspecies-level analyses alters predictions and provides more biologically-realistic predictions of habitat suitability across the species' range. The realized niche of the species may be constrained by competition, while the fundamental niche of the species is actually much greater. *Pinus contorta* should maintain a large portion of its current range over the next century, but the response of the species to changing climate will vary by subspecies. The geographically-constrained subspecies, c*ontorta* and *murrayana*, are limited by both physiological tolerance and biotic interactions. These subspecies will not respond to changing climate in the same manner as subspecies *latifolia*. Management and conservation of *P. contorta* must be addressed at the subspecies level and account for the adaptations specific to each geographic range.

Predictions from species distribution models will not provide precise estimates of habitat loss. The true direction and magnitude of climate change is unknown, and understanding tree species' response to modern climate change will require better knowledge of geographic patterns of climatic adaptation. Interactions between habitat loss, unpredictable disturbance regimes, and rapid climate change are likely to impact a species a ability to adapt and migrate (Jump and Penuelas 2005). Regardless, species are likely to be impacted by this change, and knowledge on the potential response of our most ecologically and economically valuable species will be crucial to conservation and management efforts in light of a rapidly changing climate. Species range shifts have been predicted for many species and ecosystems (e.g. Malcolm et al. 2002, Morin et al. 2008, Notaro et al. 2012), and the ability of species to persist will depend on the responses of local populations (Sork et al. 2010). This is important for tree species, which are thought to be highly adapted to local conditions (Hamrick 2004, Savolainen et al. 2007, Aitken et al. 2008). Species distribution models provide a reasonable baseline for understanding how climate is likely to impact the distribution and persistence of *Pinus contorta*, one of western North America's most ecologically and economically valuable tree species.

Table 4.1: ClimateWNA variables for past (1900), current (2010), and future (2080) climate. Presented is a subset of population-level data from each Pinus contorta subspecies.

Subspecies	Latitude	Longitude	Mean Annual Temperature (°C)			Mean Coldest Month Temperature (°C)			Mean Annual Precipitation (mm)			Number of Frost-Free Days		
			1900	2010	2080	1900	2010	2080	1900	2010	2080	1900	2010	2080
contorta	39.28	-123.76	11.6	12	15.3	8.6	9.3	12.3	1074	1104	1217	341	345	363
	42.19	-124.37	11.6	12.1	15.4	7.5	8.5	11.3	2041	2136	2321	346	349	363
	46.56	-124.04	9.8	10.2	13.3	4.6	5.6	8.7	1840	2005	2345	309	319	353
	49.35	-123.01	8.5	9	12.7	1.1	2.4	6.3	2103	2357	2682	274	289	351
	53.33	-129.71	7.1	7.6	11.1	0.6	1.9	6.6	4037	3626	4517	263	278	349
	59.37	-135.82	1.7	2.5	6.8	-12	-10.3	-2.6	994	1029	1308	142	153	214
latifolia	43.12	-122.04	4.3	4.5	8.3	-2.4	-1.5	2.6	1076	1219	1282	113	126	200
	45.11	-118.23	5.1	2.7	9.8	-4.3	-5.4	2.5	768	1610	963	161	108	261
	48.15	-117.14	6.8	7.4	11.3	-4.6	-3.4	1.3	616	724	822	173	192	276
	52.21	-122.39	2.9	3.4	7.3	-10.5	-8.9	-3.8	392	462	523	138	148	213
	56.12	-120.94	0.9	1.8	5.5	-15.6	-13.2	-7.4	367	453	588	139	155	195
	59.96	-130.34	-3.7	-2.7	1.7	-17.8	-15.9	-7.8	464	480	639	92	101	149
murrayana	34.13	-116.91	5.4	6	9.7	-2.1	-1.6	1.9	1104	1170	1059	122	139	199
	37.14	-119.10	4	4.1	8	-1.2	-1.2	2.4	1084	1159	1304	121	134	208
	39.26	-120.55	8.5	8.4	12.5	1.6	1.5	5.8	1660	1735	1945	197	205	281
	40.20	-121.27	8.1	8	12.1	-0.4	-0.3	4.2	932	964	1092	164	177	256
	41.19	-121.75	9.5	9.5	13.5	1.4	1.6	6	1506	1670	1862	221	232	306
Average difference (1900 to 2080)					**+ 3.8**			**+ 5.1**			**+ 232**			**+ 64**

Table 4.2: Mean growing season variables for *Pinus contorta* and each subspecies. Parameters were derived from ClimateWNA and Illingworth Provenance Trial (British Columbia, Canada) data. Values derived for use in ECOCROP modeling included: minimum temperature for growth (T_{min}), maximum temperature for growth (T_{max}), minimum temperature for optimal growth (T_{optmin}), maximum temperature for optimal growth (T_{optmax}), minimum rainfall for growth (R_{min}), maximum rainfall for growth (R_{max}), minimum rainfall for optimal growth (R_{optmin}), maximum rainfall for optimal growth (R_{optmax}), and minimum and maximum growing periods (G_{min} and G_{max}).

Model Run	T_{min} (°C)	T_{optmin} (°C)	T_{optmax} (°C)	T_{max} (°C)	R_{min} (mm)	R_{opmin} (mm)	R_{opmax} (mm)	R_{max} (mm)	G_{min} (days)	G_{max} (days)
contorta	1	11	14	18	300	600	900	1300	110	160
latifolia	0.5	10	14	17	125	250	450	600	70	150
murrayana	1.2	16	20	28	70	100	175	200	110	220
Full species model	0.5	10	15	18	150	250	500	1100	70	150

Table 4.3: Estimates of suitable habitat (in percent of landscape of western North America). Percentages are based on grid cells of suitable habitat of all grid cells used in prediction. Extent of analysis ranged from 30 to 70 degrees latitude and -170 to -100 degrees longitude. Relative range size (RRS) values assess the area predicted in correlative modeling (MaxEnt) against that predicted in mechanistic modeling (EcoCrop). The RSS values for change in area evaluate current versus future habitat for each model. $p < 0.05$ for all comparisons

Model	Current Area (%)			Future Area (%)			Δ in Area (%)			
	MaxEnt	EcoCrop	RRS	MaxEnt	EcoCrop	RRS	MaxEnt	RRS	EcoCrop	RRS
contorta	1.6	2.99	-0.90	0.56	2.2	-2.94	-64	-1.77	-26	-0.35
latifolia	22.4	20.4	0.09	11.5	13.3	-0.15	-43	-0.92	-30	-0.54
murrayana	0.25	7.17	-0.93	0.08	4.1	-49	-67	-2.03	-41	-0.73
Full species model	27.5	31.9	-0.16	17.6	18.3	-0.04	-30	-0.54	-36	-0.75

Table 4.4: Contribution of climate variables to model predictions in the MaxEnt models of current and future habitat suitability. **BOLD** values were the most important variables in determining species' occurrence. Receiver-operating area under the curve (AUC) values were used to evaluate model performance.

Model	Mean Annual Temp (°C)	Min Coldest Temp (°C)	Mean Annual Precip (mm)	Precip Driest Month (mm)	Precip Wettest Month (mm)	AUC Scores
contorta	3.3	6.5	**85.4**	13.0	0.9	0.98
latifolia	**40.5**	11.7	13.0	**31.9**	0.4	0.94
murrayana	**87.7**	2.9	0.9	0.4	8.1	0.99
Full species model	**48.0**	11.5	16.7	**22.3**	1.5	0.98

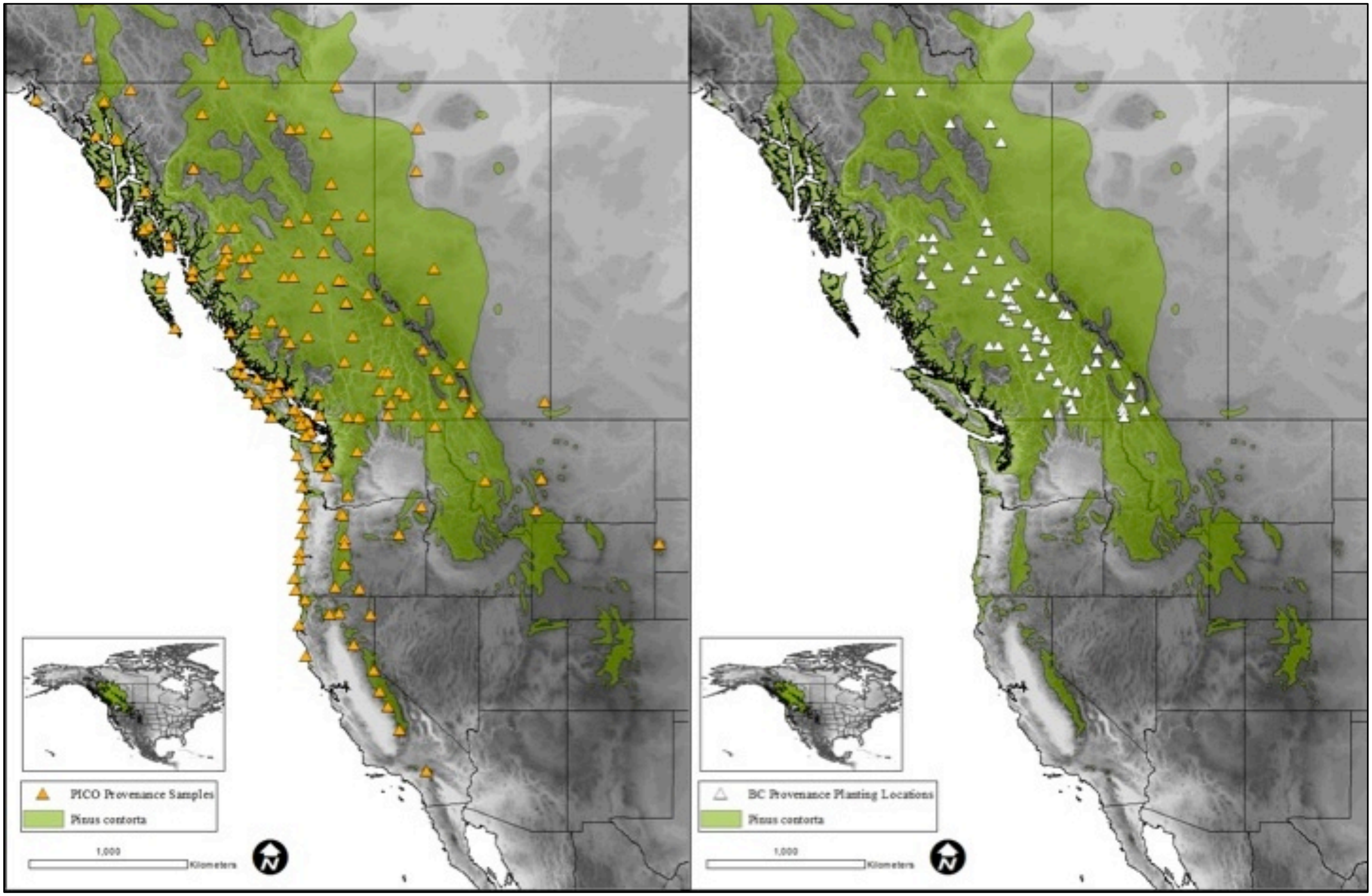

Figure 4.1: Illingworth Provenance Trial source populations (left) and planting locations in British Columbia, Canada (right). Data from these trials was used to estimate physiological tolerances of *Pinus contorta* populations to temperature and precipitation.

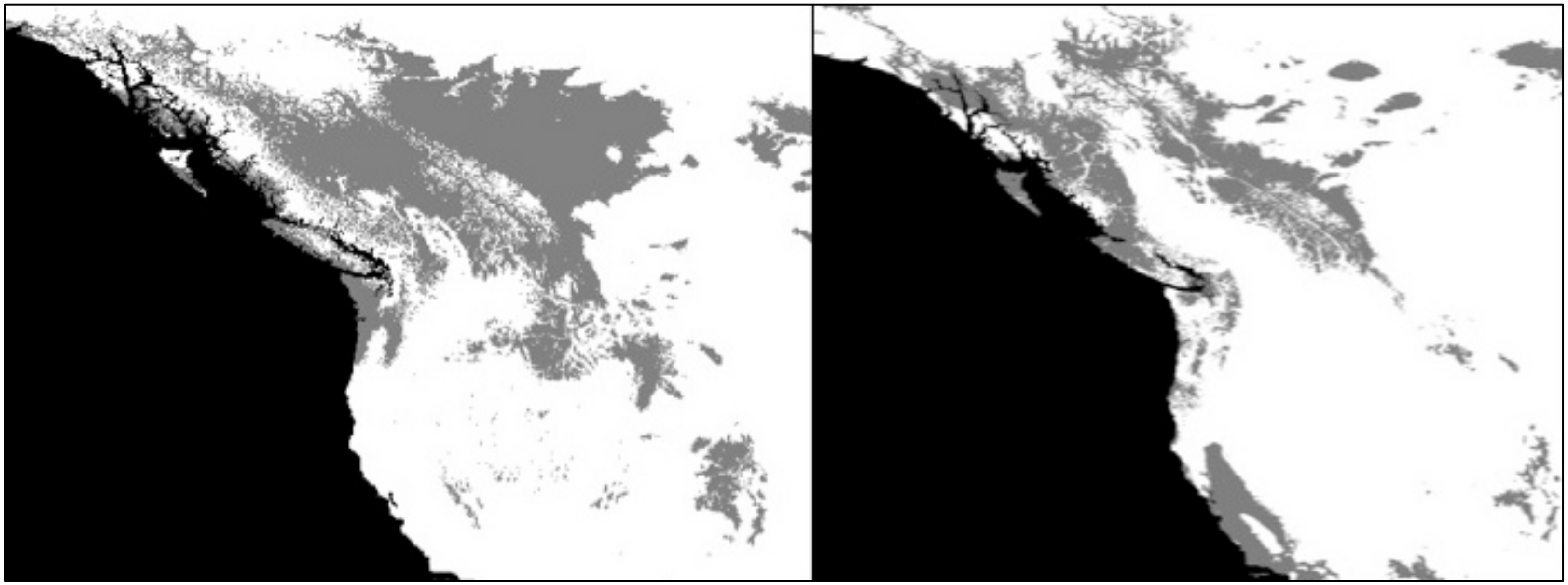

Figure 4.2: Species-level predictions of *Pinus contorta* suitable habitat in 2080 (A2 scenario) in MaxEnt (left) and EcoCrop (right). White = unsuitable, grey = suitable.

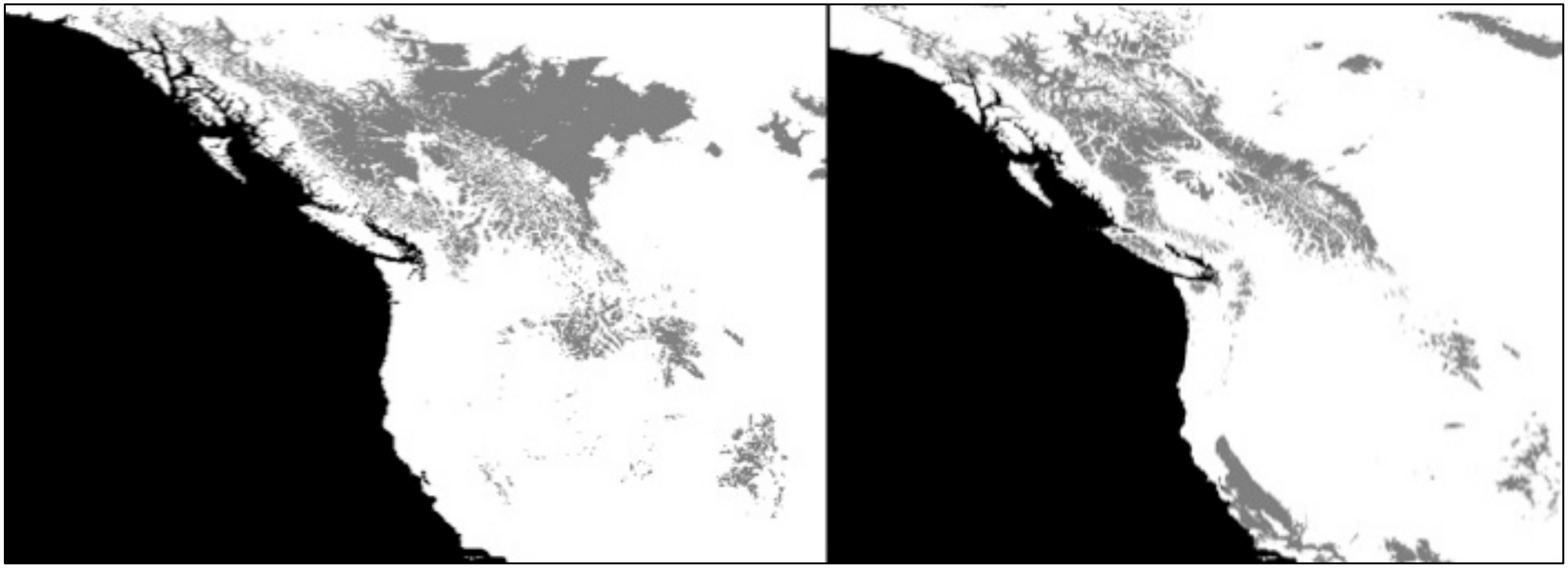

Figure 4.3: Predictions of subspecies *latifolia* suitable habitat in 2080 (A2 scenario) in MaxEnt (left) and EcoCrop (right). White = unsuitable, grey = suitable.

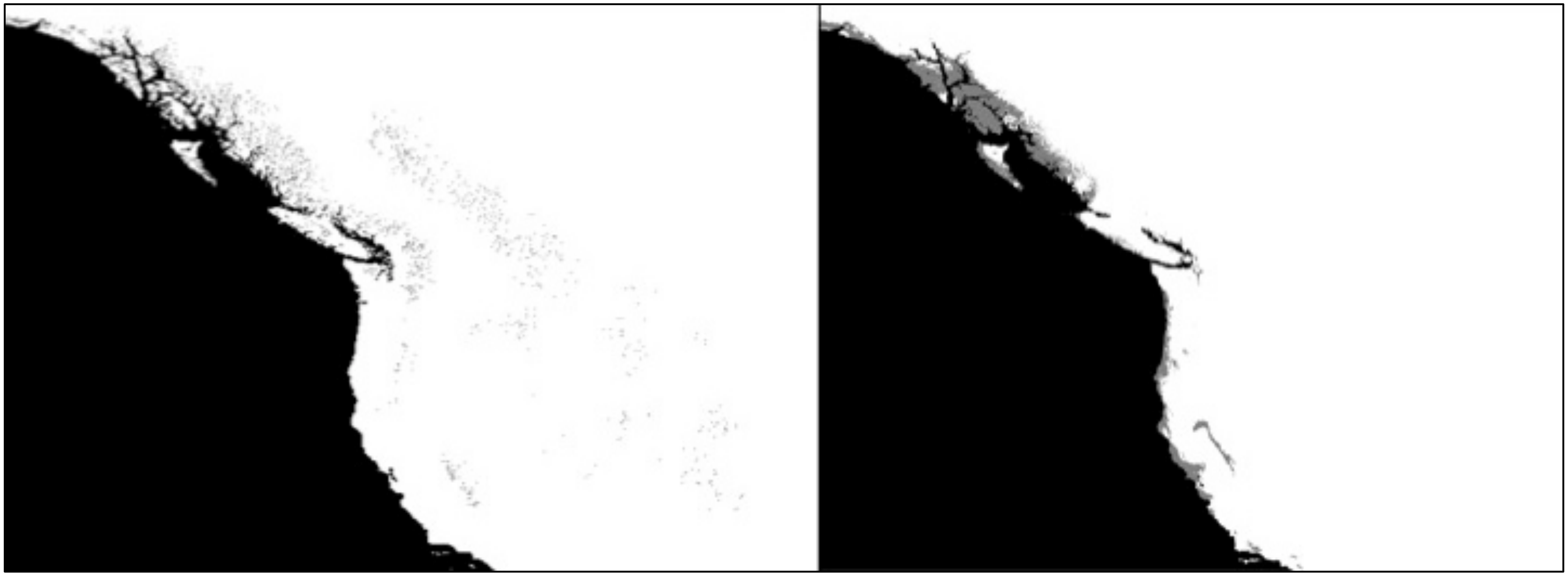

Figure 4.4: Predictions of subspecies *contorta* suitable habitat in 2080 (A2 scenario) in MaxEnt (left) and EcoCrop (right). White = unsuitable, grey = suitable.

Figure 4.5: Predictions of subspecies *murrayana* suitable habitat in 2080 (A2 scenario) in MaxEnt (left) and EcoCrop (right). White = unsuitable, grey = suitable.

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Appendix 4.1

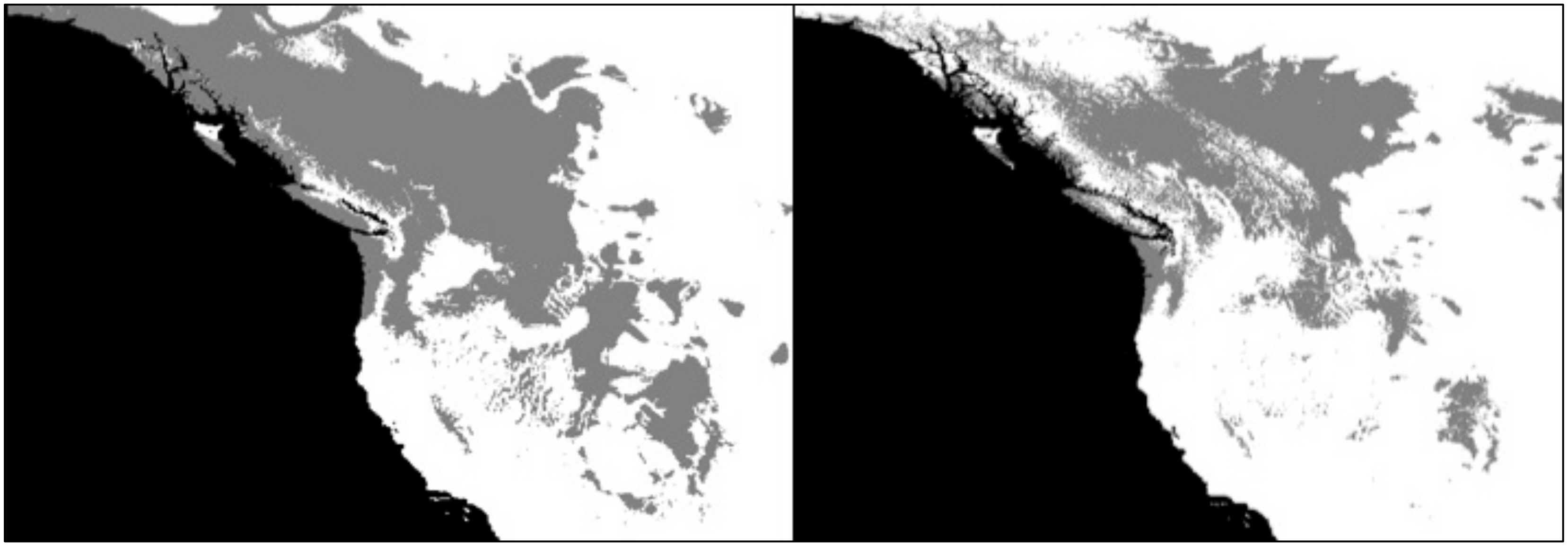

Figure A.4.1: MaxEnt species-level predictions of *Pinus contorta* suitable habitat under current (2010, left) and future (2080, A2, right) conditions.

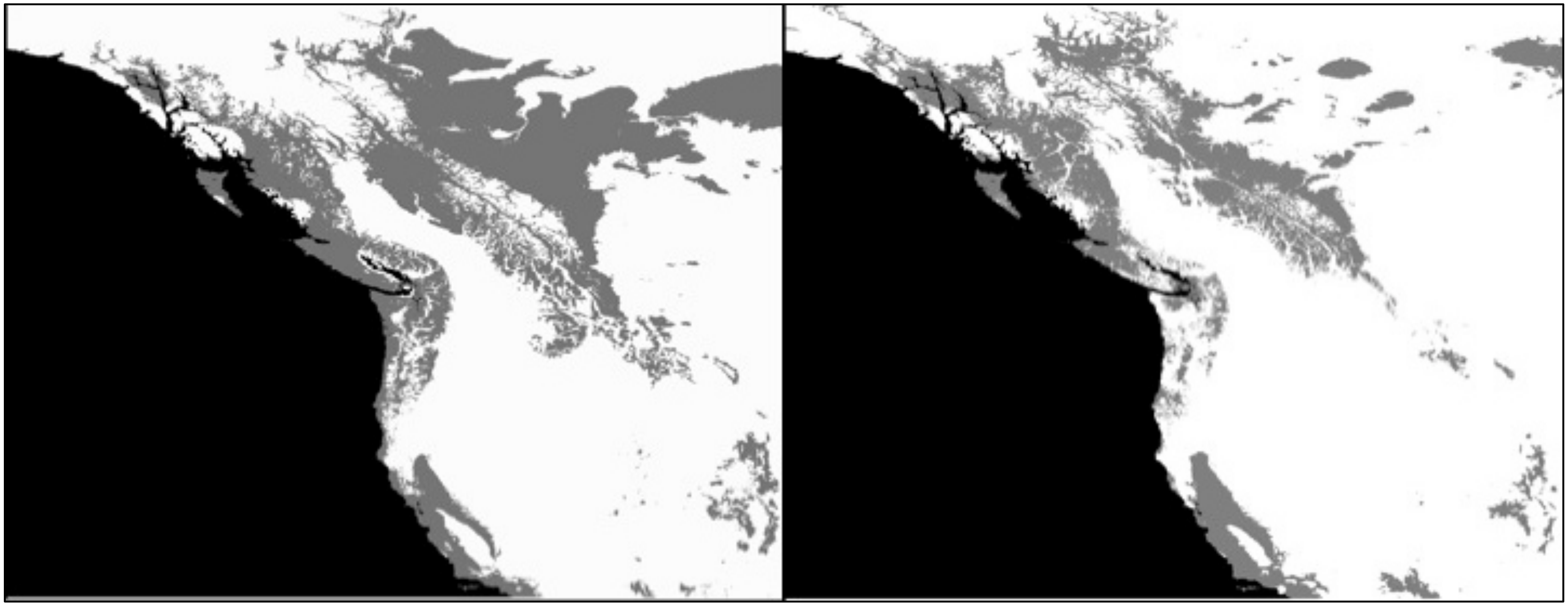

Figure A.4.2: EcoCrop Species-level predictions of *Pinus contorta* suitable habitat under current (2010, left) and future (2080, A2, right) conditions.

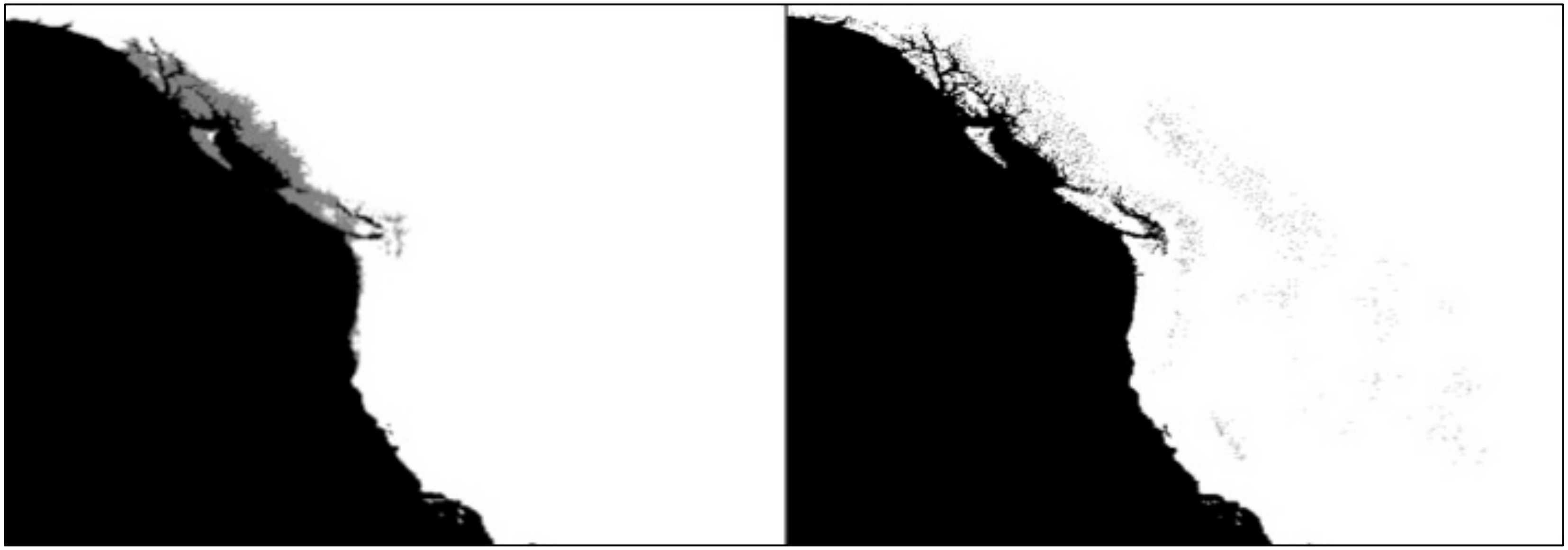

Figure A.4.3: MaxEnt predictions of subspecies *contorta* habitat under current (2010, left) and future (2080, A2, right) conditions.

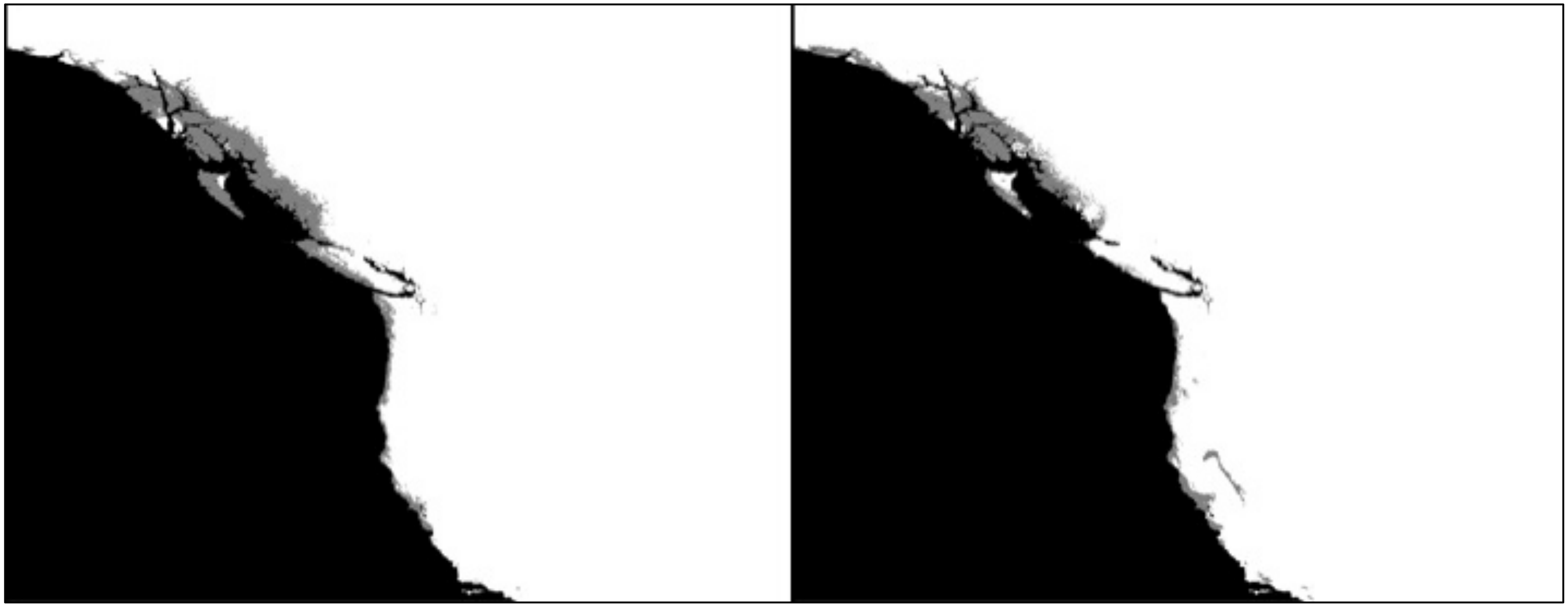

Figure A.4.4: Predictions of subspecies *contorta* habitat under current (2010, left) and future (2080, A2, right) conditions in EcoCrop.

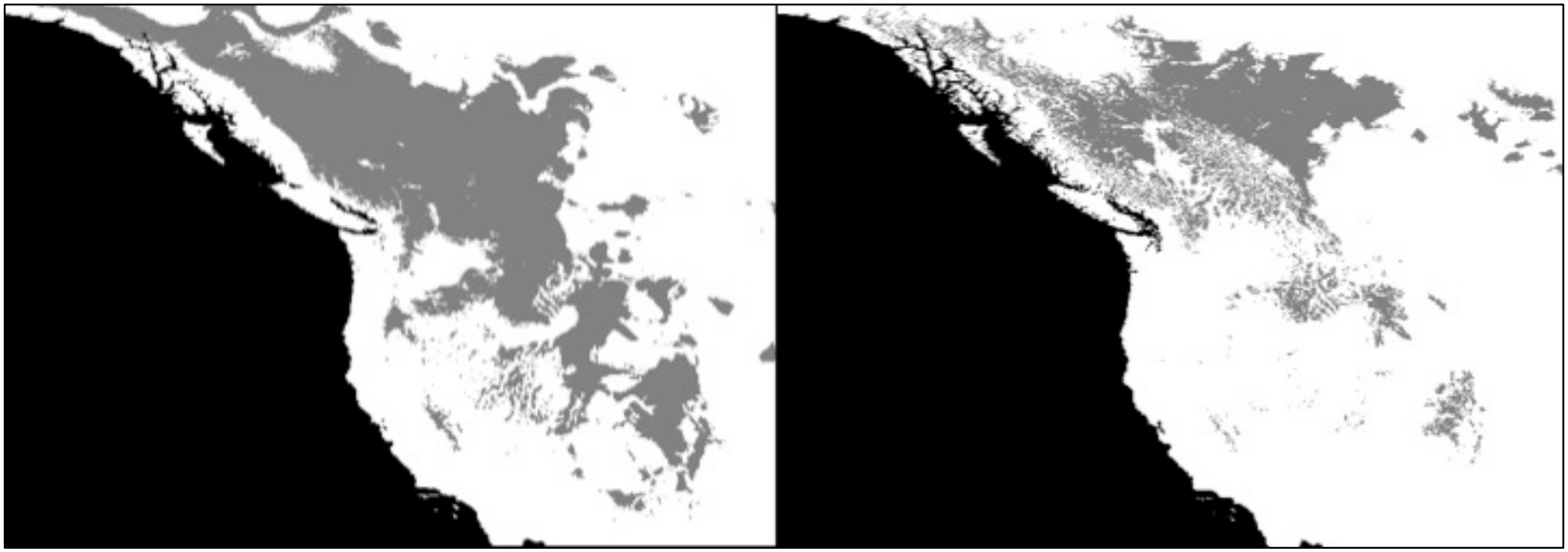

Figure A.4.5: MaxEnt predictions of subspecies *latifolia* habitat under current (2010, left) and future (2080, A2, right) conditions.

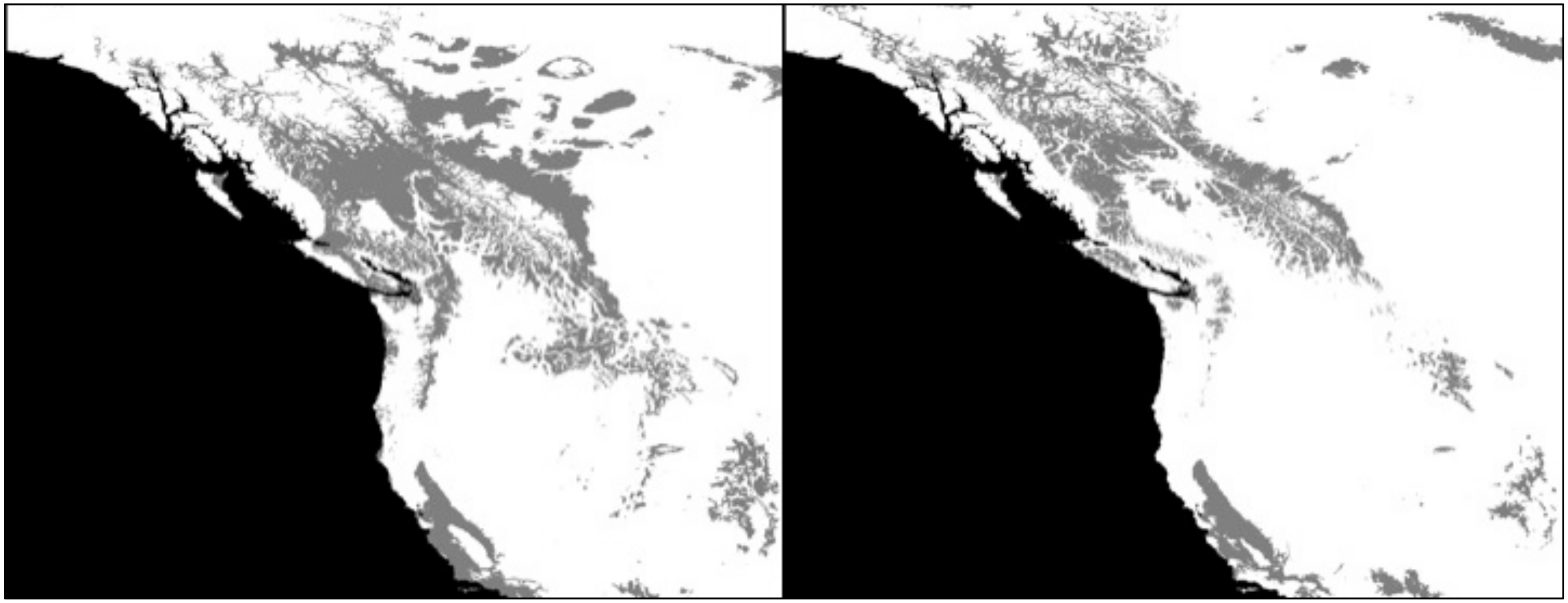

Figure A.4.6: EcoCrop predictions of subspecies *latifolia* habitat under current (2010, left) and future (2080, A2, right) conditions.

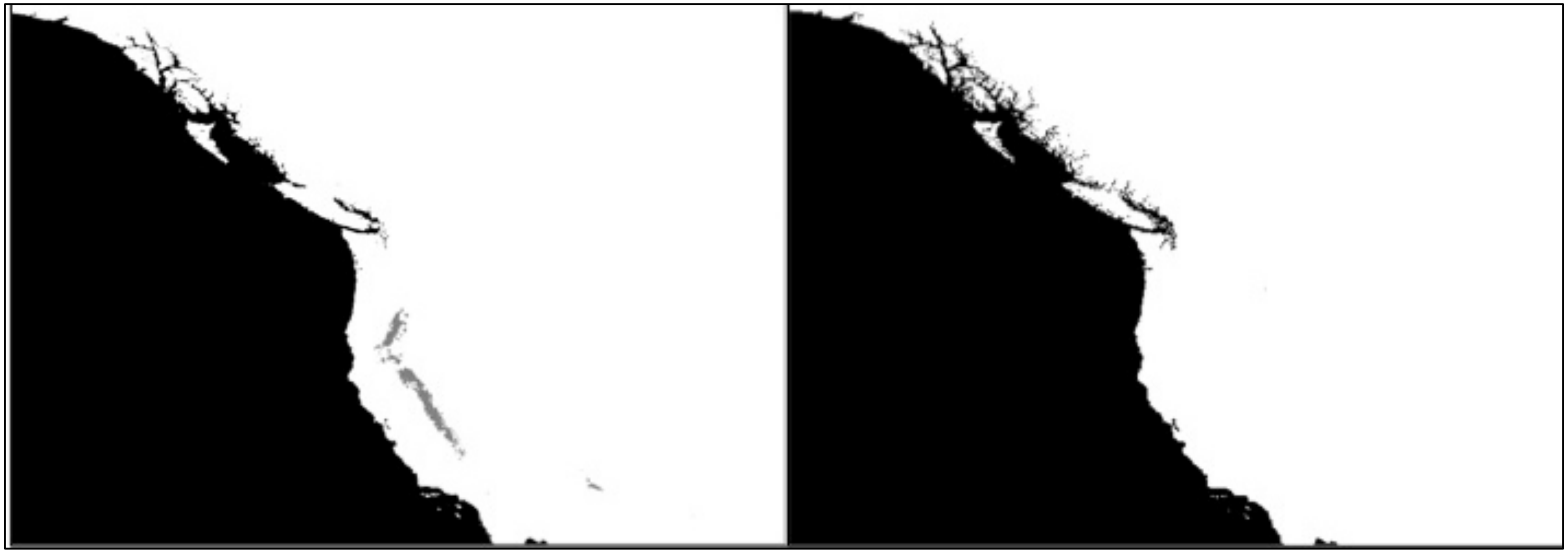

Figure A.4.7: MaxEnt predictions of subspecies *murrayana* habitat under current (2010, left) and future (2080, A2, right) conditions.

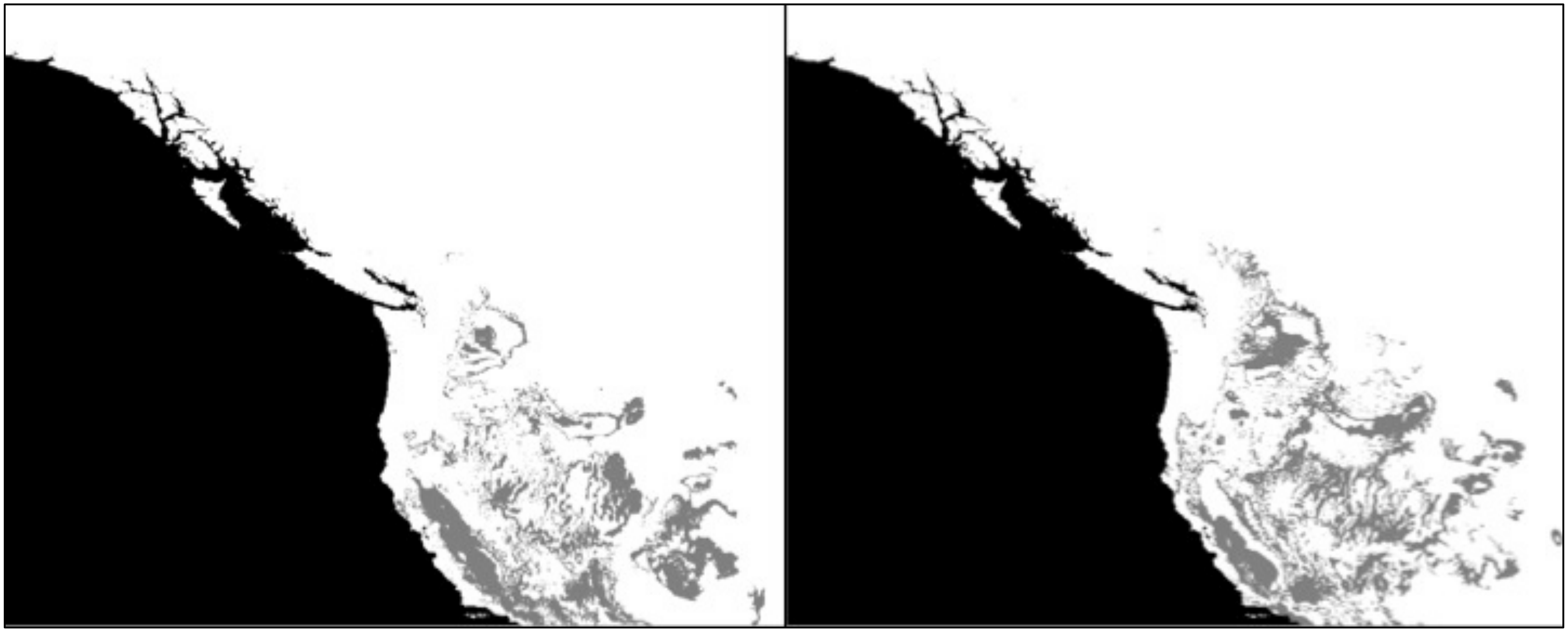

Figure A.4.8: EcoCrop predictions of subspecies *murrayana* habitat under current (2010, left) and future (2080, A2, right) conditions.

5 Synthesis

My dissertation research evaluated the relationship between distributional patterns of tree species and the processes driving these patterns from local to continental scales. I addressed three questions: 1) Which local abiotic and biotic processes are most important in determining the distribution of tree species along a hydrologic gradient in southeast Alaska? 2) How is genetic variation partitioned across the range of *Pinus contorta*, and is this variation explained by geographic or landscape variables? 3) How will *Pinus contorta* respond to predicted climate change?

At the local scale, I assessed the role of abiotic and biotic constraints in limiting three tree species (*Pinus contorta, Picea sitchensis,* and *Tsuga heterophylla*) along a hydrologic gradient in southeast Alaska. Model predictions identified abiotic variables, including soil nitrogen, pH, and depth to water, as the primary factors limiting species' success in anaerobic wetland ecosystems. Competition was identified as the limiting factor in aerobic forest ecosystems.

At the continental scale, I quantified the impact of historic evolutionary processes in shaping patterns of genetic diversity across the range of *Pinus contorta,* a widespread and morphologically variable species. Gene flow is high across the range of the species, and patterns of variation are most strongly influenced by landscape barriers to gene flow and the environmental variation associated with its heterogeneous range. This suggests that, despite widespread gene flow, subspecies are adapted to local conditions. I then used correlative and mechanistic species distribution models to evaluate potential, future habitat suitability at the species and subspecies levels of *Pinus contorta*. Model results predict that *P. contorta* will maintain a large portion of its current habitat, but two of the more geographically constrained subspecies will lose a significant portion of suitable habitat.

My work provides an understanding of the ecological and evolutionary processes shaping tree species distributions across a gradient of temporal and spatial scales, from historic to current timeframes and local to range-wide extents. Results from my research show that different processes determine patterns of distribution across this gradient of scales. Linking these patterns and processes will be essential for forest management and conservation in light of a rapidly changing climate.