CLIMATE VARIABILITY AND TREELINE DYNAMICS IN YELLOWSTONE AND GRAND TETON NATIONAL PARKS

by

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of the requirements for the degree

of

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ABSTRACT

Understanding the impacts of climate variability on high-elevation forests is of great importance due to the interest in upper treeline as an indicator of future change in protected mountain systems. While the location of upper treeline is primarily controlled by temperature, investigation of local treeline processes reveals considerable complexity in the spatial and temporal responses of species to various climatic parameters. The focus of the work presented in this thesis is to increase the understanding of the bioclimatic drivers of upper treeline species distribution and abundance in Yellowstone and Grand Teton National Parks. The species of interest in this ecosystem include: subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and whitebark pine (*Pinus albicaulis*). The abundance of whitebark pine is of particular interest due to its role as a food source for grizzly bears (*Ursus arctos*) and its recent decline in many systems due to the combined impacts of an introduced pathogen and native insect outbreaks. Using information on the current distribution of these treeline species, as well as data from soil surveys and spatially interpolated climate data, I was able to model future occurrence of treeline species across the Yellowstone landscape under various climate scenarios. These models provide managers with predictions of possible landscape-scale changes in subalpine forests over the next century. In addition, I used the influence of biophysical setting to examine the spatial and temporal response of species composition and abundance to moisture availability. Moisture availability has been shown to affect local processes, such as growth and recruitment of conifer species, on short temporal scales. Thus, processes that are more closely linked to moisture may serve as important indicators of future change. The results of this research provide information about alpine treeline dynamics that will allow managers to make knowledgeable decisions to protect these forest resources in the face of future change.

CHAPTER 1

THESIS OVERVIEW

Introduction

Understanding the impacts of global climate change on species distributions has become a focal point in ecology and natural resource management. Evidence shows that temperatures have increased substantially over the past century, and accurately forecasting future change has become a priority for climate change scientists (National Research Council, 2006). Of particular interest to ecologists, however, is developing an understanding of the ecological effects of climate change on biota. Studies addressing this issue have recently become prevalent in the ecological and climate-change literature (e.g., Inouye *et al.*, 2000; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Thomas *et al.*, 2004; Menzel *et al.*, 2006), and results have begun to raise the awareness of natural resource managers of changes that might occur in wilderness areas under their jurisdiction.

Responses of organisms to climate change are varied depending on the life history of the species. For long-lived, non-migratory species such as conifers, one of the most common responses is the alteration of species distributions. Insights from the paleorecord provide examples of species-specific shifts in response to past climate change, and future change is expected to lead to novel community assemblages, as opposed to groups of species shifting in unison (Davis & Zabinski, 1992; Whitlock, 1993; Bartlein *et al.*, 1997; Davis & Shaw, 2001). Defining the relationship between climate variables and historic and current species distributions can enhance our ability to predict future changes as climate models are modified to more accurately forecast changes.

The focus of the work presented here is alpine treeline, a dynamic ecotone that represents the limit of upright tree growth at high elevations. Alpine treeline represents a good system in which to study the effects of climate on vegetation because it is primarily controlled by abiotic factors (Körner, 1998; Körner & Paulsen, 2004). In addition, historic records present evidence of treeline responding to climate fluctuations throughout the past centuries and as recently as the last 100 years (Elliot-Fisk, 1983; Brubaker, 1986; Lloyd & Graumlich, 1997; Lloyd *et al.*, 2003; Bunn *et al.*, 2005; Lloyd, 2005). Since many treeline processes (e.g., growth rates, elevation) are sensitive to climatic parameters, it may also serve as a useful indicator of future change.

National parks serve as excellent areas in which to study the impacts of global change on vegetation community composition due to their pristine nature and relative lack of human-induced change (e.g., land-use change). However, while the national park system encompasses a rather expansive amount of land throughout the U.S., the parks serve as islands within a complex matrix of change and, as such, are not exempt from the impacts of large-scale threats, such as changing climate. Thus, to manage these relatively unaltered systems for maximum resilience to future change, it is necessary to understand historic and current changes that have occurred and to construct models that provide managers with the information they need to make informed choices for the future.

Integrating climate change and natural resource management is difficult for a variety of reasons. The accessibility of good-quality data in a format that is useful for managers is rare or non-existent for most parks. When the data is available, it is difficult for managers to incorporate possible future changes due to the uncertainties present in most models of future change and the apparent inability to control the processes that are causing the change. However, due to the influence of climate as a major driver of all ecosystems, it is imperative that climate variability and change be incorporated in some way into future natural resource planning. The first step towards this integration is designing research that can identify an association between climate and changes that are currently occurring within park boundaries.

The research contained within this thesis broadly addresses the impacts of climate on alpine treeline within the boundaries of Yellowstone and Grand Teton National Parks. Specifically, I sought to answer the following questions: 1) how will subalpine conifer species respond to predicted future changes in climate parameters; and 2) how do subalpine conifer species respond to spatial and temporal variability in moisture availability? When considered jointly, the answers to these questions provide insight into treeline forest community dynamics that will allow managers to make knowledgeable decisions to protect these forest resources in the face of future change.

The subalpine forests of the Greater Yellowstone Ecosystem are of particular importance due to the occurrence of whitebark pine, a species of special concern. Whitebark pine is a main food source of the grizzly bear (*Ursus arctos*), and its survival is threatened by a variety of factors, including an introduced pathogen, native insect outbreaks and changing fire and climate regimes (Tomback *et al.*, 2001). While the majority of management and monitoring efforts have been focused on understanding infection and infestation levels within whitebark pine stands, the frequency and magnitude of these disturbance agents are also dependent upon climate factors (Koteen, 2002; Logan & Powell, 2001; Logan *et al.*, 2003). In addition, the direct impacts of climate on whitebark pine have not previously been addressed at the scale of this study in these parks.

By designing a study that directly addresses the impacts of climate on treeline conifer species, I was able to show an association between climate and changes in subalpine forests of Yellowstone and Grand Teton National Parks. In the first chapter of this thesis, I develop a model using a robust statistical technique that establishes a relationship between bioclimatic variables and current species distribution. I then use the model to project possible future changes in the distribution of these species under three different scenarios. In the second chapter of the thesis, I address the spatial and temporal influence of moisture on species composition and abundance. Moisture is a particularly significant and rarely studied influence on treeline forests due to its importance in recruitment of individuals above current treeline and successful establishment of seedlings within the treeline ecotone (Germino *et al.*, 2002; Daniels & Veblen, 2004). Both of these processes—a change in elevation due to new recruits above current forest boundaries and densification of current treeline due to increased seedling establishment—can be useful indicators of change that can be monitored over long time scales. This thesis, therefore, provides important insights into subalpine forest community dynamics that can be incorporated into future management decisions to ensure the existence of treeline forests that are resilient to future change.

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CHAPTER 2

INFLUENCE OF BIOCLIMATIC VARIABLES ON TREELINE CONIFER DISTRIBUTION IN THE GREATER YELLOWSTONE ECOSYSTEM: IMPLICATIONS FOR SPECIES OF SPECIAL CONCERN

Introduction

Anomalous warming in the late 20th century (relative to previous centuries) has been documented and is anticipated to increase in the future (National Research Council, 2006). While species might respond to warming in distinct ways that are dependent upon their individual life histories, non-migratory species are likely to respond by shifting their geographical ranges, and evidence of such changes are emerging on the global scale (Parmesan *et al.*, 1999; Parmesan & Yohe 2003; Root *et al.*, 2003). In addition, paleoecological studies have documented individualistic responses of numerous taxa (including conifers) in the form of modifications of their spatial distributions, and future projections indicate that shifts in species' ranges might need to occur at unprecedented rates to match predicted changes in climatic variables (Davis & Zabinski, 1992; Whitlock, 1993; Bartlein *et al.*, 1997; Davis & Shaw, 2001).

Understanding the relationship between vegetation distribution and biophysical variables has been an integral part of biogeographical studies, and a better understanding of these relationships can improve our ability to predict future ecological responses to climate change (Bartlein *et al.*, 1997; Iverson & Prasad, 1998; McKenzie *et al.*, 2003; Bunn *et al.*, 2005; Norris *et al.*, 2006). Biophysical envelope models (also called environmental niche models) have become an increasingly common method for describing the influence of current and future climate on the distribution of species (e.g., Bartlein *et al.*, 1997; Iverson & Prasad, 1998; Hannah *et al.*, 2002; McKenzie *et al.*, 2003; Prasad *et al.*, 2006; Lawler *et al.*, 2006). By ‘training’ a model on current species distributions and biophysical parameters and assuming a static relationship between climate and vegetation in the future, predictions of future changes in distributions under various climatic regimes can be developed (Hannah *et al.*, 2002). These models detail species-specific responses to changes in physical parameters and increase understanding of processes controlling current and future species distributions.

Upper treeline represents a dynamic equilibrium between climate and vegetation, making it a good system in which to study forest community responses to climate. Trees in these ecosystems are under tremendous environmental stress, which can be greatly amplified or moderated by small changes in temperature or precipitation (Lloyd & Graumlich, 1997). Because treeline is believed to be limited worldwide by temperature, species inhabiting this ecotone are expected to be sensitive to temperature increases (Tranquillini, 1979; Rochefort *et al.*, 1994; Körner, 1998; Bassman *et al.*, 2003; Smith *et al.*, 2003; Körner & Paulsen, 2004). In addition to temperature, recent studies have shown that precipitation is influential to species establishment in this ecotone (Germino *et al.*, 2002; Daniels & Veblen, 2004).

Upper treeline, with its relative lack of human influences (e.g., such as land-use changes and hydrological diversions), is an ideal place to examine the impacts of climate on conifer species. National parks include extensive alpine and subalpine habitats and, therefore, provide substantial amounts of non-impacted land on which to conduct studies of future change. With the addition of the Inventory and Monitoring Program (I&M), the National Park Service has also expanded efforts to better understand impacts of climate variability on park resources.

My objective in this study was to improve understanding of the relationship between conifer species that comprise upper treeline in Yellowstone (YELL) and Grand Teton National Parks (GRTE) and biophysical controls on their distribution. Specifically, I focus on three conifer species that occupy treeline in the national parks of the Greater Yellowstone Ecosystem: whitebark pine (*Pinus albicaulis* Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). It was the goal of this study to focus specifically on treeline within park boundaries to better define the relationship between bioclimatic variables and the spatial distribution of high-elevation species within the parks. I also focused on using publicly available data on bioclimatic variables in order to present the model as an example of a low-cost method for incorporating climate change scenarios into natural resource management. The inclusion of ecosystem drivers and their effects on ecosystem function is especially important for natural resource management in protected areas, such as national parks, due to the limitations of stationary political boundaries and the subsequent impacts of these boundaries on the management of natural resources across large ecosystems that encompass numerous land-management agencies (Halpin, 1997).

The practical use of biophysical envelope models for describing future distributions of species is often limited because these models do not incorporate competitive interactions, dispersal ability or evolutionary change. In addition, these models assume equilibrium conditions exist between climate and vegetation that can then be applied to future climate-vegetation relationships (Woodward & Beerling, 1997; Davis *et al.*, 1998; Pearson & Dawson, 2003). However, niche models are particularly applicable in high-elevation ecosystems that are dominated by long-lived species that respond relatively slowly to environmental change (Pearson & Dawson, 2003). Two previous studies have explored the use of biophysical envelope models for projecting future climate impacts on forests in the Yellowstone region. Romme and Turner (1991) conceptually examined the consequences of three possible future climate scenarios on spatial extent and elevation of forest zones in the Greater Yellowstone Ecosystem. In addition, Bartlein *et al.* (1997) examined potential future distributions of various tree species within the Yellowstone region using a coarse-resolution climate model to understand the impacts of doubling carbon dioxide on species' ranges. I believe the focus on long-lived upper treeline conifer species and the use of a robust statistical technique that has strong predictive power exploits the positive aspects of envelope modeling and minimizes the downfalls of such a technique.

Methods

Study Area

Yellowstone and Grand Teton National Parks comprise the core of the Greater Yellowstone Ecosystem. Together, they represent approximately 2.5 million acres of reserves straddling the Wyoming, Montana and Idaho borders. YELL is dominated by a relatively flat volcanic plateau, with three major mountain ranges bordering the plateau, providing high-elevation subalpine and alpine habitats. This distinct topography has led to the description of two major climates for YELL, with the highest temperatures and lowest precipitation occurring in the large valleys of the northern portion of the park and graduating to lower temperatures and higher precipitation in the southwestern corner of the plateau (Despain, 1987; Whitlock & Bartlein, 1993). Grand Teton National Park also encompasses a wide variety of topography, including the Teton Range and numerous hectacres of riparian corridors and morainal lakes. Most of the precipitation for high-elevation areas in both parks is contained within the annual snowpack, which can reach five to ten meters during heavy snowfall years (National Park Service, 2006).

Soils in the Yellowstone region are highly influenced by the volcanic history of the region. Most soils found on lower-elevation plateaus are rhyolites of volcanic origin, while higher-elevation forests and meadows are underlain by andesites (Despain, 1990). Rhyolitic soils are comparably low in nutrients (particularly calcium) and are mostly sand, while andesitic soils are higher in plant nutrients and are texturally dominated by clay (Despain, 1990). Thus, vegetation species that require more nutrients and deeper rooting depths are believed to preferentially inhabit andesitic sites (Despain, 1990).

Vegetation Source Data

Data on the distribution of treeline species in YELL and GRTE was obtained from the USDA Forest Service Forest Inventory and Analysis Program (FIA). The goal of FIA is to determine the amount of timber available on public and private forested lands throughout the US by inventorying regularly spaced circular sample plots across the landscape (US Forest Service [USFS], 2001). For specific information on the sampling design used by the FIA Program, please refer to the FIA field guide (USFS, 2001).

Plot-level data obtained for this study included the geographic coordinates of each plot, topographic variables (including elevation, slope and aspect) and the number and size of all trees with a diameter at breast height (dbh) > 2.5 cm (where dbh is measured at 1.37 m above the ground). I converted species abundance data (e.g., dbh and number of stems of each species) to presence/absence values associated with each of the FIA plot locations. From these data a point shapefile was developed in ArcMap 9.1 (Environmental Systems Research Institute [ESRI], 2005) to show the location of each of the sample plots across the Yellowstone landscape (Figure 2.1).

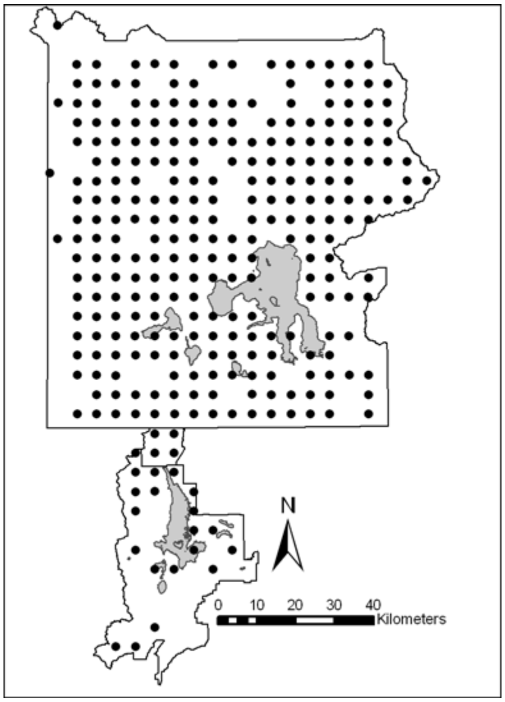


Figure 2.1. Map of the spatial distribution of FIA plots (black dots) that were used in the study. Areas without dots are either water or were missing data.

Climate Data

Climatic parameters were obtained from the DAYMET climate model, which uses spatial interpolation techniques and raw weather station data to account for variations in climate across the landscape due to topography and elevation (Thorton *et al.*, 1997). Mean values for the period 1980-1997 for 20 variables (Table 2.1) were downloaded as grids and clipped to the geographic extent of the study area. I then overlaid the vegetation plots on the DAYMET grids and extracted the values for the climatic variables at each of the plot locations.

Table 2.1. Bioclimatic parameters used as predictor variables in the models. Climate variables represent the mean value over the 18-year period from 1980-1997 at a 1-km scale.

Climate variables	*Soil variables*
Climate variables	Soil variables
Average air temperature	Depth to bedrock
Daily maximum temperature	Bulk density for 11 layers
Daily minimum temperature	Hydrologic soil group (4 groups)
Maximum summer (JJA) temperature	Porosity for 11 layers
Maximum winter (DJF) temperature	Rock fragment texture for 11 layers
Minimum summer (JJA) temperature	Rock fragment volume for 11 layers
Minimum winter (DJF) temperature	Sand, silt and clay fraction for 11 layers
Average summer (JJA) temperature	Soil texture for 11 layers
Average winter (DJF) temperature	Available water capacity at 100, 150 and 250cm depth
Maximum July temperature	
Maximum January temperature	
Minimum July temperature	
Minimum January temperature	
Total annual precipitation	
Total winter precipitation	
Total summer precipitation	
Daily average water vapor pressure	
Frost days	
Growing degree days	
Daily total shortwave radiation	

Soils Data

Soils data were derived from CONUS-SOIL digital soil maps, based on data from the USDA Natural Resources Conservation Service as part of the State Soil Geographic Database program (Miller & White, 1998). The goal of the CONUS-SOIL dataset is to provide soils data for GIS-based analyses in a systematic format across the continental US. Eleven variables (Table 2.1) that described the texture, water holding capacity and depth of the soil were used (Miller & White, 1998). Raster datasets at a 1-km resolution were downloaded, clipped to the study area and soil variables were extracted for each of the vegetation plot locations.

Future Climate Scenarios

Future climate predictions for biophysical envelope modeling are generally taken from global circulation models (GCMs); however, the applicability of these models at a regional scale has been questioned due to their coarse resolution (Bartlein *et al.*, 1997). Therefore, I chose to examine the sensitivity of treeline species to possible changes in climate by using one possible scenario of future climate that falls within the predicted future range of climate variables predicted by GCMs for the Northern Rockies and Yellowstone region (e.g., Bartlein *et al.*, 1997; Hansen *et al.*, 2001) but does not follow a specific model of future climate. This model was used to predict future presence/absence values at each location under three climate change scenarios: (1) an increase in temperature by 4.5°C and an increase in precipitation by 35%; (2) an increase in temperature by 4.5°C only; and (3) an increase in precipitation by 35% only. Theoretically, these three scenarios demonstrate the individual effects of changing temperature and precipitation on species distributions as well as the combined effect of changing both variables. Based on warming rates observed during the past century and future projected changes (Hansen *et al.*, 2001; National Research Council, 2006), this scenario serves as a conservative estimate of possible future changes in the region.

Data Analysis

All analyses were performed in the R 2.3.1 statistical environment (R Core Development Team, 2006). I used the random forest prediction method for understanding current and future relationships between vegetation distribution and climatic and soil parameters. Random forest is a recently developed modeling technique that is based on classification (and regression) tree analysis (CTA [Breiman, 2001]). Due to their hierarchical nature, random forest and CTA are capable of capturing non-linear relationships in predictor variables, which can be particularly useful with climate and soil variables that often exhibit complex relationships. However, random forest departs from CTA by developing hundreds to thousands of classification trees where each tree is built using a random subset of the data and a randomly chosen suite of predictor variables at each node. The trees are then aggregated. Thus, many trees are grown and collected to provide more stable models and error rates, whereas CTA is highly influenced by minor variations in the data (e.g., different random subsets of samples often produce substantially different models). Few parameters in the random forest model can be manipulated (e.g., the number of trees grown, the number of variables to try at each split), and the outcome is not very sensitive to modifications of these parameters. I optimized the number of classification trees grown (1000) and predictor variables tried at each split

(93, or 66%) to minimize the ‘out-of-bag’ (OOB) error estimate, which is described below (Liaw & Weiner, 2002). No overfitting of trees—a common occurrence in CTA—occurs when using random forest. Thus, random forest is believed to be a useful modeling method for making future predictions (Prasad *et al.*, 2006).

Random forest provides an ‘out-of-bag’ error estimate, which is calculated as an error rate based on the samples that are withheld from the analysis. Therefore, it might be unnecessary to split datasets into ‘training’ and ‘testing’ subsets, which is advantageous with small datasets (Liaw & Weiner, 2002; Lawrence *et al.*, 2006). The initial FIA dataset was relatively small and, therefore, I wanted to use the entire dataset to develop the model. Because random forest is a relatively new analysis technique, however, I compared the error rates for the model using the entire dataset and a random subset of the data (e.g., a 50-50 split) used for training and testing the model. These results showed that error rates were very similar among the models, with differences in error rates ranging from 0.09-2.19% (Table 2.2). Thus, I chose to use the full dataset for model building. I used the model developed in random forest to predict the presence or absence of each species for each of the 10,246 1-km raster cells within the boundaries of Yellowstone and Grand Teton National Parks currently and under each of the three climate scenarios.

To explore more closely the relationships between the predictor variables and the distribution of the species, I developed variable importance plots. Random forest calculates the importance of a predictor variable by calculating the increase in prediction error when the out-of-bag samples for that variable undergo permutation while all other predictor variables are held constant (Liaw & Weiner, 2002). In practice, variable importance is plotted as the mean decrease in accuracy of the model when the aforementioned process is carried out for each predictor variable.

Table 2.2. Error rates for the models using the full and split data sets.

	Subalpine fir (n=157)	*Engelmann spruce (n=119)*	*Whitebark pine (n=56)*
Full dataset (n=275)	33.45	33.81	23.27
Training dataset (50%)	33.57	34.31	23.36
Testing dataset (50%)	35.04	32.11	23.36

To determine if model error rates were ‘better than random’, I calculated a Kappa statistic using the confusion matrices. Kappa statistics are indices that account for chance agreement that may occur if values were randomly assigned to each cell across the landscape. Thus, comparing the actual and chance agreement, along with the associated p-values, allowed me to assess the degree to which the model correctly predicted presence and absence values compared with random chance (Congalton & Green, 1999).

Results

Model Results

The models show a decrease in the percentage of plots occupied by all treeline species when temperature increases (Table 2.3). All species showed an increase (albeit slight for whitebark pine and Engelmann spruce) with increased precipitation. Increasing both parameters lead to a decrease in all species.

The random forest package allows for the development of plots that show the relative importance of each of the predictor variables to the model. The following predictor variables were most influential in model building: hydrological soil group b, which refers to soils with moderate infiltration capacities, for subalpine fir; summer precipitation for Engelmann spruce; and average daily maximum temperature for whitebark pine (Figure 2.2). While climatic variables dominated the models for all species, soil variables play a more important role for spruce and fir than for whitebark pine (Figure 2.2). The variable importance plot showed that bulk density, a measure of the water retention potential of the soil, of the upper-most soil layers (approximately 10 cm [Miller & White, 1998]) was important for distinguishing the location of Engelmann spruce stands. However, subalpine fir was more directly impacted by the bulk density of lower layers (layer 5, which occurs at 30-40 cm depth), as well as the fraction of clay in the soil at greater depths (Figure 2.2).

Table 2.3. Percentage of area predicted to be occupied by treeline species under four climate scenarios.

	Subalpine fir	*Engelmann spruce*	*Whitebark pine*
Current climate	42.56	28.69	12.18
Increased temperature	14.13	2.98	0.02
Increased precipitation	52.80	30.66	13.02
Increased temperature and precipitation	17.28	5.02	0.02

Model Evaluation

Model evaluation results suggest that the random forest prediction method was able to identify current species with a level of accuracy ranging from 66.55% for the model of subalpine fir distribution to 76.73% for the model of whitebark pine distribution. All models had a level of accuracy between 66-77% (Table 2.2). Error rates were lowest for the whitebark pine model, compared with those for Engelmann spruce and subalpine fir, which is probably due to the specialist nature of whitebark pine, as opposed to the more generalist spruce and fir species. The inability to differentiate microsite conditions at a 1-km scale likely contributed to the difficulty in predicting locations of spruce and fir, which commonly co-occur.

The capacity of the model to correctly distinguish between occupied and unoccupied sites is another important aspect of model evaluation (Guisan & Zimmerman, 2000). Confusion matrices are commonly used in assessing the accuracy of classifications in many different fields, such as remote sensing, and quantify the level of agreement (or disagreement) between the input data and model predictions (Lillesand & Keifer, 1999). I used confusion matrices to calculate class error rates for unoccupied sites that were classified as occupied (e.g., false positives, errors of comission) and occupied sites that were classified as unoccupied (e.g., false negatives, errors of omission). Full results are in Table 2.4. Kappa statistics suggest that all three models classified presence and absence of treeline species more accurately than a random classification (subalpine fir: $\kappa=0.31$, $p<0.0001$; whitebark pine: $\kappa=0.15$, $p=0.01$; Engelmann spruce: $\kappa=0.31$, $p<0.0001$). However, false negative error rates were particularly high for whitebark pine. Likely explanations for these errors are outlined in the discussion section, and caution should be used when interpreting the results of these models.

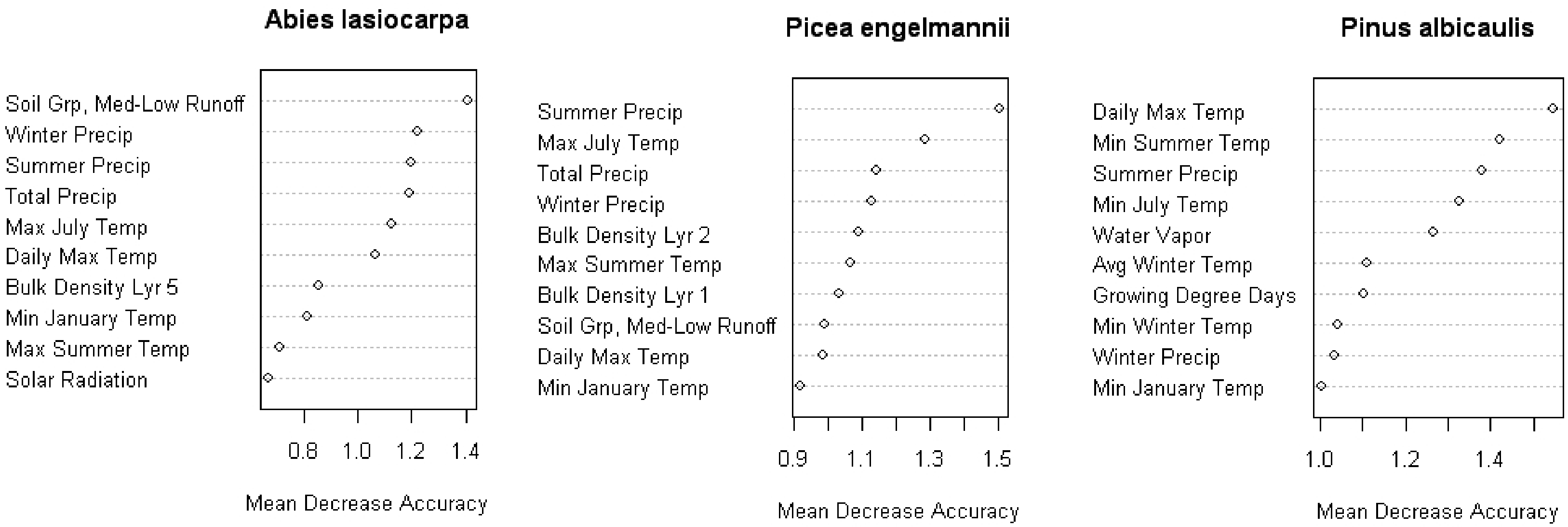


Figure 2.2. Variable importance plots for subalpine fir (left), Engelmann spruce (middle) and whitebark pine (right).

Mapped Results

An important aspect of biogeographic modeling is to understand the spatial changes in treeline conifer distributions that could occur under various future climate scenarios. Thus, I mapped current and future distributions of treeline conifer species for each of the 1-km raster cells within the boundaries of Yellowstone and Grand Teton National Parks to determine changes in the spatial distribution of these species.

When temperature and precipitation increase, subalpine fir is predicted to decrease in mid- and high-elevation areas and to be present only in the highest elevations and wettest mid-elevation regions (Figure 2.3). If only temperature increases, subalpine fir decreases in mid- and high-elevation areas and is present only in the highest, wettest habitats (Figure 2.3). Subalpine fir experiences a substantial decrease in dry, high-elevation areas, such as northern YELL, with drought-like conditions. With an increase in precipitation, subalpine fir is expected to increase, mostly in wet middle elevations (Figure 2.3).

Engelmann spruce shows a decrease in middle and high elevations with increased temperature and precipitation and is only present at the highest elevations (Figure 2.4). With increased temperature only, Engelmann spruce shows a similar response, decreasing at all elevations (Figure 2.4). Increased precipitation leads to a relatively unchanged distribution compared to the current distribution (Figure 2.4).

Whitebark pine nearly disappears from the park with a scenario of both increased temperature and precipitation and a scenario of only increased temperature (Figure 2.5).

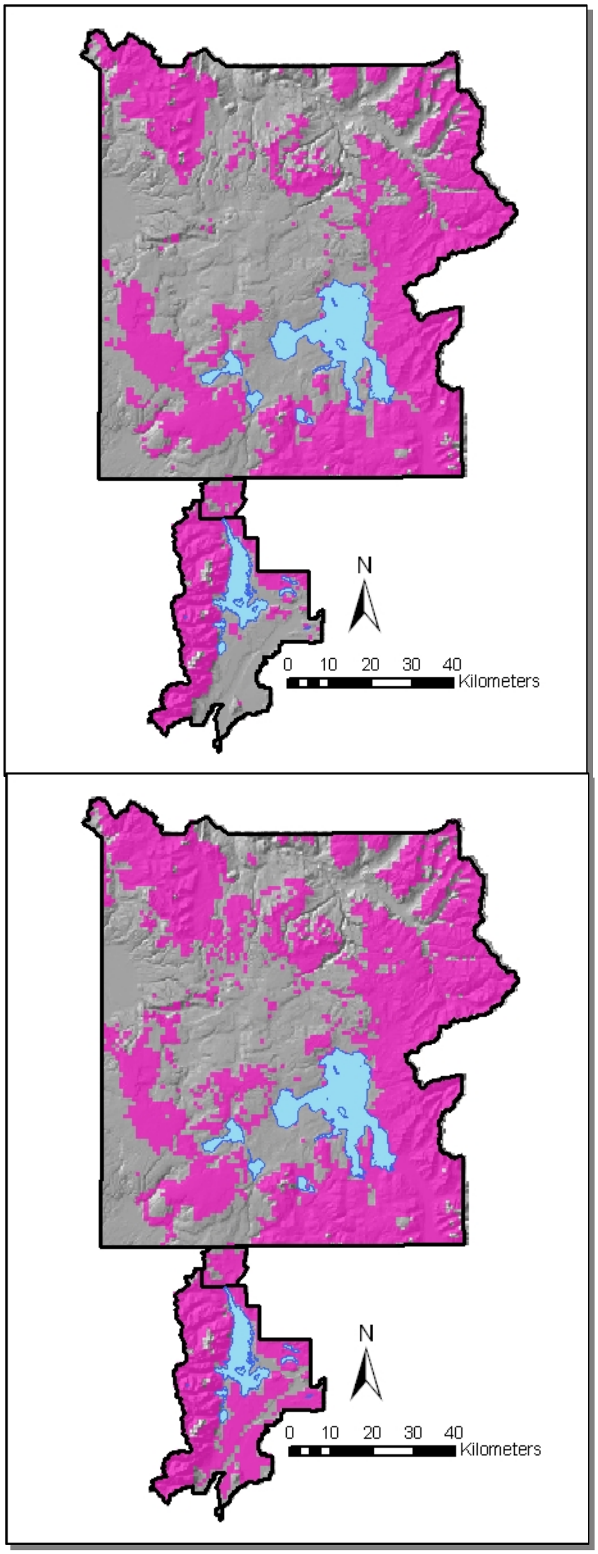


Figure 2.3. Distribution of subalpine fir under current conditions (top) and a scenario of increased precipitation (bottom).

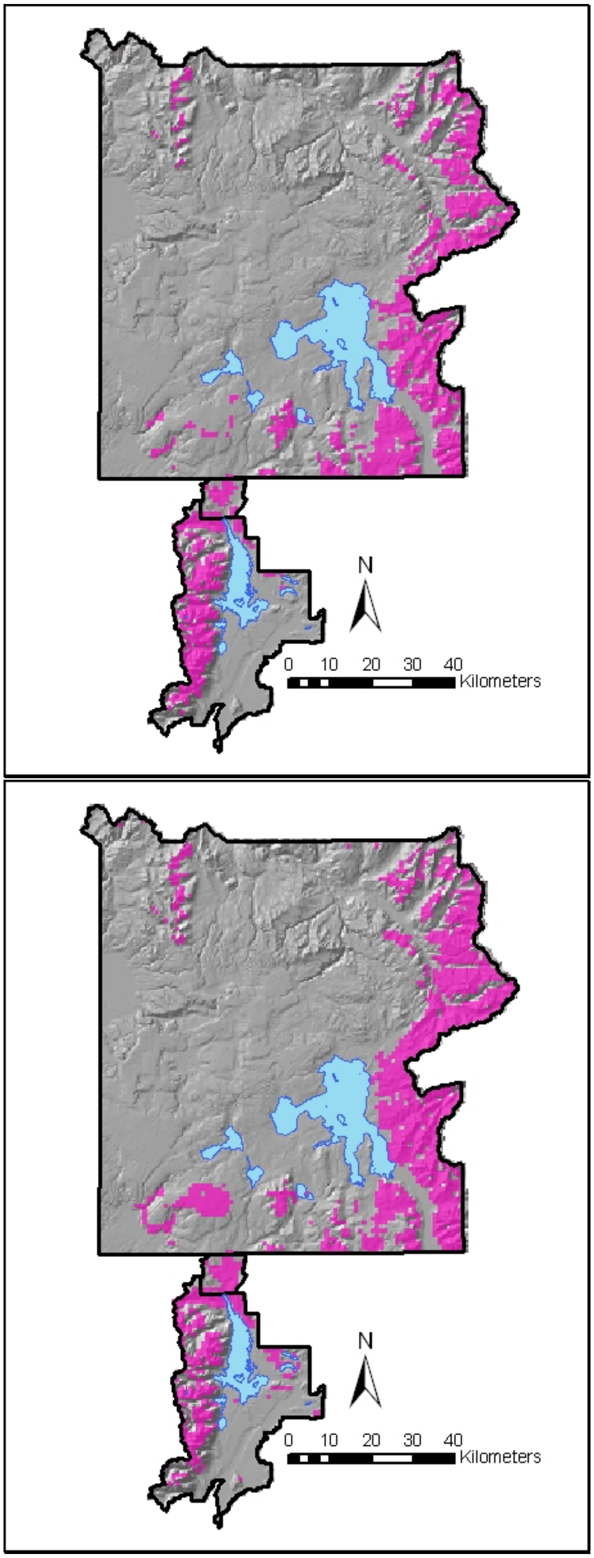


Figure 2.3. (cont.) Distribution of subalpine fir with increased temperature only (top) and increased temperature and precipitation (bottom).

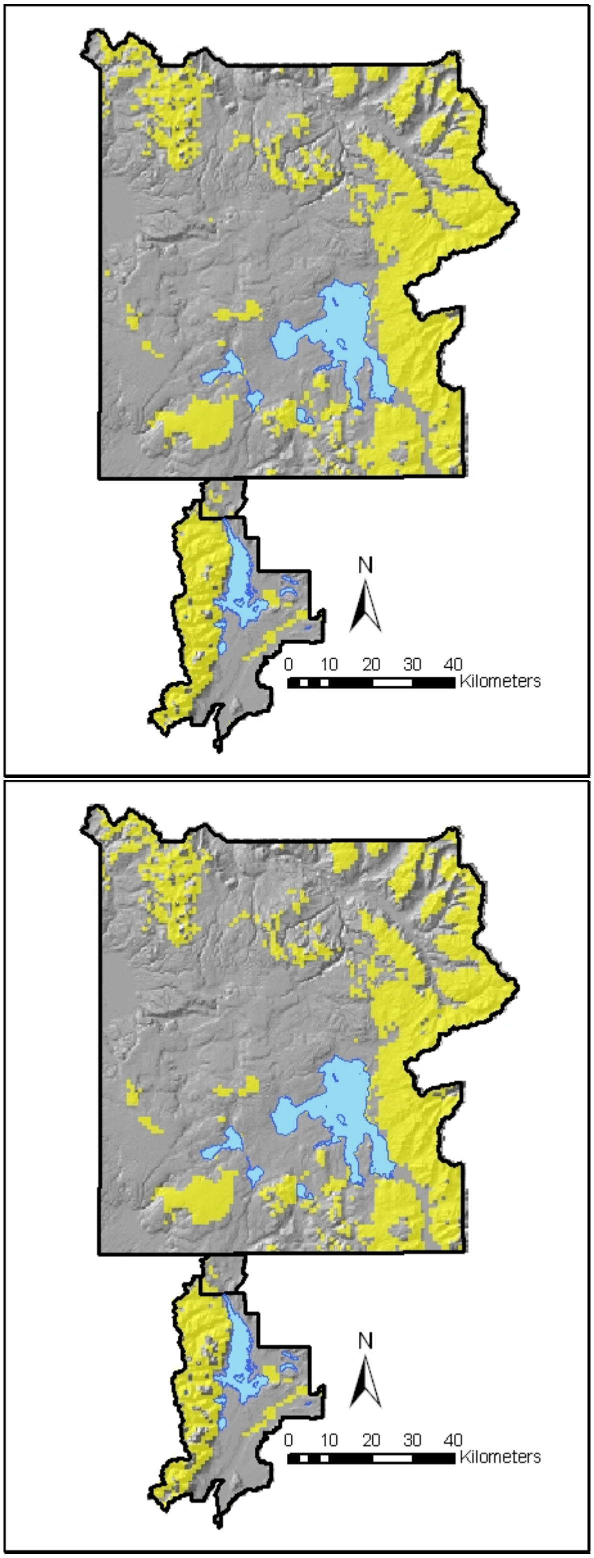


Figure 2.4. Distribution of Engelmann spruce under current conditions (top) and a scenario of increased precipitation (bottom).

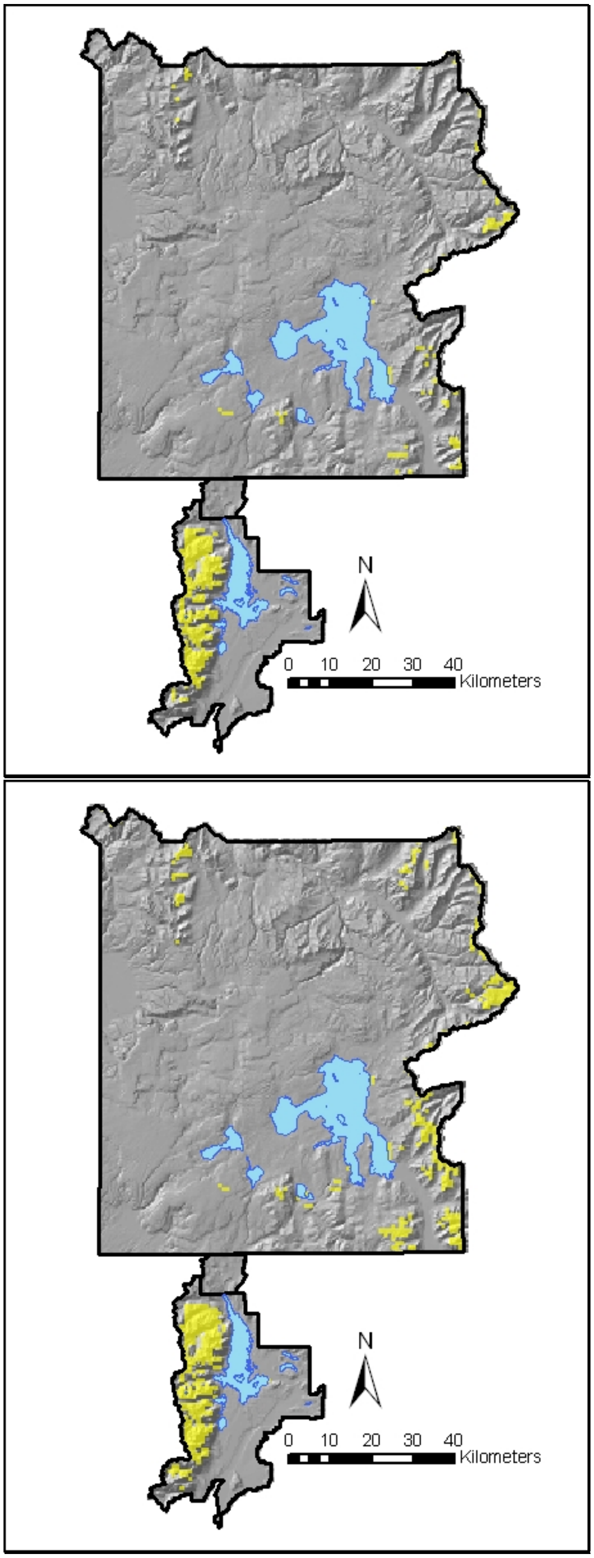


Figure 2.4. (cont.) Distribution of Engelmann spruce with increased temperature only (top) and increased temperature and precipitation (bottom).

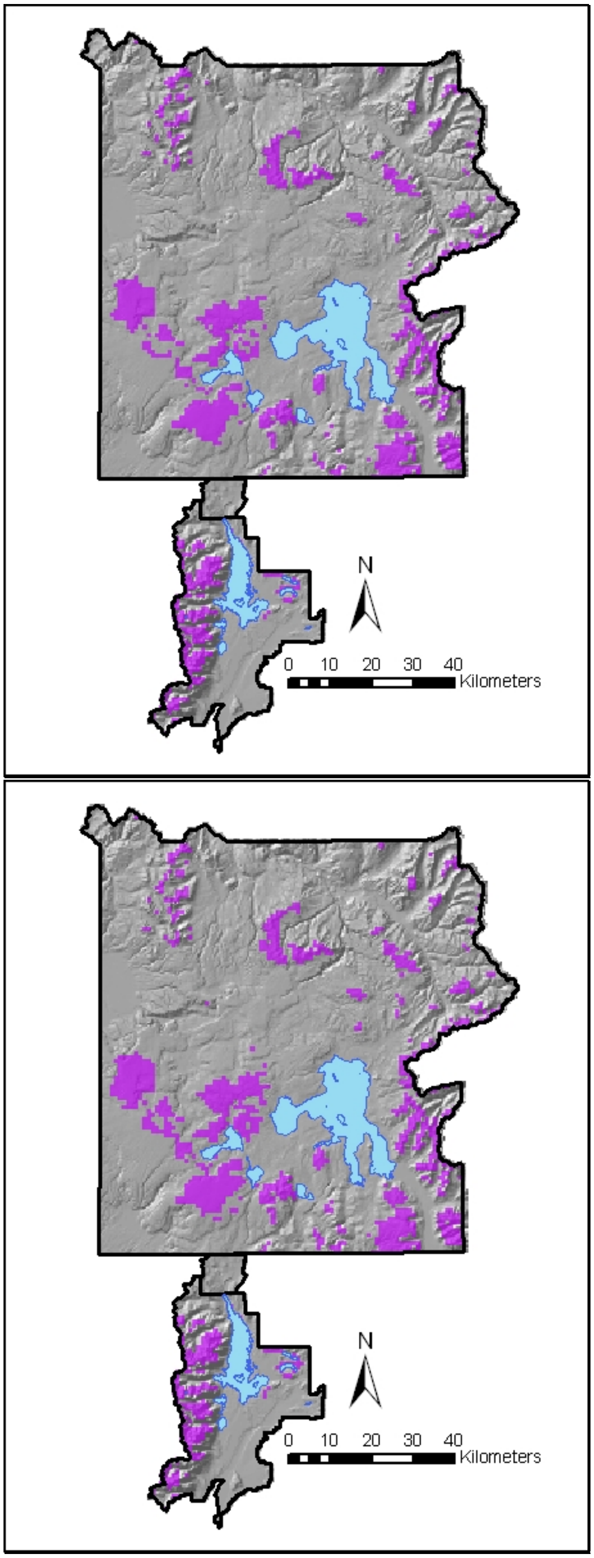
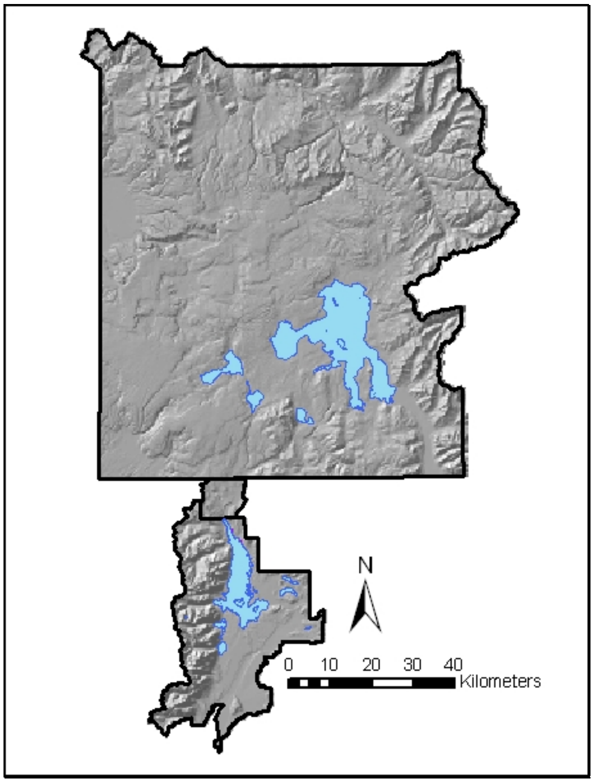


Figure 2.5. Distribution of whitebark pine under current conditions (top) and a scenario of increased precipitation (bottom).



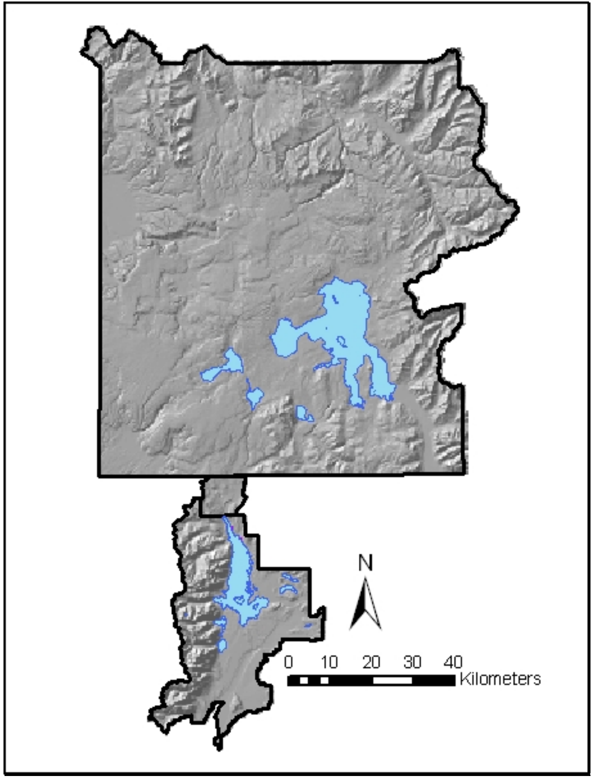


Figure 2.5. (cont.) Distribution of whitebark pine with increased temperature only (top) and increased temperature and precipitation (bottom).

The distribution remains relatively unchanged with an increase in precipitation (Figure 2.5).

Discussion

These models demonstrate the complex response of conifer distributions to changing climate scenarios. Under a scenario of increased temperature, as well as a scenario of increased temperature coupled with increased precipitation, the models show a substantial decrease in the overall distribution of treeline conifer species across the Yellowstone landscape. This supports the existing hypothesis that the response of long-lived, non-migratory species, such as treeline conifers, to increased temperatures is upslope movement to higher elevations (Innes, 1991; Rochefort *et al.*, 1994; Lloyd & Graumlich, 1997; Millar *et al.*, 2004). All of the species modeled in this study inhabit the coldest and wettest forest zones (Alexander *et al.*, 1990; Alexander & Shepperd, 1990; Arno & Hoff, 1990). Because the autecology of many treeline species prevents them from inhabiting warmer zones, the species modeled here experience a decrease in overall habitat with an increase in temperature (Tranquillini, 1979; Alexander *et al.*, 1990; Alexander & Shepperd, 1990; Arno & Hoff, 1990). In contrast, an increase in precipitation leads to an increase (albeit small in the case of whitebark pine and Engelmann spruce) in the area occupied by treeline conifers. Since these species inhabit relatively wet areas on the landscape, higher precipitation leads to an increase in inhabitable mid-elevation cells that also fall within the temperature requirements of the species. Whitebark pine, as a true subalpine species, is found near the summits of most peaks in YELL and GRTE with only small areas of currently non-forested alpine zone into which to migrate (Despain, 1990). In addition, physical factors such as wind and drifting snow can prevent establishment of individual trees above current treeline, even if climate parameters are compatible with successful recruitment. Therefore, it is expected that an increase in precipitation would lead to a proportionally small increase in the area occupied by whitebark pine.

Table 2.4. Comission and omission error rates.

	Subalpine fir	*Engelmann spruce*	*Whitebark pine*
Comission (false positive)	41.53	29.49	9.13
Omission (false negative)	27.39	39.50	78.57

Precipitation and soil variables play a larger role in the models for subalpine fir and Engelmann spruce than for whitebark pine. Temperature variables dominate the whitebark pine models, following the autecology of this specialized subalpine species that is highly influenced and limited by growing season temperature. Because Engelmann spruce is more likely to grow in areas with accessible water tables than to require specific physical soil properties, the importance of shallow bulk density is probably a reflection of its establishment on sites that provide ample water availability in the upper soil layers (Alexander & Shepperd, 1990). In contrast, according to these models, the importance of water availability at greater depths appears to be more important to subalpine fir. Yet, the distribution of subalpine fir is also likely to be tightly linked to competitive interactions, as it is known to establish on sites that are ‘too wet or too dry for its common associates’ (Alexander *et al.*, 1990).

It should be noted that because the climate and soils variables are inherently spatially and temporally autocorrelated and the groups of variables are intercorrelated, it is difficult to interpret the importance of each variable to the model separately. It is instead more likely that groups of variables are acting together to influence the presence or absence of each species. With rapidly changing climate, the correlation among climatic and edaphic variables is likely to vary in the future. Shifts in soil fauna and microbial communities could occur in relation to changes in plant distribution, which may lead to changes in the availability of carbon and nitrogen (Hausenbuiller, 1985). However, major changes on short temporal scales are likely to be due to changes in soil moisture properties, as increases in temperature will lead to earlier snowmelt runoff and, consequently, earlier soil moisture recharge, which may lead to earlier desiccation of soils (Hamlet *et al.*, *in review*).

Changes in the spatial distribution of treeline conifers are coupled with relative moisture across the Yellowstone landscape, emphasizing the importance of moisture availability to treeline composition and structure. The influence of moisture on treeline dynamics has long been overlooked in long-term, large-scale studies in favor of examining the effects of increased temperature, since treeline is believed to be controlled by temperature worldwide (e.g., Tranquillini, 1979; Innes, 1991; Körner, 1998; Camarero & Gutiérrez, 2004, but see Daniels & Veblen, 2004). For instance, under drought-like conditions, high elevations in YELL and GRTE become dominated by spruce-fir forests, with a decrease in the area occupied by whitebark pine. With an increase in precipitation, the probability of occurrence of all treeline species increases across the landscape.

However, while the spatial distribution of Englemann spruce and whitebark pine remain relatively unchanged, subalpine fir increases in the wettest, mid-elevation areas. Thus, the spatial implications of increased precipitation are an increase in fir-dominated forests in the wettest mid-elevation areas, which could lead to the replacement of whitebark pine in mid-elevation, mixed-conifer forests.

The models for whitebark pine substantially under-predict presences (e.g., high omission error rates), and caution should be used when interpreting current and future distribution maps. Possible explanations for these error rates are most likely based on the biology of this species and the interaction between climate and multiple factors driving its distribution across the landscape. For example, it is the only one of the three species that is dispersed by animals instead of wind. Clark's nutcrackers (*Nucifraga columbiana*) tend to disperse whitebark pine seeds in open areas and on ridges (Tomback *et al.*, 2001) and, as such, whitebark pine is often found on sites that may not be climatically optimal, but on which it can establish. Furthermore, significant dieback of whitebark pine stands in the GYE and beyond is occurring due to blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*) and changing fire regimes. Thus, mortality rates are likely higher than they would be under normal circumstances due to these factors, which makes predicting the distribution of whitebark pine using only climatic and soil variables difficult. In addition, climate, fire, pine beetle outbreaks and blister rust infection are interrelated processes, and these relationships are integral to understanding the distribution of this species and should be incorporated into future distribution models. Thus, it is evident that a first-order, process-based model for this system is inadequate and biology is likely to play an important role in whitebark pine distribution. Therefore, introducing meta-population dynamics (Dobson, 2003) to explain dispersal mechanisms and disturbance models to integrate factors driving high mortality rates are extremely important for future modeling efforts. The current models, however, should be interpreted with caution, and the future models of whitebark pine distribution likely under-represent the species on the landscape.

Management Implications

Existing models have emphasized the impact of the following processes on treeline forest dynamics: changing fire regimes and their impact on successional pathways due to fire suppression practices in the 20th century (e.g., Keane, 2001; Kipfmueller & Kupfer, 2005); increased infestations by introduced pathogens (Koteen, 2002); and more frequent and intense outbreaks of native pests (Logan & Powell, 2001; Logan *et al.*, 2003; Logan & Powell, *in review*). However, few studies have emphasized the importance of the direct impact of climate on treeline conifers—especially whitebark pine—in the region (exceptions include Romme & Turner, 1991; Bartlein *et al.*, 1997).

Whitebark pine is considered a ‘keystone’ species in the subalpine forests of western North America (Arno & Hoff, 1990; Tomback *et al.*, 2001). Its large seeds are high in fat and provide an important food source to seventeen animal species throughout its range—most notably the threatened grizzly bear (Tomback *et al.*, 2001). However, it is believed to be ‘functionally extinct in more than a third of its range’ due to the combined effects of white pine blister rust, an introduced pathogen, outbreaks of the native mountain pine beetle and changing fire regimes (Tomback *et al.*, 2001; Kendall, 2003).

The current study highlights the impacts of a changing climate on the treeline forests of the Yellowstone region, which in some areas are currently dominated by whitebark pine. Given future predicted changes in climate, it is reasonable to predict an overall decrease in pine-dominated subalpine forests in YELL and GRTE. However, of greater importance to land managers is the implication that whitebark pine is likely to decrease in the driest mid- and high-elevation forests in northern and central Yellowstone National Park—the areas in which it is currently dominant (Despain, 1990; McCaughey & Schmidt, 2001). From a forest ecology perspective, a loss of high-elevation whitebark pine forests in northern Yellowstone would lead to an overall decrease in genetic diversity and loss of subalpine habitat connectivity. This change would, in turn, impact species that are dependent on whitebark pine, including animal species, such as Clark's nutcrackers (the primary seed dispersal agent for whitebark pine) and grizzly bears, and understory plant communities, which rely on the open-grown canopies that are typical of whitebark pine stands (Bassman *et al.*, 2003).

However, from the perspective of ecosystem management, especially in relation to the threatened grizzly bear, the predicted loss of mid-elevation, mixed-pine forests in drier areas of the ecosystem might be of utmost management importance. Mixed whitebark pine forests are highly valuable to grizzly bears because they provide more suitable habitat than monotypic stands for red squirrels, which harvest the cones from whitebark pines and cache them in middens (Mattson & Reinhart, 1997). Grizzly bears then dig up middens in order to find whitebark pine seeds. Without these forests, whitebark pine seeds become unavailable as a food source for grizzly bears, causing the bears to move to lower elevations to find alternate food sources (Mattson *et al.,* 2001). As grizzlies move to lower elevations, they are more likely to experience conflicts with humans (Mattson *et al.*, 2001). Thus, to most effectively manage the subalpine forests of YELL and GRTE in the face of a changing climate, it is perhaps most important to focus attention on monitoring dry mid- and high-elevation forests in the Yellowstone region as harbingers of long-term change in the ecosystem.

Conclusions

The results of this modeling exercise suggest a possible change from pine-dominated, high-elevation forests in the Yellowstone region to spruce-fir dominated forests. In a system that has already experienced a shift from whitebark pine-dominated forests to spruce-fir complexes (Bassman *et al.*, 2003), it is worth noting that the changes modeled in this study might exacerbate this shift and could lead to further decreases in whitebark pine. While this result alone might cause heightened concern for species of special concern in the Greater Yellowstone Ecosystem, it is important to also consider that the influence of other large-scale ecosystem drivers might provide additional threats to these resources. To most accurately predict the future status of these species, it is necessary to couple the results of a climate model such as the one employed in this study with an enhanced understanding of the impacts of land-use change (e.g., Hernandez, 2004), shifting fire cycles (e.g., Keane, 2001), introduced pathogens (e.g., Koteen, 2002) and native pests (e.g., Logan *et al.*, 2003) on habitat availability. Only then can natural resource managers truly implement well-informed management practices.

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CHAPTER 3

SPATIAL AND TEMPORAL INFLUENCE OF MOISTURE AVAILABILITY ON SUBALPINE FORESTS OF THE GREATER YELLOWSTONE ECOSYSTEM

Introduction

The effects of global climate change on species and communities have been identified in a variety of systems and are varied in form and spatial and temporal scale. For instance, studies have shown changes at relatively small spatial scales and with individual species or communities, as well as across large spatial scales that incorporate entire continents and a plethora of taxa (e.g., Walther *et al.*, 2002; Parmesan & Yohe, 2003; Camarero & Gutiérrez, 2004; Breshears *et al.*, 2005; Debinski *et al.*, 2006; Menzel *et al.*, 2006). These shifts are revealed in the form of phenological changes and associated match-mismatch issues (e.g., Inouye *et al.*, 2000; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Menzel *et al.*, 2006), shifts in geographical range (Parmesan *et al.*, 1999; Parmesan & Yohe 2003; Root *et al.*, 2003), increased risk of extinction (Thomas *et al.*, 2004) and additional responses that are more closely related to overuse of resources by humans (e.g., exacerbating the effects of overfishing [Stenseth *et al.*, 2002]). In addition to these studies of recent shifts, paleorecords of environmental change are available to show the effects of past variability on long-lived species (e.g., Brubaker, 1986; Davis, 1989; Graumlich, 1993; Whitlock, 1993; Lloyd & Graumlich, 1997).

Quantifying the response of ecological communities to past climate change has important implications for the interpretation of predicted responses to future change. Using paleoecological data to better understand past changes can provide insights into site- and species-specific responses that are difficult to model given uncertainties in future global climate change predictions (Swetnam *et al.*, 1999; Bunn *et al.*, 2005; Lloyd, 2005). For instance, while most organismal (e.g., tree rings, pollen from lake sediment cores) and instrumental historical records demonstrate a substantial increase in temperature over the past century, changes in precipitation appear to operate at more local scales, with some areas experiencing increases in moisture while others become increasingly droughty (Walther *et al.*, 2002; Lloyd, 2005). Uncoupling the combined effects of temperature and precipitation will allow for a more knowledgeable interpretation of future predictions (Bunn *et al.*, 2005).

Alpine treeline marks an ecotonal boundary that is largely controlled by abiotic factors (Körner, 1998; Körner & Paulsen, 2004). Thus, it represents an important system in which to study the effects of climate on biotic communities. Treeline has been shown to respond to fluctuations in climatic variables in the past (Elliot-Fisk, 1983; Brubaker, 1986; Lloyd & Graumlich, 1997), and responses to recent changes are evident in some systems (Lloyd *et al.*, 2003; Bunn *et al.*, 2005; Lloyd, 2005). Recent changes often take the following forms: 1) increased radial growth of upright, mature individuals; 2) increased growth of krummholtz; 3) advances of treeline elevation through seedling establishment beyond current treeline boundaries; and 4) increased density of trees due to the facilitation of seedling establishment in closed subalpine forest (Villalba & Veblen, 1997; Lloyd *et al.*, 2003; Daniels & Veblen, 2004; Lloyd, 2005; Bunn *et al.*, 2005). While the location of treeline worldwide is strongly correlated with temperature, precipitation has been shown to affect more local processes, such as growth and recruitment and, therefore, may be an important influence on future change in the subalpine forest ecosystem (Germino *et al.*, 2002; Daniels & Veblen, 2004).

National parks represent excellent natural laboratories within which to study the effects of global climate change, mostly due to their pristine nature and lack of confounding factors at high elevations, such as land-use change. National parks and other protected natural areas (e.g., US Forest Service Wilderness Areas) have the added advantage of encompassing many of the high-elevation regions in the mountainous west of the United States, providing protected subalpine and alpine habitats in which to conduct observational studies of past change. High-elevation habitats in the Greater Yellowstone Ecosystem (GYE) are of particular importance due to the abundance of whitebark pine, a species of special concern, in these areas. Yellowstone (YELL) and Grand Teton (GRTE) National Parks represent the core of the GYE, which is the largest intact ecosystem within the conterminous United States. This ecosystem encompasses a precipitation gradient from drier forests in the northern part of YELL and the Gallatin Range to wetter forests in the Teton Range. Thus, the parks of the GYE represent an excellent area in which to study the effects of moisture on subalpine forest species composition throughout space and time.

My broad objective was to examine the spatial and temporal influence of moisture availability on species composition in subalpine forests in the national parks of the

Greater Yellowstone Ecosystem (GYE) along a moisture gradient. Treeline in this system is dominated by three species: subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and whitebark pine (*Pinus albicaulis* Engelm.). This study is one of few that examine biophysical setting on subalpine forests (e.g., Villalba *et al*., 1994; Bunn *et al.*, 2005) and represents the first analysis of habitat setting on species composition in subalpine forests in the GYE. My specific objectives, thus, were to test the hypothesis that species abundance is correlated with total precipitation. I tested this hypothesis across space and back through time by utilizing the aforementioned precipitation gradient and historical climate data. In addition, I sought to determine if a correlation exists between precipitation and the total number of stems in each plot. These questions, when analyzed jointly, allowed me to investigate the sensitivity of subalpine forests in the GYE to precipitation across space and through time and can provide valuable information to assist managers in interpreting models of future change in the ecosystem.

Methods

Study Area and Site Selection

The study region is enclosed within the boundaries of Yellowstone and Grand Teton National Parks in the northwestern corner of Wyoming and including small areas of Montana and Idaho (Figure 3.1). The Yellowstone landscape is dominated by a high-elevation volcanic plateau, surrounded by mountain ranges that provide subalpine and alpine habitat. The landscape of Grand Teton, in contrast, is dominated by the Teton

Range juxtaposed sagebrush-steppe and riparian habitat. These landscape features provide varied climatic regimes for vegetation communities in the region. It is said that Yellowstone has two climates: a drier climate dominated by summer precipitation in the northern valleys of the park and a wetter climate dominated by winter snowpack in the southwestern corner of the park (Despain, 1987; Whitlock & Bartlein, 1993). This wetter climate is also present in Grand Teton, especially in the mountainous areas in the western portion of the park. These two climate regimes, which can also be reclassified as a precipitation gradient across the ecosystem, impact the composition of vegetation communities.

While the parks of the GYE encompass a substantial number of mountain peaks, relatively few contain treeline that is controlled by climate (as defined below), as opposed to being controlled by topography and disturbance processes. For the purposes of this study, I defined climatically controlled treeline as the end of upright growth of conifers (thus eliminating the krummholtz zone) that occurs on peaks that do not exhibit considerable impacts from topographic controls (e.g., cliff bands) and physical processes (e.g., avalanche activity) that may artificially depress treeline. These guidelines eliminated a substantial portion of the mountains within the boundaries of the parks as potential sampling area, but allowed me to attribute differences in treeline composition and structure to climatic and biotic controls, as opposed to physical controls.

Climate Data and Plot Selection

I stratified treeline forest demography plots along a precipitation gradient developed using climate data from the DAYMET climate model, which spatially interpolates weather station data across the landscape and adjusts values for topographic variation (Thorton *et al.*, 1997). I downloaded a grid of total annual precipitation averaged over the period 1980-1997 at 1-km resolution. I developed a treeline coverage by classifying all areas on the landscape above 9,000 ft (2743 m) as possible treeline and adding a 500 ft (152 m) downhill buffer (Despain, 1990). I then clipped the grid to treeline and classified the cells into four precipitation quartiles (Figure 3.1). Because the GYE is a fire-dominated system, it was also necessary to eliminate areas that were known to have burned by overlaying a spatial coverage of fires that occurred within park boundaries. Because records of area burned are only available for the period from 1881 to present and, thus, some plots may have experienced fires before this time that were not represented in the spatial coverages, I also inspected each plot in the field for evidence of fire scars and charcoal. In addition, due to park regulations, I eliminated all bear management areas within YELL where entry was not permitted during the snow-free season.

Forest Demography Data

I sampled eight 20x20m plots across four precipitation quartiles (32 total plots) within park boundaries (Figure 3.1). Once suitable subalpine forest habitats were located using the guidelines described above, plots were randomly placed at treeline. I recorded the geographic coordinates of the plot center and perimeter using a Trimble GeoExplorer XT GPS unit. Within each plot, I extracted an increment core as close to the base of the tree as possible from each individual with a diameter at breast height (dbh) >10 cm and recorded the species, dbh and height at which the core was taken. Dbh was measured at

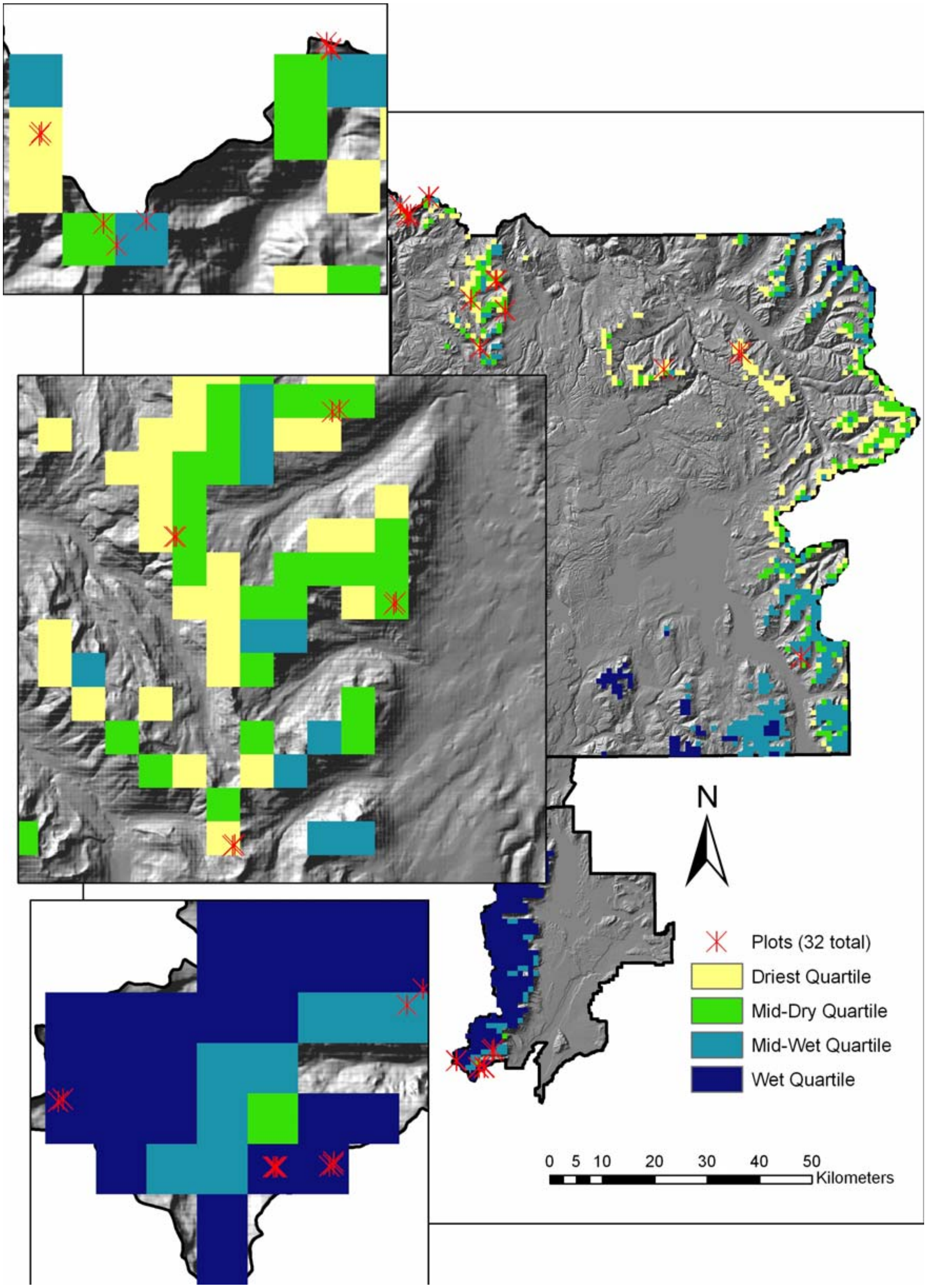

Figure 3.1. A map showing the location of sampling plots across the Yellowstone landscape and the distribution of plots of each precipitation type.

1.37m above ground level on the upslope side of the tree. For trees <10 cm dbh and >0.5 m in height, I recorded the species, basal area, height and number of branch internodes of each individual. I also tallied the number and species of all trees <0.5 m in height. Although I realize the limitations of these definitions, hereafter I will refer to all trees with a dbh <10 cm and height >0.5 m as 'saplings' and all trees <0.5 m in height as 'seedlings', while those trees with dbh >10 cm will be referred to as 'mature individuals'. Due to National Park Service regulations in proposed wilderness areas (such as Yellowstone National Park), I was not permitted to core saplings and seedlings. However, the majority of the analyses are focused on those individuals for which I obtained an increment core.

Increment cores were mounted and sanded in the laboratory. Establishment dates were determined by visually cross-dating rings and making corrections for missed pith and the number of years required for the tree to grow to core height (using age-height regressions described below). For cores that did not contain the pith, a circular template was fitted to closely match the width of the inner-most curved rings. The number of missing rings was then estimated by counting the number of rings on the pith locator template that would be required to reach the pith (Applequist 1958). Cores where germination dates could not be definitively established (e.g., due to heart rot or missing pieces) were not used in the analyses. This yielded a total of 359 cores (subalpine fir: n=83; whitebark pine: n=177; Engelmann spruce: n=99), with a mean age of 140 years ± 3.8 (mean ± 1 SE). To develop age-height regressions, 30 individuals of each species with dbh <10 cm were destructively sampled from surrounding US Forest Service lands at similar elevations (>9000 ft [2743 m]). I collected seedlings from similar biophysical settings to those trees that I sampled within the parks. The height and basal diameter of each of these individuals were recorded, and thin, cross-sectional discs were cut from each sample. The rings were counted and cross-dated along two radii for each disk and an age-height regression was established for each species ($R^2>0.33$, $p<0.001$; subalpine fir: $y=13.70+0.35x$; whitebark pine: $y=36.91+0.20x$; Engelmann spruce: $y=24.16+0.90x$). These equations were used to correct to core height for those individuals from which I extracted an increment core.

Changes in tree species composition and abundance were established by grouping estimated germination dates into 10-year intervals, centered on each decade (e.g., trees that established from 1895-1904 are centered on a decade at 1900). To develop spatial and temporal correlations of species composition with precipitation, I used both DAYMET data (as described above) at 1-km resolution for the period from 1980-1997 and PRISM data at 4-km resolution from 1895-2004 (PRISM Group, 2004). PRISM data were used because they represent historical climate data for the last 110 years, thus allowing for an examination of historical patterns of successful recruitment, which are not possible using DAYMET data.

Data Analysis

All analyses were conducted in the R 2.3.1 statistical environment (R Core Development Team, 2006). Associations between species abundance and spatial variability in total annual precipitation were explored using Pearson's product-momentum correlation coefficients. Due to the autocorrelation inherent in climate data, I examined the residuals from the correlations of species and precipitation with Moran's I. This test showed that the errors did not violate the assumption of independence.

To examine correlations between species abundances and precipitation through time, I used a combination of non-metric multidimensional scaling (NMDS) as a way to represent the data visually and biplots that display the correlation between the species abundance data and precipitation data through time. NMDS is an unconstrained ordination technique and differs from more popular constrained ordination techniques, such as Canonical Correspondence Analysis (CCA), in that it configures sites in ordination space based on species abundance instead of on underlying gradients that are then used to constrain the ordination. The goal of NMDS is to minimize stress by maximizing the correlation among the distances calculated from a dissimilarity matrix (McCune & Grace, 2002).

I used NMDS as another way of looking at correlations between species abundances and historical variability in precipitation. For this analysis, I used the Bray-Curtis dissimilarity matrix to represent the 'ecological distance' among my plots (Bray & Curtis, 1957). NMDS was performed using the VEGAN 1.8-2 contributed package in R (Dixon, 2003). Using the 'metaMDS' function from the VEGAN package allowed me to run NMDS using multiple starts to minimize the stress of the configuration (Dixon, 2003). I chose to perform NMDS using two dimensions, yielding a stress of 3.38% for the data assessing historical variability (McCune & Grace, 2002). Although I realize this is a fairly insignificant reduction in the number of dimensions of the dataset, since only three species are present in the plots, it represents a useful way to visualize the correlation between species abundance and precipitation over time. To examine historical variability in precipitation availability and species abundance in the plots, I plotted the ordination scores for each decade (from 1495-1974) and then overlaid species centroids, which are calculated as a weighted average of the species abundance for each decade. I then extracted the ordination scores for the last eight decades (1895-1974) for which I have climate data and correlated the ordination scores for those decades to total annual precipitation. I then plotted a biplot vector on the ordination to represent the correlation between total precipitation and the ordination axes. I repeated this biplot process for summer and winter precipitation to compare the correlation between seasonal precipitation and species abundance.

Results

Effects of Spatial Variability in Moisture on Species Composition

Spatial variability of species composition was evident across the precipitation gradient, as represented by the spatially interpolated climate data. I found a significant positive relationship between total annual precipitation and subalpine fir and Engelmann spruce abundance using the site classification based on DAYMET data (Figure 3.2; Table 3.1). I found a strong and significant negative relationship between total annual precipitation and whitebark pine presence and abundance (Table 3.1). The direction and relative magnitude of these relationships were similar using the PRISM data for the last century, although the relationship between PRISM total annual precipitation and subalpine fir abundance was not significant at the $p<0.05$ level (Table 3.1). In addition, I evaluated the relationship between total precipitation using the DAYMET data and the total number of stems, the total number of 'saplings' and the total number of 'seedlings' in the plots. I found no significant relationship between the total number of stems, saplings or seedlings and the total annual precipitation of the plots (Table 3.2).

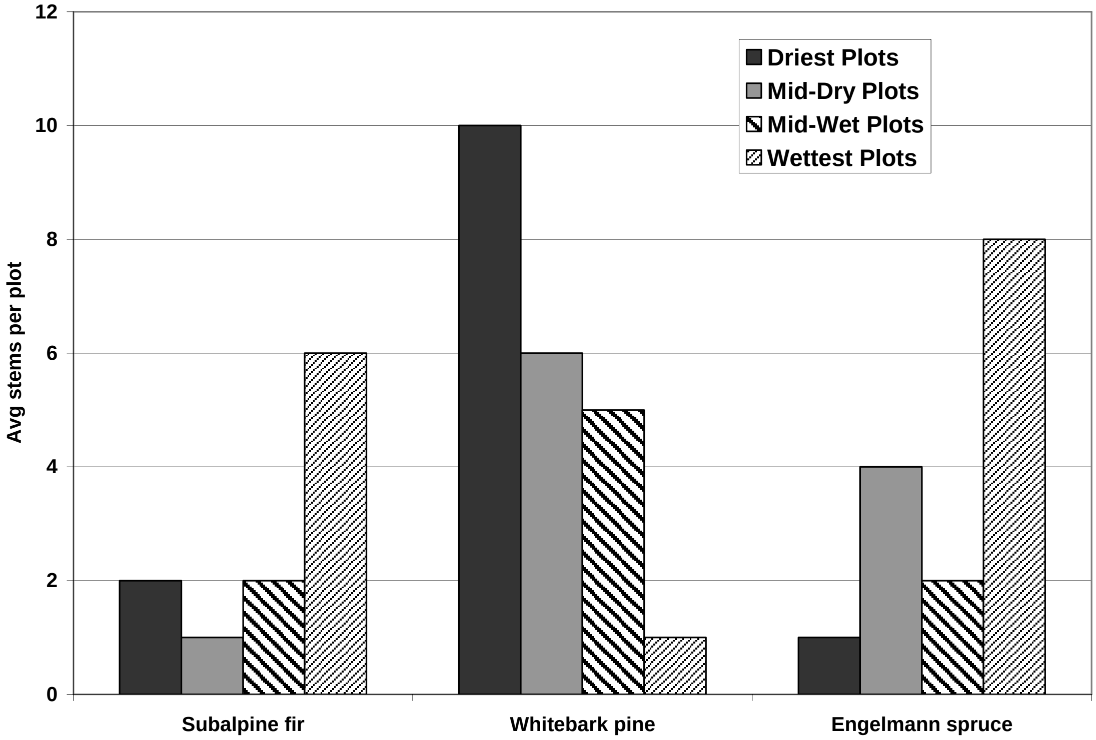

Figure 3.2. Barplot of the average number of stems of each species in plots stratified across four precipitation regimes.

While I attempted to sample across the entire landscape, the results may be complicated by possible pseudoreplication within each DAYMET or PRISM raster cell (e.g., multiple plots located within one cell). However, the limitations of the resolution of the spatially interpolated climate data, in addition to the relatively small amount of climatically controlled treeline within the study area, prevented all samples from being completely independent. This is a common problem with landscape ecology studies but can be overcome by using an integrative approach that incorporates modeling and observational studies (Wu & Hobbs, 2002). I acknowledge this limitation in the data but point to the results of bioclimatic envelope modeling (Chapter 2) to support the results that spruce and fir are positively correlated with precipitation, as compared with whitebark pine, in the study system.

Table 3.1. The correlation between species abundance and climate data using Pearson's product-momentum correlation coefficients and associated p-values.

	DAYMET data	*PRISM data*
Subalpine fir	r=0.377; p=0.03	r=0.251; p=0.17
Engelmann spruce	r=0.427; p=0.01	r=0.420; p=0.02
Whitebark pine	r=-0.682; p<0.0001	r=-0.619; p=0.0001

Effects of Historical Variability in Moisture on Species Composition

I examined the variability in the number of individuals that successfully recruited during 10-year intervals for the period 1895-1974. Because I was not permitted to extract increment cores from smaller individuals in the plots, I have chosen to eliminate them from the analyses of historical variability in moisture on species composition in the plots. Therefore, only trees for which I have definite germination dates were used in the analyses, and these trees established during or before the decade from 1965-1974. Because the DAYMET data only represents a mean value for a 17-year period, I chose to use the spatially interpolated climate data from the PRISM model to establish a relationship between climate variability and species composition through time.

Table 3.2. The correlation between average number of seedlings, saplings and total stems per plot and total annual precipitation using Pearson's product-momentum correlation coefficients and associated p-values.

	Pearson's r
Seedlings	r=0.261; p=0.15
Saplings	r=-0.047; p=0.80
All stems	r=0.111; p=0.54

Of the total number of mature individuals that successfully recruited into the plots over time (from 1495-1965), 42.94% established during or after 1895. This represents 45.24% of mature individuals of subalpine fir, 49.49% of Engelmann spruce and 37.64% of whitebark pine. The following percentages of mature individuals established during or after 1895 in each of the plot types (precipitation quartiles): 36.73% of mature individuals in the driest plots; 58.14% of mature individuals in the mid-dry plots; 52.22% of mature individuals in the mid-wet plots; and 24.71% of mature individuals in the wettest plots. Figure 3.3 shows the recruitment of stems in each of the plot types throughout the past five centuries by decade and species.

I also performed NMDS on the historical species establishment data. I produced plots of ordination scores and overlaid species centroids and a biplot vector showing the correlation between species abundance and precipitation variables (Figures 3.4-3.6). These plots allowed me to examine more closely the relationship between historical precipitation and successful species establishment. All three plots (including summer, winter and total precipitation) show a correlation between precipitation and abundance of Engelmann spruce over time. The species scores are shown in Table 3.3. I measured the goodness of fit of the ordination by plotting the observed dissimilarity (as calculated by the dissimilarity matrix) to the ordination distance using a Shepherd plot, which yielded a

R^2=0.996, indicating a good fit between the ordination distance and the observed dissimilarity, as calculated by the Bray-Curtis index (Figure 3.7).

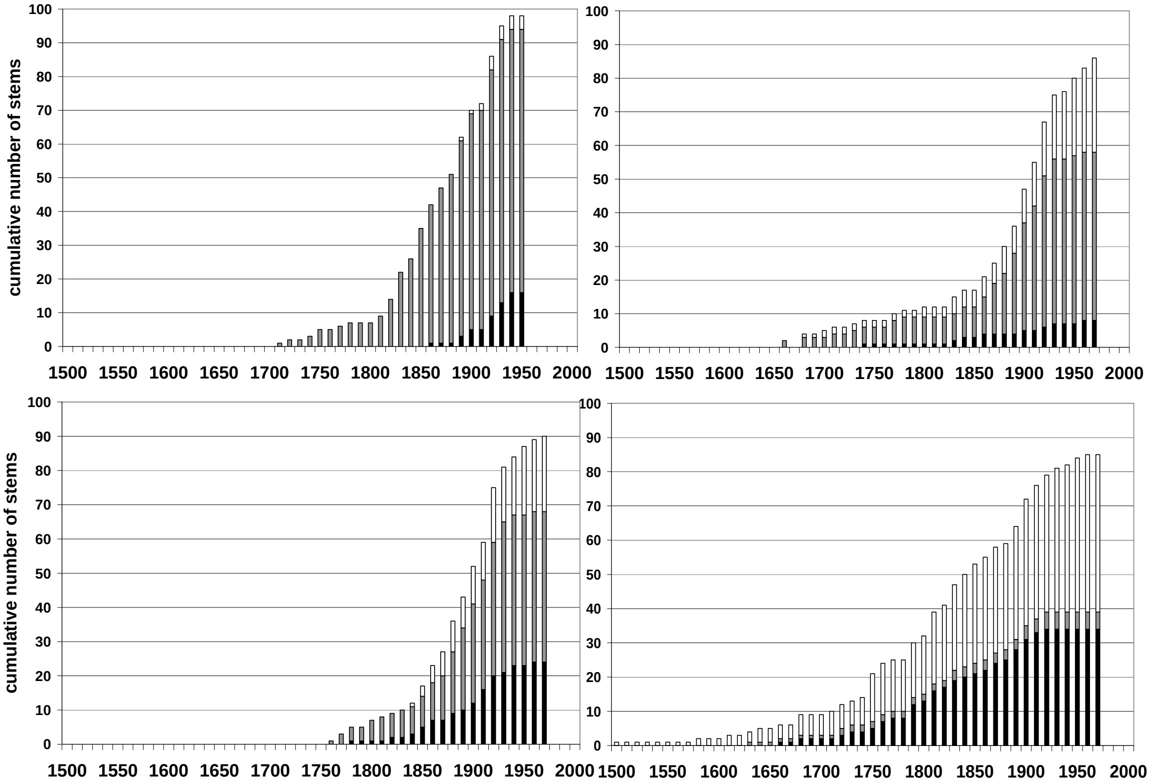

Figure 3.3. Barplots showing the recruitment of stems of each species through time. Dry plots are shown in the upper left, mid-dry in the upper right, mid-wet in the lower left and wet in the lower right. White bars are Engelmann spruce, gray bars are whitebark pine and black bars are subalpine fir.

Discussion

This study highlights the complex interactions between species composition and habitat setting even across a relatively small and species depauperate area and provides information that will allow for more realistic interpretations of future change in the ecosystem. Using both correlation and ordination methods for analyzing the spatial and temporal variability in species composition of subalpine forests in the GYE allows me to view the data in both a linear fashion and understand the relationship of the species abundance over time in multidimensional space.

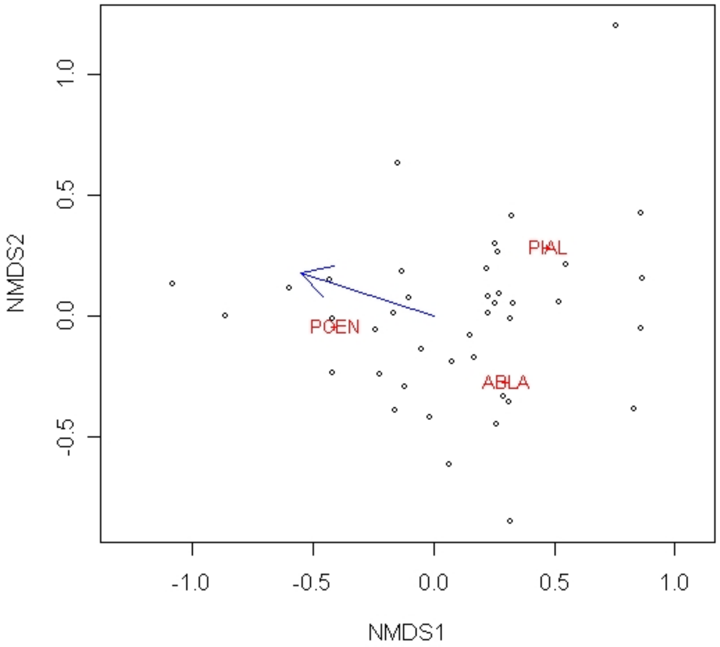

Figure 3.4. A plot of the two dimensions of the NMDS analysis. Red text indicates species centroids, which are labeled by the following species codes: subalpine fir=ABLA, Englemann spruce=PCEN, whitebark pine=PIAL. The blue arrow represents the correlation of total annual precipitation to axes 1 and 2.

The relationship between species abundance and total annual precipitation follows species autecology and competitive dynamics in this system. For instance, it is to be expected that moisture-loving and shade-tolerant species such as subalpine fir and Engelmann spruce are positively correlated with moisture across the ecosystem, while drought-tolerant whitebark pine is negatively correlated with moisture due to competitive interactions. The higher degree of difficulty in modeling fir with respect to moisture suggests that the establishment of fir across the landscape is dependent upon multiple other factors, such as soil properties and successional pathways. In fact, juvenile individuals of subalpine fir are often found germinating beneath mature individuals of whitebark pine and Englemann spruce, which serve as nurse plants and provide microsite conditions that favor the survival of subalpine fir seedlings (Tomback *et al*., 2001). These results agree strongly with the results presented in Chapter 2, which show that subalpine fir responds strongly to both moisture- and soil-related variables.

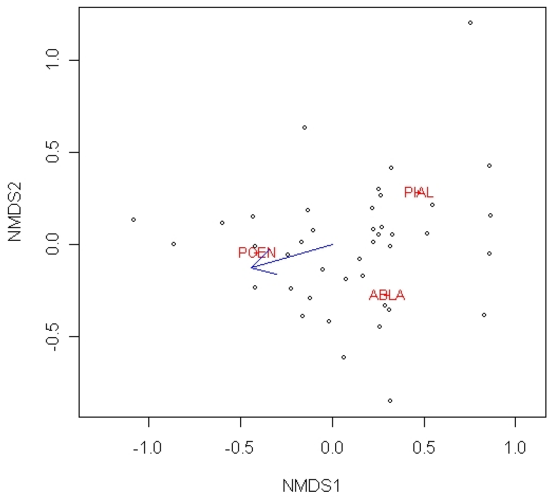

Figure 3.5. A plot of the two dimensions of the NMDS analysis. Species codes are shown in Figure 3.4. The blue arrow represents the correlation of winter precipitation to axes 1 and 2.

The lack of a relationship between the number of stems of all life stages and total annual precipitation is somewhat surprising. However, because these species are living in extreme environments that are dominated by short growing seasons and low temperatures, it is likely that successful recruitment is more closely related to temperature than precipitation, as water is not a limiting factor in high-elevation forest ecosystems, due to large amounts of persistent snowpack (Grace *et al*., 2002). The relationship between temperature and the number of stems is an area that should be explored in further work that examines the impact of biophysical setting on species composition. Data that establish the importance of temperature on species composition of subalpine forests are critical to disaggregating the influence of temperature and precipitation on these systems.

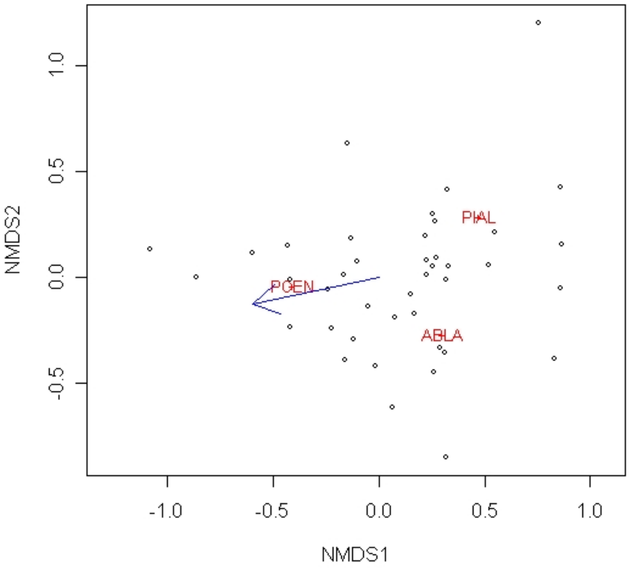

Figure 3.6. A plot of the two dimensions of the NMDS analysis. Species codes are shown in Figure 3.4. The blue arrow represents the correlation of summer precipitation to axes 1 and 2.

Analysis of the historic variability in precipitation revealed that precipitation is positively correlated with Englemann spruce through time as well as across space. Almost half of the total number of stems that successfully established in the plots recruited during or after 1895. While it is to be expected that trees establishing at any ecotonal boundary (e.g., upper treeline, lower forest border) will be younger than those contained within closed forests, it may be possible that trees are establishing at higher elevations due to warming during the 20th century, as has occurred in the past (e.g., Lloyd & Graumlich, 1997; Grace *et al.*, 2002). While I cannot specifically address this question using the PRISM spatial climate data because is it based on instrumental records that are only available for the 20th century, long-term records suggest that the past century has been anomalously warm compared with at least the previous four centuries and possibly the last millennium (National Research Council, 2006). When sorted by species, it is interesting to note that fewer mature individuals of whitebark pine established during the past century as compared with subalpine fir and Engelmann spruce. The most likely ecological explanation for this result is the facilitation of fir and spruce germination by mature individuals of whitebark pine acting as nurse plants (Tomback *et al.*, 2001). This result underscores the importance of understanding the biology of the species and their competitive interactions even in an environment that is predominately controlled by abiotic factors. However, the results do not necessarily suggest limited recruitment by whitebark pine in the plots; in fact, the proportion of seedlings and saplings of each species was quite variable across plots and did not favor any particular species. This study does suggest, however, that the number of individuals of whitebark pine that have successfully recruited into the population was lower during the 20th century than during the previous three centuries combined. Yet, without a better understanding of the population dynamics of the seedling and sapling stages of these species, it is difficult to make definitive conclusions about recruitment success over time.

Overall, this study highlights the importance of spatial and temporal variability of moisture across the GYE. It is important to note, however, that the correlation between

Table 3.3. Correlations of species to the first and second dimensions of the NMDS analysis, calculated by using weighted averages of species abundance by decade.

	NMDS using decades	
	Axis 1	Axis 2
Subalpine fir	0.3022076	-0.27132801
Engelmann spruce	-0.4069501	-0.04021228
Whitebark pine	0.4713141	0.28718153

plot type and species abundance is not as strong when using PRISM climate data for the past century as it is when using DAYMET data for the period from 1980-1997. Several possible reasons exist for this difference. First, PRISM data is provided at a 4-km resolution for the past century, while DAYMET data is provided at a 1-km resolution. Because of the variability in topography, especially at high elevations, 4-km resolution climate data may not be adequate to understand the relationship between species and moisture. Second, because I used DAYMET data to stratify the plots into quartiles during study design, it is to be expected that correlations with species composition may be stronger when using these data in the analyses. Finally, the fact that the relationship between species abundance and precipitation differs depending on the length of the climate record used highlights the importance in understanding long-term climate variability and the limitations of relying on shorter-term averages typically used in climatology. When comparing plot classifications, while most of the plots classified as ‘dry’ and ‘wet’ using the DAYMET data remained in those categories over the past century, a number of the ‘mid-dry’ and ‘mid-wet’ plots would have been classified differently had I used the PRISM data to categorize the plots. Once again, this could be due to historical variability that is not reflected in averages from the period from 1980-

1997 or the spatial variability that is lost when moving to coarser-resolution data. It is thus important to understand the implications of both the length of the record and the resolution of such data when incorporating climate variability into regional resource analysis.

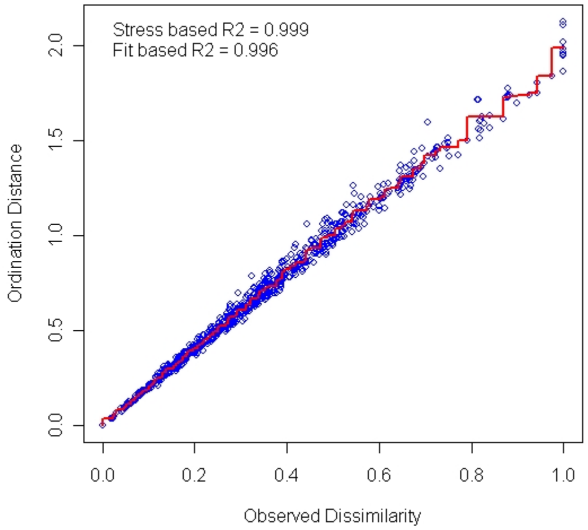

Figure 3.7. Shepherd plot showing the correlation between the distance from the dissimilarity matrix and the ordination distance for NMDS analysis.

While understanding the effects of topographic variables on species abundance and composition was not part of the original study design, I was able to examine correlations between species abundance and site characteristics, such as slope and aspect, within plot type to determine if local topography was influential. I found no significant correlation between species abundance and slope or aspect within plot type (p>0.3). While this does not definitely rule out local topographic variables as a factor in species composition and abundance, especially since these variables are incorporated into the spatially interpolated climate data, it suggests that species are more closely correlated with precipitation at this spatial scale. Monitoring high-elevation systems at this spatial scale is hindered by inaccessibility, and the effort required to sample at this spatial scale would be much greater had I taken into account local topographic variation. Thus, while many advantages exist for monitoring treeline forests as an indicator of climate change, it is not without limitations, such as significant requirements of time and resources to conduct such monitoring.

Conclusions

Quantifying the effects of climate change on subalpine conifer species composition and abundance is important for accurately interpreting forecasts of future change. By focusing specifically on the impacts of moisture availability on species abundance through space and time, I was able to better understand the sensitivity of subalpine forest community composition to precipitation. I was also able to provide information that should allow for a more fluid interpretation of models of future change in these systems, given that global circulation models currently do not agree as to the magnitude and direction of future precipitation change.

This work highlights the influence of both climatic and competitive interactions among species on treeline composition. Given the strong negative association between precipitation and abundance of whitebark pine, competition and other biotic factors (e.g., dispersal) are likely important mediating factors in where whitebark pine is a dominant component of treeline in the GYE. I can also speculate that successional processes might be occurring at treeline in the GYE, with higher proportions of spruce and fir successfully establishing during the last century. This could possibly lead to a lower number of successful recruits of whitebark pine into the subalpine forest. When coupled with bioclimatic envelope models that show species-specific responses to climate change over time (as described in Chapter 2), these data offer valuable insights into the spatial and temporal dynamics of treeline species composition.

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CHAPTER 4

THESIS CONCLUSIONS

Summary and Conclusions

Understanding the potential impacts of global climate change on ecosystems is a burgeoning area of interest within the science community. The manner in which ecosystems respond to change is still relatively unknown; however, the need for such information and its integration into natural resource management are pivotal for responsible stewardship of resilient forest ecosystems. The results of this thesis contribute important information about mechanisms for change in subalpine forests of the Greater Yellowstone Ecosystem and, thus, provide managers with some of the tools they need to incorporate a large-scale and long-term driver, such as climate change, into future management decisions.

The response of treeline conifers to climate variability is a complex process that is dependent on a variety of factors, including biophysical setting and the individualistic response of species. The work presented in this thesis highlights the unique responses of species to climate variability. Both studies suggest that successful establishment of Engelmann spruce, which is classified as a moisture-loving and shade-tolerant species, is tied to moisture availability and soil properties. Meanwhile, whitebark pine is influenced most strongly by temperature variables and is able to persist on dry, exposed sites that are inhospitable to spruce and fir. Subalpine fir in this ecosystem occupies sites opportunistically and, thus, its distribution appears to be closely linked to biotic than abiotic interactions.

The effects of climate on subalpine forest species distributions carries heightened importance due to the prevalence of whitebark pine, a species of special concern, in subalpine forests of the study region. Models of the response of species to scenarios of future climate suggest a possible replacement of whitebark pine forests by spruce-fir complexes, if temperatures indeed rise at the projected rate. This shift in forest community assemblages could lead to decreased availability of whitebark pine seeds, which represent an important food source for grizzly bears in the ecosystem. Because changes in forest community composition occur at time scales that are relatively slow compared with most other management concerns, the general perception is that a change in this system will have a relatively small ‘ripple’ effect on species that depend upon these resources. However, with the added impacts of white pine blister rust, mountain pine beetle and changing fire regimes, the threat of climate to whitebark pine populations may proceed quickly and through multiple pathways.

In addition to the direct management implications of this work, the research presented in this thesis describes the use of robust statistical techniques to provide valuable insights into the ecology of treeline conifers. These insights offer valuable information for determining the manner in which treeline may be monitored as an important indicator of climate change in the future. Understanding the individualistic responses of species is often forgotten during the management decision-making process. Furthermore, while choosing to monitor treelines for evidence of change is intuitively appealing due to the substantial influence of abiotic processes as compared with human-induced change, the manner in which treeline is monitored can be complex. Shifts in elevation, changes in establishment rates, increases and decreases in radial growth and alterations of community assemblages are all possible effects of climate change on treeline. However, the temporal and spatial scales at which these processes operate can vary greatly. Moreover, some of these processes may be more tightly linked to changes in temperature, precipitation or combinations of both, in addition to other processes, such as modification of evapotranspiration rates, soil moisture availability and snowpack.

Treeline ecosystems, and particularly those that are enclosed within protected areas, provide valuable natural laboratories in which to conduct research on the impacts of global change to forested systems. It is imperative to protect these systems for future generations, and fostering responsible stewardship of ecosystems that are resilient to change is one of the best ways to ensure that this occurs. The insights provided here, as well as a wealth of paleoecological and treeline-specific research, can move managers closer to making well-informed decisions that protect these natural systems from large-scale changes that are occurring both within and around the jurisdictional boundaries of national parks.

APPENDIX A

RELATIVE INFLUENCE OF INDIRECT VERSUS DIRECT (AND RESOURCE) GRADIENTS ON PREDICTING CONIFER DISTRIBUTION

This appendix explores the relative importance of topographic and climatic parameters on the distribution of treeline species in Yellowstone and Grand Teton National Parks, based on the random forest models described in Chapter 2. Topographic variables, such as elevation, slope and aspect, are often referred to as ‘indirect gradients’ that “replace a combination of different resources and direct gradients in a simple way” (Guisan *et al.*, 1999; Guisan & Zimmerman, 2000). The relative importance of indirect gradients compared with direct and resource gradients, such as temperature and soil textural characteristics, can be important in biophysical envelope modeling because it gives an indication of the ability of the model to explain tree distribution based on physiological parameters alone. A model that is based on indirect gradients uses more precise topographic variables derived from digital sources (e.g., high-resolution digital elevation models). Meanwhile, models based on direct and resource gradients theoretically can be applied to a much larger geographic area because they provide more physiologically meaningful information about vegetation distribution (Guisan *et al.*, 1999; Guisan & Zimmerman, 2000).

To explore the relative importance of indirect, direct and resource gradients to these models, the correlations between topographic and climatic parameters were calculated and the error rates for models with and without topographic variables were compared. Correlations were highest between elevation and average and maximum temperature variables, such as average air temperature, daily maximum air temperature and maximum summer temperature (Table 1). Correlations between elevation and precipitation were relatively low in comparison ($r<0.7$; Table 1). Lower correlations between precipitation and topographic variables are likely due to the spatial variability in moisture availability throughout the Yellowstone region, as discussed in Chapters 2 and 3 and referenced in Despain (1987) and Whitlock & Bartlein (1993). The spatial location (e.g., geographic coordinates) of the plots is probably highly influential to the availability of moisture across the landscape. However, because the exact coordinates of FIA plots are not available for public use, it is impossible to examine this relationship in depth.

Table A.1. Correlations for climate variables and elevation (all p values ≤ 0.01). JJA=composite June, July and August; DJF=composite December, January and February.

Variable	*r values*
Average air temperature	0.9019
Daily minimum temperature	0.7618
Daily maximum temperature	0.9395
Minimum January temperature	0.4462
Maximum January temperature	0.8209
Minimum July temperature	0.7321
Maximum July temperature	0.8866
Minimum summer (JJA) temperature	0.7374
Average summer (JJA) temperature	0.8224
Maximum summer (JJA) temperature	0.8843
Minimum winter (DJF) temperature	0.5132
Average winter (DJF) temperature	0.7333
Maximum winter (DJF) temperature	0.8531
Total precipitation	0.4269
Winter (DJF) precipitation	0.3066
Summer (JJA) precipitation	0.6752

Since the correlations between temperature and topographic variables are relatively strong, models that use only direct and resource gradients should perform nearly as well as models that also incorporate topographic variables. This result is reflected in the error rates for models with and without topographic variables included

(Table 2). Error rates are comparable for both models, indicating that the climatic variables from the topographically adjusted DAYMET data reflect the influence of topography on climate.

Table A.2. Error rates for the models with and without topographic variables.

	Subalpine fir	*Engelmann spruce*	*Whitebark pine*
Including topographic variables	30.91	33.09	20.00
Not including topographic variables	33.45	33.81	23.27

The correlation between elevation and other important climate-related biophysical variables was also calculated. These variables include growing degree days, frost days, solar radiation and water vapor pressure. As elevation increases, the number of growing degree days decreases (r=0.9150), while the number of frost days increases (r=0.7723). Water vapor pressure decreases with elevation (r=0.6271) and solar radiation is unrelated to elevation (r=0.1540). While the relationship between water vapor pressure and elevation is not as strong as the relationship between elevation and other biophysical variables, water vapor pressure and temperature (due to adiabatic cooling) decrease with elevation, which is expected (Aguado & Burt, 1999). Both water vapor pressure and daily shortwave radiation have relatively weak relationships with the topographic variables, which is likely due to the scale at which the DAYMET data are compiled. The influence of water vapor pressure and solar radiation on species distribution is dependent upon local topographic controls and may not be reflected in the 1-km scale of the data used in this study.

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