PREDICTING THE DISTRIBUTION OF WHITEBARK PINE *(PINUS ALBICAULIS)* IN WASHINGTON STATE

by

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ABSTRACT

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Whitebark pine is a five-needle pine native to western North America. The species is considered to be at risk from the combined effects of the introduced disease white pine blister rust, mountain pine beetle attack, disrupted fire cycles, and global climate change. In Washington State, whitebark pine occurs in relatively dry upper montane and subalpine habitats in the Cascade Range, and in the northeastern corner of the state in the western margin of the Rocky Mountains. A small population occurs in subalpine habitat in the northeastern rainshadow region of the Olympic Mountains. Distribution of whitebark pine in Washington State tends to be patchy, and the species has not been mapped at a fine scale. An effective conservation strategy for any species must be based on accurate information about the extent and distribution of the species within the region of interest. This study investigated topographic and climate characteristics of whitebark pine habitat in Washington State. The topographic variables included in the analysis were elevation, slope, and aspect. The climate variables were average annual precipitation, length of frost-free period (mean and median number of frost-free days), and minimum, maximum, and mean annual temperature. Simple z-tests comparing these variable values between sites having documented presence or absence of whitebark pine show significant differences for elevation, slope, length of frost-free period, and minimum and mean annual temperatures. A range map based on these statistically significant variables correlates closely with known whitebark pine presence. These results may prove useful in future efforts to more finely model whitebark pine habitat in Washington State.

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Predicting the distribution of whitebark pine *(Pinus albicaulis)* in Washington State

INTRODUCTION

Whitebark pine

Whitebark pine (*Pinus albicaulis* Engelm.) is a five-needle pine that occurs in high-elevation areas of western North America (fig. 1). It is one of the five "stone pine" species in family *Pinaceae*, section *Strobus*, subsection *Cembrae* (Price, Liston, and Strauss 1998). Stone pines are characterized by their five-needled fascicles; indehiscent cones; and large, edible, wingless seeds that are dispersed primarily by birds—in particular, nutcrackers of the genus *Nucifraga* (Corvidae). The only stone pine native to the North American continent, whitebark pine grows in upper montane and subalpine habitats in the Canadian Rocky Mountains; the Rocky Mountains of Montana, Wyoming, Idaho, and northeast Washington; and in the Cascade and Blue Mountains of Washington and Oregon. A small population inhabits the Olympic Mountains in northwestern Washington State. The species occurs in patches in the Sierra Mountains in California (MacDonald, Cwynar, and Whitlock 1998). There are a few isolated occurrences of whitebark pine in Nevada.

Whitebark pine is not a commercially valuable timber species—its economic and social importance are most closely associated with wilderness aesthetics and back-country recreation (Keane 2000). Whitebark pine is also closely associated with the grizzly bear (*Ursos arctos*)—whitebark pine seeds make up a substantial portion of the bear's diet (Mattson and Reinhart 1994; Mattson et al. 2001). Whitebark pine is of special ecological interest because of its mutualistic relationship with the Clark's nutcracker (*N. columbiana*), (Tomback 1982; Mattes 1994; Lanner 1996). Whitebark pine cones do not open by themselves, nor do mature cones fall from the trees on their own (Lanner 1982). Clark's nutcrackers harvest whitebark pine seeds by breaking apart the cones with their strong beaks. A sublingual pouch allows the birds to harvest and carry dozens of seeds at once. Each bird caches three to five or more seeds at a time in loose substrates such as mineral soil, gravel, pumice, and forest litter. A single nutcracker can cache an astounding number of seeds—in the range of 30,000 or more seeds in some 9000 or 10,000 caches in a good cone crop year—of which they may retrieve only one-third (Tomback 2001). Seeds that are not retrieved may germinate. The nutcracker's seed-caching behavior provides the primary means of whitebark pine seed dispersal and regeneration (Tomback 1982, 2001).

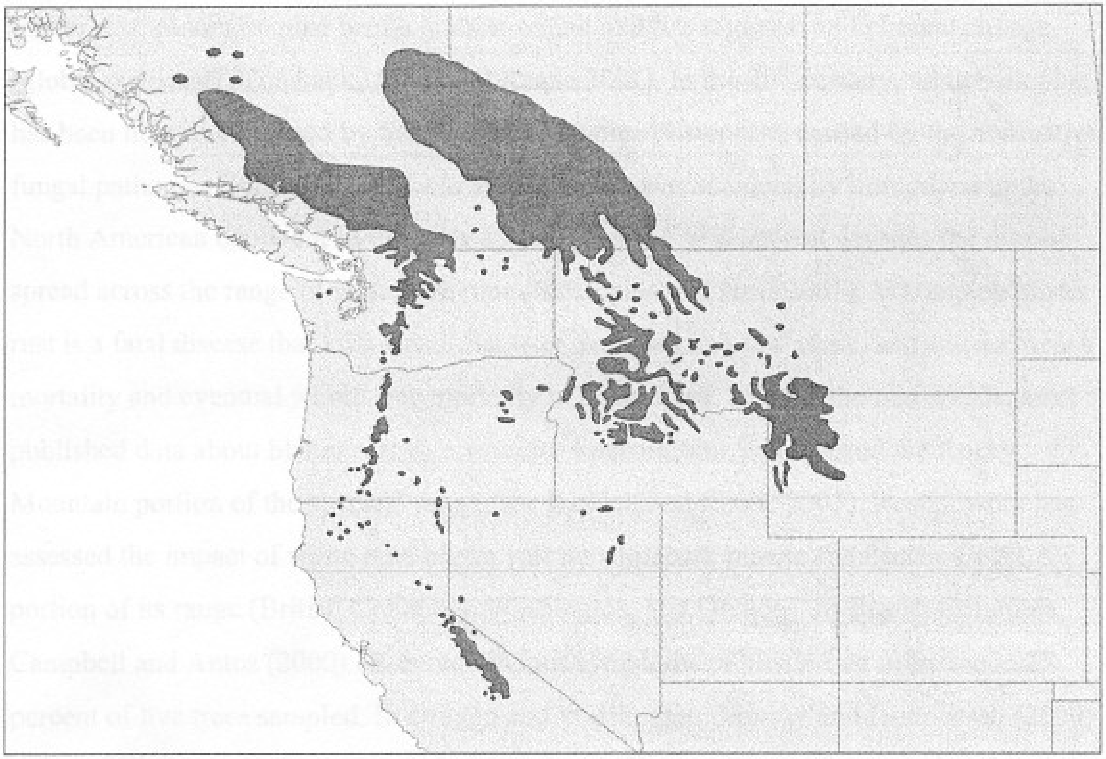

Figure 1. Range of whitebark pine (U.S. Geological Survey 1999—digitized representation of Little 1971)

Whitebark pine is considered a keystone species of high-elevation ecosystems (Tomback and Kendall 2001). The term "keystone species" was first used by Robert Paine to describe the central role of a low abundance predator (a *Pisaster sp.* starfish) in maintaining biological diversity in a tidepool ecosystem (Paine 1969). A keystone species is a species whose presence is crucial in maintaining the organization and diversity of its ecological community, and whose effect on the community is disproportionately large relative to its abundance. (Mills et al. 1993; Power et al. 1996). Whitebark pine's keystone functions include retaining snowpack and regulating runoff; pioneering disturbed sites and initiating forest succession; providing microsites in which other vegetation can become established; and providing crucial food and shelter for wildlife (Tomback and Kendall 2001).

Whitebark pine and whitebark pine ecosystems are currently considered to be at risk of serious range-wide decline as a result of four agents: the introduced disease white pine blister rust; mountain pine beetle infestation; altered fire regimes; and climate change (global warming) (Tomback, Arno, and Keane 2001). In the 20th century, whitebark pine has been heavily impacted by the disease white pine blister rust, caused by the non-native fungal pathogen *Cronartium ribicola* Fisch., which was accidentally introduced to the North American continent in the early 1900s. Over the next several decades the disease spread across the range of whitebark pine (McDonald and Hoff 2001). White pine blister rust is a fatal disease that kills small-diameter trees within a few years, and causes branch mortality and eventual whole-tree mortality in larger trees. Prior to the mid-1990s, most published data about blister rust infection in whitebark pine emphasized the Rocky Mountain portion of the species' range (see Kendall and Keane 2001). Recent work has assessed the impact of white pine blister rust on whitebark pine in the Pacific Coast portion of its range (British Columbia, Washington, and Oregon). In British Columbia, Campbell and Antos (2000) observed obvious symptoms of blister rust infection in 27 percent of live trees sampled. In Oregon and Washington, Murray and Rasmussen (2000) reported 20 percent infection in whitebark pine in Oregon's Crater Lake National Park. Goheen et al. (2002) found a 46 percent infection rate in live whitebark pine on the Umpqua National Forest in southwestern Oregon. Doede (2004) documented blister rust in 10 to 100 percent of live trees in stands on Washington's Gifford Pinchot National Forest. Shoal and Aubry reported rates of blister rust incidence ranging from 0 to 73 percent of live trees on eight national forests in Washington and Oregon (Shoal and Aubry 2006).

Mountain pine beetle (*Dectroctonus ponderosae* Hopkins) (Coeleoptera: Scolytidae) populations are currently increasing in western North America, and the insect is causing rising levels of mortality to mature whitebark pine (Logan and Powell 2001; Perkins and

Roberts 2003). Mountain pine beetle is native to North America, and typically exists at low (endemic) population levels in low- to mid-elevation lodgepole pine forests, but the species periodically erupts into epidemic population levels, causing widespread mortality of pine hosts (Bartos and Gibson 1990). An extensive mountain pine beetle epidemic in the early 1900s ravaged whitebark pine in the western United States. Mortality is rapid—usually within a single season. Mountain pine beetles preferentially attack larger diameter trees (Perkins and Roberts 2003). For whitebark pine, this means that large trees less vulnerable to white pine blister rust are susceptible to mountain pine beetle attack. In addition, there is growing concern that global warming may result in both increased mountain pine beetle activity and improved success of mountain pine beetle in high-elevation ecosystems (Logan and Powell 2001; Carroll et al. 2003).

In many parts of its range, particularly in the upper montane ecosystems of the Intermountain West and on other sites where whitebark pine is an early seral rather than a climax species, whitebark pine is considered to be fire-dependent: it relies on a cycle of natural fire to reduce or eliminate competition from more shade-tolerant tree species. Mature whitebark pines are relatively fire-resistant, and can survive low- and moderate-severity fire. Decades of active suppression of forest fires have interrupted natural fire cycles and promoted the expansion of other tree species onto whitebark pine habitat, leading to declines in whitebark pine presence on the landscape (Arno 1986, 2001; Arno, Parsons and Keane 2000). The increased fuel loading represented by this additional vegetation means that fire, when it does occur, is more likely to be severe and stand-replacing, killing whitebark pines as well as other tree species.

Climate change presents a risk as well, because it is associated with both increased mountain pine beetle activity in higher elevation forests (Logan and Powell 2001; Carroll et al. 2003) and projected loss of substantial portions of suitable subalpine habitat (Romme and Turner 1991; Warwell et al. 2006; Rehfelt et al. 2006). Whitebark pine ecosystems, due in part to their inherent remoteness and the fact that a significant proportion of whitebark pine habitat occurs on protected public lands (national parks, national forests, and designated wilderness), are considered to be geographically well protected from direct anthropogenic impacts (Scott et al. 2001). However, the well-documented range-wide decline of whitebark pine as a result of these indirect agents indicates that simple geographic protection may not be sufficient to conserve this species.

Habitat modeling and management needs

In order to develop an effective conservation strategy for any targeted at-risk species, community, or ecosystem, it is necessary to understand as precisely as possible both the known and predicted distribution of the conservation target (Groves 2003; Rushton et al. 2004). Spatial modeling that maps the species' distribution and potential habitat is especially useful as a communication tool between ecologists and land managers (Turner et al. 1995). Geographic Information Systems (GIS) are becoming an increasingly important tool for both displaying known distributions, and for identifying characteristics of sites where the conservation target is found. Maps modeling current and predicted distributions can be generated based on these characteristics. The Gap Analysis Program (GAP) of the US Geological Survey, National Biological Information Infrastructure is one example of this practice. The mission of the GAP is to identify the habitats of species and plant communities that are not adequately represented in existing conservation lands: "By identifying their habitats, GAP Analysis gives land managers and policy makers the information they need to make better-informed decisions when identifying priority areas for conservation" (US Geological Survey National Biological Information Infrastructure 2007).

The simplest application of a GIS to identify habitat is straightforward mapping of known presence (and absence, if available) of the conservation target. Comparing presence with other site attributes—for instance, latitude, longitude, climate, elevation, topography, geology, soils, vegetation type, forest cover, and land use—can generate ranges of these variables that are associated with the presence of the species, community, or ecosystem of interest. This information can be used to display simple spatial habitat models, or the data can be analyzed statistically to identify which of the attributes are most important in predicting suitable habitat.

bioclimatic modeling (predicting biological responses to climate change), Rehfeldt et al. (2006) caution that the accuracy of predictions depends heavily on the precision of the global climate model used as a basis for the predictive modeling, and on the appropriateness of the scenario chosen. They also assert that finer-grained analyses are needed on smaller scales—landscapes rather than continents or bioregions. In contrast, Hargrove and Hoffman (2000) offer a GIS-based, statistical, "niche hypervolume" technique to predict changes in the distribution of any plant or animal species across the continental U.S. given changes in environmental conditions, and advocate a centralized data repository; land management agencies could either draw data from the repository, or contribute improved data to it.

BACKGROUND

The need to map whitebark pine

In the summer of 2002, as a biological science technician for the U.S. Forest Service, I began conducting surveys of whitebark pine stands on five National Forests in Washington State: the Olympic, Mt Baker-Snoqualmie, Colville, Wenatchee and Okanogan National Forests. The primary objectives of these surveys were to assess the impacts of white pine blister rust and mountain pine beetle on the species and on whitebark pine ecosystems, and to locate and map occurrences of whitebark pine. Whitebark pine had not been systematically mapped on these forests, largely because it is not a commercially important species in the state, and also because it tends to occur on remote, high-elevation sites that are infrequently visited and that can be quite difficult to access.

In order to locate our whitebark pine study sites, we relied initially on anecdotal evidence and generalizations about the species, as well as on the local knowledge of experienced Forest Service employees. Depending on the experience of the sources and the accuracy of their observations, this can be an excellent starting point for mapping, particularly for relatively small, well-delineated areas. For instance, as part of a project to develop a habitat suitability model for the Clark's nutcracker, whitebark pine locations in the upper Oldman River sub-basin in the Rocky Mountains of southern Alberta, Canada were initially mapped based primarily on anecdotal information, with the intent of ground-truthing and using the resulting presence/absence data to develop more accurate maps (Blouin 2006).

Anecdotal indicators of probable whitebark pine presence in Washington State included elevations above 1525 meters (5000 feet); fairly steep slopes; aspects between southeast (112.5 degrees) and west (270 degrees); and relatively exposed, rocky terrain inhospitable to the establishment other tree species. Guided by this anecdotal evidence and by direct analysis of aerial photographs, our project developed a reasonable skill at "intuitive mapping" to identify probable locations of whitebark pine. We used, ground-truthed, and refined this process for several years as we surveyed and mapped whitebark pine stands across the state.

While this technique served the purpose of locating whitebark pine-dominated stands for blister rust surveys, it tended to miss smaller stands and areas where whitebark pine occurred as a minor component in relatively dense mixed-species stands, especially at the lower limits of the above-1525-meter zone. While en route to the targeted stands, we frequently encountered whitebark pine growing on east- and north-facing slopes, widely scattered across relatively flat, grassy meadows, and as a minor species in dense mixed-species stands between 1525 and 1830 meters in elevation. In general, the anecdotal information was very useful in identifying sites where whitebark pine was a dominant landscape feature, but it overlooked site and stand types where the species has a less obvious presence. Some sort of less biased, more scientifically-based predictive mapping was needed.

Climate and topography as a basis for mapping plant species distribution

Climate is considered to be a good predictor of plant species occurrence (Woodward 1987). Box (1994) determined that moisture balance and seasonality in temperature and precipitation control the potential distributions of vegetation types. Weaver (1990) characterized climates of whitebark pine woodlands using data from sites in the Rocky

Mountains known to have whitebark pine, but did not attempt to distinguish between sites with and without whitebark pine. McKenzie et al. (2003) found distinct correlations between two climate parameters (annual mean daily temperature and maximum winter snowpack accumulation) and whitebark pine presence in Washington State, but whitebark pine was not a primary subject of their 14-species study of conifer distribution.

The U.S. Forest Service and other land management agencies frequently use both climate and topography to delineate and map vegetation types. Forested plant association groups and potential natural vegetation (PNV) groups are described by both climatic and topographic characteristics (Kuchler 1964; Henderson et al. 1989, 1992; Lillybridge et al. 1995). PNV is the climax vegetation that would be expected to occupy a site in the absence of disturbance (including climate change). PNV is an expression of environmental factors, including topography and climate.

Project objectives

The principal objective of this exercise was to describe the topographic characteristics and the "bioclimatic envelope" or "climate space" associated with whitebark pine occurrence in Washington State. The bioclimatic envelope model defines, for selected parameters, the upper and lower limits within which a plant group or type is expected to occur (Box 1981, 1994). Because it relies solely on climate parameters and does not consider the many other factors that are involved in determining the distribution of plant species, such as biotic interactions and temporal vegetation dynamics, the bioclimatic envelope model is inherently coarse-scaled and general, but it can provide a useful starting point for habitat modeling (Pearson and Dawson 1993).

The terms "envelope" and "niche" are related terms used to describe generalities about factors controlling plant species' distributions, but niche characterizations are typically more specifically defined. For instance, the physiology-based "physiological niche" or "fundamental niche" of a species is described as those conditions under which the species would grow in a laboratory or nursery. This is an idealized niche that explicitly does not take into account competitive (i.e. seral) and dynamic influences of other species. Those impacts reduce the space of the fundamental niche, shaping the "ecological" or "realized" niche (Ellenberg 1953 and Hutchinson 1957, as cited in Prinzing et al. 2002). Although dynamic biological factors such as competition and seral stage are not directly considered in this thesis, it is likely that such factors contributed to the absence of the species on local levels or near the margins of its range, and are thus indirectly reflected in the presence/absence data. The current study, then, based on both presence and absence under field conditions, goes somewhat beyond defining the generalized climate envelope for whitebark pine, but does not directly describe whitebark pine's ecological niche in Washington State.

In addition to describing whitebark pine's bioclimatic envelope, a secondary goal was to identify which, if any, of these parameters are strongly associated with whitebark pine presence, and could potentially be used as predictive variables in future efforts to generate a mathematical model to predict whitebark pine presence on a finer scale, perhaps incorporating synergistic effects of these and other pertinent parameters. The current analysis is intentionally simple, using readily available data and simple statistical techniques. It is outside the scope of this thesis to perform the more complex statistical analyses that are typically used to generate such predictive models.

Null hypothesis

The null hypothesis for this study can be stated as follows: *in Washington State, there are no statistically significant differences in climatic and topographic parameters between sites over 1525 meters in elevation having documented presence of whitebark pine, and sites over 1525 meters in elevation having documented absence of whitebark pine.* Simple statistical analysis of climate and topographic characteristics associated with precise geographic locations of sites having documented presence or absence of whitebark pine allow testing of this hypothesis. Even if the analysis provides no grounds for rejecting this null hypothesis, elucidating the ranges of the climatic and topographic variables representing sites having known whitebark pine presence might at least permit more refined intuitive mapping and contribute to future efforts to predict the species' distribution within the state.

METHODS AND MATERIALS

Study area

The study area is Washington State, the most northwest of the continental United States. Climatic conditions vary widely across the state—the Cascade Mountains divide the state into two distinct climatic regimes. Mild, wet, maritime conditions near the Pacific coast extend into the western foothills of the Cascade Range, and the western slopes of the Cascade Range typically receive heavy annual snowfall. East of the Cascades conditions are much drier, with colder winter and hotter summer temperatures.

While this study considers Washington State in general, national forest lands within the state are the particular focus. Washington State contains all or part of seven national forests: the Olympic National Forest on the Olympic Peninsula in the northwest corner of the state; the Mt Baker-Snoqualmie, Gifford Pinchot, and Okanogan and Wenatchee National Forests spanning the entire north-to-south length of the Cascade Mountain Range down the center of the state; the Colville National Forest in the state's northeast corner; and a small portion of the Umatilla National Forest in the state's southeast corner. Because whitebark pine's lower elevational limit in the state is estimated to be around 1525 meters, these national forests, plus three national parks—Olympic National Park, North Cascades National Park, and Mount Rainier National Park—encompass nearly all the state's mountainous territory, and hence nearly all of the state's whitebark pine habitat. The remaining mountainous areas are either on Indian Reservations—the Colville Indian Nation and the Yakama Indian Nation, both in eastern Washington—or on state-owned lands—the Loomis State Forest immediately east of the Okanogan National Forest, and lands administered by the Washington Department of Natural Resources and the Washington Department of Fish and Wildlife. In all, about 80 percent of potential whitebark pine habitat in the state is on national forest system lands, 14 percent lies within national park boundaries, and the remaining 6 percent is on tribal or state-owned lands. Figure 2 shows elevations over 1525 meters in Washington State. The background is a shaded relief of the state's topography. National Forest System lands are outlined in black.

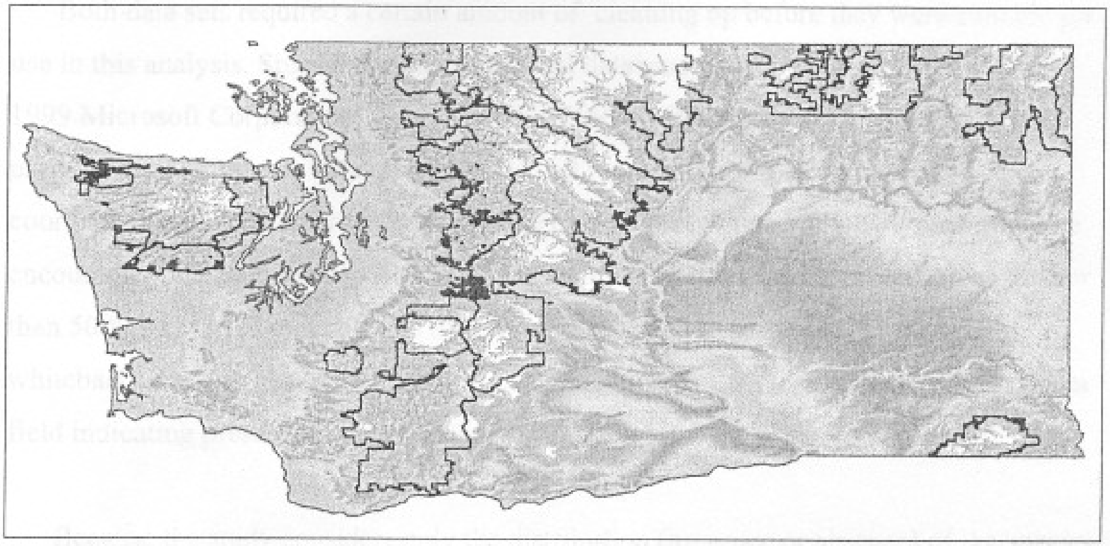

Figure 2. Shaded relief map of the state of Washington, showing elevations above 1525 meters (shaded white) ,and National Forest System boundaries (black outlines)

Presence and absence data

Two USDA Forest Service data sets were used for this analysis: Continuous Vegetation Survey (CVS) plot data, and the combined Ecology Plot/Potential Natural Vegetation (PNV) plot database developed and maintained by the Area Ecology Programs of the US Forest Service, Region 6. The CVS data represent vegetation plots installed between 1993 and 1996 on Forest Service lands in Washington and Oregon (US Forest Service Region 6) on a randomly selected 2-mile by 2-mile (1.25 kilometer by 1.25 kilometer) grid. In wilderness areas, the grid is expanded to 4-miles by 4-miles (2.5 kilometers by 2.5 kilometers). All plant species encountered in each CVS plot are identified and recorded. The Eco/PNV database contains plot data used for determining plant association groups for several national forests in Washington State (Henderson et al. 1989; Lillybridge et al. 1995), and in the PNV model developed by Henderson (1997). Ecology plots and PNV plots are typically non-randomly-located 1/10-acre (405 square-meter) plots. Because the identity of all plant species encountered on the plots in the CVS and Eco/PNV databases is recorded, it was possible to derive both presence and absence data for whitebark pine: presence for plots where the species was encountered, and absence for the plots where whitebark pine was not among the species recorded.

Both data sets required a certain amount of cleaning up before they were suitable for use in this analysis. Spreadsheet and relational database software (Excel 2000, ©1985-1999 Microsoft Corporation; Access 2000, ©1992-1999 Microsoft Corporation) were used for the preliminary data cleanup. First, all records missing geographic site coordinates removed. In order to restrict the data to sites where whitebark pine might be encountered, the data set was limited to sites with field-recorded elevation values greater than 5000 feet (1525 meters). The data were then sorted to separate sites on which whitebark pine was observed from those on which it was not observed, and a binary data field indicating presence ("1") or absence ("0") of whitebark pine was added.

Because the study considers only the distribution (presence or absence) of the species, data concerning percent cover and cover type (overstory or regeneration) were disregarded. Again, this was to ensure that no instance of whitebark pine presence would be overlooked—plots varied from containing only a single whitebark pine sapling to having whitebark pine as the dominant overstory tree species. In a number of instances different records contained identical unique plot identifiers, geographic coordinates, and survey dates, but different data. Where whitebark pine presence or absence was consistent throughout all the records for that unique location, one instance of that site was retained. Where whitebark pine presence or absence was not consistent in such a situation, all of the suspect records were eliminated. In some instances two or more plot records had different unique identifiers but identical geographic coordinates. Again, where all the recorded data, including whitebark pine presence or absence, were consistent for those coordinates, a single instance of the plot was retained. Otherwise all the suspect records were removed from the data set.

Once the initial comparisons and cleanups were complete, the remaining plots were mapped using GIS software (ArcGIS 9.0, ©1999-2004, ESRI Inc.). Points that appeared outside of the geographic extent of the databases (outside the boundaries of national forest system lands in Washington State) were removed. The mapped points were then compared to a 10-meter digital elevation model (DEM), and any plots that did not fall into the elevation range of 1525 meters and above were eliminated. The 10-meter DEM was chosen because of its fine-scale spatial resolution. After all the GIS-based clean up was complete, the ultimate data set contained 2728 unique sites, of which 803 contained whitebark pine (the "present" sites) and 1925 did not (the "absent" sites). Figure 3 is a map of the sites included in the analysis.

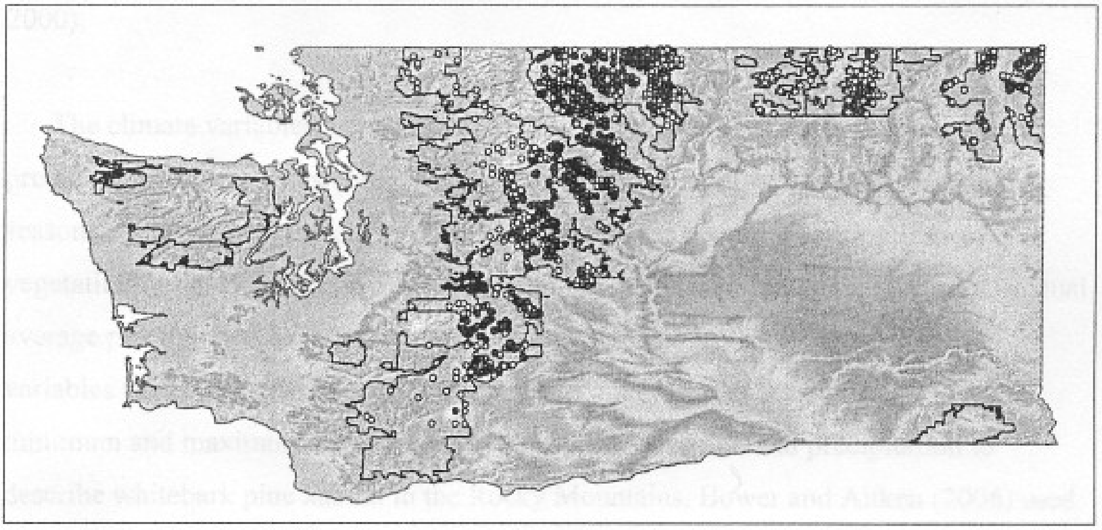

Figure 3. Sites in the dataset: whitebark pine PRESENT (dark dots) and ABSENT (light dots). Black lines indicate national forest boundaries.

Topographic and climatic data

Three topographic and six climatic variables were used in this analysis. The topographic variables of interest were elevation (ELEV), slope (SLOPE), and aspect (ASPECT). The climatic variables were average annual precipitation (PRECIP); mean length of frost-free period (FFDMEAN) and median length of frost-free period (FFDMED); mean annual temperature (TMEAN), average minimum annual temperature (TMIN), and average maximum annual temperature (TMAX). All nine of these variables were chosen for both their applicability and their availability.

Of the three topographic variables, elevation was selected to determine if there was a strong association between any particular elevational stratum (above 1525 meters) and whitebark pine presence. Slope and aspect were chosen because literature and anecdotal evidence suggest that, as a result of nutcracker caching site preferences, whitebark pine is more likely to be found on steep south-facing slopes, (Tomback 2001). Incorporating slope and aspect in the analysis would test this observation. Elevation, slope, and aspect are also used to characterize forested plant associations on national forests across the study area (Henderson et al. 1989, 1992; Lillybridge et al. 1995), and are considered important regional factors in determining vegetation patterns (Guisan and Zimmerman 2000).

The climate variables were chosen because of climate's close association with predicting plant species occurrence (Woodward 1987), and Box's (1994) finding that seasonality in temperature and precipitation control the potential distributions of vegetation types. Box specifically lists maximum and minimum temperatures and annual average precipitation as important factors. Other studies have used these climatic variables to identify characteristics of whitebark pine habitat. Weaver (2001) uses minimum and maximum annual temperatures and average annual precipitation to describe whitebark pine habitat in the Rocky Mountains. Bower and Aitken (2006) used frost-free days to characterize geographic variation in cold-hardiness in a laboratory study of whitebark pine seedlings. McKenzie et al. (2003) included mean annual temperature, annual precipitation and length of frost-free period in their study identifying climatic and biophysical limits to conifer species distributions on several national forests in Washington State. Inquiries about availability of spatial climate data sets for the study area revealed that frost-free period data were available for both mean and median length of frost-free period. In order to see if one of these measures was a better predictor of whitebark pine than the other, both were used in the analysis.

Spatial data for average annual precipitation (PRECIP) came from the U.S. Forest Service. The data were in the form of a GIS polygon coverage. Units for PRECIP were originally in inches, and were converted to centimeters for this analysis. The remaining climate data were obtained from The Climate Source (www.climatesource.com), a private company that distributes climate data developed by the PRISM group (www.prismclimate.org), housed at Oregon State University in Corvallis, Oregon. These data were in the form of spatial grids with a 2-kilometer resolution (the finest resolution available at that time), and represent data collected over the 30-year period from 1971 to 2000. Units of temperature are 10ths of a degree Celsius. Frost-free period values are the average length, in days, of the annual frost-free period. Using the spatial join and Spatial Analyst features of ArcGIS, values for the six climate variables were extracted for all sites in the presence/absence data set.

While field-recorded values for the topographic characteristics elevation, slope, and aspect were present in the original data, for the purpose of this analysis the values for these three variables were extracted from the 10-meter DEM using the Spatial Analyst feature of ArcGIS. A DEM and its derivatives (i.e., slope, aspect) are usually quite accurate, even in mountainous regions (Guisan and Zimmerman 2000), so extracting these topographic variable values from the DEM rather than relying on field-recorded values allowed for consistency across the entire data set. Units of elevation are in meters above sea level, and range from 1525 to 2555. The full range of values for slope, expressed in degrees, is 0 to 90, with the value of 0 indicating a flat site. The full range of values for aspect, expressed as the compass direction, in degrees, toward which the site faces, is 0 to 360, with -1 for flat. Of the 2728 data points in the presence/absence data set, only five had ASPECT values of -1; whitebark pine was absent from all five of those sites. To prevent these rare flat aspect values of -1 from influencing the results for this variable, those five sites were not included in the analysis of ASPECT.

DATA ANALYSIS AND RESULTS

This analysis was performed using Excel spreadsheet software (Excel 2000, ©1995-1999, Microsoft Corporation). All of the variables except ASPECT were continuous linear variables with roughly normal distributions, so z-tests could be used to compare the differences between their distributions in the presence and absence data subsets. Figures 4 through 11 display histograms for the distributions of these variable values for the present and absent data subsets.

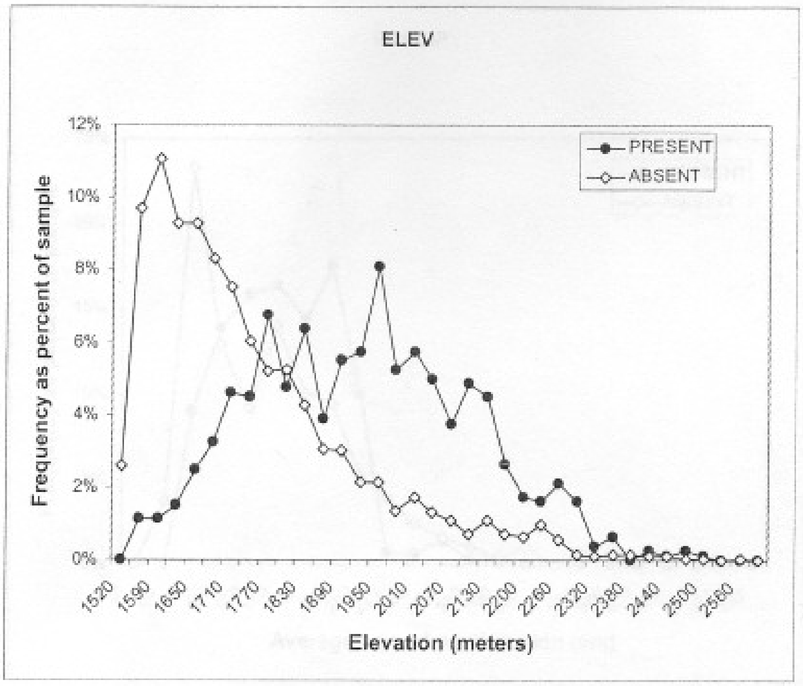

Figure 4. Distributions of elevation (ELEV) for sites with known whitebark pine presence or absence

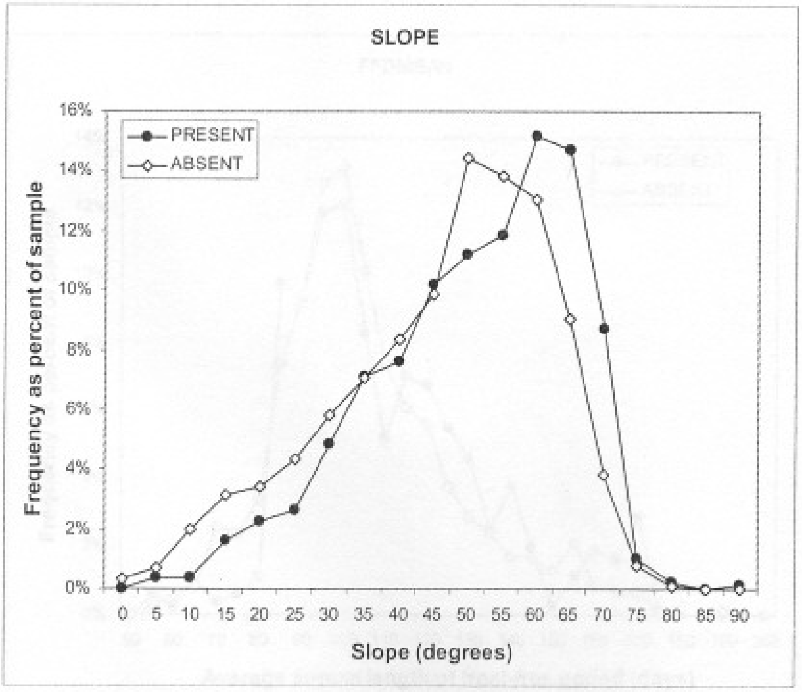

Figure 5. Distributions of slope (SLOPE) for sites with known whitebark pine presence or absence

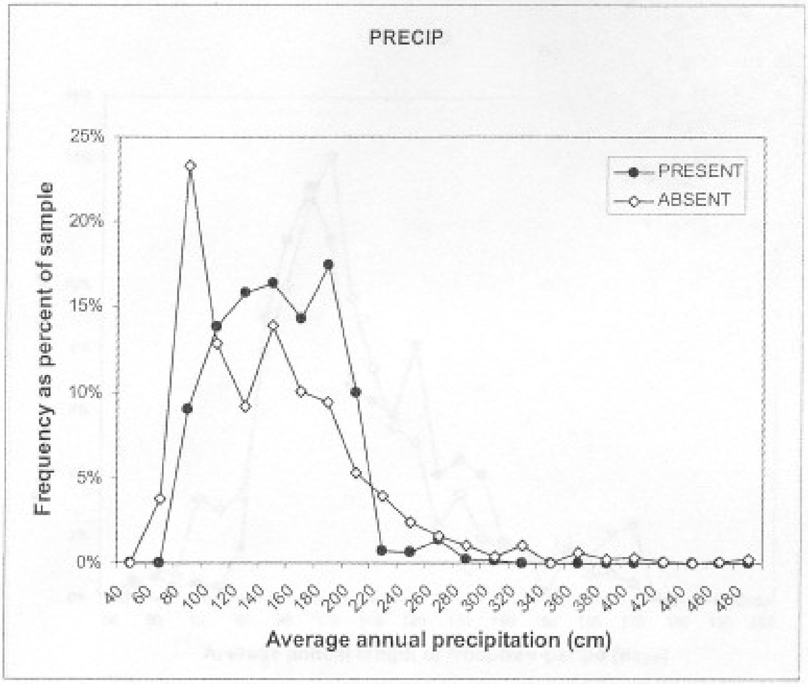

Figure 6. Distributions of annual average precipitation (PRECIP) for sites with known whitebark pine presence or absence

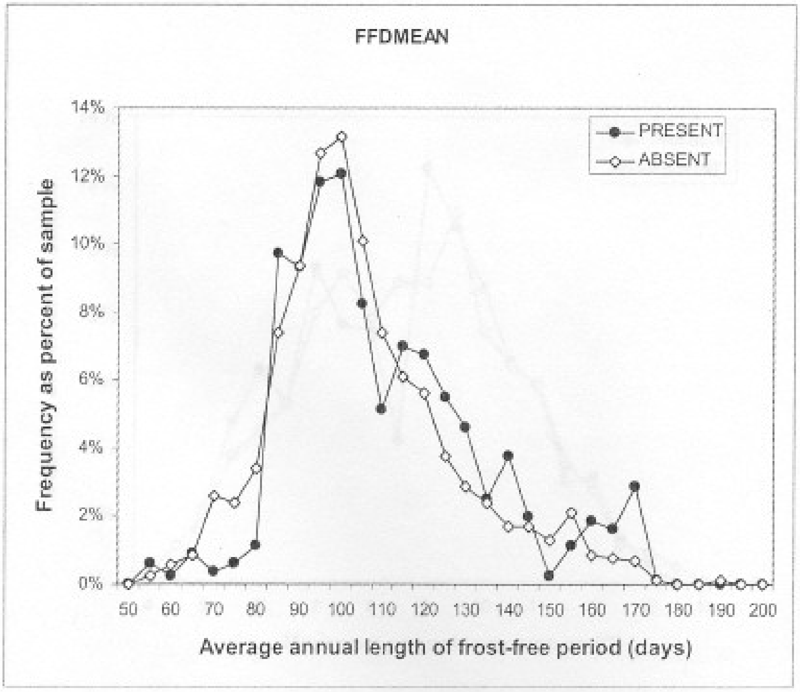

Figure 7. Distributions of mean length of frost-free period (FFDMEAN) for sites with known whitebark pine presence or absence

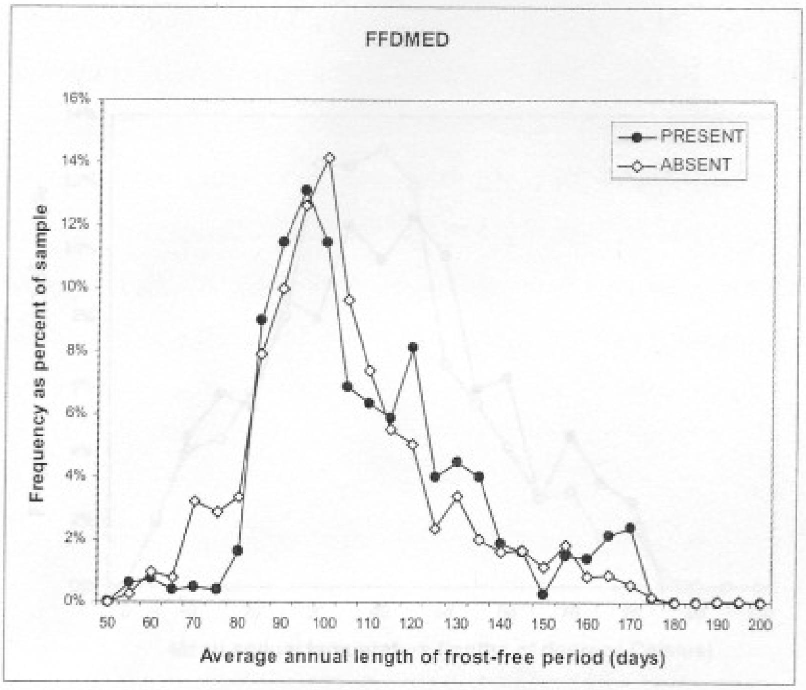

Figure 8. Distributions of median length of frost-free period (FFDMED) for sites with known whitebark pine presence or absence

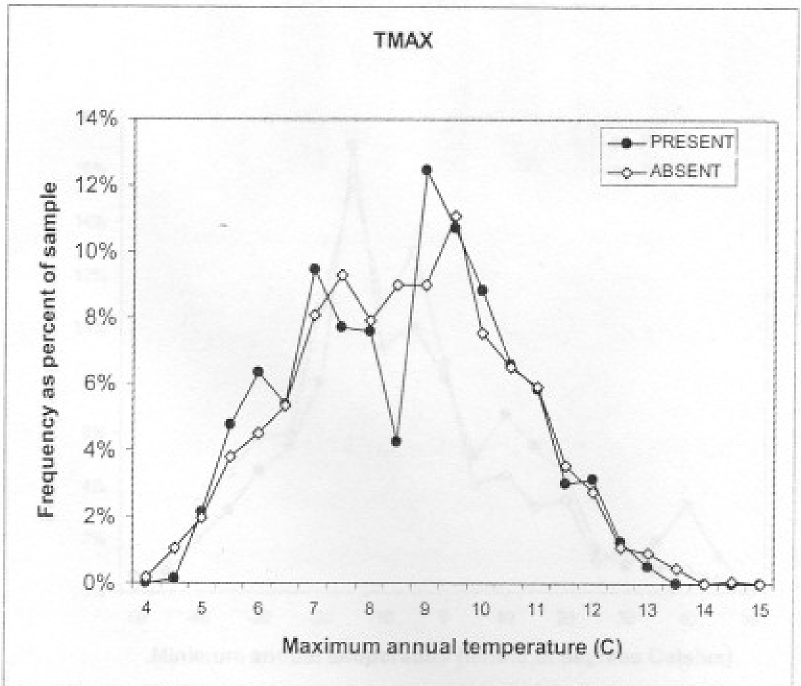

Figure 9. Distributions of average maximum annual temperature (TMAX) for sites with known whitebark pine presence or absence

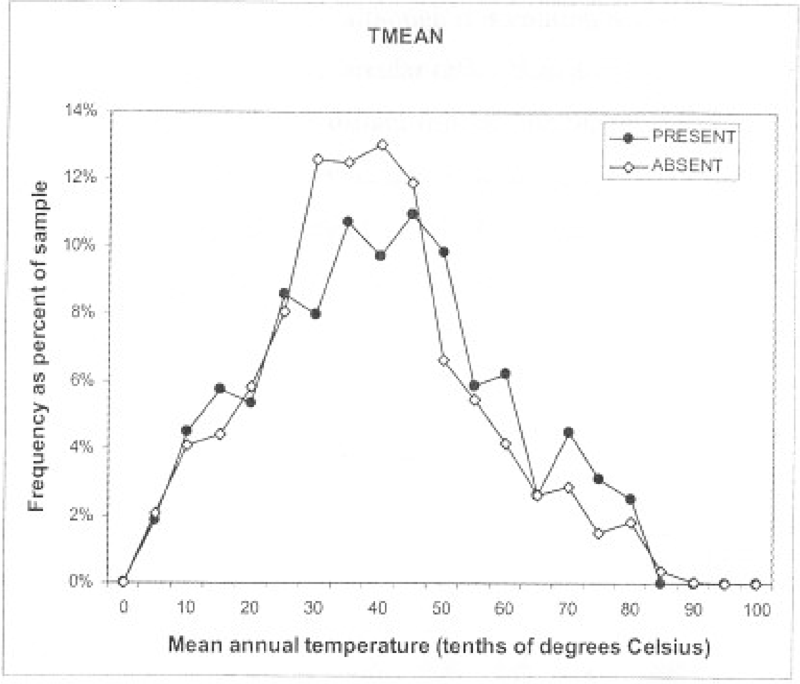

Figure 10. Distributions of mean annual temperature (TMEAN) for sites with known whitebark pine presence or absence

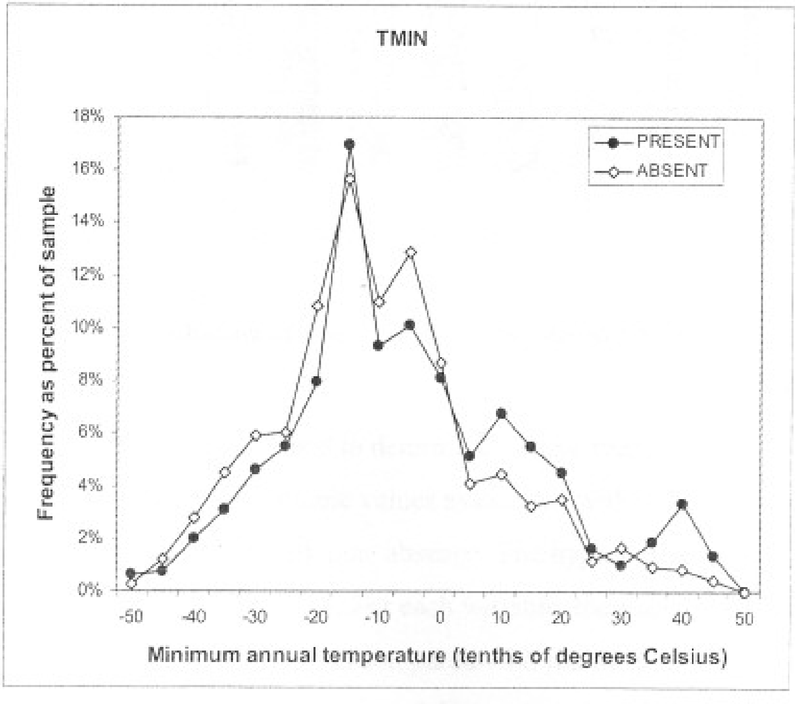

Figure 11. Distributions of average minimum annual temperature (TMIN) for sites with known whitebark pine presence or absence

The variable ASPECT, although it is continuous within its 360-degree limit, actually represents increments of a circular rather than a linear range—0.0 is adjacent to 359.9 instead of 360 increments distant from it, and the greatest physical distance between two values occurs when the mathematical difference between them is 180. Hence, calculating a simple mathematical mean for ASPECT is meaningless. Figure 12 shows a bar histogram for ASPECT, with the familiar 45-degree increments of north (N, 337.5-22.5 deg), northeast (NE, 22.5-67.5 deg), east (E, 67.5-112.5), etc. on the x-axis.

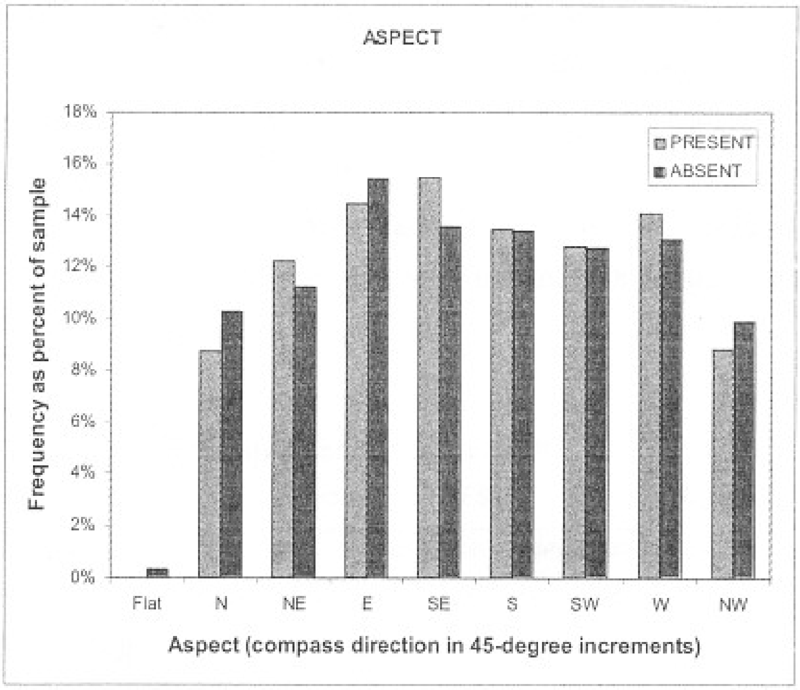

Figure 12. Distributions of aspect (ASPECT) for sites with known whitebark pine presence or absence

Z-tests were performed to determine if there were any statistically significant differences between variable values associated with whitebark pine presence and those associated with whitebark pine absence. The hypothesized mean difference was 0 (zero), and alpha was fixed at 0.05. For each variable, the mean of the values associated with whitebark pine presence was compared with the mean of the values associated with whitebark pine absence. Results of the z-tests return a "P-value" (P) indicating the probability that the means of the compared distributions are equal. A variable having a

P-value equal to or less than the chosen alpha (in this case 0.05, or 5.00×10^{-2}) indicates that there is a statistically significant differences between the mean of the whitebark pine present and whitebark pine absent distributions for that variable.

Six of the nine variables tested showed statistically significant differences between sites with and without whitebark pine. These findings of statistical significance disprove the null hypothesis that there are no significant differences in these simple topographic and climatic parameters between sites where whitebark pine is present and sites where it is absent in Washington State. Table 1 shows descriptive statistics and the results of significance testing for all the variables. In order to allow for mathematical calculations on ASPECT, a cosine transformation was used for this variable—only its P-value is displayed in table 1. The six variables with statistically significant P-values are emphasized in bold font. Note that the temperatures are all annual averages based on 24-hour daily readings, so their ranges incorporate both daytime and nighttime values, and are narrower than might be expected.

Table 1. Descriptive statistics and z-test results

	Whitebark pine PRESENT					Whitebark pine ABSENT					
Variable [a]	min.	max.	median	mean	st. dev.	min.	max.	median	mean	st. dev.	P (z-test) [b]
ELEV (ft)	1527	2500	1915	1916	183	1525	2555	1677	1727	174	**0.00**
SLOPE (deg)	0.0	89.0	50.8	48.4	14.5	0.0	79.0	46.9	43.9	15.6	**2.40×10^{-13}**
ASPECT (cosine) [c]	-	-	-	-	-	-	-	-	-	-	1.86×10^{-1}
PRECIP (cm)	68.6	281.9	134.6	135.5	38.4	43.2	469.9	124.5	131.7	64.4	5.86×10^{-2}
FFDMEAN (days)	55.0	172.0	103.0	108.2	23.2	55.0	190.0	100.0	103.5	21.6	**5.35×10^{-7}**
FFDMED (days)	54.0	172.0	101.0	107.1	23.2	54.0	194.0	98.0	102.1	21.7	**1.89×10^{-7}**
TMAX (deg C) [d]	4.1	12.8	8.7	8.4	1.9	4.0	14.4	8.5	8.5	1.9	5.26×10^{-1}
TMEAN (C) [d]	0.3	8.0	3.8	3.9	1.8	0.3	8.6	3.6	3.7	1.7	**8.40×10^{-3}**
TMIN (C) [d]	-5.1	4.4	-1.1	-0.7	1.9	-5.1	4.3	-1.3	-1.1	1.7	**2.91×10^{-8}**

a Variables with statistically significant P-values are in bold font.

b Alpha = 0.05

c In order to allow for mathematical calculations on ASPECT, a cosine transformation was used for this variable—only its P-value is displayed

d For ease of interpretation, all temperature values have been converted from the original units of 0.1C to units of 1C.

Statistically significant differences between presence and absence

Of the three topographic variables, both ELEV ($P \leq 0$) and SLOPE ($P \leq 2.4 \times 10^{-13}$) showed statistically significant differences between the presence and absence data subsets. For ELEV, the difference occurs within the already restricted elevational range of 1525 meters and above. Within this range the present sites were relatively normally distributed, while the absent sites were concentrated in the lower elevations (fig. 4). For SLOPE, whitebark pine presence was more frequently associated with sites having steeper slopes (fig. 5).

Visual analysis of the histograms for ASPECT reveals no apparent trends in that variable, either on a degree-by-degree basis (not shown) or in the more familiar increments of 45 degrees (fig. 12). On a degree-by-degree basis, no one-degree range captured more than 0.87 percent of either the presence or absence subset. A cosine transformation for this parameter revealed a non-significant P-value ($P \leq 1.86 \times 10^{-1}$).

For the climate variables, PRECIP ($P \leq 5.86 \times 10^{-2}$) was not significantly different between present and absent sites, although there is a trend toward lower average annual precipitation on the sites where whitebark pine is present (fig. 6). Both FFDMED ($P \leq 1.89 \times 10^{-7}$) and FFDMEAN ($P \leq 5.35 \times 10^{-7}$) did show significant differences between the present and absent sites, with FFDMED showing a slightly greater significance. Of the three temperature variables TMIN ($P \leq 2.91 \times 10^{-8}$) showed the greatest significance; TMEAN was also significant ($P \leq 8.4 \times 10^{-3}$), but TMAX was not ($P \leq 5.25 \times 10^{-1}$).

DISCUSSION

Bioclimatic envelope of whitebark pine

Based on the descriptive statistics for climate parameters associated with whitebark pine presence in table 1, a simple bioclimatic envelope for the species in Washington State can be described this way: whitebark pine occurs in areas above 1525 meters in elevation having average annual precipitation of 69 to 282 cm (median 135); a frost-free period of 54 to 172 days (median 107); and mean annual temperatures of 0.3 to 8.0

degrees C (median 3.8), with average maximum annual temperatures of 4.1 to 12.8 degrees C (median 8.7), and average minimum annual temperatures of -5.1 to 4.4 degrees C (median -1.1).

Using ELEV and the two most statistically significant climate variables (FFDMED and TMIN), with a confidence interval of 95 percent [mean +/- 1.96 x (st. dev.)] for each variable, the predicted range for whitebark pine above 1525 meters in elevation in Washington State would be those geographic areas between 1557 and 2275 meters in elevation having a median frost-free period of 83.9 to 130.3 days, and average minimum annual temperatures of -2.6C to 1.2C. Figure 13 displays this range, overlaid on Little's (1971) more general range map.

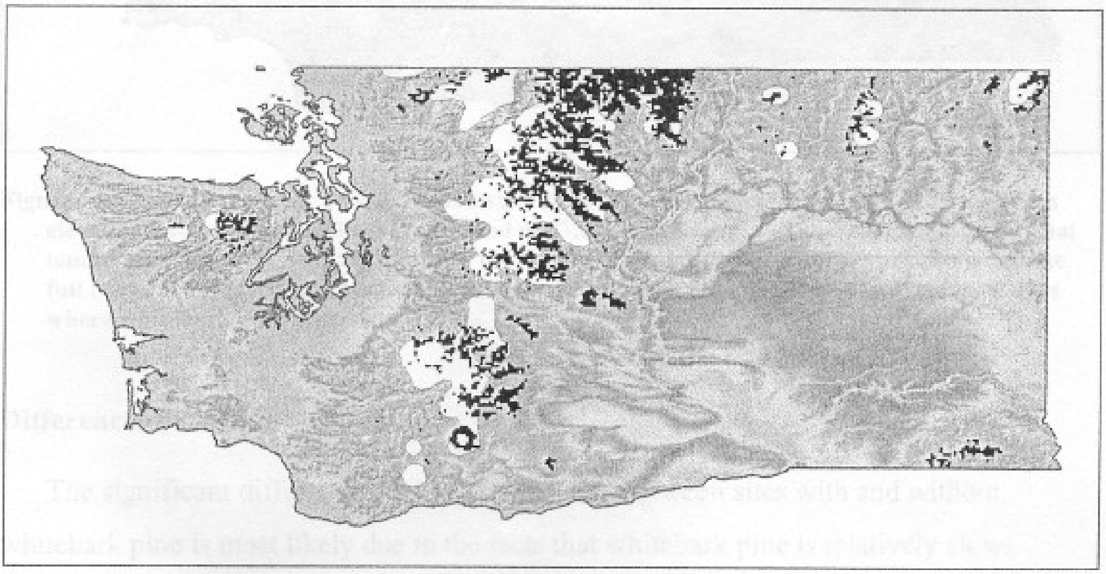

Figure 13. Shaded relief map of Washington state showing (in black shading) the areas between 1557 and 2275 meters in elevation having a median frost-free period of 83.9 to 130.3 days, and average minimum annual temperatures of -2.6C to 1.2C (the 95% confidence intervals for these three variables). The Little (1971) range map is underlaid in white.

Interestingly, further limiting the range predicted by the 95 percent confidence interval of ELEV, FFDMED, and TMIN (fig.13) with the full range of PRECIP for the sites where whitebark pine was present (68.6 to 281.9 cm/year) provides an even better representation of the sites with documented whitebark pine presence. Figure 14 displays this combination, overlaid with both the "present" sites in the dataset and a handful of additional known whitebark pine sites on the Olympic Peninsula and in North Cascades and Mount Rainier National Parks.

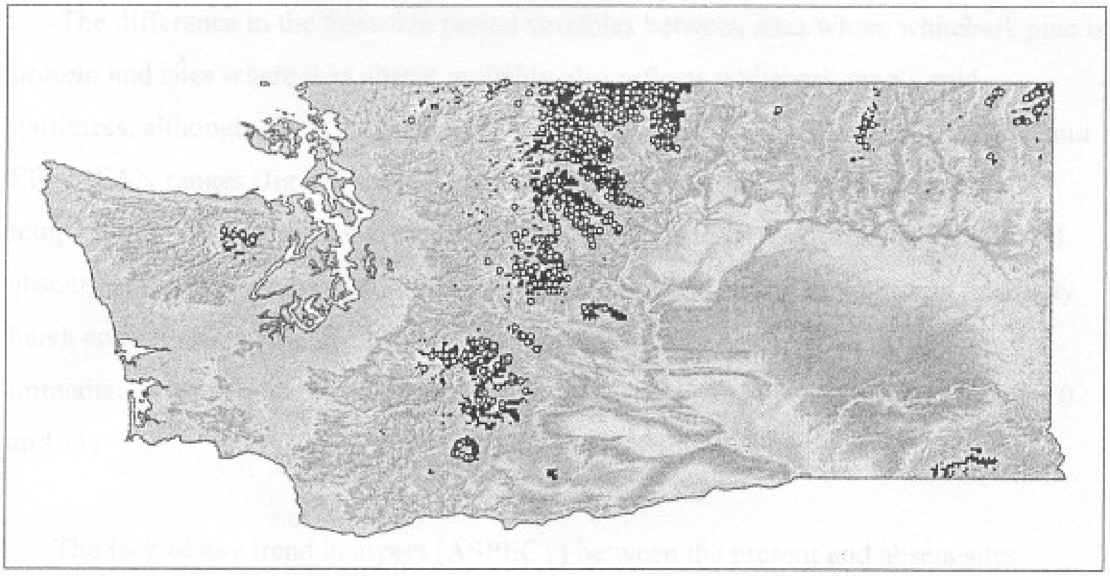

Figure 14. Shaded relief map of Washington state showing areas between 1557 and 2275 meters in elevation having a median frost-free period of 83.9 to 130.3 days, and average minimum annual temperatures of -2.6C to 1.2C (the 95% confidence intervals for these three variables), and the full range of PRECIP for sites with documented whitebark pine presence. Dots represent sites where whitebark pine is present.

Differences between variables

The significant difference in elevation (ELEV) between sites with and without whitebark pine is most likely due to the facts that whitebark pine is relatively slow-growing and is not shade-tolerant(Arno 2001)—it is out-competed on lower elevation sites by other tree species (fig. 4). I have encountered an occasional straggly whitebark pine sapling on sites as low as 1400 meters, but such strays are unlikely to survive in the typically dense forest conditions found at these elevations. Conversely, whitebark pine does extremely well in the harsher conditions encountered at higher elevations and near the subalpine treeline, and is able to persist on these sites where other tree species are unable to establish and survive (Arno 2001). Whitebark pine's positive association with steeper slopes (SLOPE) (fig. 5) is probably based on similar competitive factors.

Whitebark pine is considered to be relatively drought-tolerant and cold-hardy compared to co-occurring tree species in Washington State (Arno and Hoff 1990), and its ability to colonize and persist on steeper, higher-elevation sites reflect these characteristics.

The difference in the frost-free period variables between sites where whitebark pine is present and sites where it as absent probably also reflects whitebark pine's cold-hardiness, although this is apparent as a trend only in the upper end of the FFDMED and FFDMEAN ranges (figures 7 and 8). Similarly, differences in average minimum temperature (TMIN) and mean annual temperature (TMEAN) between the present and absent data subsets probably also reflect whitebark pine's ability to withstand relatively harsh conditions. Again, these trends are apparent in the z-test results, but are not immediately evident in the descriptive statistics (table 1) and the histograms (figures 10 and 11)

The lack of any trend in aspect (ASPECT) between the present and absent sites (fig.12) probably reveals an observer bias inherent in the anecdotal reports associating whitebark pine primarily with southerly and westerly aspects. My own field observations indicate that, while whitebark pine occurs on all aspects, it tends to be more dominant (and hence more prominent) on the south- and west-facing slopes indicated in anecdotal reports. On the moister, more shaded northerly and easterly aspects it tends to be suppressed by shade-tolerant species. An analysis that considered whitebark pine dominance (as relative percent cover) instead of simple presence and absence might reveal stronger associations with this parameter.

The lack of a statistically significant difference in average annual precipitation (PRECIP) ($P \leq 5.86\text{x}10^{-2}$) between sites with and without whitebark pine was unexpected. Both in terms of frequency of occurrence and of dominance on a site, whitebark pine presence diminishes rapidly as one moves westward across the Cascade Crest into the moister maritime climate. While it just misses statistical significance at an alpha of 0.05, including the full range of PRECIP associated with whitebark pine presence (68.8 to 281.9 cm/year) with the statistically significant variables ELEV, FFDMED, and TMIN on a map depicting whitebark pine presence and absence noticeably improved the correlation between the species' predicted range and whitebark pine presence (fig 14).

Comparison with other studies

Using data drawn from four study locations—one each in California, Oregon, Montana, British Columbia, and Alberta—Weaver (2001) describes the climate of whitebark pine ecosystems as follows: for minimum temperatures, an absolute minimum of -36C, with an average January minimum of -13C; for maximum temperatures, an absolute maximum of 29C, with an average July maximum of 19C; for the 4.3 month growing season, a mean temperature of 9C. Each of these temperature parameters represents a different measure than the average annual mean, minimum, and maximum temperatures considered in this thesis—because Weaver's average values are averaged over shorter time periods, they are less moderate than the annual averages used here, and not readily comparable. Weaver's reported growing season of 4.3 months (approximately 129 days assuming a 30-day month) is longer than the 107 frost-free days reported here, a discrepancy which may be attributable to differences between Weaver's definition of growing season month (months with moist soils and average air temperature above 0C) and the stricter delineation of frost-free days. Weaver's value for annual precipitation for these four whitebark pine sites is 705mm, or 70.5cm, which is considerably less than the mean of 135.5cm reported in this thesis, and is actually quite close to the 68.6cm minimum. Washington State has a generally wetter and milder climate than those prevalent in the four sites included in Weaver's analysis, and whitebark pine's climatic envelope in Washington apparently reflects those differences. Weaver reports that precipitation in whitebark pine habitat ranges from 60cm to 160cm per year, while the range reported here in table 1 runs from 69cm to 282. Weaver's values reflect the conditions prevalent on his various study sites, and are not transferable to Washington State.

McKenzie et al. (2003) included annual precipitation, mean annual temperature, and frost days among the variables analyzed in a study modeling climatic and biophysical controls on conifer species distributions in Washington State. They also included aspect. They drew their data from the US Forest Service's Area Ecology database, and from data collected for a study of Grizzly Bear habitat. Their study of 14 conifer species covered the Wenatchee, Okanogan, and Colville National Forests, and was not elevation-limited. Although plots in which whitebark pine was present comprised only 2.7 percent of their dataset (284 of a total of 10,653 sites), they included the species because of its rarity and its considerable management interest. McKenzie et al.'s study was a modeling study, investigating generalized linear models to predict the habitat conditions and limiting factors for each species. Climate variables were the most frequent of the predictor variables they identified. Whitebark pine was present in only three of the seven geographic data subsets they tested—the grizzly bear habitat study sites, the Wenatchee National Forest, and those two sets combined—and was successfully modeled in all three. The three predictive variables that appeared for whitebark pine were annual mean daily temperature (all three areas), maximum winter snowpack (one area), solar radiation (one area), and evaporative water loss (one area). The statistically significant correlation of annual mean temperature with whitebark pine presence in this thesis compares favorably with McKenzie et al.'s results for this variable. Neither this study nor McKenzie et al.'s identified average annual precipitation as a statistically significant predictive variable.

The U.S. Geological Survey has produced a climate-vegetation atlas for North America that characterizes range-wide climatic conditions for selected North American conifers and hardwoods (Thompson et al. 1999). This atlas uses the existing range maps developed by Elbert Little (i.e., Little 1971) and extracts the ranges of the climatic parameters delineated by those range maps. The assumption is made that the species of interest is consistently present within that range, and absent outside of it. The scale used by this continental-level atlas is coarse—a 25km by 25km grid. For whitebark pine, the range of which encompassed 589 of these grid points, Thompson et al. (1999) report average annual temperatures of -4.8C to 10.2C; and annual precipitation of 28.5cm to 437cm. Given the very broad ranges for these two climate variables, it is likely that the data in the atlas are not elevation-limited. In contrast, the dataset used in this thesis was intentionally limited from below at the 1525-meter level, and effectively limited from above at the 2555-meter level, the highest elevation in the dataset.

Project summary

This study produced a range map for whitebark pine in Washington State that is considerably more refined and accurate than the 1971 Little range map. However, using the data and methods described, I was unable to determine any fine-scale predictive differences between sites with and without whitebark pine within that range. The data set does not provide a finely-enough scaled representation of whitebark pine presence and absence, especially (and ironically) in those open, whitebark pine-dominated stands near timberline. In the Pacific Northwest, this stand type usually occurs in relatively small patches on open slopes and in narrow stringy stands near summits and along ridge systems. It is probable that 2x2-mile (non-wilderness) or 4x4-mile (within wilderness) sampling technique in the primary data source (the CVS plots) simply skips over many of these stands. Also, with the small (0.1-acre) circular plots, it is entirely likely that plot data from a plot that did land in such a stand might not indicate presence of whitebark pine, because the entire plot area occurred in one of the wide spaces between trees, resulting in a false negative ("absent") value. This indicates that a much finer-grained sampling strategy, or the use of larger sample plots, or perhaps something else altogether would more accurately represent whitebark pine presence or absence on a local scale.

With the rapid development of high-resolution satellite imagery and LIDAR technology, it may be possible to use these remote-sensing technologies to visually identify whitebark pine locations with a high degree of accuracy. Combining data obtained using this technology in a GIS with similarly high-resolution climate and topographical data could reveal fine-scale predictive factors that are undetectable using the data and methods of this current study.

SUGGESTIONS FOR FURTHER ANALYSIS

Improving the statistical method

This thesis identifies significant differences between several basic climatic parameters associated with whitebark pine presence and whitebark pine absence in Washington State. This study was intentionally simple, using readily available climate data and a somewhat wide-ranging, non-randomized presence/absence data set. This initial analysis can contribute to the development of a model to predict the presence distribution of whitebark pine in Washington State on a finer scale.

Statistician Nobuya Suzuki, PhD, of Oregon State University provided valuable advice on how to proceed with the next step toward such a modeling effort. Dr. Suzuki identified binary logistic regression as the appropriate statistical method, with whitebark pine presence or absence as the response variable. This method calculates the odds of a selected binary outcome—in this case, the odds of whitebark pine presence on a given site—based on the values of the variables (the climatic and topographic factors) for that site. Dr. Suzuki recommended using multi-model inference based on Akiake's information criteria (AIC) (Akiake 1973) as the method of model analysis (see Burnham and Anderson 1998 for detailed information about AIC and its basis in information and likelihood theory). This method allows for sound comparison between multiple models. AIC has been shown to have several advantages over traditional significance testing (Greaves et al. 2006), and is becoming increasingly popular for ecological modeling (Fidler et al. 2006). AIC has been used in several recent ecological modeling studies in the Pacific Northwest, including a study of habitat use by northern spotted owls in Oregon (Glenn et al. 2004), and preferential selection of different types of in-stream wood structures by beavers in Washington (MacCracken and Lebovitz 2005). More broadly, Jarnevich et al. (2006) used AIC to model native species diversity and non-native species invasions across the continental U.S.

To be credible and robust, statistical analysis requires a designed sampling strategy. A more sophisticated analysis of the presence/absence data set used in this study should be restricted to the non-random CVS plots, and within those plots should be further restricted to either the plots within the boundaries of designated wilderness (4-mile grid), or those outside of wilderness (2-mile grid). The analysis should also be limited to a single cohesive geographic area—for instance, one national forest, or one of Omernik's level 3 ecoregions (Omernik 1987; McMahon et al. 2001). This dramatically reduces the dataset, but would allow for sound statistical analysis of smaller geographic units.

In order to avoid collinearity in such a modeling effort, only one of the closely related frost-free period variables, and one of the temperature variables should be selected. In this study, FFDMED and TMIN showed the strongest associations with whitebark pine presence, and were the better choices for frost-free day and temperature parameters, but study on a smaller geographic area might yield different results. If the model were intended to predict only certain types of stands—for instance, stands where whitebark pine is a dominant overstory component—the binary response field indicating presence (1) or absence (0) in the dataset could be revisited, and the positive value of the response variable limited to only the subset of "present" sites where the species showed the desired relative dominance in that cover type.

Additional factors to consider

There are certainly additional factors that may play a role in the fine-scale distribution of whitebark pine in Washington State. Clark's nutcracker cache site preferences probably influence the distribution of whitebark pine across a landscape (Tomback, Hoffman and Sund 1990), as might fire disturbance history (Keane et al. 1990; Morgan and Murray 2001). All of the three studies with which the results of this thesis were compared (Weaver 2001; McKenzie et al. 2003; Thompson et al. 1999) consider a greater variety of climate variables than does this thesis. More detailed climate data such as absolute maximum and minimum temperatures, seasonal precipitation, solar radiation, and variables having to do with air movement, soil moisture, and drought could be used to more finely distinguish sites with and without whitebark pine. Parameters derived from interactions between climate and topography, such as the slope position and topographic moisture variables used in PNV models, might also contribute to whitebark pine presence or absence. Soils and underlying geology may have an effect, as well. Austin (1980) differentiates between three types of environmental gradients whose factors have predictive value for vegetation modeling, based on their level of physiological influence on plant growth: indirect gradients that have no direct physiological effect (elevation, topography, geology); direct gradients that do have physiological influence but are not consumed (temperature, soil pH); and essential resource gradients (food, water, light). Competition and ecological interactions along these gradients are important in developing realistic vegetation models (Austin 1990, 2002).

Ultimately, a good habitat model must rely on ecologically relevant factors, identifying a priori which parameters are truly pertinent to both the species under consideration and the particular geographic scale of the analysis. The level of complexity should be limited to the question the model is intended to address, and to the level of analysis the data will support (Burnham and Anderson 2002). The tendency to include parameters covering every conceivable environmental and ecological influence can result in unwieldy, over-complicated models, and potentially in unnecessary and expensive data-gathering and delays. Starfield and Bleloch (1991) demonstrate that simpler models are often more powerful than complicated ones, even for inherently complex ecological systems. They recommend starting with relatively simple models, testing them repeatedly to determine their effectiveness and identify what might be missing. The purpose of empirical data analysis is not to produce the "true model", but to generate a parsimonious, best approximating model based on good data, and develop statistical inference from the model (Burnham and Anderson 2002). It is evident even from this relatively simple study and analysis of whitebark pine habitat in Washington State that there is no lack of direct and derived variables from which to choose.

REFERENCES

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B. N.; Csaki, F. F., eds. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary. 267–281.

Arno, S.F. 1986. Whitebark pine cone crops: a diminishing source of wildlife food. Western Journal of Applied Forestry 1:92-94.

Arno, S.F. 2001. Community types and natural disturbance processes. In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 74-88.

Arno, S.F.; Hoff, R.J. 1990. Whitebark pine. In: Burns, R.; Honkala, B.H. (tech. cords.). Silvics of North America. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, D.C. vol.2, 877 p.

Arno, S.F.; Parsons, D.J.; Keane, R.E. 2000. Mixed-severity fire regimes in the northern rocky mountains: consequences of fire exclusion and options for the future. In: McCool, S.F.; Cole, D.N.; Borrie, W.T.; O'Loughlin, J. (comps.). 2000. Wilderness science in a time of change conference—Volume 5: Wilderness ecosystems, threats, and management; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-5. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 225-232.

Austin, M.P. 1980. Searching for a model for use in vegetation analysis. Vegetation 42:11-21.

Austin, M.P. 1990. Community theory and competition in vegetation. In: Grace, J.B.; Tilman, D. (eds.), Perspectives on plant competition. Academic Press, California.: 215-238.

Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological modeling 157:101-118.

Bartos, D.L.; Gibson, K.E. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. In: Schmidt, W.C., ed. Proceedings–Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. Department of Agriculture, Forest Service, Intermountain Research Station. General Technical Report INT-270: 171-178.

Blouin, F. 2006. The Southern Headwaters at-risk project: a multi-species conservation strategy for the headwaters of the Oldman River. Volume 3: Landscape management—selection and recommendations. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Repotr No. 105, Edmonton, Alberta.

Bower, A.D.; Aitken, S.N. Geographic and seasonal variation in cold hardiness of whitebark pine. Canadian Journal of Forest Research 36: 1842–1850.

Box, E.O. 1981. Macroclimate and plant forms: an introduction to predictive modeling in phytogeography. Tasks for vegetation science, Vol. 1. The Hague: Dr. W. Junk BV, Publishers. 258p.

Box, E.O. 1994. Factors determining distributions of tree species and plant functional types. Vegetation 121:101-116.

Campbell, E.M.; Antos, J.A. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. Canadian Journal of Forest Research 30:1051-1059.

Carroll, A.L.; Taylor, S.W.; Régnière, J.; Safranyik, L. 2003. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: Shore, T.L.; Brooks, J.E.; Stone, J.E. (eds.). Mountain pine beetle symposium: challenges and solutions. October 30-31, 2003, Kelowna, British Columbia. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC:223-232.

Carroll, C.; Zielinksi, W.J.; Noss, R.F. 1999. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath region, U.S.A. Conservation Biology 13/6:1344-1359.

Dinerstein, E.; Powell, G.; Olson, D.; Wikramanayake, E.; Abell, R.; Loucks, C.; Underwood, E.; Allnutt, T.; Wettengel, W.; Ricketts, T.; Strand, H.; O'Connor, S.; Burgess, N. 2000. A workbook for conducting biological assessments and developing biodiversity visions for ecoregion-based conservation. World Wildlife Fund; Conservation Science Program; 249p. Available: http://conserveonline.org/coldocs/2003/10/13wkbk.pdf. Accessed March 7, 2007.

Doede, D. 2004. Unpublished survey data including incidence and intensity of white pine blister rust infection in whitebark pine on the Gifford Pinchot and Mt Hood National Forests.

Fidler, F.; Burgman, M.A.; Cumming, G.; Buttrose, R.; Thomason, N. 2006. Impact of Criticism of Null-Hypothesis Significance Testing on Statistical Reporting Practices in Conservation Biology. Conservation Biology 20:1539–1544.

Glenn, E.M.; Hansen, M.C.; Anthony, R.G. 2004. Spotted owl home-range and habitat use in young forests of western Oregon. Journal of Wildlife Management 68:33-50

Goheen, E.M.; Goheen, D.J.; Marshall, K.; Danchok, R.S.; Petrick, J.A.; White, D.E. 2002. The status of whitebark pine along the Pacific Crest National Scenic Trail on the Umpqua National Forest. USDA Forest Service, Pacific Northwest Research Station. General Technical Report PNW-GTR-530. 21p.

Groves, C.R. 2003. Drafting a conservation blueprint: a practitioner's guide to planning for biodiversity. Washington D.C.: Island Press. 457p.

Guisan, A.; Zimmerman, N.E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Hansen-Bristow, K.; Montagne, C.; Schmid, G. 1990. Geology, geomorphology, and soils within whitebark pine ecosystems. In: Schmidt, W.C.; McDonald, K.J. (comps.). Proceedings—symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource: Bozeman, MT, March 29-31, 1989. Gen. tech. rep. INT-270. Ogden, UT: U.S. Dept. of Agriculture, Forest Service, Intermountain Research Station: 62-71

Hargrove, W.W.; Hoffman, F.M. 2000. An analytical assessment tool for predicting changes in a species distribution map following changes in environmental conditions. 4th international conference on integrating GIS and environmental modeling (GIS/EM4):
problems, prospects and research needs. Banff, Alberta, Canada, September 2 - 8, 2000. Available: http://www.colorado.edu/research/cires/banff/pubpapers/104/. Accessed March 7, 2007.

Henderson, J.A. 1997. The PNV Model – A gradient model for predicting environmental variables and potential natural vegetation across a landscape. Draft, revised November 2001. Mt Baker-Snoqualmie National Forest, Seattle, Washington. 102p.

Henderson, J.A.; Lesher, R.D.; Peter, D.H.; Shaw, D.C. 1992. Field guide to the forested plant associations of the Mt Baker-Snoqualmie National Forest. USDA Forest Service, Pacific Northwest Region, R6-ECOL-TP-028-91. 196p.

Henderson, J.A.; Peter, D.H.; Lesher, R.D.; Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. USDA Forest Service, Pacific Northwest Region. R6-ECOL-TP-001-88. 502p.

Jarnevich, C.S.; Stohlgren, T.J.; Barnett, D.; Kartesz, J. 2006. Filling in the gaps: modelling native species richness and invasions using spatially incomplete data. Diversity and Distributions 12:511–520.

Keane, R.E. 2000. The importance of wilderness to whitebark pine research and management. In: McCool, S.F.; Cole, D.N.; Borrie, W.T.; O'Loughlin, J. (compilers). 2000. Wilderness science in a time of change conference—Volume 3: wilderness as a place for scientific inquiry; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-3. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 84-92.

Keane, R.E. 2001. Successional dynamics: modeling an anthropogenic threat. In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 159-192

Keane, R.E.; Stephen F. Arno, S.F.; Brown, J.K.; Tomback, D.F. 1990. Modelling stand dynamics in whitebark pine (Pinus albicaulis) forests. Ecological Modelling 51:73-95.

Kendall, K.C.; Keane, R.E.. 2001. Whitebark pine decline: infection, mortality, and population trends. In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 221-242

Kuchler, A.W. 1964. The potential natural vegetation of the conterminous United States. American Geographic Society Special Publication No. 36.

Lanner, R.M. 1982. Adaptations of whitebark pine for seed dispersal by Clark's nutcracker. Canadian Journal of Forest Research 12:391-402.

Lanner, Ronald M. 1996. Made for each other: a symbiosis of birds and pines. Oxford University Press. 170p.

Lillybridge, T.R.; Kovalchik, B.L.; Williams, C.K.; Smith, B.G. 1995. Field guide to the forested plant associations of the Wenatchee National Forest. USDA Forest Service General Technical Report PNW-GTR-359. Pacific Northwest Research Station. 336p.

Lillybridge, T.R.; Kovalchik, B.L.; Williams, C.K.; Smith, B.G. 1995. Field guide for forested plant associations of the Wenatchee National Forest. Gen. Tech. Rep. PNW-GTR-359. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 335 p.

Little, E.L., Jr. 1971. Atlas of United States trees, volume 1, conifers and important hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1146, 9 p., 200 maps.

Logan, J.A.; Powell, J.A. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist. Fall 2001.

MacCracken, J.G.; Lebovitz, A.D. 2005 Selection of in-stream wood structures by beaver in the Bear River, southwest Washington. Northwestern Naturalist 86/2: 49-58.

MacDonald, G.M.; Cwynar, L.C.; Whitlock, C. 1998. The late Quaternary dynamics of pines in northern North America. In: Richardson, D.M. (ed.). Ecology and Biogeography of Pinus. Cambridge University Press: 122-136.

Mattes, H. 1994. Coevolutional aspects of stone pines and nutcrackers. In: Schmidt, W.C.; Holtmeier, F.-K. (comps.). Proceedings—international workshop on subalpine stone pines and their environment: the status of our knowledge. USDA Forest Service, Intermountain Research Station, Ogden, Utah. General Technical Report INT-GTR-309: 13-35.

Mattson, D.J.; Kendall, K.C.; Reinhart, D.P. 2001. Whitebark pine, grizzly bears, and red squirrels. In: In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds.). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 120-136.

Mattson, D.J.; Reinhart, D.P. 1994. Bear use of whitebark pine seeds in North America. In: Schmidt, W.C.; Holtmeier, F.-K. (comps.). Proceedings—international workshop on subalpine stone pines and their environment: the status of our knowledge. USDA Forest Service, Intermountain Research Station, Ogden, Utah. General Technical Report INT-GTR-309: 212-220.

McDonald, G.I.; Hoff, R.J. 2001. Blister rust: an introduced plague. In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 193-220.

McKenzie, D.; Peterson, D.W.; Peterson, D.L. 2003. Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. Journal of Biogeography 30:1093-1108.

McMahon, G.; Gregonis, S.M.; Waltman, S.W.; Omernik, J.M.; Thorson, T.D.; Freeouf, J.A.; Rorick, A.H.; Keys, J.E. 2001. Developing a spatial framework of common ecological regions for the conterminous United States. Environmental Management 28 (3).

Mills, L.S.; Soule, M.E.; Doak, D.F. 1993. The keystone-species concept in ecology and conservation. BioScience 43: 219-224.

Morgan, P.; Murray, M.P. 2001. Landscape ecology and isolation: implications for conservation of whitebark pine. In: Tomback, D.F.; Arno, S.F.; Keane, R.E. (eds). Whitebark pine communities: ecology and restoration. Washington D.C.: Island Press: 289-309.

Murray, M.P.; Rasmussen, M.A. 2000. Non-native blister rust disease on whitebark pine at Crater Lake National Park. Northwest Science 77: 87-91.

Omernik, J.M., 1987. Ecoregions of the conterminous United States (map). Annals of the Association of American Geographers 77:118-125.

Paine, R.T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91-93.

Perkins, D.L.; Roberts, D.W. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. Forest Ecology and Management 174, 495-510.

Power, M.E.; Tilman, D.; Estes, J.A.; Menge, B.A.; Bond, W.J.; Mills, L.S.; Daily, G.; Castilla, J.C.; Lubchenco, J.; Paine, R.T. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Preston, K.L; Rotenberry, J.T.; Knick, S.T. 2006. GIS-based niche modeling for mapping species habitat. Gap Analysis Bulletin 14. Available: ftp://ftp.gap.uidaho.edu/products/bulletins/14/Preston_bulletin14.pdf. Accessed March 7, 2007.

Price, R.A.; Liston, A.; Strauss, S.H. 1998. Phylogeny and systematics of Pinus. Pages 49-68 in Richardson, D.M. (ed.). Ecology and Biogeography of Pinus. Cambridge University Press. 527p.

Prinzing, A.; Durka, W.; Klotz, S.; Brandl, R. 2002. Geographic variability of ecological niches of plant species: are competition and stress relevant. Ecography 25: 721–729.

Rehfeldt, G.E.; Crookston, N.L.; Warwell, M.V.; Evans, J.S. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences (167) 6:1123-1150.

Richard G. Pearson, R.G.; Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12: 361–371

Romme, W.H.; Turner, M.G. 1991. implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. Conservation Biology 5:373-386.