Assessment of Great Basin Bristlecone Pine (Pinus longaeva D.K. Bailey) Forest Communities Using Geospatial Technologies

David Richard Burchfield
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Assessment of Great Basin Bristlecone Pine (*Pinus longaeva* D.K. Bailey)

Forest Communities Using Geospatial Technologies

David Richard Burchfield

A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Assessment of Great Basin Bristlecone Pine (*Pinus longaeva* D.K. Bailey) Forest Communities Using Geospatial Technologies

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Doctor of Philosophy

Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey) is a keystone species of the subalpine forest in the Great Basin and western Colorado Plateau ecoregions in Utah, Nevada, and California. Bristlecone pine is also the world’s longest-lived non-clonal organism, with individuals occasionally reaching ages up to 5,000 years old. Because of its longevity, bristlecone pine contains an important proxy record of climate data in its growth rings. Despite its ecological and scientific importance, bristlecone pine’s distribution and associated environmental drivers are poorly understood. Geospatial technologies, including unmanned aircraft systems (UAS), remote sensing, geographic information systems (GIS), and spatial modeling techniques can be used to quantify and characterize biotic and abiotic factors that constrain the fundamental and realized niches of bristlecone pine and other subalpine forest species. In Chapter 1, we describe workflows and important technical and logistical considerations for collecting aerial imagery in mountainous areas using small UAS, enabling high-quality remotely sensed datasets to be assembled to study the ecology of subalpine forests. In Chapter 2, we discuss a unique outlier population of bristlecone pine found in the Stansbury Mountains, Utah. We used GIS to delineate boundaries for five small stands of bristlecone pine and examined two competing hypotheses that could explain the species’ presence in the range: 1) that the current population is a relict from the Pleistocene, or 2) that long-distance dispersal mechanisms led to bristlecone pine’s migration from other mountain ranges during or after the warming period of the Pleistocene/Holocene transition. Potential migration routes and barriers to migration were considered in our effort to understand the dynamics behind the presence of this unique disjunct population of bristlecone pine. Chapter 3 describes a comprehensive mapping effort for bristlecone pine across its entire distribution. Using data from historic maps, vegetation surveys, herbarium records, and an online ecological database, we compiled nearly 500 individual map polygons in a public-facing online GIS database representing locations where bristlecone pine occurs. Using these occurrence data, we modeled the suitable habitat of the species with Maximum Entropy (MaxEnt), examining the relative importance of 60 environmental variables in constraining the species distribution. A probability map was generated for bristlecone pine, and the environmental variables were ranked in order of their predictive power in explaining the species distribution. We found that January mean dewpoint temperature and February precipitation explained over 80% of the species distribution according to the MaxEnt model, suggesting that the species favors drier air conditions and increased snowfall during winter months. These three studies demonstrate that geospatial tools can be effectively used to quantify and characterize the habitat of bristlecone pine, leading to improved management and conservation of the species in the face of multiple threats, including mountain pine beetle (MPB), white pine blister rust (WPBR), and possible habitat constriction due to climate change.

Keywords: Great Basin bristlecone pine, spatial ecology, UAS, MaxEnt, GIS, *Pinus*
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CHAPTER 1

sUAS-based Remote Sensing in Mountainous Areas: Benefits, Challenges, and Best Practices

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ABSTRACT

Small unmanned aircraft systems (sUAS) offer key benefits over manned aircraft and satellite platforms used for remote sensing research, such as high spatial resolution, portability, simplicity of implementing ground control, affordability, and lack of reliance upon third-party imagery providers. Mountainous areas, which we define as locations that are higher than 2500 meters in elevation and that contain slopes greater than 25°, pose a number of challenges to sUAS mapping operations that other environments do not, including reduced aircraft performance, cold temperatures, high winds, and limited accessibility. The purpose of our paper is to identify these challenges and discuss workflows used to mitigate these difficulties to achieve greater logistical and operational efficiency. We used a DJI Inspire 2 multirotor aircraft to conduct mapping missions in remote, mountainous areas to support subalpine forest inventory and assessment in Nevada and southern Utah. We identified several potential obstacles to collecting high-quality aerial image data in environments with high topographic variability and landscape heterogeneity. We found that sUAS are very useful and practical when performing mapping missions in these circumstances when operators account for potential environmental limitations (e.g. poor weather, shortened flight times due to atmospheric conditions, line-of-sight challenges, difficulty implementing ground control across steep sites, ensuring applicable aviation regulations are observed) and technological capabilities (terrain following, flight duration, etc.). This work has implications for a wide variety of scientific and management disciplines that involve low-altitude remote sensing research in mountainous areas.

Keywords: UAS; UAV; drone; mountains; terrain; elevation; topographic mapping
INTRODUCTION

Small unmanned aircraft systems (hereafter abbreviated sUAS), defined in the U.S. as unmanned aircraft weighing less than 55 lbs. (14 C.F.R. Part 107, 2016), have become ubiquitous in their use in several disciplines in recent years. Perhaps the most widespread use of sUAS currently is as a remote sensing platform. sUAS are often equipped with high resolution RGB, multispectral, and thermal infrared sensor packages. Their relatively low cost (compared to manned aircraft and satellite remote sensing platforms) and rapid deployment capabilities are ideal for low-altitude scientific imaging applications. Two basic types of sUAS are available—fixed wing and multirotor systems. Off-the-shelf fixed-wing sUAS are suitable for surveying larger areas at relatively higher altitudes above ground level (AGL) (e.g. 160 hectares in 45 minutes at 122 meters AGL), while multirotor sUAS are by their nature generally less efficient and can cover smaller areas on a single flight (e.g., 40 hectares in 25 minutes at 122 meters AGL). However, multirotor systems have other advantages, including their ability to stop and hover, fly slowly, and easily descend to a lower altitude for more detailed imaging of a small area of interest. Additionally, multirotor systems, e.g., the DJI Inspire 2 (Dà-Jiāng Innovations, Shenzhen, China), tend to cost less than fixed-wing systems with similar capabilities.

sUAS have been used as remote sensing platforms to support a wide variety of applications, such as emergency management, agronomy, cadastral mapping, and infrastructure inspection (Silvagni et al. 2017; Knot et al. 2016; Shi et al. 2016; Crommelinck et al. 2016). Use cases are also numerous in environmental disciplines, including forestry, range management, wildlife management, geology, and oceanography (Linchant et al. 2015; Tang and Shao 2015; Laliberte, Winters, and Rango 2011; Eisenbeiss 2009). Relatively few academic papers have been published about conducting UAS-based remote sensing missions in mountainous locations,
which are common settings for environmental research in many regions of the world. Still fewer
detail challenges encountered and best practices for flight operations. Ambrosia et al. (2011)
described missions conducted using a NASA-modified MQ-9 Predator B, dubbed Ikhana, for
wildfire observation and firefighting coordination in several mountainous areas across the
western United States. This large fixed-wing aircraft has a 400-lb sensor payload capacity and
can fly up to 13,700 m in altitude for durations approaching 24 hours. The Ikhana flies well
above the tops of mountains and is more suited to providing situational awareness rather than
high-resolution mapping capabilities. Ragg and Fey (2013) used two small UAS—a fixed-wing
QUEST-UAV and a TWINS-NRN multicopter—outfitted with an RGB sensor to monitor an
active rock slide at 2,900 m in the Austrian Alps. They described several challenges operating
sUAS in this setting, including thin air, cold temperatures, strong and unpredictable winds, poor
GNSS reception, and large differences in scale caused by steep slopes. Mirijovsky and
Langhammer (2015) studied the morphodynamics of a montane stream system in the Czech
Republic using a Canon DSLR camera mounted aboard a Mikrokopter Hexa XL multirotor
system. They were able to create a multitemporal digital elevation model (DEM) dataset using
structure-from-motion photogrammetry, from which they measured bank erosion rates. Gruen,
Zhang, and Eisenbeiss (2012) discuss a workflow for sUAS-based 3D modeling of an
archaeological site at 2930 m elevation in Bhutan. Their article focuses primarily on their
process for processing the data and does not provide much detail on sUAS mapping procedures.

Mapping snow and ice cover are common applications for sUAS in high-altitude sites.
Syromyatina et al. (2015) performed mapping flights with a Geoscan 101 fixed-wing UAS over
two glaciers at altitudes ranging from 3400–3900 m MSL in the Tavan Bogd mountains in
Mongolia. De Michele et al. (2016) used a SenseFly Swinglet-CAM fixed-wing UAS to
characterize snow depths in an alpine location in northern Italy using multitemporal RGB imaging. Buhler et al. (2017) detailed methods for reconstructing three-dimensional depictions of homogeneous snow surfaces following avalanches. They provided a useful perspective on the challenges of flying in a subalpine location (their study sites were in Switzerland and Austria), such as steep slopes, high elevation differences, and unfavorable atmospheric considerations, including low temperatures and high winds that exceeded the recommended limits for the Falcon 8 multirotor UAS they used.

The purpose of this paper is to discuss how multirotor sUAS can be effectively used to conduct remote sensing missions in mountainous areas to support environmental research. Our objectives are to present techniques for operating sUAS in challenging operational environments in mountainous areas, to explain how to overcome difficulties related to the operational environment, and to develop a set of best practices for operating sUAS within these conditions. Additionally, we describe our methods and the best practices for collecting high-quality aerial image data in mountainous areas, which we define as locations where steep slopes (> 25°) and high elevations (> 2500 meters MSL) create logistical challenges for sUAS-based mapping—challenges that are not present at study sites in low-elevation and topographically flat locations. These challenges include reduced thrust and shorter flight times due to reduced air pressure, cold temperatures, strong winds, problems with variable scale and resolution when mapping areas with steep slopes or significant topographic relief, difficulty maintaining visual line-of-sight (VLOS) with the UAS, and following current regulations from the Federal Aviation Administration (FAA) governing sUAS flights in the United States (14 C.F.R. Part 107, 2016). Our team successfully conducted mapping missions with sUAS at study sites in mountainous areas 17 times during 2017–2018, gaining valuable experience that has helped us develop
specialized standard procedures for aerial imaging flights in locations with rugged terrain at high elevations.

MATERIALS AND METHODS

Data collection for this project was accomplished as part of a larger study to map subalpine forest stands in the Great Basin and Colorado Plateau ecoregions at a fine spatial scale. Study sites were selected based upon their forest species composition, accessibility, and topography. In total, seven sites in Utah and Nevada, U.S.A. were mapped using an sUAS during this project (Figure 1.1; Table 1.1).

To accomplish the mapping missions, we selected a DJI Inspire 2 sUAS platform (Figure 1.2). The Inspire 2 is a quadcopter designed for aerial photography and videography applications. One benefit of the Inspire 2 is its compatibility with various gimbaled cameras manufactured by DJI. We selected the DJI Zenmuse X4S camera system with integrated gimbal, which includes a 1-inch size RGB sensor with a fixed 94-degree field of view lens. An additional feature of the Inspire 2 is its ability to raise its landing legs after takeoff, providing the camera with an unobstructed 360-degree rotation capability while in flight. During some missions in which detailed spectral data were required, we used a Micasense Rededge-M multispectral camera (Micasense Inc., Seattle, Washington, U.S.A.). The Rededge-M is a small five-band multispectral imager designed for use aboard sUAS. It offers discrete bands centered at 475 nm (blue), 560 nm (green), 668 nm (red), 840 nm (near-infrared), and 717 nm (red-edge), offering the capabilities to produce natural color and color infrared imagery, along with various vegetation indices that make use of the near-infrared and red-edge bands in tandem with a visible band (typically red).
The Inspire 2 is controlled via the DJI Cendence transmitter in tandem with an Apple iPad Pro (Apple Inc., Cupertino, California, U.S.A.) that functions as a computer ground control station. DJI’s Go 4 iOS app provides a live view of the video feed from the Inspire 2’s camera, along with real-time telemetry information such as GPS position, battery status, altitude, distance, and camera settings. The DJI software developer’s kit (SDK) enables third party developers to create applications that leverage the functionality of the sUAS and the ground station software to offer enhanced capabilities, such as aerial mapping. After evaluating several iOS applications designed for mapping with DJI UAS, our team selected the Maps Made Easy Map Pilot for DJI app (www.mapsmadeeasy.com). This application has several useful features, including a terrain-following mode, a live map view that showed image footprints during each flight, and the ability to pre-cache basemap imagery in remote locations without reliable cellular data service. The application was programmed to capture images at 75% overlap in both the forward and side directions, from an altitude of 121 meters above ground level. The camera exposure settings were automatically selected by the app, while white balance was manually set to the “Sunny” option during each flight to avoid issues with white balance variations associated with the use of the automatic white balance setting. Images were captured in the JPEG file format.

To improve the georectification accuracy of orthoimagery and photogrammetric point cloud models produced from these missions, we needed to establish absolute ground control within the areas we mapped (Mirijovsky and Langhammer 2015; Pix4D 2019). We created 24 ground control point (GCP) panels made from plywood boards cut to 0.6 m x 0.6 m dimensions. These square panels were painted with a checkerboard pattern to improve their visibility from the air, and to create obvious and well-defined center points that would serve as the actual GCP
locations (Figure 1.3). These GCPs were laid out at each site in a uniform pattern prior to conducting sUAS mapping flights. Distances between GCPs depended upon the total area of each site. The primary goal in GCP placement was to focus on the corners and edges of each site, then to place several GCPs in a uniform pattern between the edges and corners of the area of interest. After placement, a Trimble GeoExplorer 6000 GNSS (Trimble Inc., Sunnyvale, California, U.S.A.) was used to collect differential precision Global Positioning System (GPS) data (latitude, longitude, and elevation) at each GCP location.

Following data acquisition, our team used Pix4Dmapper software (Pix4D SA, Lausanne, Switzerland) to post-process the imagery gathered on each mission. Pix4Dmapper is a photogrammetric mapping software package that uses Structure-From-Motion algorithms to produce orthomosaics, point clouds, and digital surface models (DSMs) from aerial imagery collected with a high percentage of overlap between adjacent images (Pix4Dmapper User Manual 2019; Westoby, Hambrey, and Glasser 2012). Following processing with Pix4D, the data products were imported into GIS software (e.g. ArcGIS) for further processing and information extraction.

RESULTS AND DISCUSSION

Benefits, drawbacks, and logistics of sUAS-based imaging in mountainous areas

UAS offer several key advantages over manned aircraft and satellite platforms when imaging in mountainous areas. First, UAS can fly close to the ground and collect ultra-high resolution data in locations where manned aircraft would not be able to fly safely due to the danger of colliding with terrain or other terrestrial features (Laliberte, Winters, and Rango 2011). Second, sUAS can be easily transported in a four-wheel drive vehicle, or even carried by a
A key disadvantage of sUAS compared to higher-altitude platforms is their inability to provide mapping coverage over large geographic areas. The maximum acreage we could cover in a single 15–20 minute mapping flight at 122 m AGL with the Inspire 2 was typically around 32 hectares. Because of this coverage area limitation, multirotor sUAS similar to the Inspire 2 are best suited for mapping small research plots with areas up to 40 hectares. Fixed-wing sUAS offer greater endurance than multirotor systems, but our team opted for a multirotor for reasons that will be discussed below.

A logistical aspect of operating sUAS is adhering to the regulatory structure that governs their operation for commercial purposes (14 CFR Part 107—hereafter “Part 107”). Two key provisions of Part 107 are the altitude and distance restrictions on sUAS flights: sUAS are limited to operating up to 400 feet (122 meters) above ground level (AGL) and within visual line-of-sight (VLOS) of the remote pilot-in-command (RPIC) (14 C.F.R. Part 107, 2016). These two restrictions can be waived by the FAA under certain circumstances if an acceptable safety case is made. Many mapping missions would benefit from operating a UAS above 122 m and beyond VLOS distances to increase the aircraft’s ability to image larger areas per flight, albeit at a coarser spatial resolution. Another requirement of Part 107 is that RPIC candidates must obtain a remote pilot certificate (RPC) with an sUAS rating from the Federal Aviation Administration (FAA) to conduct or supervise sUAS operations for commercial purposes (14 C.F.R. Part 107, 2016). This certification requires the candidate to pass a written examination that tests their knowledge of weather, airspace, and operating limitations for sUAS. Then, after initial
certification, remote pilots must pass a recertification test every 24 calendar months. This examination system has proved burdensome for some remote sensing scientists because of the need to learn seemingly complex aviation regulations, procedures, and jargon that are foreign to their area of specialization. Notwithstanding, the regulations in Part 107 represent significant progress toward standardizing sUAS flights in the United States (see Hardin et al. 2018, 9-11).

Platform selection—fixed wing vs. multirotor

We decided early in the planning process for this project to utilize a multirotor sUAS instead of a fixed-wing system. Multirotors have the disadvantages of reduced aerodynamic and power efficiency (due to the energy spent by the motors creating lift for hovering and maneuvering), and generally shorter endurance. Their advantages lie in their ability to stop and hover, maneuver slowly around steep slopes and obstacles, and take off and land without a large area nearby to serve as a runway (~75-100 m minimum distance for most fixed-wing aircraft) (Ragg and Fey 2013). Few or none of the sites we mapped had sufficient open space for fixed-wing takeoff and landing operations. Moreover, DJI multicopters (DJI does not offer fixed-wing UAS models) have a sophisticated software developer’s kit (SDK) that allows third-party developers to write sophisticated mapping applications for DJI aircraft that control the functions of the on-board camera and provide navigation over the area of interest. There are several of these apps available for the iOS and Android platforms, including DroneDeploy, Pix4Dcapture, and the Map Pilot for DJI app that we selected (described above).

Besides maneuverability, another advantage of multirotor systems (including DJI products) is low cost. The system we acquired, the DJI Inspire 2, cost ~$3600 for the airframe and gimbaled Zenmuse X4S RGB camera. We also purchased additional batteries (six pairs total) for extended operational capabilities in remote areas, a rapid charging station, a
GoProfessional hard case (GPC Custom Cases Inc., San Diego, California, U.S.A.) for transporting the Inspire 2 to study sites, a DJI Cendence transmitter (an upgrade from the stock transmitter), and an Apple iPad Pro to serve as the ground control station. The total investment for the Inspire 2 with accessories was around $7500. The un-gimballed Micasense Rededge-M multispectral camera could be optionally mounted to the Inspire 2 camera port using a custom 3D-printed adapter we designed. Total costs for the Rededge-M were approximately $5000. Off-the-shelf fixed-wing platforms that were comparable in their mapping capabilities were much more expensive. For example, the Sensefly eBee Classic (Sensefly, Cheseaux-sur-Lausanne, Switzerland) fixed-wing platform with RGB and multispectral sensor capabilities costs around $25,000, about twice the price of the Inspire 2 system with the Micasense Rededge-M camera. The primary benefit of the eBee over the Inspire 2 is its 50-minute maximum endurance, which we did not consider to be worth the additional cost to our project. Furthermore, we were concerned that a fixed-wing sUAS would not be able to fly slowly enough or be sufficiently maneuverable to handle the complex terrain present in the mountainous environments where we operated.

Challenges of operating sUAS in mountainous areas

sUAS, and aircraft in general, perform less efficiently at high elevation than they do at altitudes near sea level. Lower air density in high altitude locations means wings and rotors produce less lift and propellers produce less thrust than they would achieve at sea level. The reduced efficiency results in diminished aircraft endurance, or flight time, which limits the total area that can be mapped on a single flight (Ragg and Fey 2013). “Density altitude” is defined as the altitude at which a given air density occurs in the standard atmosphere (Guinn and Barry 2016). Aircraft operations at high density altitudes (i.e. at high altitudes and on hot days) result
in diminished thrust and lift due to the reduced atmospheric density. DJI addresses the problem of reduced thrust at higher altitudes by selling high altitude propellers for the Inspire 2 that have a greater pitch than the standard propellers, thereby producing more thrust in thinner air. Additionally, wind velocity tends to have greater potential at high altitudes and can be a factor in reducing aircraft endurance when flying upwind legs during a mapping mission. Finally, cold ambient air temperatures reduce the efficiency of the Inspire 2’s lithium polymer (LiPo) batteries, creating an additional variable that can have an impact on flight endurance (Ragg and Fey 2013). We learned that we needed to carefully evaluate weather forecasts prior to departure to our field sites, paying special attention to the temperature and wind velocity forecasts. Our Inspire 2 achieved flight times ranging from ~15-20 minutes, depending upon flight elevation, windspeed, and ambient air temperature. Cold temperatures can also have a negative impact on crew comfort and performance during mapping flights. Due to the reduced flight times we experienced due to the aforementioned phenomena inherent to high mountainous areas, we invested in a total of six sets of flight batteries and a rapid charging station (powered via wall outlet or generator) to enable us to quickly land and swap batteries during aerial mapping missions that could not be completed on a single flight.

Line-of-sight problems are also common in mountainous areas. Per Part 107, the RPIC must maintain visual line-of-sight with the aircraft at all times during the flight operation (14 C.F.R. Part 107, 2016). Additionally, the aircraft uses a line-of-sight 2.4 GHz radio control link that must be maintained during flight. If the aircraft descends over a ridge away from the pilot’s location, the radio control link is lost. Although the flight software typically uploads all mission waypoints to the aircraft before flight and the aircraft continues to fly normally when radio signals are lost, the RPIC must still maintain visual line-of-sight with the aircraft (14 C.F.R. Part
Addressing radio- and visual line-of-sight challenges should be done during the pre-flight safety briefing. When possible, the UAS pilot should be pre-positioned on an elevated location within the study site to minimize the chance of losing both radio- and visual line-of-sight with the aircraft while in flight. During at least two of our mapping missions, the RPIC was forced to abort the automated mapping mission in order to avoid losing line-of-sight with the aircraft. As a last resort, we configured our Inspire 2 to use its “smart return-to-home” capabilities. In this mode, if the transmission signal is lost, the aircraft will return to its takeoff location using its built-in obstacle avoidance sensors to navigate over trees and slopes. An additional option for reducing the chances of losing visual line-of-sight is to use a designated visual observer (VO), who can aid the RPIC in maintaining visual line-of-sight (14 C.F.R. Part 107, 2016). During missions with particularly complex terrain or obstacles, or that require flight near the edge of visible range, it can be useful for the pilot to have a small network of VOs distributed across the flight area and communicating with the pilot and each other via two-way radios.

*Variable resolution and scale*

Another problem we encountered when mapping in locations with steep slopes was dealing with variable resolution and scale in the imagery. When the sensor is far from the ground, it produces an image of coarser spatial resolution (and smaller scale) than when it is flown close to the ground. In locations with extremely steep slopes, the ground may be both close and far within the mapping area, or even within the same image (e.g. Figure 1.4), resulting in variable scale and resolution. Apart from causing difficulties in post-processing (Ragg and Fey 2013), this phenomenon presents a challenge from a regulatory standpoint because Part 107 mandates a maximum flight altitude of 400 feet (122 m) AGL. At a topographically rugged site,
this altitude rule may be quickly exceeded unintentionally if a “flat” flight plan is used (constant height MSL). To maintain safe and legal flight, mapping must be done in a way that maintains the altitude of the sUAS at a constant height AGL (Figure 1.5). We searched for a mapping software application that could produce flight plans that would keep the Inspire 2 at 122 m AGL or below regardless of the terrain. The Map Pilot for DJI (MP) app was selected because it includes a terrain following mode. The elevation dataset used by the MP app is derived from the Shuttle Radar Topography Mission dataset collected by STS-99 in February 2000 (30-meter spatial resolution). When the user identifies the location of the mapping flight (drawn in the app as a rectangle or polygon boundary feature) and specifies the desired forward overlap and sidelap, MP creates an elevation profile for the ground beneath the flight path, then calculates another elevation profile for the flight path to maintain a desired height above ground level. We found this functionality to be reliable, even in terrain that included nearly vertical topography that we expected would confound the accuracy of the terrain following mode.

The MP app and terrain following feature generally functioned as advertised—we did experience an occasional problem (probably a software glitch) in which the Inspire 2 would reach the end of a flight line and pause for up to a minute before turning onto the next flight line and resuming the mission. This delay seemed especially pronounced when the sUAS needed to make an elevation adjustment as it proceeded to the next flight line. More than being a simple annoyance, this delay reduced the effective mapping endurance of the aircraft. The total flight endurance of the Inspire 2 was also visibly reduced by the terrain-following feature when compared with missions flown at a constant height MSL because of the additional battery capacity that was consumed to allow the UAS to climb and descend constantly throughout the flight.
Ground control

Due to the precision distance and area measurements that would be made from the imagery collected during this project, we implemented ground control at each site prior to mapping. After trial and error while testing various methods, we created the GCP boards described above. Transporting the boards around each site was made easier by loading them into a mainframe backpack designed for hunters to transport game meat. Using the supplied straps, we were able to attach a stack of 10–12 GCPs on the backpack frame. A team of two was required to accomplish each task when placing and measuring the GCPs. One team member carried the backpack with GCP boards, while the other carried the GPS receiver used to collect the coordinates at each location. The second team member also carried a hammer and stakes, and drove a stake into the ground through a hole in the center of the GCP board so it would not move during the mapping flight. We found this to be particularly important on steep slopes because GCPs can easily shift out of position if they are disturbed.

While very important to the overall goals of the project, the process of placing ground control targets was often tedious and difficult due to steep terrain. To streamline this process, prior to visiting each site, we would use GIS software to create a rough map of the site boundaries with intended GCP locations positioned at regular intervals. We used smartphone mapping apps (e.g., Collector for ArcGIS and Gaia GPS) to navigate to the desired positions for the GCPs. However, cliffs, scree slopes, and areas of bare rock often thwarted our efforts to place GCPs in the desired locations. We quickly learned to prioritize placing GCPs first near the corners of the site, then along the edges, and finally within the interior. This strategy seemed to improve global accuracy of the photogrammetric modeling of the scene in Pix4Dmapper, resulting in precisely georectified orthomosaics and digital surface models. If GCPs were only
placed within the interior of the site and not at the corners and edges, local accuracy near the points tended to be adequate, but the global model accuracy often suffered.

Newer UAS such as the DJI Phantom 4 RTK offer near-direct georeferencing capabilities that may reduce the number of GCPs needed or eliminate them altogether. These systems work by communicating with an on-site GPS base station that has been left to average its signal over several minutes or hours, resulting in a highly accurate base point. The UAS measures its location relative to the base station to refine the accuracy of the geotags produced during the mission, which in turn results in a more accurate photogrammetric model in post-processing. We have not yet had the opportunity to use the Phantom 4 RTK, but we believe it could be very promising for precision mapping in mountainous areas with minimal GCPs.

CONCLUSIONS

We mapped seven subalpine forest sites using sUAS during 2017-2018 and encountered several challenges associated with mapping in mountainous locations. These challenges included weather factors and reduced aircraft performance at high altitudes, regulatory challenges related to flight altitude, line-of-sight issues, problems with variable resolution and scale, and difficulties with ground control placement over steep terrain. We learned how to overcome each of these problems using off-the-shelf or simple custom solutions to produce high-quality aerial image data at our study sites, and we believe these lessons we have outlined will be of great value to any research group conducting sUAS mapping operations in similar settings. We have found that sUAS are excellent platforms for remote sensing applications in mountainous areas, and we believe that this area of research is ripe for further development.

Funding: This research was funded by the Charles Redd Center for Western Studies.


Figure 1.1: Locations of the seven subalpine forest sites mapped using sUAS within the Great Basin and Colorado Plateau ecoregions. Map data courtesy of Esri, Garmin, USGS, NOAA, and NPS.
Figure 1.2: DJI Inspire 2 with DJI Zenmuse X4S camera in operation at Highland Peak, Nevada.
Figure 1.3: (Left) Staking a ground control point (GCP) target at Ford Ridge, Utah. GCP boards are made of 0.6 m x 0.6 m plywood painted to be highly visible from the air. (Right) An RGB aerial image of a GCP target in position at Spruce Mountain, Nevada (captured from 122 m AGL).
Figure 1.4: Nadir aerial photograph showing trees along a steep slope (~55° average). The top-right of the image has a finer scale (higher spatial resolution) than the bottom-left of the image due to the rapidly changing elevation. The changes in elevation are reflected in the relative sizes of the trees.
Figure 1.5: Diagram comparing UAS mapping missions flown at a constant height AGL (above ground level) versus a constant height MSL (above mean sea level). Flight at a constant height AGL (i.e. terrain following) allows the UAS to remain under the 400-foot (122 m) maximum altitude set by the FAA, even while navigating across rugged terrain, and mitigates problems related to variable scale and resolution.
Table 1.1: Descriptions of seven subalpine forest sites mapped using sUAS.

<table>
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<tr>
<th>Site Number</th>
<th>Site Name</th>
<th>State</th>
<th>Mountain Range</th>
<th>Mean Elevation (m)</th>
<th>Max Slope (°)</th>
<th>Total Area Mapped (ha)</th>
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<td>Schell Creek Range</td>
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<td>2827</td>
<td>39</td>
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<tr>
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<tr>
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<td>2587</td>
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CHAPTER 2

Revisiting Bristlecone Pine (*Pinus longaeva*) in the Stansbury Mountains, Utah

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ABSTRACT

Great Basin bristlecone pine (*Pinus longaeva*) presence in the Stansbury Mountains of north-central Utah has been reported prior to the year 2020, but these reports lack definitive stand boundaries, adequate population characterization, and the delineation of individual stands of trees. In summer 2020, we identified and documented the presence of five separate stands of bristlecone pine in the Stansbury Mountains. These stands are removed from the nearest bristlecone populations in other mountain ranges by a distance of 120 km; as such, they represent a unique outlier population of the species. We used GPS data to create a geographic information system (GIS) database delineating the five stands we identified, and sampled tree age and size in one of the stands for comparison with other populations in the Great Basin. We present here two hypotheses to explain the occurrence of bristlecone pine in the Stansbury Mountains: first, that this population is a relict from a time when bristlecone pine was widely distributed across the Great Basin, and second, that the species arrived in the range via long-distance dispersal (LDD) mechanisms at some point during or after the Pleistocene/Holocene transition (ca. 12,000 $^{14}$C YBP). *Neotoma* (wood rat) midden data suggest that bristlecone pine was absent or at least not
widespread in the northern Bonneville basin during the late Pleistocene, but midden data are sparse for the Stansbury Mountains and surrounding ranges. Additionally, we present possible migration pathways that the species could have taken to reach the Stansbury Mountains from the southern Bonneville Basin, where it was widespread during the late Pleistocene, using the largest extent of Lake Bonneville as a limiting boundary. Hypothesized migration vectors include windborne LDD events or transport by granivorous birds. We also postulate that a small population of bristlecone pine may be present in the Oquirrh Mountains to the east of the Stansbury Mountains based upon the existence of similar habitat characteristics there, as well as our identification of a likely mis-determined 1964 voucher specimen from the Oquirrh Mountains that appears to be of bristlecone pine.

INTRODUCTION

Great Basin bristlecone pine (*Pinus longaeva*, hereafter “bristlecone pine”) is a subalpine conifer species found in isolated populations across the Great Basin and western Colorado Plateau U.S.A. (Bailey 1970). It is well-known for being among the oldest tree species on earth (Schulman 1958, Currey 1965). Bristlecone pine primarily grows on limestone- and dolomite-derived soils across an elevation range of 2200 to 3600 m (Bailey 1970). Bristlecone pine is found in Utah, Nevada, and eastern California (Lanner 1984, Welsh 1993, Charlet 1993) with the southernmost population of the species occurring in the Panamint Range of California (36.18° N) and the northernmost populations in the Ruby Mountains (40.64° N) and Spruce Mountain (Pequop Mountains) (40.55° N) of the central Great Basin in Nevada. In Utah, bristlecone pine extends from the Pine Valley Mountains in Washington County (37.32° N) to the West Tavaputs Plateau in Duchesne County (39.99° N) (see Appendix A for voucher information for aforementioned locations).
D. K. Bailey (1970) described Great Basin bristlecone pine as a separate species from Rocky Mountain bristlecone pine (*P. aristata*). He described several locations where the environmental conditions were assumed to be suitable for bristlecone pine occurrence, but where vouchers were lacking. One location he identified was the Stansbury Mountains (Bailey 1970). In 1978, Kay and Oviatt published a report describing a single bristlecone pine individual that they observed along an arête in the central portion of the range. This report included a general location and site description of this tree, while explaining that conditions were potentially suitable for additional populations to occur (Kay & Oviatt 1978). Taye (1983) identified isolated stands of bristlecone pine as infrequent but locally dominant on limestone slopes in the range, although he did not provide specific information regarding the location of these stands or individual trees. Additional information about bristlecone pines in the Stansbury Mountains has been recorded in the form of herbarium vouchers—one collected by P. Kay in 1977 (from the tree described in Kay & Oviatt 1978), another collected by A. Taye in 1979, and a third by S. Langer in 1994 (Appendix A). Taye’s and Langer’s vouchers were collected within 1 km of Kay’s original voucher along ridges on the east side of Deseret Peak, the range’s high point. These reports are notable because they describe a population of bristlecone pine that is highly disjunct from other known populations. The nearest known populations are in the Deep Creek Mountains, UT, ca. 122 km to the west-southwest, and the House Range, ca. 129 km to the south-southwest (Appendix A). The Stansbury Mountains population is currently the northernmost identified population of bristlecone pine in Utah at 40.47° N, rivaling the latitudes of the aforementioned northernmost populations in Nevada.

The origin and timing of arrival of bristlecone pine into the Stansbury Mountains remains uncertain. The paleogeography of conifer species in the western United States has been
extensively characterized in the literature (Wells 1983, Thompson 1984, Rhode & Madsen 1995, Rhode 2016). A common source of late Quaternary paleobiogeographic records is in the form of vegetation fragments, primarily from tissue found within the strata of excavated woodrat (Neotoma spp.) middens (Wells 1983). Neotoma middens typically contain needles, seeds, and other plant matter that can be identified (Wells 1983). Individual plant fragments are $^{14}$C-dated to approximate the time when a particular species was established at the midden location.

Midden records indicate that bristlecone pine was dominant in the southern Bonneville Basin during the late Pleistocene, between 37,000 and ~10,000 $^{14}$C YBP (Wells 1983, Madsen et al. 2001). Available Neotoma midden evidence (Wells 1983, Thompson 1984, Rhode 2016) suggests that the upper Bonneville Basin, including the Stansbury Mountains, was dominated by limber pine during that period, and that bristlecone pine might have been absent above about 40° N latitude (Wells 1983, Rhode 2016). More extensive sampling of Pleistocene-aged samples from the region is needed to confirm this possibility. An unpublished Neotoma midden record of bristlecone pine on Swasey Mountain (39.380° N, 113.321° W; elev. 2386 m, ~11,000 $^{14}$C YBP; data on file USDA Forest Service, Shrub Sciences Laboratory, Provo, Utah) combined with a widespread modern distribution supports a conclusion that this species has had a continuous presence on the northern end of the House Range since at least the late Pleistocene. From these midden records, it could be assumed that a transition from bristlecone pine dominance to limber pine dominance occurred between the House Range and the Onaqui Mountains. Unfortunately, there are large gaps in the midden records for the upper Bonneville Basin, and the genesis of the small outlier population on the Stansbury Mountains remains unexplained.

The objective of this paper is to characterize prior ambiguous observations of the extent and structure of extant stands of bristlecone pine in the central Stansbury Mountains by producing a
map that delineates the location and size of each stand. Additionally, we speculate regarding two possible mechanisms that could explain how and when bristlecone pine arrived at this mountain range.

1. Bristlecone pine was present in the range during much or all of the last (Wisconsin) glacial stage (≈ 75,000-11,000 YBP), having arrived under much colder than modern climate conditions, and the current stands are high-elevation remnants of a larger, earlier population.

2. Bristlecone pine colonized the Stansbury Mountains at approximately its modern elevational range under warmer climatic conditions of the terminal Pleistocene (Pleistocene/Holocene transition) or during the Holocene (<11,000 YBP) via long-distance dispersal mechanisms.

METHODS

Study area description

The Stansbury Mountains are located in the eastern Great Basin, in Tooele County, 62 km WSW of Salt Lake City, Utah. Like most mountain ranges in the Great Basin, the crest of the range trends from north to south and is bounded on either side by low-elevation semi-arid desert valleys, with Skull Valley located to the west and Rush and Tooele valleys to the east (Lanner 1971, Taye 1983). The range extends from Johnson Pass (elev. 1981 m) where it meets the Onaqui Mountains, north to the Great Salt Lake. The range rises to its highest point, Deseret Peak, at 3362 m. Ridgelines extend both north and south of Deseret Peak, forming a high, narrow crest. The total length of the range is approximately 45 km, and it is 21 km wide at its greatest width (Taye 1983). Geologically, the Stansbury Mountains are described as a massive eastward-
tilted fault block with a steep western escarpment and more gradual eastern slopes. The core consists of Precambrian Prospect Mountain quartzite, with abundant Paleozoic limestone and dolomite occurring on the north and south ends of the range, and east of Deseret Peak (Rigby 1958).

The distribution and composition of vegetation vary with elevation, slope, and aspect across the range. On west-facing slopes, Utah juniper (*Juniperus osteosperma*) and Rocky Mountain juniper (*J. scopulorum*) grow in scattered stands, with singleleaf pinyon (*P. monophylla*) occurring primarily on north-facing aspects at low and middle elevations. The east side of the range supports riparian ecosystems that follow stream corridors in canyon bottoms. These sites are dominated by narrowleaf cottonwood (*Populus angustifolia*) and boxelder (*Acer negundo*) at lower elevations. Aspen (*Populus tremuloides*) is present along streams and within higher-elevation sites interspersed among montane mixed-conifer forests. White fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) are common in canyons at lower elevations.

At middle elevations (between 2350 and 2450 m) limber pine (*P. flexilis*), Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are common. Along the crests of the range (above 3050 m), these three species are also present, but often grow as matted stands of krummholz (Lanner 1971). Bristlecone pine is found within this upper high elevation zone, commonly associated with limber pine, Douglas-fir, subalpine fir, and Engelmann spruce (Lanner 1971, Taye 1983). The summit of Deseret Peak is devoid of trees (Lanner 1971). The ridgeline to the east of Deseret Peak averages between 3000 and 3120 m, with Engelmann spruce, limber pine, and bristlecone pine common along its length. Tree line in the area is between 3200 and 3290 m, with only Deseret Peak rising above this height (Taye 1983).
Assessment of Great Basin bristlecone pine in the Stansbury Mountains

We used historic voucher records describing the distribution of bristlecone pine to approximate the locations of potential trees or stands within the Stansbury Mountains. These voucher data were compiled as part of a study mapping and characterizing the overall distribution of bristlecone pine throughout western North America (Burchfield et al. 2021). Our search efforts were assisted with information provided by personal communication with Langer (2019), who had collected voucher specimens of bristlecone pine in the Stansbury Mountains on limestone substrate near Point 10,042, 1.6 km east of Deseret Peak (“Point 10,042” refers to an unnamed peak shown on the USGS topographic quadrangle map of the area). Langer provided estimated GPS coordinates along the ridgeline north and south of Point 10,042 of additional sites where bristlecone pines were assumed to be present (Langer, personal communication 2019). In June 2020 we conducted an initial scouting trip to the range. In the vicinity of the coordinates provided by Langer, we identified three distinct stands of bristlecone pine on east-facing slopes in the upper reaches of the Bear Fork of East Hickman Canyon (hereafter Bear Fork, Stand 5), and the White Pine Fork of Box Elder Canyon (hereafter White Pine Fork N and S, Stands 3 and 4, respectively) that had not been identified or described previously. Vouchers were collected from Stands 3 and 4 and deposited at the S.L. Welch Herbarium (Appendix A).

In July 2020, we made a second visit to the ridgeline east of Deseret Peak via the Mill Fork Canyon trail. Observations made of conifers in this area led to the discovery of two additional bristlecone pine stands (hereafter Mill Fork W and E, Stands 1 and 2, respectively). We visited the area a third time in August 2020 to obtain radial cores from Stand 4 to determine the average tree age within the stand. Ten bristlecone pines were opportunistically selected within the stand (randomized sampling proved difficult due to steep slopes), and radial cores
were extracted from the trees using a 24-inch Haglöf increment borer (Haglöf, Långsele, Sweden). Slope and aspect were measured for each tree using a TruPulse 360 Rangefinder (Laser Technology, Centennial, Colorado, USA). Core samples were collected at heights below 1.0 m above ground level through actively growing wood (live cambium) to extract a maximum number of rings available for age estimation. Out of the 10 cores, three reached tree pith, while seven did not. Failure to reach tree pith was a result of either 1) being only slightly off of the pith, and because of time limitations, samples close to pith were deemed sufficient for the study, or 2) reaching dead, decayed wood when core sampling, which resulted in a partial core of solid wood being obtained. Trees were selected for sampling in an effort to represent total variation in tree size and age classes, as well as differences in terrain characteristics (slope and aspect) within the stand.

Sample cores were preserved in paper straws and later glued to wood mounts after drying. Mounted cores were sanded using progressively finer sandpaper, starting with 150 grit paper, and ending with 600 grit paper, using a 53.3 x 7.6 cm. belt sander. Subsequently, cores were sanded by hand using 9-micron finishing film until individual cells were distinguishable in cross-section. Growth-ring series were aged using a simple ring count approach to develop estimates of tree ages. In cores that approached but did not intersect pith (i.e. were within 1 cm. of pith) the number of missing rings were estimated using a pith indicator (Applequist 1958, Speer 2010). For cores that did not come close to pith (those that ended in rotted wood), estimated age was determined by using DBH measurements to approximate the length of the missing wood (from core end to pith). The average growth rate of each incomplete core’s innermost 3 full centuries of growth (centuries were measured at even 100-year marks, such as 1500, 1600, etc.) was then calculated. This growth rate was applied to the estimated missing
length of wood to pith, giving an approximate total number of rings for each incomplete core. We acknowledge that this method is limited; crossdating is needed to definitively date these trees, but was impossible due to the small number of core samples we obtained.

During each visit, we collected numerous digital photographs of each stand we encountered. The photographs were tagged with geographic coordinates (latitude, longitude, and elevation values), and plotted using Google Maps (Google, Mountain View, California, USA) and ArcGIS Pro (Esri, Redlands, California, USA) to produce boundary polygons for each stand. For the stands we did not visit due to steep terrain and time constraints (Mill Fork W and Mill Fork E), we used Gaia GPS, a mobile GPS mapping application (Outside, Boulder, Colorado, USA), to draw boundary polygons. This application offers the capability of pre-caching topographic maps and high-resolution aerial imagery for use in remote areas where cellular data connectivity is unavailable. We viewed the Mill Fork W and E stands through binoculars from the bottom of Mill Fork Canyon, compared visible terrain features with those present on the pre-cached topographic map in Gaia GPS, then drew the stand boundaries accordingly.

Compilation of bristlecone pine distribution data for the late Pleistocene and early Holocene

We utilized the USGS-NOAA Packrat Midden Database (USGS 2021) to compile midden records for bristlecone pine and limber pine within western Utah and eastern Nevada for 12,000 ± 2000 14C YBP. This time period was chosen because it encompasses much of the Pleistocene/Holocene transition period during which time these species migrated to their modern distributions. Only midden strata that corresponded to this Pleistocene/Holocene transition period were considered, as some middens also included strata that were dated to other time periods. We restricted the analysis to bristlecone pine and limber pine due to their relative dominance (among conifers) in the region compared to other species during this time period.
(Wells 1983). The midden records were plotted on a map using ArcGIS Pro. Additionally, a GIS file for the maximum extent of Lake Bonneville was obtained (Utah AGRC 2021) and plotted in ArcGIS Pro for analysis of possible bristlecone pine migration routes.

RESULTS

Analysis of surveyed bristlecone pine stands

Four of the five stands we mapped are located on limestone or limestone-shale substrates, while the remaining stand grows on Prospect Mountain Quartzite, north of the lone tree described by Kay and Oviatt (1978). The stand found on quartzite (Stand 1) is located north of Point 9,841 on the lower, rocky portion of the ridge. These geology types are consistent with substrates found at other bristlecone pine stand locations (Wright & Mooney 1965).

The smallest of the five newly identified stands (Stand 3) is located approximately 150 meters northeast of Point 10,042 and corresponds to the voucher collected by Taye (1979). We counted eight mature trees and two juvenile bristlecone pine individuals in this stand. Trees are growing on steep, rocky limestone slopes positioned above White Pine Fork Canyon. Limber pine is co-dominant with bristlecone pine in this stand. The two stands south of Point 10,042 (Stands 4 and 5) are larger in area. The White Pine Fork South stand is located northeast of Point 10,230 on east facing slopes (Figure 2.1). Bristlecone pine is dominant within the stand, with scattered limber pine, Engelmann spruce, Douglas-fir, and subalpine fir present in the vicinity. The White Pine Fork South stand (Stand 4) contains a large number of ancient, weathered bristlecone pines (Figure 2.2). The southernmost stand (Stand 5) we identified lies within the Bear Fork drainage and is similar in size to the White Pine Fork South stand, with a slightly lower mean elevation (Figure 2.1; Table 2.1).
**White Pine S (Stand 4) tree measurements**

Within Stand 4, sampled trees ranged in size from 22 to 172 cm diameter at breast height (DBH) (Table 2.2). Mean DBH for all sampled trees was 80 cm. The mean elevation of the sampled trees was 3053 m. Slope ranged from 52.0° near the north end of the stand, to 37.2° near the stand center, with a mean slope of 41.0° among the sample locations. Aspect varied slightly throughout the stand, ranging from 41° to 78° (NE to ENE) with a mean of 59.6° (ENE).

The position of Stand 4 appears to be representative of most other portions of the Stansbury ridgeline where bristlecone pine occurs. Trees are generally restricted to steep, east-facing slopes of the ridge. Bristlecone pine rarely reaches the ridge, and when it does, only scattered trees are present and limber pine becomes dominant. These characteristics fit closely with Taye’s description of bristlecone pine occurrence in the range (Taye 1983). Additional conifer species co-occurring with bristlecone pine on the ridgeline are common juniper (*Juniperus communis*), Engelmann spruce, and Douglas-fir.

**Age distribution**

Estimated ages for sampled trees varied by an order of magnitude, consistent with the wide variability in individual tree DBH. The youngest tree was 80 years old, while the oldest estimated age for a tree we cored was 1784 years. Based on our visits to the stand, we estimate that the sampled trees are representative of all trees across the stand. Large trees in the stand (DBH > 80 cm) grow on a wide range of slopes, with some trees on steep, rocky terrain, while others are located on more gentle slopes where soil accumulation is evident. The oldest trees in the stand exhibit growth patterns outlined by LaMarche (1969), in which growth is limited to a portion of the tree’s circumference. This allows old (greater than 1500 years) trees to maintain a
constant ratio of green to non-green tissue, even when trunk circumference becomes large (> 6 meters) (Wright and Mooney 1965). Cores from trees 1, 8, and 9 provide the longest history of growth in the stand. A marked trend toward smaller rings from 1300 to 1400 A.D. could correspond to the end of the Medieval Warm Period and beginning of the Little Ice Age.

**DISCUSSION**

*Disjunct nature of the Stansbury Mountains bristlecone pine population*

The characteristics of the bristlecone pine population we identified in the Stansbury Mountains are similar to other populations in the eastern and central Great Basin. The five stands we mapped lie between 2560 m and 3118 m, which is consistent with the species’ typical elevation range (Fryer 2004). Dominant soil series in these stands include Lundy, Podmor, and Datemark, which are each found within bristlecone pine stands in the Deep Creek Mountains to the southwest (California Soil Resource Lab 2021). Vegetation associations are also typical of other bristlecone pine populations in Utah and Nevada (Hiebert & Hamrick 1984). Despite these similarities to other populations, the Stansbury Mountains population is unique because of its large distance from the next closest known populations in the Deep Creek Mountains, the House Range, and the West Tavaputs Plateau.

*Paleobiogeography of bristlecone pine and limber pine in the Bonneville Basin*

Modern records of conifers in the Bonneville Basin during the late Pleistocene and early Holocene indicates low probability for bristlecone pine to reach the Stansbury Mountains given known dispersal mechanisms. This extant bristlecone pine population in the Stansbury Mountains may be a remnant of an undocumented presence of the species in the northern Bonneville Basin sometime prior to the Pleistocene/Holocene transition, when cooler
temperatures facilitated montane conifer presence at low elevations. A warming climate during the early Holocene makes it seem more likely that bristlecone pine reached the Stansbury Range prior to that time, as the suitable habitat area for this species would have declined sharply under warmer conditions. *Neotoma* midden records from the late Pleistocene (ca. 12,000 YBP) suggest that bristlecone pine was dominant in mountains and foothills of the east-central Great Basin (Wells 1983; Thompson 1990). Middens have not yet been discovered in the Stansbury Mountains that document bristlecone pine occurrence during the Pleistocene.

*Neotoma* midden records from other portions of the Bonneville Basin suggest that bristlecone pine was present on thin or skeletal soils as low as 1660 meters at the north end of the Confusion Range in west-central Utah (11,880 ± 170 14C YBP) (Wells 1983). This elevation is near the maximum level of Lake Bonneville at 1550 meters (Wells 1983). The lake maintained this level between 18,600 and 18,000 14C YBP, and later subsided to the Provo Level (1450 meters MSL), where it stabilized for 2,000 years (ca. 17,000 – 15,200 14C YBP) (Benson et al. 2011; Oviatt 2015). Throughout the Provo Level period, Lake Bonneville continued to occupy low passes between the House Range and the Stansbury Mountains. As temperatures gradually increased after the last glacial maximum (ca. 18,000 YBP), treeline (including bristlecone pine) moved upslope into cool, dry mountain ranges where they are currently located (Betancourt 1984). The Stansbury Mountains offer a relatively small area of suitable habitat for bristlecone pine compared to other ranges (e.g. House Range, Utah; Deep Creek Mountains, Utah; Snake Range, Nevada), which could explain the small, fragmented nature of modern bristlecone pine stands near the highest elevations in the range. Competition from other conifer species in areas with higher-quality soils and shallower slopes may further explain the species’ highly restricted distribution (Beasley & Klemmedson 1980). Based on available data, we propose two
hypotheses to explain the arrival and modern presence of bristlecone pine in the Stansbury Mountains.

Pleistocene refugium mechanism

Extant bristlecone pine stands in the Stansbury Mountains could be a relict population that was continuously present in the range during all or much of the Wisconsin Glacial Stage (75,000-11,000 YBP). During the late Pleistocene (ca. 12,000 YBP) and into the Pleistocene/Holocene transition (warming) period, midden records indicate that bristlecone pine was widespread within montane environments in the central and southern Great Basin (Wells 1983, Thompson 1990). However, midden data from calcareous soils in the northern Bonneville Basin are sparse, and bristlecone pine material is absent from the single Pleistocene-age midden record from the Stansbury Mountains (at Devil’s Gate at the south end of the range, 1825 m elevation), which only contains material from subalpine fir and limber pine from 12,370 ± 60 14C YBP (USGS 2021). Limber pine was the dominant conifer in the northern Bonneville Basin during this period, while bristlecone pine transitioned to dominance in the southern portion of the basin (Figure 2.3). Complex relationships between multiple conifer species and climatic changes during this period make it difficult to determine both the timing and migration route of bristlecone pine to the Stansbury Mountains. Additionally, a near absence of bristlecone pine in Neotoma middens north of the Confusion Range in western Utah during the Pleistocene/Holocene transition further complicates the task of identifying both the timing and route of bristlecone pine migration to the Stansbury Mountains. The aforementioned unpublished midden record from the northern House Range is evidence that the species was present in upland areas north of the Confusion Range during this period, though it is impossible to determine the
northern extent of the distribution without additional midden data from the Pleistocene/Holocene transition period.

*Long-distance dispersal (LDD) mechanism*

Alternatively, if bristlecone pine was not present in the vicinity of the Stansbury Mountains during the Pleistocene, we hypothesize that seeds could have traveled to the range via long-distance dispersal (LDD) mechanisms at some time during or after the Pleistocene/Holocene transition. This mechanism seems to be the most likely cause of bristlecone pine’s arrival in the Stansbury Mountains, regardless of whether the migration occurred in the Pleistocene or Holocene, but the timing and possible migration pathways are important to consider.

Bristlecone pine seeds are small (6 – 8 mm in length), winged, and are typically spread across short distances via wind dispersal (Lanner 1988, Fryer 2004). Clark’s nutcracker (*Nucifraga columbiana*) forages for pine seeds and caches them at longer distances, particularly in higher elevation stands, which results in germination in a small percentage of caches (Lanner 1988, Chambers et al. 1999). While the LDD capability of bristlecone pine under typical conditions has not been studied extensively, the likelihood that seeds from the nearest populations in the Deep Creek Mountains, House Range, or West Tavaputs Plateau could reach the Stansbury Mountains in a direct linear path seems very low, based on seed dispersal research from other pine species (McCaughey, Schmidt & Shearer 1985, van Wilgen & Siegfried 1986, Benkman 1995). However, studies have shown that tree species can move rapidly via uncommon dispersal events, which can cause seeds to travel greater distances than what would be expected within a specific time period (Clark et al. 1995, Powell & Zimmerman 2004).
Dispersal mechanisms may include interactions with high winds, water movement, or transport by birds (Clark et al. 1998), the latter seeming quite likely with bristlecone pine during the late Pleistocene, when Lake Bonneville covered valley bottoms around the Stansbury Mountains and other mountain ranges where bristlecone pine is now present. Clark’s nutcracker has been shown to disperse seeds some 30 km (Schaming 2016), and it seems feasible that seed transport to the Stansbury Mountains from nearby ranges could have occurred over several generations. Because of bristlecone pine’s affinity for limestone soils (Bailey 1970), it appears probable that dispersal of seeds may have occurred as a series of LDD events that delivered seed from one suitable habitat area to the next across an unknown time frame.

A likely scenario is that bristlecone pine could have reached the Stansbury Mountains via wind- or bird-borne seed dispersal through a series of desert mountain ranges extending northward from the House Range. Following this route, migration would have occurred via a series of separate establishment events beginning at the vicinity of Swasey Mountain in the House Range (where the species has been present since at least 11,000 $^{14}$C YBP), arriving at the Stansbury Mountains through a linear sequence of mountain ranges including the Thomas Range, Drum Mountains, Keg Mountain, Simpson Mountains, Sheeprick Mountains, and Onaqui Mountains (Figure 2.4). The lowest elevation along this route is found at the Old River Bed (feature shown on 1:24,000 USGS topographic quadrangle) between Keg Mountain and the Simpson Mountains, at around 1386 meters. During the maximum level of Lake Bonneville, this pass would have been submerged at a depth of approximately 160 meters. Access between the House Range and the Stansbury Mountains would have been possible only by crossing three channels of the lake between the House Range and the Simpson Mountains (Figure 2.4). Geology appears favorable for this pathway, with the substrate formations (or similar
formations) mentioned in Table 2.1 repeated in the Drum Mountains, Sheeprock Mountains, and Onaqui Mountains (Croft 1956, Cohenour 1957, Hintze 1978, Dommer 1980), although bristlecone pine is apparently not extant in these ranges, or at least it has not been documented. Despite the favorable geological characteristics in these ranges, modern climatic conditions may not be suitable for bristlecone there. If bristlecone pine did establish there in a past climate, it has become extirpated under the modern climatic regime.

Bristlecone pine could also have conceivably reached the Stansbury Mountains via a southeastern approach, coming from either the Wasatch Plateau or Pahvant Range, where the species exists today (Figure 2.4). This route minimizes dispersal across Lake Bonneville. To determine which of the two options (a southwest or southeast route) is more likely, a comparison of genetic samples from bristlecone pine populations at multiple sites (the Stansbury Mountains, House Range, Wasatch Plateau, and Pahvant Range) would be required. However, taking weather patterns into account (prevailing winds move from west to east across the Great Basin), bristlecone migration via the southwest approach is more plausible under a wind dispersal scenario, as arrival at the Stansbury Mountains would likely be facilitated by prevailing weather patterns.

Potential for bristlecone pine occurrence in neighboring ranges

The Stansbury Mountains have likely served as a refuge for bristlecone pine as the elevation range of bristlecone pine occurrence has narrowed since the end of the Wisconsin Glacial Stage (Wells 1983). The Oquirrh Mountains, located 45 km east of the Stansbury Mountains, are another location in the northern Bonneville Basin where other small, isolated stands of bristlecone pine could be present. These stands could be of a similar origin to those found in the Stansbury Mountains. A bristlecone pine voucher was collected in 1964 from the
Oquirrh Mountains by Col. Lynn Mitchell, a USFS forest ranger (Appendix A), and was later re-determined to be limber pine (Thomsen 2011). Upon careful inspection of this voucher via digital photograph, we question the accuracy of this determination as limber pine and suggest that it is likely bristlecone pine. Unfortunately, the ambiguous location description of the voucher (at an elevation of 2745 meters in the Oquirrh Mountains) is insufficient information to locate the vouchered tree without an extensive search of the range. The northern and central Oquirrh Mountains are composed of Paleozoic limestone (Tooker and Roberts 1962), and as such would offer suitable habitat for bristlecone pine. The Onaqui Mountains, to the south of Stansbury Mountains, provide another possible location of undiscovered bristlecone pine stands. Although this range is lower in its maximum elevation (2750 meters), the Onaqui Mountains lie along a possible migration route of bristlecone pine to the Stansbury Mountains during the Pleistocene or Pleistocene/Holocene transition (Figure 2.4). A thorough search of both ranges is needed to determine whether additional populations might be present. Additionally, *Neotoma* midden records from these ranges from the Pleistocene/Holocene transition are needed to establish whether bristlecone pine was present in these areas during that period.

*Future work*

This study represents only a preliminary analysis of this disjunct population of bristlecone pine. More data is needed to understand the paleobiogeography of this species in the Stansbury Mountains. Genetic characteristics of this population should be compared with the nearest populations in the Great Basin to the south and west, and the Utah high plateaus to the southeast. Discovery of nearby *Neotoma* middens may shed further light on bristlecone pine distribution in the Stansbury Mountains and adjacent ranges during the Pleistocene and early Holocene. Additionally, further work should be performed on producing a crossdated climate
chronology using bristlecone pine wood from the Stansbury Mountains (see Salzer, Pearson & Baisan 2019). This climate history should be of great interest because of the close proximity of this bristlecone pine population to a major urban center in Salt Lake City.

ACKNOWLEDGEMENTS

The authors wish to express our gratitude to the Charles Redd Center for Western Studies for funding our travel to the Stansbury Mountains. Additionally, we express deep appreciation to David Charlet for his proofreading assistance, and to Theresa Whitesell for her insightful review of literature concerning seed dispersal by Clark’s nutcracker (*Nucifraga columbiana*).
LITERATURE CITED


Oviatt, C.G. 2015. Chronology of Lake Bonneville, 30,000 to 10,000 yr BP. *Quaternary Science Reviews*, 110, 166-171.


FIGURES

Figure 2.1: Map of Great Basin bristlecone pine occurrence in the Stansbury Mountains.
Figure 2.2: Ancient bristlecone pine individuals growing on steep limestone substrate in the White Pine South stand. Photograph courtesy of Otto De Groff.
Figure 2.3: Map of relative abundance of bristlecone pine and limber pine material in individual *Neotoma* midden strata dated to the Pleistocene/Holocene transition period (12,000 ± 2000 $^{14}$C YBP) in the Bonneville Basin. Bristlecone pine transitions from dominance in the south to absence in records from the northern portion of the basin. Labels indicate the approximate radiocarbon date of each midden record (e.g., $12.4K = 12,400$ $^{14}$C YBP). Data courtesy of the USGS-NOAA North American Packrat Midden Database and Esri.
Figure 2.4: Hypothetical bristlecone pine migration routes to the Stansbury Mountains. Known extant stands of bristlecone pine are displayed as red points (Burchfield et al. 2021). The maximum shoreline elevation of Lake Bonneville (1550 meters MSL) is shown (Chen & Maloof 2017, Utah AGRC 2021).
### Table 2.1: Topographic and geologic characteristics of the five stands of Great Basin bristlecone pine mapped in the Stansbury Mountains (USGS 2021, UGS 2021).

<table>
<thead>
<tr>
<th>Stand Name</th>
<th>Stand Area (ha)</th>
<th>Mean Elevation (m)</th>
<th>Mean Slope (degrees)</th>
<th>Mean Aspect (degrees)</th>
<th>Geology</th>
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<tr>
<td>Mill Fork W (Stand 1)</td>
<td>6.6</td>
<td>2669</td>
<td>42.8</td>
<td>123.3</td>
<td>Prospect Mountain Quartzite (Podmor series)</td>
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<tr>
<td>Mill Fork E (Stand 2)</td>
<td>3.8</td>
<td>2918</td>
<td>35.9</td>
<td>44.3</td>
<td>Cambrian carbonates and shales (Datemark and Podmor series)</td>
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<tr>
<td>White Pine Fork N (Stand 3)</td>
<td>0.4</td>
<td>3014</td>
<td>36.2</td>
<td>118.3</td>
<td>Wheeler Formation and Swasey Limestone (Lundy series)</td>
</tr>
<tr>
<td>White Pine Fork S (Stand 4)</td>
<td>4.3</td>
<td>3055</td>
<td>37.5</td>
<td>69.0</td>
<td>Pierson Cove Formation (limestone) (Lundy series)</td>
</tr>
<tr>
<td>Bear Fork (Stand 5)</td>
<td>3.9</td>
<td>2958</td>
<td>38.0</td>
<td>80.0</td>
<td>Pierson Cove Formation (limestone) (Lundy series)</td>
</tr>
</tbody>
</table>
Table 2.2: Measurements from the ten bristlecone pine individuals sampled within White Pine S (Stand 4). Additional samples are needed to facilitate crossdating and the development of a climate chronology from this population.

<table>
<thead>
<tr>
<th>Core Number</th>
<th>Ring Count</th>
<th>Est. Inner Ring Year (AD)</th>
<th>DBH (cm)</th>
<th>Radius Estimate (cm)</th>
<th>Core Length (cm)</th>
<th>Estimated Age</th>
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<tr>
<td>1</td>
<td>997</td>
<td>1023</td>
<td>94.7</td>
<td>47.4</td>
<td>33.9</td>
<td>1320</td>
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<tr>
<td>2</td>
<td>446</td>
<td>1574</td>
<td>95.3</td>
<td>47.6</td>
<td>13.1</td>
<td>1784</td>
</tr>
<tr>
<td>3</td>
<td>515</td>
<td>1505 (pith)</td>
<td>41.2</td>
<td>20.6</td>
<td>18.9</td>
<td>515</td>
</tr>
<tr>
<td>4</td>
<td>335</td>
<td>1685</td>
<td>59.2</td>
<td>30.0</td>
<td>29.9</td>
<td>345</td>
</tr>
<tr>
<td>5</td>
<td>1147</td>
<td>873</td>
<td>130.8</td>
<td>65.4</td>
<td>44.0</td>
<td>1516</td>
</tr>
<tr>
<td>6</td>
<td>80</td>
<td>1940 (pith)</td>
<td>22.0</td>
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<td>10.5</td>
<td>80</td>
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<tr>
<td>7</td>
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<td>92.5</td>
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<td>10</td>
<td>113</td>
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<td>25.7</td>
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APPENDIX A: Voucher information for referenced plant collections.

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<tr>
<th>Location</th>
<th>Mountain Range</th>
<th>State</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation (m)</th>
<th>Collector</th>
<th>Herbarium/a</th>
<th>Year</th>
<th>Species</th>
</tr>
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<tbody>
<tr>
<td>1.2 mi ESE of Deseret Peak (stand 4)</td>
<td>Stansbury Mountains</td>
<td>UT</td>
<td>40.4511</td>
<td>-112.8046</td>
<td>3063</td>
<td>De Groff 18</td>
<td>BRY</td>
<td>2020</td>
<td>Juniperus communis</td>
</tr>
<tr>
<td>1.2 mi ESE of Deseret Peak (stand 4)</td>
<td>Stansbury Mountains</td>
<td>UT</td>
<td>40.4511</td>
<td>-112.8046</td>
<td>3063</td>
<td>De Groff 19</td>
<td>BRY</td>
<td>2020</td>
<td>Picea engelmannii</td>
</tr>
<tr>
<td>1.2 mi ESE of Deseret Peak (stand 4)</td>
<td>Stansbury Mountains</td>
<td>UT</td>
<td>40.4511</td>
<td>-112.8046</td>
<td>3063</td>
<td>De Groff 17</td>
<td>BRY</td>
<td>2020</td>
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<tr>
<td>1.0 mi E of Deseret Peak (stand 3)</td>
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<td>UT</td>
<td>40.4604</td>
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<td>3048</td>
<td>De Groff 28</td>
<td>BRY</td>
<td>2020</td>
<td>Pinus flexilis</td>
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<td>Thomas Creek Canyon</td>
<td>Ruby Mountains</td>
<td>NV</td>
<td>40.6426</td>
<td>-115.4058</td>
<td>2743</td>
<td>Holmgren 6273</td>
<td>BRY</td>
<td>1972</td>
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<tr>
<td>Spruce Mountain</td>
<td>Pequop Mountains</td>
<td>NV</td>
<td>40.5509</td>
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<td>BRY</td>
<td>1981</td>
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<td>Burger Peak</td>
<td>Pine Valley Mountains</td>
<td>UT</td>
<td>37.3224</td>
<td>-113.5030</td>
<td>3100</td>
<td>Higgins 14398</td>
<td>BRY</td>
<td>1984</td>
<td>Pinus longaeva</td>
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<tr>
<td>Right Fork Lake Canyon</td>
<td>West Tavaputs Plateau</td>
<td>UT</td>
<td>39.9921</td>
<td>-110.7377</td>
<td>2365</td>
<td>Goodrich 25877</td>
<td>BRY</td>
<td>1998</td>
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<td>Ridge between Mill Fork and Dry Lake Fork</td>
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<td>2743-3200</td>
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<td>Oquirrh Mountains, elevation 9000 ft.</td>
<td>Oquirrh Mountains</td>
<td>UT</td>
<td>-</td>
<td>-</td>
<td>2743</td>
<td>Mitchell s.n.</td>
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<td>Telescope Peak</td>
<td>Panamint Range</td>
<td>CA</td>
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<td>De Groff 29</td>
<td>BRY</td>
<td>2020</td>
<td>Pseudotsuga menziesii</td>
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CHAPTER 3

A Comprehensive Distribution Map and Habitat Suitability Model for Great Basin Bristlecone Pine (Pinus longaeva D.K. Bailey)

David R. Burchfield\textsuperscript{1}, Otto W. De Groff\textsuperscript{4}, Stanley G. Kitchen\textsuperscript{2}, David A. Charlet\textsuperscript{3}, Douglas H. Page\textsuperscript{4}, Constance I. Millar\textsuperscript{5}, Douglas J. Merkler\textsuperscript{6}, Gregory W. Taylor\textsuperscript{1}, Héctor G. Ortiz\textsuperscript{1}, and Steven L. Petersen\textsuperscript{1}

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ABSTRACT

Great Basin bristlecone pine (Pinus longaeva D.K. Bailey) is a long-lived subalpine conifer native to the western United States. Bristlecone pine is considered a keystone species of high-elevation Great Basin sky island forests, yet detailed distribution data and information about constraining environmental factors for the species are lacking. We compiled a distribution dataset consisting of 490 individual bristlecone pine forest stands covering nearly 100,000 ha in Utah, Nevada, and California to enable improved monitoring of the species and enhanced understanding of forest succession dynamics. These data were sourced using records from herbaria, an internet-based ecological database, government vegetation surveys and extensive field surveys. We field-verified approximately 60\% of mapped bristlecone pine stands in cooperation with a network of collaborators. We used this occurrence data to train a Maximum
Entropy (MaxEnt) Habitat Suitability Model (HSM) covering the entire known distribution of bristlecone pine. Sixty environmental variables representing climatic, topographic, and edaphic factors were considered in the model and ranked by relative importance in constraining the MaxEnt model to the current known distribution of bristlecone pine. The model was regenerated using the 10 most influential variables that showed an insignificant correlation ($|r| < 0.7$) with all other variables to reduce possible effects of collinearity. A second model was produced using only climatic and topographic variables to fill coverage gaps in our soil variables, and the two resulting probability maps were merged. Both models performed well using the AUC metric of model fit—the models achieved values of 0.967 and 0.954, respectively. The variables that contributed the most predictive power to both models were mean dewpoint temperature and mean precipitation values for the months of January and February, respectively (> 80% predictive power), although other climatic, edaphic, and topographic factors were also shown to be useful for refining the distribution model. Our model’s occurrence probability map will serve as a valuable resource for conservation of bristlecone pine populations and assessing risk in the face of multiple threats, such as fire disturbance, MPB, and WPBR. Additionally, we intend to project the model to characterize the potential response of the species distribution to anticipated climate change in the region.

INTRODUCTION

Great Basin bristlecone pine (*Pinus longaeva*; hereafter bristlecone pine) is a subalpine tree species native to the U.S. states of Utah, Nevada, and California. Bristlecone pine is a member of *Pinus* subsection *Balfourianae*. It shares this subsection with two other closely related North American pine species, the foxtail pine (*Pinus balfouriana*) and the Rocky Mountain bristlecone pine (*Pinus aristata*). Bristlecone pine is typically associated with limber
pine (*P. flexilis*) in montane forested systems, referred to as the “Limber Pine-Bristlecone Pine zone” (Grayson 1993) and is considered a keystone species in montane forest communities in the Great Basin and western Colorado Plateau ecoregions (Eidson, Mock & Bentz 2018).

Bristlecone pine has shown tremendous scientific importance due to its longevity. Dendrochronologists have used ancient bristlecone pine wood to study climate patterns since the 1950s (Ferguson 1969). Individual trees in the White Mountains in eastern California have been dated through ring-counting and cross-dating techniques to be nearly 5000 years old (Currey 1965; Lanner & Conner 2001). Using ring-width analysis methods on wood from ancient trees (both living and dead), dendrochronologists have developed climatic chronologies to 8000+ years B.P. (Feng & Epstein 1994; Salzer, Pearson & Baisan 2019). Additionally, bristlecone pine wood has been used to calibrate radiocarbon dating methods (Ferguson & Graybill 1983).

Across much of its distribution, bristlecone pine frequently occurs in small, isolated patches, mainly in high-elevation, topographically rugged environments, and only rarely does this species form uniform forest stands that cover large areas (e.g. Mt. Charleston, Nevada, White Mountains, California) (Hiebert & Hamrick 1984; Bunn et al. 2018). However, the species distribution is not well-documented at finer spatial scales. The factors that control its distribution are also poorly understood and have not been studied extensively. We found two studies that attempted to model bristlecone pine distribution or establishment drivers. Gray (2017) utilized a raster-based random forest (RF) spatial modeling approach using bristlecone pine presence and absence data, and concluded that elevation, texture (derived from Landsat satellite imagery), and slope were important drivers of bristlecone pine distribution. Hankin & Bisbing (2021) examined the effects of snowpack conditions on the regeneration of bristlecone, limber, and whitebark pines after fire disturbance, and found that greater snowpack has a negative effect on bristlecone
pine establishment. LaMarche & Stockton (1974) examined the effects of seasonal temperature and precipitation on bristlecone pine (*Pinus longaeva* and *P. aristata*) growth patterns (as opposed to establishment frequency) as measured by tree-ring widths, showing a wide range of growth responses to climatic factors that varied by site.

Multiple studies have also shown that soil characteristics are important for establishment and persistence of bristlecone pine—the species has an affinity for alkaline, calcareous soils, but its occurrence has occasionally been documented on other soil types as well (Wright & Mooney 1965; Currey 1965; Orlemann, Flinders & Allphin 2017). Additionally, ectomycorrhizal spore bank occurrence has been demonstrated to be important for establishment of bristlecone pine (Shemesh et al. 2019). Other edaphic and climatological variables that account for the species distribution at a global scale have not been explored in-depth, nor have distribution maps been published for the entire species range at a detailed scale. A comprehensive map of the species distribution is needed for improved management and conservation. Moreover, a detailed distribution map will lead to improved understanding of habitat requirements and site suitability for bristlecone pine establishment and survival. Furthermore, we propose a Habitat Suitability Modeling (HSM) approach to aid in characterization of environmental drivers of bristlecone pine distribution.

HSM, also known as Species Distribution Modeling (SDM) or Ecological Niche Modeling (ENM), is a commonly used tool in ecology and biogeography (Yackulic et al. 2013; Phillips et al. 2017). An HSM is a prediction of environmental suitability for a species within an area of interest (Phillips et al. 2017). The inputs to HSM algorithms are geo-referenced environmental variables (e.g. climate, topography, and soils) and species presence and/or absence data. Three of the most popular correlative HSM algorithms are BIOCLIM, random...
forest (RF), and Maximum Entropy (MaxEnt) (Evans et al. 2011; Booth et al. 2014; Phillips et al. 2017). MaxEnt has the advantage of using species presence data in tandem with environmental variables to quantify relative probability of occurrence—no absence data is required (Yackulic et al. 2013). This presence-only approach contrasts with other modeling methods that rely on both presence and absence data. Meaningful absence data is often challenging to collect, while there are many sources of presence data available (e.g. herbarium voucher records, iNaturalist).

MaxEnt provides as outputs both a map of relative occurrence rate (ROR) (Fithian & Hastie 2012; Merow, Smith & Silander 2013, also termed “suitability index” by Royle et al. 2021) and an analysis of variable contributions to the distribution model. Relative occurrence is expressed via a complementary log-log (cloglog) transform, which can be cautiously interpreted as occurrence probability provided certain statistical assumptions are met (Phillips et al. 2017). These assumptions include independence of presence samples (i.e. that they are a result of random or representative samples) and constant probability of detection across sample locations (Yackulic et al. 2013).

This study has two primary objectives:

1. To create a detailed spatial database of known stands of bristlecone pine using a variety of available data sources. These presence points will be mapped using GIS and used as an input for MaxEnt habitat suitability modeling.
2. To develop a model-based prediction for the distribution of bristlecone pine in relation to key environmental variables. We will use MaxEnt habitat suitability modeling to identify environmental factors that aid in characterization of the fundamental niche of the species (Roughgarden 1974). We predict that a combination of topographic, edaphic, and climatic variables will prove to be important drivers of the distribution and habitat niche of the species.

METHODS

Compilation of PILO occurrence data

In order to model the distribution of bristlecone pine, we compiled all available presence data for the species, building from historic mapping efforts, government vegetation surveys from the National Park Service and U.S. Forest Service, herbarium records, internet databases, and extensive field work. The overall distribution of Great Basin bristlecone pine had been mapped at least four times in the past, which provided historical context and a starting point for our mapping effort. Initially, bristlecone pine was not recognized as a separate species from the closely related Rocky Mountain bristlecone pine (P. aristata)—maps created before 1970 aggregated the distributions of the two species (Bailey 1970). E. N. Munns of the U.S. Forest Service published perhaps the first distribution map for P. aristata (including P. longaeva) in his 1938 atlas “The Distribution of Important Forest Trees of the United States” (Munns 1938). This map was merely an estimate of the species distribution, and the atlas did not list specific sources for the map data. Several locations are erroneously shown where bristlecone pine is now known to be absent (Figure 3.1).
In 1966, W. B. Critchfield and E. L. Little produced a map of the distribution of Rocky Mountain bristlecone pine (including Great Basin bristlecone pine) for their atlas “Geographic Distribution of the Pines of the World” (Critchfield & Little 1966). This map was copied in Little’s well-known “Atlas of United States Trees” (Little & Viereck 1971). The authors listed only four unpublished sources of information for their map for bristlecone pine as a whole, including two from California and one from Utah. These sources are presumably U.S. Forest Service vegetation surveys conducted in those states. This map is both highly generalized and incomplete, displaying polygons for the locations of just 11 populations within the borders of Utah, Nevada, and California, with 17 additional point markers indicating “isolated occurrences” in those states (Figure 3.1).

In his 1970 taxonomic and geographic study of Pinus subsection Balfourianae, which identified Great Basin bristlecone pine as a separate species distinct from Rocky Mountain bristlecone pine and foxtail pine (P. balfouriana), D. K. Bailey created a map of P. longaeva using herbarium records and conducting site visits to verify the presence of the trees in several locations. He examined 600 specimens, aggregated them into localities, and geo-located them as point features on a paper map. Bailey also drew a rough polygon on his map representing an estimated absolute outer boundary of Great Basin bristlecone pine populations (Bailey 1970) (Figure 3.1).

Most recently, D. A. Charlet, in his book “Atlas of Nevada Conifers: A Phytogeographic Reference” (Charlet 1996), produced a map of known bristlecone pine stands across the state of Nevada. He mapped the locations of 72 herbarium collections in 17 mountain ranges in Nevada, which were plotted as point features on a map of Nevada with boundaries representing mountain range extents (Figure 3.1).
Each of these maps, while highly useful, showed limitations related to map scale or data type. The Munns and Little maps often drew broad, generalized polygons that covered entire mountain ranges, including some ranges where bristlecone pine does not occur. Bailey’s map delineated an outer boundary of the distribution, but occurrences within the distribution were shown as point features instead of polygons representing population extents. Similarly, Charlet’s map of the species distribution in Nevada, while highly precise, was based on herbarium occurrence records with only latitude and longitude values for each occurrence, precluding any sort of analysis where the extent of populations or individual stands might be important. Nevertheless, it is important to note that the quality of these maps has improved over time as the availability of vegetation distribution data has expanded, allowing researchers to map these data at finer spatial scales. These maps, along with a thorough literature review of bristlecone pine population locations, gave us a starting point for field visits that allowed us to produce species presence data in preparation for HSM.

We compiled stand-level distribution data for the entire known range of bristlecone pine, which encompasses portions of the states of Utah, Nevada, and California. A “stand,” in a forestry context, is defined as “a contiguous community of trees uniform in composition, age and size class distribution, spatial arrangement, site quality, condition, or location to distinguish it from adjacent communities” (Nyland 2016). We opted to focus on the “composition” and “location” aspects of this definition in our mapping approach, identifying forested areas in which bristlecone pine is at least a minor but consistent component of the forest. The approach generally worked well due to the patchy, fragmented nature of most populations of the species. We did not identify a minimum stand size for inclusion in our map—stands were identified that were smaller than 1.0 hectare in area. The compilation of these stand data was a multi-year effort.
that involved gathering bristlecone pine distribution information from numerous sources, including vegetation surveys, herbarium records, iNaturalist observations (California Academy of Sciences, San Francisco, California), high-resolution aerial imagery (e.g. USDA NAIP imagery), and firsthand reports from scientists, foresters, and land managers. These known stand location polygons were digitized and assembled into an Esri geodatabase for display in an ArcGIS Online-based web mapping application (Esri, Redlands, California, USA). Apart from the stand polygons, attribute data were also assembled for each stand and recorded in the geodatabase, including a name, unique identifier, the mountain range or region, county, and state where the stand is found, the stand area, the source of the stand data, a web link to photographs of the stand (if available), and attribution to the photographer. Due to the difficulty of reaching many bristlecone pine stands, we also assigned an “access class” to each stand to quantify the ease of access, i.e. easy (a road passes through the stand), moderate (a road approaches to within 0.5 miles/0.8 km of the stand), and difficult (no road exists within 1.0 mile/1.6 km of the stand).

A total of 490 stand polygons were produced from the aforementioned mapping effort. Each of the stand polygons was tagged based on what data sources were used to create the stand. In cases where multiple sources were used, a secondary source tag was assigned (Figure 3.2). 296 (60.4%) of the stands were directly field verified by BYU Geospatial Habitat Analysis Laboratory (GHAL) staff or collaborators via site visits. An additional 64 stands (13.0%) were derived from geolocation information included with herbarium voucher records or iNaturalist observations and were verified to a high degree of confidence using aerial imagery. In sites directly field verified by GHAL staff, presence of bristlecone pine within the polygon area was confirmed, and the stand boundaries were validated to the extent this was possible by hiking around the stand and estimating the boundaries using binoculars, and in some cases, drones. Due
to the rugged terrain in which many of the stands are found, it was often problematic to directly verify the boundaries, and in these cases they were estimated from aerial imagery by interpreting vegetation and soil patterns. 198 records from our database were either partially verified or derived from other sources deemed to be unreliable and received an “unverified” tag. These stands were excluded from the MaxEnt analysis. We acknowledge that there are likely to be errors of omission (type II errors) in the dataset due to under-estimation of bristlecone habitat areas. Errors of commission (type I errors) are also likely to be present, but in a more limited quantity due to the methodology we used.

Following completion of the stand mapping effort, we analyzed the current protected status of mapped stands using the USGS Protected Areas Database of the United States (USGS 2020). We used ArcGIS Pro to perform a geometric intersection of bristlecone pine stands with each of four GAP status classes to quantify the area of bristlecone pine habitat included in each class.

*Maximum Entropy habitat suitability modeling*

The MaxEnt HSM package required species presence data as an input, which necessitated the conversion of our stand polygons to a point-based table of samples consisting of latitude and longitude coordinates (WGS 84) for each sample. Prior to this conversion, we refined our presence dataset by eliminating observations that were not directly verified via site visits, herbarium vouchers with precise geolocation, or iNaturalist records. This greatly increased the reliability of the presence dataset for modeling purposes and reduced the number of largely redundant samples. Following the database cleanup process, we used the Generate Random Points tool in ArcGIS Pro 2.7.1 (Esri, Redlands, California, U.S.A.) to create a point feature
class consisting of random points selected from within bristlecone pine stand polygon boundaries. We specified a minimum distance of 800 m between each randomly placed point to avoid excessive spatial clustering of presence samples. The 800 m spacing threshold was used because it was the same distance as the spatial resolution of our environmental predictor variables, and it allowed us to avoid the chance that multiple presence samples would fall onto the same cell of our predictor rasters. The smallest stand polygons received only one sample point, while the largest polygons were able to receive up to 1000 points using the 800 m spacing constraint. Latitude and longitude were calculated for each sample in the feature class, and the attribute table was exported as a comma-separated value (CSV) file for input into MaxEnt. This process yielded 371 samples representing locations where bristlecone pine was known to be present. Due to the comprehensive nature of the presence dataset and the random selection of sample points, we assumed that the input data was unbiased, which is an important assumption of MaxEnt modeling (Yackulic et al. 2013; Phillips et al. 2017).

The other primary input required in MaxEnt is a series of environmental predictor raster variables, which represent environmental phenomena that may constrain the distribution of the species of interest, including climate, soils, and topographic variables. Climate variables we selected as model inputs consisted of 30-year (1980–2010) annual and monthly normal values for total precipitation, mean dewpoint temperature, and minimum and maximum temperatures obtained from the PRISM Climate Group (PRISM 2019) at 800 m spatial resolution. These variables were selected in an exploratory sense because it was unknown which climatic factors would prove important for bristlecone pine occurrence. Additionally, Topographic Ruggedness Index (TRI) (Riley, DeGloria & Elliott 1999), slope, aspect, and total solar radiation (Fu & Rich 2002) values derived from PRISM elevation data were included as model inputs. These were
calculated using tools in ArcGIS Pro and were derived from the PRISM elevation dataset.
gSSURGO (Soil Survey Staff 2020) soil data for available water supply (AWS) (expressed as
centimeters of water per centimeter of depth) (NRCS 2016), calcium carbonate (CaCO$_3$)
concentration (percent of carbonates in the fraction of the soil less than 2.0 millimeters in size)
(NRCS 2016), and pH were rasterized and resampled to match the 800 m spatial resolution of the
PRISM datasets. AWS is a measure of the quantity of water that soil is capable of storing for use
by plants, and is influenced by the soil’s concentration of rock fragments, organic matter, and
texture (Wieczorek 2014; NRCS 2016). This represented a condensed format for characterizing
multiple variables that were deemed possibly important for establishment of bristlecone pine.
Studies have indicated that bristlecone pine tends to grow on alkaline soils containing high
concentrations of CaCO$_3$ (Wright & Mooney 1965; Bidartondo, Baar & Bruns 2001; Smithers &
North 2020). CaCO$_3$ and pH were selected to test the importance of those influences on
bristlecone pine distribution (Table 3.1).

Due to limitations of the gSSURGO dataset, there were coverage gaps among the soil
variables. These gaps were primarily located in mountainous portions of California and central
Utah in areas where detailed soil surveys have not been completed, and would produce coverage
gaps in the resulting MaxEnt model probability maps. Because we were interested in the effects
of these soil variables despite the coverage gaps, we decided to produce one model with the soil
variables included, and a second model that only included the PRISM data and derived variables.
Before input into MaxEnt, all predictor variable rasters were clipped to a modified version of

To aid in variable selection, an initial run of MaxEnt was performed using all variables to
establish relative importance of the variables using the permutation importance table provided in
the MaxEnt output. We used ENMTools (Warren et al. 2019) to produce a correlation matrix (Pearson’s $R$) of the top variables to evaluate multicollinearity. Variables were discarded if they produced a significant correlation ($|r| \geq 0.7$) with a more important variable (higher on the permutation order table). We selected the 10 most important insignificantly correlated variables for inclusion in the final model to reduce possible negative effects of collinearity on model transferability (see Feng et al. 2019).

We used the MaxEnt Java program (version 3.4.1) (Phillips et al. 2017) to generate our species distribution models for bristlecone pine. We configured the program to produce 10 replicates of the model, then average the resulting cloglog values into a composite map to reduce noise on the final output model probability map. Samples were set aside during each replicate run as test data used for $k$-fold cross-validation (Mosteller & Tukey 1968; Radosavljevic & Anderson 2014). Two separate models were produced using MaxEnt. The first included gSSURGO soil data as environmental variables, despite the large coverage gaps associated with those data (“with-soil model”). Additionally, a second model was generated that excluded the soil data (“no-soil model”). This allowed us to produce a MaxEnt probability map for areas that lacked gSSURGO coverage. It also allowed us to compare the relative strength of the two modeling approaches and determine whether certain climatic or topographic variables were important in either or both approaches.

The “Mosaic to New Raster” tool in ArcGIS Pro was used to merge the probability maps for the two models by giving the higher-quality model (with-soil) probability map mosaic priority over the lower-quality model (no-soil) probability map, but using the no-soil model to fill in the aforementioned gaps in the with-soil map. Additionally, scattered missing values (no-data cells) resulting from the input raster variables were filled using the “Elevation Void Fill”
function in ArcGIS Pro. The resulting composite raster was resampled using a cubic convolution method in order to smooth the final output for improved visualization (Keys 1981).

RESULTS

*Distribution map for Great Basin bristlecone pine*

Using the stand polygon dataset, we produced a map of known bristlecone pine occurrences using a proportional point symbology to highlight differences in relative sizes of contiguous stands (Figure 3.3). We mapped 490 stand polygons encompassing 99,808 ha of forests in Utah, Nevada, and California that contained bristlecone pine as at least a minor component.

We segmented the total distribution into four regional groupings based upon apparent spatial clusters. These roughly followed physiographic boundaries in the case of the Utah High Plateaus (UHP) grouping (hydrographic Colorado Plateau), while the Central Great Basin (CGB), Southern Great Basin (SGB), and Western Great Basin (WGB) groupings were drawn based upon the large distances between bristlecone pine populations found in those groupings (Figure 3.3). Additionally, stands tended to be smaller ($\bar{x} = 167$ ha) and more scattered among the CGB population when compared to the large contiguous stands prevalent in the SGB and WGB populations ($\bar{x} = 3578$ and 833 ha, respectively). Mean stand size in the UHP stands was even smaller at 71 ha. To further test the robustness of these groupings in characterizing regional differences in environmental conditions within bristlecone pine populations, we randomly sampled the elevation values ($n = 1000$) within stand polygons in each grouping and performed a pairwise Wilcoxon rank sum test using R (R Core Team 2021; Wilcoxon 1946). We produced a box-and-whisker plot for visualization using ggplot2 (Wickham 2016) (Figure 3.4). Most pairs of
groupings were significantly different, indicating that the regional groupings we selected displayed significant differences in environmental factors related to elevation. Other interactions between regional groupings and environmental variables would be explored after determining which variables proved most important in our MaxEnt models.

MaxEnt models

Variables used in model development

Following the initial run of MaxEnt to determine variable importance, we re-analyzed the dataset using only the top 10 insignificantly correlated variables (with-soil model) (Figure 3.5). To fill the coverage gaps found in the soil data, we created an additional model using the seven topographic and climatic variables that remained after removing the soil variables (AWS, CaCO₃, and pH) (no-soil model).

MaxEnt model results

Total model performance is characterized by the area under the receiver-operator curve (AUC) and represents the probability that a randomly chosen occurrence sample is ranked higher than a randomly selected background point (Merow, Smith & Silander 2013). An AUC value close to 1.0 represents a high probability and therefore high model performance (Syfert, Smith & Coomes 2013). Our MaxEnt model (mean of 10 replicates) with soil variables included achieved an average test AUC value of 0.967 with a standard deviation of 0.007. The 10 most influential variables in the model are displayed in Table 3.2. The MaxEnt model without soil variables included achieved an average test AUC value of 0.954, with a standard deviation of 0.008.
Variable importance and response

January mean dewpoint temperature and February mean precipitation were the most influential variables in both models, accounting for 90.3% and 82.3% of the total importance in the with-soil and no-soil models, respectively (Table 3.2).

MaxEnt output graphs showing variable response curves are shown in Figure 3.6 and Figure 3.7. The variables used in both models showed similar responses between models. After determining which variables MaxEnt showed to be most important for constraining bristlecone pine distribution, we randomly sampled values for the top two variables (January mean dewpoint temperature and February mean precipitation) in bristlecone pine stands using the same methodology previously discussed to determine whether the regional groupings showed significant differences. The pairwise Wilcoxon rank sum test again showed significance for both variables among most regional groupings, lending further support to the groupings we selected. We produced box-and-whisker plots to visualize the differences in these variables in each regional grouping (Figure 3.8).

Composite HSM probability map

The composite HSM probability map is shown in Figure 3.9. Modeled high-cloglog areas consistently aligned with observed topographic, climatic, and edaphic factors typical for bristlecone pine habitat.

Bristlecone pine protected status

A summary of GAP status information for mapped bristlecone pine stands is shown in Table 3.3. 81,243 ha (81.4%) of mapped bristlecone pine stands were listed as being currently managed for
biodiversity (GAP 1 and GAP 2). However, a large proportion of protected stands are listed as being managed for multiple uses, including extractive and off-highway vehicle use (GAP 3). 1,785 ha are not found in protected areas (GAP 4).

DISCUSSION

Variable importance

January mean dewpoint temperature (tdewpoint01) and February mean precipitation (precip02) were the most influential variables in both models (Figure 3.10). This indicates that winter air dryness and precipitation are important factors in bristlecone persistence, likely resulting from a competitive advantage over other species that are less adapted to extreme cold and desiccation during winter months. Variable response curves show that occurrence probability increases logarithmically with February precipitation, which aligns with LaMarche & Stockton’s (1974) observations of a positive correlation between mid-winter precipitation and bristlecone pine cambial growth in the White Mountains, California. The month of February is a key period for snowpack accumulation in high-elevation mountainous regions of the western U.S., and the interaction between bristlecone pine occurrence and may be related to long persistence of February precipitation in the form of snow, followed by a subsequent slow release of water and warming temperatures in the spring (see Harpold et al. 2015). The interaction between occurrence probability and January dewpoint temperature is more complex, represented by a narrow range of optimal dewpoint temperatures between -17 and -11°C, then a rapid decrease in occurrence probability (suitability) above -11°C. Bristlecone pine may outperform other species in these conditions that result in a higher probability of occurrence.
January mean dewpoint and February mean precipitation were highly correlated with other variables thought to be important in constraining the distribution of bristlecone pine. For example, January mean dewpoint showed a high negative correlation with elevation ($r = -0.92$) and could be considered a surrogate for elevation in the HSM. Additionally, the edaphic variables we used (CaCO$_3$ concentration, pH, and AWS) did not account for a large percentage of the total permutation importance, but they did appear to constrain mapped areas of high probability better than the climatic and topographic variables by themselves.

The two variables that contributed most to the MaxEnt model showed significant differences among the regional groupings we established for the overall range of bristlecone pine. This indicates differences in importance of environmental factors among genetic subpopulations of the species. Therefore, bristlecone pine’s fundamental niche is likely to vary across space and among genetically different subpopulations. Additional analysis is needed to characterize these potential genetic differences among regional groupings.

*MaxEnt cloglog map interpretation*

The composite map of MaxEnt-derived cloglog values that combined values from the with-soil and no-soil models performed well based upon visual comparison with available bristlecone pine occurrence data. Map areas with high cloglog values generally showed locations where bristlecone pine presence has been documented (i.e. where the species’ fundamental and realized niches aligned), with several exceptions. For example, the Diamond Mountains of Eureka County, Nevada appear on our map with generally high cloglog values along the crest of the range, but no bristlecone pine has yet been documented in this location (Charlet 1996). The Diamond Mountains may represent a region that provides bristlecone pine’s fundamental niche,
but unknown factors have prevented its establishment within this area. Conversely, an area of high cloglog values around the Chokecherry Benchmark in the southern Snake Range in eastern Nevada, where no bristlecone pine had been mapped, led us to a recent internet report of bristlecone pine occurrence there, confirming our model’s prediction in that location (Gathright 2020). We anticipate that this model will aid in location of additional undocumented populations of bristlecone pine.

Model limitations

Our model has two limitations that should be mentioned. First, the spatial resolution of the PRISM datasets we used as environmental predictor variables (800 m) was appropriate for such a large area, but it could be too coarse to effectively characterize important fine-scale variation in variables such as total solar radiation, slope, and aspect. There could have been local variations in these phenomena that would explain bristlecone pine occurrence with greater discrimination, but those local variations could have been averaged out due to the relatively coarse scale we selected (see Levin 1992). Second, as previously discussed, there were large gaps in the gSSURGO soil data we used in the analysis. MaxEnt does not provide a means to ignore the gaps in one variable, so all variables get cropped to the extent of the variable that covers the smallest land area. This led to large holes in our bristlecone pine occurrence predictions in several areas that are known to contain bristlecone pine populations, resulting in the need to create a separate model without soil data. This second model was used to fill the gaps in the soil rasters, but its overall performance indicated lower reliability (Wright & Mooney 1965). Additionally, limitations in the accuracy of the gSSURGO data may be a source of error in model predictions.
We also acknowledge the likelihood that, across such a wide distribution area, certain subpopulations of bristlecone pine are likely to be more sensitive to specific environmental factors than other subpopulations. A blanket modeling treatment of the entire species distribution may preclude representation of important genetic groupings within the species that are constrained to different ecological niches. In order to study these subpopulations and their respective niches, it would be necessary to conduct extensive genetic testing on the species, identify genotypic groupings, and conduct modeling among each genetic group to determine the relative importance of environmental variables among the subpopulations.

*Iterative modeling approach*

These results represented the latest iteration of our modeling workflow. Our approach was to create MaxEnt distribution models, then search for areas of high probability where no bristlecone pine was known to occur, then field-verify those locations where possible (see Rhoden et al. 2017). This led us to document several populations that were previously unknown or undocumented in herbaria, e.g. O’Neal Peak, Nevada (Snake Range), Kern Mountains, Nevada, and Howell Peak, Utah (House Range). These newly verified locations were, in turn, used to improve our database of presence samples and to create new models. We plan to continue using this iterative modeling approach to find additional undocumented populations.

**CONCLUSION**

This study resulted in the most comprehensive distribution dataset for Great Basin bristlecone pine to date and used the resulting occurrence data to model the species distribution based upon 60 environmental variables. The resulting model showed that the species is sensitive to a combination of topographic, climatic, and edaphic variables that constrain the species to its
current ecological niche. We intend to use this model to estimate the response of Great Basin bristlecone pine to warming climatic conditions. Bristlecone pine is a subalpine conifer with an already limited, fragmented distribution, and we would expect its range to contract under a warmer climate. Modifying the PRISM data to represent anticipated warming regimes and projecting our model to those conditions is a continuation of this work that we hope to pursue.

We also plan to maintain the Great Basin bristlecone pine distribution database and continue to field-verify stands to iteratively improve the dataset. As data for newly documented stands become available, we will update the database. This will be an important dataset for forest scientists, researchers, and land managers as they monitor the overall health of the species in the face of multiple potential threats, including white pine blister rust (WPBR) and mountain pine beetle (MPB) infestations that have caused high mortality in other high-elevation pine species.

Mapped bristlecone pine stands are largely found within protected areas, including national parks, designated wilderness areas, and national forests. However, we estimate that 93% of the total mapped habitat area is contained within mixed-management areas where extractive activities could impact bristlecone pine populations. Further research should be performed to quantify the effects of these activities on overall health of the species and to determine whether additional protection is needed.

The bristlecone pine distribution database and associated web mapping application will continue to be hosted by the BYU Geospatial Habitat Analysis Laboratory (GHAL), and the database will be made freely available to interested parties. The permanent link for the bristlecone pine web mapping application is found at https://bristlecone.byu.edu.
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Little, E. L. (1979). Four varietal transfers of United States trees [*Persea borbonia pubescens, Populus fremontii mesetae, Quercus turbinella ajoensis, Pinus aristata longaeva*]. *Phytologia.*


Figure 3.1: Historic map data for Great Basin bristlecone pine (1938-1993).
Figure 3.2: Pie chart of source tags assigned to mapped bristlecone pine stand polygons. 558 tags were assigned to 490 polygons, meaning that ~14% of stand polygons were derived from more than one source. 198 polygons (~40%) were tagged as “need additional verification” and were excluded from the HSM analysis.
Figure 3.3: Proportional point map showing the distribution of stands of Great Basin bristlecone pine (*Pinus longaeva* D. K. Bailey). Dashed lines enclose regional groupings of bristlecone pine populations: Utah High Plateaus (1), Central Great Basin (2), Southern Great Basin (3), Western Great Basin (4). Basemap data courtesy of Esri.
Figure 3.4: Notched box-and-whisker plot showing elevation distributions for randomly selected points within bristlecone pine stands in each regional grouping. Notches represent the confidence interval around the median (Chambers 2018). Asterisks denote significance level when comparing each group with other groups using the pairwise Wilcoxon rank sum test. *** denotes significance at the 0.01 level; “ns” means not significant.
Figure 3.5: Correlation heat map of the 10 selected variables. Cells in the heat map are colorized based on the Pearson’s $r$ value between variables.
Figure 3.6: Variable response curves for with-soil model.
Figure 3.7: Variable response curves for no-soil model.
Figure 3.8: Notched box-and-whisker plots of January mean dewpoint temperature (top) and February mean precipitation (bottom). Asterisks denote significance level when comparing each group with other groups using the pairwise Wilcoxon rank sum test. *** denotes significance at the 0.01 level; ** denotes significance at the 0.05 level; “ns” means not significant.
Figure 3.9: MaxEnt-derived composite HSM probability map for bristlecone pine. Bailey’s estimated outer extent of bristlecone pine distribution is shown as a dashed gray line (Bailey 1970).
Figure 3.10: Plot of predicted suitability for January mean dewpoint temperature versus February mean precipitation. White points represent the locations of MaxEnt bristlecone pine presence training data in environment space.
Table 3.1: MaxEnt environmental predictor variables.

<table>
<thead>
<tr>
<th>Environmental Predictor Variables</th>
<th>Number of variables</th>
<th>Variable code</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRISM elevation (m)</td>
<td>1</td>
<td>elevation</td>
</tr>
<tr>
<td>Slope (derived from PRISM elevation) (°)</td>
<td>1</td>
<td>slope</td>
</tr>
<tr>
<td>Aspect (derived from PRISM elevation) (°)</td>
<td>1</td>
<td>aspect</td>
</tr>
<tr>
<td>Topographic Ruggedness Index (derived from PRISM elevation)</td>
<td>1</td>
<td>tri</td>
</tr>
<tr>
<td>Annual total solar radiation (derived from PRISM elevation) (Wh/m²)</td>
<td>1</td>
<td>solar_radiation</td>
</tr>
<tr>
<td>PRISM 30 year normal monthly and annual precipitation (mm)</td>
<td>13</td>
<td>precip_XX</td>
</tr>
<tr>
<td>PRISM 30 year normal monthly and annual dewpoint temperature (°C)</td>
<td>13</td>
<td>dewpoint_XX</td>
</tr>
<tr>
<td>PRISM 30 year normal monthly and annual maximum temperature (°C)</td>
<td>13</td>
<td>tmax_XX</td>
</tr>
<tr>
<td>PRISM 30 year normal monthly and annual minimum temperature (°C)</td>
<td>13</td>
<td>tmin_XX</td>
</tr>
<tr>
<td>USDA/NRCS gSSURGO available water storage, 0-50 cm (cm/cm)</td>
<td>1</td>
<td>soil_aws</td>
</tr>
<tr>
<td>USDA/NRCS gSSURGO calcium carbonate (CaCO3), 0-50 cm (cm/cm)</td>
<td>1</td>
<td>soil_caco3</td>
</tr>
<tr>
<td>USDA/NRCS gSSURGO pH (1-to-1 water), 0-50 cm</td>
<td>1</td>
<td>soil_pH</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>60</td>
</tr>
</tbody>
</table>
Table 3.2: Variable permutation importance for MaxEnt model with soil data vs. model with no soil data.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Importance (with-soils model)</th>
<th>Importance (no-soils model)</th>
</tr>
</thead>
<tbody>
<tr>
<td>January Mean Dewpoint</td>
<td>76.5%</td>
<td>68.1%</td>
</tr>
<tr>
<td>February Precipitation</td>
<td>13.8%</td>
<td>14.2%</td>
</tr>
<tr>
<td>June Precipitation</td>
<td>2.0%</td>
<td>3.1%</td>
</tr>
<tr>
<td>July Mean Dewpoint</td>
<td>1.8%</td>
<td>6.4%</td>
</tr>
<tr>
<td>Topographic Ruggedness</td>
<td>1.6%</td>
<td>6.9%</td>
</tr>
<tr>
<td>Soil Available Water Storage</td>
<td>1.6%</td>
<td>N/A</td>
</tr>
<tr>
<td>Soil pH</td>
<td>0.9%</td>
<td>N/A</td>
</tr>
<tr>
<td>Soil CaCO₃ Concentration</td>
<td>0.9%</td>
<td>N/A</td>
</tr>
<tr>
<td>Total Solar Radiation</td>
<td>0.7%</td>
<td>0.4%</td>
</tr>
<tr>
<td>July Precipitation</td>
<td>0.3%</td>
<td>1.0%</td>
</tr>
</tbody>
</table>
Table 3.3: Protected status information for mapped stands of bristlecone pine. Spatial overlap between GAP 2 and GAP 3 classes results in the total exceeding 100%. Data courtesy of the USGS Protected Areas Database of the United States.

<table>
<thead>
<tr>
<th>GAP Status Code</th>
<th>Hectares</th>
<th>Percent of Total</th>
<th>GAP Code Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>54,242.9</td>
<td>54.3%</td>
<td>Managed for biodiversity - disturbance events proceed or are mimicked</td>
</tr>
<tr>
<td>2</td>
<td>27,000.2</td>
<td>27.1%</td>
<td>Managed for biodiversity - disturbance events suppressed</td>
</tr>
<tr>
<td>3</td>
<td>92,949.5</td>
<td>93.1%</td>
<td>Managed for multiple uses - subject to extractive (e.g. mining or logging) or OHV use</td>
</tr>
<tr>
<td>4</td>
<td>1,785.1</td>
<td>1.8%</td>
<td>No known mandate for biodiversity protection</td>
</tr>
</tbody>
</table>

**Total Mapped Habitat Area:** 99,810.3