Climate warming alters fuels across elevational gradients in Great Basin bristlecone pine-dominated sky island forests

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Abstract:

Little is known about fuel characteristics and dynamics in GBBP communities, and current monitoring programs inadequately quantify the surface and canopy fuels of this system. Using the Forest Inventory Analysis (FIA) plot variables of tree species, height, diameter at breast height (DBH), canopy base height (CBH), coarse (CWD) and fine (FWD) woody debris counts, and canopy fuels measurements, this paper examines the effects of climate-induced changes to fuel loading, fire hazard and risk on predicted changes in fire behavior and severity. Field transects were installed using FIA protocols along environmental gradients. Plots were located every 22 chains or ~440 meters along random transects on Mt. Washington in the Great Basin National Park (GBNP) and in the nearby Mt. Moriah Wilderness, NV. Additional plots were installed at Notch Peak (UT), Cave Mountain (NV), and Wheeler Peak (GBNP, NV). Linear regression showed that all classes of FWD decreased with elevation, and only 1000-hr fuels remained constant across elevational transects. This, combined with lower CBH and foliar moisture and increasing temperatures due to climate change, increases fire potential at the Great Basin bristlecone pine treeline, threatening the oldest individuals of this iconic species. New information about discontinuous fuels will aid in management of high elevation alpine treeline forests.

Keywords: Great Basin bristlecone pine; Wildland fuels; Climate change; Treeline forests

1. Introduction:

High elevation five needle pines are declining throughout western North America from climate warming, mountain pine beetle (*Dendroctonus ponderosae* Hopkins), white pine blister rust (*Cronartium ribicola*), and the alteration of naturally occurring fire regimes (Gibson et al., 2008). Climate change effects are especially acute in sky islands, the isolated mountains surrounded by valleys of the Great Basin, as warming temperatures alter tree community distribution and contribute to increased surface fuels. Changing air temperature and precipitation may interact with fire regimes to shorten times to ignition and lower temperatures at ignition from lower moisture content (Gill et al. 1978) of lower elevation populations. Great Basin bristlecone pine (*Pinus longaeva* Bailey) is a high elevation, five needle pine, located near treeline and grows in isolated sky islands of California, Nevada, and Utah. Great Basin bristlecone pine (GBBP) are mainly adapted to survive low-severity surface fires (Zavarin and Snajberk, 1973), however fire-scarred GBBP are found at lower elevations with fire tolerant ponderosa pine (Lanner, 1999). Climate induced changes to the fire regime will alter surface and canopy fuel loading, species composition, fire hazard and risk, and fire behavior and severity on GBBP forests (Schoennagel et

al., 2004). Additionally, the amount, arrangement, and continuity of GBBP fuels vary with elevation, community species composition, and time. Fuel loadings are strongly influenced by fire history and site characteristics providing a proxy for temperature change; however, these gradients have yet to be quantified.

1.1 Climate change and fire in treeline communities

GBBP are among the oldest organisms on earth. Their distribution is limited to the highest elevations (2700-3700m) in mountain ranges of the Great Basin of the western United States. Because populations are isolated, effects of a warming climate are projected to be particularly acute (Bower et al., 2011). Increasing temperatures are expected to result in pine mortality and introduction of invasive weeds and lower elevation conifers, consequently changing surface fuels composition (Flannigan et al., 2000; Gibson et al., 2008). Historically, fire was thought to be infrequent in GBBP communities at high-elevation sites because stands are open and productivity is low. When fires did occur at high elevations, they were usually small, low-severity surface fires (Bailey, 1970; Bradley et al., 1992). Moisture and climate have more influence on treeline stand dynamics than fire (Lanner, 1988, 1985). Early studies suggested that low tree density and sparse litter in the sub-alpine GBBP forests near treeline did not contain enough fuels to carry fire (Bradley et al., 1992; Lamarche, 1967; Lanner, 1988). At lower elevation sites, the role of historical fire regimes in dictating past stand characteristics and current distribution is not fully known, yet it is likely GBBP experienced a variable fire regime across gradients of site productivity and fuels connectivity. Fuels can be sufficient to carry fire in denser, low-elevation sites where GBBP occurs in mixed forests with limber pine (*Pinus flexilis* James) and/or Engelmann spruce (*Picea engelmannii* Parry) (Bidartondo et al., 2001). GBBP have a low resistance to fire, due to thin bark and low branches and retain their 2.5-3.5 cm needles up to 25-30 years (Bailey, 1970), increasing needle accumulation in crowns and on the surface under GBBP when compared to lower elevation pine species (Jenkins, 2011).

Limited studies of the closely related Rocky Mountain (RM) bristlecone pine (*Pinus aristata* Engelm.) and limber pine communities have found fire scars indicative of frequent, low intensity surface fires in sites that border grassy openings (Coop and Schoettle, 2011). Stand-replacing fire could be the primary disturbance regime for RM bristlecone pine, with a fire return interval of approximately 300 years (Baker, 1992). Evidence suggests that fire severity for RM bristlecone forest types varied through time and space (mixed-severity fire regime) as climate changed at centennial to millennial time scales (Coop and Schoettle, 2011). Additionally, frequent fire presumably played an important role in restricting RM

bristlecone pine at lower elevations in pre-settlement times (Coop and Schoettle, 2011). Physical limitations on forest structure, such as age and density, affect the accumulation of surface fuels and crown fuels. For example, a study from boreal forests in Finland indicates a site's disturbance history is the determining factor for fuels quantity and decay class distribution (Aakala, 2010). While Baker (1992) found that stand-replacing fires in RM bristlecone pine initiated regeneration, little is known of post-fire succession in mixed-conifer forests containing GBBP. It is important to understand the fire history of GBBP/limber pine/Engelmann spruce and other montane forests in the Great Basin to develop appropriate adaptation strategies for managing these systems with a warming climate.

Most wildfire and fuel models were designed for vegetation types that burn frequently, are characterized by continuous surface fuels, or are of interest to fire management (Rothermel 1972). Thus, discontinuous fuel associated with GBBP are not represented by traditional fuel models, and might be more similar to heterogeneous systems like piñon juniper woodlands. Extensive characterization of piñon juniper woodlands have examined the sparse surface fuels and discontinuous tree canopies that curtail fire spread under low wind conditions (Floyd et al., 2008; Huffman et al., 2009; Miller et al., 2000; Romme et al., 2009). One physics-based fire model was applied to piñon juniper woodlands and results suggest sparse fuels in heterogeneous forests propagate fire because dead needles on the ground provide surface fuels, and allow increased winds through the canopy and sub-canopy (Linn et al., 2013). A fire behavior study in arid vegetation communities in Australia developed models to predict the sustainability of fire spread, fire type (surface or crown), rate of spread and flame height in a discontinuous fuel type (Cruz et al., 2013). They found that sustainability of fire spread was a function of litter fuel moisture with wind speed having a secondary but still significant effect. The continuity of fine fuels was also significant. Initiation of crown fire was primarily determined by wind speed. Cruz et al. (2013) presented the need to find threshold conditions for sustained fire propagation based on wind speed and fine fuel moisture content. While fire spread models could be helpful for assessing fuel changes in GBBP, validation data are unavailable, and therefore are outside the scope of this study.

1.2 Environmental gradients

Environmental gradients relate factors such as elevation, temperature, water availability, light, and soil nutrients, or their closely correlated surrogates. Forest composition usually changes along environmental gradients in predictable ways (Peet, 2000). For example, elevation is often a surrogate variable which approximates changes in temperature and moisture (Peet, 2000). At lower elevations, moisture and temperature may allow for a forest to reach full crown closure, although a mid-elevation site might not

reach full crown closure. At upper alpine treeline (the edge of the habitat at which trees are capable of growing, found at high elevations and in frigid environments) tree density and decomposition is typically limited by a short growing season. However, high severity disturbances are rare (low frequency and high intensity) allowing for large tree size diversity (Miller 1997).

1.3 Fuels composition across environmental gradients

Understanding how fuels structure and composition varies across environmental gradients in Great Basin sky islands is necessary to predict how fire frequency and intensity may change at high elevations with a warming climate. Studies that have modeled severity and length of forest fire season employing general circulation models (GCMs) have estimated that seasonal severity ratings may increase by 10–50% over most of North America, (Flannigan et al., 2000) suggesting that fire is an predominate agent of change and has the potential to overshadow direct effects of climate change on species distribution and migration. Our best tool at estimating the potential fire intensity of vegetation communities, or the amount of energy released during a fire, is fine and coarse woody debris surveys (Brown, 1974), yet fuels vary greatly depending on topography, meteorological influences, fuel type and characteristics of previous disturbance. Warming temperatures, lower humidity, and lower fuel moisture increase the potential for high severity fires (Abatzoglou and Williams, 2016; Littell et al., 2016). Research is needed that will help managers plan for transitions to new conditions and habitats, manage migrations along expected climatic gradients, prepare for higher-elevation insect and disease outbreaks, and anticipate forest mortality events and altered fire regimes (Millar et al., 2007).

The objective of this paper is to quantify spatially discontinuous fuel structure across changing environmental gradients in GBBP stands. This information is useful to understand how climate change affects the fire regime and GBBP health and abundance. We assume that elevation is a surrogate for warming air temperatures. To understand how global climate change will alter wildland fuels, we quantified differences in GBBP fuels and how fuels differ across elevation gradients. We compare the relationship between forest structure and environmental gradients to predict changes in surface and canopy fuels of GBBP communities with increasing temperatures. A comprehensive stand assessment and fuel survey of this iconic species provides a foundation upon which management decisions and dialogue can be based. Consequently, this research is valuable for forest and fire planning and management, as well as prioritization and design of restoration efforts and climate change adaptation strategies.

2. Study Site:

The geographic extent of sampling was limited to sky islands of the Great Basin of Nevada and western Utah. Sample sites were at Washington Peak, NV (38.90°, -114.31°, 3,475 m), Wheeler Peak, NV (39.00°, -114.30°, 3,415 m), and Mt. Moriah, NV (39.29°, -114.20°, 3,300 m). Additional individual plots were installed at Cave Mountain, NV (39.16°, -114.61°, 3,230 m), and Notch Peak, UT (39.14°, -113.40°, 2,800 m).

The Great Basin of California, Nevada, and Utah has an arid climate characterized by Basin and Range topography, with numerous high mountain peaks and low intermountain valleys. Upper treeline is approximately 3,300 m and lower treeline is approximately 2,100 m (Thompson and Mead, 1982). Mountains and basins create steep environmental gradients, which greatly influence the composition and structure of vegetative communities (Peet, 2000). As mentioned, fires are infrequent in high elevation GBBP forest due to sparse fuels (Figure 1C). Yet this is not the case at the lower treeline of GBBP communities, which are dominated with shrubs and other forest species (Figure 1A). The mid elevation sites are typical of mixed conifer forests (Figure 1B).

162 Figure 1. Fuels complexes of Great Basin bristlecone pine (GBBP) communities. (A) Lower elevation communities have higher
 163 fuels from denser vegetation and shrubs. (B) Mid elevations have less fuels than lower elevations, but retain considerable 1 hr,
 164 10 hr, and 100 hr fuels. (C) Fuels in the highest elevations near treeline are mostly litter and duff under individual trees.

3. Methods:

3.1. FIA data and sampling

Data were from a combination of US Forest Service Forest Inventory and Analysis (FIA) program plots (O'Connell et al., 2015) that contained GBBP and additional study sites that were selected using expertise from local US Forest Service and National Park Service personnel. The FIA variables collected at each plot were tree species, height, diameter at breast height (DBH), canopy base height (CBH - the vertical distance between the surface fuels and live canopy fuels), seedling and sampling counts, and surface fuels measurements. All 34 plots that contained GBBP in the FIA database from Utah, Nevada and California were examined for forest structure and fuel loading. The FIA program uses a three phase sampling design covering all public and private land in the United States (Bechtold and Patterson, 2005; O'Connell et al., 2015). In Phase 1, remote sensing and aerial photography classify forested lands, percent tree cover, and forest use (Bechtold and Patterson, 2005). In Phase 2, four 7.3 m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with subplot 1 in the center and subplots 2, 3, and 4 at azimuths of 0°, 120°, and 240°, respectively, from the center of subplot 1 measure tree species, size, and density (O'Connell et al., 2015) (Figure S1-B). Phase 3 measurements assess forest health such as tree crown, soil, and lichen conditions, and down woody material (Bechtold and Patterson, 2005; Woodall and Monleon, 2010) and are not yet available in much of the U.S.

Due to the relatively small sample of FIA plots with GBBP, 76 additional plots using FIA Phase 2 protocols were installed along elevational gradients to assess changes in GBBP communities (total plots = 110). From the lowest elevation plot (2827 m), subsequent plot centers were located by pacing approximately 400 m up the fall line (mean distance between plots from GIS = 418 m) (Figure S1-A). If no trees were located at the 400 m interval, this point was skipped. Survey plots are fixed radius plots, which were modified FIA plots (Figure S1-B), each containing four subplots. Every plot contained at least one GBBP. Other species included limber pine (*Pinus flexilis* James), Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* var. *latifolia* Nutt.), Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Beissn), aspen (*Populus tremuloides* Michx.), piñon pine (*Pinus edulis* Engelm.), juniper (*Juniperus spp.*), mountain mahogany (*Cercocarpus ledifolius*), and ponderosa pine (*Pinus ponderosa* Douglas).

3.2. Fuels sampling

We quantified fuel loading, specifically the dry weight biomass of fuel per unit area (kg m^{-2}) of four major surface fuel components: litter (freshly fallen non-woody material which includes leaves and

cones), duff (partially decomposed biomass whose origins cannot be determined), fine woody debris (FWD; 0–7.6 cm diameter), and coarse woody debris (CWD, >7.6 cm diameter; commonly referred to as logs or 1000 hr fuels). Estimates of CWD biomass are often used for large-scale fire/fuel and carbon monitoring efforts while FWD comprise a substantial portion of fuel loadings and, to a large extent, determine fire behavior (Burgan and Rothermel, 1984). Down woody material, which includes twigs, branches, stems, and tree boles in and above the litter was sampled using Brown’s method (also called the line-intersect or planar-intersect method) (Brown, 1974). This transect method is used by FIA and Fire Ecology Assessment Tool/Fire Effects Monitoring and Inventory System (FEAT/FIREMON) Integrated (FFI) programs (Lutes et al., 2009). Brown’s method samples both fine and coarse woody material by diameter class by counting and measuring the size of all woody pieces in the vertical sampling plane. The diameter classes correspond to the 1 hr (<1cm), 10 hr (1-2.5cm), 100 hr (2.5-7.6cm), and 1,000 hr (>7.6cm) fuel classes used in the U.S. National Fire Danger Rating System (Deeming et al., 1977). Tallies of 1 hr and 10 hr fuels were made along the distal 1.83 m of the fuels transects, while 100 hr fuels were made on 3.05 m, and 1000 hr fuels were made on 7.32 m of the transect (Figure S1-B). Volume and weight were calculated by applying estimates of the woody material’s specific gravity following Brown (1982).

3.3. Tree-specific fuels sampling

Jenkins (2011) described the distribution of surface and aerial fuels under whitebark pine (*Pinus albicaulis* Engelm.) forests which are similar to other alpine treeline five-needle pine forests. He defined the pine fuel zone as fuels lying within the drip line of a tree and the non-pine fuel matrix as the area between adjacent trees. While installing our fuels transects, we observed similar surface and aerial fuel distribution in GBBP communities as whitebark pine forests (Figure 1C). In high elevation GBBP stands, we expect that fuel influence on surface fire behavior will be a function of the distribution of pine fuel zone and non-pine fuel matrix. The pine fuel zone will increase as stand density increases and may compose 100% of the surface fuel matrix in very dense stands (Jenkins, 2011). To quantify this unique patchy and discontinuous fuel complex, we measured litter and duff of 105 trees in the four cardinal directions (NSEW) under three trees from each plot (Figure 2). From the plot center, the closest GBBP tree within the northern third (300°-60°), south-eastern third (60°-180°), and south-western third (180°-300°) were selected for sampling. In each cardinal direction away from the sample tree bole, litter and duff depth were measured at 60 cm intervals until the end of the tree crown (Figure 2).

Figure 2 Sample design for individual tree surface fuels. From the plot center (inset) the closest GBBP tree within the northern third (300° - 60°), south-eastern third (60° - 180°), and south-western third (180° - 300°) of plots were selected for sampling. Litter and duff were measured in the four cardinal directions (NSEW) under the three trees. In each cardinal transect, litter and duff depth were measured at 60cm intervals until the end of the tree crown was reached.

3.4. Fuels cover and continuity

While there is a large shrub component (up to 90%) in some of the lowest elevation occurrences of GBBP (Figure 1A), shrubs are rare or absent in most stands. Fuels cover is important because it describes the size of the fuel gaps that limit fire propagation. We assessed the relative amounts of fuels continuity by utilizing Landsat satellite images. The August 24, 2012 Landsat-7 Enhanced Thematic Mapper (ETM+) image was chosen because it was the cloud-free image closest to the dates of field sampling. The spectral indices Normalized Difference Vegetation Index (NDVI), Brightness, and Greenness estimate fuels cover

and continuity. NDVI is a graphical indicator to assess whether a pixel contains live green vegetation. It is based on the ratio of the red and near-infrared (NIR) spectral values, computed as $NDVI = (NIR-RED) / (NIR+RED)$ (Xavier, 2004). Brightness is an estimate of bright or dark soil values, and greenness is a measure of green vegetation. Brightness and Greenness are the first two components of a tasselled cap transformation (Huang, 2002), a method for enhancing spectral information content of Landsat TM data. Landsat pixels represent a uniform 30 by 30 m spectral sample, a larger spatial extent than our field plots, which gives a broader overview of fuels continuity. We intersected field plots with the calculated indices of the Landsat pixel. When our field plots were at the margins of pixels, we averaged the values for all pixels that intersected a plot.

3.5. Canopy fuels

Canopy fuels are the main fuel layer supporting crown fire spread (Cruz et al., 2003). Canopy base height (CBH) is the vertical distance between the surface fuels and live canopy fuels. CBH influences the likelihood of crown fire initiation and the interaction between combustion of surface and canopy fuels (Cruz et al., 2003). We collected CBH at 16 plots and used this and other forest structure variables such as DBH and tree height, to calculate several variables to assess the canopy structure and crown fire potential of GBBP stands. Canopy length (CL), the average length of the canopy fuel stratum, was calculated by subtracting CBH from tree height and averaging it over the stand. Canopy fuel load (CFL) in $kg\ m^{-2}$ was estimated using the allometric foliage weight equations from Brown (1978). As mentioned in Cruz et al. (2003), no published allometric equations were found for GBBP, so whitebark pine was used as a surrogate based on similarity in the tree crown structure. Canopy bulk density (CBD) in $kg\ m^{-3}$, is a measure of how closely canopy fuels are packed. It reflects the likelihood that fire can move through the forest and was calculated as CFL/CL (Cruz et al., 2003). Stand density (trees ha^{-1}) was calculated using FIA tree expansion factors (US Department of Agriculture, 2007) as an estimate for inter-crown distance (ICD). ICD is the distance from one tree crown to an adjacent tree crown and is less in high-elevation five-needle pine stands compared to stands of other pine species with similar basal areas (Jenkins, 2011).

3.6. Foliar moisture content

To assess live foliar moisture content (FMC), needles were randomly selected from four GBBP trees at three different elevations (low = 2640 m, mid = 2910 m, high = 3160 m) during the first week of July, August, and September, 2012 ($n = 36$). Approximately 20 g of live needles from each sample were

weighed to the nearest 0.01 g and then oven-dried at 105° C for 48 hours and reweighed to obtain a dry weight (Matthews, 2010). Samples were kept frozen until processed. FMC was computed as the percentage of the oven-dry weight to dry foliage weight.

3.7 Data analysis and statistics

Forest floor CWD and FWD transect counts were converted to weight of fuel per unit area (kg m^{-2}) following Brown (1982). Litter and duff weight per unit area (kg m^{-2}) was estimated from depth measurements by using the equation developed for foxtail pine (*Pinus balfouriana* Grev. et Balf.), a close relative to GBBP (van Wagtenonk et al. 1998). Regression coefficients via generalized linear models (GLM) were developed relating forest floor mass to elevation. To characterize surface fuels dissimilarity along environmental gradients, a non-metric multi-dimensional scaling (NMDS) ordination based on a matrix of Euclidean dissimilarities was calculated on FWD, CWD, litter and duff amounts. NMDS collapses information from multiple dimensions to fewer dimensions, so that data can be visualized and interpreted (McCune et al., 2002) (Figure S3 in supplemental information). Stand densities in trees hectare^{-1} were calculated for each plot using the tree expansion factors (coefficient used to scale each tree on a plot to a per-area basis) in the FIA user manual (O'Connell et al., 2015). Regression coefficients were also calculated for stand density (trees ha^{-1}) and height to live crown for the same elevational gradients. Post hoc mean comparisons using Tukey-Kramer tests were used when a significant difference among elevation class was identified in canopy fuels. A generalized linear model (GLM) with a negative binomial link was fit to the litter and duff measurements made in the four cardinal directions under the sampled individual trees. We used the negative binomial distribution because data with many zero values cause over-dispersion, or greater variability than would be expected. GLMs are mathematical extensions of linear models that do not force data into unnatural scales, and thereby allow for non-linearity and non-constant variance structures in the data (Hastie and Tibshirani, 1990). The negative binomial distribution generates realistic heterogeneity representative of spatial clustering of individuals and other small-scale processes (Bolker, 2008). All statistics were completed using R statistical software (R Development Core Team, 2015).

4. Results:

4.1. FWD and CWD fuels loading

The mean weight of fuel per unit area (kg m^{-2}) for low (2700–3000m), mid (3000–3300m), and high (3300–3500m) elevation classes are reported in Table 1. As elevation increases, FWD and CWD decrease, limiting the surface fuels available to carry a fire. Separate regression coefficients were calculated for each FWD and CWD class (Table 2, Figure 3) by elevation. All slope coefficients were significant ($p < 0.001$) except for the largest class (1000-hr fuels). All FWD classes, litter, and duff are highly correlated. CWD is not strongly correlated to any other classes (Figure S2). NMDS ordination of the fuels classes is characterized by high linear fit ($R^2 = 0.99$) and a low stress value (0.058) indicating a good representation of all variables in two dimensions. The ordination was highly correlated with elevation and slope indicating that all measurements of fuels (except CWD) change with elevation (Figure S3).

Figure 3 Coarse and fine woody debris (CWD and FWD), litter and duff in kg m⁻² versus elevation in Great Basin bristlecone pine communities. Regression coefficients for all fuel sizes except 1000-hr fuels were significant ($p < 0.001$) including litter and duff. Shaded areas are the 95% confidence intervals.

Table 1

Mean weight of fuel per unit area (kg m⁻²) and standard error (kg m⁻²) for fine woody debris (FWD), coarse woody debris (CWD), and litter and duff fuel at low, mid and high elevations. (Litter and duff depth measured in mm in parenthesis).

Elevation		1hr	10hr	100hr	1000hr	Litter (mm)	Duff (mm)
Low	Mean	0.12	0.21	0.49	3.94	0.85 (9.6)	18.6 (7.4)
	SE	0.02	0.03	0.08	0.96	0.11 (1.2)	4.2 (1.6)
Mid		0.04	0.10	0.32	3.79	0.62 (7.1)	12.0 (4.8)

	SE	0.01	0.02	0.06	0.90	0.07 (0.7)	1.7 (0.7)
High	Mean	0.03	0.08	0.15	2.77	0.43 (4.8)	7.2 (2.9)
	SE	0.01	0.02	0.04	0.79	0.08 (0.9)	1.9 (0.7)
All	Mean	0.06	0.12	0.31	3.50	0.61 (6.9)	12.1 (4.8)
	SE	0.01	0.01	0.04	0.53	0.05 (0.6)	1.4 (0.6)

Table 2

Regression coefficients of fuel per unit area (kg m^{-2}) weight for FWD, CWD, litter and duff fuel classes by elevation. N.S. = not significant.

Fuel class	Slope	Intercept	<i>p</i> -value	Sig-level	R^2
1-hr	-0.0002	0.696	<0.001	***	0.301
10-hr	-0.0003	1.116	<0.001	***	0.182
100-hr	-0.0007	2.671	<0.001	***	0.016
1000-hr	N.S.	N.S.	N.S.	N.S.	
litter	-0.0010	3.75	<0.001	***	0.161
duff	-0.0010	3.71	<0.001	***	0.170

4.2. Stand density, fuels cover, and community composition

GBBP stand density (trees ha^{-1}) also significantly decreased with elevation (Figure 4). Stand density is an important contributor to the continuity of surface and aerial fuels (Cruz et al., 2003). Only 13% of variability is explained by the regression model ($R^2 = 0.133$), likely due to only examining stands that have at least one GBBP in the plot. If nearby forest stands at mid elevations (2600-3000 m) were included, there would likely be higher stand densities. Stand density index (SDI) (Reineke, 1933; Shaw, 2000), describes density that is sensitive to the diameter of the trees, and was calculated for all trees and for each plot. The SDI was not significant, however SDI is best used as a summary variable in even aged stands (Shaw, 2000). SDI is less applicable to long lived GBBP communities, in which very old trees may have a relatively large DBH with little live crown compared to more typical timber producing conifer species. The number of species that make up forest communities also decreases with elevation, from up to 8 dominate tree species at lower elevations to mostly GBBP, limber pine and Engelmann spruce at upper alpine treeline. At lower and mid elevations, GBBP makes up only a minor component (7-14%) of the mixed forest community, growing with other lower elevation tree species including white and subalpine fir, piñon/juniper species, ponderosa pine and Douglas-fir (Figure 4).

Figure 4 Stand density (trees hectare⁻¹) versus elevation. Points are density at each individual plot with actual elevation, bar-graph is species density parsed into 100 m bins.

More important than fuel loads are the size of the fuel gaps that limit fire propagation. The results from the Landsat indices of vegetation cover reiterate the findings from CWD and FWD sampling. As elevation increases, NDVI and Greenness decrease, indicating less vegetation and fuels available to carry a surface fire. Conversely, as elevation increases, Brightness (a measure of exposed soil) also increases, indicating larger gaps between trees, or less continuous fuel cover (Figure 5).

Figure 5 NDVI, Brightness, and Greenness (Landsat-7 ETM+, August 24, 2012) versus elevation in Great Basin bristlecone pine communities. Regression coefficients were all significant ($p < 0.001$). Shaded areas are the 95% confidence intervals.

4.3. Canopy fuels

Canopy base height declined significantly with elevation ($p < 0.001$, $R^2 = 0.74$) (Figure 6). As elevation increased, the branches of GBBP were closer to the ground, which could facilitate fire into the crown of the trees. All crown fuels metrics vary by elevation (Table 3). Tree height, CBH and crown length (CL) decreased with increasing elevation, while available crown fuel load (CFL) and crown bulk density (CBD) increase with elevation (Table 3).

Figure 6 Great Basin bristlecone pine crown base height (CBH) (the distance from the ground to the first tree branches) versus elevation. Shaded areas are the 95% confidence intervals.

Table 3

Great Basin bristlecone pine canopy fuels: tree height (Ht), canopy base height (CBH), diameter at breast height (DBH), Canopy length (CL), Canopy fuel load (CFL), and Canopy bulk density (CBD) average for low, mid and high elevations classes. Different lower case letters (a, b, c) indicate significant differences between elevation classes ($\alpha = 0.05$).

Elevation	Ht (m)	CBH (m)	DBH (cm)	CL (m)	CFL (kg m^{-2})	CBD (kg m^{-3})
Low	12.9 ^a	0.9 ^a	37.3 ^a	12.0 ^a	0.36 ^a	0.03 ^a
Mid	12.0 ^a	0.9 ^a	54.3 ^b	11.0 ^a	1.12 ^b	0.09 ^a
High	7.5 ^b	0.6 ^b	74.6 ^c	6.9 ^b	1.84 ^b	0.22 ^b

Foliar moisture content (FMC) at the three elevations sampled also significantly decreased at the upper elevation site (ANOVA with $p < 0.001$) while the mid and low sites were not significantly different (Figure 7). FMC varied significantly by month. September had the highest FMC and July the lowest (Figure 7) with values likely influenced by monsoonal precipitation events.

Figure 7 Live foliar moisture content (FMC) collected from Great Basin bristlecone pines at low, mid, and high elevations.

4.4. Individual tree fuel loading

Measurements of litter and duff in the four cardinal directions (NSEW) directly beneath GBBP trees showed higher litter and duff fuel loads near the bole of the tree (Figure 2, Figure S4, and Figure 8 Fitted curve of regression model of combined litter and duff around the bole of a tree. Fitted curves in each cardinal direction correspond to logistic regressions with a negative binomial link.). A negative binomial model was fit to the combined litter and duff for each cardinal direction (Figure S4). The fitted curve for each cardinal direction was draped on a surface (mm of litter and duff) around the tree to visualize fuel loads underneath an individual tree (Figure 8). While there might not be sufficient fuels between individual trees to carry a surface fire, nearly each individual tree had a pocket of litter and duff directly beneath it.

Figure 8 Fitted curve of regression model of combined litter and duff around the bole of a tree. Fitted curves in each cardinal direction correspond to logistic regressions with a negative binomial link. (Vertical exaggeration = 300x)

6. Discussion:

The sky islands of the Great Basin are predicted to experience a 2-4 °C increase in March-April mean temperature, a 60-100% decrease in mean April snow water equivalent (SWE), yet possibly experience a 10-20% increase in October-April precipitation by the end of the 21st century (Scalzitti et al., 2016). While there is uncertainty in how climate change will affect mountain regions of the Great Basin, extensive research has modelled probable affects. Salzer et al. (2014) used tree ring chronologies to show that GBBP have a positive growth-response to increasing temperature at elevations 60–80 vertical meters below treeline in the White Mountains of California. Chronologies from 80 m and farther below treeline are sensitive to precipitation change (similar to lower elevation chronologies) and do not correlate strongly with temperature (Salzer et al., 2014). Using dynamical downscaling and applying a mean

monthly perturbation to boundary conditions to simulate future climate, the role of temperature and precipitation in spring snowpack variability has been modeled throughout the western U.S. (Scalzitti et al. 2016, IAP-Climate Change Assessment). Assuming that GBBP treeline communities are temperature limited, it is reasonable to expect the stands to more closely approximate the conditions that are currently at the mid and low elevations (historically 2-4 °C warmer on average). Our research indicates that if climate warming changes fuel conditions, then the frequency of fire in GBBP systems at low and mid elevations could increase where stands are typically denser and surface fuel is greatest. While rare, wild fires such as The Carpenter 1 fire in southern Nevada (July, 2013; 36.25, -115.69) and the Phillips Fire in Great Basin National Park, (September, 2000; 38.90, -114.31) that started in lower elevation fuel types and moved through the crowns of GBBPs with the aid of extreme fire weather, could become more likely. The accumulation of fuels in lower elevation vegetation communities have proven to amplify the effects of fire in the high elevation/low fire return interval systems.

Warmer temperatures will likely increase the number of days in each fire season that FWD will be at its driest. FWD are fast drying fuels, which greatly affect ignition and spread of surface fires; CWD responds to changes in moisture and temperatures over months and affect the latency of wildfires more than the rate of spread. FWD (1 hr, 10 hr, and 100 hr fuels) for all fuel sizes decreased with elevation in GBBP transects (Figure 4), although this pattern did not hold for CWD (1000 hr fuels). Litter depth in GBBP sites ranged from 12 mm at the lower elevation sites to 5 mm at treeline sites while duff depth ranged from 10 mm to 3 mm, respectively. While the trend of decreasing surface fuels with elevation is consistent across most fuels types, there is considerable variation across the sample sites (R^2 values ranged from 0.15 to 0.30). Disparities could be from the influence of other species, such as Engelmann spruce and limber pine, that contribute to stand structure, composition, and fuels. When surface fuels are contiguous, flames easily advance across the landscape, conversely, surface fires do not spread with discontinuous fuels, such as those in this study's high elevation sites. This confirms previous observations that fires in low-density stands near treeline were likely rare and small, due to the scarcity and discontinuity of fuels (Bailey 1970). Litter and duff depths found in other Great Basin fuels plots ranged from mean depths of 20 mm and 6 mm, respectively, at the Clover Mountains dominated by ponderosa pine, to 12 and 3 mm, respectively, at Mount Irish dominated by piñon juniper (Cheek et al., 2012). Yet we measured litter fuel depths closer to 35 to 50 mm, which consider the high amounts of litter fuels that are directly beneath individual trees (Figure S4 and Figure 9). Litter fuel depths decrease to values closer to the FIA measurements at about 3 meters from any individual tree. Combined with patches of shrubs and prostrate spruce thickets, fire susceptibility may be higher than indicated by FIA measurements since FIA plot centers are usually not located directly beneath trees. If fire starts in low elevations and extreme

fire weather exists, the unique patchy fuels found at mid and high elevations could make upper elevations more susceptible to fire. This is not apparent from standard fuel models developed for lower elevation fuel types.

Drier fuels at all elevations increases fire hazard. Additionally, for GBBP, CFL and CBD increase at higher elevations (Table 3), resulting in denser crown fuels within individual trees. Crown fires likely are dependent upon weather, especially atmospheric stability and wind speed. Crown fire prediction models use canopy bulk density (CBD) as the index of canopy fuel characteristics to determine whether fire will initiate and spread either vertically or horizontally through a forest canopy. CBH is another important factor in predicting crown fires (Scott, 2006). CBH is less than 50 cm at the highest elevations of GBBP (Figure 6 *Great Basin bristlecone pine crown base height (CBH) (the distance from the ground to the first tree branches) versus elevation.*), and live FMC (Figure 7) decreased from 80-87% at low elevations to 71-78% at the highest elevations. This suggests that while the likelihood of a surface fire decreases with elevation, the potential for crown fire and spotting is still present. Thus, the greatest fire threat to GBBP growing near treeline is from fires ignited in the mixed conifer forests below and progressing as crown fires into pure GBBP stands during which threshold wind conditions and fuel moistures are exceeded. More research is needed to identify wind speed and fuel moisture threshold conditions that would sustain fire propagation.

In other Great Basin forest types, CBD at Mount Irish (37.64, -115.40) ranged from 0.04 to 0.18 kg m⁻³ in juniper types, to 0.02 to 0.23 kg m⁻³ at the Clover Mountains (37.40, -114.33) (Cheek et al., 2012), indicating higher severity potential crown fire behavior at low elevations. Crown fires normally occur because of steep topography, high wind speeds (Wolf, 2003), and canopy bulk density (CBD) of 0.05 kg m⁻³ or more (van Wagendonk 2006). While the samples of GBBP at the low elevations had relatively low CBD (0.03 to 0.09 kg m⁻³, Table 3), these trees are co-located with other tree species (piñon, juniper, and ponderosa pine) so that CBD and ICD sometimes support crown fire and high surface fuel loads. The composition and structure of the adjacent forests at the lower elevation margins of GBBP varied greatly and often have a large shrub component. A thorough inventory of these lower margins is necessary to predict the hazard to GBBP. GBBP pines at the highest elevations had a mean CBD of 0.22 kg m⁻³ in the areas with the lowest CBH, while the ICD at these elevations becomes too large to carry a crown fire. While CBH and FMC decrease in GBBP at higher elevations (Figure 7 and Figure 8), the decreased stand density (Figure 5), which likely reduces ICD (Jenkins, 2011), reduces the probability of a moving crown fire. The higher CBD values at high elevations may not be representative however, because many of these ancient trees become krumholtz (twisted and deformed) with only a portion of the tree remaining alive, which means that the allometric equation derived for whitebark pine may not be applicable to these trees.

Fires that spread beyond individual trees are dependent on increasing fuel types and amounts from climate warming and introduction of lower elevation species.

For decades, fire suppression has contributed to forest stand-level effects such as: increases in woody fuel loading, canopy cover, vertical fuel distribution, canopy stratum, and fuel continuity, which in turn leads to increased fire intensity, severity, and size as fuels increase and become more connected. Interestingly however, fire suppression, which produced unnatural fuel accumulations in most locations in the American West, was not applied to high elevation pine forests where GBBP are located (Schoennagel et al., 2004). Regardless, quantifying GBBP fuels is important for forest management. Large, severe fires have sizable economic implications when considering the costs of fire suppression, loss of valuable timber, poor air quality, soil erosion, as well as impacts on downstream water quality. Although stand replacing fires are rare, the more precise data and analysis presented here identifies areas that are the most susceptible to fire. Management of GBBP stands might be novel or unprecedented, but fuels management could have large impacts on preventing stand replacing fire in these highly prized communities. How GBBP communities regenerate is also of great interest. Post-fire establishment may be favored in certain mixed conifer ecotones, lower-elevation limestone soils, and other sites that are marginally productive for other conifer species but relatively good for GBBPs.

Considering the recent ecological impacts of mountain pine beetle epidemics and blister rust in whitebark and limber pines, a major component of treeline in the northern Rocky Mountains, more attention to insect and disease epidemics in GBBP communities is needed. Recently, tree chemistry research showed that bark beetles are not attracted to GBBP (Gray et al., 2015). Tomback and Resler (2007) examined the cascading ecological effects of losing treeline whitebark pine and expected changes in landscape vegetation patterns in the context of climate change. They speculate that exotic pathogens could potentially confound predictions of treeline responses to global warming in many geographic regions and other communities (Tomback and Resler, 2007). Resistance of GBBP to blister rust is unknown, yet laboratory experiments suggest GBBP lack genetic resistance (Kinloch Jr and Dupper, 2002). More research is needed on these topics.

7. Management Implications:

Overall, our knowledge of GBBP ecosystems is poorly understood. For example, GBBP longevity still remains a mystery, but improved understanding may be beneficial for creating appropriate adaptation strategies to manage this species with a changing climate. Historically, GBBP pine stands experienced

low to high severity fires, and fuels structures changed considerably across elevational gradients. In low elevation, mixed species stands, fuels are often heavy and in close proximity to anthropogenic ignition sources. Yet at high elevations, GBBP typically grow on limestone outcroppings that provide little or no surface fuels to propagate a wildfire. In other words, stands are non-uniform so it is difficult to make blanket fire response predictions. In the absence of fire, stands are likely to exhibit gradual infilling by other local conifer, shade-tolerant tree species or invasive weed species with climate warming. Tree species that occur at the high-elevations and xeric margins provide ecological services that likely cannot be replaced. Climate change may manifest as warming temperatures with more days of extreme fire weather and reduced snowpack. Management in response to these threats to GBBP must balance a range of concerns and may include both the application and prevention of fire. How should fuels distribution be spread across the landscape? Should there be diversity at the stand level or in a mosaic of different patches and age distributions? How will we manage this with respect to climate change? Finally, how might management tools, including fire (or the lack thereof), be best used to encourage such conditions? Applied research is needed to gain insight into these questions. More research and improved fire models for patchy fuels are needed to predict and identify appropriate fire management to protect valuable stands, promote regeneration, and diversify age classes.

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