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Range-wide conservation of *Pinus aristata*: a genetic collection with ecological context for proactive management today and resources for tomorrow

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Abstract Tree species are highly vulnerable to anthropogenic environmental change, and are increasingly being challenged by non-native pests and climate change. Rocky Mountain bristlecone pines are long-lived, exhibit delayed maturation, have low genetic diversity, and inhabit cold, high-elevation environments. They are threatened by the non-native disease white pine blister rust, warming temperatures, changing precipitation patterns, and altered disturbance regimes. The goal of this work was to (1) sample the range-wide genetic diversity of bristlecone pine for ex situ seed and tissue collections and research before the populations are impacted, (2) assess the health and ecological conditions of the species across its geographic range (61 stands) to provide a baseline by which to evaluate future changes, and (3) assess relationships between stand and regeneration characteristics and topographic, geographic, and climatic factors to identify vulnerabilities and proactive management interventions to increase population resilience. Local variation in topoclimate was strongly related to stand structure, composition, health, and regeneration. Bristlecone pine currently showed only minor impacts from insects and pathogens, but relationships between cone production and regeneration with climate variables suggest vulnerabilities to projected climate change. Both cone production and seedling regeneration were also linked to stand structure and ground cover that provide opportunities for proactive in situ management to increase population size to mitigate potential future climate- and pathogen-driven declines. These efforts represent the first proactive coordinated range-wide genetic collection design and forest health assessment for a threatened, but not yet impacted, tree species and offers a model for other species at risk.

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Introduction

Globally, tree species are increasingly threatened by anthropogenic environmental change (Oldfield et al. 1998), including overexploitation and deforestation (Aljos et al. 1993; Oldfield et al. 1998), climate change (McKenney et al. 2007; McDowell and Allen 2015), native and introduced insects and pathogens (e.g. Hansen et al. 2000; McDonald and Hoff 2001), and altered disturbance regimes (e.g. Williams et al. 1999; Savage and Mast 2005). Trees are keystone organisms in ecological systems and their losses impart profound consequences for biological diversity and ecosystem function. The speed that these threats can impact forest ecosystems requires rapid adaptive approaches to reduce vulnerabilities and mitigate impacts at relevant temporal and spatial scales (Jacobs et al. 2015; Stanturf 2015). Once demographic thresholds are crossed ecosystem recovery becomes limited, necessitating active intervention to restore ecosystem function (Jacobs et al. 2015; Nunez-Mir et al. 2015; Stanturf 2015). Unfortunately, the timely development and implementation of appropriate management and conservation strategies is often constrained by both insufficient scientific understanding and reactive, rather than proactive, management responses. These deficiencies are particularly acute for large, long-lived organisms with delayed maturity, inherently protracted population dynamics, and slow rates of migration—the rate at which a forest can be lost from a landscape is many orders of magnitude faster than the rate at which a forest might be re-established.

Rapid directional selection imposed by non-native pathogens increases the urgency for proactive approaches that incorporate an evolutionary perspective into forest management (Ennos 2015). The conventional sequence of responses to a new invasion is prevention, detection, control and management, and restoration and rehabilitation (U.S. Department of Agriculture Forest Service 2013). The first two elements are often grouped under "early detection and rapid response" and eradiation attempts continue into control and management activities along with efforts to contain the spread and mitigate the invasive species' impacts. Finally, if eradiation fails and impacts are realized, restoration is prioritized for valued resources. Often ex situ conservation of impacted native species is not initiated until the restoration phase as a last resort to preserve genetic resources prior to potential species or population extirpation. Restoration of degraded ecosystems is often met with limited success (see Jacobs et al. 2015 and reference therein); consequently, prioritizing gene conservation earlier in the invasion process before the threatened tree species incurs high mortality may be more effective at preserving species-wide genetic diversity. These collections can serve as an archive and can also accelerate development of genetic solutions (e.g. disease resistance detection and development, adaptive seed transfer guidelines) and, in conjunction with ecological research, can guide proactive management to sustain and increase the resilience of threatened ecosystems before they reach their tipping point (Schoettle and Sniezko 2007; Coop and Schoettle 2011; U.S. Department of Agriculture Forest Service 2013; Crow 2014).

Rocky Mountain bristlecone pine (*Pinus aristata*; henceforth bristlecone pine) ecosystems of the southern Rocky Mountains and US southwest offer an opportunity for proactive conservation and intervention. Bristlecone pine is a high-elevation species that

occurs on xeric sites, including alpine tree lines, windswept ridges, and dry, rocky, south-facing slopes of Colorado, northern New Mexico, and northern Arizona (Peet 1978; Veblen 1986; Baker 1992). Bristlecone pine occupies sites beyond the physiological limits of most other tree species and the forests it forms provide wildlife habitat, watershed protection, and recreational experiences that are irreplaceable (Schoettle 2004). The southern Rocky Mountains are at the infection front of the lethal disease white pine blister rust (WPBR) caused by the non-native pathogen *Cronartium ribicola*. Bristlecone pine is susceptible to WPBR (Blodgett and Sullivan 2004) and the disease is expected to continue to spread through much of the bristlecone pine distribution (Howell et al. 2006). Bristlecone pine's restricted high-elevation habitat and narrow geographic range also puts it directly in the crosshairs of a warming climate. Temperatures have increased 0.5–1 °C throughout the southern Rockies during the last 30 years and high elevation habitats may be warming even more quickly; a shift toward a greater percentage of precipitation falling as rain rather than snow in the western United States is also predicted (McWethy et al. 2010). Species niche models predict that bristlecone pine's current climatic niche may entirely vanish from the Rocky Mountain region by 2090 (Crookston 2012).

Sustaining successful regeneration and diverse age class structures across the landscape is essential to support adaptive capacity when faced with novel stresses (Aitken et al. 2008; Field et al. 2012). Low species and population level genetic diversity, exceedingly long generation times, and slow recruitment suggest bristlecone pine has an inherently low capacity for rapid adaptive response to ongoing and projected ecological changes (Schoettle et al. 2012a). Bristlecone pine trees can be very long-lived, with some of the oldest recorded specimens surviving for over 2400 years, and have delayed maturation, taking 30–50 years for a seedlings to produce seed bearing cones and much longer to produce a full cone crop. Extremely delayed post-fire regeneration, coupled with poor dispersal into burn interiors (Coop and Schoettle 2009) suggest that populations of bristlecone pine are likely to be negatively impacted by increases in forecasted wildfire activity and severity (Westerling et al. 2006; Moritz et al. 2012). Understanding the natural reproductive and regeneration processes can help assess a species' vulnerabilities and define how and when to manage them to promote a sustainable population in the presence of novel stressors (Schoettle et al. 2012a). While bristlecone pine is well adapted to conditions under which it evolved, its life history traits do not position it well, without management intervention, for a future in the Anthropocene.

Vulnerability of bristlecone pine populations to expected environmental changes compels expanded basic and applied research for appropriate proactive in situ management and conservation and ex situ conservation (Schoettle and Sniezko 2007; Schoettle et al. 2012a). The work presented here includes (1) range-wide seed and tissue collections for ex situ conservation and research, (2) range-wide characterization of patterns of stand structure, composition, reproduction, and health, and (3) assessment and definition of relationships between stand characteristics (with special attention on reproduction), abiotic site factors, and climate. This provides the infrastructure for an integrated ecological and genetic research and conservation program for bristlecone pine (e.g. Burns et al. 2008; Schoettle et al. 2011, 2012a). To the best of our knowledge, these efforts represent the first time a tree species has been subject to a proactive coordinated range-wide forest health assessment, genetic collection design, and research program.

Methods

Study area

The geographic range of Rocky Mountain bristlecone pine is centered on the southern Rocky Mountains of central and southern Colorado and it extends south along the length of the Sangre de Cristo range into northern New Mexico, and an isolated population also occupies high elevations in San Francisco Peaks of Arizona (Fig. 1; Online Resource 1). Our sampling was intended to include approximately equal representation from six putative seed collection areas that exhibit genetic divergence (Schoettle et al. 2012a), including the (1) Front Range, (2) Mosquito and Sawatch ranges, (3) San Juan and La Garitas, (4) Wet Mountains and northern Sangres de Cristo Mountains (within Colorado), (5) southern Sangres de Cristo Mountains (within New Mexico), and (6) San Francisco Peaks (Arizona) (Fig. 1; see Online Resource 1). Sample sites were also stratified by elevation: the elevational range of bristlecone within each zone was divided into bands of 150 vertical meters (500 ft); one or two sites was sampled within each band, when access and conditions permitted. Three other criteria for site inclusion were based on logistical criteria for cone collection: that sample areas be located within lands managed by the USDA Forest Service, be accessible by road or trail, and contain at least ten mature, cone-producing trees with a minimum separation of 60 m (200 ft). Locating sample areas within this scheme was facilitated through prior knowledge and previous research, communication with land managers and local experts, and field reconnaissance.

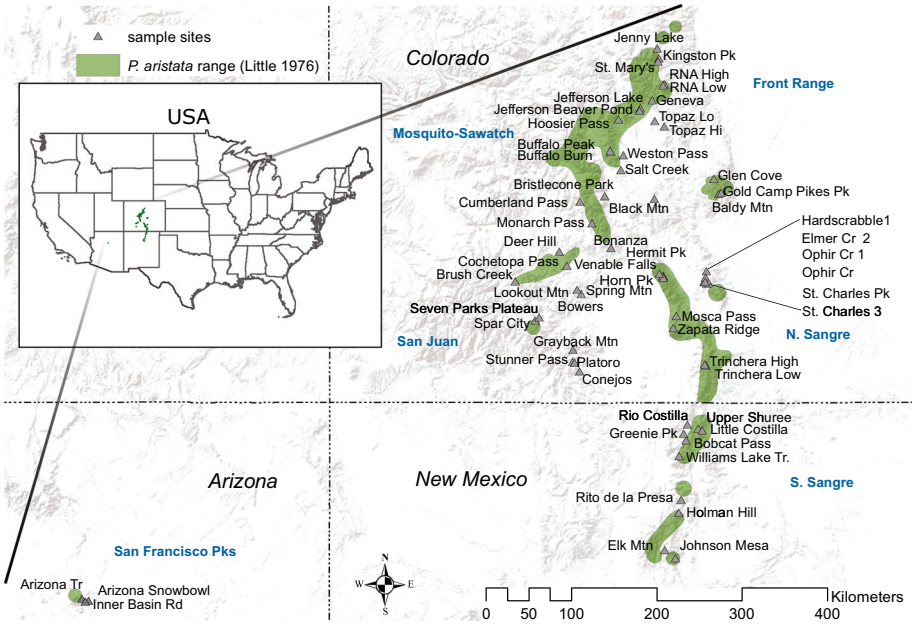

Fig. 1 Locations of 61 study sites across the range of Rocky Mountain bristlecone pine with seed collection areas labeled in *blue*. List of sites by seed collection area are shown in Online Resource 1

Seed and tissue sampling methods

We targeted seed and foliage collections from ten individual seed trees from each site (objective 1); seeds were collected in 2003, 2005, 2008, 2009, 2010, 2011, 2012, and 2014. All seed collections were from open pollinated trees and cones. WPBR was evident at one site at the time of sampling (Mosca Pass, CO) (Blodgett and Sullivan 2004); trees with and without blister rust infections were sampled. For all the other sites that had no evidence of WPBR, trees were not selected for any phenotype other than being cone-bearing. Sampled trees were located a minimum of 60 m (200 ft) apart from one another, they were tagged, and their coordinates recorded; elevations were noted upon mapping of the coordinates. Seed was extracted by hand and stored at −18 °C. A subset of each seed lot is stored in a USDA Forest Service permanent gene conservation archive at the USDA Agricultural Research Service National Lab for Genetic Resources Preservation (Fort Collins, CO) and the working collection is retained by USDA Forest Service Rocky Mountain Research Station (Fort Collins, CO). Foliage samples for DNA analyses were collected from each seed tree; three to four healthy fascicles were placed in a 15 ml screw-top centrifuge tube (Corning Life Sciences, NY) with 10 ml indicating silica gel beads (Macron, Grade 47; 10–18 mesh) and stored in a cooler until returning to the lab where they were transferred to the −18 °C freezer.

Ecological sampling methods

Field sampling methods were modified from whitebark pine (Tomback et al. 2004) and limber pine (Burns et al. 2011) monitoring protocols. Sample plots were placed in stands in locations that were approximately representative of overstory structure and composition across the site. Plots were installed and assessed in 2010 and 2011. Plots were 930 m^2 (60.96 × 15.24 m; 200 × 50 ft) and monumented with two rebar stakes at the midpoint of each short edge, with 0.75-m PVC sleeves labeled with plot number. Locations (UTM, WGS 84) were recorded for each stake. Common Stand Exam (USDA Forest Service 2012) codes were used where possible. For all trees (>1.37 m in height), species, dbh, and health status were recorded. For trees with multiple boles (broad, vertical stems), each stem was measured separately but allotted to the same individual. For trees with a shrub-like physiognomy, the basal area was measured at the root-shoot interface (diameter at root crown; d.r.c.)—a standard practice for woodland trees such as piñon pine and juniper species that commonly exhibit brushy physiognomy. For all five-needle pines, crown class, percent canopy kill, crown condition (no visible WPBR branch infections, <25% branches infected, 25–50% branches infected, >50% branches infected), percent of outer branch tips with maturing cones, and number of cones per crown was estimated. Five-needle pine seedlings (<1.37 m) were also tallied across the entire 930-m^2 plot. Cone production was similar among the two years for which plots were assessed (2010, 2011) and they were not mast years for bristlecone pine. Our cone collection experience indicates that bristlecone pine forests have bumper cone crops at uneven intervals. Unlike other masting pine species, bristlecone pine appears to have a bet-hedging strategy by investing annually in first year conelets on some trees on most sites and in non-masting years many of the conelets abort in the spring of the second year before seed maturation. Consequently, while some years produce greater cone crops than others, and cone production is present most years at some level. The conditions that promote successful fertilization, cone maturation, and seed production are not known for this species.

Within each plot, three 0.004 ha, 3.6-m radius circular fixed area subplots (0.01 acre, 11.8-foot radius) were nested at equal intervals (15.2, 30.5, and 45.7 m) along the long axis. Within each subplot, we tallied all tree seedlings by species. We estimated the percent ground cover by the three most extensive categories/plant species. Cover was also estimated for *Ribes* species in each subplot. At each plot, abiotic variables measured included elevation (m), slope (%), slope aspect (°), slope position, and disturbance history. Climatic parameters (Table 1) for each site were generated from thin-plate spline climate models (Rehfeldt 2006; data downloaded from http://forest.moscowfsl.wsu.edu/climate/). Rather than monthly mean values, we focused our analyses on derived climate variables most closely tied to western US tree species distributions (Rehfeldt et al. 2006).

Data analysis

To characterize current bristlecone stand condition (objective 2), summary statistics for characteristics of interest (e.g. live bristlecone density, average crown condition, total cone production, etc.) were calculated for each sample plot and for the entire sample of 61 sites. Many of these summary statistics are given below.

Table 1 Derived climate variables estimated (normalized for 1961–1990) by thin plate spline surfaces (Rehfeldt 2006, available at http://forest.moscowfsl.wsu.edu/climate/)

Climate variable	Definition	Range among source locations		
		Mean	Max	Min
mat	Mean annual temperature (°C)	0.9	4.5	−2.2
map	Mean annual precipitation (mm)	631	1033	327
gsp	Growing season precipitation, April to September (mm)	363	474	218
mtcm	Mean temperature in the coldest month (°C)	−9.0	−4.3	−13.5
mmin	Mean minimum temperature in the coldest month (°C)	−17.1	−11.8	−21.7
mtwm	Mean temperature in the warmest month (°C)	12.0	16.9	9.4
mmax	Mean maximum temperature in the warmest month (°C)	19.8	24.6	15.8
sday	Julian date of the last freezing date of spring	189	201	155
fday	Julian date of the first freezing date of autumn	230	246	216
ffp	Length of the frost-free period (days)	39	78	15
dd5	Degree-days >5 °C (based on mean monthly temperature)	688	1298	342
gsdd5	Degree-days >5 °C accumulating within the frost-free period	281	917	83
d100	Julian date the sum of degree-days >5 °C reaches 100	163	188	133
dd0	Degree-days <0 °C (based on mean monthly temperature)	1328	2055	638
mmindd0	Degree-days <0 °C (based on mean minimum monthly temperature)	2995	3829	1943
smrpb	Summer precipitation balance (Jul + Aug + Sep)/(Apr + May + Jun)	1.6	2.9	0.8
smrsprpb	Summer/spring precipitation balance (Jul + Aug)/(Apr + May)	1.8	2.7	0.8

Variables were estimated for each bristlecone pine site location and mean, maximum, and minimum values presented here

To examine relationships between stand composition, topography, climate, health, and reproduction (objective 3), we utilized linear and generalized linear models to test for the effects of a suite of environmental variables on three stand attributes of high interest: stand health, reproductive capacity (cone quantity), and regeneration (abundance of seedlings). To identify which dependent and independent variables to include in these models, we first examined the correlation structure between all measured variables. From several measures of each of the three stand attributes of interest (health, cones, and seedlings) we selected a single dependent variable to model, choosing the variable that showed the highest correlations (Pearson's r) to related measures. For example, to select the variable that best represented cone quantity at any given site, we considered (a) average number of cones/tree, (b) total cones/ha, and (c) cones/live bristlecone basal area. Cones/tree showed strong correlations to both the other two variables whereas total cones/ha and cones/live basal area were less strongly correlated. Similarly, we selected the number of seedlings/sample (bristlecone pines <1.37-m height per 0.03 ac) and percent healthy trees (percent of bristlecone pines with <5% crown loss) as dependent variables representing regeneration and stand health. Log-transformed cones/tree and percent healthy trees were modeled using linear models; seedlings/sample was modeled as a generalized linear (Poisson distribution) model. To reduce the number of possible predictor variables in any given model, we following a modified procedure recommended by Hosmer and Lemeshow (2000). First, we examined the correlations between predictors and response variables; second, only those with an absolute value of Pearson's $r > 0.20$ and $P < 0.25$ were included in any subsequent regression models. We used a stepwise elimination to identify the linear or generalized linear model that minimized Akaike's Information Criterion (AIC) and retained predictors significant at $P < 0.05$. All analyses were conducted in R (R Core Development Team 2015).

We tested for differences in stand composition, condition, reproduction, and climate between putative seed zones using a multi-response permutation procedure (MRPP, R package Vegan; Oksanen et al. 2016). MRPP tests whether pairwise within-group distances are significantly less than that expected from randomized groups over many permutations. Significance was determined following 10,000 permutations.

Results

Climate characteristics

The climate envelope for bristlecone pine, as characterized by 61 plots sampled here (Table 1; Fig. 1), spans a mean annual temperature (MAT) from −2.2 to 4.5 °C and mean annual precipitation (MAP) of 327 to 1033 mm. The northern Sangres supports bristlecone pine stands under the widest range of MATs while stands within the San Juan/La Garitas zone varied the widest in MAP (Fig. 2). MAT and MAP vary predictably in relation to each other in most mountain ranges with bristlecone pine occupying cooler sites with greater precipitation associated with the elevation gradient (Fig. 2). The San Juan/La Garitas stands revealed two different relationships between MAT-MAP that appear to distinguish the northern and southern portions of the area; the sites in the other mountain ranges followed their single respective relationships (Fig. 2). The more southern mountain ranges show the characteristic increase in summer precipitation from the North American Monsoon.

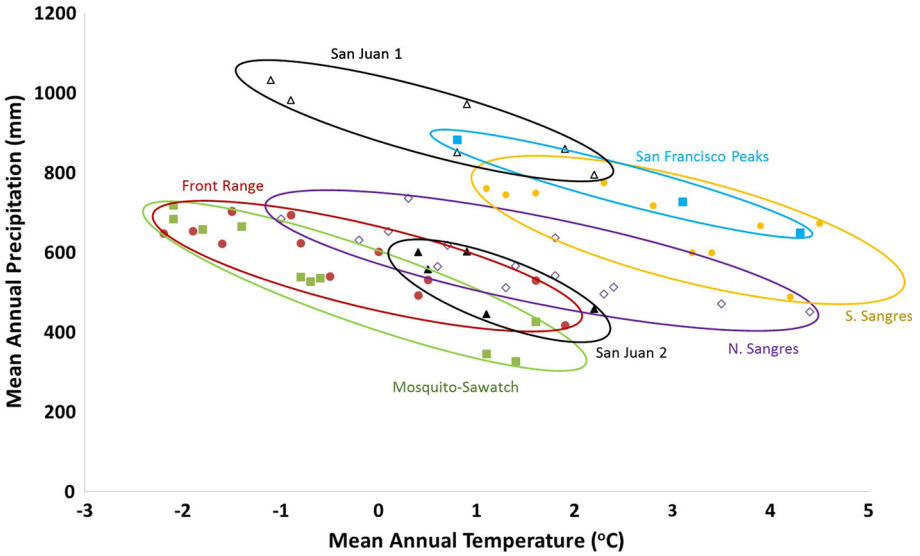

Fig. 2 Relationship between mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm year^{-1}) among the bristlecone pine stands sampled in this study by mountain range-zone. Linear correlations were significant for each zone, except the San Juan zone that revealed two relationships reflected the northern and southern portions of the area. Linear correlations (r^2) ranged from 0.53 (San Juan 2, Colorado) and 1.00 (San Francisco Peaks, Arizona)

Seed and tissue collections

Seed collections were successfully collected from most of the 61 sites for which plots were installed. In some cases seed yield was too poor or the sites too steep for cone collections and alternative sites within the seed collection area were sampled (Online Resource 1). Three to four fascicles were collected from each seed tree as a resource for genetic and genomic research. These are the first range-wide collections of bristlecone pine seed and genetic material.

Site and stand characteristics

Sixty one sites were sampled across the study area (Fig. 1), including 3–14 sites in each seed collection zone (see Online Resource 1), and a total of 2375 bristlecone trees were examined. Elevations of sample sites ranged from 2721 to 3676 m, with a mean of 3249 m. These mature bristlecone stands generally occupied upper landform positions, with most stands occurring on shoulder (14 sites) and backslope (32 sites) positions. Slope inclination at sample sites averaged 40.1%, but ranged from 3 to 88%. Stands were predominantly located on south (135°–225°; 25 sites) and west (225°–315°; 23 sites) aspects. Stands exhibited a wide range of disturbance histories. Evidence of fire was present at 21 sites, including trees with fire scars or scorch marks indicating low-severity fire and dead trees killed by higher-severity burns at several sites. Evidence of historic cutting was observed at 19 sites, and old mining activity was also found in several sites. However, nearly half (28 sites) of all sample sites showed no evidence of recent disturbance.

Table 2 Composition of tree species at sampled stands by live and dead basal area, density, and number of stands in which each species occurred

Species	Live BA (m^2 ha^{-1})	Dead BA (m^2 ha^{-1})	Live density (ha^{-1})	Dead density (ha^{-1})	Number of stands
Abies concolor	0.17	0	1	0	2
Abies lasiocarpa	0.15	0	16	0	11
Picea engelmannii	3.22	0.22	128	3	37
Picea pungens	0.14	0	2	0	6
Pinus aristata	22.06	2.23	385	34	61
Pinus contorta	0.03	0	1	0	3
Pinus edulis	0.01	0	1	0	3
Pinus flexilis	2.08	0.07	38	2	24
Pinus ponderosa	0.26	0	4	0	6
Populus tremuloides	0.48	0.15	92	27	18
Pseudotsuga menziesii	0.47	0.01	7	0	11

Stand density (all live trees >1.37 m tall) ranged from 86 to 1776 ha^{-1}, averaging 676 ha^{-1}. Within sampled stands, bristlecone pine was the most abundant tree (11–1141 ha^{-1}, mean 386 ha^{-1}), followed by Engelmann spruce (*Picea engelmannii*) and aspen (*Populus tremuloides*; Table 2).

Ribes species, the alternate hosts for WPBR, were frequent but minor components of bristlecone pine understories, occurring in 24 sites (39%). *Ribes* cover averaged only 2% in plots in which it occurred. The most common species was wax current (*Ribes cereum*, 13 sites, mean cover in these sites was 1.9%, average across all samples was 0.4%), followed by gooseberry current (*Ribes montigenum*, 10 sites, where it averaged 1.8, 0.3% across all samples) and whitestem gooseberry (*Ribes inerme*, 4 sites, 1.2, 0.1% across all samples).

Understory plant cover in bristlecone pine sites was generally sparse: litter (23% mean cover), rock (20%), and bare soil (9%) accounted for most ground cover. The five most abundant understory species were Arizona fescue (*Festuca arizonica*, 3.6%), mountain muhly (*Muhlenbergia montana*, 2.5%), Thurber's fescue (*Festuca thurberi*, 2.3%), Parry's oatgrass (*Danthonia parryi*, 1.8%), and common juniper (*Juniperus communis*, 1.4%).

Stand health

Bristlecone pines were generally healthy, with very little insect or disease damage. However, many trees exhibited substantial crown dieback that was not attributed to insects or other agents (Figs. 3, 4). Of 2375 assessed trees, 70.1% were classified as healthy, showing 0–5% damage. Of the remainder, 19.5% were declining (>5–50% damage), 2.2% were classified as dying (>50% damage), 0.5% were recent dead (fine twigs still present), and 7.8% were old dead. WPBR was not found on bristlecone pine in sample plots at any site but infected bristlecone pine trees were identified in the greater area of the Mosca Pass site. At the Mosca Pass site, WPBR was found on five limber pines in the sample plot but no rust was found on the bristlecone pines within the sample plot. Other stem cankers were only found at one site, Ophir 3, where one tree appeared infected with western gall rust (*Endocronartium harknessii*). Mountain pine beetle (*Dendroctonus ponderosae*) was also noted only at one site, Jefferson Beaver Ponds, and on a single tree. Twig beetles

Fig. 3 High-elevation bristlecone pines exhibiting characteristic partial cambial dieback and gnarled physiognomy at Bristlecone Park, 3676 m

(*Pityophthorus*, *Pityogenes*, and/or *Pityoborus* spp.) were the most commonly noted pest, occurring at 13 of 61 sites (see Online Resource 2). However, at these sites, twig beetle damage averaged only 1.38%. Minor damage by animals (e.g. elk antler rubs, porcupines) was noted at ten sites. Recent fire damage was noted at four sites, and other sources of abiotic damage such as lightning, wind, and avalanche were recorded at ten sites. Human activity (sawed branches) had caused damage to trees at two sites.

Many trees exhibited partial dieback from unknown but apparently abiotic causes. At higher elevations, trees frequently exhibited dieback of larger branches or substantial portions of the crown, as well as cambial dieback (Fig. 3). Additionally, trees at a range of lower elevation sites showed dieback of branch tips that appeared to have occurred within the past decade, and were likely linked to recent drought. These phenomena were recorded in the field as "old dieback", and occurred at 58 of 61 sites, where damage averaged 9.05%. Bristlecone stand health, estimated as the inverse of percent canopy kill, was positively predicted by mean minimum temperature and summer/spring precipitation balance, and negatively related to stand basal area and mean annual temperature (% healthy canopy $= 102.7 - [0.18 *$ total basal area (m^2 ha^{-1})] $+ [1.14 *$ mean minimum temperature of the coldest month (C)] $+ [8.4 *$ summer/spring precipitation balance ((Jul + Aug)/(Apr + May))]; $r^2 = 0.29$; $P < 0.001$; 56 d.f.).

Reproduction and regeneration

Cone production of bristlecone pine was highly variable within and across sites during the two plot assessment years, and averaged 9 ± 17 cones/tree and 2979 ± 3217 cones/ha, though only two sample sites (Glen Cove and Greenie Peak) lacked any cone production. Cone production was often observed to be highest at treeline sites. Cone production within

Fig. 4 Patterns of branch dieback at a moderate elevation site at Spring Mountain, 3390 m

sites was strongly negatively related to stand density and positively related to the number of degree days <0 °C ($\log_{10}$ cones/tree = 0.09 − [0.0008 * total tree density (ha^{-1})] + [0.0005 * degree days < 0]; $r^2 = 0.44$; $P < 0.001$; 56 d.f). Two other models produced similar low AIC values (ΔAIC ≤ 2; Table 3); rather than degree days <0, these showed a negative relationship to mean maximum temperature [−0.07 * mean maximum temp (°C)] or the mean temperature of the coldest month [−0.07 * mean temp of coldest month (°C)]. At the level of individual trees, cone production was weakly related to tree basal area ($r^2 = 0.05$, $P < 0.001$, 2177 d.f.).

The average density of bristlecone pine seedlings (<1.37 m in height) was 148 ha^{-1}, but ranged from 0 to 750 ha^{-1}. Three models produced nearly identical AIC scores (Table 3). Seedling density in the top model was strongly positively related to cone production (cones ha^{-1}), percent canopy health, and percent cover by bare soil (seedlings/0.012 ha sample = −0.386 + [0.00008 * cones ha^{-1}] + [0.04 * percent healthy bristlecone pine] + [0.51 * percent cover by bare soil]; family = poisson (link = log); null deviance 179.7; residual deviance 153.8; McFadden pseudo-$r^2 = 0.18$; $P < 0.001$; 56 d.f).

Table 3 The r^2, P, and AIC for the top three best fitting models predicting stand canopy health (percent of bristlecone pines with canopy health ≥95%), reproductive capacity (cone crop), and current regeneration (seedling density)

Model	r^2	P	AIC
Canopy health			
(1) Health ~ total ba + mmin + mat + smrsprpb	0.29	<0.001	404.9
(2) Health ~ PIAR ba + mmin + mat + smrsprpb	0.27	<0.001	406.1
(3) Health ~ total ba + mmin	0.22	<0.001	408.4
Reproductive capacity			
(1) Cones ~ tree density + dd0	0.41	<0.001	95.3
(2) Cones ~ tree density + mmax	0.40	<0.001	96.6
(3) Cones ~ tree density + mtcm	0.39	<0.001	97.3
Regeneration			
(1) Regen ~ total ba + cones/ha + health + bare soil	0.18[a]	<0.001[b]	255.8
(2) Regen ~ total ba + cones/ha + gsp + health + bare soil	0.19[a]	<0.001[b]	256.0
(3) Regen ~ cones/ha + health + bare soil	0.18[a]	<0.001[b]	256.3

Definitions for dependent variables are as follows: health, percent of undamaged canopy; cones, $\log_{10}$ (mean cones/live bristlecone pine tree); regen, bristlecone seedlings/sample unit. Listed predictor variables are: total ba, total tree basal area/stand (all species); tree density, total number of trees/stand; cones/ha, number of bristlecone pine cones per unit area; mmin, mean minimum temperature of the coldest month; mat, mean annual temperature; mmax, mean maximum temperature of the coldest month; mtcm, mean temperature of the coldest month; dd0; total degree days <0 °C; smrsprpb, summer/spring precipitation balance (July + Aug)/(Apr + May); gsp, growing season precipitation Apr–Sept

[a] Generalized linear (poisson) model: model r^2 is estimated as the McFadden pseudo-r^2

[b] Generalized linear (poisson) model: model P value is calculated from an asymptotic Chi-square statistic based on deviance accounted for in the model compared to a null model

The two other best-fitting models (Table 3) either included a positive relationship between seedling abundance and growing season precipitation [+0.0015* Apr–Sept precipitation (mm); Model 2] or excluded both total stand basal area and growing season precipitation (Model 3).

The six geographic seed collection zones exhibited significant differences in climate (MRPP $P < 0.001$) and reproduction ($P = 0.018$), but not in stand composition or tree health (MRPP $P > 0.05$ for each test).

Discussion

Across the geographic range of Rocky Mountain bristlecone pine, seed and tissue collections were made (objective 1), patterns of stand structure, composition, disturbance history, reproduction, and health were characterized (objective 2), and relationships between stand characteristics, abiotic site factors, and climate were tested and defined (objective 3). This integrated range-wide sampling of genetic material, ecological site characterization, and climate interactions provide fundamental knowledge and resources for a threatened species before impacts by strong directional biotic (WPBR invasion) and abiotic (climate change) forces are realized, and thereby provide a framework for current research and intervention and a basis for future research and comparisons. Range-wide

genetic collections for bristlecone pine, designed to capture a representative sample of the genetic diversity of the species, targeted populations across elevational gradients within each of six geographic zones. This collection provides baseline resources to detect genetic bottlenecks or shifts in the future, while retaining the pre-impact genetic diversity ex situ. In addition, the tissues provide resources now for researching genetic resistance to WPBR, adaptive variation, evolutionary history, and genetic diversity, and seed transfer and assisted migration strategies, as well as a myriad of other basic and applied questions related to species in mountain habitats. The seed collections also provide the start of a seed bank for artificial regeneration projects which have begun in some areas.

For many timber species, historical stand data are available yet for species with little timber value such information is often lacking; this study provides the scientific foundation and site network for Rocky Mountain bristlecone pine before the species declines providing the opportunity to assess ecological and genetic shifts in real time in the future with repeat sampling. Dendrochronological techniques can recreate pre-impact stand structures (e.g. Austin et al. 2016) and post-impact genetic conservation collections from surviving tree populations can help archive remaining genetic diversity (e.g. Jetton et al. 2013, 2015) however some rare alleles or whole populations may have been lost. Gathering range-wide genetic resources and ecological data for threatened, but not yet impacted, forest species reduces the risk of lost diversity in conservation archives and research materials and provides insights for management interventions to increase ecosystem resilience to proactively mitigate impacts that could lead to population extirpation or severe impacts to ecosystem services.

Range-wide, mature Rocky Mountain bristlecone pine stands exhibited a rather narrow range of variation in stand structure, composition, regeneration, and stand health. Variation in these stand attributes was largely related to local topographic and elevational variation, rather than regional or geographic differentiation. Overall, bristlecone pine tends to occupy xeric, southwest-facing slopes at moderate to high elevations, with high ground cover by rock, litter, and bare soil. Variation in stand structure and composition across our sites largely confirms patterns previously reported by earlier investigators (Baker 1992; Ranne et al. 1997), including frequent canopy associations with Engelmann spruce and aspen, and with understory species including Arizona and Thurber's fescue, mountain muhly, and common juniper.

We did not find substantial geographic differences in patterns of stand conditions, though the geographic regions differed in climatic characteristics and cone production. Ranne et al. (1997) also found geographic variation in stand understory composition, which they associated with differences in geologic substrate—extrusive igneous in the San Juan range, sedimentary in the Sangres, and intrusive igneous elsewhere. While these differences are likely to lead to variation in edaphic properties, they did not appear to lead to clear geographic differentiation in stand condition among our sampled sites.

Within any given mountain range, bristlecone pine stands generally showed a predictable pattern of variation along an elevational gradient. Sites at lower elevations tended to be more open, and frequently occurred on shallower slopes with grassier understories, often bordering open meadows or grasslands. At increasing elevations and higher slope positions, bristlecone pine stand density and basal area increased. Ground cover in closed canopy stands was commonly dominated by needle litter and wood. Within some parts of its range, these stands contain a substantial component of Engelmann spruce. It also seemed that such stands were entirely absent from some parts of bristlecone pine range, perhaps where conditions were sufficiently mesic to promote complete competitive dominance by Engelmann spruce. At the highest elevations, bristlecone pine was again found in

patchy stands at alpine treeline, with high variability in stand density, but a large proportion of older trees with high levels of dieback (Fig. 3).

In general, bristlecone pine stands currently showed very little damage by pathogens or insects. WPBR was found only at one site, Mosca Pass. Cankers were not found on any bristlecone pines within our sample plots, though they are present on bristlecone pine in the greater Mosca Pass area (Blodgett and Sullivan 2004). Cankers were well developed on the infected limber pine trees in the sample plot, their absence on bristlecone in the plot suggests lower susceptibility or slower disease development in bristlecone compared to limber pine (Schoettle et al. 2011; Jacobi et al. 2017). Likewise, mountain pine beetle, another agent of high management concern for which bristlecone pine is a host, was only found to have impacted one tree at one site, though it was noted at other sites outside our plots. This site, Jefferson Beaver Ponds, is located towards the northernmost edge of bristlecone distribution, closest to the extensive mountain pine beetle outbreak affecting lodgepole and limber pine in north-central Colorado (Cleaver et al. 2015). Twig beetles (*Pityophthorus*, *Pityogenes*, and/or *Pityoborus* spp.) were the most widely observed source of damage. Little is known about these insects, which eat the cambium and kill twigs and small branches of drought-stressed trees, and may kill small trees when conditions allow episodic outbreaks (Fairweather et al. 2006).

Beyond clear effects of insects and pathogens, many trees in our samples exhibited some level of dieback within the canopy, lateral branches, or bole of individual trees [not to be confused with stand-level dieback (Mueller-Dombois 1988)]. Partial cambial dieback (bark-stripping) of bristlecone pines, common on high-elevation and exposed sites, has been widely reported previously as a response to wind or other sources of physical damage (Fig. 3) (e.g. Schauer et al. 2001). However, we also observed substantial recent crown and branch dieback (Fig. 4) across a wide range of sites. Such canopy-level dieback has been associated with fungal pathogens in a number of tree species (e.g. Úrbez-Torres et al. 2013); no obvious signs or symptoms of causal agents were present to help explain the branch dieback in bristlecone. Episodes of prolonged or severe drought, as have been experienced recently in the southern Rockies (Smith et al. 2015), can also contribute to hydraulic failure and branch dieback (Scott et al. 1999; Koepke et al. 2010; Spetich et al. 2016) and may be a factor here. As with self-pruning (Mäkelä 1997) in response to light limitations, perhaps these patterns of dieback in bristlecone pine represent an adaptive response to limitations of key resources in the harsh environments this species inhabits.

Bristlecone pine reproduction and regeneration capacity, as measured by cone production and seedling abundance, respectively, were strongly predicted by a suite of structural and environmental variables. Cone production was highest in low-density stands composed of large, mature trees on cold sites, particularly high-elevation ridgelines. Climate influences on the periodicity of cone production for other species of *Pinus* have been examined within a single site or region, and generally show increasing production in years with higher summer temperature and precipitation (e.g. Despland and Houle 1997; Mutke et al. 2005). Why bristlecone pine showed increased cone production at colder sites across its range, whether the positive effects of cold winter temperature are most beneficial for cone initiation, fertilization, or maturation, and how this pattern might be influenced by inter-annual variability, are not known. However, the pattern we observed is suggestive of a potential sensitivity of bristlecone pine cone production to warming climate. Increased cone production in low-density stands suggests that mechanical treatments (particularly those that remove competing tree species) may be useful management strategies for increasing cone production for bristlecone pine trees.

Cone count was one predictor of bristlecone pine seedling density, suggesting at least some correlation between cone production and propagule availability. Not surprisingly, seedling density was also strongly positively related to growing season precipitation in the second best-fitting model, again suggesting potential climate vulnerability. Large scale disturbance can contribute to pulses of bristlecone pine regeneration (Coop and Schoettle 2009; Baker 1992) yet our findings support previous conclusions that within-stand establishment events regularly occur and generate mixed-aged bristlecone pine stands over time (Brown and Schoettle 2008). Increased seedling density with bare soil and reduced stand cover suggests prospects for proactive stand management to increase bristlecone populations prior to blister rust impacts. Likewise, the high elevation stands opened by Engelmann spruce mortality caused by the recent spruce beetle (*Dendroctonus rufipennis*) epidemic in the southern Rockies may stimulate natural regeneration of bristlecone pine; in addition, inclusion of rust-resistant bristlecone pine seedlings in the reforestation planting stock can help increase the bristlecone pine population size and the frequency of disease resistance in anticipation of rust invasion (Schoettle and Sniezko 2007).

The health and functioning of the ecosystem can determine its response to management intervention. This can be demonstrated with examples from WPBR management in high elevation five-needle pines habitats. Genetic resistance to WPBR exists in each North American five-needle pine species, but it is at low frequency and is not distributed evenly across each species' distribution (see Sniezko et al. 2014). However, the presence of this resistance provides a much more optimistic prognosis for the species than those novel pathosystems for which genetic resistance to the pathogen is not within the natural genetic diversity of the host (e.g. Jacobs et al. 2013). This variation can help forecast the differential trajectory of populations upon invasion and therefore their management priorities and prescriptions. The proactive collection of seeds from naïve populations enables the baseline frequency of resistance to WPBR in populations to be estimated using existing screening technologies. If the naïve population has genetic resistance to WPBR, efforts to increase natural regeneration, through thinning in bristlecone pine forests for example, will increase the population size such that upon *C. ribicola* invasion and selection (i.e. mortality of susceptible genotypes) a larger population with a greater frequency of resistance will remain (Schoettle et al. 2012b). However, if one applies the same logic to an impacted forest, one with putatively resistant survivors but few individuals after high WPBR-caused mortality, attempts to stimulate regeneration have had only partial success due to seed and dispersal limitations (Keane and Parsons 2010). If the naïve population is found to have little to no genetic resistance to WPBR, planting seedlings with genetic resistance into the healthy population will provide time for those seedlings to approach reproductive maturity before high mortality of the older age classes is realized thereby maintaining ecosystem functions. Alternatively, planting resistant seedlings into a heavily impacted stand will restore the population over time but until the planted seedlings reach reproductive maturity (which may take several decades or more), the population has no ability to recover from other disturbances. The earlier resistant seedlings can be established or planted in a healthy populations the shorter the window of time the resilience of the population and ecosystem is compromised upon invasion. When intervention precedes ecosystem impairment, i.e. proactive intervention, natural processes are still functioning and outcomes can be more easily predicted. These examples can be adapted and applied to stress tolerance, rather than disease resistance, traits and could be generally referred to as incremental or anticipatory adaptive management (see Stanturf 2015); however it would be more accurate to term them proactive management since a key element of their potential is the timing of their implementation in relation to ecosystem condition. In addition, the proactive intervention

approach can be applied to portions of a species' distribution rather than entire distribution. Attention is often focused on the heavily impacted species or areas yet opportunities for effective intervention to support conservation goals exist in threatened but not yet impacted areas and may offer less uncertainty.

Conclusions

To the best of our knowledge, this study represents the first proactive range-wide gene conservation collections and assessment of the health and ecological conditions of a threatened, but not yet impacted, tree species. The ex situ bristlecone pine seed and tissue collections provide timely opportunities for genetic, genomic, evolutionary, and ecological research as well as establish a conservation archive collection and provide the beginnings of a seed bank to support artificial regeneration efforts. The in situ ecological assessment provides a baseline to compare future conditions and clues to bristlecone pine's vulnerabilities and how to manage regeneration to increase the resilience and adaptive capacity of the species. Overall, we found that local, rather than regional, variation in topoclimate was related to patterns of stand structure, composition, health, and regeneration. Across its range, bristlecone pine currently shows very few impacts of insects or fungal pathogens, but relationships between cone production and regeneration with climate variables suggest vulnerabilities to climate change and we know this species is susceptible to WPBR. Bristlecone pine cone production and seedling regeneration were however associated with stand structure and ground cover, which provide opportunities for proactive in situ conservation management to increase reproductive success and help mitigate potential future climate- and pathogen-driven declines.

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