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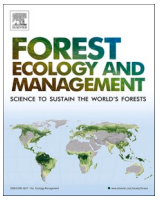

Is whitebark pine less sensitive to climate warming when climate tolerances of juveniles are considered?

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ABSTRACT

Whitebark pine (*Pinus albicaulis*) (PIAL) is a proposed threatened species that plays a keystone ecological role in the Greater Yellowstone Ecosystem (GYE). Its population response to climate change is of high interest to managers because climate-induced declines may adversely affect critical ecosystem services that this species provides. While previous studies of reproductive size classes of the species have projected dramatic reductions in area of suitable habitat under climate warming scenarios, it has been suggested that the species can tolerate warmer and drier conditions if seedlings and saplings are not competitively excluded by other conifer species. Thus, we asked if juvenile-sized PIAL are found in warmer and drier locations than larger individuals, under the assumption that competitive exclusion would require several years to decades to influence the distribution of regenerating PIAL. We used a new genetic technique to distinguish non-cone bearing PIAL from the more warm-dry tolerant limber pine (P. *flexilis)* among samples collected along transects extending from lower treeline to the subalpine around the GYE. Predictor data on climate and water balance were obtained from a 250-m spatially explicit data product. We used a stochastic gradient boosting model to predict probability of presence of PIAL < 1 cm dbh (diameter at breast height) and >=1 cm dbh as a function of these predictors. We discovered that smaller diameter PIAL were not proportionally more abundant at lower elevations, suggesting that competitive exclusion may not be the primary mechanism limiting this species' low elevation distribution. In contrast, the small size class PIAL were slightly less warm-dry tolerant than larger individuals. This suggests that the zone of regeneration of PIAL has shifted upwards in elevation in recent decades, perhaps associated with the observed warming in the GYE. In comparison to a previous study of reproductive-sized trees (>20 cm dbh) from a coarser (1.6 km) sampling frame, however, the predicted zone of suitable habitat of PIAL (<1 cm dbh) was 122 m lower in elevation. We conclude that consideration of the fine-scale distribution of PIAL near lower treeline suggests that the tree species is slightly less sensitive to climate warming than found by previous studies of reproductive-sized trees, but, nonetheless, large range contractions of PIAL in GYE are likely under projected future climates.

1. Introduction

Increased knowledge of species respond to climate change is critical to developing strategies to conserve them under human induced global warming. In the case of sessile and long-lived species such as trees, this requires an understanding of the species' autecological tolerances to environment, synecological responses to other species, and adaptations for responding to disturbances (Jackson et al., 2009). Accordingly, "Understanding the Rules of Life" is one of the National Science Foundation's 10 Big Ideas and has the goal of "elucidating the sets of rules that predict an organism's observable characteristics, its phenotype" (National Science Foundation, 2020). This challenge will require detailed studies of how species performance results from the interactions of the biotic, abiotic, and environmental components of the ecosystem.

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Such studies are especially important for keystone species, which have a disproportionately large influence on the web of life in a place.

Whitebark pine (*Pinus albicaulis*) (PIAL) is a native conifer of the Western U.S. that many consider a keystone species in the sub-alpine environment. Its seeds provide an important food source for animals such as the grizzly bear (*Ursus arctos*), red squirrel (*Tamiasciurus hudsonicus*), and Clark's nutcracker (*Nucifraga columbiana*) (Tomback et al., 2001). It also serves other ecosystem functions such as stabilizing soil, moderating snowmelt and runoff, and facilitating establishment of other species (Keane et al., 2017). PIAL has experienced a substantial decline in the past two decades within the U.S. Northern Rockies due to high rates of infestation from the mountain pine beetle (*Dendroctonus ponderosae*) and infections from white pine blister rust (*Cronartium ribicola*), resulting in an 80% mortality rate within the adult population (Landguth et al., 2017; MacFarlane et al., 2013). The severity the recent mountain pine beetle outbreak has been associated with climate warming and is projected to become even more severe in the future (Buotte et al., 2016). The PIAL is also thought to be sensitive to the direct effects of future climate change (Chang et al., 2014; Coops and Waring, 2011; McLane and Aitken, 2012). As we wrote the final draft of this paper, the U.S. Fish and Wildlife Service proposed to list PIAL as a threatened species under the Endangered Species Act (Fish and Wildlife Service, 2020) due to population declines driven by "white pine blister rust, … the mountain pine beetle, altered fire regimes, and the effects of climate change".

Population response of PIAL to climate change is of high interest to managers in the Greater Yellowstone Ecosystem (GYE) because of the species' proposed listing and its beneficial ecological role (USFS, 2011). Two methods of inferring species response to climate change, however, have found or projected opposite population responses of PIAL to past or projected future warming scenarios. Species distribution models (SDMs) were parameterized based on climate and geomorphic conditions of where reproductive-sized PIAL occurs as recorded in the Forest Inventory and Analysis Project (FIA) (Chang et al., 2014). These SDMs projected large reductions in area of suitable habitat across the GYE under future climate change scenarios. In contrast, vegetation reconstructions based on fossil pollen data indicated increases in the proportional abundance of PIAL-type pollen during the warm period centering on 10,000 years B.P. (Iglesias et al., 2015).

The discrepancies in results between these studies may be due to a lack of knowledge of the regeneration climatic niche of PIAL relative to the adult climate niche (Hansen et al., 2016). Climate is often a limiting factor for tree species in montane environments and the climate tolerances of seedlings and saplings may differ with those of adults due to differences in rooting depth, carbohydrate storage, and other factors (Jackson et al., 2009). The climate regeneration niche of PIAL is poorly know because of confusion with the congener limber pine (*Pinus flexilis*) (PIFL).

Field inventory methods are often unable to distinguish PIAL from PIFL in the absence of mature cones. The needles, bark, and overall morphology of both species are sufficiently similar to prevent accurate and consistent species identification for non-cone bearing trees. Cones are often absent in sampled trees because individuals have not reached reproductive age; cones were not produced due to unsuitable weather conditions; or seed predators removed the cones. PIFL thrives in warmer and drier conditions and reaches peak abundance in lower treeline forests in the GYE (Hansen et al., 2016). Thus, confusion in species identity is likely between non-cone bearing PIAL and PIFL individuals in the zone of overlap. Similarly, fossil pollen of five-needle pine cannot be resolved to species and the expansion of pine in the paleo record may be PIFL rather than PIAL (Iglesias et al., 2015).

Previous studies of PIAL tolerance to climate have either ignored this species identification issue (Bell et al., 2014, Monleon and Lintz, 2015) or restricted analysis to reproductive-sized trees under the assumption that they were correctly identified by the presence of cones (Chang et al., 2014). Thus, the results of these studies may be in question if the samples used to quantify the regeneration niche of PIAL included some PIFL individuals and/or the regeneration niche of PIAL differs from that of adult trees.

In fact, the projected range contraction of PIAL in the Greater Yellowstone Ecosystem under furure climate scenarios (Chang et al., 2014) was called into question because junenile trees were not included in the analysis. Buermeyer et al. (2016) suggested that PIAL is able to regenerate in warmer and drier settings than where adults are found, but are competitively excluded from these lower treeline settings by other conifer species. PIAL is relatively shade intolerant (Keane et al., 2007) and competition for light by more rapidly growing conifer species such as Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) is hypothesized to kill juvenile PIAL from sites that meet their climate tolerances leading to adult sized individuals not occurring in these sites (Buermeyer et al., 2016). Under conditions where fire or other disturbances remove this competition, PIAL may be able to occupy lower elevations (Flanary and Keane, 2019). Therefore, the SDM analysis of Chang et al. (2014), based on the presence of only adult sized PIAL trees, may have failed to detect actual lower-elevational distributions of regenerating PIAL and over-predicted the contraction of whitebark pine's range under future climate scenarios.

The ability to distinguish non cone-bearing PIAL from PIFL is necessary to resolve the regeneration niche of PIAL. Fortunately, Alongi et al. (2019) developed a straightforward genetic approach to distinguish non cone-bearing PIAL from PIFL using restriction endonucleases (Alongi et al., 2019). The chloroplast *matK* PCR amplicon of PIAL cleaves into two fragments with the restriction enzyme BsmaI, whereas the chloroplast *psbA-trnH* PCR amplicon of PIFL cleaves into two or three fragments with the restriction enzyme PsiI. Alongi et al. (2019) then used these chloroplast regions as genetic barcodes to identify needles from PIAL and PIFL samples and found the results validated well against visual species identification from cone-bearing trees.

Taking advantage of this new genetic identification method, we quantified the climate niche for juvenile-sized PIAL (<1 cm diameter at breast height (dbh)) and that of larger individuals. This was done by recording the locations of juvenile-sized PIAL and larger PIAL (>=1 cm dbh) across elevation gradients in the GYE and quantified climate and water balance correlations (at a 250-m resolution) to the probability of presence of each PIAL size class.

We then used these field results to project distributions of climate suitable habitats for juvenile-sized and larger PIAL across the GYE and compared this result to that of Chang et al. (2014) who investigated PIAL sensitivity to projected future climate in GYE. The objective was to determine if the area of suitable habitat predicted under current climate for juvenile and adult individuals from our studies was similar to or different from that predicted by Chang et al. (2014) for reproductive-sized individuals. If the distribution of climate suitable habitat for the current period predicted by our analyses extended to substantially lower elevations and warmer and dryer conditions to that of Chang et al. (2014), this would suggest that PIAL is less sensitive to future projected climate warming than suggested by that study.

The Chang study differed from ours in that they used a coarser climate data set (800 m compared to our 250 m data) and the field plot locations in the data set they used were offset by 1.6 km by FIA to protect land owner privacy. To better understand the influence of the 'fuzzed' locations of the Chang et al. (2014) samples and the coarser predictor data, we projected current PIAL climate suitable habitat using unfuzzed FIA data matched with the 250 m climate and water balance used for analyzing our field samples to see if this resulted in differing PIAL distributions under current climate.

Thus, the goal of the study was to determine if PIAL is less sensitive to climate warming if the climate tolerances of juveniles are considered. Specific objectives were as follows.

1. Compare the warm dry tolerances of juvenile-sized PIAL to sapling and larger sized PIAL to test if previous studies of only larger trees

underestimated warm and dry climate tolerances of the species, as is suggested by the hypothesis that PIAL can tolerate conditions at lower treeline but is competitively excluded from those environments.

2. Evaluate if the spatial extent of suitable habitats of PIAL in the GYE differs between analyses for adult sized trees (likely to be cone-bearing and correctly identified) and analyses of our data for genetically identified PIAL of all size classes, and draw inference about sensitivity to projected climate warming.

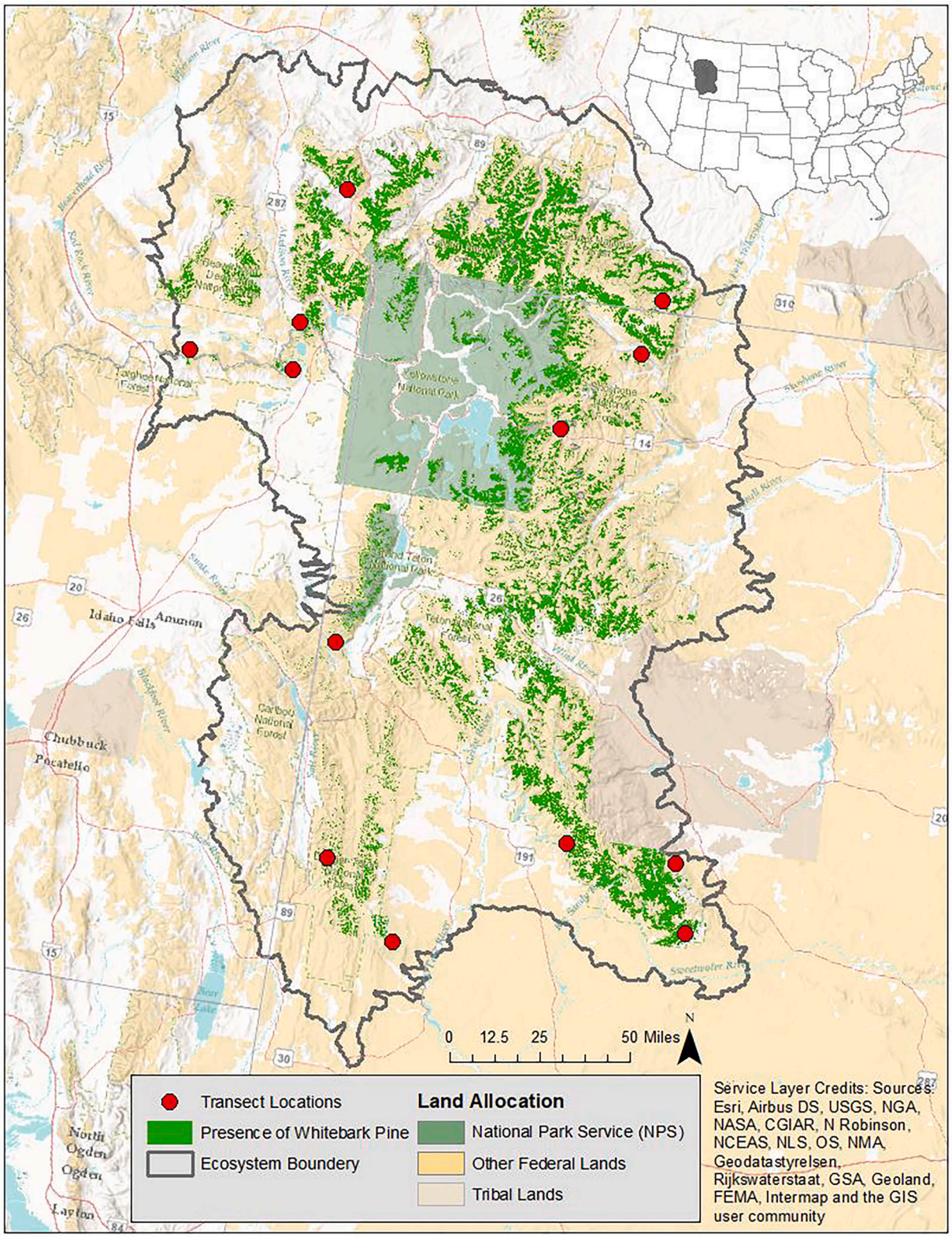

Fig. 1. Map of the Greater Yellowstone Ecosystem showing the distribution of PIAL, land allocation, and location of the 13 transects within each of the four cardinal quadrants of the GYE.

2. Methods

2.1. Study area

While PIAL is distributed across most mountain ranges of western North America, we studied only populations within the GYE (Fig. 1). The GYE includes Yellowstone National Park, Grand Teton National Park, and a number of state and federally managed forests. It occurs across the mid- to high-elevation region in the Northern Rocky Mountains of western North America (Hansen and Phillips, 2018). The GYE study area encompassed 150,700 km^2 with an elevational gradient from 522 to 4,206 m that included portions of 14 mountain ranges.

The GYE region experiences a cold continental climate with more warm and dry conditions at lower elevations and more cool and wet conditions at higher elevations and across much of the Yellowstone plateau. Temperatures in the region have been increasing since 1948, with the most pronounced warming in the winter and summer months (Sepulveda et al., 2015). Warming winter temperatures have led to reduced snow accumulation and earlier snowmelt (Sepulveda et al., 2015). The future climate of the GYE is expected to be warmer and drier than present (Chang et al., 2014).

Vegetation communities vary with elevation (Despain, 1990). PIAL dominates the forest at upper treeline in many locations but occurs as a subordinate to other species down to mid forest elevations. PIFL has the widest elevational distribution among tree species extending from the subalpine zone down to lower treeline. Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occur in subalpine forests along with PIAL. Lodgepole pine (*Pinus contorta*) is most abundant in mid-elevation forests. Douglas fir (*Pseudotsuga menziesii*) dominates lower treeline forests. Juniper (*Juniperus scopulorum*) and sagebrush (*Artemisia tridentata*) occupy valley bottoms and toe slopes.

2.2. Field sampling

We collected needles from PIAL and PIFL along 13 transects distributed among the four compass quadrants of the GYE that were located to span environmental gradients from lower tree-line to the mid elevational distribution of PIAL (ca 2740 m) (Fig. 1). The current distribution of PIAL in the GYE was derived from the GYCC whitebark pine map (USFS, 2011). Lower treeline was identified from inspection of large scale photography (i.e., Google Earth Imagery). Three or four transects were placed within each of the four compass quadrants of the GYE shown in Fig. 1. Transect locations were determined based on the following criteria:

- knowledge or evidence the presence of PIAL (USFS, 2011) and PIFL (Wilson et al., 2013) along the transect;
- historic growing season temperature and water balance within the limits of PIAL as summarized by Chang et al. (2014);
- forest canopy cover from > 0 to <= 50% to capture the conditions typical for regenerating five-needle pine; and
- accessible by road or trail to facilitate timely sampling.

Transects varied in length as determined by distance from lower treeline to the mid elevation zone of PIAL and were 60 m wide. Four equal interval elevation zones were identified along each transect (termed elevation quartiles) to facilitate stratification of five-needle leaf samples across elevation. Potential five-needle pine absence points (required for the statistical analyses) were randomly placed along the transects, with 5 points located in each of the elevation quartiles. The digital transect files were loaded onto smart phones, allowing the field crews to locate the transects, elevational zones, and potential absence points on the ground.

Field crews collected leaf samples and data for up to six five-needle pine trees within each elevation quartile along each transect for a total of about 24 tree samples per transect. The crews first hiked along the transect to identify the distribution of candidate trees along the transect. On the return along the transect, they collected samples from five-needle pine trees prioritized by:

1. size class < 1 cm dbh in order to get adequate samples of seedlings;
2. even distribution along the elevation zone to facilitate representative sampling of abiotic settings; and
3. proximity to transect centerline for ease of sampling.

The crews also collected up to two samples from cone-bearing trees in each elevation quartile along each transect. These samples were used to validate species identification from genetic analysis of needles in the lab.

Data recorded for each leaf sample included: GYE compass quadrant; transect name; elevation quartile (lower, second, third, upper), sample number (1–6 within each quartile), tree identification (PIAL, PIFL, Unknown) based on cones present in the tree, tree dbh; observer, date, latitude; longitude; and elevation. The protocol for sampling leaves was to collect three fascicles of five needles from each sampled tree. The fascicles from each tree were placed a plastic bag with a data card. Data written on the card stock included: transect name; elevation quartile (lower, second, third, upper); and sample number. The bags were then stored in a dry, cool, and dark environment until delivered to the genetics lab for analysis.

The crews also inspected each of the previously located potential absence points. Data recorded for each potential absence point included: GYE compass quadrant; transect name; elevation quartile (lower, second, third, upper), potential absence sample number (PA1–PA5 within each quartile), five-needle status within 30 m of the point center (absent, present). If PIAL or PIFL were found in the potential absence points, samples were collected to fill out the six samples required for each elevation quartile. A total of 253 potential absence points were originally identified. Field inspection found that 73 of these did not have 5-needle pine trees and these sites were used as absence points in the niche modeling. We subsequently added 27 absence points along the transects near lower treeline. This was done by overlaying the transects and sample points on earth imagery in ESRI ArcGIS and selecting locations in the transect near lower treeline that were clearly non-forested.

Genetic identification of the leaf samples was done based on haplotypes of the chloroplast *psbA-trnH* spacer and the *matK* locus and the validation of the results against the cone-bearing trees was done as described in Alongi et al. (2019).

2.3. Climate data

We used a high resolution (250 m) climate and water balance data set developed by Landguth et al. (2017) for their study of PIAL blister rust susceptibility across the Northern Rockies. The variables were temperature, solar radiation, snowpack, evapotranspiration, and soil moisture (Table 1). Water balance predictors were calculated using a Penman-Monteith based model as in Dobrowski et al. (2015) and a simple bucket model from Lutz et al. (2010), Dobrowski et al. (2015); Lutz et al. (2010). The climatic and soil inputs to these models were downscaled from PRISM 800 m data (Holden et al., 2016), SSURGO data and WINDNinja data as described in Landguth et al. (2015).

We selected these data because 250-m resolution better matches the scale of our sampling design than the other coarser-resolution data sets that are available (e.g., PRISM, DAYMET). Moreover, the variables that were available overlap with the climate and water balance variables found in previous studies to be highly associated with tree species distributions (e.g., Chang et al., 2014; Landguth et al., 2017; Piekielek et al., 2015)). These data were summarized by Spring (April, May, June) and Summer (July, August, September) averages for the period 1981–2010 and clipped to our study area. The climate data were associated with each PIAL sample point and with each absence point.

Table 1
Predictor variables used in the analysis. The data are 250 m resolution and are from Holden et al. (2016).

Group	Variable	Growing season period
Climate	Maximum air temperature	Spring (AprMayJu0 Summer (JulAugSep)
	Minimum air temperature	Spring (AprMayJu0 Summer (JulAugSep)
	Water vapor pressure	Spring (AprMayJu0 Summer (JulAugSep)
	Growing degree days	Growing Season (Apr-Sep)
	Shortwave radiation	Spring (AprMayJu0 Summer (JulAugSep)
	Snow water equivalent	April
Water balance	Soil water deficit	Spring (AprMayJu0 Summer (JulAugSep)
	Potential evapotranspiration	Spring (AprMayJu0 Summer (JulAugSep)
	Actual evapotranspiration	Spring (AprMayJu0 Summer (JulAugSep)

2.4. Statistical analysis

A stochastic gradient boosting model (gbm) (Friedman, 2002) was used to create bioclimate niche models of juvenile-sized PIAL (<1 cm dbh) and larger PIAL (>=1 cm dbh) to evaluate Objective 1. Gradient boosting is an ensemble learning technique that generates additive regression models by iteratively parameterizing a function based on the residual error of the last decision tree. Gradient boosting models have the advantage of accommodating missing data, outliers, and can handle complex interactions (Elith et al., 2008). Additionally, gbm greatly outperformed Random Forest in our projection accuracy.

Absence points for the PIAL models included locations of PIFL presence and five-needle pine absence points. Model evaluation was performed under a variety of methods. An out-of-bag (OOB) error estimate was calculated by comparing the modeled probability of presence using approximately two thirds of the field data, while withholding a subset of the remainder. Accuracy was evaluated by calculating: 1) the sensitivity, representing the true positive rate (TPR), 2) the specificity, representing the true negative rate (TNR), 3) the receiver operator characteristic curve (AUC). The importance of a specific predictor variable was calculated by examining the increase in prediction error within the OOB sample when the predictor variable was permuted while others were held constant (Pedregosa et al., 2014). The rate of prediction error with permutation of a specified variable can be interpreted as the level of dependence of presence or absence response to that variable (Cutler et al., 2007).

We also assessed relative contributions of each predictor variable to the predicted probability of presence with importance plots. Conditional density plots were used to determine the occurrence of the two size classes of PIAL individuals with respect to important predictor variables, controlling for the effects of other predictors. We then identified the threshold values for each important predictor for modeled probability of presence for each PIAL size class by determining the minimum value of each predictor and the lower 2.5th percentile for modeled probability of presence. These lower values were compared among the two size classes to evaluate warm and dry tolerances.

Model projections of climate suitable habitat were geographically constrained to elevations that were represented in sampling (2042–3055 m) using a digital elevation model. Suitable habitat was determined using a binary classification in which the probability of presence threshold was the value at which the ratio of sensitivity to specificity was equal to 1.

To address Objective 2, the spatial extents of suitable habitats were compared between the models derived from our field data of genetically identified individuals of individuals < 1 cm dbh, and individuals >= 1 cm dbh, and models from two FIA-derived data sets for reproductive-sized PIAL.

One of the FIA-derived models was from the previous habitat suitability analysis of Chang et al. (2014). This model was pertinent to the study because it was used to project PIAL habitat suitability under future climate scenarios and drew the important conclusion that area of suitable habitat is substantially reduced compared to the historic period. The FIA data were restricted to individuals > 20 cm dbh under the assumption that this size class represents cone-bearing individuals that were correctly identified in the field. Chang et al. (2014) used the "fuzzed" FIA data that are publicly available. FIA plots are located on a hexagonal grid with one plot measured in the field for approximately every 2,428 forested hectares (Bechtold and Patterson, 2005). Publicly available plot locations sampled prior to 2001 were fuzzed within 1.6 km of the actual locations, and additional swapping procedures are applied to a subset of plots, to protect landowner privacy and sample integrity (Smith, 2002). Predictor data were derived from the 30- arc-second (~800 m) monthly Parameter-elevation Regressions on Independent Slopes Model (PRISM), a derived product that interpolates local station measurements across a continuous grid (Daly et al., 2002). PRISM data includes monthly average minimum temperatures, maximum temperature, mean temperature, and mean precipitation. All monthly data were averaged for the temporal extent of 1950–1980 for the bioclimatic niche model.

Because the Chang et al. (2014) analysis was done at a coarser resolution (~800 m) and with uncertainty in geolocation, we derived a new SDM model using unfuzzed FIA data (Burrill et al., 2018). This model was based on exact plot locations, thus reducing uncertainty in georeferencing with the same 250-m predictor data used in the analyses of our field data. The FIA plot locations were joined to the Landguth et al. (2015) predictor data by FIA staff to avoid inaccuracies that could have resulted from using the publicly available "fuzzed" coordinates. FIA crews used the best available field-based guidelines to distinguish PIAL (e.g., (Arno and Hoff, 1989; USFS, n.d.). Crews also looked for cones on nearby trees when cone-bearing trees were not present on a plot. FIA plots with >=1 PIAL individual > 20 cm dbh were classified as presence. Plots with no PIAL individuals were classified as absences. The habitat suitability modeling and extrapolation for this data set were done using random forest (Breiman, 2001), the same technique as the Chang et al. (2014), computational limitations would not allow for a gradient booting approach to this analysis. All assessment of these models followed the same methods as Objective 1. We included in the analysis FIA plots in the same elevation range as the field data.

We then compared the spatial characteristics of suitable habitat resulting from analysis of our field data, Chang et al. (2014), and our new analysis based on unfuzzed FIA locations, all within the elevation limits of our field sampling. For comparison across different models of PIAL presence, suitable habitat was determined for each model using a binary classification in which the probability of presence threshold was the value at which the ratio of sensitivity to specificity was equal to 1. The spatial characteristics of suitable habitat were: percent of study area within the modeled elevation range, mean elevation, and upper 97.5th to lower 2.5th percentile of predicted presence. If the results for the genetically identified data show a larger extent of suitable habitats at lower elevations than the two FIA data analyses for adult sized individuals, this would suggest that the FIA based analyses were biased towards PIAL having suitable habitats only in colder and wetter settings and that Chang et al. (2014) overestimated PIAL sensitivity to projected future climate change.

3. Results

A total of 302 leaf samples were collected along the 13 transects and genetically identified. Among these, 45 samples were visually identified by the presence of seed cones (16 PIAL and 29 PIFL). The other 257 tree samples were identified by strictly genetic analysis. Genetic analysis identified 205 samples as PIAL and 97 as PIFL. Of the 45 samples

identified using seed cones, genetic identification matched visual identification.

3.1. Objective 1. Evaluating climate tolerances of PIAL size classes.

We found that the distribution of PIAL was strongly related to the climate and water balance predictors for both dbh size classes as evidenced by high confidence in the statistical models. The gbm statistical model for PIAL < 1 cm dbh displayed an out-of-bag (OoB) error rate of 15% with greater errors of omission (85%) than commission (45%) (Table 2). The AUC was 0.82 for this size class, displaying high relatively specificity and sensitivity. Threshold probability of presence for a binary classification was selected at 0.33 (i.e., where sensitivity = specificity). Diagnostics for the random forest model of PIAL >=1 cm dbh were similar.

The two PIAL size classes differed in the climate and water balance factors that contributed most to the statistical models. Summer maximum temperature had the highest variable importance for both PIAL size classes (Fig. 2). Spring maximum temperature and spring PET were also important for the smaller size class. For the larger size class, summer AET, spring SWE and spring maximum temperature were of high importance. The nature of the relationship between PIAL distribution and climate and water balance predictors also differed between the two size classes based on the partial dependence plots (Fig. 3). For PIAL < 1 cm dbh, probability of presence dropped with increasing spring and summer maximum temperatures and with spring PET. For PIAL >=1 cm dbh, probability of presence dropped with spring and summer maximum temperature and increased with summer AET and with April SWE.

Thresholds in climate and water balance tolerances associated with the warmer/drier 2.5th percentile of modeled presence revealed that the small size class was limited to cooler spring and summer maximum temperatures and lower spring PET than the larger size class (Table 3). The smaller size class tolerated lower levels of summer AET and April SWE, but these variables had relatively low importance in the model.

3.2. Objective 2. Comparing spatial extents of modeled suitable habitats.

The differences in climate tolerance of the two PIAL size classes resulted in the range of predicted presence for the small size class covering ~ 38% of the modeled area compared to the larger size class covering 44% (Table 4, Fig. 4). The predicted presence of the smaller size class also had a substantially higher lower elevational limit than the larger size class.

The random forest models for the two FIA data sets of reproductive sized trees (>20 cm dbh) performed well. The out-of-bag (OOB) error rates were about 16% for both with good balance of omission and commission and the AUC values were 0.91 and 0.88, displaying high relatively specificity and sensitivity.

Compared with the small size class from the field data model, the spatial distributions of suitable habitat for the two FIA data sets were somewhat smaller in area (about 30% of the modeled area) and had a higher lower elevation threshold (122 m). The model for the unfuzzed FIA data and finer grain size of analysis had spatial patterns of suitable habitat very similar to the Chang et al. (2014) data set.

Table 2
Confusion matrix from out-of-bag analysis for PIAL < 1 cm dbh, and PIAL >=1cm dbh.

Diagnostic	PIAL < 1	PIAL >= 1
Receiver operator characteristic curve	0.82	0.81
Out-of-bag error rate	0.15	0.17
Total	39	41
Commissions	33	34
Omissions	6	7
Threshold probability presence	0.33	0.4

4. Discussion

Give the disproportionately large influence PIAL has on subalpine ecosystems and its recent listing as a proposed threatened species, it is of high importance to better understand the species' potential response to future climate change. The broad goal of this study was to contribute to improving understanding of PIAL's sensitivity to climate change as a basis for mitigation and adaptation strategies to sustain the species in the GYE (see (USFS, 2011).

The high rates of mortality of PIAL from blister rust and mountain pine beetles across its range in the past two decades have raised alarm regarding potential impacts on ecosystem function, mutualistic species, and the population viability of PIAL in western ecosystems (Keane et al., 2017). It is perhaps ironic that the key need is to better understand the physiological tolerances of PIAL to climate. Such information is widely available for other tree species in silvics manuals (Burns and Honkala, 1990). Some factors that limit the lower range of PIAL are not fully known because the inability to distinguish it in the field from PIFL in the absence of reproductive tissue. The warm and dry tolerant PIFL overlaps in range with PIAL leading to inability to map the distribution of non-reproductive PIAL vs PIFL from lower treeline to the core of PIAL habitat at higher elevations.

Overcoming the limitations of species identification, would allow testing of hypotheses on the factors limiting the species at lower elevations. One hypothesis is that establishment of seedlings and growth of young trees may be limited by physiological intolerance to warm temperatures and/or low plant water availability (Hansen et al., 2016). An alternative hypothesis is that young PIAL are able to tolerate climatic conditions at lower elevations but are competitively excluded by other faster-growing tree species (Buermeyer et al., 2016).

Using a new genetic technique to uniquely identify PIAL, we quantified the climate and water balance characteristics of locations where seedling PIAL occurred relative to those for larger PIAL size classes. Under the assumption that competitive exclusion was unlikey for recently established individuals, we examined if seedling sized individuals occurred in warmer and drier locations than larger individuals whose distribution may have been filtered through the effects of competition with faster growing conifer species.

In contrast to this prediction, we found that juvenile-sized PIAL individuals were not found in warmer and drier settings than larger trees. The juvenile-sized trees, in fact, were not found in the warmest and driest locations occupied by larger size classes. Consequently, the statistical projection of suitable habitat across the GYE based on climate and water balance was 14% smaller and 200 m higher in elevation for juvenile-sized individuals than for larger individuals.

Our study is the first to quantify the lower elevation climate limits of PIAL. Several previous studies found that probability of presence of reproductive-sized PIAL was associated with relatively cool summer temperatures, late spring snowpack, higher summer precipitation, and lower summer vapor pressure deficit typical of subalpine settings (Bell et al., 2014; Chang et al., 2014; Schrag et al., 2008; Weaver, 2001). However, the higher temperature tolerances of PIAL seedlings and samplings were relatively unknown. One laboratory experiment (Jacobs and Weaver, 1990) found that optimal temperatures for photosynthesis of seedlings from the GYE were well above the summer temperatures typical of where PIAL is found in the GYE (Hansen et al., 2016). Studies elsewhere in the range of PIAL found that the species increased in growth rate with increasing minimum temperature (Millar et al., 2012) and increased in density and basal area in response to warmer, wetter conditions (Dolanc et al., 2013). Our results advanced on these previous studies by establishing that PIAL of all size classes were limited to cooler and moister locations generally above 2100 m, which is well above lower treeline.

It remains difficult to determine to what extent the realized niche of PIAL is a subset of its fundamental niche as limited by interspecific competition. Evidence that competition limits PIAL density and/or

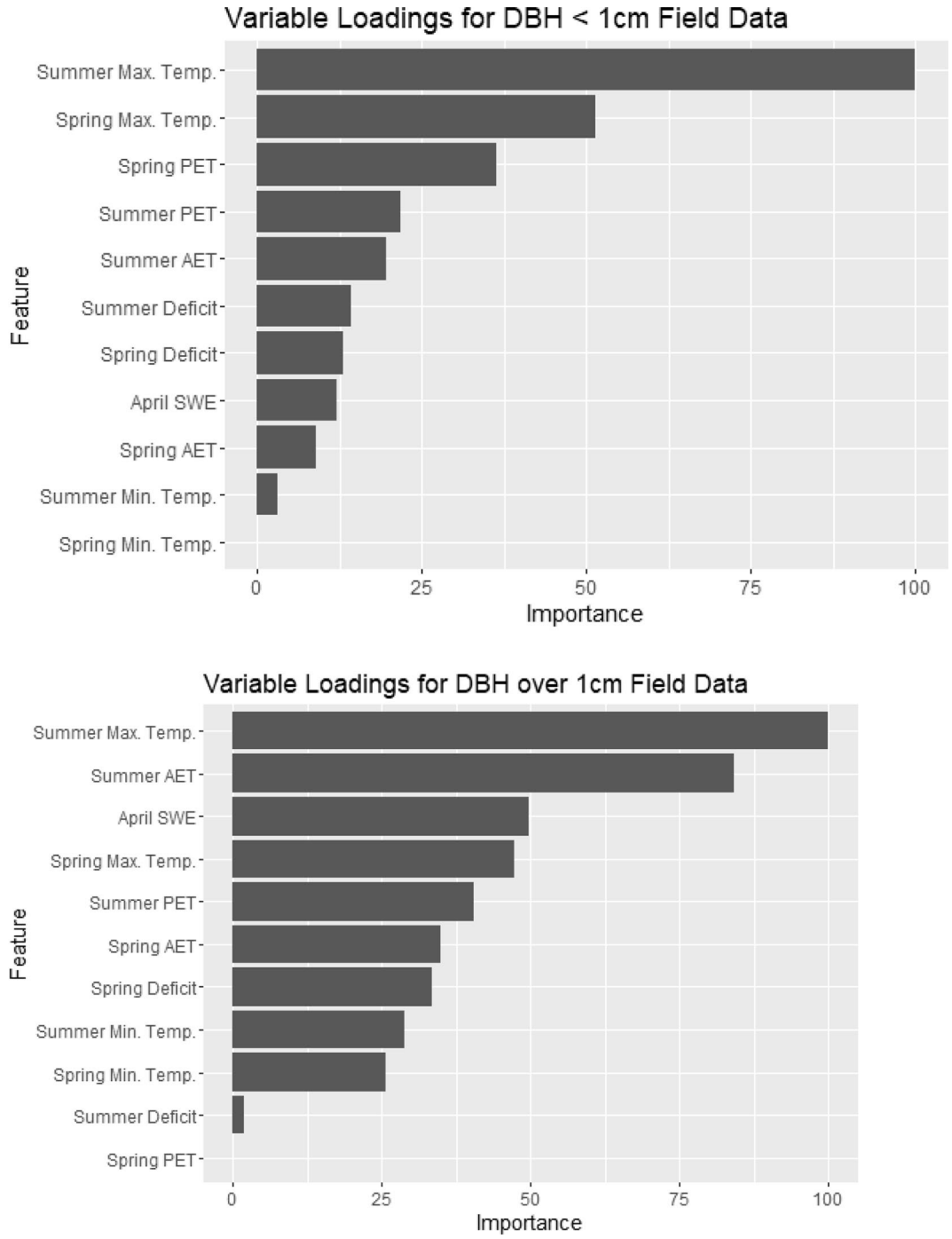

Fig. 2. Relative importance of variables included in boosted regression tree analysis of PIAL < 1 cm dbh versus PIAL >=1 cm dbh.

growth rates is reasonably strong in the wetter and warmer portions of the species range. For example, Campbell and Antos (2003) found that PIAL in western British Columbia was inhibited early in succession by lodgepole pine and later in succession by subalpine fir and Engelmann spruce(Campbell and Antos, 2003). Other evidence of competition was found in lower elevations in western Montana, where individual PIAL and subalpine fir were observed to be farther apart than expected if the trees were distributed randomly, implying competition for resources, whereas at high elevations, the two are found closer together potentially due to facilitation (Callaway, 1998). Keane et al. (2007) provided the most direct evidence of competitive effects when they observed a significant increase of PIAL diameter growth rate in the first five years after experimental removal of other tree species (See also (Retzlaff et al., 2018)).

In the colder and drier GYE, a study of co-occurrence of conifer species found little evidence of competitive effects on probability of presence or basal area of PIAL at low to mid elevations and only weak evidence for a negative competitive effect in the subalpine zone (Chang et al., 2014). It is also important to note that reductions in growth or density due to competition need to be severe to cause actual competitive exclusion of a species from a habitat. While competition is widely documented among tree species, competitive exclusion is rare (Clark et al., 2014). Our finding that juvenile-sized PIAL individuals had cooler and wetter climate thresholds than larger individuals contradicts the hypothesis that competitive exclusion is an important mechanism limiting the lower elevational distribution of the species in the study

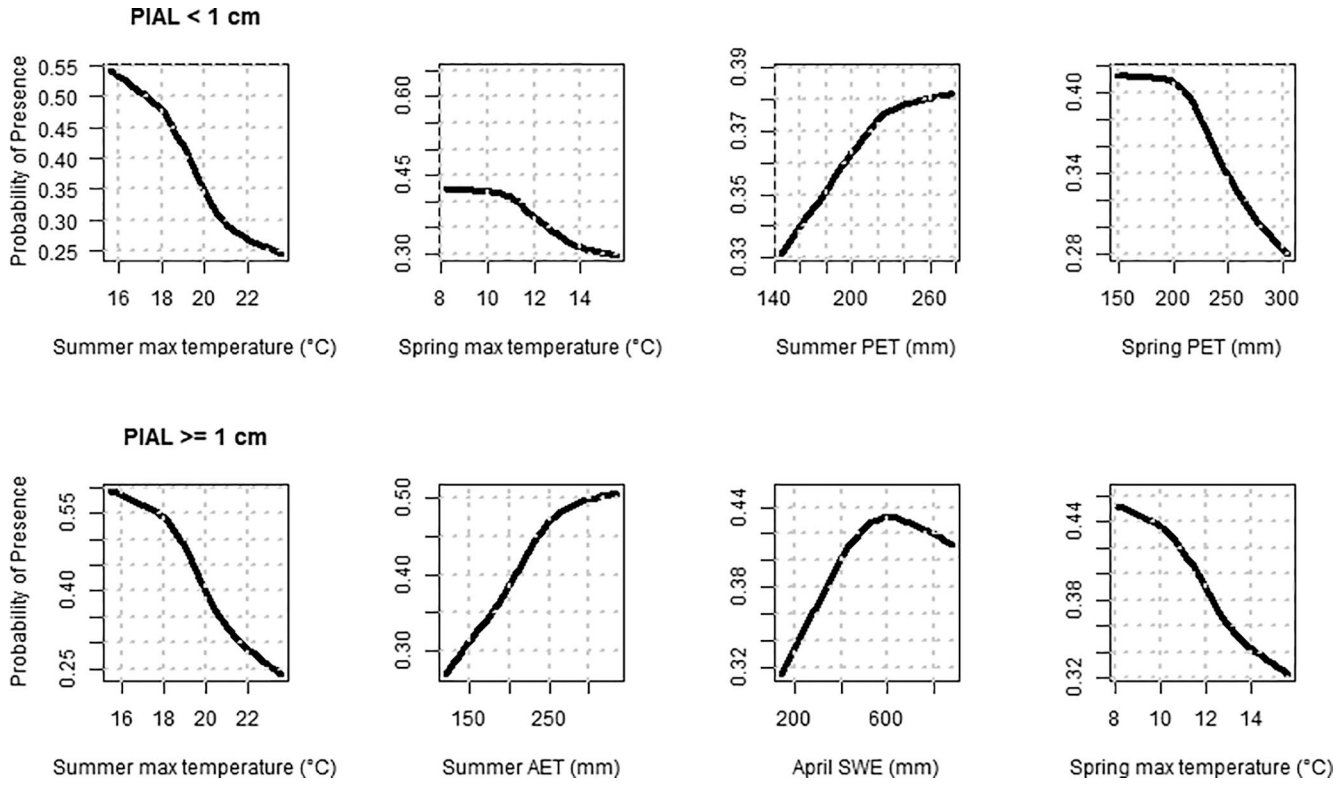

Fig. 3. Partial dependence plots for important variables from boosted regression tree analysis of PIAL < 1 cm dbh and PIAL>=1 cm dbh presence.

Table 3
Levels of the predictor variables associate with the lower to upper 2.5th percentile of modeled presence of the two Whitebark pine size classes.

Variable	2.5th Percentile	
	PIAL < 1 cm dbh	PIAL >= 1 cm dbh
Tmax summer	15.6–20.2 °C	15.7–22.6 °C
Tmax spring	7.8 °C – 12.3 °C	7.9–14.26 °C
Spring PET	157.8–249.9 mm	159.6–257.5 mm
Summer AET	176.6–295.2 mm	182.5–295.68 mm
April SWE	185.9–930.4 cm	206.2–920.5 cm
Summer PET	145.6–223.5 mm	147.1–228.4 mm

Table 4
Spatial dimensions of modeled binary presence within the elevational zones of the study for PIAL with data derived from our field samples and from our two FIA based analyses (reproductive sized trees > 20 cm dbh and likely accurately identified by species).

Diagnostic	Field sample data set (<1 cm dbh)	Field sample data set (>=1 cm dbh)	Fuzzed FIA data set from Chang et al., 2014	Unfuzzed FIA data set
Percent of study area	38.27%	44.42%	31.07%	28.29%
Mean elevation (m)	2668	2721	2734	2733
2.5% elevation (m)	2302	2102	2424	2424

area.

Our results, in fact, suggest that the warmer and drier conditions in the GYE since 1980 (Gross et al., 2016) have resulted in an upward shift in the lower elevational limit of PIAL establishment. Differences in climatic requirements for tree adult survival versus regeneration can result in regional regeneration failures and have influenced past changes in species distributions in the dry forest systems of the western United States (Jackson et al., 2009). Studies of the distributional responses of seedlings along elevational and latitudinal gradients provide evidence of upslope or northward migration (Vitasse et al., 2012) as well as range contraction (Zhu et al., 2012) in response to recent climate change. A study of six conifer species including PIAL across the western U.S. found that predicted probability of occurrence of seedlings were lower than probabilities of tree occurrence for all six species (Bell et al., 2014).

Based on the studies cited above, we suggest that the PIAL individuals now at the lower limit of their distribution established in previous decades under cooler conditions and are able to tolerate the warmer and dryer conditions, possibly because their roots extend to deeper and moister soil layers. Seedlings, in contrast, may not be able to establish under these conditions due to inadequate water balance within their shallower rooting zone. Thus, quite in contrast to the prediction of Buermeyer et al. (2016) that PIAL may expand under climate change because increased fire reduces competition from other conifers, our results are consistent with the prediction of Chang et al. (2014) that suitable habitat for PIAL will contract to higher elevations under climatic warming.

Our results offer tangential inference regarding this question of PIAL response to projected climate warming. Chang et al. (2014) used fuzzed FIA data for reproductive-sized trees (>20 cm) to model suitable habitat across the GYE for the historic period and to 2100 under climate scenarios. They found that suitable habitat was projected to move upslope and contract in area by 2100. We thus compared modeled suitable habitats for the current period from our field data for both size classes with the modeled historic suitable habitat from the Chang et al. (2014) data set. The objective was to determine if inclusion of the non-reproductive size classes of PIAL led to modeled suitable habitat being larger in area and extending to lower elevations. If so, it is reasonable to conclude that area of suitable habitat projected for 2100 climate scenarios would be larger than found by Chang et al. (2014).

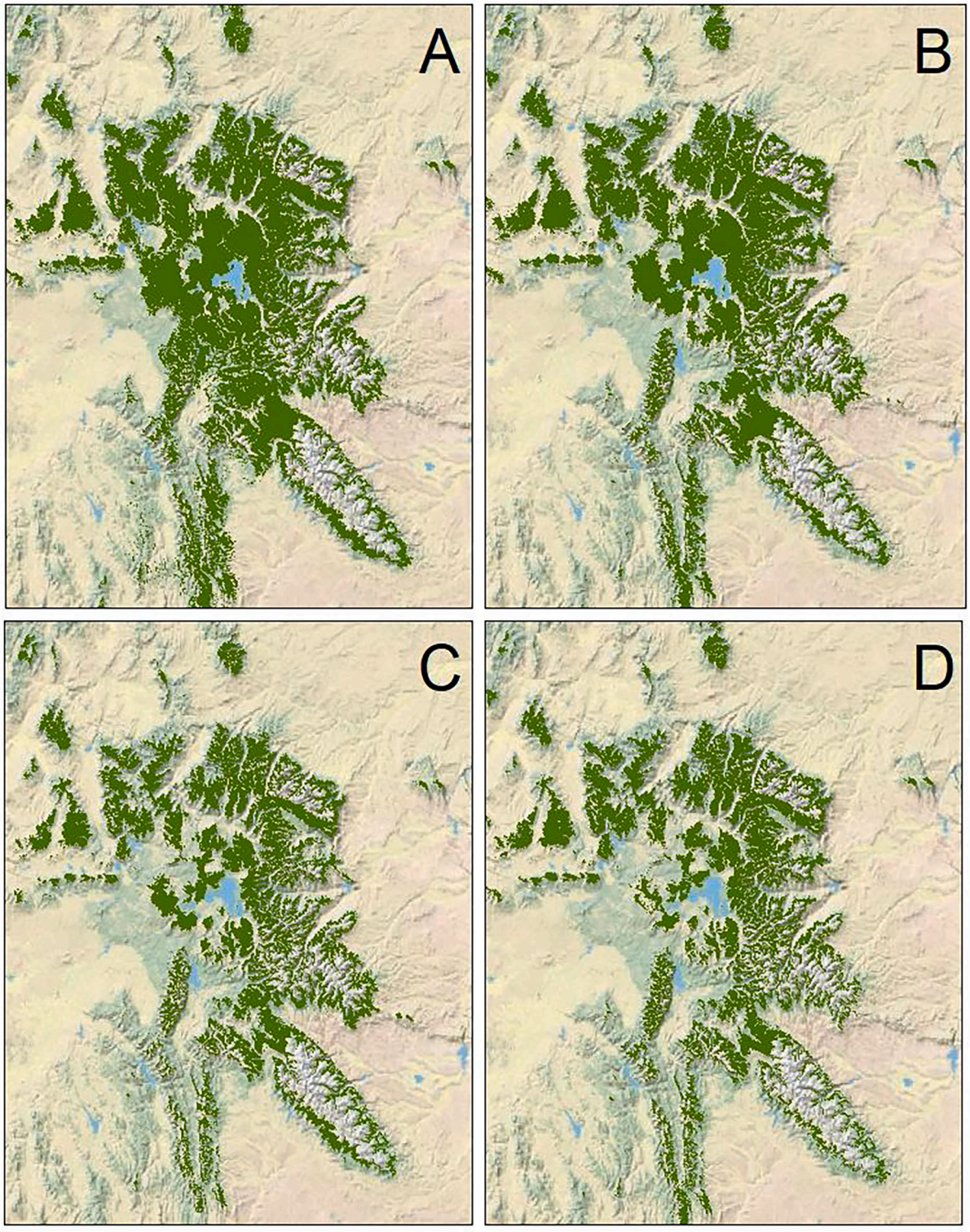

Fig. 4. The modeled presence of PIAL from field data of all PIAL >=1cm dbh (A). and field data of all PIAL < 1 cm dbh (B). Chang et al., 2014 (C) from a model of reproductive sized (>20 cm dbh) trees derived from unfuzzed FIA data (D).

We found that suitable habitat as modeled from our field data for PIAL < 1 cm dbh was 20% larger in area and extended 122 m lower in elevation than that modeled from the Chang et al. (2014) data. This suggests that the Chang et al. projections of PIAL suitable habitat in 2100 somewhat over-projected range contraction under climate change. The data sets for the two models differed in grain size of analysis (250 m vs 1 km), in locational accuracy (the Chang data was + -1.6 km in geolocation), and in the predictor data sets (Holden et al. 2016 vs the original PRISM data). The Holden dataset was designed to resolve topographic variations in temperature, snowmelt and soil water balance, and this may explain some of the differences in mapped suitability (i.e. microclimates). Thus, we also ran a model for unfuzzed FIA data for reproductive-sized trees merged with the 250 Holden et al. (2016) predictor data to see if its results differed from those from the Chang

et al. (2014) derived model. Modeled suitable habitat was nearly identical from the two FIA data sets. This suggests that the differences between results from our field data and from the Chang et al. data set were not due to differences in grain size or predictor data sets.

We feel our study design of sampling all size classes of PIAL along transects from lower treeline to mid elevations better captured the lower limits of PIAL than either of the two FIA data sets. We found the elevational limit of projected suitable habitat to extend about 120 m lower for PIAL < 1 cm dbh and 300 m lower for PIAL > 1 cm dbh than for the FIA data sets. This finding suggests that the GYE PIAL may retain more area of suitable habitat under future climates than projected by Chang et al. (2014). Nonetheless, large range contractions are still likely. Additional studies are needed to project PIAL habitat suitability under climate change with models parametrized with the climate tolerances documented in this study.

The primary management implication of this work is that efforts at protecting and restoring PIAL will be most successful if they take into account the climate tolerances of the species and spatially locate treatments with consideration of projected future climates. The Greater Yellowstone Coordinating Committee (GYCC), an interagency coalition of representatives from all federal agencies in the GYE, prepared a strategy aimed at protecting and restoring WBP across federally managed lands in the GYE (USFS, 2011). The GYCC WBP strategy outlined specific protection and restoration actions for managing WBP under current conditions. The management actions identified by the GYCC can be broadly categorized as planting of blister-rust-resistant PIAL seedlings, thinning (for competition removal, to promote regeneration, or to reduce mortality risk from mountain pine beetle), mountain pine beetle protection (using insecticides and pheromones to protect selected trees or stands), and fire use (either wildland fire use planning to protect cone-bearing PIAL trees from fire mortality or prescribed fire).

A framework for spatially distributing these strategies in the context of climate change was recently developed and recommended for application across the GYE (Ireland et al., 2018). A key component of that framework was to place each of the four strategies across the landscape with respect to PIAL habitat suitability. Three zones were recognized. Core is locations where climate is currently suitable and the climate is projected to remain suitable for PIAL. Suitable locations that are projected to become less climatically suitable were labeled “deteriorating zones”. “Future zones” were those areas, which are currently climatically unsuitable but are projected to improve in suitability in the future. These zones were defined by the habitat suitability modeling of Chang et al. (2014).

We recommend that our results be used to develop new projections of habitat suitability for seeding and larger sized PIAL under future scenarios and the zones of Ireland et al. be modified accordingly. This would allow the GYCC WBSC to proceed with placing the protection and restoration strategies across the landscape based on the best current scientific information.

5. Conclusions

In total, our results advance the current state of knowledge of PIAL in the GYE with regard to climate and water balance tolerances, elevational distribution, and fundamental vs realized niche. We documented for the first time the warm, dry limits of PIAL in the field in the GYE. We found no evidence consistent with the hypothesis that PIAL can tolerate warm dry conditions at lower treeline but are competitively excluded there. In contrast to this, the smallest size classes (and presumably the youngest) were associated with wetter and cooler settings. This suggests that the zone of regeneration of PIAL has shifted up in elevation in recent decades, perhaps associated with the observed warming in the GYE. Finally, our results suggest that published studies of PIAL response to future climates may have slightly over-predicted contraction of suitable habitats. Our results provide a basis for better parameterizing models of climate suitability to better ascertain the level of range contraction possibly in the ecosystem under future climates.

The major implication of these findings is that PIAL may well be highly sensitive to future climate change and undergo substantial reductions in area of suitable climate. To more accurately assess potential responses, data that distinguishes PIAL from PIFL across all age classes should be used to parameterize species distribution models and mechanistic simulation models. Such studies should be better informed about the physiological and demographic mechanisms that underlie PIAL performance across climate gradients. Thus, we recommend adequately scaled field and greenhouse experiments of PIAL response to climate, water balance, and competition, and mechanistic simulation projections parametrized accordingly. Such studies are needed to better inform on the climate settings that may best promote the management and restoration goals of federal agencies for PIAL (Ireland et al., 2018; USFS, 2011).

CRediT authorship contribution statement

Andrew J. Hansen: Conceptualization, Methodology, Writing - original draft. **Alyson East:** Software, Formal analysis, Data curation, Visualization, Writing - review & editing. **Robert E. Keane:** Conceptualization, Methodology, Resources, Writing - review & editing. **Matt Lavin:** Methodology, Resources, Writing - review & editing. **Kristin Legg:** Resources, Writing - review & editing. **Zachary Holden:** Methodology, Formal analysis, Resources, Data curation, Writing - review & editing. **Chris Toney:** Methodology, Formal analysis, Resources, Data curation, Writing - review & editing. **Franklin Alongi:** Methodology, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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