ENVIRONMENTAL RESEARCH
LETTERS

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RECEIVED
27 March 2025

REVISED
12 August 2025

ACCEPTED FOR PUBLICATION
19 August 2025

PUBLISHED
2 September 2025

LETTER

Whitebark pine in the United States projected to experience an 80% reduction in climatically suitable area by the mid-21st century

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Keywords: whitebark pine, species distribution model, moving window regression, climate change, endangered species, *Pinus albicaulis*

Supplementary material for this article is available online

Abstract

Whitebark pine (WBP; *Pinus albicaulis*) is a five-needle conifer tree species native to the western United States (US) and southwestern Canada. In the US, this ecologically important species is listed as 'threatened' under the Endangered Species Act because of population declines from compound stressors, including climate change, introduced white pine blister rust (WPBR), widespread outbreaks of mountain pine beetle, and altered fire regimes. Species recovery depends primarily on planting WBP seedlings that are resistant to WPBR, but suitable planting locations are likely to shift under climate warming. We modeled and mapped WBP climatic suitability in the US using forest inventory data and fine-scale (∼220 m) climate datasets under reference period (1961–1990) and mid-21st century climatic conditions. We projected an 80% reduction in the area climatically suitable for WBP by the mid-21st century. Moreover, 75% of the climatically suitable area for WBP under mid-21st century climate is located in designated wilderness areas and national parks. This could challenge WBP recovery efforts, as these protected areas strive to reduce human manipulation of ecological systems. WBP climate suitability maps resulting from our models can be used to identify priority or 'target areas' where planting will have the highest likelihood of success and to identify areas within the WPB's current range that are most vulnerable to rapid change should high-severity wildfires or mountain pine beetle outbreaks occur. Mapping WBP reference period and mid-21st century climate suitability is a fundamental step to efficiently prioritize restoration areas and develop a successful recovery program.

1. Introduction

Climate change is affecting forested lands globally and challenging resource managers to identify strategies to mitigate or adapt to changing ecosystem processes (Millar *et al* 2007, Keenan 2015). In western North America, these impacts include longer and more severe periods of drought (Hammond *et al* 2022), increasing fire activity (Parks and Abatzoglou 2020), and reduced post-fire forest recovery in many ecosystems (Davis *et al* 2019, Kemp *et al* 2019). These climate effects are altering where trees can establish and grow, leading to potential changes in the distribution and dynamics of major forest community types (Hansen *et al* 2001). Shifting distributions pose significant management concerns and greatly complicate recovery planning for species in decline that may be experiencing compound stressors.

Whitebark pine (WBP; *Pinus albicaulis*) is a five-needle conifer tree species native to the western United States (US) and southwestern Canada (figure 1). It generally inhabits cold, upper subalpine environments (Arno and Hoff 1990, Tomback *et al* 2001b) and is dependent on seed dispersal by the bird Clark's nutcracker (Tomback 1982). Considered both a keystone and foundation species, WBP promotes biodiversity, provides ecosystem structure, and influences ecosystem dynamics in high-elevation communities across its range (Ellison *et al* 2005, Tomback and Achuff 2010). For example, WBP establishes rapidly in subalpine environments after high-severity fire or other disturbances, facilitates community development, protracts snow melt at upper elevations, and produces large seeds that are an important food for several animal species (Tomback *et al* 2001b, 2016).

However, these important ecosystem services are at risk, with 51% of WBP standing trees dead throughout its US range as of 2016 (Goeking and Izlar 2018). Factors leading to this decline include the disease white pine blister rust (WPBR), the mountain pine beetle, altered fire regimes, and climate change (Tomback and Achuff 2010, Dudney *et al* 2020). A warming climate can have a direct impact on WBP through increasing drought and associated tree stress, but can have an indirect impact on WBP by promoting mountain pine beetle outbreaks and larger, more frequent fires at higher elevations (Bentz *et al* 2010, Higuera *et al* 2021). Consequently, WBP was listed as 'threatened' by the US Fish & Wildlife Service (USFWS) in January 2023 under the Endangered Species Act (ESA), thereby motivating restoration efforts.

Restoring WBP throughout its range requires mitigating the effects of WPBR, as only a small percentage of WBP trees are naturally resistant to this pathogen. Across Oregon and Washington, for example, Sniezko and Liu (2022) found that resistance to WPBR is highly variable geographically, and there is low (10%) survival for the majority of trees tested. However, there are some populations with high levels of genetic resistance (Sniezko and Liu 2022). Key strategies for restoring WBP include building resilience through planting WPBR-resistant seedlings and protecting WPBR-resistant trees from wildfire and mountain pine beetle infestation (Hoff *et al* 2001, Keane *et al* 2012). The National WBP Restoration Plan proposes prioritizing restoration and conservation treatments in core areas that represent 20%–30% of WBP range within a given land ownership jurisdiction (Tomback and Sprague 2022). The core area approach aims to increase genetic resistance to WPBR and allow effective seed dispersal by Clark's nutcracker (within and outside of core areas), which can spread WPBR-resistant genotypes. To maximize success and resource-use efficiency, restoration actions may need to be targeted to elevations and terrain predicted to retain WBP under climate change (Keane *et al* 2022, Tomback *et al* 2022). In other words, areas where WBP was historically prevalent may become less suitable under a warming climate (Chang *et al* 2014, Hansen *et al* 2021), and restoration in these trailing edge areas (see Parks *et al* 2019) may be less effective. Understanding the geographic distribution of areas climatically suitable for WBP under a warmer climate can help in the design and implementation of successful restoration strategies (Schrag *et al* 2008).

Our overarching goal is to determine how climate change will affect the geographic distribution of WBP in the US in the foreseeable future at a scale useful for management applications. Our approach is to model climatic suitability using forest inventory plots and high-resolution (∼220 m), topographically resolved climate datasets under both reference period (1961–1990) and mid-21st century climates. Our study encompasses the entire US WBP range, therefore complementing, expanding upon, and updating regional (e.g. Schrag *et al* 2008, Chang *et al* 2014) and geographically broader studies (Warwell *et al* 2006, McKenney *et al* 2007) that used coarser climate inputs and, in some cases, input data with less precise coordinates. We also sought to explicitly quantify and summarize climatic suitability in designated wilderness and other protected areas (i.e. National Parks) that have a disproportionate representation of the WBP range (Keane 2000, Tomback and Sprague 2022). Due to institutional, logistical, administrative and philosophical constraints that may limit restoration activities, an explicit focus on these protected areas underscores potential challenges that need collaborative and creative solutions to foster successful WBP restoration (Tomback *et al* 2022).

2. Methods

2.1. Data

We modeled WBP presence/absence in the US (figure 1) as a function of climate. WBP

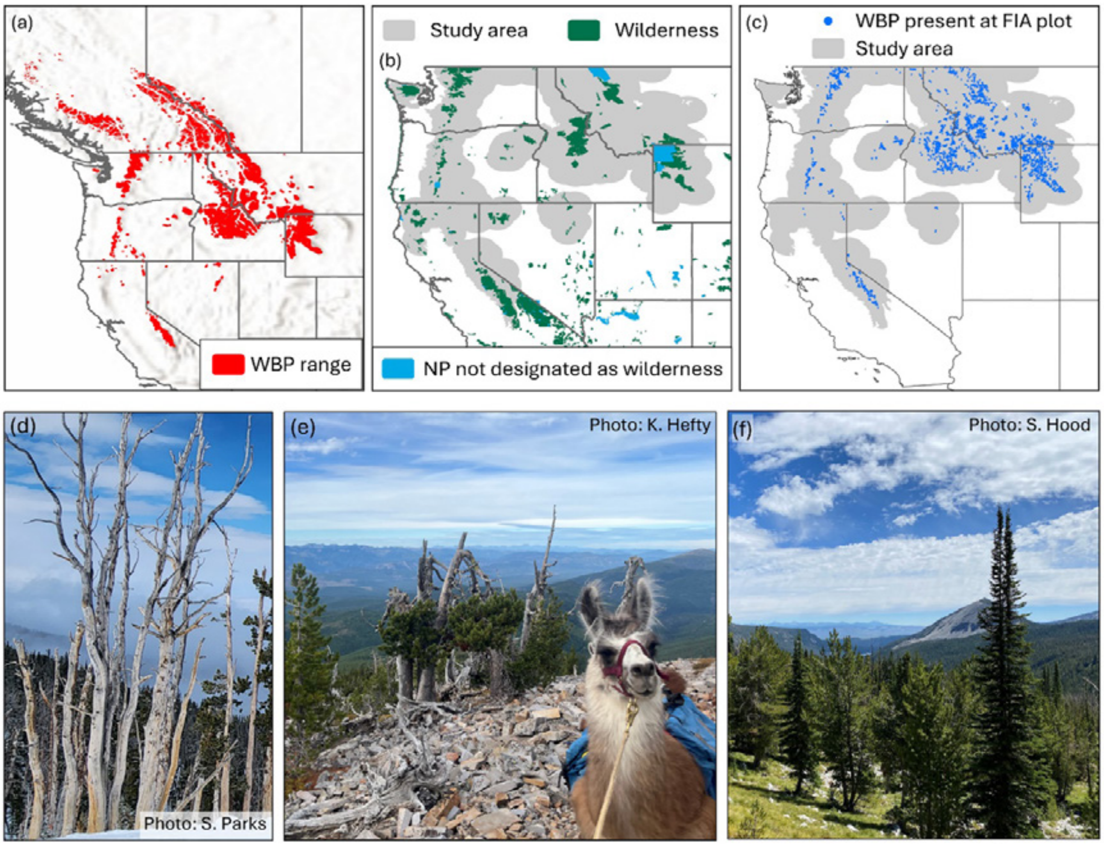

Figure 1. Maps showing the range of WBP in western North America (Smith and Collingwood 2014) (a), our study area defined by the USFWS (US Fish & Wildlife Service 2023) overlaid with protected areas (b) and the distribution of WBP at Forest Inventory and Analysis plots (c). Pictures show several dead WBP trees northeast of Yellowstone National Park (d), Chester the llama posing on a rocky ridge with declining WBP trees in western Montana (e), and a healthy WBP forest in southwestern Montana (f).

presence/absence was identified using plot data from the USDA Forest Service Forest Inventory and Analysis (FIA) program (Bechtold and Patterson 2005); plots in our study were measured from 2007 to 2021. WBP was considered present if a live seedling or live or dead sapling or tree was recorded on the plot. Dead saplings and trees were included because we assumed the reference period climate (described below) supported WBP establishment and survival even if WBP later succumbed to climate warming, wildfire, WPBR, or mountain pine beetles. WBP was assumed to be absent on non-forest plots. We did not use WBP data from other sources because they may be spatially biased, often document WBP presence but not absence, do not cover the entire study area, or have inconsistent sampling protocols across land ownership or administrative agency.

At each FIA plot, we extracted four climate variables (figure S1): annual climatic water deficit (CWD), annual actual evapotranspiration (AET), mean low temperature in January (T_{min}), and mean high temperature in July (T_{max}). Although FIA adds small errors to the publicly available plot coordinates and swaps the locations of some plots (termed 'perturbed coordinates') to protect landowner privacy and prevent differential management of plots, we used actual coordinates to extract the climate data. All climate variables were obtained from TopoTerra (Hoecker *et al* 2025; resolution ∼220 m), a downscaled characterization of TerraClimate (Abatzoglou *et al* 2018), and represent annual means (i.e. climate normals) spanning 1961–1990 (hereafter the 'reference period'). TopoTerra products provide an improvement over many other gridded climate datasets because they account for the influence of slope and aspect (i.e. solar insolation), with variables exhibiting warmer and drier conditions on slopes with southern aspects compared with corresponding northern aspects. Most other downscaled climate datasets use elevational lapse rates (Behnke *et al* 2016, Wang *et al* 2016) and therefore cannot account for fine-scale, topographically driven differences in solar insolation. TopoTerra exhibits high agreement with weather station T_{min} and T_{max}: $R^2 = 0.94$ and 0.95, respectively (Hoecker *et al* 2025). Future climate conditions were also obtained from TopoTerra and correspond to a 2 °C increase above pre-industrial global mean temperature that will likely manifest by the mid-21st century (Friedlingstein *et al* 2014). We used these four variables (CWD, AET, T_{min} and T_{max}) because (1) they, or variants thereof, are known to influence tree species distributions (including WBP) (Lutz *et al* 2010, Chang *et al* 2014, Davis *et al* 2016, Hansen *et al* 2021) and (2) these are the

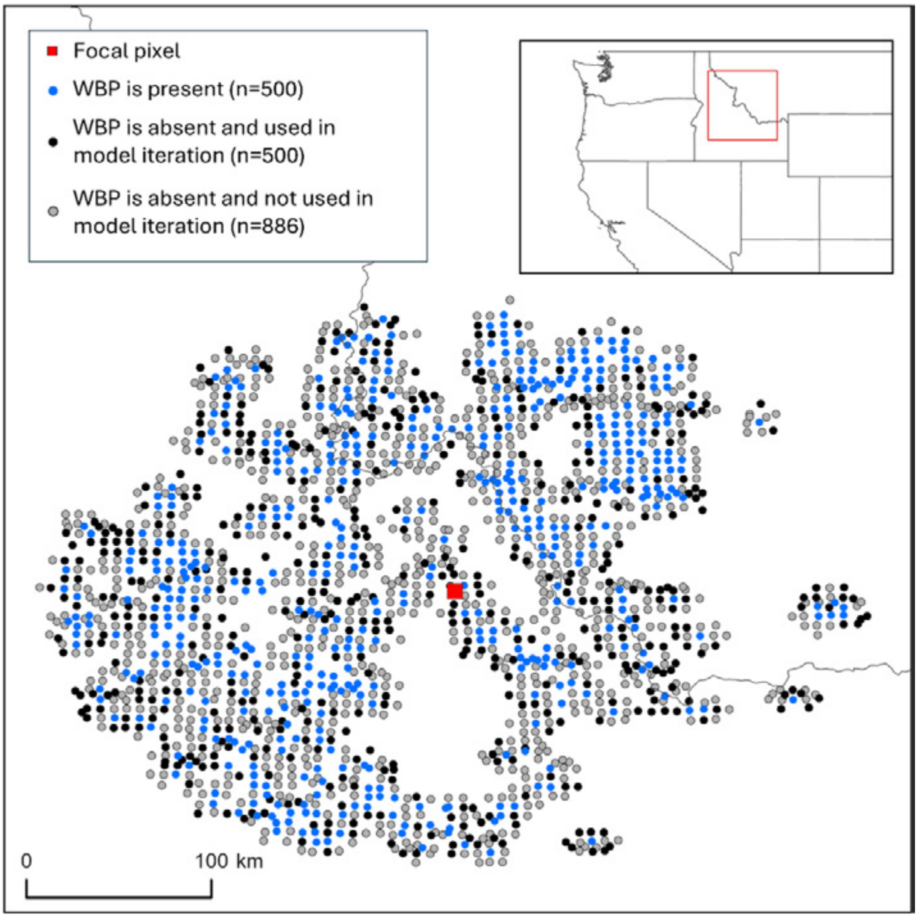

Figure 2. Example showing the FIA plots used in the moving window regression for a focal pixel. For each focal pixel (red box), the 500 nearest FIA plots with WBP present are selected (blue dots). Then, all FIA plots with WBP absent within 10 km of the WBP-present plots are identified, and 500 of those are randomly selected (black dots) for input into the logistic regression model describing the probability of WBP presence (the random selection of 500 WBP-absent plots was iterated five times; see Methods). With this approach, a unique logistic regression model was produced for each 220 m pixel (see figure 5); there are ∼21 million pixels/models in the study area. The red box in the inset map shows the spatial extent of this example. The FIA plot locations in this figure show the perturbed coordinates, although unperturbed coordinates were used for data extractions for use in the models.

only variables provided by TopoTerra (Hoecker *et al* 2025). Model performance testing (see below) further supported our choice of the four climate variables. The topographically sensitive downscaled TopoTerra product at ∼220 m resolution provides added value compared with other climate datasets with more variables but without topographically sensitive downscaling. The analyses and interpretations are restricted to WBP analysis units identified by the USFWS (US Fish & Wildlife Service 2023) (figure 1). The USFWS-defined region was delineated to ensure that modeling efforts did not miss any important areas or areas with potential occurrence, as there were several accounts of occurrence of WBP at lower elevations and lower-quality habitat than previously expected.

2.2. Modeling and analyses

As the relationship between WBP presence/absence and climate may be expected to vary over the analysis area (i.e. spatial non-stationarity) (Brunsdon *et al* 1996), we used a spatial moving window regression approach (Lloyd and Shuttleworth 2005, Yu *et al* 2023). The moving window regression identifies the best model for each pixel as represented by the model coefficients and fits. This approach is robust as each pixel has its own unique model (>20 million pixels/-models). To do this, we built a generalized linear model (family = 'binomial'; hereafter logistic regression) for each ∼220 m pixel in the study area ($n \sim$ 21 million pixels/models) (figure 2), as follows: (1) We identified the nearest 500 FIA plots with WBP present. We chose 500 WBP plots to ensure that we had enough data to produce robust models but not so many that the spatial variability produced by the moving window regression is obscured. (2) We identified all FIA plots with WBP absent within 10 km of the FIA-present plots. Given the relative sparseness of FIA plots (plots are ∼5 km apart), the 10 km search criterion ensures that an adequate number of WBP-absent plots are available for modeling. (3) We randomly selected 500 of these WBP-absent plots to create a balanced dataset of 500 WBP-present and 500

WBP-absent plots. (4) We performed logistic regression using the 1000 observations of WBP presence/-absence as a function of the four climate variables. A second-order polynomial was used for all climate variables to account for non-monotonic relationships. (5) We applied the model to predict the probability of WBP presence for the pixel under the reference period climate. (6) The model was then used to predict the probability of WBP presence under mid-21st century climate.

Because the random selection of 500 WBP-absent plots introduces some variability, steps 3–6 were repeated five times; we averaged the results (steps 5 and 6) to stabilize the reference period and mid-21st century predictions. After these steps were completed for all ∼21 million pixels in the study area, we built raster datasets depicting WBP climatic suitability under reference period and mid-21st century climate. Model performance was assessed using the area under the curve (AUC) statistic derived from the receiver operating characteristic curve; the AUC results of the five iterations (steps 3–5) were averaged and mapped. Lastly, it is worth noting that we also evaluated models using both 100 and 250 WBP-present and WBP-absent plots; we determined that these models resulted in some undesirable spatial artifacts and chose to use 500 WBP-present and 500 WBP-absent plots in the models, as described above.

This process resulted in gridded datasets depicting WBP climatic suitability (based on a probability with a range of zero to one) for reference period and mid-21st century climate for WBP in the US. To simplify descriptive analyses, we converted our continuous probability surfaces to binary surfaces, where pixels with climatic suitability $\geqslant$0.50 were considered 'climatically suitable'. We chose 0.50 as the threshold because we used balanced datasets in our models (i.e. an equal number of WBP present and absent). We then compared areas characterized as climatically suitable in both time periods, thereby producing gridded datasets depicting regions of WBP contraction, stability, and expansion under mid-21st century climate. We also quantified the extent of area climatically suitable for WBP in designated wilderness areas and/or national parks for both time periods. Note that portions of some national parks are congressionally designated wilderness, but some national parks do not have designated wilderness (figure 1(b)). We validated the binary classification by calculating the commission and omission error rates, which measure the percent of WBP-absent FIA plots that were classified as WBP-present and WBP-present FIA plots that were classified as WBP-absent, respectively. In addition to all the WBP-present plots, we selected WBP-absent plots within 10 km of the FIA-present plots for this validation. Although we used a probability threshold of 0.5 to define areas as climatically unsuitable/suitable, other thresholds could be used or multiple categories could be defined depending on the user and the intended use.

We also calculated the relative importance of each climate variable for each pixel in the study area. This required that we produce four additional models for every pixel, with each model excluding one of the variables. We then calculated the AUC for each of these models, the interpretation being that larger reductions in AUC when a given variable is removed, compared with the full model, indicate a higher relative importance of that variable. We calculated the relative influence for each variable as follows (Parks *et al* 2018):

$$\text{relative influence}_i = \frac{\text{AUC.full} - \text{AUC.no.var}_i}{\sum_{i=1}^{i=4}\left(\text{AUC.full} - \text{AUC.no.var}_i\right)} \times 100$$

where AUC.full is the AUC of the full model, AUC.no.var is the AUC of the model excluding any particular variable, and i represents one of the four variables. In models in which the AUC.no.var is greater than AUC.full, indicating that the model performs better without the variable of interest, the numerator, and thereby the relative influence of the variable, is set to zero. This issue was evident on only ∼2.5% of the pixels in the analysis area, the overwhelming majority of which were quite distant from documented WBP occurrences. Consequently, this artifact has a negligible impact on our study.

Lastly, we explored the climatic settings that exhibit decreasing versus increasing WBP climatic suitability (i.e. the trailing edge versus leading edge; Liang *et al* 2018) to gain a broad-scale understanding of those climate domains with high WBP vulnerability to a warming climate. We approached this by selecting only those records (i.e. pixels) with a probability $\geqslant$0.5 (i.e. climatically suitable) in either time period and then subtracted mid-21st century (figure 3(b)) from reference period climatic suitability (figure 3(a)). We used a linear model to assess the difference in suitability between the two time periods as a function of reference period $T_{\max}$, which was overall the most important variable in the models (see Results).

3. Results

Compared with the reference period climate (1961–1990), our models predicted an 80% reduction in the climatically suitable area for WBP by the mid-21st century (figures 3 and 4, table 1). In wilderness and national parks, we showed a 79% reduction in area climatically suitable for WBP, and when considering only wilderness, a 67% reduction (table 1). Proportionally, we predicted an overall shift towards protected areas in terms of the area climatically suitable for WBP. In the reference period, 50% of the

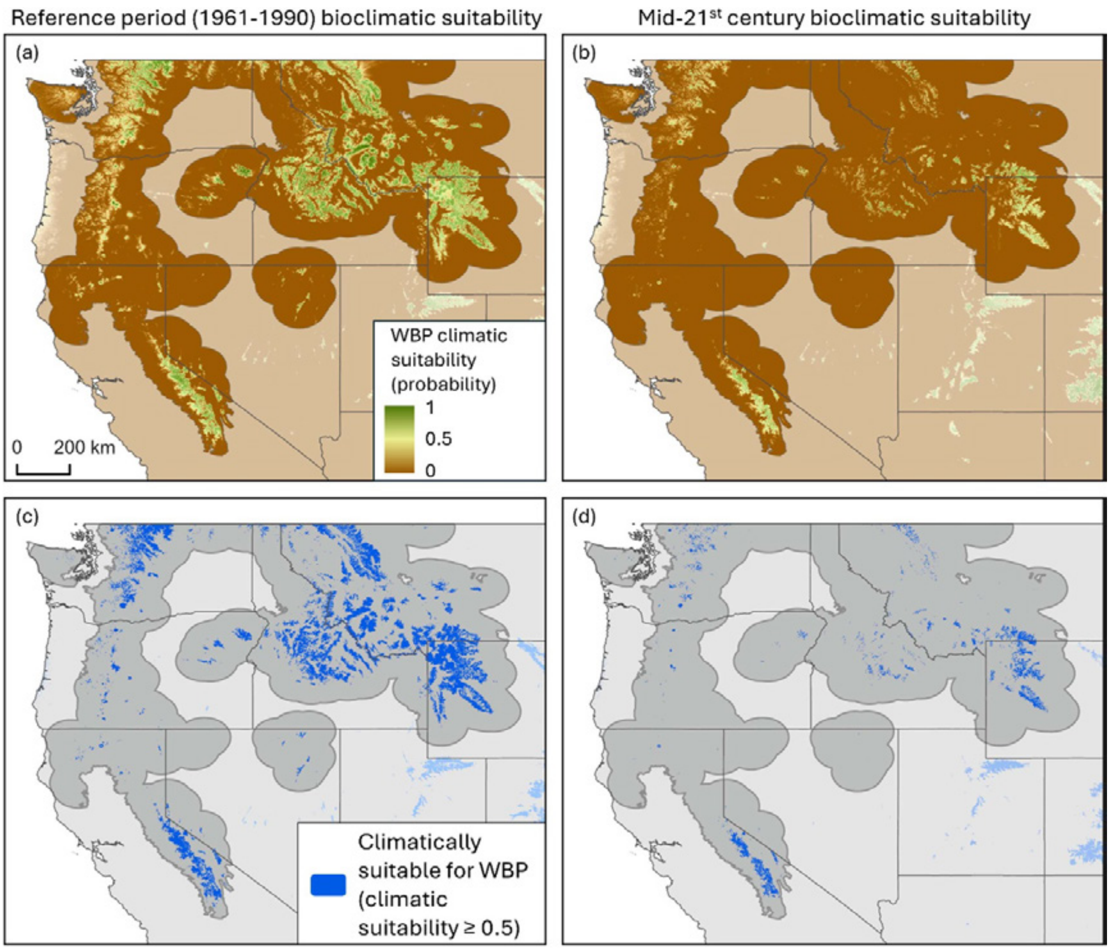

Figure 3. Maps showing the continuous ((a), (b)) and binary ((c), (d)) climatic suitability for WBP under the reference period (1961–1990) ((a), (c)) and mid-21st century climate ((b), (d)). The semi-transparent region is outside the study area and was modeled for discussion purposes (see Discussion); these areas are not included in any of our other results.

climatically suitable area was located in wilderness and national parks; this increased to 75% under mid-21st century climate. When considering only wilderness (i.e. excluding non-wilderness national parks), 41% of the area identified as climatically suitable for WBP was located in designated wilderness in the reference period; by the mid-21st century, this increased to 69%. Of the regions expected to show an expansion in area climatically suitable for WBP (figure 4), 86% of the area was located in designated wilderness and national parks.

Overall, our moving window regression models performed well, with an average AUC of 0.875, although there was some variability in model performance (figure S2). T_{max} was overwhelmingly the most influential variable in the models (figure S3); the mean relative importance for T_{max} was 76.5%. The second most influential variable was T_{min} (mean relative importance 16.1%), followed by AET (4.4%) and CWD (2.9%). There was considerable spatial variability in the relative importance of T_{max} and other variables; for example, the relative importance of T_{min} increased and T_{max} decreased in the Pacific Northwest (figure S3). For the binary classification (figure 3(c)), the commission and omission error rates were 6% and 14%, respectively.

WBP climatic suitability between the reference period and mid-21st century exhibited substantial decreases in warmer, lower-elevation climatic settings (i.e. the trailing edge; figure 4(d)). For example, when reference period T_{max} is 21 °C, WBP suitability (probability) is reduced by 0.56 (average across all models) under mid-21st century climate. Note that this finding (figure 4(d)) encompasses the average relationship across the study area even though there may be finer-scale and regional differences because of the moving window logistic regression (figure 5).

The model suggests there are several areas outside the study area that are climatically suitable for WBP (figure 3) under reference period climate and will continue to be so under mid-21st century climate, such as the Uinta Range in northeastern Utah, the Bighorn Mountains in north-central Wyoming, and the southern Rocky Mountains in Colorado. Even within the study area, there are mountain ranges with high WBP climatic suitability where WBP is not present (e.g. the White Mountains just east of the Sierra Nevada).

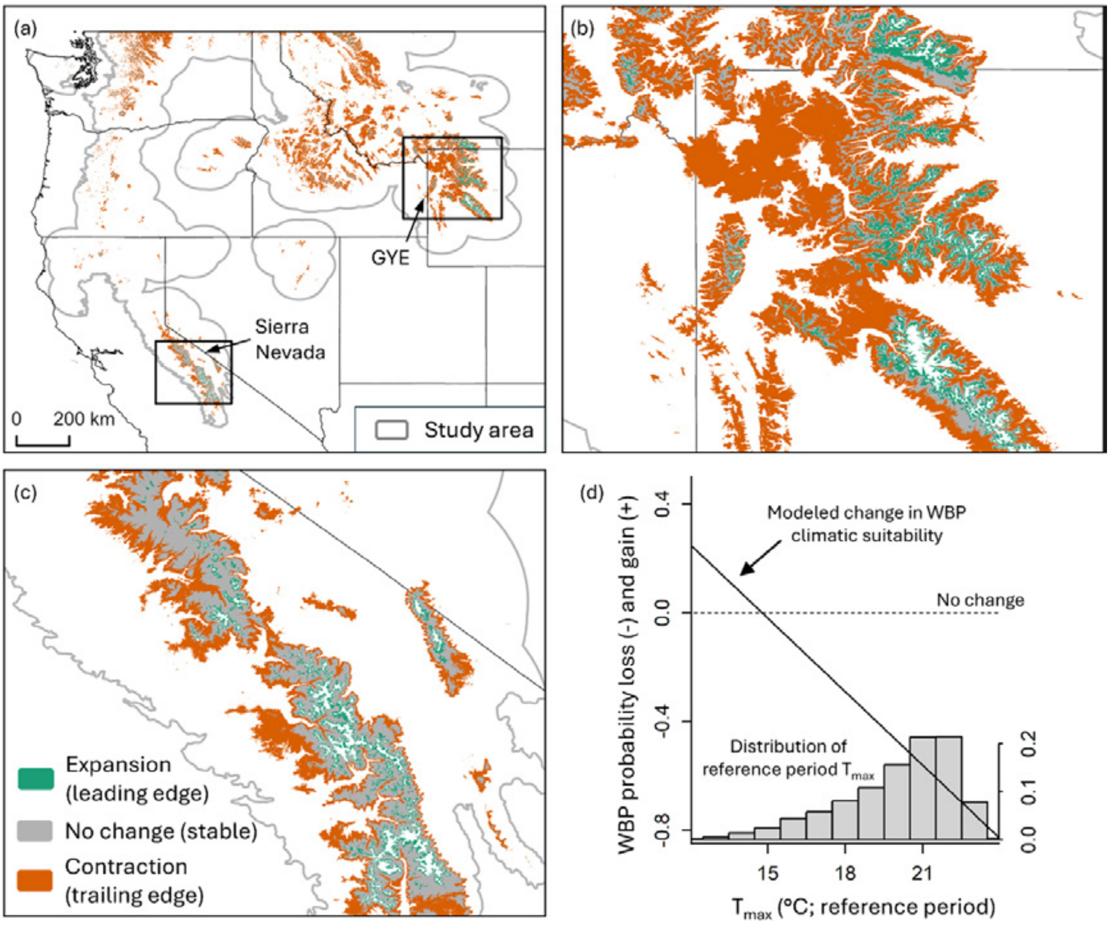

Figure 4. Maps showing areas of expansion (leading edge), no change (or stable), and contraction (trailing edge) in terms of areas climatically suitable for WBP for the study area (a), the Greater Yellowstone Ecosystem (b), and the Sierra Nevada (c). These were produced by subtracting the reference period binary classification (figure 3(c)) from the mid-21st century binary classification (figure 3(d)). Modeled change in WBP climatic suitability between the mid-21st century and the reference period (figure 3(b) versus (a)) along a gradient of reference period T_{max} is illustrated by the solid descending line in (d). This shows that most of the reduction in reference period WBP climatic suitability (i.e. the trailing edge) occurs where reference period T_{max} ranges from 18 °C to 22 °C. This is intended to serve as a broad interpretation, as this relationship varies across the analysis area given that we used moving window regression to conduct our study. The histogram in (d) shows the statistical distribution of reference period T_{max} for pixels that are considered climatically suitable (probability ⩾ 0.5) in either time period.

Table 1. Total area identified as climatically suitable (probability ⩾ 0.5) for WBP for the study area, designated wilderness and/or national park (NP), and designated wilderness.

	Climatically suitable for WBP		
Area of interest	Reference period (1961–1990) (km^2)	Mid-21st century (km^2)	Change between time periods
Core study area	142 690	28 048	80% reduction
Wilderness and/or NP	70 967	21 113	79% reduction
Wilderness	58 034	19 284	67% reduction

4. Discussion

Our models predict an 80% reduction in the area climatically suitable for WBP in the US by the mid-21st century. These models show reductions in the climatically suitable area at lower elevations and in warmer settings, with some limited expansions of climatically suitable area upslope (figure 4). These findings are consistent with several other observational and modeling studies showing similar responses of WBP (Hamann and Wang 2006, Schrag *et al* 2008) and other tree species in mountainous terrain (Lenoir *et al* 2008, Monleon and Lintz 2015). Mean maximum temperature in July (T_{max}) was overwhelmingly the most influential climate predictor of suitability, which is consistent with other studies of WPB in the Greater Yellowstone Ecosystem (GYE) (Hansen *et al* 2021) and Idaho (Airey and Taylor 2024). The general decline in WBP climatic suitability with increasing T_{max} (figures 4(d) and 5) supports

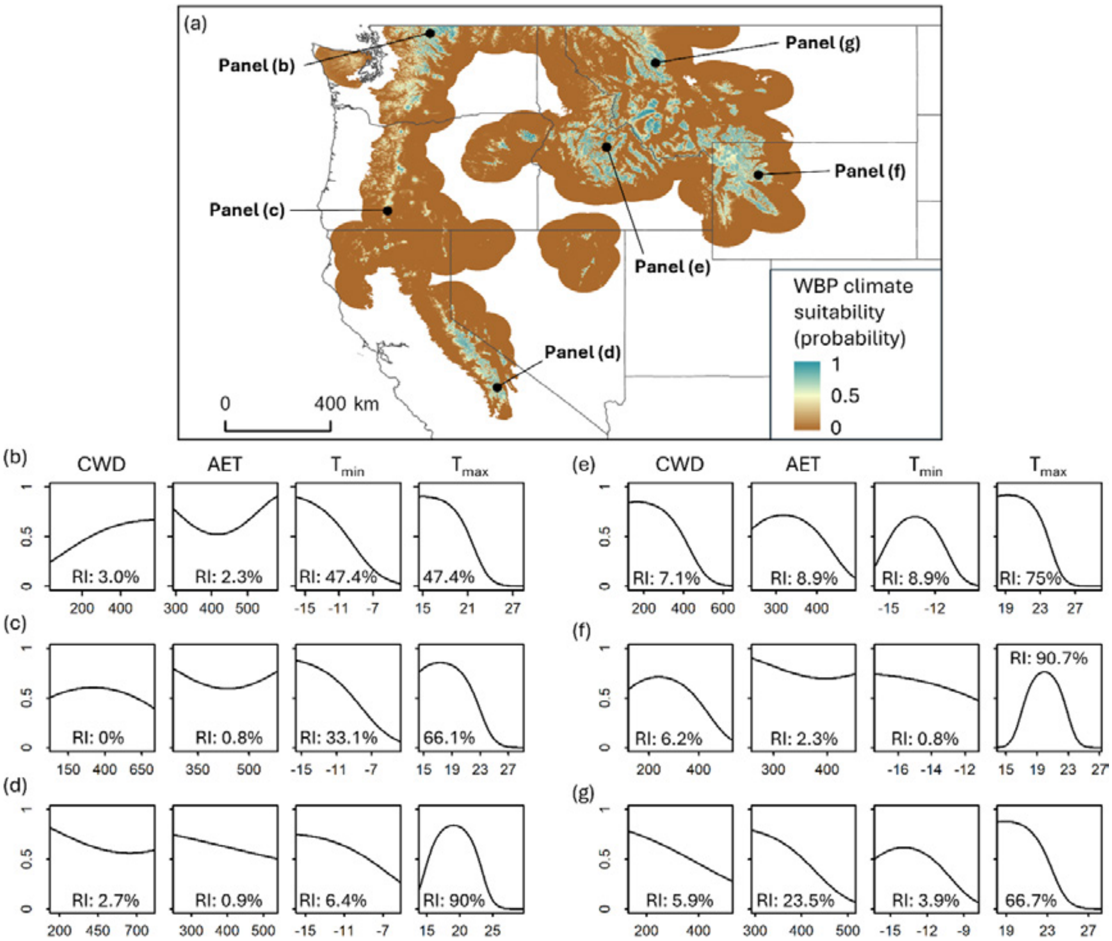

Figure 5. Examples illustrating the relationships between WBP climatic suitability and each of the four variables used in the models. The map shows climatic suitability under reference period climate (1961–1990) and the locations of six pixels (a), each with its own model and corresponding relationships (b)–(g). The *y*-axes represent the probability of suitability as predicted by the logistic regression model for the pixel. For each pixel, variables with higher relative importance (RI) indicate those with the strongest influence on WBP climatic suitability.

previous work showing increased WBP mortality with warming temperatures (Young *et al* 2023).

A recent study by Pederson *et al* (2025) documented a site in the GYE in which receding glacial ice exposed a stand of mature, downed and long-dead WBP trees. The study revealed that during the mid-Holocene (∼5500 years ago), WBP trees lived at much higher elevations than they do today (∼180 m elevation above the contemporary treeline), thereby lending empirical support to our models. Our models show very low climatic suitability for this GYE site under reference period climate (probability = 0.20) but high suitability under mid-21st century climate (probability = 0.76) (figure S4). As summer temperatures similar to the mid-Holocene are expected to emerge over the coming years in this region, the findings of Pederson *et al* (2025) provide an interesting corroboration of our projected WBP climatic suitability (figure S4).

In the US, approximately 88% of the WBP's range is managed by federal agencies, including the Forest Service (74%), National Park Service (10%), and Bureau of Land Management (4%) (US Fish & Wildlife Service 2020). The high-resolution (∼220 m) gridded datasets produced in our study may help inform agency restoration efforts from local to national scales, for example by helping to identify restoration 'core areas' (Jenkins *et al* 2022, Tomback and Sprague 2022). Furthermore, the products we have produced can support federal agency land use planning by providing valuable spatial datasets for evaluating potential overlap of projects that may affect WBP and helping to facilitate 'section 7' ESA consultations, which requires consultation with the USFWS on federal projects that may affect ESA-listed species. The datasets could help determine when, or more specifically where, certain levels of consultation or conservation measures are required. Restoration actions and recovery criteria will be developed under the USFWS's Whitebark Pine Recovery Plan, which is currently in preparation, and the spatial datasets we produced can make this plan and other USFWS decisions more defensible. Also, our findings are relevant to other ESA-listed species, such as the Canada lynx, North American wolverine and grizzly bear, whose use of WBP may be important to their life cycle or which may share similar climatic needs with WBP. Although our study directly addresses the need for range projections for a legally protected species in the US, the methods here are transferable to numerous countries with existing national forest inventories (Corona *et al* 2011). For example, although our model was calibrated and applied within the US, our methods could be reproduced for the Canadian range of WBP if sufficient ground observations exist.

As WBP restoration will require significant investment in personnel and funding, agencies may consider spatially prioritized, climate-informed management strategies (Ireland *et al* 2018) that maximize the probability of success (Jenkins *et al* 2022). That is, restoration actions could be prioritized to areas that will remain climatically suitable for WBP for the foreseeable future (Keane *et al* 2022). For example, areas that are expected to remain climatically stable or even areas with expanding WBP climatic suitability (i.e. the leading edge) (figure 4) could be prime sites for restoration activities such as planting WPBR-resistant seedlings. Planting in such areas could be important in increasing the return on investments incurred in the seedling production process. Planting in climate-appropriate areas could reduce planting failures while also optimizing the investment in WBP restoration efforts in general. Conversely, it might be wise to discount trailing edge sites for some restoration activities (e.g. planting WPBR-resistant seedlings and direct seeding efforts) (Pansing and Tomback 2019, Gilbert *et al* 2020). However, trailing edge populations, particularly if they have high genetic diversity or WPBR resistance, could still be important for some restoration activities, such as limiting severe wildfire (see Slaton *et al* 2019), protecting trees from mountain pine beetle infestation, and seed collection. Our maps could therefore be paired with fire and insect risk maps (Potter and Conkling 2022, Jaffe *et al* 2024) to identify areas that could benefit from fuel reduction and restoration treatments to reduce the likelihood of high-severity wildfire and mountain pine beetle outbreaks.

By the mid-21st century, our results show that 75% of the area climatically suitable for WBP will be concentrated in wilderness and national parks. Yet these areas have legally mandated goals to minimize modern management interventions. The ‘untrammeled’ character (i.e. intentional management interventions are generally discouraged) is a key pillar in managing designated wilderness; however, maintaining ecological communities such as WBP ecosystems (i.e. naturalness) is also fundamental for wilderness management (Cole and Yung 2012, Landres *et al* 2015). Wilderness law and policy allow management intervention to support species conservation if the specific actions are minimized to the greatest extent possible. Since the recovery of WBP is not likely to occur without intervention given the prevalence and lethal impacts of WPBR (Hoff *et al* 2001, Tomback and Achuff 2010), restoration in protected areas will almost certainly be required if society intends to recover and ultimately delist WBP. Thus, restoration strategies such as ‘direct seeding’ (sowing seeds rather than planting seedlings) could be viewed as more appropriate since they may be less intrusive (Pansing and Tomback 2019, Tomback *et al* 2022). The charge to ‘recover and delist’ WBP under climate change, given the projected 80% reduction in area climatically suitable for WBP by the mid-21st century, may entail further agency discussion and development of management strategies.

Like most studies projecting species’ range shifts under a warming climate, disequilibrium dynamics must be considered when interpreting our findings, meaning that there could be a lag in the time it takes for species to undergo range shifts (Bertrand *et al* 2016, Johnstone *et al* 2016). Disequilibrium may occur on the trailing edge of a species range because large mature trees have access to resources (e.g. water) that buffer against a warming climate and are able to persist even though seedlings of the same species may be unlikely to establish and grow (Jackson *et al* 2009). WBP generally occurs in energy-limited environments and has been experiencing increased growth and resin duct defenses under recent warming trends that may bolster resistance to mountain pine beetle (Dudney *et al* 2023, Kichas *et al* 2023) and also contribute to disequilibrium in the trailing edge. Likewise, disequilibrium may occur on the leading edge of a species range due to dispersal limitations and competition with extant species that prevent movement into new climatically suitable areas (Svenning and Sandel 2013), although WBP is effectively dispersed by Clark’s nutcrackers (Tomback 1986, Tomback *et al* 2016). Some of these factors may slow WBP trailing edge contractions and leading edge expansions, but we posit that a large reduction, if not the projected 80% reduction, in area climatically suitable for WBP by the mid-21st century is plausible given non-climatic factors such as WPBR and climate-mediated disturbances such as wildfire and mountain pine beetle. This is exemplified by the findings of Goeking and Izlar (2018) who found that 51% of standing WBP trees in the US were dead as of 2016, with most of the mortality occurring in the previous 10–20 years.

Our models did not explicitly incorporate the effects of biotic (i.e. competition and mountain pine beetle) and abiotic interactions (i.e. wildfire), which are increasingly recognized as important factors influencing current and future ranges of some species (HilleRisLambers *et al* 2013, Sanczuk *et al* 2024). We argue, however, that our models *implicitly* incorporate these factors to a certain degree. Our low model commission rate (i.e. WBP is absent but model predicts present) and omission rate (i.e. WBP is present but model predicts absent) further supports this reasoning. Our model commission rate in particular is much lower than the commission rate by Schrag *et al* (2008), who urged caution that their model did not well reflect abiotic and biotic factors influencing WBP occurrence. In addition, many of the tree species that competitively exclude WBP, such as lodgepole pine and subalpine fir (Iglesias *et al* 2015), are generally more prevalent in lower-elevation and warmer settings than WBP (Hansen *et al* 2016, van Wagtendonk *et al* 2020). Therefore, areas of lower WBP climatic suitability in the elevations just below the WBP climatic 'sweet spot' are probably more climatically suitable for these competing tree species, which also have greater shade tolerance than WBP and thus are more likely to thrive in lower-elevation, denser forests (Arno and Weaver 1990). As the areas of climatic suitability for these competing tree species move upslope with climate change (cf Gray and Hamann 2013), they are likely to displace existing WBP, hence the large area of WBP trailing edge (figure 4). Likewise, WBP has about the same fire resistance as competing species such as lodgepole pine and subalpine fir (Stevens *et al* 2020, Hood *et al* 2021), suggesting that high-severity fire regimes are likely to limit the distribution of WBP. As wildfire is generally more severe (and lethal to WBP) in the warmer climatic environments that also support tree species that can outcompete WBP due to differences in life history traits, such as higher seed production and shade tolerance (Campbell and Antos 2003), our models implicitly capture, at least to some degree, the effect of high-severity fire regimes on the distribution of WBP. It is worth noting, however, that high-severity fires also create conditions favorable for the establishment of WBP seedlings (via seed dispersal through Clark's nutcracker into burned areas) (Tomback *et al* 2001a), although large patches of high-severity fire may reduce the likelihood of WBP recruitment (Leirfallom *et al* 2015).

The findings of our study are focused on geographic areas in proximity to observed WBP occurrences and are guided by the distribution of WBP in the US as assembled by the USFWS (figure 1) (US Fish & Wildlife Service 2023). However, we also modeled WBP climatic suitability beyond the defined study area (across all 11 western states) to provide a more comprehensive view of potential range, and found that there are several areas outside the study area that are climatically suitable for WBP (figure 3). In these areas, biogeographic history and seed-dispersal limitations are likely to have prevented WBP from establishing (Tomback 1982, Jorgensen and Hamrick 1997). Nevertheless, these areas of high climatic suitability outside the current WBP range may provide restoration opportunities (managed relocation; assisted migration), while noting that such activities may be controversial (Schwartz *et al* 2012).

5. Conclusions

Our study used consistent datasets across the US range of WBP to produce high-resolution (∼220 m) maps of WBP climatic suitability under reference period (1961–1990) and mid-21st century climate that may be useful to land management agencies tasked with recovery efforts. Our products may be useful to land management agencies who want to tailor restoration efforts to areas that are climatically suitable to WBP under climate change or that intersect with areas at high risk of wildfire or mountain pine beetle outbreak. For example, planting seedlings resistant to WPBR may be more successful in areas where WBP is projected to be stable or expand under mid-21st century climate (figure 4). Nevertheless, the projected 80% reduction in area climatically suitable for WBP under mid-21st century climate will challenge WBP restoration efforts. These challenges may be magnified by the procedural management constraints in wilderness and national parks (Boerigter *et al* 2025), where the majority of the climatically suitable area for WBP is concentrated under mid-21st century climate. Given the prevalence and lethal impacts of WPBR (Hoff *et al* 2001), recovery of WBP is not likely to occur without management intervention (Tomback *et al* 2001b, Meyer *et al* 2023). Overcoming restoration constraints inside and outside protected areas will almost certainly be required to preserve WBP as an ecologically important subalpine species.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.6084/m9.figshare.29485691.v1.

Acknowledgment

We thank A Hendrix and T Spector for providing feedback over the course of this project and the dedicated FIA teams who collected and processed the field data. This research was supported in part by the US Fish & Wildlife Service (USFWS) and USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USFWS, USDA or US Government determination or policy.

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