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Quantifying current and potential future impacts of balsam woolly adelgid infestation on forest biomass

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ABSTRACT

Balsam woolly adelgid (*Adelges piceae;* BWA) is an invasive forest pest in the US whose infestation in fir forests can cause widespread tree mortality. A growing body of evidence suggests that the severity of BWA's effects is linked to climatic conditions, where sites featuring seasonally warmer temperatures tend to demonstrate higher degrees of insect-induced forest degradation. Thus, a warming climate may promote the expansion of BWA-driven damage, particularly in highly susceptible subalpine fir (*Abies lasiocarpa*) forests. The degree to which climate change may foster BWA infestation and the relationship between current and future infestation damage severity are largely unknown. To understand BWA's potential climate-driven impacts on subalpine fir forests now and in the future, we built a field-validated, spatially explicit predictive model that estimates BWA infestation severity as a function of locally downscaled temperature variables. Using only four seasonal temperature variables, our model was able to explain over 78% of variance in measured severity. We applied that model to the prediction of severity for five different time periods (2020, 2040, 2060, 2080, and 2100), with the 2040 and onward predictions being driven by four separate climatic shared socioeconomic pathways (SSP126, SSP245, SSP370, and SSP585). These high resolution (~30 m) maps were compared to spatially coincident modeled estimates of subalpine fir aboveground biomass, the results of which provide valuable insight into the degree to which BWA may drive forest degradation, loss of ecosystem services, and increase in available fuels. In northern Utah, the southeasternmost extent of BWA infestation in the western US, the two major mountain ranges, Wasatch and Uinta, demonstrated very different climatic susceptibility to infestation damage, with the former being highly exposed to BWA-induced degradation under even moderate climate projections, and the latter being fairly robust against BWA's effects in all but the most extreme climate scenarios. In 2020, 41% of the study area's subalpine fir biomass is climatically exposed to some level of damage from BWA. By 2100, even under moderate climate projections (SSP245), 79% will be exposed, with 37% predicted to feature relatively high severity. By placing our results within the context of the Resist, Accept, Direct land management framework, we offer spatially explicit guidance to inform current and future silvicultural practices to mitigate future damage to subalpine fir forests at the leading edge of BWA expansion in the western US.

1. Introduction

In a warming climate, forests are being exposed to increased stress from both biotic and abiotic drivers (Allen et al., 2010; Anderegg et al., 2016; Hartmann et al., 2022). In moisture-limited portions of the Western US, elevated temperatures coupled with severe and extended droughts have pushed trees beyond their survival capacity, causing widespread mortality events in a range of forest and woodland ecosystems (Buotte et al., 2019; Stanke et al., 2021; Thorne et al., 2018). Stressed trees are also more susceptible to damage and mortality from other agents, such as forest pests (Canelles et al., 2021). Furthermore, warmer temperatures can also promote the survival and reproduction of insects who feed on trees, resulting in population growth and spread well beyond historical levels (Jactel et al., 2019). Changing climatic

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conditions can be particularly favorable to nonnative invasive insects, allowing them to readily spread, colonize, and thrive in the absence of natural predators (Gutierrez and Ponti, 2022; Logan et al., 2020). These compounding factors create a set of conditions that are ripe for widespread declines in forest health.

Forest degradation results in a decrease or loss of critical ecosystem services, such as carbon sequestration, snowpack retention, provision of habitat, sourcing of wood products, and recreation, among others (Gao et al., 2020; Riccioli et al., 2019). Aboveground biomass (AGB) acts as an important proxy for many of the services that trees provide, representing the mass of live aboveground vegetation, typically per unit area (Duncanson et al., 2019). It is directly related to the amount of carbon stored in vegetation, is an important predictor of habitat quality, can be used to estimate timber economic value, and acts as the basis for quantifying fuel loads and consumption thereof due to fire (Melito et al., 2018; Soriano-Luna et al., 2018; Temesgen et al., 2015). And, importantly, many studies have mapped AGB with high accuracy using a range of remote sensing and geospatial datasets (Lu et al., 2016). Accordingly, maps of AGB can provide an important basis for evaluating potential effects of climate-induced forest degradation (Gao et al., 2020).

The balsam wooly adelgid (*Adelges piceae*; hereafter BWA) is a nonnative invasive forest insect introduced to North America from Europe in the early 20th century (Davis et al., 2020). With separate introductions on the east and west coasts, the insect has spread slowly but widely throughout the US over the last hundred years (Havill et al., 2021). Its effects in the northwestern US have been particularly acute, with widespread mortality resulting from infestation primarily of subalpine fir (*Abies lasiocarpa*) (Hain, 1988; Zilahi-Balogh et al., 2016). BWA is a very small (<1 mm), mostly wind-dispersed sapsucking insect whose effects on tree health are highly variable by location and site characteristics (Davis et al., 2022; Lass et al., 2014; Mitchell and Buffam, 2001). In sites with favorable climatic conditions, BWA can cause widespread tree mortality (Hicke et al., 2023). Several studies have demonstrated positive relationships between a range of seasonal and annual temperature-based climate variables and infestation presence or severity (Campbell et al., 2023; Hicke et al., 2023; Hrinkevich et al., 2016a; Mitchell and Buffam, 2001). On the ground, the most apparent diagnostic symptom for detecting BWA infestation is the appearance of swollen branch nodes, or gouts – a defensive response mechanism to the insects' toxic saliva (Mitchell, 1966). BWA-induced damage to the cambium, xylem, and phloem resulting from severe infestation inhibits water transport and nutrient flow within heavily infested trees (Davis et al., 2022). Particularly when faced with a complex of other stressors at warmer sites, such as drought, bark beetles, or various pathogens, BWA can severely degrade *A. lasiocarpa* tree health to the point of mortality, a process that often takes place over the course of several years (Hrinkevich et al., 2016b; Mitchell and Buffam, 2001).

Given BWA's tendency to drive forest degradation at warmer sites, climate change may promote damage in areas where the insect's effects have either been limited or non-existent due to current climate conditions (Campbell et al., 2023; Hicke et al., 2023; Hrinkevich et al., 2016a). In the western US, the spatiotemporal edge of known infestation is northern Utah, where symptoms were first identified in 2017 (Davis et al., 2020; Havill et al., 2021; Jordan, 2023; Rideout, 2023). Accordingly, this region acts as an important area for studying the current and potential future impacts of BWA infestation. In a recent study, Campbell et al. (2023) developed a model capable of accurately predicting BWA infestation damage severity based solely on temperature-related annual and seasonal climatic variables. Given their model's powerful predictive ability, potential future BWA infestation damage severity can be evaluated by leveraging a similar modeling approach driven by climate data representing a range of future emissions scenarios.

Beyond mapping severity, providing a useful measure of BWA infestation impacts to AGB can bolster our understanding not only of where the insect may cause damage (i.e., BWA exposure), but how that damage may influence important ecosystem services, now and in the future (Anderson-Teixeira et al., 2021; Charles and Dukes, 2007; Fei et al., 2019). The results of such an analysis could help us understand potential effects of BWA infestation on the carbon cycle, on wildland fire fuel loads, on habitat quality, on recreational value, and even property value (Anderegg et al., 2023). They could also inform strategic management decisions aimed at mitigating not only present but, perhaps more importantly, future damage to an economically and ecologically important forest system. Using the "Resist, Accept, Direct" land management framework as an exemplary decision-making basis, there are several scenarios that can emerge from the combined spatially explicit evaluation of BWA infestation damage severity and *A. lasiocarpa* biomass (Fig. 1) (Lynch et al., 2021; Schuurman et al., 2022). Armed with this information, forest managers can efficiently and effectively devote resources towards addressing the ongoing and future effects of BWA. To the authors' knowledge, there are currently no biological or chemical controls on BWA populations that can be effectively and efficiently applied at broad spatial scales, limiting silvicultural treatments to the promotion of non-host species.

With the overarching goal of better understanding the current and future relationship between BWA and *A. lasiocarpa* at the spatiotemporal forefront of BWA expansion in the western US, the specific objectives of this study are to:

1. Develop a new model for predicting BWA infestation damage severity as a function of high-resolution climate data.
2. Apply that model to predict current (2020) and potential future (2040, 2060, 2080, and 2100) infestation damage severity, based on four different climate shared social pathways (SSP126, SSP245, SSP370, and SSP585).
3. Model and map *A. lasiocarpa* AGB throughout northern Utah using a large suite of geospatial and remote sensing datasets in conjunction with a large database of forest inventory data.
4. Compare current and future severity to *A. lasiocarpa* AGB to assess impacts of BWA infestation damage and identify areas where exposure to degradation is likely to be highest.

2. Materials and methods

2.1. Study area

This study focuses on the Uinta-Wasatch-Cache National Forest in northern Utah (Fig. 2). The study area was chosen as it represents the southeasternmost extent and leading edge of BWA spread in the western US. It falls towards the southern, warm, dry end of *A. lasiocarpa*'s wide range, which stretches as far north as Alaska, making the species particularly susceptible to future climatic changes in this region. *A. lasiocarpa* is among the most abundant tree species in the relatively low species richness forests here; thus, widespread losses to of the species could have an outsized impact on ecosystem structure. It is also a region where outdoor recreation is a major economic driver, with the Uinta-Wasatch-Cache National Forest bordering major population centers, the largest of which is Salt Lake City. It is home to 12 ski resorts, most of which contain *A. lasiocarpa* forests, the loss of which would have important effects on the resorts' aesthetic and recreational value.

There are two major mountain ranges in the study area (Fig. 2). The Wasatch Mountains are oriented primarily north-south in the central portion of the study area. The Uinta Mountains run primarily east-west in the eastern portion of the study area. Taken together, they separate the Great Basin to the west from the Wyoming Basin to the northeast and the Colorado Plateau to the southeast. The Wasatch Mountains are somewhat lower in elevation, ranging from 1287 – 3629 m (mean = 2228 m), than the Uintas (2048 – 4109 m, mean = 2978 m). They are also warmer, with a mean annual temperature ranging from 1.8 – 11.8°C (mean = 6.1°C), than the Uintas (-2.9 – 6.7°C, mean = 1.8°C). The two ranges have similar annual precipitation totals, with the Wasatch Mountains having a wider range (297 – 2051 mm/year) but a lower

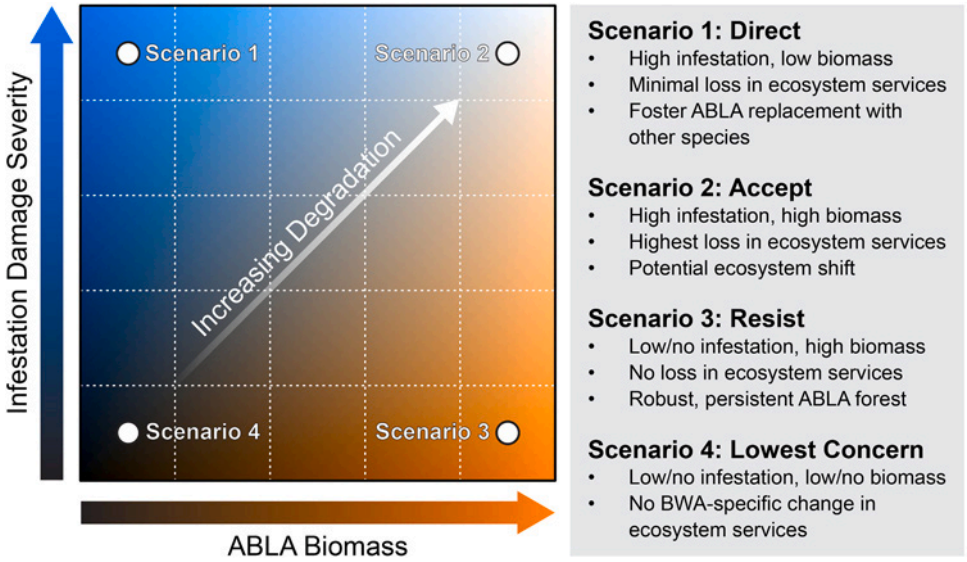

Fig. 1. An example of how the combined, spatially explicit understanding of BWA infestation and *A. lasiocarpa* AGB can be used to inform strategic land management decision-making using the Resist, Accept, Direct framework. Abbreviations: BWA = balsam woolly adelgid; AGB = aboveground biomass; RAD = Resist, Accept, Direct.

mean (mean = 683 mm/year), than the Uintas (276 – 1168 mm/year, mean = 752 mm/year) (PRISM Climate Group, Oregon State University, 2019; Wang et al., 2016). Both ranges feature an abundance of *A. lasiocarpa*, providing ample host material for BWA. Based on our field data (described in the next section), USDA Forest Service aerial detection surveys, local expert knowledge, and the modeling work by Campbell et al. (2023), the lower, warmer Wasatch Mountains have been exposed to a much higher degree of BWA infestation severity than the higher, cooler Uinta Mountains.

2.2. Field data

Between 2021 and 2022, we sampled 58 field plots within the Uinta-Wasatch-Cache National Forest to characterize BWA infestation damage severity (Fig. 2) (Campbell et al., 2023). Plot locations were selected with the intent of capturing variability in BWA infestation and damage, spatial coverage within the National Forest, and landscape characteristics (elevation, species assemblages, etc.). Each plot was a 15 m-radius circle wherein every tree greater than 5 cm in stem diameter at breast height (1.37 m above forest floor) was evaluated for the following criteria: species, status (live, new mortality = some foliage retained, old mortality = no foliage present), stem diameter at breast height, the presence of a dead tree top, and the proportion of dead foliage present (in 10% increments). For *A. lasiocarpa* trees, a series of BWA-specific severity indicators were also evaluated. The first among these was wool density, or the number of wools present on the lower 6 ft (1.83 m) of the tree bole. In highly infested trees, BWA's woolly coating can be seen as small white tufts on a tree's stem; thus, the density thereof is one way to measure infestation severity. The second BWA-specific measure was gout severity, which summarized the size and number of gouts visibly present on a tree's branches and twigs. We attempted to characterize gout severity for the entire tree, though our ability to identify small gouts in upper portions of the canopy were limited, so the lowest, most visible branches often served as the primary frame of reference. The third measure was the presence of one or more crown deformities in the tops of the trees – highly infested trees tend to manifest stunted terminal branches, stunted lateral branches, and/or a curled top. Each of these infestation and damage indicator metrics (dead top, foliage dieback, wool density, gout severity, and crown deformities) was normalized on a scale from 0 to 1, and averaged for each tree, resulting in a mean damage score (MDS) for each tree.

BWA rarely acts in isolation to kill a tree, often joined by one or more of several additional damage agents, such as bark beetles, twig beetles, defoliator insects, fir broom rust, and pathogens. To distinguish BWA-specific damage from that of other agents, we also estimated a "BWA agent score" (BAS) and "other agent score" (OAS), which attempted to summarize our interpretation of the overall health impact on the tree from BWA or other sources. Both ranged from 0 (no evidence) to 3 (severe effects). A tree heavily impacted by BWA with no evidence of other agents may receive a BAS of 3 and OAS of 0. A tree heavily impacted by both BWA and bark beetles may receive a BAS of 3 and OAS of 3. The proportion of damage on a given tree attributable to BWA (pBAS) was calculated as BAS divided by the sum of BAS and OAS. A tree with a BAS of 1 (or 100%) indicates that some BWA-specific damage was evident but no other agents were detectable.

As a result, each tree was assigned two scores: MDS, representing an amalgamated measure of tree damage, and pBAS, representing the proportion of damage attributable to BWA. The product of those two numbers produced a BWA damage score (BDS) that ranged from 0 to 1 and characterized BWA's specific impacts on tree health. BDS for every *A. lasiocarpa* tree was averaged per plot, the result of which was used to represent stand-level infestation severity. This measure served as the response variable for subsequent severity modeling. Plot-level mean BDS theoretically ranges from 0 to 1, though a 1 would mean every tree in the plot would have the highest possible values for all damage indicator metrics (i.e., MDS = 1) with no evidence of any agents other than BWA. In our field data, BDS ranged from 0 to 0.49, with a median of 0.12.

2.3. Modeling infestation severity

To construct a model for predicting BWA infestation damage severity as a function of climatic conditions, we used spatially downscaled data from ClimateNA (Wang et al., 2016). ClimateNA enables the generation of high resolution monthly, seasonal, and annual climate variables derived from PRISM and WorldClim through an elevation-informed bilinear interpolation process (Daly et al., 1997; Fick and Hijmans, 2017). In addition to modeling historic normal periods, the software also has a series of built in projected monthly, seasonal, and annual projections based on a range of different shared socioeconomic pathways (SSPs), which link socioeconomic development scenarios to different levels of greenhouse gas emission-induced radiative forcing (O'Neill et al., 2014;

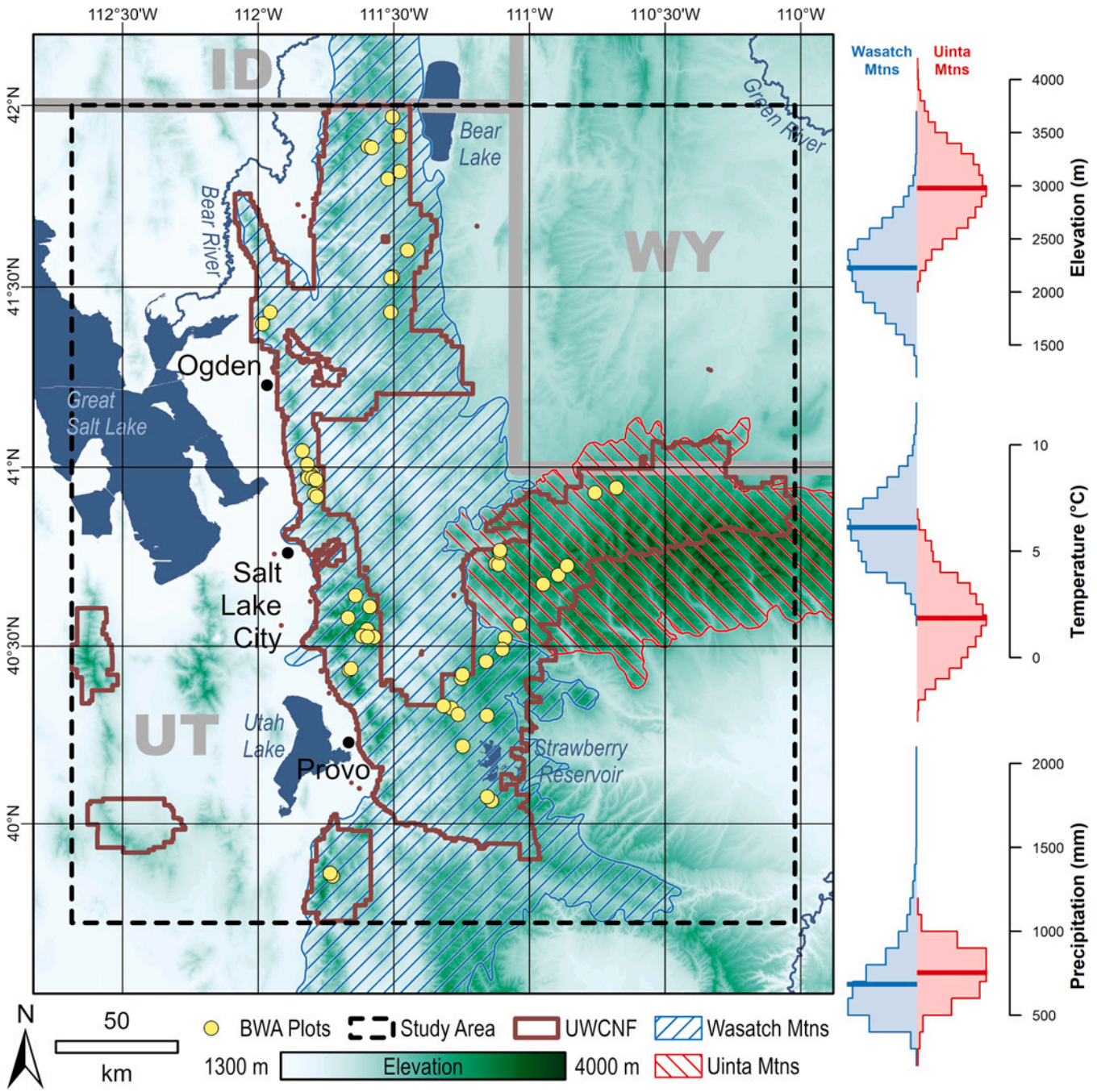

Fig. 2. Study area map featuring field plot locations within which BWA infestation severity was evaluated. Wasatch and Uinta mountain range data adapted from the EPA Level IV ecoregions. Climate data derived from ClimateNA, and represents the range of mountain range climate conditions within the study area only. Abbreviations: BWA = balsam woolly adelgid; UWCNF = Uinta-Wasatch-Cache National Forest.

Riahi et al., 2017). Given the strong relationships between BWA infestation damage and climate, ClimateNA is as an ideal data source for evaluating present and future impacts of BWA at a high spatial resolution. The SSPs evaluated in this study include SSP126 (the most sustainable pathway, with 2.6 W/m^2 of radiative forcing by 2100), SSP245 (a "middle of the road" pathway with 4.5 W/m^2 of forcing), SSP370 (a pathway resulting from increased nationalism and conflict and an associated shift away from addressing climate change, with 7.0 W/m^2 of forcing), and SSP585 (a pathway that emphasizes growth in fossil fuel development, with 8.5 W/m^2 of forcing) (Riahi et al., 2017). A host of annual and seasonal climate variables were derived to represent recent (2010 – 2020 decadal mean) and future (2040, 2060, 2080, and 2100, for each aforementioned SSP) climatic conditions (Table A1) (Wang et al., 2016). We used a 1 arc-second (approximately 30 m) resolution digital elevation model as the basis of downscaling; as a result, all of the climate variables were produced at the same spatial resolution.

Our model has three key assumptions. First, since none of our predictors directly represent forest health decline (i.e., no remotely sensed measures of spectral change over time), we are modeling climatic exposure to BWA infestation damage. Second, we are not modeling BWA's capacity to spread over space and time directly; thus, we are assuming that, BWA will have had an equal opportunity to reach all portions of the study area within the modeled time frames. Third, by predicting future climatic exposure to BWA, we are assuming the currently observed insect-climate relationships will persist into the future, which we cannot validate at present.

Modeling was done using random forests, given their ability to handle many collinear predictors and non-linear relationships, avoid overfitting, and provide a robust evaluation of predictor variable importance (Breiman, 2001; Matsuki et al., 2016; Tomaschek et al., 2018). We used the ranger package in R to construct and tune our models, and the terra package for processing predictor data and generating predictive maps (Hijmans et al., 2023; R Core Team, 2021; Wright and Ziegler, 2017). Using a random grid search and leave-one-out cross-validation approach, we tuned the following hyperparameters: the number of features evaluated at each decision tree split, the minimum decision tree node size, the fraction of samples used to train decision trees in the bagging process, the number of trees, and the number of features/predictors to use in modeling. The last hyperparameter, number of features, was tuned through two separate runs of a random forest model on each iteration. The first run included all candidate predictors, and the second run only included the *n* most important predictors according to permutation importance, where *n* was determined from the random grid search. Among 2000 random combinations of these hyperparameters, the set that yielded the lowest combined rank for the coefficient of determination (R^2) and the root mean squared error (RMSE) was selected and used for building a final model. To test the degree to which spatial autocorrelation may be present in model performance evaluation, we conducted a buffered leave one out cross-validation (Ploton et al., 2020). In this framework, data from each plot is iteratively set aside and used to test a model built from other plots outside of a buffer distance of interest. This ensures that nearby plots are not being used to both train and test the model, and that proximity alone is not inflating model performance. We tested buffers from 0 (simple leave one out) to 20 km at an interval of 500 m. The final model was applied to the 2020 data to yield a predictive map of current infestation severity. It was also applied to every combination of years (2040, 2060, 2080, and 2100) and SSP (SSP126, SSP245, SSP370, SSP585) to generate predictive maps representing potential future infestation. Relationships between the final set of climatic predictor variables and the response variable (infestation severity) were evaluated through the calculation of accumulated local effects, which are similar to partial dependence, but more robust against collinearity (Apley and Zhu, 2020).

2.4. Modeling *A. lasiocarpa* AGB

To map *A. lasiocarpa* AGB, we used a large suite of geospatial and remote sensing predictor datasets along with a large database of USDA Forest Service Forest Inventory and Analysis data (Bechtold and Patterson, 2005). In the interest of developing a regionally robust model, rather than simply using the Forest Inventory and Analysis plots within the study area, we opted to use those found within a bounding box around a 200 km buffer around the Uinta-Wasatch-Cache National Forest. A total of 12,506 plots with true ("unfuzzed") plot locations were used. A series of quality and relevance filters were performed on the Forest Inventory and Analysis data to reach this number, including: (1) removing plots that were measured prior to 2010; (2) removing plots that were not sampled; (3) removing plots that were not collected with the national design; (4) removing plots where multiple conditions were present; (5) removing plots without measurements in all four subplots; and (6) removing plots that had been disturbed, according to LANDFIRE, since measurement. For each plot, the following metrics were computed: (1) total AGB of all live trees; (2) total AGB of all live *A. lasiocarpa* trees; (3) proportional AGB of all live *A. lasiocarpa* trees; and (4) presence/absence of any live *A. lasiocarpa* trees. Only trees greater than 12.7 cm at breast height (1.37 m from top of forest floor) were included in AGB calculations.

We compiled a large set of spatial predictor datasets, each at 30 m spatial resolution, aimed at capturing valuable AGB predictive capacity (Table A2). These included the same set of 2010 – 2020 decadal seasonal and annual climatic means from Table A1. They also included a suite of topographic variables derived from a digital elevation model. We used Google Earth Engine to derive an array of spectral predictors (raw band reflectance and derived vegetation indices) representing "early season" (days of year 150 – 225, or May 30 – August 13) and "late season" (days of year 226 – 300, or August 14 – October 27) conditions, composited from quality-filtered pixels from Landsat 8 and 9 Tier 1 Level 2 surface reflectance data from 2017 – 2022 (Gorelick et al., 2017; Vermote et al., 2016). The quality filtering removed pixels containing clouds and cloud shadows, as well as radiometrically saturated pixels. Among the filtered pixels for each time frame, a median was used to derive a single representation of spectral conditions. We also used the Earth Engine implementation of Landtrendr to produce several predictors summarizing disturbances (i.e., timing, magnitude, etc.) from 1985 – 2021 (Kennedy et al., 2010). Lastly, we acquired a range of derived map products representing vegetation type, structure, and disturbance from the University of Maryland's Global Land Analysis & Discovery (GLAD) group (Hansen et al., 2013; Potapov et al., 2021), LANDFIRE (Rollins, 2009), and the National Land Cover Database (NLCD) (Jin et al., 2019).

The modeling workflow for AGB mapping was nearly identical to that of BWA infestation damage severity (random forests with 2000-iteration random grid search hyperparameter tuning). One key difference was that instead of a leave-one-out cross-validation approach, a 70%/30% random training/test split was used to assess performance, given the large volume of reference data. We modeled *A. lasiocarpa* AGB in two ways. The first was directly – that is, *A. lasiocarpa* AGB, in Mg/ha for each Forest Inventory and Analysis plot used as the response variable. The second was a more indirect approach, achieved by generating models for total (all species) AGB (in Mg/ha), *A. lasiocarpa* proportional AGB (in %), and *A. lasiocarpa* presence/absence (binarily represented as 1 and 0, respectively). The product of these three datasets (total × *A. lasiocarpa* proportion × *A. lasiocarpa* presence) yielded a secondary estimate of *A. lasiocarpa* AGB, for comparison. The better of the two *A. lasiocarpa* AGB maps (direct vs. indirect) was selected and used as the basis of comparison to BWA infestation damage severity.

The resulting *A. lasiocarpa* AGB map, which represented approximately 2020 conditions, was compared to each of the BWA severity maps, present and future for all modeled climate scenarios, on a per-pixel basis. This enabled the evaluation of how much AGB (in Mg) would be affected by varying levels of infestation damage severity. To distill the future projections of the BWA-AGB relationship into a singular and moderate representation, we compared 2020 severity to a 2040 – 2080 mean of SSP245-modeled severity, the results of which highlight likely near-term climatic exposure to BWA's effects in a spatially explicit manner. It is important to note that we relied solely on our 2020 *A. lasiocarpa* AGB map as the basis of this comparative analysis, rather than attempting to project future AGB in a changing climate, so results must be interpreted through the lens of that caveat.

3. Results

3.1. Current BWA-climate model

The current (2020) climate model performed well, explaining 78.9% of variance in observed severity, and yielding an average predictive error (RMSE) of 0.070, according to a leave-one-out cross-validation (Fig. 3A). The model selected four predictors among the candidate list of 80 (Table A3), including minimum spring temperature (tmin_sp), annual number of frost-free days (nffd), degree-days below zero in autumn (dd_0_at), and number of frost-free days in spring (nffd_sp), in order of decreasing importance (Fig. 3B; Table A1). Relationships between predictor and response variables all pointed towards the same trend: higher temperatures (i.e., higher minimum temperatures, more frost-free days, lower subzero degree-days) are correlated with more severe BWA infestation damage (Fig. 3C-F). All accumulated local effects plots revealed inflection points that separated low/no severity from higher severity. Higher severity tended to occur in areas with: (1) minimum spring temperatures greater than −3°C; (2) number of annual frost-free

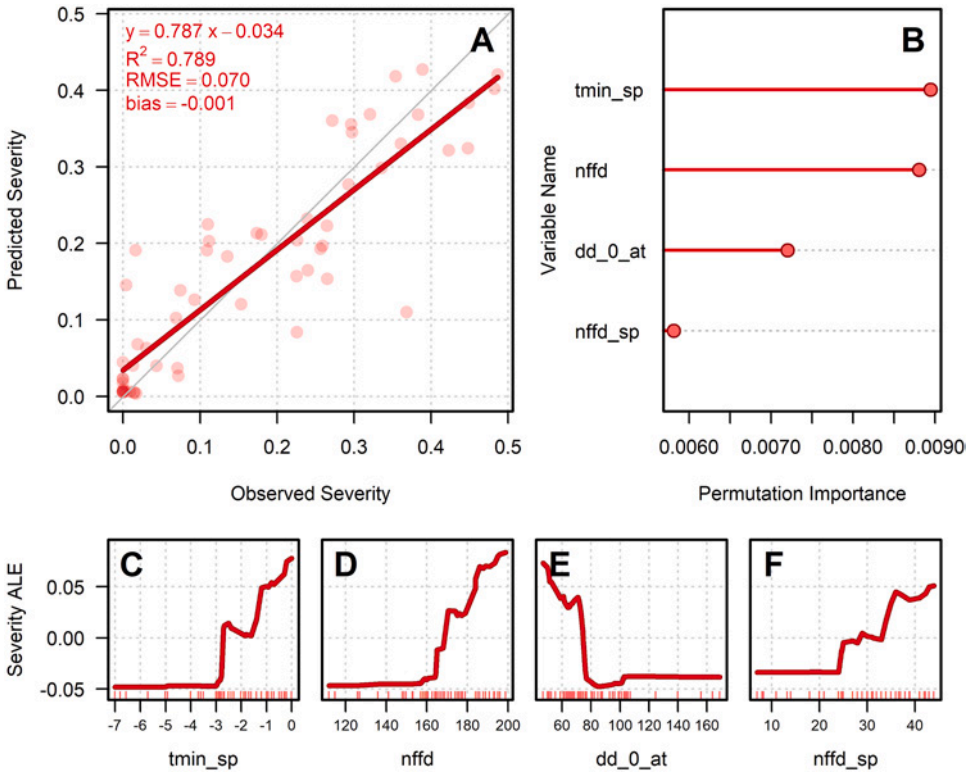

Fig. 3. BWA infestation damage severity model results, including (A) predicted versus observed severity, compiled from a leave-one-out cross-validation approach; (B) variable importance plot, with values representing the increase in mean squared predictor error resulting from random permutation of predictor variables; and (C-F) accumulated local effects plots of the predictor variables, characterizing their individual relationships with modeled severity. Abbreviations: ALE = accumulated local effects; tmin_sp = minimum spring temperature (°C); nffd = number of annual frost-free days; dd_0_at = subzero (chilling) degree-days in autumn; nffd_sp = number of spring frost-free days.

days greater than 160; (3) autumn chilling degree-days lower than 80; and (4) number of spring frost-free days fewer than 25. The buffered leave one out cross-validation revealed that spatial autocorrelation appears to play a relatively minor role in model evaluation (Fig. 4). Model performance does decrease slightly with increasing buffer distances up until about 10 km, after which performance levels off with R^2 values only 0.02 lower and RMSE values only 0.006 higher than the unbuffered leave one out cross-validated results.

3.2. AGB models

The performance of the AGB models varied by response variable. The total (all tree species combined) AGB model performed very well (R^2 = 0.769; RMSE = 15.120 Mg/ha; bias = +0.292 Mg/ha) (Fig. 5A). The proportional *A. lasiocarpa* AGB model's performance was somewhat lesser (R^2 = 0.390; RMSE = 0.066; bias = 0.006) (Fig. 5B). The *A. lasiocarpa* presence/absence model performed well, though the overall accuracy (0.975) should be treated cautiously, given the vastly uneven distribution of samples across classes (Fig. 5C). The F1 score, robust to uneven sample sizes, captures a more reliable measure of performance at 0.744. This model's relatively better results than those of the proportional AGB model suggest that *A. lasiocarpa* is comparably easier to detect in a binary fashion than to quantify along a continuous spectrum of AGB abundance. Ultimately, our interest was in deriving a map that represented an approximation of *A. lasiocarpa* AGB, and we compared two different approaches for doing that: (1) modeling it directly (Fig. 5D); and (2) modeling it as the product of total AGB, *A. lasiocarpa* AGB proportion, and *A. lasiocarpa* presence/absence (Fig. 5E). The latter approach, though more analytically complex, yielded improved results over the direct approach (R^2 = 0.448; RMSE = 6.177 Mg/ha; bias = 0.360 Mg/ha). Removing the one very high AGB outlier point from the performance assessment yields improved fit metrics (R^2 = 0.481; RMSE = 5.672 Mg/ha), albeit with a slightly higher bias (0.399 Mg/ha). The best sets of hyperparameters for each of these models can be seen in Table A4, which revealed that the AGB models were much more complex than the BWA-climate model, particularly in terms of the numbers of features needed to construct the trees. This is not

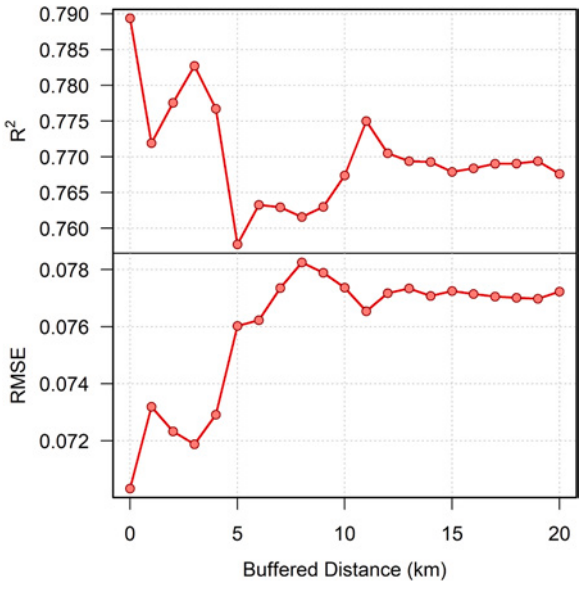

Fig. 4. Results of the buffered leave one out cross-validation analysis, revealing trends in R^2 and RMSE with increasing buffer distance. Abbreviations: R^2 = coefficient of determination; RMSE = root mean squared error.

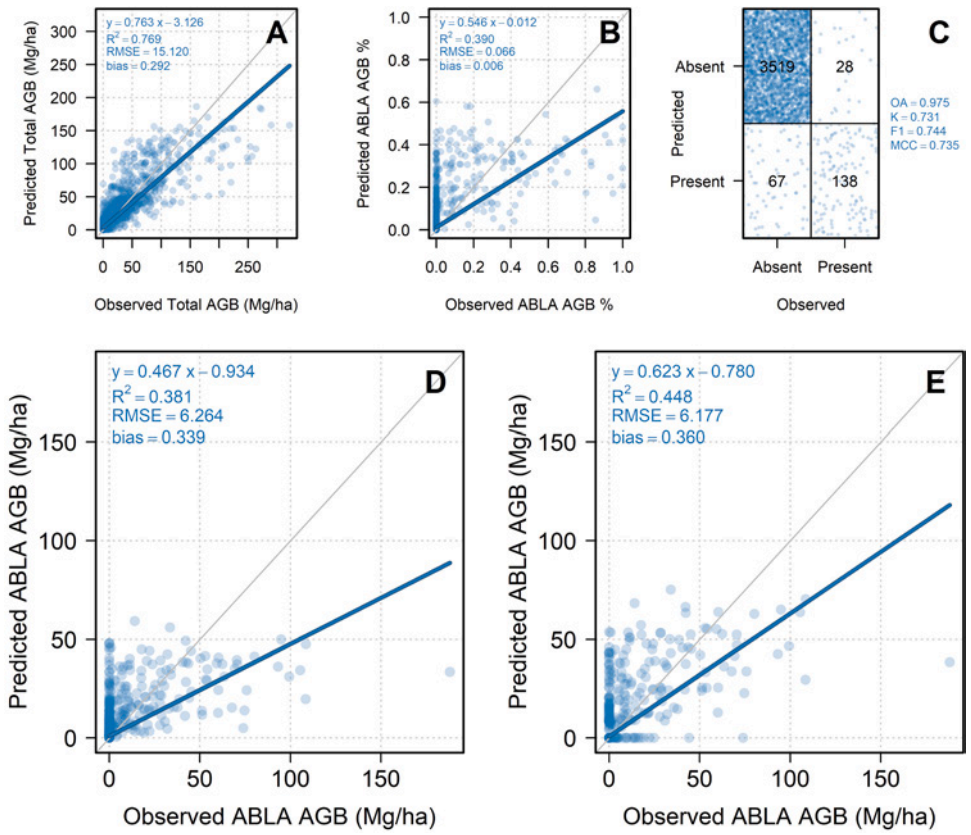

Fig. 5. Biomass modeling results, including (A) predicted versus observed total AGB (all tree species); (B) predicted versus observed *A. lasiocarpa* proportional AGB; (C) predicted versus observed *A. lasiocarpa* presence/absence; (D) predicted versus observed *A. lasiocarpa* AGB, modeled directly; and (E) predicted versus observed *A. lasiocarpa* AGB modeled as the product of total AGB multiplied by *A. lasiocarpa* proportion subset to *A. lasiocarpa* presence. All of the above are based on a 30% test dataset set aside from the original sample of Forest Inventory and Analysis plots used in this study. Abbreviations: AGB = aboveground biomass (Mg/ha); ABLA = *Abies lasiocarpa*; RMSE = root mean squared error; OA = overall accuracy; K = kappa coefficient; F1 = F1 score; MCC = Matthews correlation coefficient.

unexpected, given the much larger sample size and less easily-predictive relationships between predictor and response variables in comparison to the BWA-climate model.

As seen in Fig. 6, clear patterns in *A. lasiocarpa* AGB emerged throughout the study area, with the highest totals being found in the central and northern Wasatch Mountains and the western Uinta Mountains. In higher-elevation portions of the central and eastern Uinta Mountains, *A. lasiocarpa* is still present, as indicated by the presence/absence map, but comprises a much smaller portion of total AGB. Our experience in the field tells us that these areas are more likely to be dominated by Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*). Throughout the study area, there are 4737 km^2 of mapped *A. lasiocarpa*, totaling 11.2 Tg of AGB.

3.3. Future BWA-climate projections

To provide insight into study area-wide trends in how *A. lasiocarpa* forests may be exposed to climatic conditions that promote BWA infestation damage now and in the future, we compared our *A. lasiocarpa* presence/absence map to ClimateNA-modeled temperature variables for each combination of SSP (SSP126, SSP245, SSP370, and SSP585) and year (2020, 2040, 2060, 2080, and 2100) (Fig. 7). SSP126 demonstrates a small midcentury uptick in temperatures, frost-free days, and a small decrease in chilling degree-days, followed by a subsequent return to values similar to those found in 2020. On the opposite extreme, SSP585 demonstrates strong trends towards values in the predictor variables most closely linked to BWA infestation damage severity. For example, the most important predictor, tmin_sp, depicts a scenario in which the majority of *A. lasiocarpa* is found within areas expected to have low infestation damage, according to accumulated local effects, in 2020. Conversely, by 2100, the model predicts the opposite – that most *A. lasiocarpa* will fall within areas where temperature conditions may promote moderate or high infestation damage severity. The more moderate projections (SSP245 and SSP370) fall between these extremes, but still generally demonstrate trends towards increasing exposure to BWA-induced tree damage throughout the 21st century.

Applying the 2020-derived model to the prediction of BWA infestation damage severity across all SSPs and years reveals highly variable predictions (Fig. 8). Even in the most conservative, optimistic emissions scenario (SSP126), BWA's effects are projected to expand by 2060, given the aforementioned midcentury temperature increase. Although the models suggest that a subsequent decrease in temperature may reduce *A. lasiocarpa* forests to BWA exposure thereafter, considerable damage may have already taken place. Across all models and years, there is a clear differentiation between the projected effects of BWA on the Wasatch Mountains versus the Uinta Mountains. The former, being somewhat lower and warmer, demonstrate consistently higher exposure to BWA infestation damage. In all but the most extreme cases (e.g., SSP585 at 2100), the Uinta Mountains remain fairly robust against BWA infestation damage, given their higher elevations and associated cooler temperatures. However, the Uinta foothills, particularly on their western edge, appear consistently exposed across even the fairly conservative climate models.

3.4. BWA – A. lasiocarpa AGB comparison

A key objective of this research is not only to predict severity, but to also compare predicted severity maps to current *A. lasiocarpa* AGB maps

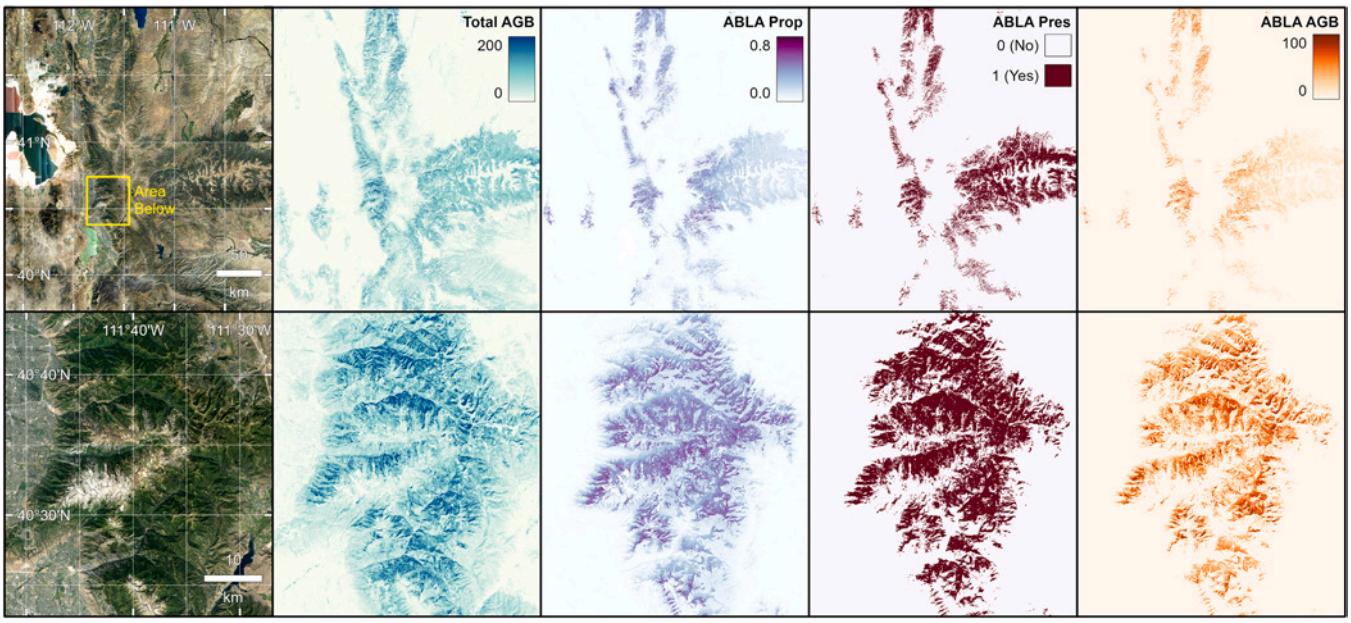

Fig. 6. Mapped biomass modeling results. The top row shows the entire study area and the bottom row shows a local-scale area within the Wasatch Mountains, shown by the highlighted box in the top left panel. Mapped results include total AGB, *A. lasiocarpa* proportional AGB, *A. lasiocarpa* presence absence, and *A. lasiocarpa* AGB computed as the product of total AGB and *A. lasiocarpa* proportion, subset to *A. lasiocarpa* presence. Abbreviations: AGB = aboveground biomass (Mg/ha); ABLA = *Abies lasiocarpa*.

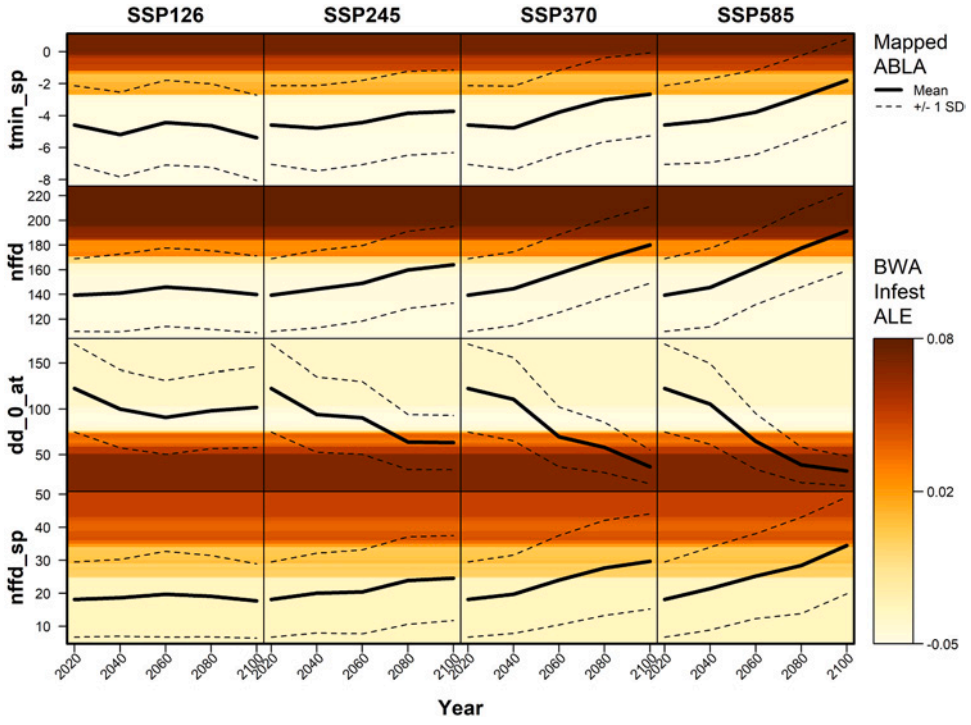

Fig. 7. Current and projected changes to the four climatic predictors of BWA infestation damage severity (rows) in areas mapped as having *A. lasiocarpa* present within the study area, according to the four different climate SSPs (columns). Plots are colored according to the accumulated local effects values from the severity prediction model (Fig. 3). Lines represent the distribution (mean and SD) of mapped *A. lasiocarpa* according to each climatic variable and SSP. Abbreviations: ABLA = *Abies lasiocarpa*; ALE = accumulated local effects; tmin_sp = minimum spring temperature (°C); nffd = number of annual frost-free days; dd_0_at = subzero (chilling) degree-days in autumn; nffd_sp = number of spring frost-free days.; SSP = shared social pathway.

to understand the exposure and potential impacts of BWA infestation. Fig. 9 provides a graphical tabulation of the potential impacts in terms of both total area and total amount of AGB affected. In 2020, 6.6 Tg or 59% of all mapped *A. lasiocarpa* AGB in our study area has modeled damage severity less than 0.05, representing uninfested or very lowly-infested conditions, with the remaining 41% featuring higher climatic exposure to BWA-induced degradation. By 2100, this higher exposure range expands to 52% under SSP126, 79% under SSP245, 99% under SSP370, and 100% under SSP585. Thus, even in the most optimistic scenario, BWA is climatically poised to drive increased forest degradation.

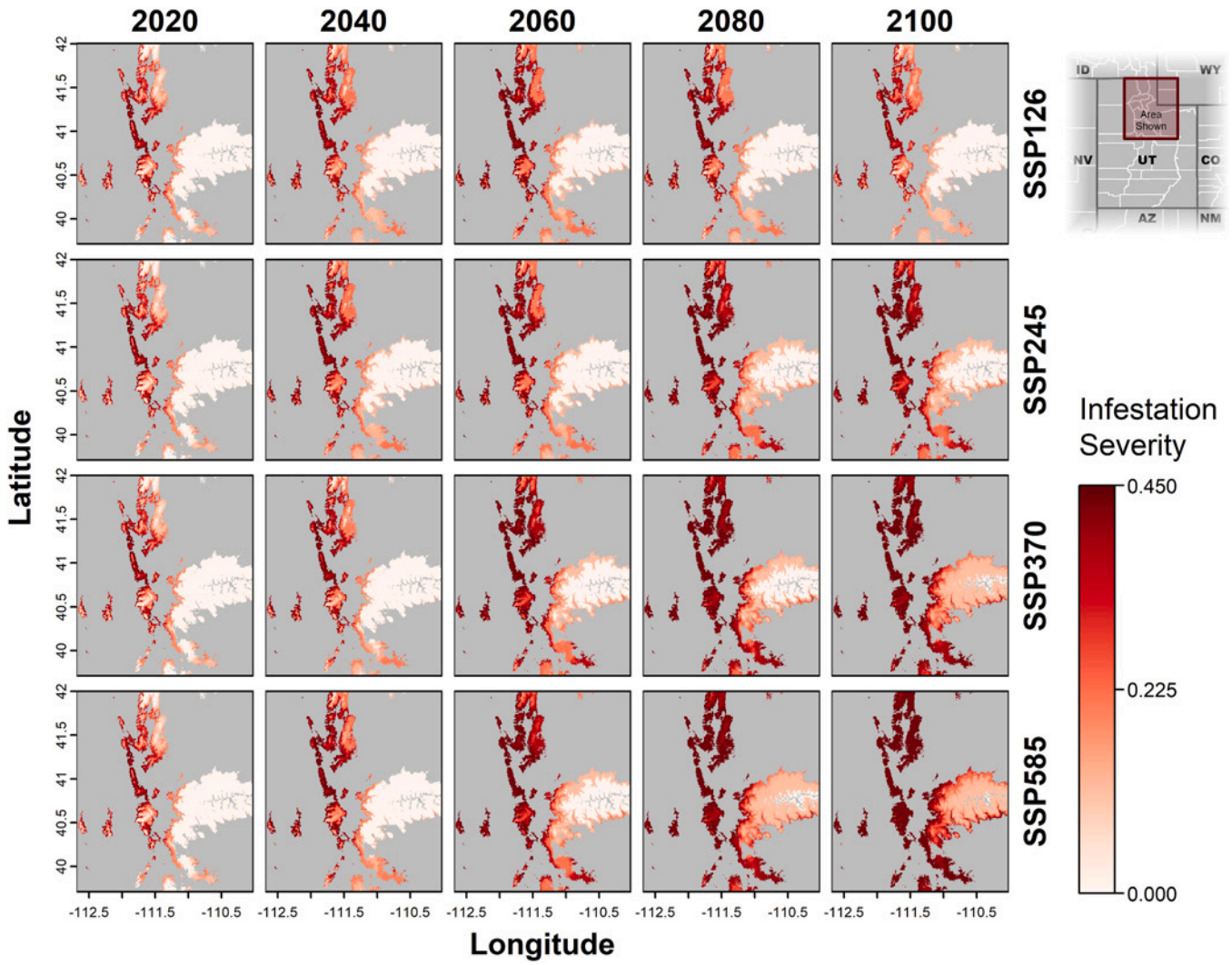

Fig. 8. Modeled BWA infestation damage severity by year (columns) and SSP (rows). Although the original prediction maps are generated at a resolution of approximately 30 m, pixels in these maps were aggregated to 900 m median values, for clarity. Abbreviations: BWA = balsam woolly adelgid; SSP = shared social pathway.

Although our continuous measure of infestation damage severity is not specifically linked to categories such as "low", "moderate", or "high", we can apply various severity thresholds to gain more insight into those areas that may be exposed to greater (or lesser) damage. For example, applying a higher severity threshold of 0.3, above which we can expect greater tree health declines and higher mortality totals, 11% of *A. lasiocarpa* AGB is currently classified as being at least that severe. Under SSP126, this proportion remains at 11% by the end of the 21st century; however, SSP245, SSP370, and SSP585 increase the modeled exposure to 37%, 53%, and 59%, respectively.

Fig. 10 conveys the spatial relationships between BWA infestation damage and *A. lasiocarpa* AGB throughout the entire study area and within a few focal areas of interest. To distill results into a simplified and reasonable set of likely outcomes, both temporally and climatically, we compare current infestation to a 2040 – 2080 average using the SSP245 climate scenario. The current model illustrates spatially variable infestation damage severity around the central Wasatch Mountains (Fig. 10 subset area 2), where high elevation portions of the Wasatch remain somewhat or entirely uninfested. The aggregated future scenario demonstrates that no longer being the case, with the entirety of the central Wasatch Mountains experiencing a high degree of exposure to BWA. An even starker temporal contrast can be seen in the northern Wasatch Mountains, such as the Bear River range depicted in subset area 1, where exposure to BWA is low at present but is projected to be severe in the near-term future. The Uinta Mountains remain largely unaffected, both at present and in the future, with the exception of the lowest-elevation portion of the range on its western edge, which exhibits a small potential increase in BWA exposure in the future.

4. Discussion

Across northern Utah, warmer parts of the *A. lasiocarpa* range were associated with dramatically higher severity of BWA outbreaks. This positive relationship between temperature-related variables and BWA infestation damage severity suggests that, in a warming climate, *A. lasiocarpa* forests will experience continued and expanded degradation. Even in the most optimistic climate projections that predict the lowest temperature increases throughout the 21st century (SSP126), an increasing amount of *A. lasiocarpa* AGB will be exposed to potential damage from BWA. Under the SSP245 scenario, as much as 1.9 Tg of AGB (~0.95 Tg of carbon, assuming carbon comprises 50% of AGB) will be exposed to the high BWA infestation damage severity by 2100 within our study area. To put this number in context, according to the Global Forest Watch, Utah forests removed a net of 2.96 Mg/year of CO_2 between 2001 and 2022 (Global Forest Watch, 2024). Thus, if we assume that forests experiencing the highest levels of BWA infestation damage

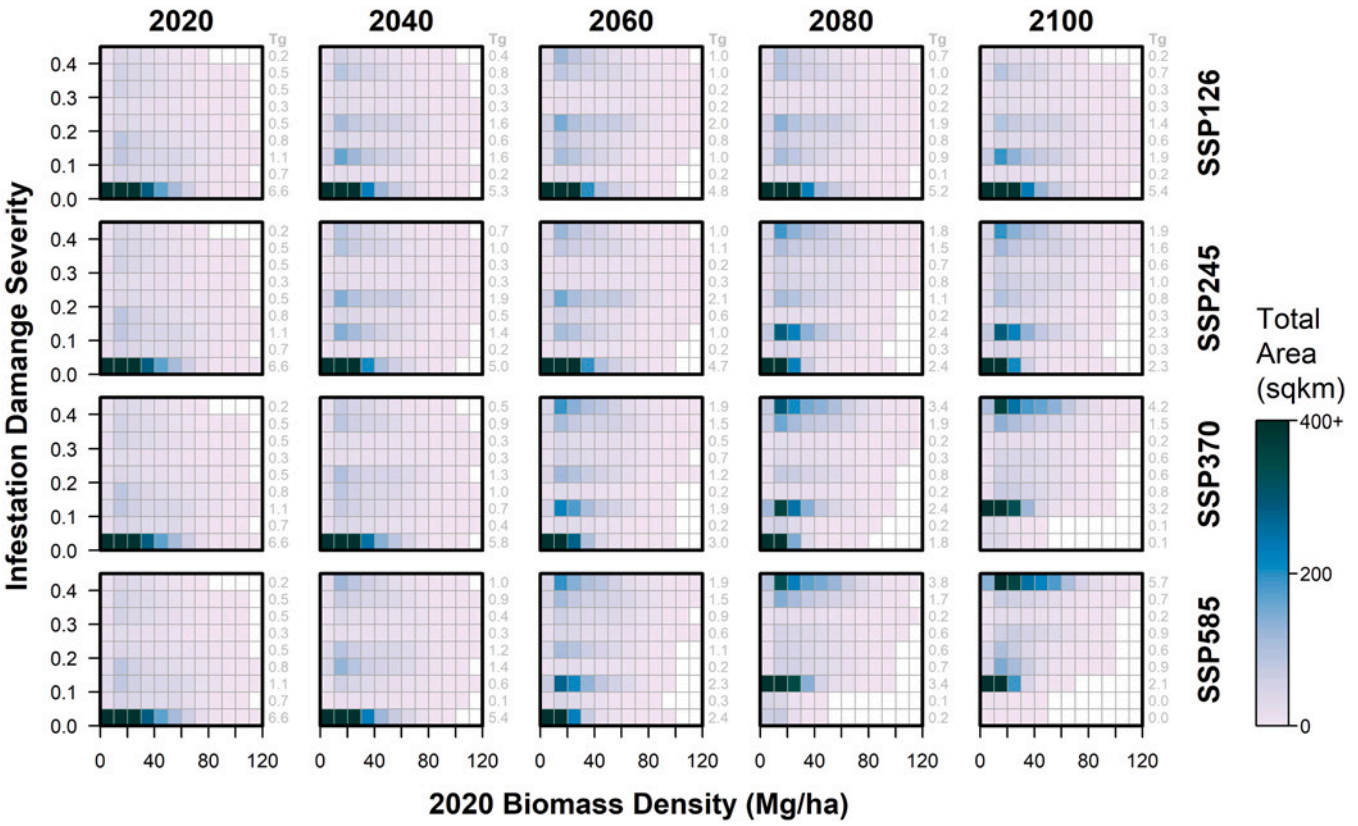

Fig. 9. Two-dimensional histogram of modeled infestation severity (y-axis) and 2020 biomass density (x-axis), by year (columns) and SSP (rows). Cells are colored by the total amount of area mapped as having a particular range of severity and *A. lasiocarpa* biomass within the study area. Gray numbers represent the total amount of AGB, in Tg, belonging to each severity range. Abbreviations: SSP = shared social pathway.

severity are likely to undergo widespread mortality, BWA may play a significant role in affecting the regional carbon budget. The Wasatch Mountains, being generally lower in elevation and warmer in temperature, are projected to experience the highest degree of exposure to BWA, in comparison to the lesser-affected Uinta Mountains. In addition, the highest *A. lasiocarpa* AGB totals are found within the Wasatch, making the Wasatch range a potential hotspot of future biomass loss due to BWA infestation.

Although no studies to date have explicitly sought to model future climate scenario-driven effects of BWA, the research we have presented adds to a growing body of recent literature surrounding the prediction of future insect spatial distribution. A large proportion of these studies have focused on agricultural pests, such as *Helicoverpa zea* (corn earworm; Zhao et al., 2022), *Oplostomus fuligineus* (large hive beetle; Abou-Shaara et al., 2021), *Homalodisca vitripennis* (glassy-winged sharpshooter; Rossi & Rasplus, 2023), *Cicadella viridis* and *Evacanthus interruptus* (leafhoppers; Zhang et al., 2023), and *Piezodorus guildinii*, to name a few. There are also several studies investigating forest pest-climate interactions, including those of *Lymantria dispar* (gypsy moth; Régnière et al., 2009), *Choristoneura fumiferana* (spruce budworm; Candau and Fleming, 2011), *Dendroctonus frontalis* (southern pine beetle; Munro et al., 2021), *Gnathotrichus materiarius* (ambrosia beetle; Witkowski et al., 2022), *Calomicrus apicalis* (leaf beetle; Şen et al., 2022), and *Tomicus yunnanensis* (common pine shoot beetle; Huang et al., 2022). A common thread to their findings is climate-fueled range expansion, with temperature increases playing a particularly important role in shifting habitat suitability in a warming climate.

An important distinction with our study is that our response variable is a continuous measure of infestation damage severity, whereas many previous studies on forest pests and climate change relied on presence-only modeling. This allows us to directly tie the prediction to ecological impacts, which we have done with the severity-AGB exposure analysis. While previous studies took place at broader spatial extents than that which we have examined, they rely on relatively coarse spatial resolutions (e.g., 1 km – 4 km). Our use of a spatially downscaled climate data not only provided the generation of a highly predictive model that captured local-scale climatic variability, but also provides a valuable level of map precision that could be directly used in land management decision-making. The Resist, Accept, Direct framework described in Fig. 1 can be used in conjunction with our projections (e.g., Fig. 10) to guide proactive and preemptive silviculture. For example, the Bear River range in the northern Wasatch Mountains represents an area poised to experience high exposure to BWA damage under even moderate climate projections. The combination of high *A. lasiocarpa* AGB and high BWA infestation damage severity would suggest a high potential for changes to ecosystem function in that region; thus, enacting a "Direct" management strategy that could promote the growth of non-*A. lasiocarpa* species could limit future loss of ecosystem services. Conversely, in areas already heavily affected by BWA, such as lower-elevation portions of the central Wasatch Mountains, management options may be limited to "Accepting" the change that is already occurring and is projected to continue into the future. As part of that acceptance, however, there may be a subsequent opportunity to employ targeted removal of dead trees as part of a fuel reduction strategy, as an abundance of BWA-caused mortality can increase available surface and canopy fuels and drive increased wildfire activity.

Our focus on northern Utah as a study area has inherent strengths and weaknesses. The strength lies in the fact that our field data and current infestation prediction model capture a relatively early stage of infestation. This promotes a valuable understanding of what near-term future conditions might look like. However, the insects' relatively brief regional residency means its effects have not yet been fully

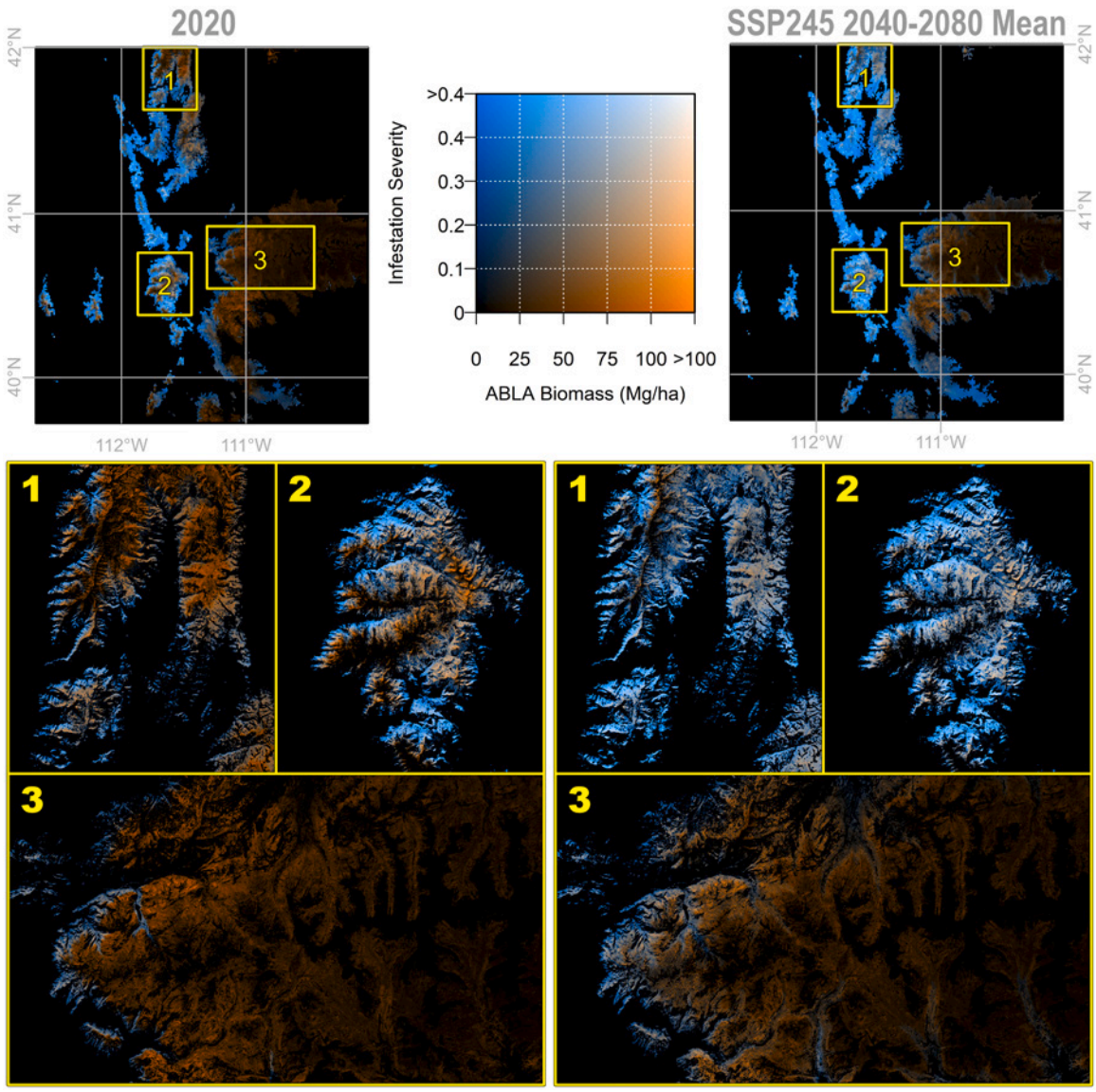

Fig. 10. Bivariate maps displaying both the modeled infestation damage severity and *A. lasiocarpa* AGB for 2020 and an average among all of the SSP-based models for 2040 – 2100. The top two maps represent the entire study area, and pixel values are aggregated to 900 m median values for clarity. The bottom six maps represent a selection of three focal areas of interest, and are shown at the original ~30 m resolution. Focal area 1 represents the Bear River range east of Logan, Utah. Focal area 2 represents the central Wasatch Mountains east of Salt Lake City, Utah. Focal area 3 represents the western Uinta Mountains. Areas in black were not mapped as having any *A. lasiocarpa* present. Abbreviations: AGB = aboveground biomass; ABLA = *Abies lasiocarpa*; SSP = shared social pathways.

realized. This is evident in our field database, where the highest measured severity was 0.49. In theory, our infestation severity metric could be as high as 1.00, which would mean every *A. lasiocarpa* tree was dead, and had the highest severity of each of the damage indicator metrics (gouting, wool density, etc.). Given that BWA's effects on trees can be drawn out over several years, it is likely that our most severe plots would yield higher severity ratings upon remeasurement in a few years. However, in the absence of such a remeasurement, and given random forests' inability to extrapolate, we can only make predictions within our constrained range of severity values. Furthermore, we do not suggest that, for example, a severity score of 0.49 is equivalent to a 49% mortality rate, as not all BWA infestation leads to mortality. Thus, our current and future predictive maps should be viewed as a holistic measure of the effects of BWA on tree health, and not strictly maps of predicted tree mortality.

An important limitation of the study is that we held *A. lasiocarpa* AGB constant to evaluate the relationship between future infestation damage and AGB. In a warming climate, particularly in this region where precipitation regimes may result in a shift from snow to rain, *A. lasiocarpa* forests will certainly undergo change. Studies have shown that *A. lasiocarpa* is likely to experience losses on the lower, warmer, drier reaches of its range (Aubin et al., 2018; Bell et al., 2014; Harris et al., 2023). Our research has shown that this coincides with areas where BWA's effects are most likely to drive tree health declines, the combination of which may significantly reduce *A. lasiocarpa* AGB. Although it may experience gains on the higher, cooler, wetter end, the degree to which those gains offset losses is highly dependent upon the degree to which uphill expansion can outpace warming. In between those habitat extremes, in the absence of disturbance or treatment, *A. lasiocarpa* AGB is likely to increase, in line with the species' typical growth and recruitment rates. The effects of holding *A. lasiocarpa* AGB constant certainly increase the error bounds at the longer projected time frames (i.e., 2100), but the nearer-term projections (i.e., 2040 – 2080) should be more stable, particularly under moderate climate change scenarios (i.e., SSP245). Projecting into the future is always challenging and has caveats; however, the powerful predictive quality of the current

BWA-climate model ($R^2 = 0.774$, RMSE = 0.073, bias = −0.002) and the sole dependence upon annual and seasonal temperature variables instills confidence in the reliability of the results.

Lastly, our results hinge on two key assumptions about BWA: that it will have an equal opportunity to spread throughout the study area within the evaluated time frames, and that population dynamics will remain constant in a changing climate. With respect to the first assumption, BWA spreads somewhat slowly, having taken over 100 years to spread from the west coast to Utah; however, the relatively confined dimensions of our study area coupled with the spatial contiguity of *A. lasiocarpa* forests in the region suggest that even with similar or slower than historical spread rates, BWA should be able to reach all portions of the study area within the projected time frames. Regarding the second assumption, although evidence based on current climatic conditions suggests a positive relationship between temperature and BWA infestation and damage (Greenbank, 1970; Hicke et al., 2023; Rideout, 2023), we do not account for temperatures enhancing or limiting BWA population growth or subsequent damage.

5. Conclusions

Utah represents the spatiotemporal forefront of BWA spread in the western US. Having only recently been detected in the state, BWA's residency and damaging effects are only in their nascency. However, our timely documentation of current effects and development of a powerful climate-based infestation severity prediction model provides a valuable glimpse into what the future may hold in this region. BWA's enhanced ability to cause tree damage and mortality in warmer areas portends a tenuous future for *A. lasiocarpa* forests of the Wasatch and Uinta Mountains, particularly in lower-elevation, warmer portions of the ranges. As with any climate scenario-driven prediction, the degree of BWA expansion is highly sensitive to both the climate model and the time frame. Focusing on the relatively moderate projections of SSP245 in nearer-term time frames (2040 – 2080), our results highlight a substantial increase in BWA-induced tree damage, with the majority of the Wasatch Mountains demonstrating high infestation damage. Coinciding spatially with the areas of highest *A. lasiocarpa* AGB within the study area, these predictions suggest potential future disruption of carbon cycling, increased available fire fuels, degraded habitat quality, and decreased recreational and aesthetic value. However, armed with the high resolution, spatially explicit information we have presented here, and with important decision-making frameworks like Resist, Accept, Direct, forest managers can develop maximally effective mitigation strategies to adapt to a changing climate.

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CRediT authorship contribution statement

Michael J Campbell: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Justin P. Williams:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Erin M. Berryman:** Writing – review & editing, Investigation, Formal analysis. **William R.L. Anderegg:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Michael Campbell reports financial support was provided by US Department of Agriculture Forest Service. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121852.

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