

Climate change shifts in habitat suitability and phenology of huckleberry (*Vaccinium membranaceum*)

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ABSTRACT

Climate change is altering the suitable habitat and phenology of plant species around the world, with cascading effects on people and animals reliant upon those plant species as food sources. Huckleberry (*Vaccinium membranaceum*) is one of these important food-producing plant species that grows in the Pacific Northwest of North America. Here, we modelled how the range and phenology of huckleberry may change as the climate changes. To address this question, we first utilized citizen scientist observations, long-term plot data, and gridded climate data to identify climate variables that best predicted the current bioclimatic niche and the timing of flowering and fruit ripening of huckleberry. We then used multi-model future climate projections for 2 time periods (2041–2070 and 2071–2100) and 2 greenhouse gas emissions scenarios (RCP 4.5 and RCP 8.5) to predict how the range and the timing of flowering and fruiting would change. The modelled bioclimatic niche for the current time period was a good match for our observations, with the model predicting a high probability of occurrence where the species was observed (AUC = 0.88). Suitable habitat for huckleberry was predicted to shrink by 5–40% across the northwestern USA by the end of the 21st century, and this reduction in predicted probability of occurrence was greatest at lower elevations, across drier portions of the current range of the species, and under the higher emissions scenario. Suitable habitat was predicted to expand at higher altitudes (> 3,050 m) and in more northern locations in British Columbia by 5–60% by the end of the 21st century. To predict how future phenological dates might shift, we developed thermal sum models for flowering and fruiting under current climate conditions and then used those models to predict how these events would change based on climate predictions. Our phenology models suggested flowering would advance 23–50 days (mean 35 days) and fruiting would advance 24–52 days (mean 36 days) by the end of the 21st century under the RCP 8.5 scenario; greater advances in phenology were shown over more northerly and higher altitude regions. These large shifts in potential range and phenology could greatly alter trophic relationships and the timing and location of traditional harvests in the future.

1. Introduction

Fruit-producing shrubs such as huckleberry (*Vaccinium membranaceum*, e.g. ‘black’ or ‘thin-leaf’ huckleberry, herein just huckleberry) contribute to the productivity and biodiversity of forest ecosystems, and are an important food source for animals (Halpern and Spies, 1995; Kerns et al., 2004). Huckleberries are used by many wildlife species, primarily for the food value of the berries, although some species will browse the leaves and stems, and the dense shrubby thickets are used as nesting habitat (Martin et al., 2011; Simonin, 2000). The berries are an

important food source for grizzly and black bears (McLellan and Hovey, 1995; Welch et al., 1997; McLellan, 2015) and the woody parts of the shrub are also eaten by moose (Pierce, 1984), elk (Edge et al., 1988), deer (Klebenow, 1965) and by many birds and small mammals (Simonin, 2000). The flowers of this species also provide significant food sources for pollinators, primarily bumble bees and other native bees (Cane and Payne, 1993).

Huckleberry forms a vital component of social history and traditional Native diets in northwestern USA and British Columbia (commonly, Pacific Northwest; Richards and Alexander, 2006;

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Turner, 2011), and serves as the basis for non-tribal recreational harvesting and small-scale commercial operations (Carroll et al., 2003; Robertson, 2014). Traditional foods such as huckleberries are key to the sense of place in many Indigenous cultures, and strong traditions exist for the collection, storage, and consumption of this species (Trusler and Johnson, 2008; Johnson et al., 2015).

Among land managers and Indigenous Peoples there is a strong interest in preserving and restoring this culturally-important plant species across the Pacific Northwest. However, to date, limited knowledge is available on the current range of huckleberry, or how climate change will impact the future range or the timing of flowering and fruiting (but see Holden et al., 2012; Roberts et al., 2014). In the past, Indigenous Peoples in the interior Columbia Basin moved to higher elevation sites in August for several weeks to collect and process berries (Hunn, 1981, 1982). However, the timing of harvest festivals (thanksgiving celebrations traditionally held prior to harvest) has become less predictable in recent decades, with berries ripening much earlier in the season than in the past (Dobkins et al., 2017). This can make it much harder for people who have jobs with regular schedules to be able to schedule time off for harvesting.

Climate change is influencing the distribution of species around the world (Walther et al., 2002; Chen et al., 2011), however, changes in distribution can vary greatly by species (Smithers et al., 2018). These changes in distribution can be rapid, as observed in the mountains of southern California, where common plant species migrated an average of 65 m up in elevation over a 30 year period in conjunction with warming temperatures and decreasing snowpack in the region (Kelly and Goulden, 2008). In the Pacific Northwest, temperatures have risen an average of 0.7 °C, summer and fall precipitation has decreased, and climatic water deficit has increased over the last century (Abatzoglou et al., 2013). Increasing temperatures and drought conditions can have strong impacts on competitive interactions of plant species and lead to reductions and/or expansions of formerly suitable habitat.

Shifting distributions of food plants, such as huckleberry, may result in altered availability and access for people and animals, and possibly increased conflict between people and animals in harvest areas (Chamberlain et al., 2018). However, existing information sources, such as general county-level range maps (USDA NRCS, 2019), are not sufficient to assess the current and projected future impact that climate change will have on the distribution of huckleberry, nor provide the specificity to develop tools to pinpoint or reduce regional vulnerability to potential changes in the range of this species. Small-scale habitat suitability models for huckleberry have been developed for the Rocky Mountains of southeastern British Columbia (Roberts et al., 2014; Lamb et al., 2017), and a model has been developed that accurately predicts huckleberry patches important to grizzly bears, also in southeast BC (Proctor et al., 2017), but range maps and climate predictions for the entire range of the species have yet to be developed.

Climate change is also having significant impacts on the phenology, or timing of seasonal biological events, of many species (Parmesan and Yohe, 2003; Guo et al., 2015; Chen et al., 2019). Climate change has altered the timing of food availability from shrubs for wildlife species such as grizzly bears (Holden et al., 2012; Roberts et al., 2014; Deacy et al., 2017), and traditional harvesters of native plants have reported increased uncertainty in harvest times directly linked to greater variability in climate (Dobkins et al., 2017). However, very limited work has focused on how changes in future climate would impact the flowering and fruiting of food-producing shrubs in the Pacific Northwest. If the timing of flowering shifts earlier with warming, but the timing of spring freezes does not advance as much in the future—freezes may damage flowers and lead to years with no fruit crops (Inouye, 2008; Augspurger, 2013). Such damage might reduce sexual reproduction and population growth of the species, as well as produce cascading impacts on the ecosystem through reduced food availability for pollinators, animals, and people (Inouye, 2000; Straka and

Starzomski, 2015).

To help address the gap in knowledge of climate impacts on huckleberry, we developed predictive models showing how climate change may impact where this plant can grow in the future, as well as potential changes in the timing of flowering and fruit production. Here, we synthesize location and life history data from multiple inventory and scientific data sources to develop climate envelope models and phenological models for huckleberry. We utilized climate envelope models to observe if the predicted range of huckleberry is likely to be altered by future changes in climate (e.g. Ara  jo et al., 2005; Hijmans and Graham, 2006; Lenoir and Svenning, 2015). To model changes in phenology, we used thermal sum models to project future changes in flowering and fruiting (Basler, 2016; Hufkens et al., 2018). Undertaking both species distribution and phenology models across the current western range of this species allows for a more complete picture of climate impacts, as it enables comparisons between how different aspects of life history influence species responses to climate change.

2. Methods

2.1. Study site

We collected data and modelled suitable habitat and phenology changes for huckleberry (*Vaccinium membranaceum*) across coastal western North America, from southern California north through British Columbia and east to central Alberta and Montana (Fig. S1). East of the continental divide, a colder and drier continental climate dominates. This region is characterized by complex topography, with steep elevational gradients from sea level to above 4000 m in the highest mountain ranges and volcanic peaks. The majority of the region has a Mediterranean climate, with wet winters and dry summers, although precipitation and temperature vary greatly across the study area (Fig. S1). The mountain ranges and low-lying coastal areas along the coast of Washington and British Columbia receive abundant precipitation in winter, and are some of the wettest places in North America with annual precipitation over 200 cm, whereas the high plateaus and basins to the east of the region are extremely dry, with mean annual precipitation of less than 20 cm possible (Dalton et al., 2013; Wang et al., 2016). Vegetation types range from temperate rainforest to dry conifer forest to cold-steppe grasslands and shrublands. Huckleberry is mainly associated with subalpine fir forests across this region.

2.2. Species data

We collected presence data for huckleberry from long-term data from federal agencies, academic research projects, citizen scientist data, and other publicly-available sources to adequately cover the current extent of the western range of the species. We obtained phenological observations from the Consortium of Pacific Northwest Herbaria, the USA National Phenology Network, the USFS Region Six Ecology program in northwestern Washington, iNaturalist, and collaborators in Montana and British Columbia, among other sources (Table 1). We removed data points that were located well outside of the western range of the species (e.g. points located east of 96° W longitude), were misidentified, or had flowering or fruiting dates that were three standard deviations or more away from the mean of the phenology observations. For example, several records from the Pacific Northwest Herbaria noted that the species was flowering in January, and we removed these outliers as they were unlikely to be true observations.

2.3. Bioclimatic data

To calculate the climate envelope model for huckleberry, 30-year climatological averages of 16 bioclimatic variables (Table 2) were acquired from AdaptWest over the western US and Canada (spatial extent: 32°–62° N, 146°–105° W; AdaptWest, 2015; Hamann et al., 2013;

Table 1

List of data sources and citations for occurrence records and phenology observations of huckleberry. The '# of records' column indicates the total number of records obtained from each data source, and in parentheses, the number of records actually used in the climate-envelope models after spatial-filtering at a 5-km radius. The 'Citation' column corresponds with the citation in the References list, and the 'Website' column indicates the web address where data were downloaded, if applicable.

Data type	Data source	# of records	Date range	Citation	Website
Occurrence	Bureau of Land Management CVS	66 (31 used in model)	1997–2011	N/A	https://www.blm.gov/or/gis/data-details.php?id=15694
Occurrence	Canadian Museum of Nature	21 (20 used in model)	1886–1989	Canadian Museum of Nature, 2018	http://collections.nature.ca/
Occurrence	USFS Ecology plots	8198 (498 used in model)	1979–2013	N/A	N/A
Occurrence	Forest Inventory and Analysis plots	7125 (1632 used in model)	2003–2015	Forest Inventory and Analysis Program, 2018	https://www.fia.fs.fed.us/
Occurrence	iNaturalist	48 (20 used in model)	2003–2017	iNaturalist, 2018	https://www.inaturalist.org/
Occurrence	Oregon Flora Project	90 (31 used in model)		Oregon Flora Project, 2018	http://www.oregonflora.org/
Occurrence	Consortium of Pacific Northwest Herbaria	856 (281 used in model)	1890–2015	CPNWH, 2018	http://www.pnwherbaria.org/data
Occurrence	National Park plots	1013 (71 used in model)	1999–2016	N/A	N/A
Phenology	Clayton Lamb and Michael Proctor	454	2014–2017	Proctor et al., 2017; Lamb, unpublished data	N/A
Phenology	USFS Ecology plots	342	1980–2013	N/A	N/A
Phenology	iNaturalist	37	2003–2017	iNaturalist, 2018	https://www.inaturalist.org/
Phenology	Consortium of Pacific Northwest Herbaria	199	1980–2015	CPNWH, 2018	http://www.pnwherbaria.org/data

Table 2

The 16 bioclimatic variables used in analysis of habitat suitability of huckleberry. The variables in bold are the seven variables remaining after an iterative variable reduction process and are the variables used in the final climate envelope model.

Bioclimatic variables
Annual Heat Moisture Index (AHM)
Hargreave's Climatic Moisture Index (CMD)
Degree-days below 0 °C (DD0)
Degree-days below 5 °C (DD5)
30-year extreme minimum temperature, °C (EMT)
30-year extreme maximum temperature, °C (EXT)
Frost-free period (FFP)
Mean annual precipitation, mm (MAP)
Mean annual temperature, °C (MAT)
Mean temperature of the coldest month, °C (MCMT)
Mean temperature of the warmest month, °C (MWMT)
Precipitation as snow, mm (PAS)
Summer heat moisture index (SHM)
MCMT – MWMT, °C, provides a measure of continentality (TD)
Hargreave's reference evapotranspiration (EREF)
Mean summer (May – September) precipitation, mm (MSP)

Table 3

The global climate models (GCMs) used in the 15-model ensembles for the climate envelope (CEMs) and phenology models. Daily temperature values were not available for all climate models, thus several different models were used for the CEMs versus the phenology models.

Ensemble GCMs used for CEMs	Ensemble GCMs used for Phenology models
ACCESS1-0	ACCESS1-0
CanESM2	CanESM2
CCSM4	CCSM4
CESM1-CAM5	CESM1-BGC
CNRM-CM5	CNRM-CM5
CSIRO-Mk3-6-0	BNU-ESM
GFDL-CM3	GFDL-CM3
GISS-E2R	MPI-ESM-MR
HadGEM2-ES	IPSL-CM5A-LR
INM-CM4	MIROC-ESM-CHEM
IPSL-CM5A-MR	NorESM1-M
MIROC5	MIROC5
MIROC-ESM	MIROC-ESM
MPI-ESM-LR	MPI-ESM-LR
MRI-CGCM3	MRI-CGCM3

Wang et al., 2016). These data are interpolated on a 1-km grid, where the contemporary climate is based on the Parameter–Elevation Regressions on Independent Slopes Model (PRISM; Daly et al., 1994), and future climate is based on downscaled global climate model (GCM) data from the Coupled Model Intercomparison Project phase 5 (CMIP5; Taylor et al., 2011). Our analysis focused on the contemporary climatological period (1981–2010), the mid-21st century period (2041–2070), and the late-21st century period (2071–2100). Our analyses over future periods were performed using the 15-model ensemble data (Table 3). In order to provide both a conservative and comparatively larger estimate of potential change, we focus on data from future experiments run under Representative Concentration Pathways 4.5 (conservative) and 8.5 (larger; RCP 4.5, RCP 8.5), though we note that emissions trajectories to date have more closely followed RCP 8.5 (Peters et al., 2012).

2.4. Phenology model data

We utilized daily interpolated climate data from 1980–2017 from Daymet (Thornton et al., 2018) to parameterize phenology models, and predict dates of flowering and fruiting for the “contemporary” time period (for phenology models this was defined as the year 2000). Daymet provides surface weather conditions for North America

interpolated from meteorological station data to a 1-km grid using the spatial convolution method of Thornton et al. (1997). Future phenological dates were then projected by forcing the parameterized model with 15 GCM model predictions and calculating the mean phenological dates across the 15 models (Table 3), using the same future time periods and RCP pathways as the climate envelope models.

2.5. Climate envelope models

Multiple methods exist for computing empirical species distribution or climate envelope models (CEM). For this analysis, we used the presence-only maximum entropy method (MaxEnt, version 3.3.3; Phillips et al., 2006). MaxEnt has been used across a wide range of applications due to its performance, ease of use, and accessibility. While no CEM is without limitations, previous studies have shown MaxEnt to perform well relative to other empirical modelling methods (e.g. Aguirre-Guti  rrez et al., 2013; Harrigan et al., 2014).

Elith et al. (2011) provide a detailed review of the statistical mechanics of the MaxEnt solution. In brief, MaxEnt uses geo-located species presence data and environmental data to quantify the species' environmental niche, which is defined as the probability of species occurrence. MaxEnt assumes a random sample of species occurrences across the geographic domain of the study area, which we define by the domain of the gridded bioclimatic variables. However, because of the spatial clustering of species location data, environmental bias is introduced, possibly reducing the model's predictive ability (e.g. Veloz, 2009; Boria et al., 2014). The heterogeneous nature of the data sources, and opportunistic collection of publicly-available data, resulted in dense clumps of observations in some areas, but much sparser observations elsewhere. Various studies have shown that addressing the spatial clustering of location data can improve model performance and reduce overfitting (Veloz, 2009; Anderson and Raza, 2010; Radosavljevic and Anderson, 2014). Boria et al. (2014) showed such improvements when location data were spatially filtered by removing duplicate localities within a given radius of one another. Following these previous studies, we spatially filtered huckleberry location data by 10-km and 5-km radii. While our initial trials showed filtered location data provide improvement as compared to the unfiltered data, little difference in model performance based on the area under curve (AUC) statistic was shown between the two filtered datasets, and mapped model output results were also comparable between the 10-km and 5-km filtered locations. Given that our study area includes complex, mountainous terrain, we chose to perform our analysis using location data filtered at a 5-km radius.

As is common in CEM studies, we utilize climate normals in our modelling efforts. In order to use variables that are likely to be directly relevant to huckleberry, we selected a set of 16 bioclimatic variables *a priori* from an available set of 27. An iterative elimination process was then performed on these variables to identify the subset for use in our modelling and analysis. Following work by Yost et al. (2008) and Baldwin (2009), MaxEnt was first run with our 16 variables, performing a jackknife test of variable importance which was used to identify the least contributing predictor, which was then removed. The predictor with the least contribution was defined as the variable with the lowest decrease in the average training gain when omitted. This stepwise process was continued until only one predictor was used for the model. For each model, the 95% confidence interval of the training gain was calculated to identify difference between models (Yost et al., 2008). The model with the most parsimonious number of predictors (Table 2) that resulted in an AUC > 0.8 and whose 95% confidence interval overlapped with that of the full model was selected to create the final distribution model for huckleberry (van Gils et al., 2014; Yost et al., 2008). For modelling the future distribution of huckleberry, the model trained on the contemporary (1981–2010) climate variables was “projected” into future climate space by applying that model to the gridded future climate data.

Following Phillips and Dud  k (2008), we utilized most of MaxEnt's default settings, which are detailed in Merow et al. (2013). However, we chose to restrict the models to linear and quadratic features in order to produce models that are easier to interpret and provide a better reflection of the relationships between climate and huckleberry (Syfert et al., 2013). Using a random subsample of 25%, we completed 10 replicated runs for each model; the subsampling approach was selected after experiments showed it to perform better (based on AUC) than *k*-fold cross-validation. For visualization and analysing geographic changes in species climate niche, we used the 10-replicate median model output. While MaxEnt provides three types of output, we selected the cumulative output for analysis as it avoids the assumptions made by the logistic output and is more easily interpreted than the raw output (Merow et al., 2013). In this output, the probability of species presence at a site ranges from 0 (low probability) to 100 (high probability); however, we note that the computation of the cumulative output from the raw output means that large variations in cumulative value do not necessarily equate to large variations in probability of presence or site suitability (Phillips and Dud  k, 2008).

2.6. Phenology models

To predict how dates of flowering and fruiting may change in the future, we used the collected phenology observations and interpolated daily mean temperature data to identify the mean accumulated daily temperature sums above a base temperature, or ‘thermal sums’ (also referred to as growing-degree days), until the flowering and fruiting dates of huckleberry in our dataset. We accessed daily interpolated climate data from 1980–2017 from Daymet (Thornton et al., 2018) using the phenoR package (Hufkens et al., 2018) in the statistical analysis program R (R Core Team, 2017). We then calculated the sum of daily mean temperatures above 0   C from January 1st for each phenology observation from 1980–2017, and used the mean value of all observations for flowering and fruiting to get thermal sum models for each phenological event. We decided to use relatively simple thermal sum models, calculated using the TT function in the phenoR package, with a starting date of January 1st for temperature sum accumulation and a base temperature of 0   C because our phenology observations were very heterogeneous over time and space, and were not collected in a systematic matter at the same sites over time (H  nninen et al., 2019). Thus, the observations used here do not necessarily indicate the first or peak observation of a phenological event. However, calculating the mean accumulated thermal sums across the many observations is likely to give an informative look at the actual accumulated temperatures required prior to peak flowering or peak fruiting (Willis et al., 2017). Previous research has shown that phenology predictions from one-time observations of phenological events, such as those that can be gleaned from herbarium specimens with flowers or fruits, are similarly accurate to more systematically collected phenology observations (Robbirt et al., 2011; Davis et al., 2015; Jones and Daehler, 2018). Thus, although our phenology observations are not as temporally precise as in some studies, they can reveal meaningful predictions for how phenology may be altered with changes in climate (Willis et al., 2017).

Next, we used the thermal sum models for flowering and fruiting to project how climate change may alter phenology in the future using projected daily temperatures for the mid- and end-of-century periods, for both the RCP 4.5 and RCP 8.5 emissions scenarios, from the NASA Earth Exchange global daily downscaled projections, following the methods of Hufkens et al. (2018). We calculated the mean predicted dates of flowering and fruiting from phenology models that used each of 15 CMIP5 daily downscaled projections (Table 3), to arrive at CMIP5 model-mean predicted flowering and fruiting dates for each future time period (mid- and end-of-century) and emission scenario (RCP 4.5 and RCP 8.5).

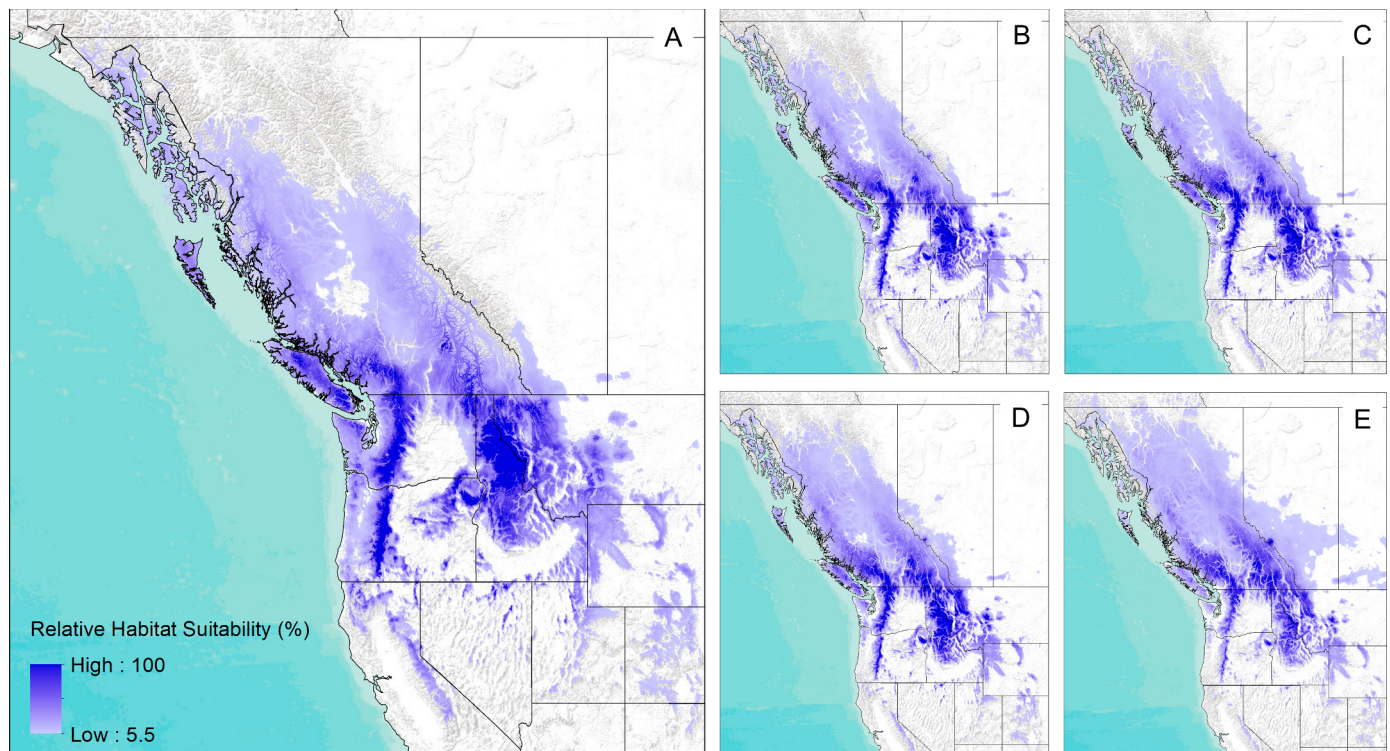


Fig. 1. Relative habitat suitability maps for huckleberry for (A) the current time period (1980–2010), and two future time periods and climate scenarios: (B) mid-century and RCP 4.5 emission scenario, (C) end-of-century and RCP 4.5 emissions scenario, (D) mid-century and RCP 8.5 emissions scenario, and (E) end-of-century and RCP 8.5 emissions scenario. We compared the current habitat suitability map to all occurrence points to decide on a lower limit for habitat suitability of 5.5% (Fig. S1), thus, all values below this limit were removed from habitat suitability maps.

3. Results

3.1. Species distribution model results

The best-fit species distribution models for huckleberry for the current time period selected seven climate variables as important predictors of habitat suitability: extreme hot temperature, average temperature of the coldest month, mean annual temperature, extreme cold temperature, annual heat-moisture index, mean summer precipitation, and moisture deficit (Table 2, Fig. S1). The species distribution model had an AUC value of 0.88, and assigned a high relative measure of habitat suitability to areas with known occurrences of huckleberry, providing an additional confirmation of model performance (Fig. 1, Fig. S2).

The future species distribution models predicted a reduction in habitat suitability for huckleberry at lower altitudes and latitudes by 5–40% (Figs. 2 and 4), and an expansion of suitable habitat at higher elevations (above ca. 3050 m) and latitudes (above c.a. 56 ° N) by mid-century by 5–60%, continuing through the end of the century (Figs. 3 and 4). The results for the RCP 4.5 and RCP 8.5 models are similar in direction, but the RCP 8.5 models project greater reduction in habitat in warmer locations and expansion of habitat in colder locations by the end-of-century period (Figs. 2–4).

3.2. Phenology model results

Phenology observations collected from our data sources spanned the years 1980 through 2017 (Table 1, Figs. S3–S6). In total, we used 97 observations for flowering and 908 observations for fruiting to calculate the mean thermal sums from January 1st through each phenological event. Flowering observations ranged from May 5th through August 10th, and fruiting observations ranged from June 28th through October 4th. The mean thermal sum accumulated January 1st through flowering

was 699, and for fruiting it was 953 (Fig. 5). The thermal sum phenology models were able to predict flowering dates to within 16 days, and fruiting to within 24 days of observed dates across the range of observations (Fig. 5, Fig. S7).

There were significant geographic differences in the advancement of huckleberry phenology across the study area (Figs. 6 and 7). Future thermal sum models projected an advance in flowering dates of huckleberry of 11–31 days, with a mean of 21 days, across the entire range by the end-of-century period under RCP 4.5, and 23–50 days, with a mean of 35 days, under RCP 8.5 (Figs. 6). Fruiting was projected to advance slightly more than flowering in the future, with an advance of 13–37 days (mean 23 days) by the end-of-century period under the low emissions pathway, and 24–52 days (mean 36 days) under the high emissions pathway (Fig. 7). For both fruiting and flowering projections, greater advances in phenological events were predicted to occur at higher latitudes and altitudes (Figs. 6 and 7). Differences between thermal sum model projections for individual CMIP5 daily temperature models were also greater at higher elevations, and greater for the RCP 8.5 than the RCP 4.5 emissions pathway (Figs. S8 and S9).

4. Discussion

Our species distribution models indicated that the range of huckleberry may contract at lower altitudes and more southern locations in the future, while climate suitability for huckleberry may increase at higher altitudes and northern latitudes. Our model included slightly different variables than the regional habitat suitability models of Roberts et al. (2014) and Lamb et al. (2017). However, in the southern Canadian Rockies, all 3 models indicated huckleberry is limited by winter temperatures, and that habitat suitability is likely to increase at higher elevations. This potential for range expansion at higher elevations and latitudes, as well as range contraction at lower elevations and latitudes, is similar to observations and predictions for other high

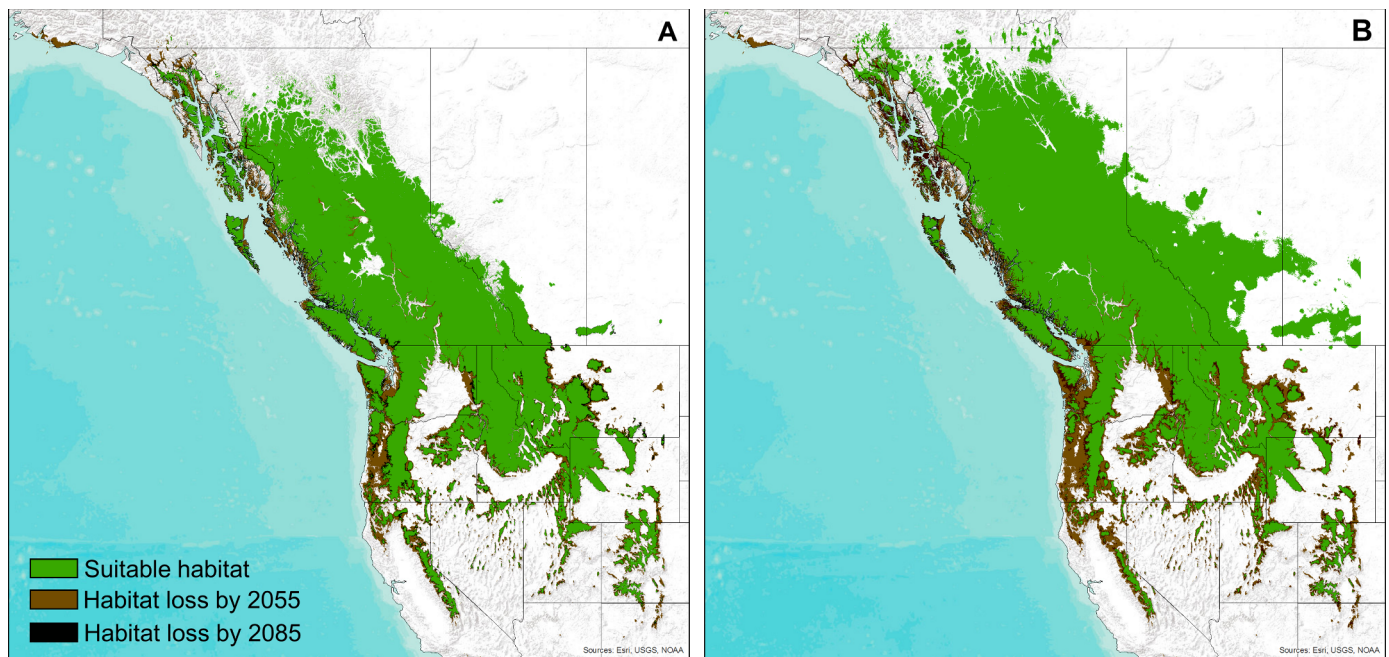


Fig. 2. Predicted range contractions of huckleberry by the end of the 21st century for (A) RCP 4.5 and (B) RCP 8.5 emissions scenarios.

elevation plant and animal species (Smithers et al., 2018). However, the velocity of change (Loarie et al., 2009; Hamann et al., 2015) in climatic variables such as minimum temperature is often relatively low in regions of complex terrain (e.g. Dobrowski et al., 2013; Parker and Abatzoglou, 2016). Expansion of suitable habitat for huckleberry at higher latitudes and altitudes may provide new opportunities for animals reliant on the species for food to move northward and upward (Roberts et al., 2014), although soil properties and soil development may be unsuitable at these sites for some time.

The phenology models projected that the timing of flowering and fruiting could advance by 11–52 days by the end of the 21st century. These large shifts in flowering time can increase flowers' exposure to frost, reducing berry crops (Straka and Starzomski, 2015). Winter and

spring temperatures may increase with climate change, driving earlier phenology, but the risk of late frost events may remain the same (Richardson et al., 2018), increasing the likelihood of frost damage for species that flower earlier with warmer temperatures (Inouye, 2008; Augspurger, 2013; Fitchett et al., 2014). Additionally, large shifts in flowering and fruiting can greatly alter trophic relationships (H  ye et al., 2013; Straka and Starzomski, 2015; Deacy et al., 2017). These results also suggest that the timing of traditional harvests associated with culturally-important species such as huckleberry may need to shift earlier in the year, perhaps by 1–2 months, to track earlier fruit ripening as the climate changes. Our projections can be utilized in conjunction with traditional ecological knowledge and observations from recent harvests to help anticipate future changes, and assist in

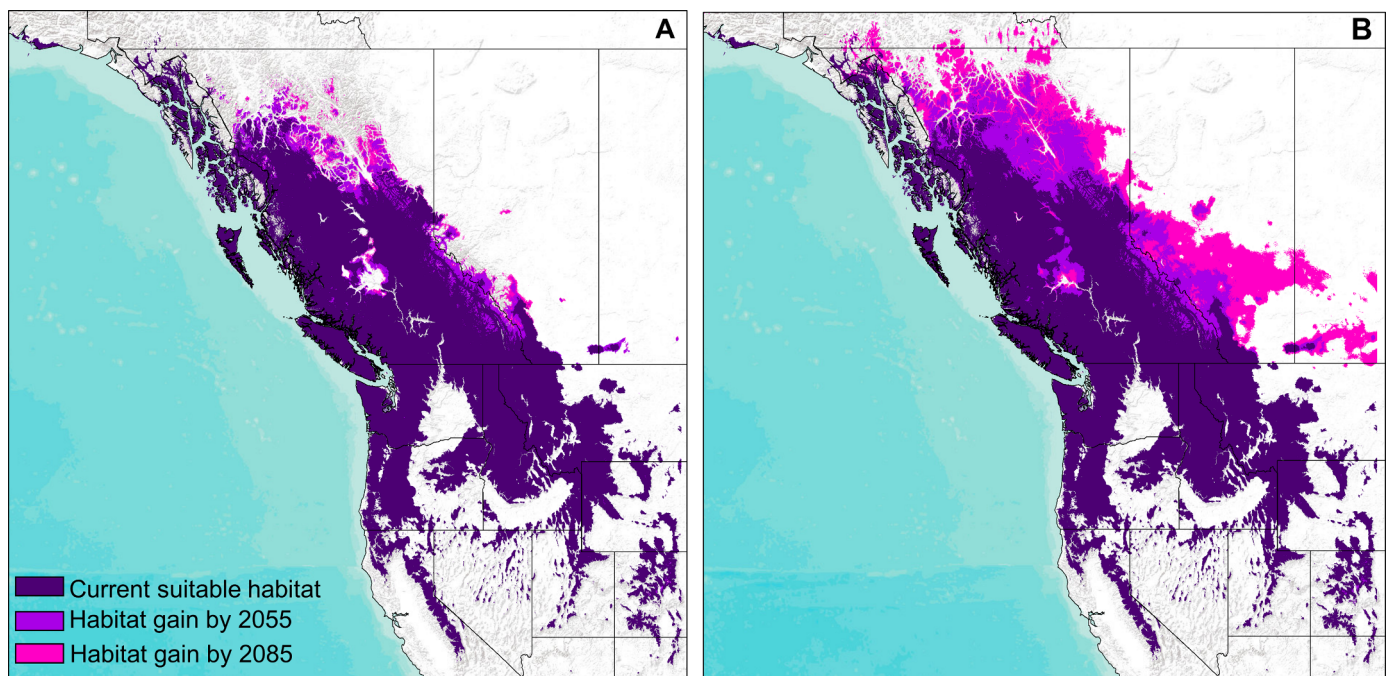


Fig. 3. Predicted range expansions of huckleberry by the end of the 21st century for (A) RCP 4.5 and (B) RCP 8.5 emissions scenarios.

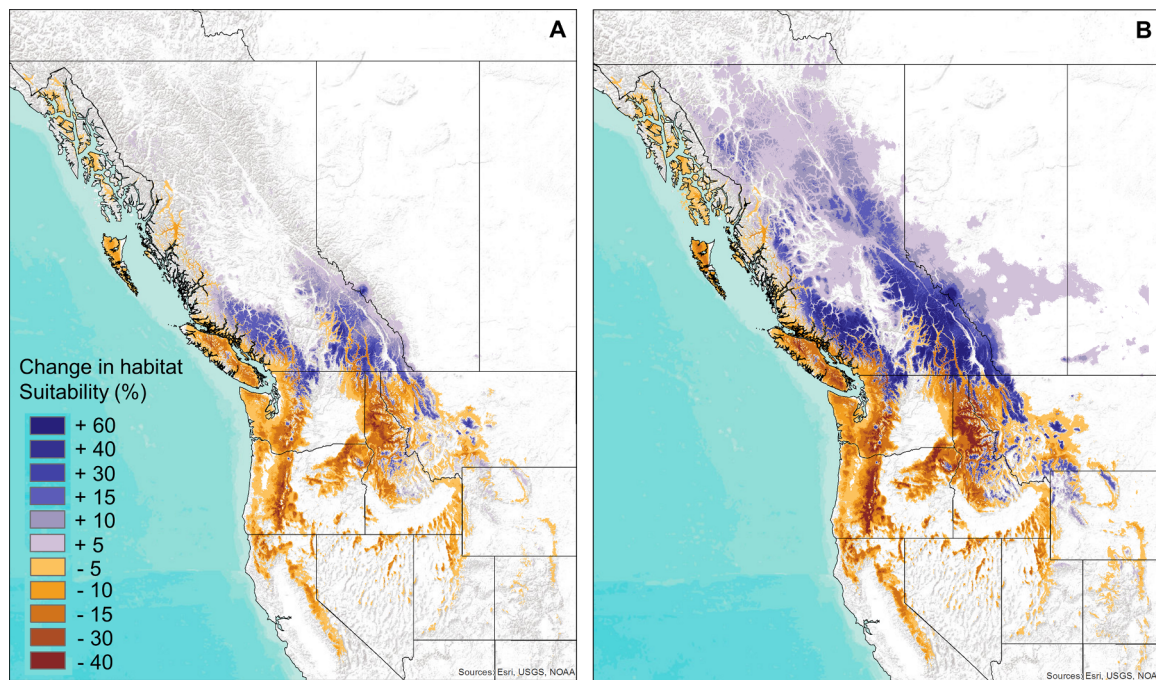


Fig 4. Predicted change in habitat suitability for huckleberry by the end of the 21st century for (A) RCP 4.5 and (B) RCP 8.5 emissions scenarios.

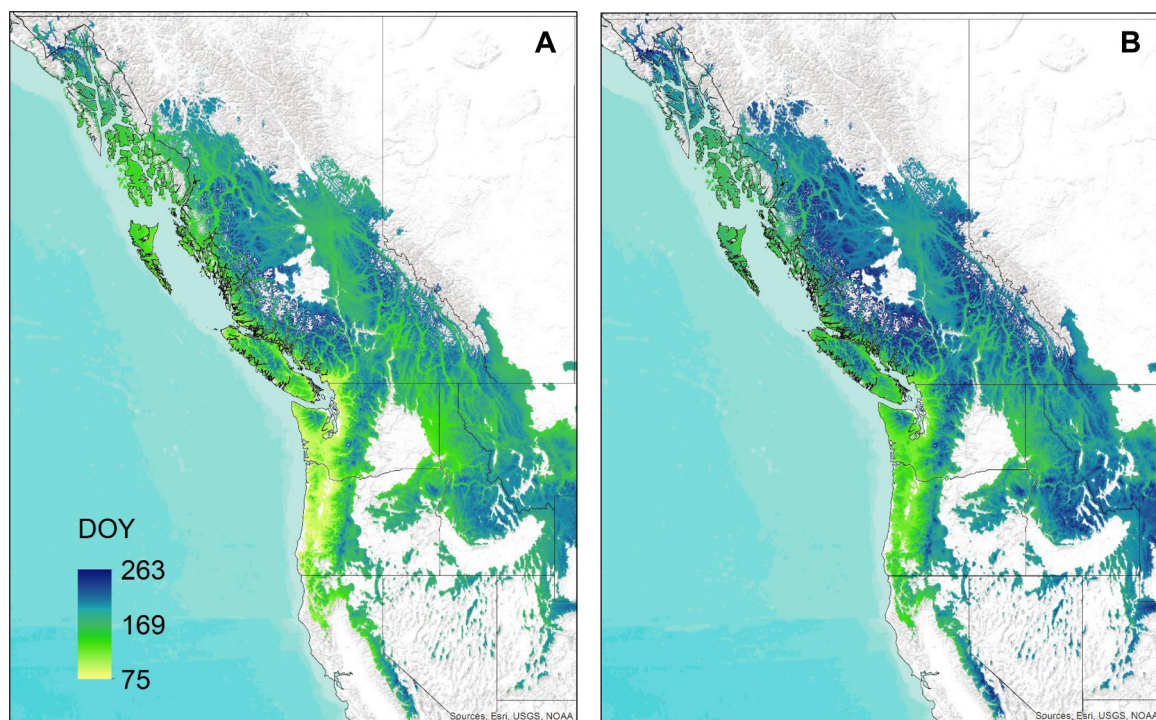


Fig. 5. Thermal sum phenology model projections for the day of year (DOY) of (A) flowering and (B) fruiting of huckleberry in 2000 based on temperature sums of Daymet interpolated daily temperature data across the current predicted range.

planning for important harvest and cultural events associated with huckleberry fruit ripening.

Comparing results from the species distribution and phenology models indicates some similarities between the different modelling approaches. Phenology models for the current time period show that northern locations are too cool to accumulate adequate forcing to result in flowering and fruiting. Interestingly—this delineation is extremely similar to the northern range limits predicted by our species distribution models for the current time period, and expansion of adequate

forcing temperatures for berry ripening in the future for phenology predictions is similar to the expansion of range in habitat suitability models. Additionally, regions with predictions for extremely early dates of flowering are not included in the current species distribution models. So, although the models use different methods to delineate suitable areas for huckleberries—there is some consistency between the results. These model comparisons show the value of looking at both mechanistic and empirical approaches to defining and predicting species range shifts (Estes et al., 2013; Parker and Abatzoglou, 2017).

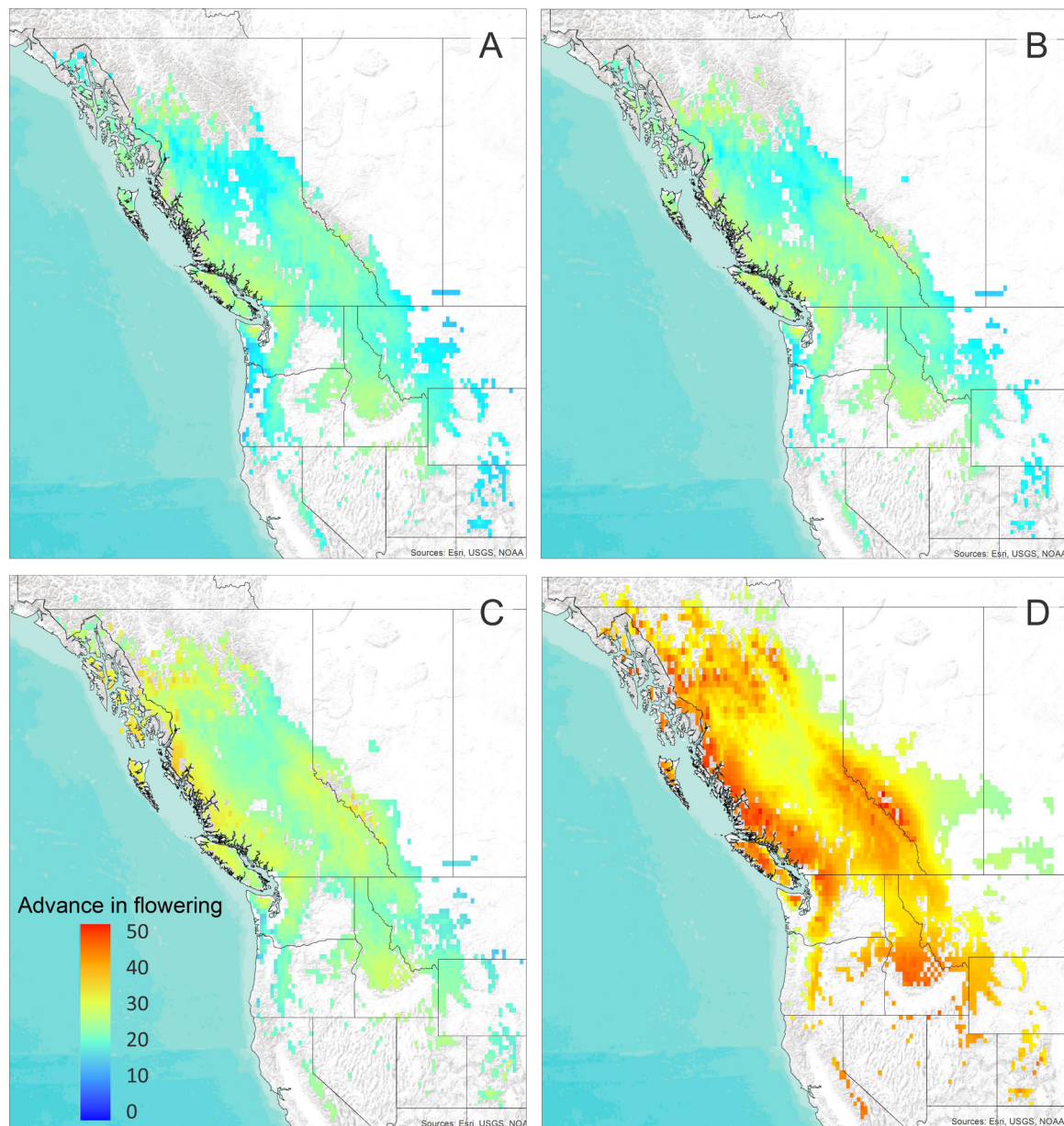


Fig. 6. Thermal sum model projections for changes in the day of year (DOY) of flowering for huckleberry for two future time periods and climate scenarios: (A) mid-century and RCP 4.5 emission scenario, (B) end-of-century and RCP 4.5 emissions scenario, (C) mid-century and RCP 8.5 emissions scenario, and (D) end-of-century and RCP 8.5 emissions scenario.

The predicted changes in distribution and phenology of huckleberry may pose challenges to the traditional users and wildlife who rely on this fruit-bearing shrub. At lower latitudes, it is possible that huckleberry harvests may be reduced in lower elevation areas historically utilized by Indigenous Peoples, and changes in the locations of traditional huckleberry harvests may be needed in the future. Similarly, restoration projects designated for the higher altitude and latitude portions of the range may be more successful in establishing huckleberry than those at lower elevations and latitudes. The altered distribution and timing of berry production will have direct effects on the wildlife that consume huckleberry. For example, grizzly bears rely on huckleberry in many regions for fat deposition and the production of cubs (McLellan, 2015). Changes in the spatial or temporal availability of this critical food source may influence seasonal habitat use, conflict, and population dynamics (Deacy et al., 2017; Lamb et al., 2017).

The poleward and upslope shift in species range shown by our predictions are consistent with other studies which have modeled

similar species retreat under observed and projected future climatic warming (e.g. (Iverson and Prasad, 2002; Kelly and Goulden, 2008; Roberts et al., 2014; Lenoir and Svenning, 2015)). While the direction of these changes is anticipated, there are several important qualifiers to take into account when utilizing the projected degree of species distribution shifts for management decisions. First, autocorrelation and collinearity among climatic variables is common and previous work has shown that variable selection and the interpretation of variable importance can be a source of uncertainty for projected future species range (e.g. Braunisch et al., 2013; Estrada-Peña et al., 2015). While the *a priori* and iterative processes we used to reduce the number of variables in the climate envelope model from 22 to 7 are founded, it cannot be assumed that the variables not included in the final model are unimportant. Biotic interactions among species, disturbances, and soil qualities also influence habitat suitability for most plant species (e.g. Lamb et al., 2017), and we do not directly test the influence of any of these factors here. Assumptions that species and communities are in

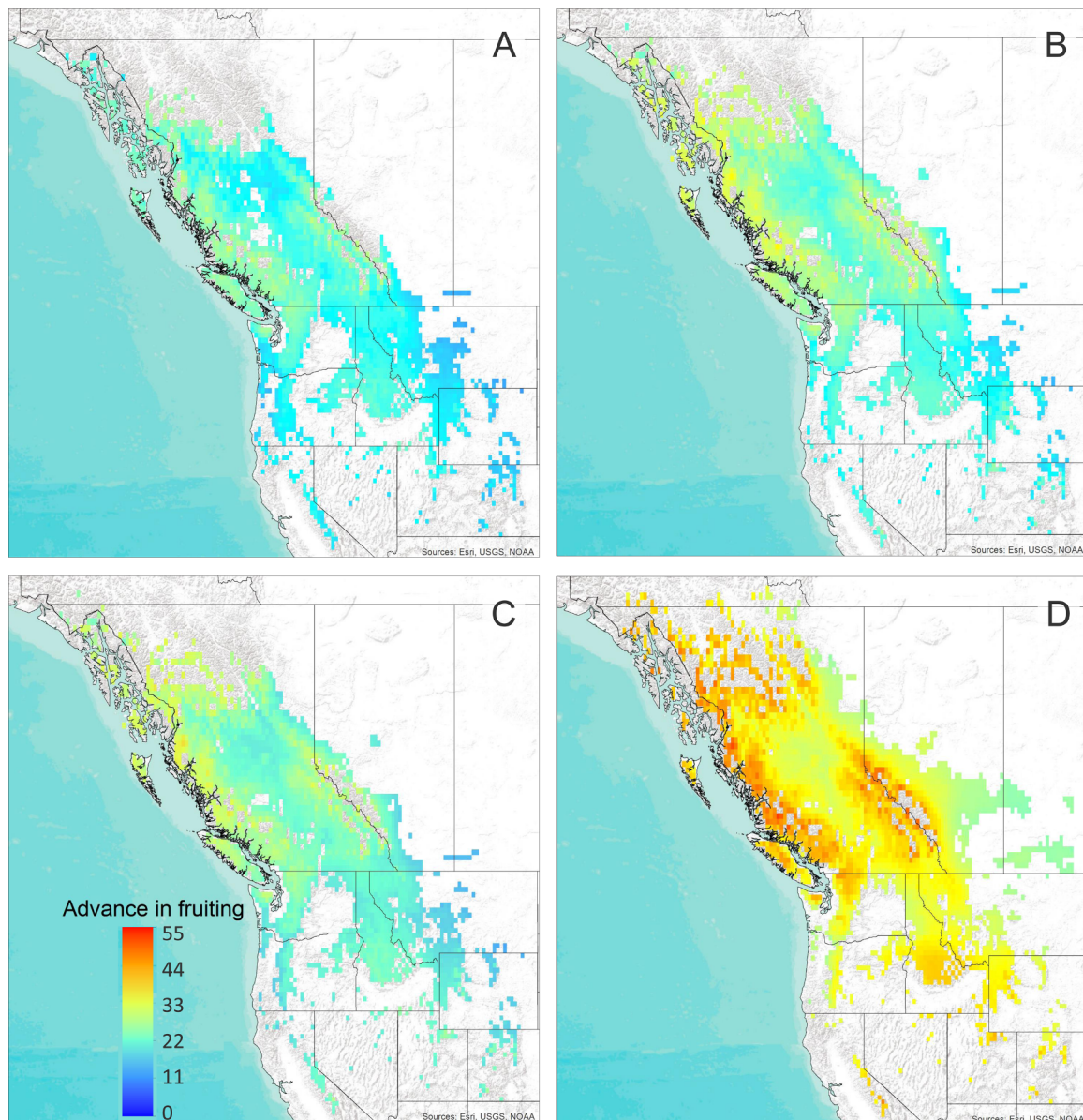


Fig. 7. Thermal sum model projections for changes in the day of year (DOY) of fruiting for huckleberry for two future time periods and climate scenarios: (A) mid-century and RCP 4.5 emission scenario, (B) end-of-century and RCP 4.5 emissions scenario, (C) mid-century and RCP 8.5 emissions scenario, and (D) end-of-century and RCP 8.5 emissions scenario.

equilibrium with climate may not hold true (Gauzère et al., 2018), and life-history traits not considered here have been shown to play an important role in species adaptive capacity (Moor, 2017) and magnitude of range shift (Lenoir et al., 2008). Finally, climate change may also have contrasting impacts on landscape versus local habitat suitability, as warmer temperatures and drier conditions may increase the probability of disturbances, such as fire, creating openings at a local scale that may lead to increased abundance and fruit production of huckleberries in burned sub-alpine regions (Minore et al., 1979; Hobby and Keefer, 2010; McLellan, 2015; Chamberlain et al., 2018; Stralberg et al., 2018).

The phenology model results should also be interpreted with caution. The observations we used to select phenology models were from multiple diverse sources, and were not standardized, likely contributing to the reduced predictive performance observed. We cannot predict with certainty whether phenology in newly suitable habitats in the future will be governed by the same factors as habitat in the current range of the species. In addition, our simple thermal sum phenology

models do not take into account other environmental factors that can influence the timing of phenology, such as the timing of snowmelt (e.g. Wadgyamar et al., 2018), photoperiod (e.g. Fu et al., 2019), or cold temperatures (chilling) over winter (e.g. Laube et al., 2014). Thus, although our phenology models project an average of a month advance in flowering and fruiting dates, actual changes in phenological events may be different if other abiotic factors mitigate the influence of warm temperatures on phenology, especially as mean yearly temperatures increase beyond the historical range of variability in the future (Chen et al., 2019).

More detailed phenological observations taken under a wide range of conditions, coupled with on-site climate data, will allow for more refined mechanistic phenological models that could possibly incorporate the influence of chilling temperatures on reproductive phenology (Harrington et al., 2010; Parker and Abatzoglou, 2017; Prevéy et al., 2018; Hänninen et al., 2019), or the interactive effects of multiple environmental cues (Flynn and Wolkovich, 2018). An adequate assessment of how chilling influences phenology can also provide

more accurate range predictions incorporating climate change (Parker and Abatzoglou, 2018). Additionally, it will be important to collect data on different phenological events (flowering and fruiting) on the same individual shrubs, as this information will help identify whether flowering and fruiting respond to separate seasonal cues, or if a set amount of time must pass after flowering for fruits to develop (Ettinger et al., 2018). Despite these limitations, the phenology models presented here are a critical first step in the direction of providing accurate projections of how phenological patterns may change in the future, and provide useful information for climate impact assessments and other management decisions that need to incorporate future changes.

The strengths of the modelling approaches used here include the large quantity of occurrence points and phenology observations collected from publicly-available data sources across the range of the species in western North America. Additionally, looking at changes in both the possible locations and timing of phenology allow for a more holistic view of how a species may respond to climate change (Estes et al., 2013; Parker and Abatzoglou, 2017; Singer, 2017). Results of our project will help managers understand how climate change is likely to affect the potential ranges and timing of fruit production of culturally-important shrub species. Information from these model projections can be used to identify geographic areas where climate change will significantly impact flowering and fruiting, help managers determine priorities for competing projects, and identify if new areas might need to be developed for traditional use. Successful restoration strategies should incorporate accurate mapping and utilize biological models that consider climate change to effectively conserve species (Hannah et al., 2002); our results can serve as decision tools to help restore populations of huckleberry by identifying regions where huckleberries are more likely to thrive in the future. These results show that the locations and timing of flowering and fruiting of huckleberry may change significantly with climate change – and these large shifts in range and phenology have the potential to greatly alter trophic relationships, plant-pollinator interactions, and the timing of traditional harvests in the future.

5. Conclusions

Our climate envelope models and phenology models projected that habitat suitability for huckleberry may decrease across much of its current range in the future, but expand at higher altitudes and latitudes, and that flowering and fruiting may advance by over a month across parts of the future range by the end of the 21st century. These landscape-scale predictions can be used as an important first step for planning management and restoration efforts of this food-producing shrub. To aid monitoring, management, and restoration plans, we recommend future research address the speed and direction of species migration, as well as the climate velocity of critical climatic variables. Future research should also address how the shifting habitat suitability and phenology of huckleberries impacts pollinators, animals, and people which depend upon the species, and the potential for climate change to alter these trophic relationships in the future.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2019.107803](https://doi.org/10.1016/j.agrformet.2019.107803).

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