Berry plant abundance but not occupancy may decline under climate change: Predicting future conditions and promoting resilience in Southeast Alaskan forests

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Research Article

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Abstract

Context

Climate change may affect the distribution and performance of many high latitude species. Plants producing fleshy, edible fruits are ecologically, economically, and socially important components of Alaskan forests, but the potential impacts of climate change on their distribution and abundance remain largely unknown.

Objectives

I developed models to project changes in habitat suitability for blueberry (*Vaccinium alaskaense* and *V. ovalifolium*) and salmonberry (*Rubus spectabilis*) in Southeast Alaskan forests under future climate change and to evaluate climatic, topographic, and forest stand conditions associated with their aerial cover (*hereafter*, cover).

Methods

I used species distribution models to compare projected habitat suitability for blueberry and salmonberry under historical climate (1990–2020) and future scenarios (SSP2-4.5, SSP 3–6.0 and SSP 5-8.5) for 2050, 2075, and 2100 in Southeast Alaskan forests. I compared projected suitability to cover and used models to evaluate environmental correlates of blueberry and salmonberry cover.

Results

Habitat suitability for blueberry and salmonberry declined in all future scenarios, but occupancy was projected to remain high. Habitat suitability was positively correlated with blueberry but not salmonberry cover. Forest stand attributes including forest type, shrub and tree cover, and stand age and size were often stronger predictors of cover than climate or topography.

Conclusions

While blueberry and salmonberry occupancy in Southeast Alaska are unlikely to decrease substantially over the 21st century, declining habitat suitability may drive reduced blueberry abundance. Relationships between forest conditions and blueberry and salmonberry cover suggest that management could support sustained abundance in the face of challenges posed by climate change.

INTRODUCTION

Global climate change has the potential to drive shifts in the distribution of species (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Chen et al. 2011; Rubenstein et al. 2023), which can have important implications for the availability of species of social, economic, or ecological importance. Climate can shape species' distributions both directly through interactions with the physiological tolerances that their fundamental niches (*sensu* Hutchinson 1957; Stevens 1989; Sexton et al. 2009; Thomas 2010), and indirectly through context-dependence in the frequency and outcomes of biotic interactions (Koh et al. 2004; Parmesan 2006; Tylianakis et al. 2008; Van der Putten et al. 2010). Changes in climatic regimes may contribute to contractions of some parts of species' distributions but can also ameliorate climatic limitations and allow for expansion of the distribution into previously unoccupied areas (Thuiller et al. 2005; Chen et al. 2011; Lenoir and Svenning 2015; Lenoir et al. 2020; Lawlor et al. 2024). Forecasts of the direction and magnitude of species' distributional shifts related to climate change are essential for projecting how ecosystems, economies, and social systems may be impacted in order to promote resilience in the face of challenges posed by climate change.

The pace of climate change in high laititude regions of the globe like Alaska is far greater than in regions closer to the equator (Rantanen et al. 2022; Ballinger et al. 2023), a pattern which is particularly concerning considering its potential to rapidly alter the distribution and abundance of species of subsistence and traditional value (*hereafter*, ST species). This concern is especially acute in the state's many rural communities, where ST species are important for promoting food security, health, and community cohesion (Wolfe and Walker 1987; Magdanz et al. 2017; Walch et al. 2018; Scaggs et al. 2021). Access of Alaskans to ST species harvesting on public lands is prioritized under state and federal law (AS 16.05.940 and Title VIII of the Alaska National Interest Lands Conservation Act of 1980); as such, actions supporting access are an important part of public land management plans in the state. Changes in the availability of ST species related to altered phenology, performance, and/or distributions have been reported for several species in Alaska and are anticipated to accelerate with future climatic shifts (Kielland et al. 2010; Moerlein & Carothers 2012; Shanley et al. 2015; Brinkman et al. 2016; Hayward et al. 2017; Herman-Mercer et al. 2020; Jones et al. 2020; Morton et al. 2024), necessitating research to forecast the direction and extent of changes in ST species distributions and availability.

Plants that produce edible fleshy fruits (*hereafter*, berry plants) are among the most commonly harvested ST plant species in Alaska; most harvesters report picking at least 19 L of berries annually, with some families harvesting more than 75 L of berries per year (Hupp et al. 2015). Berry plants provide high-quality fruit with demonstrated health benefits (Leiner et al. 2006; Neto 2007; Ogawa et al. 2008; Kellogg et al. 2010; Devore et al. 2012; Dinstel et al. 2013), and berry harvesting is an important traditional activity with spiritual and cultural significance (Callaway et al. 1998; Thornton 1999; Redwood et al. 2008; Herman-Mercer et al. 2019). Berry plants also provide forage for wildlife harvested for ST purposes (Weeden 1969; Oldemeyer et al. 1977; Hupp et al. 2013; Hanley et al. 2014). Extensive research shows that climate change may impact berry plants in Alaska and other circumpolar regions through direct impacts on performance ranging from positive (Shevtsova et al. 1997; Natali et al. 2012) to negative (Marks and Taylor 1978; Kortesharju 1995; Krebs et al. 2009; Palacio et al. 2015; Herman-Mercer et al. 2020; Mucioki 2024) and indirectly through effects on disturbance regimes (Nelson et al.

2008; Narita et al. 2015; Parkinson and Mulder 2020) or interspecific interactions (Myers-Smith et al. 2011; Pearson et al. 2013; Oakes et al. 2014; Renner et al. 2018; Parkinson and Mulder 2020; Siemens et al. 2020).

In contrast to the considerable research examining the potential for climate change to affect aspects of berry plant performance at a local scale, studies projecting the effects of climate change on the geographic distributions of berry plants in Alaska are rare. We are aware of only two studies that project how climate change may shape the future geographic distributions of some berry plants in all or part of Alaska (Hamilton et al. 2024; Rhodes 2024) and another two focused on adjacent regions of Canada and the Pacific Northwest of the United States (Prevéy et al. 2020; Hirabayashi et al. 2022). Further, we are aware of no studies that have examined potential changes in the distributions of berry plants of particular importance in Southeast Alaska, where much of the land area is administered by federal agencies and thus subject to Title VIII of the Alaska National Interest Lands Conservation Act of 1980. More research is clearly needed to explore how the distribution of berry plants may shift with projected climate change in Alaska, particularly in the Southeast portion of the state.

Projecting shifts in berry plants' distributions under future climate change can be useful for locating areas that could benefit from increased management activity. Further, identifying climatic, topographic, and/or biotic conditions that represent potential 'tipping points' beyond which berry plant abundance changes rapidly is essential for determining where and when berry plants may be threatened by changing environmental conditions. Knowledge of forest stand conditions associated with higher berry plant abundance and their relative influence compared to climatic or topographic conditions may also aid in developing management targets to promote or retain berry plant abundance in the face of changing environmental conditions.

In this study, I used a species distribution modeling (SDM) approach to evaluate habitat suitability across Southeast Alaska for two of the most commonly harvested berry species in the region under historical climate conditions and project how the distribution and abundance of climatically suitable habitat may shift through the rest of the 21st century. I also evaluated the relative importance of climatic, topographic, and forest stand correlates of each berry plant's local abundance, which may aid in developing management strategies aimed at promoting their abundance and/or harvesters' access to these plants in the future.

METHODS

All data preparation and analyses were conducted using R Statistical Software version 4.3.0 (R Core Team 2023).

Study Area

The Tongass National Forest (*hereafter*, Tongass) is the United States' largest National Forest, comprising nearly 90 percent of the land area of Southeast Alaska. Many Southeast Alaskan

communities are located along the periphery of the Tongass and berry harvesting from within the National Forest is a common practice. The Tongass is topographically complex; steep elevational gradients rising from sea level to the alpine across short distances are common. Much of the northern edge of the world's largest stretch of continuous temperate rainforest lies within the Tongass; forest overstories are generally dominated by a combination of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), but Alaska yellow-cedar (*Callitropsis nootkatensis*), western redcedar (*Thuja plicata*), and mountain hemlock (*Tsuga mertensia*) are also common in mixed conifer stands. Low-elevation riparian forests may be dominated by disturbance-associated overstory species such as red alder (*Alnus rubra*). While much of the Tongass is forested, it also includes non-forested areas such as shrub-dominated communities, meadows, wetlands, alpine tundra, glaciers, and recently deglaciated bare ground.

Study Species

Salmonberry (*Rubus spectabilis*) and blueberry (*Vaccinium ovalifolium* and *V. alaskaense*) are deciduous shrubs that produce the most commonly harvested berries in Southeast Alaska (Hupp et al. 2015). Two species (*Vaccinium ovalifolium* and *V. alaskaense*) are generally grouped together when referring to blueberry in Southeast Alaska due to their similar appearance and distributions and the fact that they are usually harvested together (Vander Kloet 1988; Viereck and Little 2007; Hupp et al. 2015). For the purposes of this study, 'blueberry' refers collectively to *V. ovalifolium* and *V. alaskaense* and analyses examining blueberry distribution and abundance group both species together. Blueberry is the most common understory shrub encountered in Southeast Alaskan forests, occurring across a broad variety of forest conditions (DeMeo et al. 1992; Martin et al. 1995; Cahoon et al. 2020). Salmonberry is more commonly associated with disturbance than blueberry but also occurs under intact canopies, particularly in canopy gaps of intermediate age to older stands (Zouhar 2019). Within western North America, blueberry is distributed from roughly southcentral Alaska to northern California and western Montana, although isolated populations have also been recorded in South Dakota. Salmonberry's distribution extends from southcentral Alaska to northern California and east into western Idaho (USDA NRCS 2024).

Presence and Cover Data

Data describing the presence or absence and aerial cover of blueberry and salmonberry were extracted from the Phase 2 vegetation dataset of the Forest Inventory and Analysis (FIA) program (Bechtold and Patterson 2005). FIA plots are randomly located within each cell of a hexagonal grid, each of which comprises 2428 hectares except in areas of intensified sampling where plots represent a smaller area. FIA plots comprise four circular 7.3 m radius subplots. As part of the Phase 2 vegetation profile protocol, FIA crews recorded the identity and aerial cover of the four most dominant vascular plant species per growth habit (forbs, graminoids, shrubs, seedlings and saplings, and large trees) that met or exceeded 3 percent aerial cover on each surveyed subplot (USDA-FS 2024). These data were recorded on all accessible forest conditions on each plot that received a ground visit within the western United States.

FIA plots are revisited on a 10-year interval; occurrence and aerial cover data for this study were taken from the most recent inventory of each plot (2010–2020).

Presence data for blueberry and salmonberry were extracted for field-visited FIA plots within all states that fell within their U.S. distributions according to the USDA Plants database (Fig. 1). The only exception was South Dakota, for which no FIA vegetation data were available; however, only a single herbarium record indicates presence of *V. ovalifolium* in the state, so it likely represents a minor part of the distribution. Each species or species aggregate was counted as present on a plot if it was recorded on any of the four subplots; it was deemed absent on the plot if it was not recorded on any of the four subplots. It is possible that blueberry or salmonberry were recorded as absent on a plot if they were present at less than 3 percent aerial cover, but for the purposes of this study, a 3 percent cover threshold for describing presence is justified considering that the focus is on the distribution of areas suitable for subsistence or traditional harvest of blueberries or salmonberries by humans, which is unlikely to occur in areas where cover is less than three percent. In this study, the term “presence” refers to presence at or exceeding 3 percent cover, and “absence” refers to less than 3 percent cover inclusive of areas of true absence.

Presence or absence records for each plot were paired with plot coordinates for model construction. With few exceptions, FIA plots are only surveyed for vegetation in forested conditions (as defined in Bechtold and Patterson 2005); as such I limited model projections for blueberry and salmonberry distributions in Southeast Alaska to forested areas of the Tongass (USDA-FS R10 2020). While FIA data do not include samples from Canada, I assumed that the spatially comprehensive nature of FIA understory vegetation data from the western U.S. is sufficient to describe the climatic tolerances of the focal species throughout their North American ranges. For a total of 27,205 plot records (Fig. 1), the occurrence dataset for blueberry contained 2,033 presences and 27,193 absences and the occurrence dataset for salmonberry contained 2,021 presences and 27,205 absences (Fig. 1).

The abundance of each berry plant was evaluated using aerial cover of each species as recorded by FIA crews on field-visited plots (*hereafter*, cover). As measures of cover can vary among different forested conditions occurring within the same subplot and among subplots within a plot, I extracted cover data for each berry plant on ground-visited plots only for the central subplot and only for those subplots that contained a single forested condition. This ensured that only a single aerial cover record existed for each set of plot coordinates, which are recorded at the center of the central subplot. As the focus of this study was on predicting cover of blueberry and salmonberry within forested areas of the Tongass, I used cover data only from forested plots within Southeast Alaska in models. This yielded 858 cover records for blueberry and salmonberry (Fig. 1). Citizen scientists participating in the Alaskan Youth Stewards program (AYS) collected an independent validation dataset (*hereafter*, AYS data) describing the aerial cover of blueberry and salmonberry across 40 forested plots with dimensions equal to that of the central subplot of an FIA plot in areas surrounding four Southeast Alaskan communities as part of this study.

Occurrence and Cover Predictors

FIA data describing the occurrence of blueberry and salmonberry throughout the western United States were paired with historical climate normals data and projected climate data extracted from the ClimateNA dataset at a 1 km resolution (v 7.5; Wang et al. 2016; Mahony et al. 2022; Wang et al. 2024). Data describing 23 annual and seasonal climatic predictors were downloaded for the 1991–2020 historical climate normals period (Table S1). Future climate projections for 2050, 2075, and 2100 were generated for the study area using a subset of 13 General Circulation Models (GCMs) from the Coupled Model Intercomparison Project (CMIP6) included in the IPCC sixth assessment report (AR6; IPCC 2023; Wang et al. 2016; Mahony et al. 2022). Shared socioeconomic pathways (SSPs) used in this report (SSP2-4.5, SSP3-7.0, and SSP5-8.5) were chosen to represent a range of social and climate change scenarios and to align with scenario prioritizations recommended by the ScenarioMIP experimental design (O'Neill et al. 2016). In addition to climatic predictors, data describing elevation, aspect, and percent slope at 30m resolution (Table S1) were used to generate aggregated 1 km resolution gridded data describing plot elevation, slope, northness, and eastness and to calculate values of terrain ruggedness index (TRI) and topographic position index (TPI) at a 1 km resolution using the terrain function within the terra package (version 1.7–29, Hijmans 2023).

Cover of blueberry and salmonberry at the subplot scale was modeled as a function of the climatic and topographic predictors described above along with forest stand attributes measured by FIA field crews. Forest stand attributes were measured on the same subplot as the cover record and included percent tree cover on the subplot, percent shrub cover on the subplot, and categorical variables describing stand age class, and the mean diameter of trees on the subplot (Table S1). Citizen scientists involved in AYS collected the same data describing forest stand attributes as those collected by FIA crews on their field plots.

Model Construction and Statistical Analyses

Occurrence Models

Prior to constructing species distribution models, I performed model selection using random forest models for the presence of blueberry and salmonberry to rank predictor importance according to the mean decease in model accuracy associated with their exclusion (Liaw and Wiener 2002). I eliminated model terms correlated with the highest-ranked predictor at $|r \geq 0.7|$ and continued this process with remaining model predictors until only non-multicollinear terms remained. These terms were included in ensemble distribution models for the two focal species. I used the biomod2 package (version 4.2-3; Thuiller et al. 2023) to build ensemble species distribution models (SDMs) for blueberry and salmonberry informed by data for their occurrence and associated climatic and topographic predictors throughout their U.S. distributions (Table S1). SDMs were calibrated using 80 percent of records and validated using the remaining 20 percent of records; the proportion of presence and absence records was identical within both the calibration and validation datasets. I conducted ten runs each of four algorithms: (1) generalized additive models, (2) multiple adaptive regression splines, (3) boosted regressions, and (4)

random forests. Any model whose True Skill Statistic (TSS; Allouche et al. 2006) exceeded 0.7 was retained in the ensemble SDM, and the weight of component model contributions to the ensemble was determined according to their accuracy as measured by each model's TSS. The accuracy of the ensemble model for each species was evaluated according to the area under the receiver operating curve (AUC) and TSS scores associated with ensemble predictions.

Projections for the probability of climatic and topographic suitability for occurrence (*hereafter*, suitability) were generated for forested areas within the Tongass National Forest under both historical climate normal conditions and future climate projections for each SSP scenario for 2050, 2075, and 2100. Continuous estimates of suitability (*hereafter*, suitability) were converted to binary classes of "suitable" or "unsuitable" (*hereafter*, binary suitability) using the threshold suitability value that maximized model accuracy according to TSS. I calculated the difference in both continuous and binary suitability projections among historical climatic conditions and each future climate scenario to generate estimates of change among current and projected future conditions. As some studies suggest that suitability may indicate the carrying capacity for a species in a particular area (VanDerWal et al. 2009; Muñoz et al. 2015; Acevedo et al. 2017), I used a generalized linear model with a negative binomial distribution to examine the relationship between predicted suitability under historical climatic conditions and cover of blueberry and salmonberry recorded on FIA plots within the Tongass. As few FIA plots in Southeast Alaska occurred in areas of low suitability, I also repeated this test using aerial cover data from the central subplot of all FIA plots within the western United States from which occupancy data were drawn to train and validate the ensemble SDM to determine whether relationships existed across a broader geographic region that contained lower-suitability areas.

Aerial Cover Models

I used generalized additive models (GAMs) to evaluate relationships between the cover of the focal species on forested plots and associated climatic, topographic, and stand attributes as described above. Although interactive effects of predictors likely exist, utilizing an additive approach allowed for clearer evaluation of potential thresholds that may exist in the tolerances of the focal species to climatic, topographic, or forest stand conditions. Preliminary model selection was implemented by first running a random forest model with all possible terms included to determine the relative contribution of each term to model accuracy, then eliminating collinear terms using the same approach as described above for SDMs. Retained terms were included in a generalized linear model with a negative binomial distribution to account for the right-skewed distribution of aerial cover data. Terms were excluded from the final model if they had < 1 degree of freedom or $P \geq 0.1$ in the initial GAM run. Model fit was evaluated by *(i)* evaluating the deviance explained by the GAM, *(ii)* comparing AIC value of the fitted model to a null model, and *(ii)* performing linear regressions of predicted values of aerial cover against values from both a validation dataset comprised of FIA data withheld from model training (a random selection of 20 percent of aerial cover records for each focal species) and the AYS validation dataset. I examined the relative contribution of each model term to model performance by determining the relative importance

value of each predictor included in the final GAM for each species (bm_VariablesImportance; biomod2; Thuiller et al. 2023). I also evaluated whether threshold values exist for each predictor beyond which cover is predicted to dramatically change by generating response curves for the relationship between model-predicted cover and variation in the value of each model term when other terms were held constant at their median (continuous predictors) or modal values (categorical predictors).

RESULTS

Species Distribution Models

Ensemble SDMs for both blueberry and salmonberry were excellent fits to data when predictions were compared to validation datasets (blueberry: AUC = 0.97, TSS = 0.843, sensitivity = 0.961, specificity = 0.929; salmonberry: AUC = 0.932, TSS = 0.753, sensitivity = 0.975, specificity = 0.884).

Using models constructed with occurrence data from the U.S. distribution of blueberry, almost all forested areas within the Tongass National Forest were predicted by the ensemble SDM to be climatically suitable for the occurrence of blueberry under climate normal conditions (99.99 percent of cells classified as suitable; Fig. 2). The relative importance values of each predictor included in the ensemble model are presented in Table S2 and associated response curves for the relationship between predicted climatic suitability and values of each predictor when holding all other predictors at their median (continuous variables) or mode (categorical variables) are included in Fig. S2. The predictors with the highest importance values for blueberry suitability were summer heat moisture index and Hargreaves reference evaporation. Predicted suitability declined precipitously from summer heat moisture index values of 0°C/cm to 78°C/cm and remained similarly low for values exceeding 78°C/cm, indicating much higher suitability under cooler and wetter summer conditions. A similar pattern existed with Hargreaves reference evaporation, where the highest predicted suitability was associated with the lowest values of reference evaporation: predicted suitability declined rapidly from values of 255–440 mm and plateaued at values exceeding 440 mm.

As with blueberry, the ensemble SDM for the occurrence of salmonberry predicted that nearly all forested areas within the Tongass National Forest were climatically suitable for the presence of salmonberry under climate normal conditions (99.4 percent of cells classified as suitable; Fig. 2). The relative importance values of each predictor included in the ensemble model are presented in Table S2 and associated response curves for the relationship between predicted climatic suitability and values of each predictor when holding all other predictors at their median (continuous variables) or mode (categorical variables) are included in Fig. S4. The predictors with the highest importance values in the ensemble model were the date of the beginning of the frost-free period and the summer climate moisture index. Suitability was predicted to be uniformly high where the beginning of the frost-free period preceded mid- to late-March and decrease dramatically in areas where the frost-free period began after late-March. Suitability was also predicted to peak in areas where summer climate moisture index was slightly greater than zero but remained similarly high at higher values, indicating higher suitability under moist to wet

conditions. Suitability was predicted to be much lower where summer climate moisture index values were negative, indicating that dry summer conditions are not favorable for salmonberry occurrence.

Maps comparing binary suitability under climate normal conditions versus projected conditions in 2100 for each SSP are presented in Fig. 2. Maps comparing climate normal conditions and projected future conditions for all SSPs and years examined in this study are presented in Figures S5 and S6. The area of forested land in the Tongass suitable for blueberry occurrence was predicted to decline slightly under all SSPs and future years examined, although these declines were generally minimal. Net percent decreases in suitable area for blueberry occurrence under future SSPs ranged from 0.39–0.82 percent in 2050, 0.44–4.27 percent in 2075, and 1.63–4.23 percent in 2100 (Table 1). Predicted decreases in forested areas suitable for salmonberry occurrence under future SSPs were similarly small. Net decreases in suitable area for salmonberry occurrence ranged from 0.62–3.65 percent in 2050, 0.08–2.99 percent in 2075, and 0.377–4.18 percent in 2100 depending upon SSP scenario (Table 1). Despite net decreases in area predicted to be suitable for the occurrence of blueberry and salmonberry under future SSPs, suitable area for their occurrence never fell below 95 percent of the study area in any scenario or year (Table 1; Fig. 2, S5, S6).

Table 1

Results of ensemble species distribution models for blueberry and salmonberry occupancy in forested areas of the Tongass for historical climate conditions (1991–2020) and all future years and SSPs. Occupied Area refers to the percent of pixels meeting the threshold for "suitable" under determinations of binary suitability described in the main text, and ΔOccupied Area describes the net change in Occupied Area between historical climate and projected future climate. Suitability reflects the mean (± 1 standard error) value of continuous suitability across forested areas of the Tongass, and ΔSuitability describes the mean (± 1 standard error) change in suitability between historical climate and projected future climate

Species	Year	SSP	Occupied Area	ΔOccupied Area	Suitability	ΔSuitability
Blueberry	Historical		99.99%		0.957 ± 0.0002	
	2050	2-4.5	99.64%	-0.35%	0.922 ± 0.0004	-0.035 ± 0.0003
		3–7.0	99.53%	-0.46%	0.911 ± 0.0005	-0.046 ± 0.0004
		5-8.5	99.18%	-0.82%	0.911 ± 0.0005	-0.046 ± 0.0004
	2075	2-4.5	99.55%	-0.44%	0.908 ± 0.0004	-0.050 ± 0.0004
		3–7.0	99.27%	-0.72%	0.904 ± 0.0004	-0.053 ± 0.0003
		5-8.5	95.72%	-4.27%	0.808 ± 0.0007	-0.149 ± 0.0007
	2100	2-4.5	98.36%	-1.63%	0.876 ± 0.0005	-0.081 ± 0.0005
		3–7.0	96.82%	-3.17%	0.797 ± 0.0007	-0.160 ± 0.0007
		5-8.5	95.76%	-4.23%	0.798 ± 0.0007	-0.160 ± 0.0006
Salmonberry	Historical		99.43%		0.878 ± 0.0003	
	2050	2-4.5	98.81%	-0.63%	0.839 ± 0.0005	-0.040 ± 0.0003
		3–7.0	95.80%	-3.65%	0.781 ± 0.0007	-0.098 ± 0.0005
		5-8.5	98.27%	-1.17%	0.842 ± 0.0006	-0.036 ± 0.0004
	2075	2-4.5	98.56%	-0.87%	0.839 ± 0.0006	-0.039 ± 0.0004

Species	Year	SSP	Occupied Area	ΔOccupied Area	Suitability	ΔSuitability
		3–7.0	99.35%	-0.08%	0.874 ± 0.0004	-0.004 ± 0.0003
		5-8.5	96.45%	-3.00%	0.823 ± 0.0007	-0.056 ± 0.0006
	2100	2-4.5	99.06%	-0.37%	0.857 ± 0.0005	-0.022 ± 0.0004
		3–7.0	95.27%	-4.18%	0.814 ± 0.0008	-0.065 ± 0.0006
		5-8.5	97.86%	-1.58%	0.825 ± 0.0006	-0.053 ± 0.0005

While binary suitability for blueberry and salmonberry presence did not change considerably between historical climatic conditions and any of the SSPs or future years examined, continuous suitability did categorically decrease under all SSP scenarios and future years examined (Table 1); decreases tended to be larger near the end of the century and with increased distance from coastal areas (Fig. 2, S7, S8). Model estimates of suitability for the blueberry presence were positively correlated with blueberry cover recorded on forested FIA plots in Southeast Alaska (z_{685} = 4.94; P = 0.0000008; Fig. 3); despite a great deal of variation in recorded blueberry cover among plots with high estimated climatic suitability, the model containing the climatic suitability term significantly outperformed the null model (χ^2_{685} = 25.77; P = 0.0000004). The same was true when cover data from all forested FIA plots throughout the U.S. distribution of blueberry were compared to model-predicted climatic suitability for blueberry occurrence across the same area ($\chi^2_{25,964}$ = 159035.2; $P < 2^{-16}$; Fig. S9). A similar positive relationship existed between recorded salmonberry cover and model-predicted climatic suitability for the occurrence of salmonberry when all forested plots within its U.S. distribution were examined together ($z_{25,964}$=56.72; $P < 2^{-16}$; Fig. S9); the model containing the suitability term significantly outperformed a null model ($\chi^2_{25,964}$ = 2724.7; $P < 2^{-16}$). However, this relationship was not significant when examined for forested plots occurring only within Southeast Alaska (z_{685}= -1.158; P = 0.247; Fig. 3); the fit of the model containing the suitability term did not differ significantly from that of a null model (χ^2_{685} = 0.704; P = 0.401).

Aerial Cover Models

The GAM for blueberry cover outperformed a null model and explained over half of the deviance in the data (ΔAIC: -468.1763; deviance explained: 50.5%; R^2_{adj} = 0.581). Forest stand attribute predictors retained in the GAM for blueberry cover included categorical descriptors of forest type, stand age class, stand size class and continuous descriptors of tree cover and shrub cover (Table 2). The only climatic predictor retained in the final GAM was winter mean temperature, and elevation was the sole topographic predictor (Table 2). Shrub cover was by far the most important predictor in the GAM for

blueberry cover and was generally positively correlated with predicted blueberry cover; a similar positive relationship existed between tree cover and predicted blueberry cover (Table 2; Fig. 4). Post-hoc pairwise Tukey tests (emmeans; Lenth 2024) showed that blueberry cover was significantly lower in stands 50 years old or older, stands characterized by larger diameter trees, and stands dominated by Sitka spruce as compared to those dominated by Alaska yellow-cedar, mountain hemlock, and western hemlock (Fig. 4). Predicted blueberry cover peaked where winter mean temperature was approximately − 1°C and decreased rapidly when winter mean temperature exceeded approximately 0°C. Blueberry cover was predicted to peak at approximately 700 m, although wide confidence intervals around model predictions indicate a relatively large degree of uncertainty in the relationship. Model predictions for blueberry cover were significantly positively correlated with observed cover data from both the withheld FIA validation dataset (R^2 = 0.490; $F_{1,170}$ = 163.4; $P < 2^{-16}$) and the AYS validation dataset (R^2 = 0.164; $F_{1,38}$ = 7.46; P = 0.0095; Fig. S10).

Table 2
Relative importance values of all terms retained in the final GAMs for aerial cover of blueberry and salmonberry

Berry Plant		Parameter	Importance
Blueberry	Shrub Cover	0.5505	
	Stand Size Class	0.0731	
	Mean Winter Temperature	0.0387	
	Stand Age Class	0.0335	
	Forest Type	0.0321	
	Tree Cover	0.0144	
	Elevation	0.0039	
Salmonberry	Forest Type	1	
	Shrub Cover	0.0048	
	Stand Age Class	0.0021	
	Temperature Difference	0.0005	
	Summer Heat Moisture Index	0.0003	
	Terrain Ruggedness Index	0.0003	

The GAM for salmonberry cover was a poorer fit than the GAM for blueberry cover; it outperformed the null model by a much smaller margin and explained less than half of the deviance in the data (ΔAIC: -68.0943; deviance explained: 43.1%; R^2_{adj} = 0.028). Forest stand attribute predictors retained in the GAM for salmonberry cover were forest type, stand age class, and shrub cover; climatic variables were summer heat moisture index and continentality; the only topographic variable was topographic

roughness index (Table 2). Salmonberry cover was predicted to peak in stands with roughly 67 percent shrub cover and in stands less than 50 years old than most older stands (Fig. 5) Sitka spruce and western hemlock stands were predicted to have significantly higher salmonberry cover than those dominated by either species of cedar, and mountain hemlock stands were predicted to have significantly higher salmonberry cover than those dominated by western redcedar (Fig. 5). Predicted salmonberry cover generally declined with increasing summer heat moisture index and continentality and increased with topographic roughness, although confidence intervals around predicted cover are quite wide (Fig. 5). Model predictions for salmonberry cover were positively correlated with observed cover data from the withheld FIA validation dataset, although the model explained little of the variation in salmonberry cover (R^2 = 0.066; $F_{1,70}$ = 11.92; P = 0.0007; Fig. S11). No such relationship was observed between model predictions for salmonberry cover and recorded salmonberry cover from the AYS validation dataset (R^2 = 0.032; $F_{1,38}$ = 1.247; P = 0.271; Fig. S11).

DISCUSSION

Nearly all forested areas of the Tongass are projected by ensemble SDMs to remain climatically suitable for the occurrence of blueberry and salmonberry throughout the remainder of the 21st century under the scenarios examined in this study. Although occupancy of these berry plants is not projected by SDMs to change substantially across the study area, significant positive relationships between projected suitability and blueberry cover indicate that blueberry may become less abundant throughout the region as suitability declines. The lack of a significant relationship between suitability and salmonberry cover in the study area makes predicting the manner in which salmonberry abundance will respond to climate change more difficult. While climatic conditions contributed to models predicting blueberry and salmonberry aerial cover at the scale of individual forest stands, several forest stand attributes proved more important than macroclimatic predictors in these models. This finding suggests that forest management activities may have strong influences on blueberry and salmonberry abundance that could potentially offset negative impacts of climate change on these species. Information regarding the relationships between blueberry and salmonberry cover and forest stand conditions may provide insight into management targets that could help in maintaining or promoting blueberry and salmonberry cover where their occupancy or abundance are expected to be negatively impacted by changing climatic conditions.

Species Distribution Models

The finding that most forested areas of the Tongass are climatically and topographically suitable for the occurrence of both blueberry and salmonberry under historical climate conditions is not surprising given the fact that salmonberry is common and blueberry nearly ubiquitous in Southeast Alaskan forests (DeMeo et al. 1992; Martin et al. 1995; Cahoon et al. 2020). Somewhat more surprising is the finding that binary suitability is projected to be largely unaffected by climate change under any scenario examined. This finding contrasts with predictions for net changes in the area of suitable habitat for berry plants

across a portion of southwest Alaska ranging from 6–33 percent losses for two other *Vaccinium* species and from a 1 percent gain to a 9 percent loss for cloudberry (*Rubus chamaemorus*, Hamilton et al. 2024), but agrees with projections from a statewide model for cloudberry that projected net increases in suitable habitat across most of the state (Rhodes 2024). The projected lack of change in blueberry and salmonberry occupancy observed in this study may be attributable to broad climatic tolerances that can be inferred from their large geographic distributions: species with wide geographic distributions that imply wider niche breadths are generally projected to have less dramatic responses to climate change than species with narrower geographic distributions and niche breadths (Thuiller et al. 2005; Slayter et al. 2013). Projections from this study's SDMs suggest that even the most extreme climate change scenarios in Southeast Alaska will only rarely yield conditions exceeding the physiological tolerances of blueberry and salmonberry. This may be because the Tongass lies near the northern edge of blueberry and salmonberry's geographic distributions; habitat suitability at the poleward edges of species ranges may decrease less than habitat suitability at the distribution's equatorward extremes or may increase as a result of climate change (Chen et al. 2011; e.g., Prevéy et al. 2020; Hirabayashi et al. 2022). However, this explanation hinges upon the assumption of niche conservatism, which asserts that the tolerances that define a species' niche are constant across space and time (Wiens and Graham 2005; Wiens et al. 2009).

The assumption of niche conservatism is a necessary component of the species distribution modeling approach used in this study (Guisan and Thuiller 2005; Peterson 2006). However, this assumption may underestimate the impacts of climate change on blueberry or salmonberry occupancy in Southeast Alaska if populations in the Tongass are locally adapted to regional conditions. When local adaptation yields narrower climatic tolerances than would be expected under niche conservatism, the space-for-time substitution underpinning SDM-based projections of suitability under future climatic conditions can result in predictions that range from underestimates to completely erroneous (Hällfors et al. 2016; DeMarche et al. 2018; Klesse et al. 2020; Evans et al. 2024; Perret et al. 2024; Kharouba and Williams 2024). Models trained with data from a relatively small geographic area can account for some amount of local adaptation but may overestimate the impacts of climate change on habitat suitability if the environmental conditions in the training data do not reflect the true breadth of focal populations' climatic tolerances (Guisan and Thuiller 2005; Araújo and Guisan 2006; Elith and Leathwick 2009). This could explain the relatively large changes in binary suitability for five berry plants projected by Hamilton et al. (2024), who trained their SDMs with occurrence data sourced from the small portion of each species' geographic distribution that fell within their study area in southwest Alaska. Studies whose SDMs were trained with data from a broader geographic area projected much less dramatic changes in the distribution of suitable habitat for three of the five species examined by Hamilton et al. (2024) and tended to project net increases in suitable habitat in Alaska and adjacent areas of Canada rather than decreases (Hirabayashi et al. 2022; Rhodes 2024).

Beyond the challenges posed by local adaptation, the possibility that novel climatic regimes may impact performance and occupancy in ways not predicted by historical relationships may also make projecting future suitability difficult (Williams and Jackson 2007; Williams et al. 2007; Veloz et al. 2012). For these

reasons, the projections of sustained habitat suitability for blueberry and salmonberry occurrence in forested areas of the Tongass throughout the rest of the 21st century may underestimate the true impact of future climate change on these species' distributions in the study area.

If relationships between climatic conditions and blueberry and salmonberry occupancy are conserved through time, examining the contributors to model predictions can offer insight into the potential drivers of future changes in suitability. Descriptors of water availability during the growing season are among the most important predictors in SDMs for the occupancy of both blueberry and salmonberry, a finding that echoes studies of the determinants of habitat suitability for other ST plants in southwest Alaska and Pacific Coast of the United States and Canada (Prevéy et al. 2020; Hamilton et al. 2024). Suitability for blueberry is highest under low values of both summer heat moisture index and Hargreaves reference evaporation and suitability for salmonberry is highest where summer climate moisture index exceeds zero, indicating that both species are intolerant of summer drought conditions. Although some metrics of growing season water limitation are accounted for in our models, they may underestimate the true severity of future drought conditions predicted for the Tongass arising from interactions between climatic conditions such as more frequent rain-on-snow events that will decrease snowpack persistence and summer runoff (Littell and Johnson *In Press*). Moreover, several studies suggest that changes in climatic variability or the frequency of extreme climatic events may also play an important role in determining occurrence and performance (Higgins et al. 2000; Parmesan et al. 2000; Zimmerman et al. 2009; Germain and Lutz 2020; Gardner et al. 2021; Perez-Navarro et al. 2021). Climatic conditions are projected to become increasingly variable and extreme weather events more common in Southeast Alaska (Littell and Johnson *In Press*), which could yield more dramatic changes in blueberry and salmonberry occupancy than those projected by this study's SDMs, which were informed by mean annual or seasonal climatic conditions.

While binary suitability for blueberry and salmonberry is not projected to be strongly affected by climate change under the SSPs I examined, continuous suitability *is* projected to experience a net decline throughout forested areas of the Tongass under all SSPs. This finding is concerning considering the strong positive relationship between climatic suitability and blueberry abundance as expressed by aerial cover. However, the implication that declining climatic suitability for occupancy under climate change will yield a concomitant decline in the abundance of blueberry should be approached cautiously. Some studies find that SDM-derived estimates of suitability display a wedge-shaped relationship with performance metrics that may predict a site's carrying capacity (Baer and Maron 2020; Jímenez-Valverde et al. 2021; Brambilla et al. 2023; Monnier-Corbel et al. 2023), while others find little to no relationship between suitability and local abundance or performance (Dallas and Hastings 2018; Lee-Yaw et al. 2021). The finding that blueberry cover is positively correlated with suitability indicates that declining suitability could drive a decrease in *potential* blueberry cover in forested areas throughout the Tongass, but several other environmental attributes could interact to determine its *realized* cover.

While salmonberry cover was positively correlated with climatic suitability for occurrence when examined across all plots within the western U.S., this was not the case when the relationship between

projected climatic suitability and salmonberry cover was examined for plots falling solely within forested areas of Southeast Alaska. This may be because the climatic and topographic predictors included in ensemble SDMs have a weaker influence on salmonberry cover than do other environmental attributes. For example, a site's disturbance history or soil conditions are known to influence the occurrence and abundance of salmonberry (Zouhar 2019); these were not directly accounted for in SDMs due to insufficient data.

Projections for negative impacts of climate change on blueberry cover but no such change in salmonberry cover align with perceived trajectories for abundance and availability of these species in Southeast Alaska. Hupp et al. (2015) documented perceptions of a recent decline in blueberry but not salmonberry abundance among environmental managers and berry harvesters in Southeast Alaska, driven at least in part by changing climatic conditions. Projected future losses of suitable habitat for blueberry occurrence in the vicinity of the southcentral Alaskan community of Hyder and for both blueberry and salmonberry occurrence near the communities of Haines and Skagway are concerning, as are model projections for declining suitability with increasing distance from coastal areas for both species.

Aerial Cover Models

Identifying environmental correlates of blueberry and salmonberry cover may help guide efforts to ensure continued access to these important ST plants under rapidly changing climate in Southeast Alaska. This may be especially useful in light of projections for slight decreases in blueberry and salmonberry occupancy in forested areas of the Tongass and the possibility that net decreases in suitability could yield concomitant decreases in cover.

It is unsurprising that shrub cover was the strongest predictor of blueberry cover included in our models, as blueberry is the most common understory shrub in the forests of Southeast Alaska (Cahoon et al. 2020). When model term selection and GAMs were re-run without shrub cover as a predictor, model fit was poorer but still outperformed the null model, indicating that shrub cover was not solely responsible for the variation in blueberry cover explained by the model (Supplemental Information). The projected decrease in blueberry cover where overall shrub cover exceeds 80 percent may be due to increases in large, taller-stature shrubs such as willows (*Salix spp.*) and Sitka alder (*Alnus viridis ssp. sinuata*) that compete with blueberry for light. However, wide confidence intervals around the predicted relationship at high levels of overall shrub cover indicate that the predicted decline in blueberry cover where overall shrub cover exceeds 80 percent should be interpreted cautiously.

Although suitability derived from the ensemble SDM was strongly correlated with blueberry cover, GAMs for blueberry cover did not contain any of the same climatic or topographic predictors as SDMs for occurrence. This may be because GAMs were built using data solely from forested plots within the Tongass while SDMs described the niche of blueberry across its U.S. distribution. Local adaptation may mean that the climatic conditions important in determining suitability across the entire U.S. distribution may not represent the strongest checks on local abundance in forested areas of the Tongass.

Response plots indicate that blueberry cover in the Tongass may decline dramatically where winter mean temperature exceeds 0°C. This finding is concerning if this threshold represents a 'tipping point' for blueberry cover in the Tongass, as many low-elevation areas of Southeast Alaska are projected to begin experiencing mean winter temperatures exceeding 0°C under future climate change (Littell and Johnson *In Press*). If increasing winter mean temperatures drive decreased blueberry cover in the low-elevation sites adjacent to Southeast Alaskan communities where a substantial amount of harvesting takes place, this could have consequences for blueberry harvest under future climate regimes. Conserving old-growth, relatively closed canopy stands and those dominated by large-diameter Sitka spruce, particularly at elevations where future winter mean temperatures are less likely to exceed ≥ 0°C, may help promote blueberry abundance in the future. Facilitating harvester access to higher-elevation harvest sites could also help to ensure continued availability of productive blueberry harvest sites in the face of projected climate change in Southeast Alaska. However, it is important to note that harvesters often prefer to harvest in locations where they have "intimate knowledge [and/or] ancestral ties" (Wheeler and Thornton 2005), so management efforts focused on promoting blueberry abundance or access to more abundant harvesting sites may not be sufficient to ensure future subsistence needs are met.

The relatively poor performance of the model for salmonberry cover compared to that for blueberry cover may have been due in large part to a lack of predictors describing sites' disturbance histories. Salmonberry is positively associated with disturbance, often occurring in canopy gaps, disturbed stands, and forest edges (Zouhar 2019). While FIA crews record data on natural disturbances and stand treatments, these disturbances must have occurred within the previous 5 years and affected 25 percent of trees over at least 0.4 hectares to be recorded (USDA-FS 2024). Thus, the types of small-scale disturbances affecting salmonberry cover in forest stands are unlikely to be reflected in FIA or captured by proxy by any other model term. Stand age was retained in the GAM and may be related to the disturbance history of a site but still reflects stand-replacing disturbances rather than small-scale disturbances resulting in the canopy gaps where salmonberry often occurs. Unsurprisingly, younger stands had greater salmonberry cover than older stands, but the large variance around model predictions indicates that other stand attributes not reflected in model predictors may modify relationships between stand age and salmonberry cover.

Forest type was the most important predictor of salmonberry cover, with the highest mean cover in stands dominated by Sitka spruce, western hemlock, and mountain hemlock. Sitka spruce is commonly associated with disturbance (Cordes 1972; Burns and Honkala 1990; Taylor 1990) and often co-occurs in mixed stands with western and mountain hemlock in Southeast Alaska (Martin et al. 1995; DeMeo et al. 1992), which may explain the higher salmonberry cover in those stand types. The negative relationships between salmonberry cover and summer heat moisture and continentality likely reflect salmonberry's tendency to thrive under high moisture availability typical of maritime climates (Zouhar 2019). While the relationships between salmonberry cover and model predictors may offer some insights into conditions associated with higher salmonberry cover, the poor fit of the model suggests that these relationships may not be particularly useful for guiding management decisions to ensure sustained salmonberry

availability in Southeast Alaska. Rather, models incorporating meaningful metrics of a site's disturbance history could be more useful for guiding management to preserve or promote salmonberry abundance.

CONCLUSIONS & FUTURE DIRECTIONS

The results of this study suggest that climate change is likely to have minimal impacts on blueberry and salmonberry occupancy in forested areas of Southeast Alaska's Tongass National Forest throughout the remainder of the 21st century. However, these projections are conservative and do not account for likely adaptation to local climatic conditions. While occupancy may not be strongly affected by climate change, declining suitability for blueberry occurrence throughout most of the Tongass National Forest may lead to substantial decreases in blueberry cover where it remains present. The potential for predicted changes in habitat suitability for salmonberry occurrence across the Tongass to affect salmonberry cover is less clear.

It is important to note that the pace of blueberry and salmonberry responses to changing climate is likely to lag behind that of climate change, a pattern that has been documented for other long-lived plants (Davis 1986; Davis 1989; Campbell and McAndrews 1993; Jackson and Sax 2010; Bertrand et al. 2011; Cotto et al. 2017). Thus, projected changes in habitat suitability may take decades to manifest as changes in blueberry or salmonberry occupancy or cover. Regardless of the timeframe in which blueberry or salmonberry populations respond to climate change, this study offers information about forest conditions associated with higher cover of these species which could help to inform management to maintain their presence and abundance in the face of changing climatic regimes.

An important limitation of this study is the use of aerial cover as a proxy for blueberry and salmonberry fruit production. Relationships between fruit production and aerial cover or plant size vary widely among sites and species (Martin 1983; Wender et al. 2004; Suring et al. 2008; Montané et al. 2016), and fruit set can be further influenced by factors including resource availability, pollen limitation, exposure to herbivory or pathogens, and genetic differences affecting allocation to vegetative versus reproductive tissues (Stephenson 1981; Ehrlén 1992; Suring et al. 2006; Drummond 2019; Parkinson and Mulder 2020; Siemens et al. 2020). Furthermore, annual rates of plant reproduction are highly sensitive to both mean climatic conditions and extreme weather events (Hedhly et al. 2009; e.g., Mingeau et al. 2000), which may mean that blueberry and salmonberry fruit yields will respond more strongly to changing climate means and variability than projections based on aerial cover alone might suggest (Mucioki 2024). To our knowledge, no quantitative data exist describing how blueberry and salmonberry fruit production vary across environmental conditions and/or geographic space nor how fruit production relates to aerial cover of berry plants in Southeast Alaska. Studies aimed at bridging this knowledge gap are an essential next step towards generating useful projections of the impacts of climate change on the abundance of these important ST plant resources in Southeast Alaskan forests.

Declarations

Competing Interests

The author has no relevant financial or non-financial interests to disclose.

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Author Contribution

K.C.B. conceived and designed the study and performed data acquisition, management, and analysis. K.C.B. wrote the manuscript and generated all tables, figures, and supplementary material.

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Data Availability

FIA data pertaining to blueberry and salmonberry occurrence and cover on all field-visited forested plots throughout the western US (including Southeast Alaska) and associated forest stand conditions are available for download from FIA DataMart at https://research.fs.usda.gov/products/dataandtools/fia-datamart. Actual FIA plot coordinates are confidential, but fuzzed plot coordinates may be downloaded from the aforementioned online source. Auxiliary climate and topographic data are available from the sources listed in the footnotes of Table S1 in the Supplementary Information.

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Figures

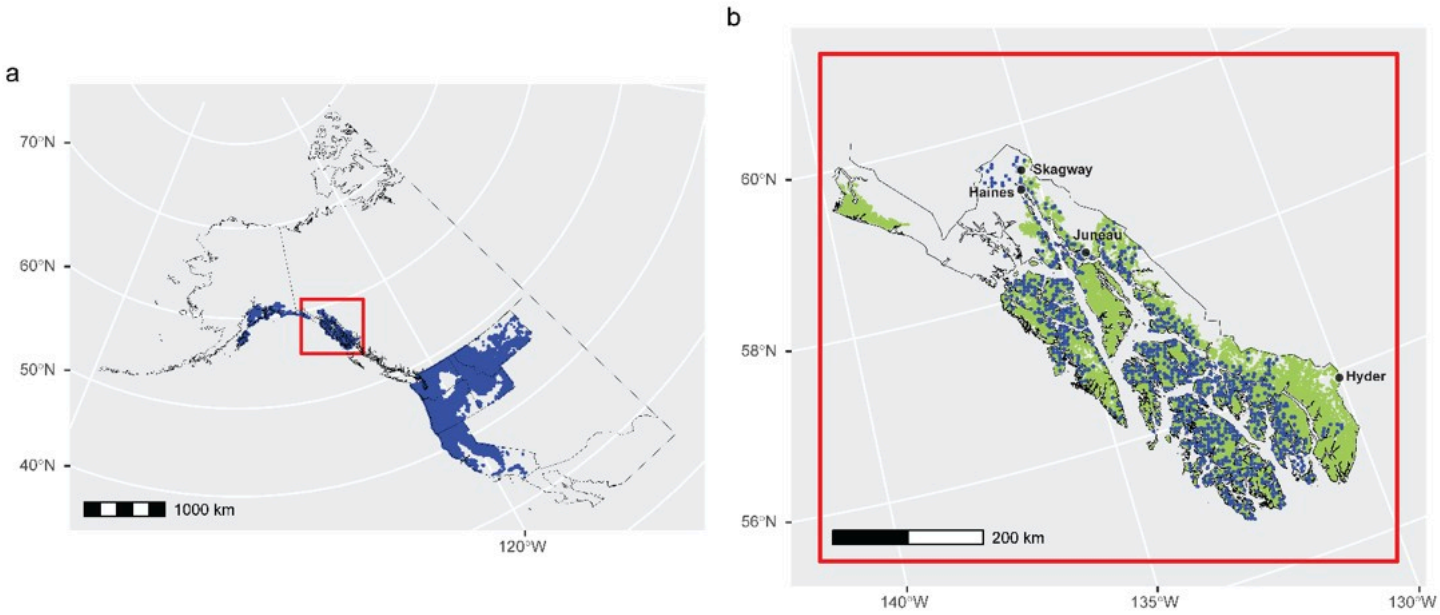

Figure 1

Study area. (a) Approximate locations of FIA plots (blue points) used to train and validate ensemble SDMs for blueberry and salmonberry occupancy. Red box indicates Southeast Alaska. (b) Approximate locations of FIA plots in Southeast Alaska (blue points) used in training and validation of both ensemble SDMs for blueberry and salmonberry occupancy and GAMs for blueberry and salmonberry aerial cover in forested areas of the Tongass National Forest (shown in green). The state capital (Juneau) and Southeast Alaskan communities mentioned in the discussion are marked with black points.

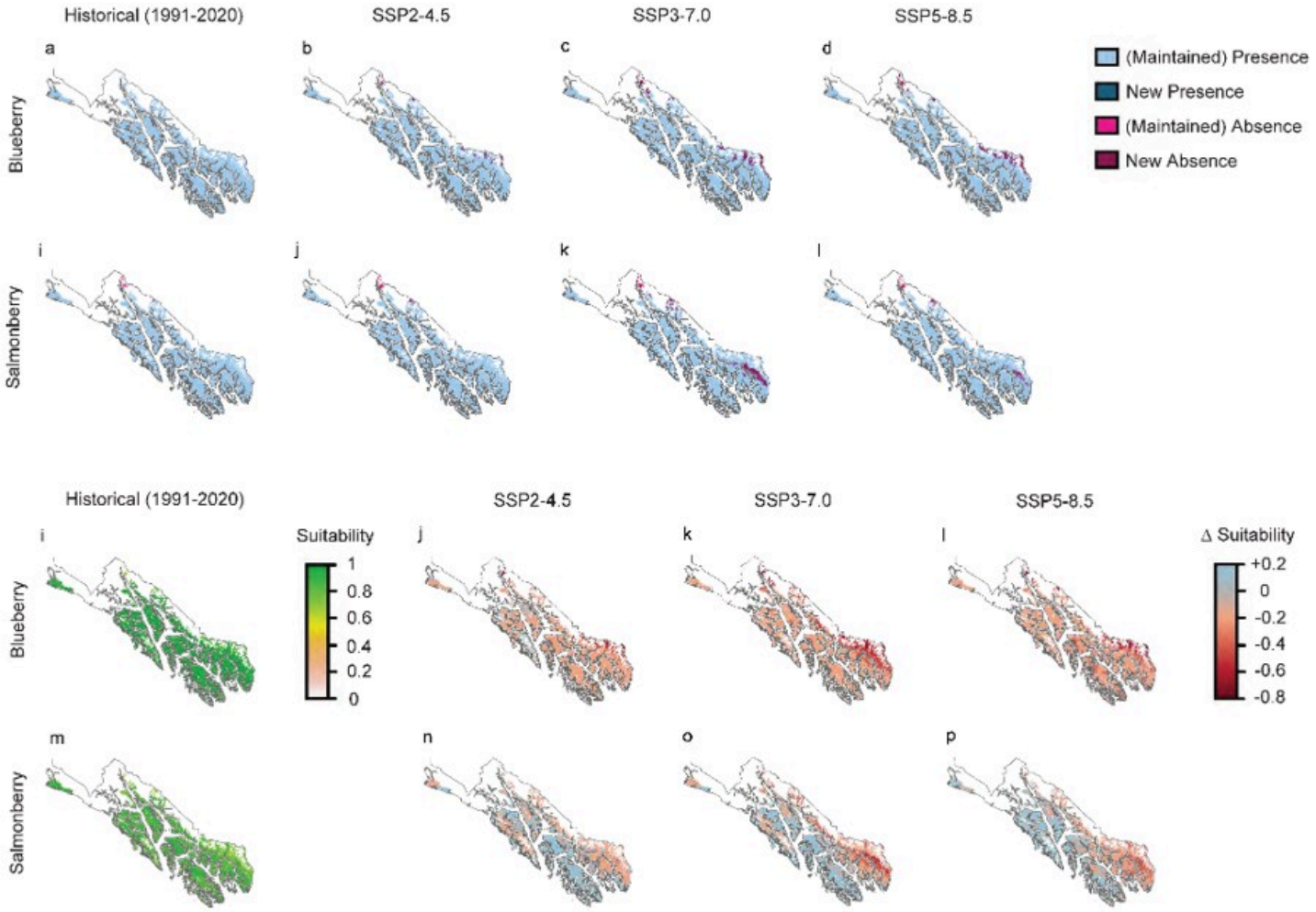

Figure 2

Projected suitability for blueberry and salmonberry presence in forested areas of the Tongass National Forest under historical climate normals and differences between suitability under historical climate normals and each SSP scenario for 2100. (a) Binary suitability for blueberry presence projected for historical climate normal conditions; (b-d) Change in binary suitability for blueberry presence between SSP scenarios and historical climate normal conditions; (e) Binary suitability for salmonberry presence projected for historical climate normal conditions; (f-h) Change in binary suitability for salmonberry presence between SSP scenarios and historical climate normal conditions; (i) Continuous suitability for blueberry presence under historical normal conditions; (j-l) Change in continuous suitability (ΔSuitability) for blueberry presence between SSP scenarios and historical climate normal conditions; (m) Continuous suitability for salmonberry presence under historical normal conditions; (n-p) Change in continuous suitability (ΔSuitability) for salmonberry presence between SSP scenarios and historical climate normal conditions

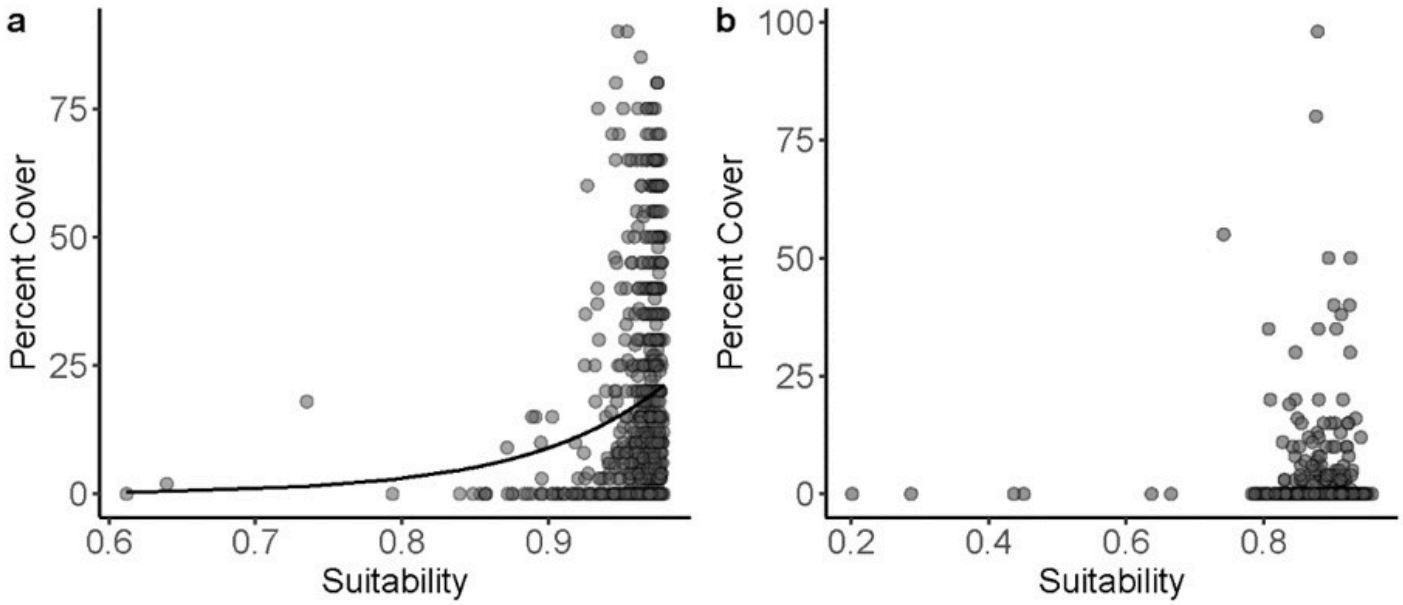

Figure 3

Suitability for occurrence projected by ensemble SDMs vs. percent aerial cover as measured by FIA crews on plots in Southeast Alaska for (a) blueberry and (b) salmonberry

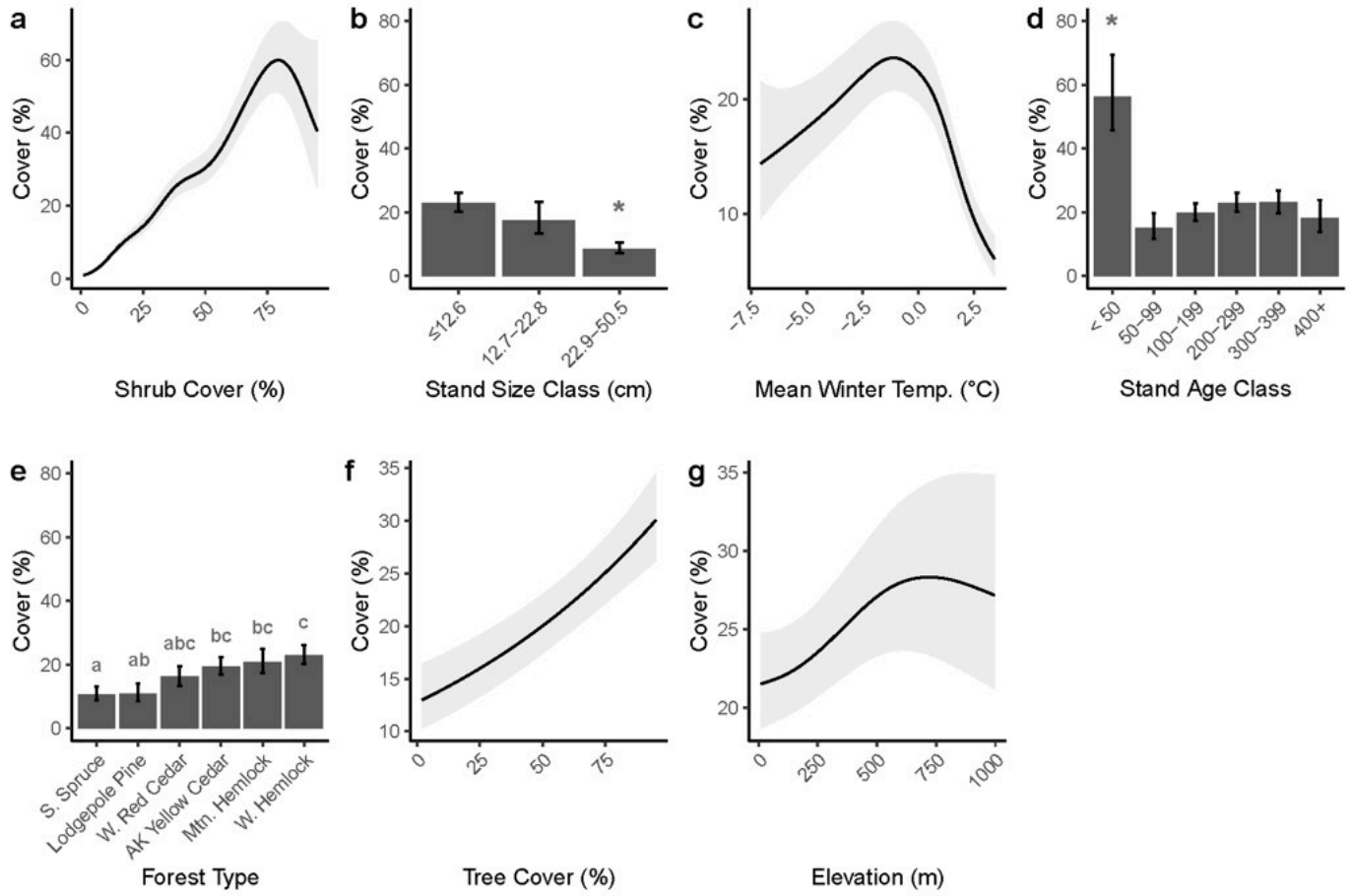

Figure 4

Response curves for projected blueberry cover (± 1 SE) across values of retained model terms when other terms were held constant at their median (continuous predictors) or modal values (categorical predictors). Asterisks and letters indicate significant differences among levels of categorical variables at *P < 0.05*. Panels are presented in order of decreasing term importance in the model

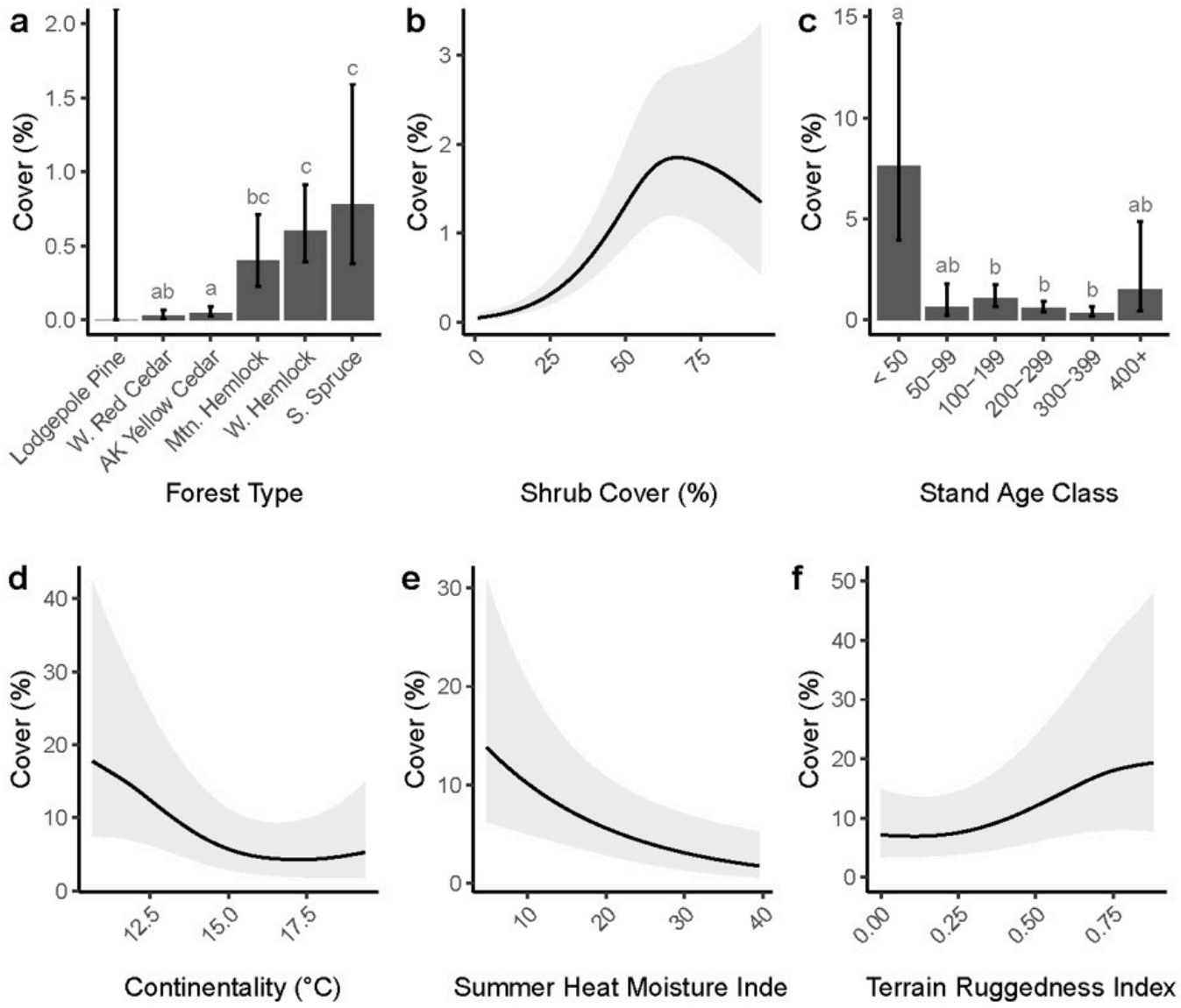

Figure 5

Response curves for projected salmonberry cover (± 1 SE) across values of retained model terms when other terms were held constant at their median (continuous predictors) or modal values (categorical predictors). Asterisks and letters indicate significant differences among levels of categorical variables at *P < 0.05*. Panels are presented in order of decreasing term importance in the model.

Supplementary Files

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