Host–parasite distributions under changing climate: *Tsuga heterophylla* and *Arceuthobium tsugense* in Alaska

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Abstract: Dwarf mistletoes (*Arceuthobium* species) influence many processes within forested ecosystems, but few studies have examined their distribution in relation to climate. An analysis of 1549 forested plots within a 14.5 million ha region of southeast Alaska provided strong indications that climate currently limits hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) to a subset of the range of its primary tree host, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), with infection varying from a high of 20% of trees at sea level to only 5% by 200 m elevation. Three types of modeling approaches (logistic, most similar neighbors, and random forests) were tested for the ability to simultaneously predict abundance and distribution of host and pathogen as a function of climate variables. Current distribution was explained well by logistic models using growing degree-days, indirect and direct solar radiation, rainfall, snowfall, slope, and minimum temperatures, although accuracy for predicting *A. tsugense* presence at a particular location was only 38%. For future climate scenarios (A1B, A2, and B1), projected increases for *A. tsugense* habitat over a century ranged from a low of 374% to a high of 757%, with differences between modeling approaches contributing more to uncertainty than differences between climate scenarios.

Résumé : Le faux-gui (*Arceuthobium* species) influence plusieurs processus dans les écosystèmes forestiers mais peu d'études ont porté sur sa répartition en lien avec le climat. Une analyse de 1 549 places échantillons boisées à l'intérieur d'une région de 14,5 millions d'hectares dans le sud-est de l'Alaska a clairement montré que le climat limite présentement le faux-gui de la pruche (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) à un sous-ensemble de l'aire de répartition de son hôte principal, pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.), avec un taux d'infection qui varie d'un maximum de 20 % des arbres au niveau de la mer à seulement 5 % vers 200 m d'altitude. Trois types de méthodes de modélisation (logistique, voisins les plus similaires et forêts aléatoires) ont été testées pour leur capacité à prédire simultanément l'abondance et la répartition de l'hôte et du pathogène en fonction des variables climatiques. La répartition actuelle est bien expliquée par des modèles logistiques utilisant les degrés-jours de croissance, le rayonnement solaire direct et indirect, la pluie, les chutes de neige, la pente et les températures minimum, mais la précision pour prédire la présence d'*A. tsugense* à un endroit donné est de seulement 38 %. Dans le cas des scénarios climatiques futurs (A1B, A2 et B1), l'élargissement prévu de l'habitat d'*A. tsugense* sur une période de cent ans varie d'un minimum de 374 % à un maximum de 757 %, les différences entre les méthodes de modélisation contribuant davantage à l'incertitude que les différences entre les scénarios climatiques.

[Traduit par la Rédaction]

Introduction

Dwarf mistletoes (*Arceuthobium* species) are important components within many forest ecosystems of North America. Obligate parasites of conifers, dwarf mistletoes serve essential functions for a number of species, ranging from providing food for the rare Johnson's Hairstreak Butterfly (Shields 1965) to hosting hyperparasitic fungi (Wicker and Shaw 1968). *Arceuthobium* species also contribute to food and habitat for birds and mammals (e.g., Hamer et al. 2008), impact processes ranging from fire disturbance to water use and carbon sequestration (Meinzer et al. 2004), and perhaps even serve as keystone species (Watson 2001). Dwarf mistletoes are also viewed as one of the most important disease agents affecting forests, with economic impacts from growth loss thought to be in the order of billions of dollars annually (Hawksworth and Wiens 1996). Infection by *Arceuthobium* species, like other forest diseases, is expected to be impacted by changing climate (Kliejunas et al. 2009). In a comprehensive review of *Arceuthobium*, Hawksworth and Wiens (1996) noted that while climate factors were probably responsible for differences in distribution between hosts and parasites, effects of climate on distribution of *Arceuthobium* are little studied.

Fig. 1. Distribution of western hemlock (*Tsuga heterophylla*) in North America.

Climate envelope modeling — predicting the distribution of a species as a function of climate — is a subset of species distribution modeling (Wiens et al. 2009). Species distribution models are founded on the niche theory concept that environmental variables can be used to describe a multidimensional space outside of which an individual species cannot survive (Vandermeer 1972). As obligate parasites, *Arceuthobium* species pose an interesting instance for climate envelope modeling: while environmental factors can directly influence their distribution, environment also indirectly limits dwarf mistletoe distribution and abundance through effects on host species. In this paper, we examine the relationships between climate and distribution and abundance of hemlock dwarf mistletoe (*Arceuthobium tsugense*) and its primary host species, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.).

Understanding of relationships between individual species of *Arceuthobium* and climate has primarily been a function of observational studies; few systematic surveys have been conducted over the large spatial regions required to understand ecoregional-level distribution (Hawksworth and Wiens 1996). Coastal Alaska is potentially an ideal location to conduct a study on the possible climate controls for a tree species and an obligate parasitic pathogen because landscape effects by other disturbances such as fire and timber harvesting are relatively uncommon.

Arceuthobium tsugense plants are dioecious and their life cycle includes an explosive discharge of viscous seeds in an approximately 3 week period from early September to late October. Seeds that are intercepted by the host tree's needles and successfully overwinter then germinate in the spring. After seeds infect host trees, an incubation period of 1 or 2 years precedes shoot production. Dwarf mistletoe flowers may develop 1–2 years after the first shoots appear and flowering occurs from June to August. Fruit maturation requires about 15 months. (Muir and Hennon 2007)

Cold temperatures can impact *Arceuthobium* species' life cycles at several different stages. Hawksworth and Wiens (1996) described an unpublished study where seedlings infected by *A. americanum* were transplanted to a site 120 m above the natural elevation limit; the dwarf mistletoe plants survived for over 20 years but fruits never matured before au-

tumn frosts. *Arceuthobium* species can also be affected by cold temperatures in winter that reduce seed germinability (Brandt et al. 2004) and freezing night temperatures in early summer that reduce pollen germinability (Gilbert and Punter 1991).

Snow can affect *Arceuthobium* reproduction because seeds must survive in tree canopies for one winter before germinating in spring. Muir and Hennon (2007) speculated that very high snow levels in northern forests could be a factor responsible for the low incidence or absence of *A. tsugense* in some areas. Heavy rainfall can also wash away seeds before they germinate (Roth 1959).

The length and warmth of the growing season are factors in *Arceuthobium* population dynamics. The maturation time of *A. tsugense* is believed to be longer in Alaska than in other parts of its range. In British Columbia, seed dispersal becomes common 5 years after inoculation (Smith 1971), but in Alaska, inoculation to seed dispersal may take longer than 12 years (Shaw and Loopstra 1991). Slower development of *A. tsugense* in young stands in Alaska has led to conclusions that *A. tsugense* is less of a problem for timber production in Alaska than in British Columbia, Oregon, or Washington (Shaw and Hennon 1991). In summary, previous research suggests that climate could limit *A. tsugense* at a number of different stages in its life cycle, influencing its rate of spread, its effects on individual trees, and its overall range.

Climate envelope analysis of species has been the focus of much previous research (Wiens et al. 2009) including work on tree species (e.g., Iverson and Prasad 1998), although we are not aware of any other climate envelope research for *Arceuthobium*. Methods used to predict range as a function of climate vary widely and include logistic regression, general additive models, neural networks, simulation modeling, and a variety of customized models. Because different modeling techniques can result in substantially different range predictions and no single modeling method is ideal for all situations, using several different methods (and validating results against independent data sets) helps to quantify and understand the component of uncertainty associated with model selection.

For many applications, nonparametric methods such as nearest neighbor imputation provide good alternatives to parametric methods such as logistic regression. Nearest neighbor imputation approaches are donor-based methods where missing values are imputed using values observed for a different unit (for details, see Eskelson et al. 2009*a*). The donors are typically determined based on a similarity metric. The Most Similar Neighbor (MSN) method (Moeur and Stage 1995), which has found widespread use in forestry applications, uses a similarity metric that is based on a canonical correlation of the response and explanatory variables. The Random Forest (RF) imputation method (Crookston and Finley 2008) determines similarity with a proximity matrix that is obtained from multiple classification and regression trees (see Breiman 2001). RF has become a popular nearest neighbor imputation method in recent years and has been shown to outperform more traditional nearest neighbor imputation methods such as MSN in a variety of applications (e.g., Eskelson et al. 2009*b*). One major advantage of nearest neighbor imputation methods is that their multivariate

Fig. 2. Location of weather stations in relation to the study area.
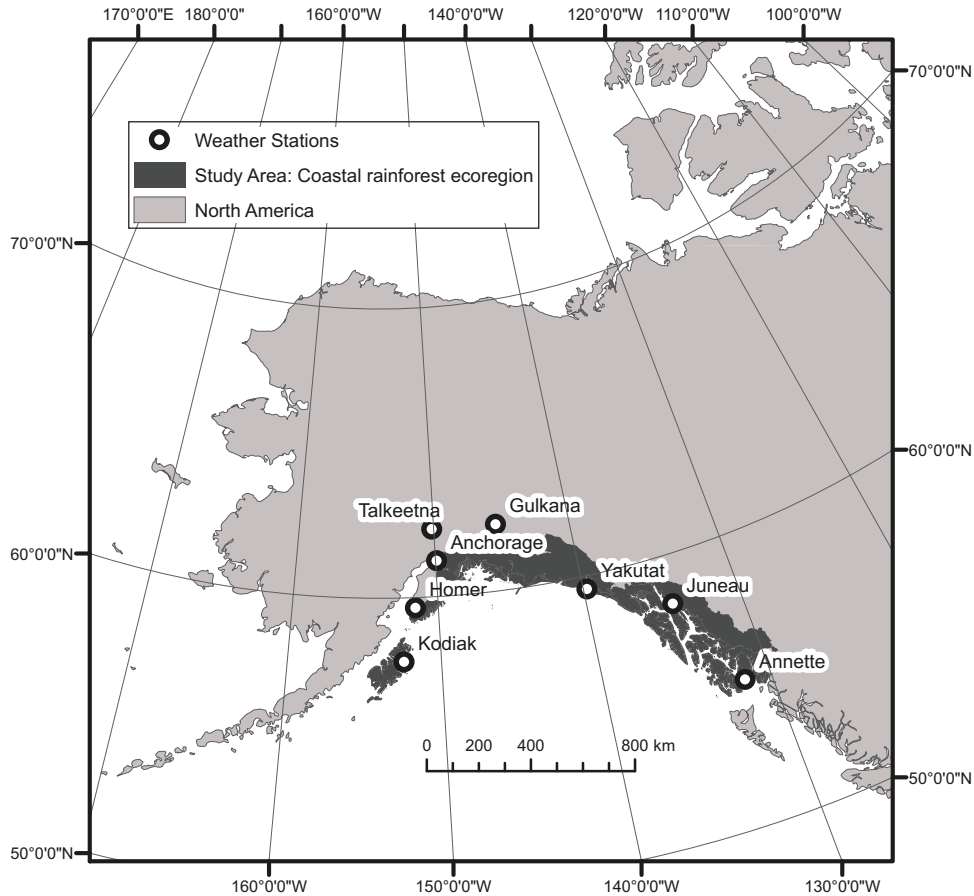
nature allows simultaneous prediction of multiple response variables (Eskelson et al. 2009*a*). Applied to prediction of a host–pathogen climate envelope, this has the advantage of never predicting combinations of response variables that do not exist in nature; thus, nearest neighbor imputation will not predict pathogen presence without a host.

While previous research on *Arceuthobium* species suggests a variety of possible mechanisms for climate effects on dwarf mistletoe range and abundance, there has been no previous study of *A. tsugense* in relation to climate at the northern extent of its range. In this paper, our objectives are to (*i*) estimate the current range and abundance of *A. tsugense* and its host species *T. heterophylla* in Alaska in relation to climate, (*ii*) develop, compare, and validate parametric and nonparametric models to predict *A. tsugense* and *T. heterophylla* distributions in the Gulf of Alaska region as a function of climate variables, and (*iii*) predict potential future distributions of *A. tsugense* and *T. heterophylla* for several possible future climate regimes.

Methods

Data for *T. heterophylla* and *A. tsugense*

We used two data sets for initial examination of the current range and abundance of *A. tsugense* and *T. heterophylla*. The first data set was from a forest inventory throughout the coastal region of Alaska. The second data set came from Washington, Oregon, and California. Thus, together, the two data sets span the northern and southern parts of the range of the *T. heterophylla* species but do not include portions of the range in the Rocky Mountains where *A. tsugense* is not found or coastal British Columbia, which uses a different inventory system (Fig. 1). Only the Alaska data set was used for climate envelope modeling because this paper focuses on those climate influences (e.g., minimum temperatures, length of growing season) that may limit *A. tsugense* at the northern portion of its range rather than climatic factors (e.g., maximum temperatures, moisture deficits) that likely limit it at the southern portion of its range.

The Alaska data set consisted of 4921 plots established between 1995 and 2003 by the Forest Inventory and Analysis program of the US Forest Service. All public and private land within the study area boundaries was included in the sampled population with the exception of national forest wilderness and Glacier Bay National Park. Of the sample, 1549 plots were forested with *T. heterophylla* trees present on 984 plots and *A. tsugense* present on 149 plots. Trees on the sample plots were selected for measurement using four 7.3 m radius subplots, with trees less than 12.5 cm diameter at breast height selected using four 2 m fixed radius areas centered on each of the four subplots. Infection by *A. tsugense* was recorded for *T. heterophylla* trees using the Hawksworth (1977) six-class rating system, but we collapsed this to presence–absence for this study, as accurately rating with the Hawksworth system can be difficult from the ground (Shaw et al. 2000). Because *A. tsugense* infection was just one of

Fig. 3. Mean annual temperature, mean minimum winter (December, January, and February) temperature, and mean annual precipitation from 1954 to 2007 for the eight primary weather stations near the study area.

◆ Mean Annual Temperature   ■ Mean Winter Minimum Temperature   △ Mean Annual Precipitation
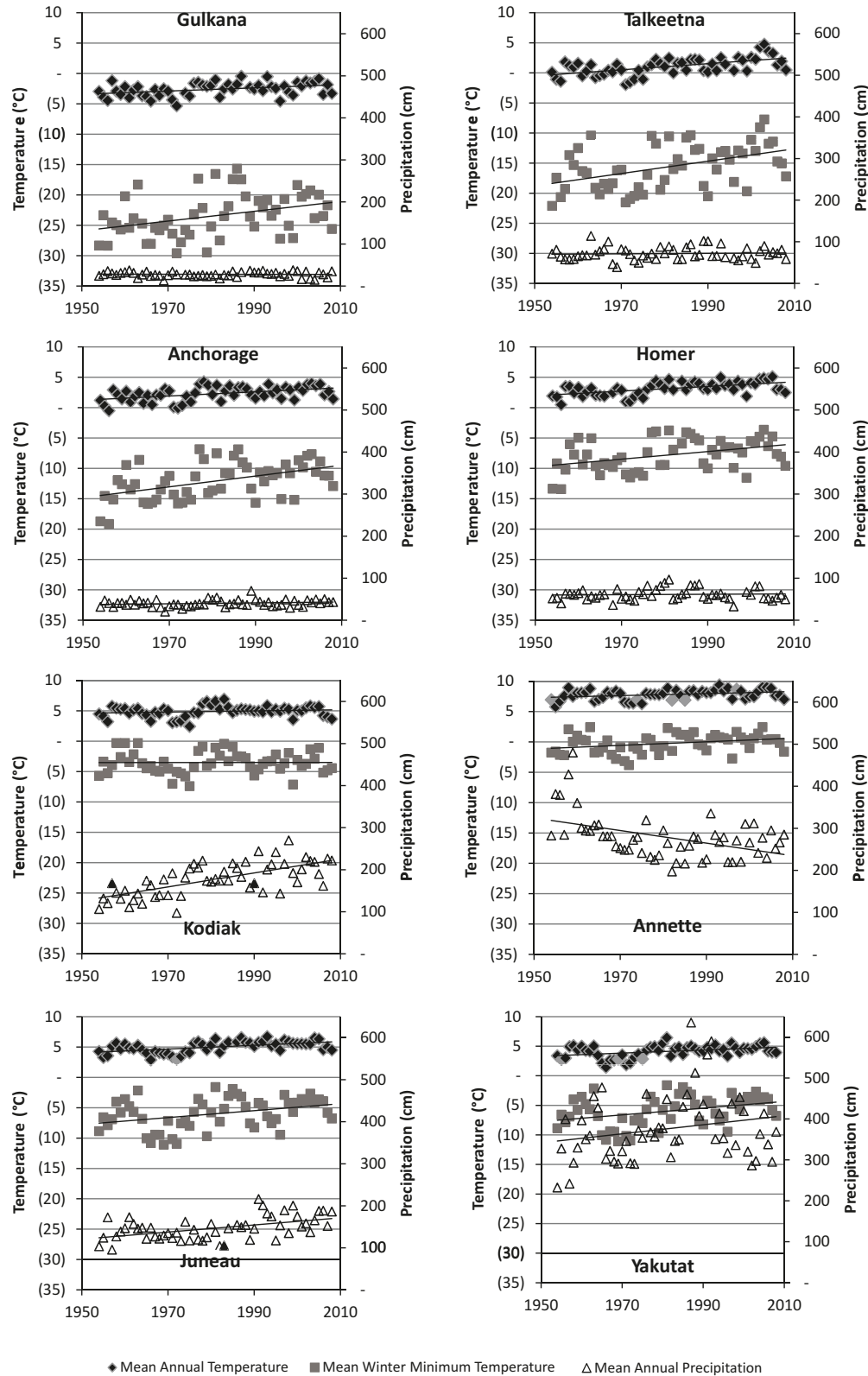
many variables collected in the inventory, it seems likely that infection would have been undercounted, although brooming and deformation from other causes could also have led to error commissions.

Arceuthobium tsugense can infect other conifers in the region such as lodgepole pine (*Pinus contorta* Douglas ex Loudon), Sitka spruce (*Picea sitchensis* (Bong.) Carrière), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière)

Fig. 4. Estimated abundance of western hemlock (*Tsuga heterophylla*) and hemlock dwarf mistletoe (*Arceuthobium tsugense*) and infection rate by elevation in southeast Alaska (longitude ≤ –138°).
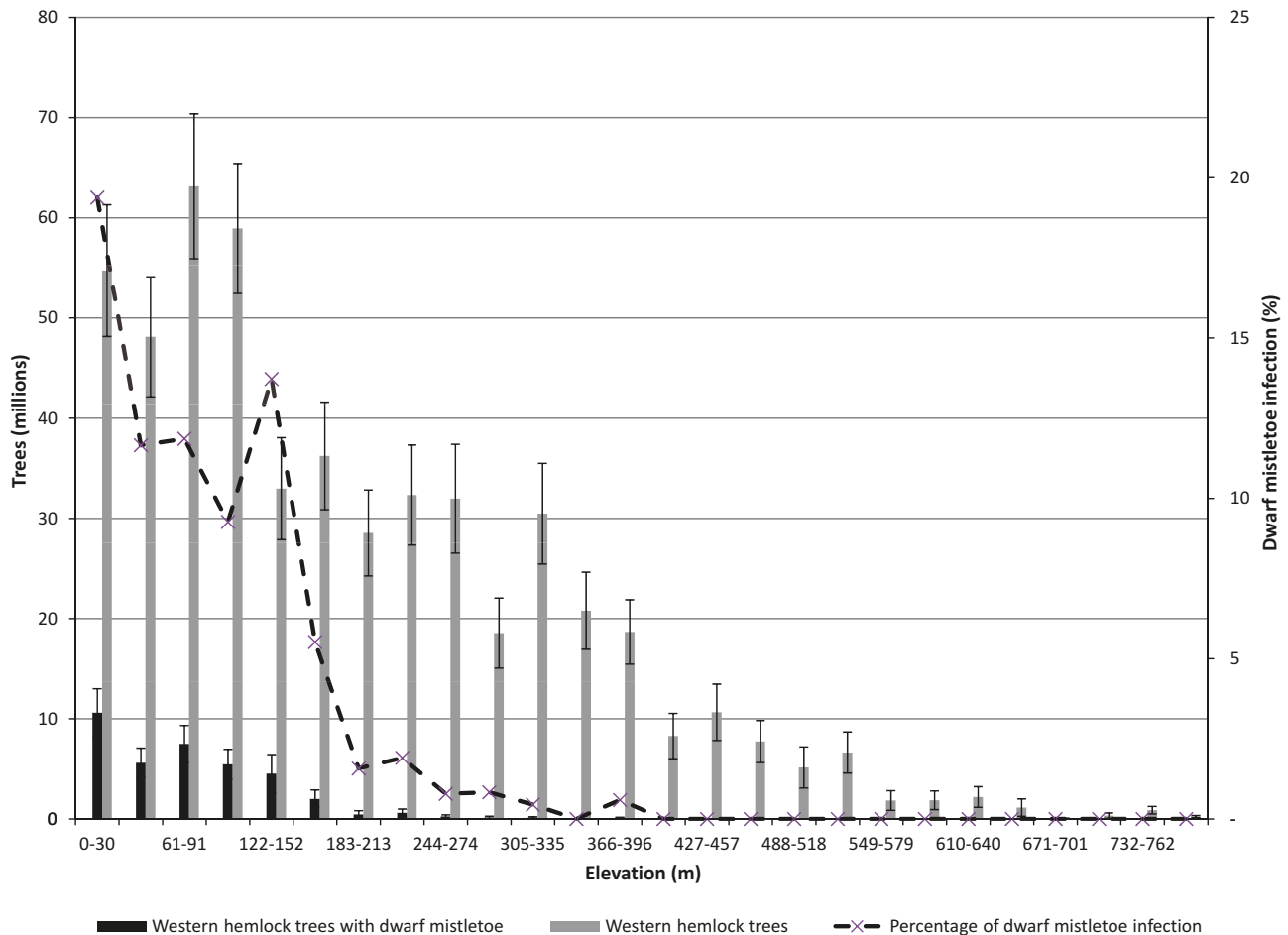
(Muir and Hennon 2007), but this is uncommon and over 96% of *A. tsugense* observations in our data set occurred in *T. heterophylla*. For our analysis, only observations of *A. tsugense* on *T. heterophylla* were used. Plots where *A. tsugense* infected *T. heterophylla* trees ranged from the Canadian border in southeast Alaska to –137° longitude, while plots with *T. heterophylla* trees extended more than 600 km further west to –149° longitude.

For initial analysis of distributions in the larger west coast region, the second data set used consisted of a sample collected by the Forest Inventory and Analysis program between 2001 and 2007 throughout California, Oregon, and Washington. These data included 1503 forested plots with *T. heterophylla* trees, with *A. tsugense* observed on 212 plots. Plots with *T. heterophylla* ranged in elevation from sea level to 1860 m and from the Canadian border south to 39° latitude in California. Estimates of area with *A. tsugense* present defined presence as at least one occurrence of *A. tsugense* on a *T. heterophylla* tree within the plot. Estimates of abundance of *A. tsugense* and distribution by elevation and climate in Alaska, Washington, Oregon, and California were made using combined ratio estimation with post-stratification (Scott et al. 2005, pp. 55–56).

Climate of the study area

The study area for the climate envelope analysis was the

14.5 million ha area encompassing the temperate rainforest ecoregion in Alaska. Weather data from all eight primary stations near our study area (Fig. 2) show a trend of increasing average annual temperature from 1954 to 2008 (Fig. 3). Assuming a linear model, mean annual temperature in the region increased at a rate of 1.5 °C per 50 years (annual increase estimated as 0.029° with a standard error of 0.009°; for a null hypothesis that slope = 0, the *p* value was 0.0015). Assuming a linear model, mean minimum winter (December, January, and February) temperatures increased at a rate of 3.0 °C per 50 years (annual increase estimated as 0.061° with a standard error of 0.022°; for a null hypothesis that slope = 0, the *p* value was 0.007). This 50 year historical trend of increasing temperatures in the Gulf of Alaska region is consistent with most General Circulation Model (GCM) projections. For example, the Hadley model (Pope et al. 2000) predicts 50 year increases of 1.4, 1.9, and 2.2 °C at Juneau and increases of 1.6, 2.5, and 2.9 °C at Homer for the B1, A2, and A1B scenarios, respectively, using a linear model from 2000 to 2100. Local climate variations, however, may not be captured by GCMs. The Pacific Decadal Oscillation, a shift in North Pacific sea temperature and currents that had a cool phase from 1947 to 1976 and a warm phase after 1977 (Mantua and Hare 2002), is a primary contributing factor to the climate in the study area.

Most GCMs predict increased precipitation for the region.

Table 1. Range of modeled climate variables in southeast and southcentral Alaska for forested plots, forested plots with western hemlock (*Tsuga heterophylla*), and forested plots with hemlock dwarf mistletoe (*Arceuthobium tsugense*).

Variable	All forested plots			*T. heterophylla* present			*A. tsugense* present		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Growing season (days >0 °C)	144	365	282	190	365	313	249	365	335
Growing days >10 °C	0	139	100.4	3	139	108	71	138	119
Growing degree-days (°C)	773	2854	2068	1214	2854	2248	1730	2854	2446
Summer evapotranspiration index	1.8	4.4	3.2	2.1	4.4	3.3	2.3	4.4	3.2
Summer climate moisture index	−8.7	28.2	3	−8.7	20.3	4.4	−4.5	10.6	3.2
Growing season radians	10.5	25.8	17.5	10.5	25.8	17.8	10.5	25.8	17.1
Lowest average minimum monthly temperature (°C)	−26.1	0.1	−6.6	−16.8	−0.8	−4.7	−8.3	−1.7	−3.6
Standard deviation of average minimum monthly temperature (°C)	4.1	12.3	5.8	4.1	8.6	5.1	4.3	6.1	4.9
Precipitation as snow (mm)	174	5041	1663	598	5041	2009	1100	3089	1849
Precipitation as rain (mm)	156	1829	733	227	1551	832	436	1069	732
Lowest average minimum monthly temperature in August–September (°C)	−1.6	9.4	6.2	2.1	9.3	7.1	5.7	9.2	7.7
Lowest average minimum monthly temperature in May–June (°C)	−3.5	7	3.3	−0.2	6.1	4.1	2.7	6	4.7
Slope (%)	0	160	29	0	160	34	0	160	32
Elevation (m)	0	884	208	0	823	199	0	396	101

Table 2. Pearson correlation coefficients for modeled climate variables in southeast and southcentral Alaska.

	SLOPE	GDD	ET	CMI	RADIANS	MINTEMP	MINTEMPSD	RAIN	SNOW	MINFALLTEMP	MINSPRINGTEMP
SLOPE	1.00	0.06	0.25	0.22	0.26	0.15	−0.22	0.32	0.18	0.10	0.04
GDD	0.06	1.00	0.30	0.15	0.12	0.80	−0.70	0.56	−0.53	0.90	0.93
ET	0.25	0.30	1.00	−0.11	0.97	0.25	−0.26	0.26	−0.07	0.25	0.24
CMI	0.22	0.15	−0.11	1.00	−0.07	0.40	−0.45	0.80	0.47	0.33	0.23
RADIANS	0.26	0.12	0.97	−0.07	1.00	0.18	−0.23	0.24	0.06	0.12	0.08
MINTEMP	0.15	0.80	0.25	0.40	0.18	1.00	−0.96	0.72	−0.34	0.91	0.82
MINTEMPSD	−0.22	−0.70	−0.26	−0.45	−0.23	−0.96	1.00	−0.77	0.20	−0.83	−0.70
RAIN	0.32	0.56	0.26	0.80	0.24	0.72	−0.77	1.00	0.16	0.66	0.54
SNOW	0.18	−0.53	−0.07	0.47	0.06	−0.34	0.20	0.16	1.00	−0.41	−0.48
MINFALLTEMP	0.10	0.90	0.25	0.33	0.12	0.91	−0.83	0.66	−0.41	1.00	0.93
MINSPRINGTEMP	0.04	0.93	0.24	0.23	0.08	0.82	−0.70	0.54	−0.48	0.93	1.00

Table 3. Coefficient estimates for fitting models with a single predictor variable and a forward-selection logistic model for prediction of hemlock dwarf mistletoe (*Arceuthobium tsugense*) and western hemlock (*Tsuga heterophylla*) occurrence (*n* = 1033).

Variable	Univariate models			
	Estimate	SE	*p*	AIC
Arceuthobium tsugense				
b_0				672
SLOPE	0.0029	0.0035	0.4088	674
GDD	0.0039	0.0004	0.0001	545
RADIANS	–0.0738	0.0415	0.0754	671
MINTEMP	0.0412	0.0059	0.0001	584
MINTEMPSD	–0.1097	0.0190	0.0001	609
RAIN	0.0004	0.0001	0.0006	672
RAIN^2	4.6×10^{-8}	2.4×10^{-7}	0.0534	671
SNOW	–0.0074	0.0012	0.0001	605
MINFALLTEMP	0.0959	0.0114	0.0001	556
MINSPRINGTEMP	0.1370	0.0155	0.0001	528
Tsuga heterophylla				
b_0				1336
SLOPE	0.0228	0.0029	0.0001	1262
GDD	0.0054	0.0003	0.0001	858
RADIANS	0.1532	0.0273	0.0001	1305
CMI	0.1999	0.0169	0.0001	1156
ET	1.4332	0.1854	0.0001	1271
MINTEMP	0.0422	0.0027	0.0001	914
MINTEMPSD	–0.1378	0.0090	0.0001	887
RAIN	0.0017	0.0001	0.0001	902
SNOW	–0.0008	0.0002	0.0013	1328
MINFALLTEMP	0.1072	0.0066	0.0001	855
MINSPRINGTEMP	0.1311	0.0078	0.0001	848

For example, the Hadley model predicts 50 year increases in average annual precipitation of 121, 135, and 168 mm at Juneau and increases in average annual precipitation of 42, 140, and 204 mm at Homer for the B1, A2, and A1B scenarios, respectively. In contrast with these predictions, historical precipitation patterns are more complex, with no single trend shown for all climate stations in the region (Fig. 3). In addition to the climate station information at Anchorage and Homer that shows relatively constant annual precipitation over the past 50 years (Fig. 3), recent research by Berg et al. (2009) documenting drying lakes and wetlands also indicates a possible ongoing change in the precipitation to evaporation balance along the western edge of our study area.

Climate variables

Potential independent variables for climate were chosen based on the review of *Arceuthobium* research and possible climate mechanisms that limit *A. tsugense* abundance and distribution in Alaska. The possible mechanisms considered were as follows: (*i*) the short growing season and cool temperatures during the growing season do not allow *A. tsugense* fruits to fully mature, (*ii*) low minimum winter temperatures reduce overwintering seed viability, (*iii*) precipitation (either rain or snow) reduces the number of seeds that can establish by causing them to be sloughed or flushed from foliage before germination, (*iv*) early autumn freezes damage fruit, and (*v*) low spring–summer temperatures damage pollen.

These mechanisms are not mutually exclusive, as climate

impacts on *A. tsugense* abundance and distribution could occur through multiple causes. The variables that were chosen to correspond to these proposed mechanisms were (*i*) "growing season variables": growing degree-days (GDD) and direct and indirect solar radiation during the growing season (RADIANS), (*ii*) "low winter temperatures": coldest mean minimum temperature over the year (MINTEMP) and variation in mean minimum temperature over the year (MINTEMPSD), (*iii*) "precipitation": precipitation as snow (SNOW) and precipitation as rain (RAIN), (*iv*) "autumn freezes": lowest mean minimum temperature in August or September (MINFALLTEMP), and (*v*) "low temperature during pollination": lowest mean minimum temperature in May or June (MINSPRINGTEMP).

Methods for deriving these climate variables are described below. Slope (SLOPE) was also added as an independent variable because *Arceuthobium*'s explosive seed dispersal results in differential ability to spread upward compared with downward (Bloomberg et al. 1980). For prediction of *T. heterophylla* distribution, two additional climate variables were selected to help explain the western boundary for *T. heterophylla* on the Kenai Peninsula. These variables were an evapotranspiration index for the growing season (ET) and a climate moisture index (CMI) representing precipitation in excess of evapotranspiration over the growing season.

Spatial precipitation and temperature information came from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2002), representing

mean values from 1961 to 1990 at a 2 km spatial resolution. PRISM's 2 km resolution is large relative to the distance between sea level and tree line in coastal Alaska, and therefore, location and elevation of each plot were used to rescale the climate data. Like Hamann and Wang (2005), we rescaled precipitation data using two-dimensional linear interpolation; however, we used geographically weighted regression to rescale temperature data. Weights (W) used for the latter were calculated as

[1] $\quad W = e^{-0.5(d/5)^2}$

where d is the distance in kilometres from the sample point to PRISM pixel centers and calculations were limited to be within a 14 km window. To avoid issues related to excessively widening or narrowing temperature differences related to independent rescaling of monthly minimum and maximum temperatures, we used geographically weighted regression to determine the average monthly temperature as well as the difference between monthly averages of minimum and maximum temperatures at each plot. We then used those rescaled data to recalculate the minimum and maximum monthly temperatures. GDD are the degrees Celsius greater than zero for each day summed over all of the days of the growing season, where growing season is defined as the calculated interval where mean temperature is above 0 °C.

MINSPRINGTEMP and MINFALLTEMP represent minimum daily temperature averaged over a month and then averaged over the years 1961–1990, with the lowest value chosen from May or June (for MINSPRINGTEMP) and August or September (for MINFALLTEMP). MINTEMP is derived by averaging minimum daily temperature over a month, then averaging minimum daily temperature over the years 1961–1990, and then selecting the lowest value from the 12 months. MINTEMPSD is the standard deviation of the minimums over the 12 months of the calendar year. ET uses the Hargreaves method described in Narongrit and Yasuoka (2003), with CMI calculated as shown in Latta et al. (2009). The solar radiation variable (RADIANS) is calculated as the sum of direct radiation (Swift 1976) and indirect solar radiation (Coops et al. 2000).

Precipitation was divided into rain and snow, with snow models adapted from Wang et al. (2006):

[2] $\quad \text{PPAS}_m = 1/(1 + e^{-(T-a)/b})$

where PPAS_m is the percentage of precipitation that falls as snow in month m, T is mean monthly temperature (degrees Celsius) at each location, and a and b are parameters that vary by month. The form of the equation is logistic, and PPAS_m is bound between the values of 0 to 1. Parameters a and b were calculated as $a = -3.39$ and $b = -2.53$ for January, $a = -1.80$ and $b = -2.10$ for February, $a = -0.33$ and $b = -1.37$ for March, $a = 0.90$ and $b = -1.29$ for April, $a = 0.27$ and $b = -1.21$ for October, $a = -2.18$ and $b = -1.88$ for November, and $a = -3.22$ and $b = -2.36$ for December, developed from fitting eq. 2 to 1954–2008 snowfall data from the eight weather stations in the region (Fig. 2). Because weather stations recorded snow depth but not snow as precipitation, snow was converted based on a ratio of 8 for snow depth to equivalent precipitation. The percentage of snow as precipitation was assumed to be zero for May through Sep-

Table 4. Results for prediction of hemlock dwarf mistletoe (*Arceuthobium tsugense*) in coastal Alaska for four candidate logistic models.

	Model A			Model B			Model C			Model D		
Number of variables	5			7			6			6		
χ^2 score	136.37			146.20			113.83			131.97		
AIC	518.47			512.26			517.92			515.09		
AIC – AIC$_{min}$	6.20			0.00			5.65			2.83		
Akaike weight	0.033			0.742			0.044			0.180		
Area under ROC curve	0.85			0.85			0.85			0.83		
Parameter	Value	SE	p	Value	SE	p	Value	SE	p	Value	SE	p
b_0	−8.965	1.475	<0.001	−6.492	2.879	0.024	−1.396	2.341	0.551	−6.943	2.811	0.014
SLOPE	0.012	0.004	0.005	0.013	0.005	0.005	0.012	0.005	0.006	0.013	0.004	0.004
GDD	0.002	0.010	0.027	0.003	0.001	0.007				0.003	0.001	0.010
RADIANS	−0.087	0.046	0.062	−0.095	0.047	0.042	−0.096	0.046	0.037			
MINTEMP				−0.077	0.027	0.004	−0.067	0.023	0.003	−0.076	0.027	0.004
MINTEMPSD				−0.198	0.066	0.003	−0.176	0.061	0.004	−0.205	0.066	0.002
RAIN	−1.2×10^{-7}	0.5×10^{-7}	0.010	−1.2×10^{-7}	0.5×10^{-7}	0.016						
RAIN^2										−6.3×10^{-4}	2.5×10^{-4}	0.011
SNOW							−3.0×10^{-3}	1.7×10^{-3}	0.083			
MINFALLTEMP												
MINSPRINGTEMP	0.090	0.030	0.003	0.120	0.033	<0.001	0.173	0.028	<0.001	0.130	0.033	<0.001

tember; while the records between 1954 and 2008 did show occasional snow during those months in some years at some locations, it was a very small portion of annual snowfall. Total annual snowfall as precipitation (SNOW) was calculated as $PPAS_m$ multiplied by precipitation for each month and summed over the year. Rainfall (RAIN) was calculated as precipitation minus SNOW.

Model development

For developing a predictive logistic model of *A. tsugense* presence, we used the probability function

$$p_i = \frac{e_i^{f(x)}}{\left(1 + e_i^{f(x)}\right)}$$

where p_i is the probability of *A. tsugense* being present at location i and $f(x)$ is a linear combination of the climate variables:

$$f(x) = b_0 + b_1 x_1 + b_2 x_2 + \ldots + b_n x_n$$

and the log odds (logit) of *A. tsugense* presence was thus

$$\ln\left(\frac{p_i}{1 - p_i}\right)$$

Logistic regression models and plots of the smoothed loess were used to examine the relationship between each climate variable and the logit for *A. tsugense*. The smoothed loess graphs suggested that there was a possible nonlinear relationship between *A. tsugense* probability and precipitation: a decline in probability after 2000 mm of total precipitation in southeast Alaska but an increase in probability at lower levels of precipitation. Thus, $RAIN^2$ was included as a possible term, leaving the set of candidate variables as SLOPE, GDD, RADIANS, MINTEMP, MINTEMPSD, RAIN, $RAIN^2$, SNOW, MINFALLTEMP, and MINSPRINGTEMP. Data for individual plots were randomly split into development (two thirds of plots) and validation (one third of plots) sets. The SAS logistic procedure (SAS Institute Inc. 2009) was used to select candidate models, with the significance level for variables to enter and leave the model set at 0.15 (Lee and Koval 1997). Because of model selection uncertainty, caused by high correlation among climate variables and limited knowledge of causal relationships, a model averaging approach (Burnham and Anderson 2002) was applied to four candidate models. The first two candidate models were selected using forward selection and backward elimination. Three variables that were significant (SNOW, RAIN, and MINFALLTEMP) as single-variable predictors were not included in either of those candidate models. To vary the models considered, two additional candidate models were chosen by selecting the best (by the Akaike information criterion (AIC)) six-variable models that included the SNOW and RAIN terms, respectively. Models with low AIC scores either did not contain the MINFALLTEMP term or, if included, the variable was not significant ($p \geq 0.15$). Accuracy of the logistic models was also assessed with receiver operating characteristic (ROC) curves, confusion matrices, and comparison of the predicted geographic range against observed locations. A similar process was used for developing logistic models for *T. heterophylla*.

In addition to the logistic models, we used two nonparametric methods for predicting *A. tsugense* distribution as a function of climate: RF imputation (Crookston and Finley 2008) and MSN imputation (Moeur and Stage 1995), implemented with R 2.10.0 (R Development Core Team 2009) and the R packages randomForest 4.5 and yaImpute (Crookston and Finley 2008). Explanatory variables used were SLOPE, GDD, RADIANS, ET, CMI, RADIANS, MINTEMP, MINTEMPSD, RAIN, $RAIN^2$, SNOW, MINFALLTEMP, and MINSPRINGTEMP. As both RF and MSN are well suited for problems with multiple response variables (Cutler et al. 2007; Eskelson et al. 2009a), presence of host and pathogen was predicted together.

To examine how *A. tsugense* and *T. heterophylla* distributions could change as a function of future climate, final models were also used to predict probability of occurrence with climate variables updated to 25, 50, and 100 years in the future. For climate projection data, we used downscaled GCM composites created by the Scenarios Network for Alaska Planning (SNAP) (2011). The composite models were made from the MPI ECHAM5, GFDL CM2.1, MIROC 3.2 (medres), UKMO HADCM3, and CCCma CGCM3.1 models, which had been chosen based on relatively good performance in an evaluation of GCMs for Alaska and Greenland by Walsh et al. (2008). The A1B (rapid economic growth, globalization, balanced energy), A2 (less economic growth but more population growth than A1, regionalization), and B1 (same population growth as A1 but more sustainable development) scenarios were used; see Nakicenovic et al. (2000) for full descriptions of scenarios. Temperature and precipitation values were projected by calculating the difference between the GCM projected value at 2011–2020, 2041–2050, and 2090–2099 and the GCM 1990–1999 base period and adding this to the PRISM values for current (1960–1990) climate. Derived climate variables such as GDD and MINSPRINGTEMP were then recalculated from the adjusted precipitation and temperature values.

Results

Current abundance and distribution of *A. tsugense*

Using the Pacific Northwest data set, an estimated 4.8% of the 2.259 billion *T. heterophylla* trees in Oregon, Washington, and California are infected with *A. tsugense*. Within the temperate rainforest ecoregion of Alaska (excluding national forest wilderness), an estimated 3.1% of 1.686 billion *T. heterophylla* trees are infected with *A. tsugense*. The estimated forest area with *A. tsugense* present is 752 000 ha in the Pacific Northwest and 376 000 ha in Alaska.

Combining the Alaska data set with the Pacific Northwest data set shows that the infection rate of individual *T. heterophylla* trees by *A. tsugense* varies by an interaction of latitude and elevation. At latitudes from 42.0 to 46.4°, the midpoint of which is near Eugene, Oregon, the mean infection rate (percentage of *T. heterophylla* trees with *A. tsugense*) was estimated as 7.0% (standard error (SE) = 1.2%). For 46.5–49.0° latitude, centered near Seattle, Washington, the mean infection rate was estimated as 3.3% (SE = 0.6%). Mean infection rate in Alaska, where latitudes are greater than 54.7°, was 3.1% (SE = 0.4%). The highest levels of infection rates within each latitudinal range were from 600 to 1400 m eleva-

Table 5. Results for prediction of western hemlock (*Tsuga heterophylla*) in coastal Alaska for three candidate logistic models.

	Model A			Model B			Model C		
Number of variables	5			6			5		
χ^2 score	610.35			613.66			601.18		
AIC	624.47			618.81			628.32		
AIC − AIC$_{min}$	5.66			0.00			9.51		
Akaike weight	0.055			0.937			0.008		
Area under ROC curve	0.92			0.92			0.92		
Parameter	Value	SE	p	Value	SE	p	Value	SE	p
b_0	0.848	1.395	0.543	−1.161	1.851	0.531	3.877	1.181	0.001
SLOPE	0.015	0.004	<0.001	0.018	0.004	<0.001	0.018	0.004	<0.001
GDD				2.8×10^{-3}	0.8×10^{-3}	<0.001			
ET									
CMI				0.129	0.024	<0.001	0.097	0.021	<0.001
RADIANS									
MINTEMP	−0.126	0.015	<0.001	−0.133	0.015	<0.001	−0.130	0.016	<0.001
MINTEMPSD	−0.307	0.037	<0.001	−0.334	0.037	<0.001	−0.348	0.038	<0.001
MINFALLTEMP									
MINSPRINGTEMP	0.214	0.019	<0.001	0.171	0.024	<0.001	0.224	0.020	<0.001
SNOW									
RAIN	8.5×10^{-4}	1.7×10^{-4}	<0.001						

tion in Oregon, from 200 to 800 m in Washington, and from 0 to 200 m in Alaska. Because *T. heterophylla* is not common in California, only 28 plots with the species were in the inventory so that reliable estimates of *A. tsugense* infection rates by elevation could not be made for California.

Within the existing broad range of *A. tsugense* in southeast Alaska (longitude $\leq$ −138°), both host and pathogen abundance decreased with elevation, but the pathogen reached an elevation threshold well before that of the host; *T. heterophylla* trees were found on plots that ranged in elevation from sea level to 825 m, while *A. tsugense* was found on plots from sea level to 396 m. The infection rate also decreased with elevation; infection by *A. tsugense* varied from a high of 20% at sea level to 5% by 200 m elevation in southeast Alaska (Fig. 4). Using the modeled climate variables, plots with *A. tsugense* had an average of an additional 22 days per year above freezing, had an additional 11 days above 10 °C, had warmer minimum spring and fall temperatures, had less solar radiation, and had less snow and rain than plots with *T. heterophylla* and without *A. tsugense* (Table 1).

Modeling results, logistic model

Most climate terms were correlated with each other (Table 2), with high correlations (>0.80) among those variables related to overall warmer temperatures (GDD, MINTEMP, MINFALLTEMP, and MINSPRINGTEMP). Fitting models for each independent variable showed that all variables except SLOPE were individually significant in predicting *A. tsugense* presence (Table 3). The sign of coefficients for most univariate (single independent variable) models corresponded to expectations, with increases in *A. tsugense* probability related to increases in the temperature variables (GDD, MINTEMP, MINFALLTEMP, and MINSPRINGTEMP). MINSPRINGTEMP created the greatest improvement in the deviance score (145) followed by GDD (129) and MINFALLTEMP (118).

Sign and magnitude of climate term coefficients were similar among the four candidate *A. tsugense* models (Table 4).

The seven-variable model (SLOPE, GDD, RADIANS, MINTEMP, MINTEMPSD, RAIN², and MINSPRINGTEMP; model B in Table 4) had the lowest AIC score and highest χ^2 score, with an Akaike weight of 0.742 (Table 4) in relation to the four candidate models. Area under the ROC curve was more than 0.83 for all four models, a value that Hosmer and Lemeshow (2000, p. 162) characterized as excellent discrimination.

For the averaged logistic model, we chose a classification cutoff value for the estimated probability of 0.276 because it resulted in a predicted 10% infection rate, which was the rate of infection observed in the developmental data set (103/1033 = 0.10). The confusion matrix showed sensitivity (*A. tsugense* presence that was classified correctly) of 38% for the development data set and 37% for the validation data set. Specificity (correctly classified absence of *A. tsugense*) was 93% for the development data set and 93% for the validation data set. Predicted values for both data sets were visually compared with the current spatial range in a GIS, and all plots that were predicted to have *A. tsugense* were within the current geographic range in southeast Alaska.

A similar process for developing logistic models for *T. heterophylla* presence resulted in three identified candidate models, with all three models having an ROC curve area of 0.92 and high significance for individual terms (Table 5). Model averaging of these three models using the Akaike weights (Burnham and Anderson 2002) and a cutoff value of 0.69 resulted in predictions with sensitivity (correct prediction of presence for *T. heterophylla*) of 90% for the development data set and 91% for the validation data set. Specificity for *T. heterophylla* predictions was 81% for the development data set and 80% for the validation data set (Table 6). A visual comparison using GIS indicated that in general the predicted range matched the observed range, with correct prediction of an absence of *T. heterophylla* on Kodiak Island and the western Kenai Peninsula. One predicted location for presence was 33 km farther northwest than the current range on the Kenai Peninsula shown by Viereck and Little (2007),

Table 6. Confusion matrix[a] showing actual versus predicted number of observations of hemlock dwarf mistletoe (*Arceuthobium tsugense*) and western hemlock (*Tsuga heterophylla*) presence in southeast and south-central Alaska using logistic, Random Forest (RF), and Most Similar Neighbors (MSN) imputation.

	Actual					
	Logistic[b]		RF		MSN	
Predicted	Present	Absent	Present	Absent	Present	Absent
Arceuthobium tsugense						
Development data set (*n* = 1033)						
Present	39	64	38	19	30	78
Absent	64	866	65	911	73	852
Validation data set (*n* = 516)						
Present	17	35	9	20	11	46
Absent	29	435	37	450	35	424
Tsuga heterophylla						
Development data set (*n* = 1033)						
Present	607	67	650	61	579	94
Absent	67	292	24	298	95	265
Validation data set (*n* = 516)						
Present	283	42	292	46	273	63
Absent	27	164	18	160	37	143

[a]Sensitivity, a metric for accuracy of predicting presence, is calculated from the confusion matrix as the percentage of observed presences that were correctly predicted. Specificity, a metric for accuracy of predicting absence, is calculated as the percentage of observed absences that were correctly predicted. For example, for the development data set and *A. tsugense*, sensitivity of the RF model is $38/(38 + 66) = 37\%$, specificity is $911/(19 + 911) = 98\%$, and bias can be understood by comparing predicted presence $((38 + 19)/1033 = 5.5\%)$ with observed presence $((38 + 65)/1033 = 10.0\%)$.

[b]Logistic model classification used a cutpoint of 0.276 for *A. tsugense* and 0.690 for *T. heterophylla*.

and overall, there were fewer predictions of *T. heterophylla* presence in forested areas bordering the Gulf of Alaska than were found in the inventory. While the two logistic models for host and pathogen had been developed separately, there were no instances in either the development or validation data set of locations where *A. tsugense* was predicted and *T. heterophylla* was not.

Modeling results, most similar neighbor and random forest models

Sensitivity of predicting *A. tsugense* presence was better for RF (37%) than for MSN (29%) for the development data set (Table 6). For the validation data set, sensitivity was better for MSN (24%) than for RF (20%). Specificity for both the development and validation sets was better for RF (98% and 96%) than for MSN (92% and 90%). MSN had a slight bias toward overpredicting *A. tsugense* presence, with 10.5% of development plots and 11.0% of validation plots predicted as having *A. tsugense* infection compared with actual rates of 10.0% and 8.9%. RF underpredicted rates of *A. tsugense* infection, with predictions of 5.6% and 5.5% for the development and validation data sets, respectively. Spatially, all plots in both data sets that were predicted to have *A. tsugense* presence were within the current geographic range of *A. tsugense* for both RF and MSN.

RF slightly overpredicted *T. heterophylla* presence, with 68.8% of development plots and 65.5% of validation plots predicted as having *T. heterophylla* compared with actual rates of 65.2% and 60.1% (Table 6). MSN was unbiased in prediction of *T. heterophylla* presence for development plots (65.2%) and slightly overpredicted *T. heterophylla* presence for the validation data set (65.1%). For MSN, sensitivity of *T. heterophylla* prediction was 85.9% for the development

data set and 88.1% for the validation data set, and specificity was 73.8% for the development data set and 69.4% for the validation set. For RF, sensitivity of *T. heterophylla* prediction was 96.4% for the development data set and 94.2% for the validation data set, and specificity was 83.0% for the development data set and 77.7% for the validation data set. Spatially, RF and MSN both correctly predicted an absence of *T. heterophylla* on Kodiak Island and the western Kenai Peninsula. While the RF-predicted range matched the actual inventory observations closely, MSN made four out-of-range predictions of *T. heterophylla* presence in the Anchorage and Kenai Fjords regions, all within 75 km from the current range.

Modeling results, prediction of future *A. tsugense* for altered climate

For *T. heterophylla*, all three models (RF, MSN, and logistic) predicted increases of 5%–18% by the fifth decade for the three climate scenarios (A1B, A2, and B1). The models showed greater differentiation by the 10th decade, with RF showing less increase than either the MSN or logistic model (Table 7). At the 10th decade, there was greater variation between modeling methods than between climate scenarios.

For *A. tsugense*, the models predicted increases of 166%–509% by the fifth decade and increases of 242%–856% by the 10th decade (Table 7). Adjusting by the amount of bias shown for the validation data set, the predicted increases are 186%–450% by the fifth decade and 374%–757% by the 10th decade. The logistic model predicted the greatest amount of increase for all three climate scenarios. Standard deviation between models (MSN, RF, and logistic) was much greater than standard deviation between scenarios (A1B, A2, and B1). While the majority of predicted potential increase of *A.*

Table 7. Projection of hemlock dwarf mistletoe (*Arceuthobium tsugense*) and western hemlock (*Tsuga heterophylla*) frequency as a percentage of modeled 1990–1999 values, by model and climate scenario, for southeast and southcentral Alaska.

	Decade			
Model and scenario	2011–2020	2041–2050	2091–2100	2091–2100[a]
Arceuthobium tsugense				
Most Similar Neighbors				
A1B	115	357	715	577
A2	171	230	739	596
B1	158	236	515	416
Random Forests				
A1B	74	166	242	384
A2	99	197	283	449
B1	93	147	236	374
Logistic				
A1B	135	464	818	724
A2	248	509	856	757
B1	305	402	645	571
Tsuga heterophylla				
Most Similar Neighbors				
A1B	100	118	149	137
A2	102	117	153	141
B1	106	109	128	118
Random Forests				
A1B	98	115	122	112
A2	103	114	123	113
B1	105	110	117	107
Logistic				
A1B	100	112	141	134
A2	102	116	143	136
B1	105	105	121	115

[a]Adjusted by the ratio of observed to predicted presence from the validation data set.

tsugense occurs in southeast Alaska within the current geographic range, there is also a westward expansion of potential infection along the Gulf of Alaska (Fig. 5).

The consistency of the logistic models for predicting pathogen presence only where the host occurred did not hold when applied to future climates. For the 2090–2100 decade, about 0.6% of predictions of *A. tsugense* presence occurred for locations where *T. heterophylla* was not predicted to occur.

Discussion

Predictions over the next century from all three climate envelope models indicated a substantial difference between potential impacts on the host tree (*T. heterophylla*) and potential impacts on the pathogen (*A. tsugense*). Results for the host tree indicated modest potential increases in abundance and range expansion. In contrast, the models predicted extremely large potential increases in abundance of *A. tsugense*, mostly within its current range but also from an 800 km westward expansion in potential habitat.

However, predictions are only for potential habitat and do not incorporate migration rates. Landscape-level dispersal of *Arceuthobium* can be viewed as a combination of short-distance explosive seed dispersal each autumn and less frequent long-distance transmission by birds and other animals (Lundquist 2005). The ability of *A. tsugense* to spread over short distances through explosive seed dispersal has been well es-

tablished. In contrast, dispersal over longer distances, while known to occur, has much more uncertainty. The presence of *A. tsugense* on many of the islands within the Alexander Archipelago of Alaska that were covered by glaciers until the end of the late Wisconsin glaciation 13 000 B.P. indicates that long-distance transmission does occur. While dispersal rates of *T. heterophylla* are also uncertain, pollen records suggest that it recolonized southeast Alaska as early as 10 000 B.P. (Ager et al. 2010) but did not reach the Prince William Sound area until about 2000 B.P. (Heusser 1983).

As dispersal is not addressed in this paper, predictions from the climate envelope models should be viewed as predictions of potential rather than actual occupancy. A related difficulty posed for this analysis is that the degree to which both species have occupied their potential climate niches is unknown. Tidewater glaciers, fjords, and mountains provide barriers to dispersal in this region, and it may be that *T. heterophylla* is still migrating westward, as is known to be the case for *P. sitchensis* (Griggs 1934).

For land managers, the prediction for large potential increases in southeast Alaska, where *A. tsugense* is already present, is of more immediate applicability than the prediction for potential range expansion westward along the Gulf of Alaska coastline. Reduced snow and longer growing seasons in southeast Alaska could allow *A. tsugense* to migrate upslope above the 200 m threshold where it is currently rare. In southeast Alaska, a change to a more favorable climate for

Fig. 5. Current distribution of western hemlock (*Tsuga heterophylla*) and hemlock dwarf mistletoe (*Arceuthobium tsugense*) from inventory data and Most Similar Neighbor current, fifth decade, and 10th decade predictions.
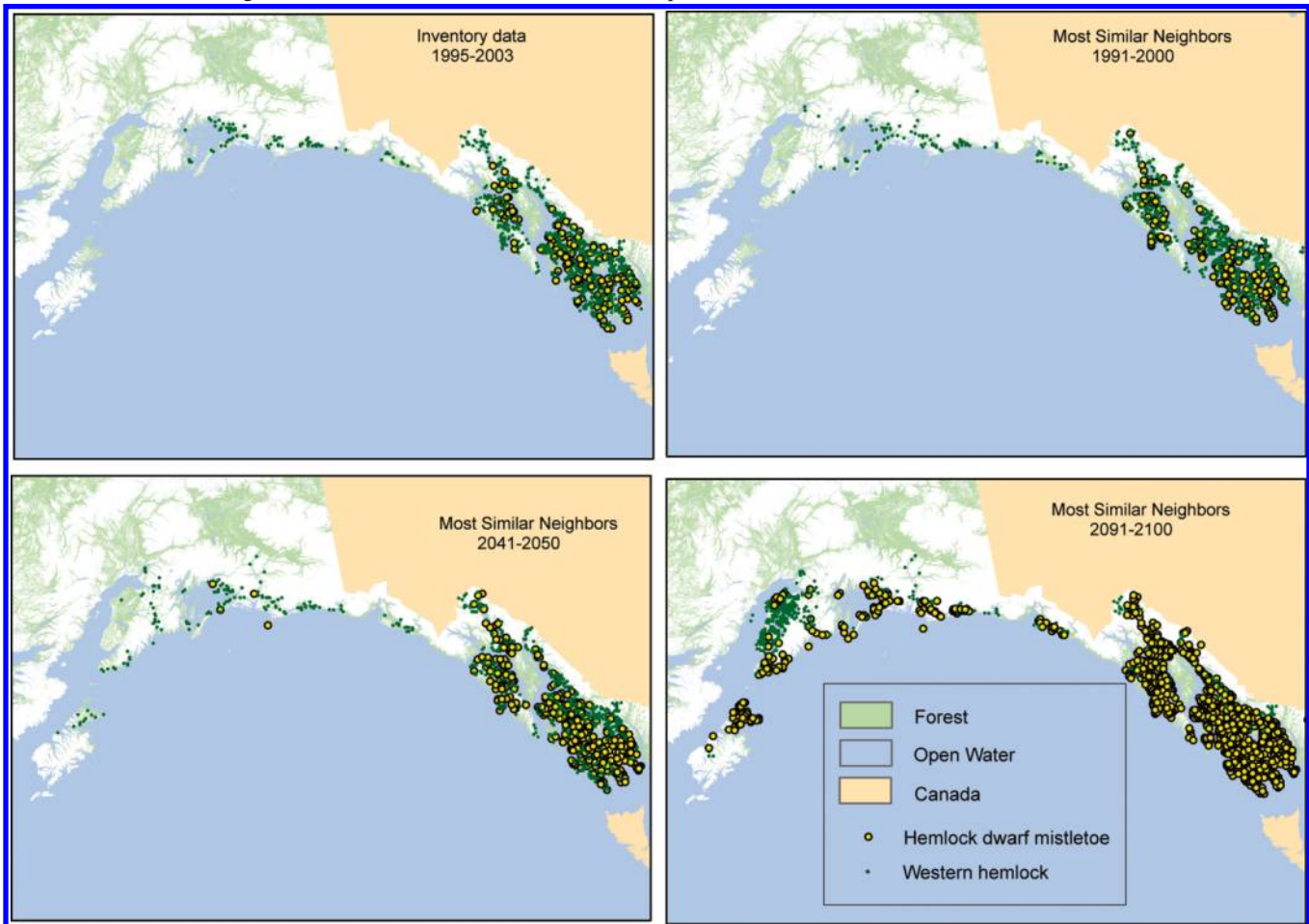
A. tsugense would allow it to reproduce more effectively with a resulting increase in disease effects (growth loss and mortality) for *T. heterophylla*. It may be that in the future, the faster rate of spread and completion of the *A. tsugense* life cycle that is currently seen in British Columbia (Muir and Hennon 2007) becomes the standard for how the pathogen behaves in southeast Alaska.

The current abundance and distribution of *A. tsugense* in the temperate rainforests of Alaska appear to be strongly related to climate. The parsimonious logistic models that we selected included explanatory climate variables of growing degree-days, rainfall and snowfall, direct and indirect solar radiation, minimum winter and spring temperatures, and variation in minimum temperatures. Most variables were correlated, and when extended to future climate scenarios, there is an assumption made that the correlation between climate variables will be the same. This seems more likely to hold true between temperature variables than for interactions between temperature and precipitation. Correlation among climate variables also means that modeling results cannot be used to reject any particular hypothesis about causal mechanisms, e.g., that limitation of range is caused by a short cool growing season rather than minimum spring temperatures or snow accumulation. In our literature review, we found that much of the previous research on *A. tsugense* has been focused on

management, and some surprisingly basic information, such as the impact of precipitation on seed establishment, or whether pollination occurs from insects or wind, is unknown. Some additional field research on causal mechanisms influencing *A. tsugense* establishment and reproduction could be helpful in refining understanding of the relationship between the phenology of *A. tsugense* and climate. An additional limitation of the models may be the use of average monthly minimum temperatures, as temperature extremes are more likely to be injurous to both *A.tsugense* and *T. heterophylla*.

None of the three modeling approaches used here (logistic models, RF imputation, and MSN imputation) was consistently best by all measures. RF showed some evidence of overfitting (through a drop in accuracy between the development and validation data sets) and underpredicted *A. tsugense* presence, although it also performed the best for prediction of the development data set. The logistic modeling approach has the advantage of having a number of well-understood diagnostics (ROC curves, AIC scores, probability plots) that can be used for comparing models and developing understanding of relationships, in contrast with the two imputation methods.

Climate envelope modeling is sometimes criticized for being too simplistic to help predict actual changes in species' distribution and abundance in that disturbance, competition, and the influence of biotic factors such as insects and patho-

gens are not considered. The methods presented in this paper help to address the last concern by modeling climate effects on both a host tree species and an infecting pathogenic species. While our expectations were that the imputation methods of MSN and RF would have an advantage by simultaneously predicting host and pathogen, this only proved to be an advantage for prediction of future climates because the logistic models did not predict the presence of *A. tsugense* without *T. heterophylla* for the current climate. It may be that *A. tsugense*'s climate range is well within *T. heterophylla*'s climate range as a result of evolution with a single primary host; multivariate prediction methods might have a stronger advantage in situations where this was not the case, e.g., where a nonnative pathogen has been recently introduced to a new host species.

Conclusion

There are strong indications that climate is currently limiting *A. tsugense* to a subset of the range of its primary host, *T. heterophylla*, in the northern temperate rainforest. Predictions from models used here suggest large increases in potential habitat for *A. tsugense* in Alaska and modest increases possible for *T. heterophylla*. While increases within the current range in southeast Alaska can occur from normal explosive seed discharges over short distances, expansion of range westward along the Gulf of Alaska is dependent on dispersal by birds and mammals, the rate of which is unknown.

Implications for southeast Alaska include reduced capacity for carbon sequestration, potential beneficial impacts for wildlife, and higher risk of negative impacts for those portions of the forest managed for timber production, which may alter silvicultural choices. The opposing influences on *T. heterophylla*, from an increase in habitat accompanied by an increase in a major pathogen, illustrate the complexity of prediction of climate impacts on plant species.

Substantial uncertainty as to the amount of potential increase in *A. tsugense* habitat exists. The use of different modeling approaches contributed more to the range of possible outcomes than did the use of different climate scenarios, suggesting that using multiple modeling approaches is beneficial to understanding uncertainty of predictions. In the future, collection and analysis of inventory data, similar to the approach used in this paper, could be helpful in monitoring the predicted increase in disease behavior.

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