



Vector-Borne Diseases, Surveillance, Prevention

Modeling Geographic Uncertainty in Current and Future Habitat for Potential Populations of *Ixodes pacificus* (Acari: Ixodidae) in Alaska

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Abstract

Ixodes pacificus Cooley & Kohls is the primary vector of Lyme disease spirochetes to humans in the western United States. Although not native to Alaska, this tick species has recently been found on domestic animals in the state. *Ixodes pacificus* has a known native range within the western contiguous United States and southwest Canada; therefore, it is not clear if introduced individuals can successfully survive and reproduce in the high-latitude climate of Alaska. To identify areas of suitable habitat within Alaska for *I. pacificus*, we used model parameters from two existing sets of ensemble habitat distribution models calibrated in the contiguous United States. To match the model input covariates, we calculated climatic and land cover covariates for the present (1980–2014) and future (2070–2100) climatologies in Alaska. The present-day habitat suitability maps suggest that the climate and land cover in Southeast Alaska and portions of Southcentral Alaska could support the establishment of *I. pacificus* populations. Future forecasts suggest an increase in suitable habitat with considerable uncertainty for many areas of the state. Repeated introductions of this non-native tick to Alaska increase the likelihood that resident populations could become established.

Key words: *Ixodes pacificus*, habitat modeling, climate change, species distribution model, extrapolation uncertainty

Ticks can transmit a wide diversity of pathogens to humans, companion animals, and wildlife and continue to be a persistent public health and veterinary concern. Although many parts of the contiguous United States have endemic populations of human-biting ticks (Eisen et al. 2017), given its high latitude, Alaska has historically been outside the geographic range of the most common medically important ticks in the country (Hahn et al. 2020). In recent years, several tick species have expanded their northern range into parts of the Palearctic where they have not been found before (Tokarevich et al. 2011, Jaenson et al. 2012, 2016, Alfredsson et al. 2017), potentially exposing new human populations to a variety of tick-borne disease agents. Although there have been no confirmed autochthonous human cases of tick-borne disease in Alaska, several species of medically important ticks have been identified in the state for the first time within the last decade (Hahn et al. 2020), raising concerns about the establishment of local populations.

Many of the non-native ticks identified in Alaska in the past several years were found on people or domestic animals that had

recently traveled out of state (Durden et al. 2016, Hahn et al. 2020). Particularly when their recent travel was to tick-endemic areas, it is possible that they brought these vectors back with them, rather than acquiring them from natural areas in Alaska. Despite the large number of travel-related tick collections, there have been several dozen non-native ticks found in Alaska since 2010 on hosts that had reportedly not recently traveled out of the state. In Anchorage, Alaska's primary urban center, *Ixodes pacificus* Cooley & Kohls (western black-legged tick) has been found on two dogs without recent travel (one in 2017 and one in 2019). While human and pet travel is likely an important route of importation of *I. pacificus* into Alaska (Xu et al. 2019, Hahn et al. 2020), migratory birds may also be a source of repeated introductions of *I. pacificus* into the state (Morshed et al. 2005, Ogden et al. 2008).

Ixodes pacificus is widely distributed on the west coast of the United States (Eisen et al. 2016) as well as a small portion of southwest Canada and is a vector of *Borrelia burgdorferi* Johnson

et al. (Spirochaetales: Spirochaetaceae), the causative agent of Lyme disease, and *Anaplasma phagocytophilum* (Foggie) Dumler et al. (Rickettsiales: Anaplasmataceae), the agent of granulocytic anaplasmosis (Foley et al. 2004). This tick species readily feeds on a wide diversity of mammalian, avian, and reptilian hosts (Castro and Wright 2007). Previous habitat distribution models have characterized the climate and land cover affinities of *I. pacificus* within its native range in the western United States (Hahn et al. 2016, Eisen et al. 2018, Porter et al. 2021). Temperature and precipitation, particularly during the cold season, were important contributing variables to models of *I. pacificus* habitat suitability in California (Hahn et al. 2016, Eisen et al. 2018). Areas of greater forest cover were an important explanatory factor in *I. pacificus* habitat models in California, Oregon, and Washington (Hahn et al. 2016, Porter et al. 2021). Land cover is also a key habitat predictor, and previous modeling studies of *I. pacificus* have used forest cover metrics that included deciduous, evergreen, and mixed forests to assess habitat (Hahn et al. 2016). Field studies of *I. pacificus* in California (Eisen et al. 2006) and the closely related *I. scapularis* Say (Acari: Ixodidae) in Minnesota (Hahn et al. 2018) have collected ticks on drags in mixed hardwood-coniferous and coniferous forests. Overall, these results suggest that within the native range of *I. pacificus*, the likelihood of an area being classified as suitable habitat increases in areas with sufficient forest cover, increasing winter temperature above 0°C, and when winter precipitation ranges from 400 to 800 mm (Hahn et al. 2016, Eisen et al. 2018, Porter et al. 2021).

Once introduced into a new environment, the ability of *I. pacificus* to survive depends on several biotic and abiotic factors including climate, plant community composition and structure, and the distribution of hosts (Medlock et al. 2013, Sonenshine and Roe 2013). Many of the most important disease vectors are ixodid (hard) ticks, which often spend over 90% of their life off-host, in-between blood meals (Needham and Teel 1991). During this time, they are in a low metabolic state (Lighton and Fielden 1995) and are particularly sensitive to local environmental conditions, such as temperature, relative humidity, and availability of dense vegetation or leaf litter to modulate their microhabitat (Sonenshine and Roe 2013). In addition to directly influencing tick survival, climatic conditions also affect several other aspects of the tick life cycle including the rate of development of immature life stages and the seasonality of host-seeking behavior (Eisen et al. 2015).

At northern latitudes, climate is likely the primary limiting factor (Gray et al. 2009). Although quite cold tolerant, *Ixodes* spp. are sensitive to freezing during long periods of extreme cold (Gray et al. 2009, Neelakanta et al. 2010, Nieto et al. 2010). During summer months, temperatures need to be warm enough for immature life stages to complete development (Padgett and Lane 2001, Ogden et al. 2004), and throughout the year, ticks are highly sensitive to desiccation. Previous studies have shown high mortality for *I. pacificus* and the closely related *I. scapularis* during periods of low humidity (Stafford 1994, Padgett and Lane 2001, Nieto et al. 2010). Thus, interactions between temperature and precipitation are likely important for survival and reproduction of *I. pacificus*.

At a regional scale, habitat distribution models can be a useful tool for assessing the invasive potential of a species in a new environment based on macroclimatic or environmental correlates of species presence within its native range (Estrada-Peña 2008, Giles et al. 2014, Raghavan et al. 2019). Although limited to a relatively small set of predictive variables, habitat distribution models can be used at a coarse scale to identify the potential distribution of a species under different climate scenarios (Estrada-Peña 2008). This approach has been used to predict the invasive potential of

Haemaphysalis longicornis Neumann (Acari: Ixodidae) in North America (Raghavan et al. 2019, Raghavan et al. 2019), *Amblyomma variegatum* (Fabricius) (Acari: Ixodidae) in Central and South America (Estrada-Peña et al. 2007), cattle fever ticks in the southern United States (Giles et al. 2014), and *Amblyomma* spp. in California (Pascoe et al. 2019). The predictions calculated from habitat distribution models can also be used to target surveillance and develop mitigation and eradication strategies prior to the establishment of local tick populations. In this study, we used habitat suitability models for *I. pacificus* in the contiguous United States to estimate potentially suitable habitat in Alaska based on present-day climate and future climate scenarios.

Materials and Methods

Study Area

Alaska encompasses portions of three biomes: temperate, boreal, and Arctic. Transitions in abiotic characteristics and biological communities between Arctic (as defined by the Circumpolar Arctic Vegetation Map; Walker et al. 2005) and boreal (as defined by the Alaska-Yukon Region of the Circumboreal Vegetation Map; Jorgenson and Meidinger 2015) are indefinite. For geographic clarity and because of the ambiguity of some transitional zones, we divided Alaska into four subregions modified from the Unified Ecoregions of Alaska (Nowacki et al. 2001) for the purpose of summarizing broad geographic patterns in our results: Temperate, Interior Boreal, Western Arctic-Boreal Transition, and Northern Arctic (Supp Fig. 1 [online only]). Hereafter, we refer to the latter three subregions as ‘Interior’, ‘Western’, and ‘Northern’, respectively. Except for the boundary between the Temperate and Interior subregions, the subregion boundaries should not be interpreted as abruptly different ecological zones.

The Temperate subregion spans Southeast Alaska and coastal Southcentral Alaska west to Kodiak Island. It consists primarily of temperate rainforests dominated by coniferous tree species, but also includes treeless coastal wetland, subalpine, and alpine communities. Because of the moderating influence of the Pacific Ocean, temperate Alaska has cool summers and mild winters with high annual precipitation (Nowacki et al. 2001). The Temperate subregion of Alaska has climatic and biogeographic affinities to the broader zone of northern Pacific temperate rainforests that stretch south from Alaska to northern California (DellaSala 2010).

The Interior subregion falls within the boreal biome as defined by Jorgenson and Meidinger (2015). Much of the subregion is covered by forest communities, and both coniferous and deciduous trees are common because of the high return interval of fire. Tundra, wetland, subalpine, and alpine communities not dominated by tree species are also present. Interior Alaska is characterized by a continental climate with short but relatively hot summers and long, cold winters. Moderate to low amounts of precipitation are typical and permafrost is discontinuous or absent (Jorgenson and Meidinger 2015).

The Western subregion includes both the Arctic as defined by Walker et al. (2005) and boreal as defined by Jorgenson and Meidinger (2015). Both tree-dominated communities and shrub- and graminoid-dominated tundra communities are widespread in the subregion and are frequently interposed. Where tundra communities are more common, tree-dominated communities often still occur on well drained landscape features, floodplains, and lake shores. Discontinuous permafrost is widespread only in certain areas, such as the Yukon-Kuskokwim Delta (Whitley et al. 2018). Winter temperatures are cold and summer temperatures are relatively cool

because of the moderating influences of the Bering Sea and Pacific Ocean. The subregion receives moderate amounts of precipitation (Jorgenson and Meidinger 2015).

The Northern subregion falls within the Arctic as defined by Walker et al. (2005). Tree-dominated communities on the south side of the Brooks Range transition to shrub- and graminoid-dominated tundra communities with increasing elevation south of the ridge crest of the Brooks Range. North of the Brooks Range ridge crest, tall shrubs occur primarily along large floodplains (Nowacki et al. 2001), and trees are rare in sheltered areas along rivers and south-facing slopes and at perennial springs (*Populus balsamifera* L. (Malpighiales: Salicaceae) only; Breen 2014). Annual precipitation is low, but soils are predominantly moist to wet because of the widespread continuous permafrost. Summers in this area are cool, and winters are cold (Nowacki et al. 2001).

Data Sources

We predicted the distribution of current and future habitat of *I. pacificus* in Alaska using two ensemble models of *I. pacificus* habitat distribution trained on data from the contiguous United States. One ensemble model was developed using *I. pacificus* presence at the county level to predict habitat suitability in the western United States (Hahn et al. 2016, henceforth ‘Western county model’). The other ensemble model was developed using individual *I. pacificus* presence records to predict habitat suitability within California at the 1 km scale (Eisen et al. 2018, henceforth ‘CA 1 km model’).

Both *I. pacificus* ensemble models used bioclimatic variables that are derived from monthly precipitation and temperature data. Though these data are available globally at roughly 1 km spatial resolution via the WorldClim dataset (Fick and Hijmans 2017), the precipitation data suffer from inaccuracies over mountainous terrain. Instead, we used climate data from the Scenarios Network for Alaska and Arctic Planning (SNAP) and calculated bioclimatic variables using the R software package, ‘dismo’ (Table 1). The historical SNAP precipitation and temperature data have a 2 km spatial resolution after SNAP downscaled them from the 0.5 degree Climate Research Unit Time Series (CRU TS) 4.0 data using the delta method. This downscaling step improved the spatial resolution of the data to more accurately reflect the local climatological conditions found in Alaska. Both *I. pacificus* ensemble models also included vapor pressure as a covariate. For these, we used downscaled vapor pressure data from SNAP, available at a 1 km spatial resolution for Alaska.

We used data from 1980 to 2014 to calculate the current climatological conditions for Alaska. These years were selected to match those used in Eisen et al. (2018). For our future forecasts, we used

climatology for the end of the century, 2070–2100. We obtained future climate projections from downscaled SNAP data that were derived from the Coupled Model Intercomparison Project, 5th Assessment Report (CMIP5/AR5) global circulation models. For this study, we used projections developed using a Representative Concentration Pathway (RCP) of 4.5 and 8.5 W/m². RCP 8.5 scenario is a worst case, ‘business as usual’ scenario, thought to be the most realistic future scenario (Schwalm et al. 2020), but we also included RCP 4.5 as an alternate future scenario. Including these two climate scenarios allows us to further explore the uncertainty in our results.

Other covariates used in the *I. pacificus* ensemble models include percent forest cover, cumulative growing degree days in December, and average summer day length. For forest cover, we used the 30 m Landsat-derived percent forest cover data (Hansen et al. 2013) resampled to a 1 km spatial resolution using Google Earth Engine (Gorelick et al. 2017). Cumulative growing degree days for December were calculated from the downscaled SNAP temperature climate data. Since these data are monthly, we approximated the daily measure using the quadratic formula specified in Springer et al. (2015). To calculate average summer day length, where we defined summer as the three warmest months, we used daily day length from Daymet (Thornton et al. 2016) for the year 2010 and averaged them for the months of June, July, and August.

We included a visual depiction for the range and spatial variation of the input covariates for the Western county (Supp Fig. 2 [online only]) and CA 1 km (Supp Fig. 3 [online only]) sets of models for the period 1980–2014 as part of the Supplementary Material.

Ensemble Modeling Approach and Visualization of Results

The *I. pacificus* ensemble models for the western United States combined the results of four (Western county model) or five (CA 1 km model) individual models of habitat suitability to produce a single consensus model. We extended this approach by estimating suitable habitat for *I. pacificus* in Alaska using each of the individual models from both studies, and then combining the results of all nine models into a single ensemble model. The modeling frameworks in the *I. pacificus* ensemble models included generalized linear model (GLM), multivariate adaptive regression spline (MARS), maximum entropy (Maxent), random forest (RF), and boosted regression tree (BRT). We used VisTrails Software for Assisted Habitat Modeling (SAHM; version 2.0) for our analysis (Morissette et al. 2013).

Each model produced a habitat suitability probability between 0.0 and 1.0. Probabilities are commonly converted to binary

Table 1. Data sources for Alaska climate and land cover covariates. All variables were resampled to 1 km. Historical conditions were calculated using 1980–2014 data. Future conditions were calculated for 2070–2100 using RCP 4.5 and 8.5

Model data	Source data resolution		Source/notes
	Temporal	Spatial	
Forests	2000s	30 m	Landsat-derived forest percentage (Hansen et al. 2013)
Day length	2010	1 km	Daymet (Thornton et al. 2016)
Temperature	1901–2015 ^a	2 km	SNAP ^b CRU TS 4.0, min and max temperature
	2006–2100 ^a	2 km	SNAP NCAR CCSM 4 RCP 4.5 & 8.5, min and max temperature
Precipitation	1901–2015 ^a	2 km	SNAP CRU TS 4.0, precipitation
	2006–2100 ^a	2 km	SNAP NCAR CCSM 4 RCP 4.5 and 8.5, precipitation
Vapor pressure	1901–2015 ^a	1 km	SNAP CRU TS 4.0, vapor pressure
	2006–2100 ^a	1 km	SNAP NCAR CCSM 4 RCP 4.5 and 8.5, vapor pressure

^aMonthly.

^bScenarios Network for Alaska and Arctic Planning (SNAP).

representations of suitable/not suitable habitat by setting a threshold value based on the optimal model sensitivity and specificity (Fielding and Bell 1997, Guisan et al. 2007). We used the model-specific optimum threshold values from the Hahn (2016) and Eisen et al. (2018) studies. Threshold values for the Western county model are as follows: GLM = 0.26, MARS = 0.31, Maxent = 0.27, and RF = 0.42. Threshold values for the CA 1 km model are as follows: BRT = 0.68, GLM = 0.474, MARS = 0.481, Maxent = 0.333, and RF = 0.49. Pixels with predicted probabilities above each threshold were classified as suitable habitat. We then combined the binary model results into a map that shows pixels where three or more models predicted suitable *I. pacificus* habitat (i.e., the ensemble model results; Hahn et al. 2021). To highlight changes from current to future climate conditions, we used a categorical change map to show pixels that do not change, pixels that change from unsuitable to suitable habitat, and pixels that change from suitable to unsuitable habitat (Hahn et al. 2021).

Final ensemble maps for both the present and future climatologies were masked, similar to Eisen et al. (2018), to limit predicted tick habitat to land cover types where ticks are commonly found. To create the land cover mask, we used the National Land Cover Database (NLCD) for the year 2016 (Wickham et al. 2017) by including the following categories (numbers refer to their classification codes): lightly developed areas (open space, 21; low intensity, 22); deciduous, evergreen, and mixed forests (41, 42, 43); and grasslands (71). We excluded medium- and high-intensity developed areas. Although scrub-shrub vegetation was included in the Eisen et al. (2018) land cover mask, shrub land cover classes are substantially different in Alaska. For example, the California scrub-shrub land cover class includes a dominant sage component that is not widespread in Alaska, and the Alaskan shrub classes include nonalpine low and dwarf shrub-dominated tundra communities that do not have analogs in California. We recognize that vegetation change during our study period will influence the distribution of tick habitat in Alaska. However, land cover and vegetation change projections suitable to our effort do not currently exist for the entire state and represent a major data gap. We therefore assumed a static land cover mask.

Evaluation of Modeling Results

The ranges of several of the climate covariates used in the *I. pacificus* ensemble models were exceeded when applying the models to some regions of Alaska. Habitat suitability predictions in areas where the new model input ranges exceeded the training ranges have a higher degree of uncertainty than areas where the input ranges were within the training ranges. Such extrapolations are commonly performed in studies making future forecasts (Elith et al. 2010, Springer et al. 2015, Hahn et al. 2021), but it is important to understand their extent. To evaluate the spatial distribution and magnitude of this uncertainty, we used multivariate environmental similarity surface (MESS) maps. Any positive MESS value indicates that the observed value is within the reference range used to train the models, while negative values denote observations beyond the training range. MESS values have an upper bound of 100, meaning the observed value is equal

to the median reference set of values. There is no lower bound for the measure. Maps of the most dissimilar (MoD) variables ('MoD maps') can be used to identify the variables driving the MESS value. See the appendix of Elith et al. (2010) for the algorithm used to calculate MESS values and the related MoD variables.

We derived predictions of present-day and future *I. pacificus* habitat suitability based on the full range of the climate covariates. Then, based on the MESS and MoD maps, we developed a second set of predictions that constrained average summer daylight and precipitation (the two variables with the largest negative MESS values for most areas) to prevent gross extrapolation of these variables.

Results

Both the unconstrained and constrained ensembles were biased to some extent. The unconstrained ensemble can be thought of as a naive application of models to Alaska, with obvious extrapolations for some covariates. The constrained ensembles address the most severe model extrapolations, and in doing so, introduce a separate set of assumptions and biases about what the future environmental conditions in Alaska might be. We define the constrained ensembles below, then present the unconstrained and constrained ensembles side-by-side before combining them to further explore the uncertainty in forecasted habitat.

Model Extrapolations in Alaska

We expected some of the input variables from Alaska to exceed the ranges of the input variables calibrated in the contiguous United States. Using the MESS measure, we found that at least six of the nine models have one or more variables for Alaska that exceed the training ranges from the contiguous United States (Supp Fig. 4 [online only]). Extrapolations are greatest for the mountainous terrain in southern Alaska (due to high precipitation in the warmest quarter of the year) and in northern Alaska (due to 24 h of daylight in the summer). These two covariates are clearly visible when looking at the most dissimilar (MoD) maps for each individual model (Supp Fig. 5 [online only]).

For precipitation of the warmest quarter (Bio18), the model ranges never exceed 226 mm, but this maximum is below the mean Alaska precipitation of 237 mm (Table 2). To prevent gross extrapolation of this variable, we constrained it to the respective model maximums of 226 mm for the Western county models and 73 mm for the CA 1 km models. Supp Fig. 6 (online only) shows the spatial effects of these constraints for current and future climatologies. Alaska's northern latitude means that the minimum summer daylight in Alaska is well above the maximum observed daylight experienced in California (Table 2). To minimize the influence of the daylight variable, we held it constant for Alaska at the California mean value of 50,601 s/d. See Supp Table 1 (online only) for additional information on the relative contribution to each model for the most problematic MoD map variables.

Table 2. Summary statistics for warm precipitation and summer daylight. Values used to constrain the Alaska model input values are in bold with italic.

Model/state	Warm precipitation (Bio18, mm)			Summer daylight (s/d)		
	Minimum	Mean	Maximum	Minimum	Mean	Maximum
Western county models	2	75	226	—	—	—
CA 1 km models	1	18	73	49,346	50,601	51,983
Alaska, 1980–2014	24	237	2,732	55,630	67,053	80,465

To visualize the influence of variables with Alaska ranges beyond the input model ranges, we mapped the *sum* of the MESS values for all nine models (Fig. 1A). Because negative values indicate that a variable is beyond the training data range, large negative summed MESS values indicate the greatest extrapolation and therefore uncertainty. After constraining precipitation of the warmest quarter and summer daylight, the smaller negative summed MESS values indicate that covariate extrapolation has been reduced substantially with no remaining obvious latitudinal or montane signals (Fig. 1B). The constrained variables improved the minimum ensemble MESS value from $-15,295$ to $-2,478$.

Prediction of Current and Future Habitat

Both the unconstrained and constrained ensembles predicted suitable habitat in much of Southeast Alaska, valleys around Anchorage, lowlands on the Kenai Peninsula, and the islands north of Kodiak (Fig. 2). Neither ensemble predicted large areas of current suitable habitat in Northern Alaska. The most striking differences between the unconstrained and constrained ensembles were that the unconstrained ensemble predicted current suitable habitat across much of Interior Alaska and a small northerly portion of Western Alaska, whereas the constrained ensemble predicted the absence of current suitable habitat across most of Interior Alaska and suitable

habitat in a small southerly portion of Western Alaska. Thus, current predictions were relatively consistent between ensembles within Temperate and Northern Alaska but contradictory for Interior and Western Alaska.

The forecast period, 2070–2100, included areas that the ensembles predicted to remain stable relative to the current period and areas that the ensembles predicted to change either from unsuitable to suitable habitat or from suitable to unsuitable habitat (Fig. 3). [Supp Fig. 7 \(online only\)](#) (unconstrained) and [Supp Fig. 8 \(online only\)](#) (constrained) show model count maps covering the current and future time periods for both future climate scenarios. Both ensembles using both climate scenarios consistently predicted habitat to remain or occur by 2100 in the coasts and inland valleys of Southeast Alaska, along the coast of Southcentral Alaska, and in the Kodiak Island group, all of which fall within the Temperate subregion. Consistent predictions for future suitable habitat occurred in portions of the Nulato Hills (between Bethel and Nome), within the Western subregion. Similarly, both ensembles for both climate scenarios predicted habitat to occur by 2100 in at least small portions of the Cook Inlet Lowlands (northeast of Anchorage and in the southern Kenai Peninsula Lowlands) and the Copper River Basin, both of which are within the Interior subregion. Most of Northern Alaska was excluded by the land cover mask, which rendered the

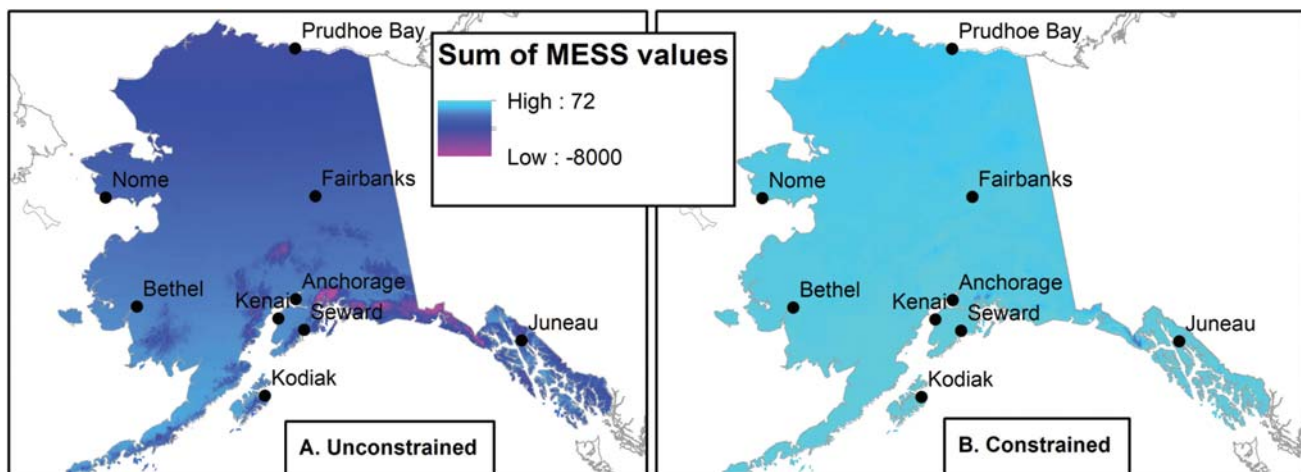


Fig. 1. Ensemble MESS maps for *I. pacificus* (CA 1 km and Western county models), 1980–2014, showing the sum of MESS values from each model. (A) The original, unconstrained ensembles and (B) the improved MESS values after constraining summer daylight and precipitation of the warmest quarter. Larger, negative values indicate more extrapolation of input variables outside the training range.

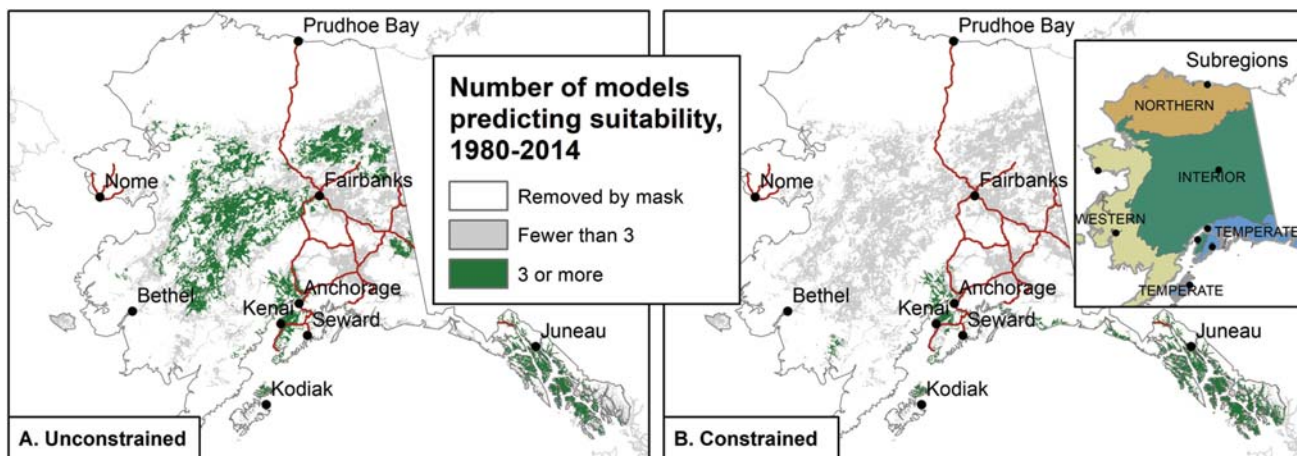


Fig. 2. Ensemble map showing (A) unconstrained and (B) constrained Alaska habitat suitability for *I. pacificus* for the period 1980–2014.

subregion insensitive to variations between ensemble and climate scenario. Thus, both ensembles under both climate scenarios predicted Northern Alaska to remain mostly devoid of suitable habitat by 2100. However, the unconstrained ensemble predicted a small portion of the south side of the Brooks Range to become suitable habitat by 2100 under both climate scenarios. The habitat predictions by 2100 within the geographic regions noted above were thus insensitive to constraints and climate scenarios.

Habitat predictions across much of Alaska were sensitive to either constraints or climate scenarios or both. To quantify broad trends in our results, we calculated the percentage area predicted for each change category (Fig. 3) relative to total unmasked area per subregion: Northern, Western, Interior, or Temperate (Table 3). We calculated percentage area rather than area to facilitate comparison among subregions, which helped identify patterns of sensitivity. Across both climate scenarios, the predicted increases in suitable habitat were largest for the unconstrained ensemble in the Interior, Western, and Temperate subregions, with more modest gains predicted by the constrained ensemble. Notably, the unconstrained ensemble under the RCP 4.5 climate scenario predicted a net decrease in habitat in Interior Alaska with the percent land area classified as unsuitable increasing more (10.1%) than the increase in suitable habitat (7.7%). Much of the predicted habitat loss under the RCP 4.5 scenario occurred in the area between Fairbanks and Bethel (Fig. 3A). In contrast, the unconstrained ensemble under the RCP 8.5 scenario predicted the same area between Fairbanks and Bethel to mostly remain or gain habitat (Fig. 3C), with more gain of habitat

than loss in Interior Alaska, which highlights Interior Alaska as the only subregion where we found substantial differences between the RCP 4.5 and RCP 8.5 future climate scenarios.

Unlike the unconstrained ensembles, the constrained ensembles predicted most of the unmasked area of Interior and Western Alaska to remain unsuitable with very little suitable habitat by 2100. Thus, differences between unconstrained and constrained ensemble results for future suitable habitat largely mirrored the results for current habitat (Fig. 2). However, one important additional difference between the unconstrained and constrained ensembles was that the constrained ensemble predicted portions of the Cook Inlet Lowlands (northern Kenai Peninsula Lowlands and in the vicinity of Anchorage) to become unsuitable by 2100. Thus, Interior Alaska was highly sensitive to both climate scenarios and ensembles, Western Alaska was somewhat sensitive to ensembles, and Northern and Temperate Alaska were mostly stable across climate scenarios and ensembles.

To further explore the uncertainty in our analysis, we combined the results from the original unconstrained models, the constrained models, and both sets of future climate scenarios (Fig. 4). As visible in Fig. 3, many of the areas of disagreement (colored gray) were driven by differences between the unconstrained and constrained models. Despite large areas of uncertainty, there were many regions in Alaska where the combined set of models provided insight into potential habitat. For example, much of Southeast Alaska is characterized by suitable habitat for *I. pacificus* in both sets of models under both climate scenarios. Valleys northwest of Anchorage, the northern tip of

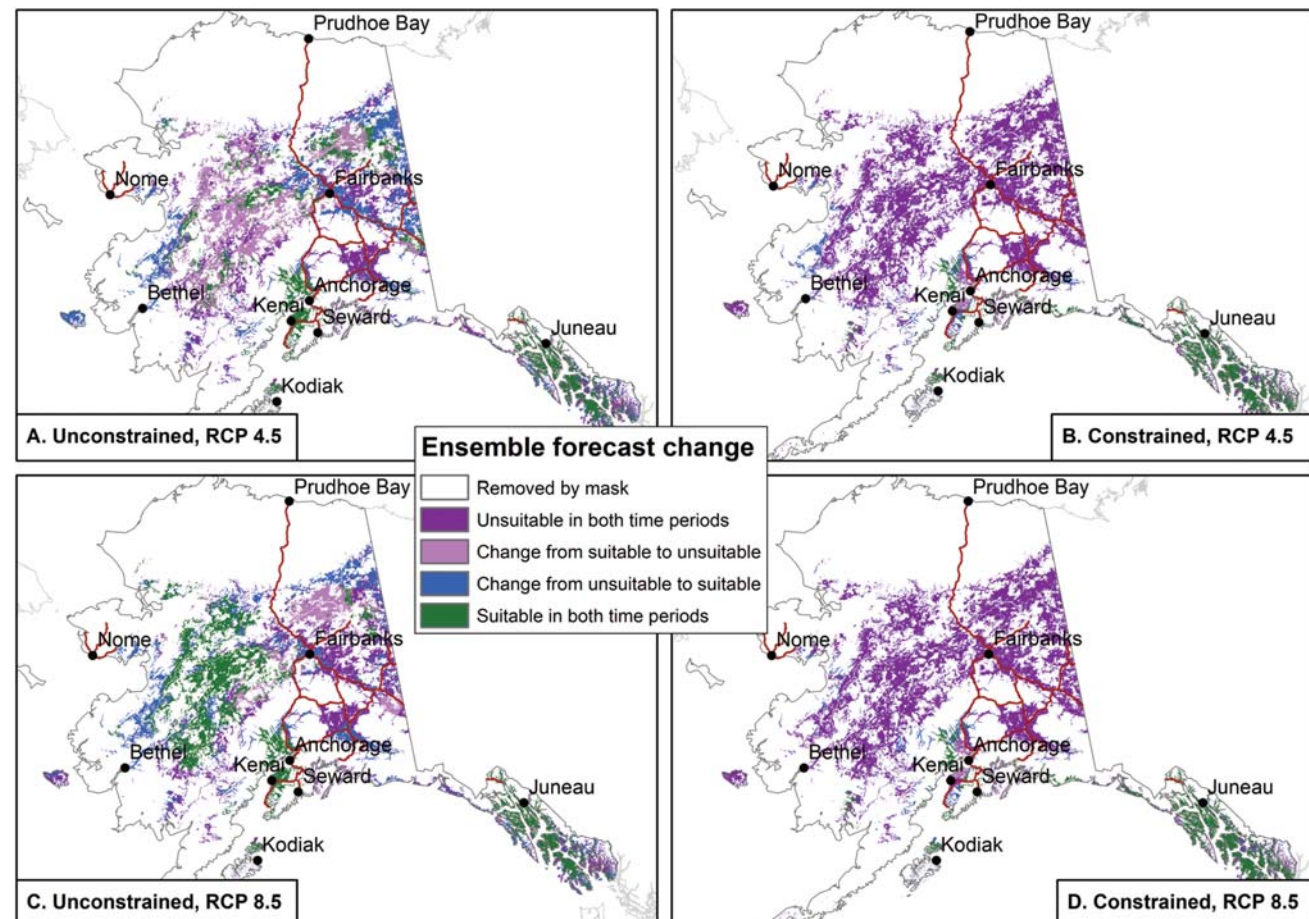
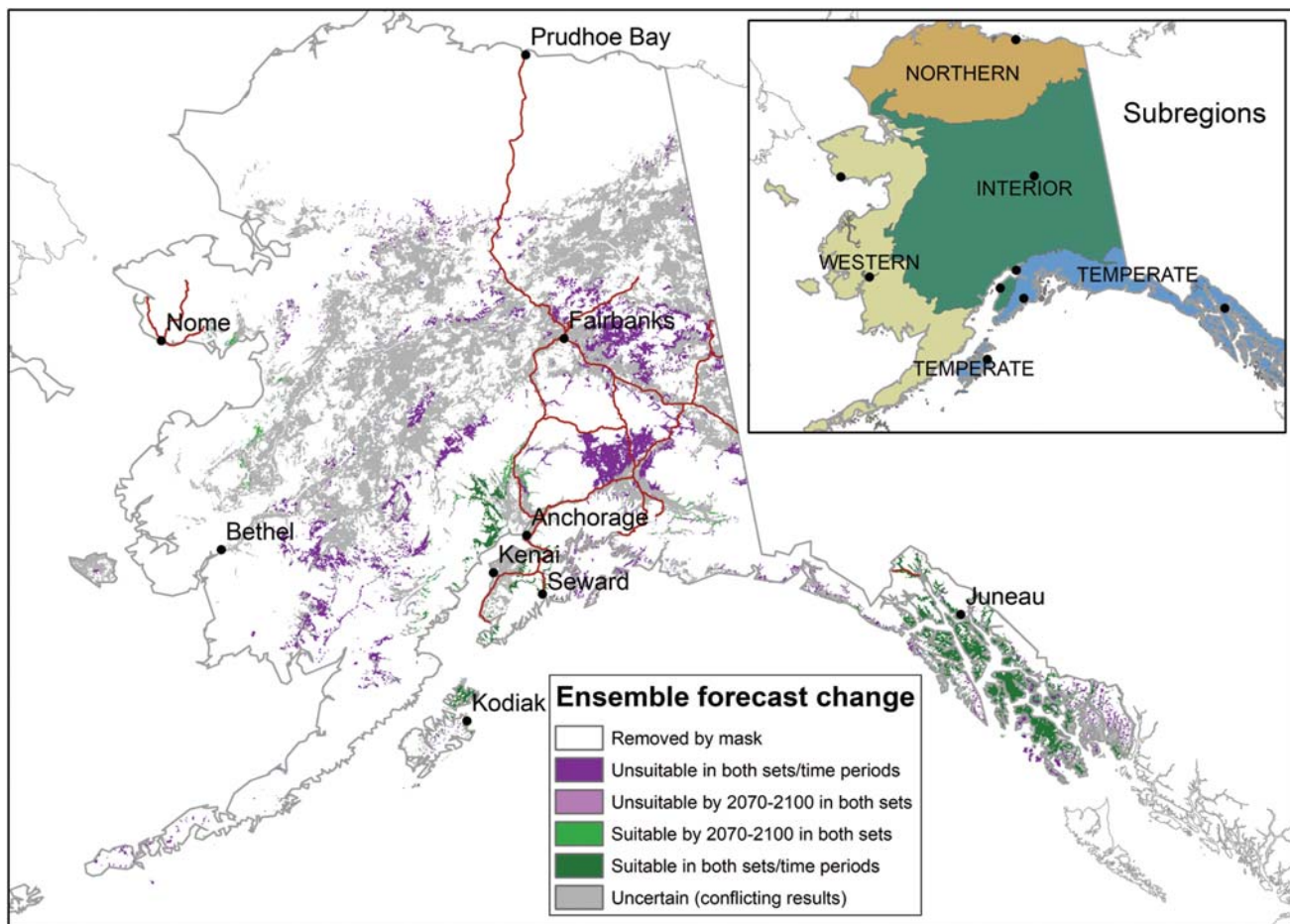


Fig. 3. Ensemble forecast change in habitat suitability from 1980–2014 to 2070–2100 for the unconstrained (A and C) and constrained (B and D) models using two future climate scenarios, RCP 4.5 (A and B) and RCP 8.5 (C and D).

Table 3. Forecast change in habitat suitability as a percentage of total unmasked area from 1980–2014 to 2070–2100 by subregion and future climate scenario for the unconstrained (Unc.) and constrained (Constr.) ensembles

Habitat area	Northern		Western		Interior		Temperate	
	Unc.	Constr.	Unc.	Constr.	Unc.	Constr.	Unc.	Constr.
RCP 4.5								
Unsuitable in both	0.4%	0.7%	2.9%	6.7%	9.0%	31.0%	7.7%	6.1%
Suitable to unsuitable	0.1%	0.0%	1.1%	0.1%	10.1%	0.3%	0.1%	0.1%
Unsuitable to suitable	0.2%	0.0%	4.5%	1.9%	7.7%	1.1%	5.8%	2.3%
Suitable in both	0.0%	0.0%	0.5%	0.3%	6.3%	0.6%	11.3%	16.3%
RCP 8.5								
Unsuitable in both	0.3%	0.7%	2.4%	7.6%	9.5%	31.0%	7.3%	5.5%
Suitable to unsuitable	0.0%	0.0%	0.1%	0.0%	4.6%	0.4%	0.3%	0.5%
Unsuitable to suitable	0.3%	0.0%	5.0%	1.0%	7.2%	1.2%	6.2%	2.9%
Suitable in both	0.1%	0.0%	1.5%	0.4%	11.7%	0.6%	11.1%	15.9%
Total unmasked area	2,492 km ²		31,696 km ²		259,404 km ²		54,872 km ²	
Total area	335,597 km ²		352,293 km ²		784,119 km ²		220,907 km ²	

**Fig. 4.** Combined results of the unconstrained and constrained ensembles for both two future climate scenarios, RCP 4.5 and RCP 8.5, showing forecast change in habitat suitability from 1980–2014 to 2070–2100.

Kodiak Island, and small pockets of land in the Nulato Hills between Bethel and Nome also appear as suitable habitat, if not now, then by the end of the century. The models also agree that large portions of the Interior subregion east of Fairbanks and the region northeast of Anchorage are, and will remain, unsuitable habitat.

The *combined* results of the unconstrained and constrained ensembles for both future climate scenarios by subregion provide a summary and the culmination of our modeling efforts and uncertainty assessment (Table 4). After applying the land cover mask,

between 1 and 33% of each subregion was available for model prediction. By looking at the subregions where the unconstrained and constrained ensembles disagree, we can learn where the model results are most uncertain. Over a quarter of the land area in Interior Alaska had conflicting results. This makes it the region with the most uncertainty in predictions of current and future tick habitat. Of the remaining unmasked area, close to 6% was consistently predicted to be unsuitable. Only 1% of the Northern region was available for model predictions after applying the land cover mask, and none was

Table 4. Forecast change in area (km²) and percentage of total area of habitat suitability from 1980–2014 to 2070–2100 by subregion for the combined unconstrained and constrained ensembles for both future climate scenarios (RCP 4.5 and 8.5)

Habitat area	Northern		Western		Interior		Temperate		Total	
Unsuitable in both sets/time periods	928	0.3%	5,604	1.6%	43,828	5.6%	9,392	4.3%	59,752	3.5%
Unsuitable by 2070–2100 in both sets	0	0.0%	0	0.0%	4	0.0%	16	0.0%	20	0.0%
Suitable by 2070–2100 in both sets	0	0.0%	1,172	0.3%	1,800	0.2%	3,040	1.4%	6,012	0.4%
Suitable in both sets/time periods	0	0.0%	100	0.0%	3,608	0.5%	23,664	10.7%	27,372	1.6%
Uncertain (conflicting results)	1,564	0.5%	24,820	7.0%	210,164	26.8%	18,760	8.5%	255,308	15.1%
Total unmasked area	2,492	0.7%	31,696	9.0%	259,404	33.1%	54,872	24.8%	348,464	20.6%
Total area	335,597		352,293		784,119		220,907		1,692,916	

consistently predicted to be or become suitable habitat. Only 9% of the Western region remained unmasked, and of this there was five times more land predicted to be unsuitable than suitable. Although 8.5% of Temperate Alaska had conflicting results, nearly 11% of the unmasked land area was consistently predicted to be suitable. Across all regions of Alaska and considering both climate scenarios, increases in suitable habitat are the largest forecast *change* category that the unconstrained and constrained ensembles agreed on with about 6,000 km² of land area in Alaska predicted to change from unsuitable to suitable habitat by 2100.

Discussion

To identify areas where humans and animals are at risk of coming into contact with ticks, we need accurate assessments of their geographic distribution (Eisen et al. 2015). Longitudinal assessments of tick occurrences demonstrate that the range of many medically important species has expanded over the past several decades in the United States (Springer et al. 2015, Eisen et al. 2016), Canada (Ogden et al. 2006, Nelder et al. 2014, Clow et al. 2017), and central Europe (Daniel et al. 2003); however, additional modeling work is needed to understand whether introduced species can survive and reproduce in these new environments.

The ensemble model results presented here are a first attempt to understand the present and future habitat in Alaska for one species of tick, *I. pacificus*. All of Alaska is vulnerable to ephemeral, introduced ticks, but introduced *I. pacificus* are only likely to survive and reproduce to establish persistent populations in areas of suitable habitat. Although using models developed in a different geographic region introduces some uncertainty into our forecasts, we have presented an approach using unconstrained and constrained models and multiple climate scenarios to identify the spectrum of uncertainty across our study region and identify consistent areas of predicted habitat. By comparing the unconstrained and constrained ensembles and examining the MESS maps, we find that much of the uncertainty in the modeled results is due to extrapolation outside of the training range of some of the covariates in the models and variation in climate projections. Within the areas of agreement, the combined ensembles show that 1.6% of Alaska currently presents suitable habitat with high certainty. Our ensembles forecast that area to increase by 25% (to 2.0% of Alaska) by the end of the century. Most of the agreement in predicted current and future habitat occurs in Southeast Alaska.

The Temperate subregion, and especially Southeast Alaska, has biogeographic and climatic affinities to temperate rainforest systems further south along the Pacific coast (DellaSala 2010), including substantial portions of the native range of *I. pacificus* (Eisen et al. 2016). The northernmost portion of the native range of *I. pacificus* in southern British Columbia is similar to the southernmost area of agreement for predicted habitat in Alaska on Prince of Wales Island.

The temperate rainforest of Southeast Alaska has mean winter temperatures near freezing, making the region sensitive to climate change (Shanley et al. 2015). The predicted present suitable habitat in Southeast Alaska likely resulted from change in climatic conditions that already occurred to make Southeast Alaska similar to the recent historic climate conditions at the northern end of the native range of *I. pacificus*. Southeast Alaska contains numerous small towns connected by sea and air that could mediate introductions through travel. Although British Columbia was not included in this study, it is probable that suitable habitat also occurs at present along the northern coast of British Columbia. Introductions and northward range expansion could eventually connect the native range of *I. pacificus* to suitable habitat in Southeast Alaska. Our models do not account for vegetation change during the time interval between our current and future predictions. In Southeast Alaska, coniferous trees are likely to expand beyond their current elevation limits (Shanley et al. 2015); thus, the agreement in future predicted habitat is likely conservative for Southeast Alaska because of the unchanging land cover mask in this study.

Beyond Southeast Alaska, agreement in predicted habitat between the unconstrained and constrained ensembles was sparse. Our ensembles predicted the forested lower slopes of mountain ranges that fringe the Cook Inlet Lowlands to either remain or become suitable habitat by 2100. Notably, however, much of the forested lowlands of the Cook Inlet Lowlands, wherein much of the human population of Alaska resides, remained or became suitable habitat only in the unconstrained ensemble. The only widely populated portion of Southcentral Alaska where our ensembles consistently predicted suitable habitat to remain or occur by 2100 was the southern Kenai Peninsula Lowlands, which are part of the Cook Inlet Lowlands in the Interior subregion. The southern Kenai Peninsula Lowlands contains many small towns interconnected by a well-developed and well-traveled road system. The area is a destination for numerous travelers from the contiguous United States and elsewhere each year because of the large and reliable salmon runs (Walker et al. 2021). Although the southern Kenai Peninsula Lowlands is a small region relative to the size of Alaska, our results suggest it is likely to provide opportunities for the establishment of resident *I. pacificus* populations in the future where interactions between ticks and humans will be likely.

The uncertainty of results across the Cook Inlet Lowlands may be caused by the interaction between temperature and precipitation: with precipitation constrained, the Cook Inlet Lowlands may be interpreted in the ensembles as subject to moisture stress sufficient to limit *I. pacificus*. Despite the high uncertainty shown by lack of agreement between the ensembles, we encourage natural resource managers to consider the habitat predictions of the unconstrained ensemble in Cook Inlet Lowlands for three reasons: 1) because most of the human population of Alaska lives in Cook Inlet Lowlands (i.e., Municipality of Anchorage, Matanuska-Susitna Borough, and Kenai Peninsula Borough), the establishment of persistent populations of

I. pacificus in this region would have the highest potential within Alaska for human health impacts; 2) the presence of Alaska's major interstate/international airport in Anchorage gives Anchorage and the surrounding areas high potential for travel-related introductions of *I. pacificus*; and 3) Anchorage serves air connections to many other parts of Alaska so that a persistent tick population in or near Anchorage could enable introductions to other parts of the state. Such diffusion of invasive species from Anchorage to surrounding habitats is well documented for other species, such as *Elodea* Michx. (Alismatales: Hydrocharitaceae) via floatplanes (Larsen et al. 2020).

The Nulato Hills (between Bethel and Nome) in Western Alaska contain areas predicted by both ensembles in both climate scenarios to become suitable habitat by 2070–2100. However, there are uncertainties in the predictions for the Nulato Hills that are not captured in the model covariates. Lower slopes and lowlands of the Nulato Hills are covered in boreal forests dominated by both coniferous and deciduous trees that are substantially different from forests within the native range of *I. pacificus*, including characteristics such as a high fire return interval. The region is relatively remote and infrequently traveled with most villages situated near the Norton Sound outside of the forested portion of the ecoregion. Introductions of *I. pacificus* from human travel are not likely now or in the future; however, persistent populations may establish through avian importation events in the future.

High uncertainty and lack of roads or major airports suggests a lower likelihood of the establishment of persistent populations in areas predicted as current habitat only by the unconstrained ensemble in Interior Alaska west and north of Fairbanks. As noted for the Nulato Hills above, persistent populations may still establish outside of areas frequently traveled by humans through avian importation events. Our results suggest that early detection and rapid response monitoring efforts for *I. pacificus* should be prioritized across the human population centers of Southeast Alaska and Cook Inlet Lowlands. As suggested by Hahn et al. (2020), proactive monitoring as a collaboration among the public, medical professionals, veterinary professionals, natural resource managers, and conservation organizations are likely necessary to prevent establishment of persistent populations of *I. pacificus* and to inform the public of high-risk locations to prevent tick-borne disease transmission.

There are a number of limitations to this exploratory work. Because the two ensemble models used in this study were calibrated based on climatic data from the contiguous United States, many of the climate variables used for the Alaska region were outside of the training range of the models. There is no gold standard for evaluating uncertainty due to extrapolation, but the MESS maps allowed us to identify which variables were furthest out of range. Additionally, due to the lack of tick presence records in Alaska, we cannot validate the model at present. Our modeling work did not address the distribution of tick hosts. All life stages of *I. pacificus* readily feed on a wide variety of hosts including dozens of species of mammals and several species of birds and reptiles (Castro and Wright 2007). Alaska is home to many small mammal species that are widely distributed, such as *Myodes rutilus* (Pallas) (Rodentia: Cricetidae, Northern red-backed vole) and *Microtus pennsylvanicus* (Ord) (Rodentia: Cricetidae, Meadow vole), both of which are active throughout the year. Although the distribution of some of these vertebrates may change in the coming decades in response to climate change, the direct impacts of temperature, precipitation, and land cover change are likely stronger limiting or enabling factors for the establishment and spread of *I. pacificus* in Alaska. Climate change is also likely to affect the host-seeking phenology of ticks, with some research suggesting that wet and cool areas that become hotter and drier will exhibit improved suitability, though

additional precipitation for wet areas may inhibit host-seeking activities (MacDonald et al. 2020).

The maps produced from this modeling effort are the first estimates of suitable tick habitat for Alaska. They are part of a larger effort to document the past and current spatial distribution of tick species in Alaska, both through passive monitoring (e.g., public outreach and veterinarian offices) and active monitoring (e.g., dragging and small mammal trapping; Hahn et al. 2020). Despite the limitation of extending habitat suitability models to new geographic areas, the results from this exploratory work can be a useful public health surveillance tool. The land area of Alaska is equivalent to about one-fifth of the land area of the contiguous United States. The area that we identified as most likely to be suitable habitat for *I. pacificus* in Alaska now and into the future totals around 33,000 km², about the size of Maryland, presenting a substantially reduced area for future studies. As such, the maps presented here can be used to help target tick surveillance efforts across the large Alaskan geographic region by focusing on the edges of the known tick distribution and areas where these models consistently predict that climate and land cover characteristics could support introduced tick populations. In an era of rapid environmental change, proactive monitoring and predictive modeling can help agencies and the public prepare for inevitable changes to vector distribution and potential disease risk.

Supplementary Data

Supplementary data are available at *Journal of Medical Entomology* online.

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