

# Cross-Scale Assessment of Potential Habitat Shifts in a Rapidly Changing Climate

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We assessed the ability of climatic, environmental, and anthropogenic variables to predict areas of high-risk for plant invasion and consider the relative importance and contribution of these predictor variables by considering two spatial scales in a region of rapidly changing climate. We created predictive distribution models, using Maxent, for three highly invasive plant species (Canada thistle, white sweetclover, and reed canarygrass) in Alaska at both a regional scale and a local scale. Regional scale models encompassed southern coastal Alaska and were developed from topographic and climatic data at a 2 km (1.2 mi) spatial resolution. Models were applied to future climate (2030). Local scale models were spatially nested within the regional area; these models incorporated physiographic and anthropogenic variables at a 30 m (98.4 ft) resolution. Regional and local models performed well (AUC values > 0.7), with the exception of one species at each spatial scale. Regional models predict an increase in area of suitable habitat for all species by 2030 with a general shift to higher elevation areas; however, the distribution of each species was driven by different climate and topographical variables. In contrast local models indicate that distance to right-of-ways and elevation are associated with habitat suitability for all three species at this spatial level. Combining results from regional models, capturing long-term distribution, and local models, capturing near-term establishment and distribution, offers a new and effective tool for highlighting at-risk areas and provides insight on how variables acting at different scales contribute to suitability predictions. The combinations also provides easy comparison, highlighting agreement between the two scales, where long-term distribution factors predict suitability while near-term do not and vice versa.

**Nomenclature:** Canada thistle, *Cirsium arvense* (L.) Scop.; reed canarygrass, *Phalaris arundinacea* L.; white sweetclover, *Melilotus albus* Medik.

**Key words:** Alaska, bioclimatic modeling, *Centaurea stoebe*, *Cirsium arvense*, climate change, *Fallopia japonica* (*Polygonum cuspidatum*) complex, invasive species, *Melilotus albus*, *Phalaris arundinacea*.

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Species' distributions are well accepted to be controlled by diverse factors at different spatial scales (Grinnell, 1917; Luoto et al., 2007; Peterson et al., 2011). Climate variables are often viewed as important at broad spatial scales for most plants, while species interactions, disturbance, fine-scale edaphic variables and land-use are believed to drive most plant distributions at the local level (Franklin, 1995; Pearson et al., 2004). The establishment of species outside their historic ranges and the subsequent ecological and economic impacts due to their establishment have fueled interest in forecasting current and future distributions of nonnative species in particular. Species distribution modeling efforts, however, rarely address the potential differences in variable contribution and model performance at different scales and resolution (see Guisan and Thuiller, 2005; Wiens, 2002) and processes involved with invasion. The need to resolve differential variable contribution and model performance at multiple scales is particularly critical for understanding and predicting expansion of invasive

## Management Implications

Effective and proactive management of invasive species requires information on both current and potential future distributions. Alaska, similar to other high latitude areas, is relatively invasion free (Lassuy and Lewis, 2013). The rapidly changing climate in this region, however, is expected to increase the area suitable for establishment for a larger number of invasive species. Here, we present results for habitat suitability models of highly invasive plants in the southern coastal region of Alaska, creating climate driven models at a regional scale and physiographic and anthropogenic models for two local regions. Using these types of models for targeted sampling of invasive plants detected more locations with less effort than nontargeted sampling (Crall et al., 2013). Our local scale models can be thought of as predicting near term establishment and distribution (potential early detection locations for management), while longer term trends in distribution may be driven by climate, especially related to the future climate scenarios at the coastal scale (potential distributions). Locations where models at both scales indicate high habitat suitability values are more appropriate targets for current control and monitoring efforts than locations identified by a model that considers factors operating at a single scale. Additionally, evaluating the areas of future suitable habitat among early invaders can help prioritize which species should be targeted for control first. If two species have similar initial distributions and similar ecological impacts, management efforts should be directed to the species with the largest possible future distribution. These models, when incorporated into an iterative sampling approach, can guide future sampling efforts. The new sampling is then used to generate future model iterations, which then provide evolving distribution models that help prioritize locations for control and restoration efforts

species in the context of rapidly changing climates and alterations of land-use patterns.

General circulation models predict that climate warming effects will be highest in northern high latitudes (Moritz et al., 2002; Serreze et al., 2000; Serreze, 2010). Significant annual and seasonal mean temperature increases have been recorded for Alaska in the past 50 yr, with highest increases in the winter (Stafford et al., 2000). Despite a cooling trend in much of Alaska in the first decade of this century attributed to the Pacific Decadal Oscillation, the northernmost regions experienced increased temperatures, and overall warming trends continued in predictions (Wendler et al., 2012). In addition, the interior Alaska growing season has nearly doubled in length in the last 100 yr, from 90 to 170 d (Wendler and Shulski, 2009) and is projected to continue to increase (SNAP 2012). Additionally, changes in climate are increasing the frequency and scale of habitat disturbances, such as wildfires and herbivorous insect outbreaks, in northern North America (ACIA, 2005; Berg and Anderson, 2006; Chapin III et al., 2008; Soja et al., 2007). These direct and indirect components of changes in climate are expected to increase the probability of establishment and spread of nonnative plant species in Alaska, which typically originate from more temperate

climates (Carlson and Cortes-Burns, 2012; Carlson and Shepherd, 2007; Sanderson et al., 2012). The spread of invasive plants in the region is of particular concern as it is currently one of few remaining intact ecosystems and this type of modeling may result in the opportunity to plan for change by incorporating these methods into an adaptive management framework (see Chapin et al., 2006; Sanderson et al., 2012).

Alaska in general is in the early stages of nonnative plant establishment (Bella, 2011; Carlson and Shepherd, 2007; Conn et al., 2003), but the frequency of introductions and establishment in natural areas is accelerating and is increasingly regarded as a potential threat to native species and ecosystems in the state (Carlson and Shephard 2007). Areas of greatest abundance and diversity of nonnative plants are concentrated in southern Alaska (AKEPIC 2012) and this region is expected to continue to have the greatest increase in future establishment of nonnative plants (Bella, 2009). Additionally, areas with large human populations and high visitation rates by tourists, such as the Kenai Peninsula, or areas with high road density and habitat disturbance (e.g., logging), such as Prince of Wales Island, are potential hot-spots for invasion and make ideal regional landscapes for exploring potential distributions of species considered ecologically threatening or damaging.

While a broad-scale prediction of potential distribution is valuable for establishing a baseline understanding of invasion patterns, smaller extent or local-scale suitability maps provide potential habitat information at a scale more applicable to day-to-day management decisions. Combining spatially explicit features as predictors at a fine scale, along with environmental predictors, may provide a better projection of the potential geographic distribution of each species than traditional niche-based modeling (Araujo and Guisan, 2006). Identifying improved methods of predictor inclusion and significance is a pressing need in bioclimatic modeling (Araujo and Guisan, 2006). Assessing predictor variable importance, distributional data quality, and modeling technique accuracy is essential to successfully apply predictive modeling (Ashcroft et al., 2011; Beaumont et al., 2008; Jimenez-Valverde et al., 2008).

Although distribution models that forecast range shifts as a consequence of climate change are inherently uncertain, careful consideration of variable inclusion in bioclimatic models specifically intended for climate change improves predictive ability (Jeschke and Strayer, 2008). A geographic model of invasive species vulnerabilities incorporating climate at the regional scale, environmental, physiographic, and anthropogenic variables at local scales, and an integrated prediction of the two provides a hybrid predictive base from which to formulate preventative policies in light of a changing climate. It also allows inclusion of potentially important local predictors that are not available at or are not as detailed for the broader spatial extent.

Here we describe habitat suitability models of five invasive plants at regional and local scales in Alaska. Models at the two different scales are tied to different stages in the invasion process. Regional scale models include factors that may control species' distributions in the long term, representing the potential distribution of the species (late stage of invasion). The local scale models include factors that may contribute to near-term establishment as well as distribution, incorporating anthropogenic factors that can be pathways of introduction and act as a proxy for propagule pressure and disturbance. Propagule pressure and disturbance are important factors at earlier stages of invasion. Specifically, we predict that (1) at the coarse scale all the invasive species' potential habitat will show a strong positive relationship between increasing suitability and increasing temperature as we hypothesize that cool temperatures are limiting factors for these species' distributions so increasing temperature with climate change will result in more suitable habitat; (2) a greater proportion of area, particularly to the north and higher elevations, will be identified as suitable in the future, again as a result of changing temperature with climate change; and (3) suitable habitat defined by local scale models will represent a smaller, more refined proportion of the landscape than suitable habitat defined by the coarse scale model as we expect climate to define distribution at a broad scale and land use/ land cover factors to be able to offer a more detailed distribution at a fine scale.

## Materials and Methods

**Study Regions and Species Sampling.** We focused on the 267,795 km<sup>2</sup> coastal ecoregions (Figure 1; Nowacki and Brock, 1995) for our regional scale models based on climate and topography at a 2 km resolution. Because this region of Alaska had the greatest establishment of nonnative plants early in the 20<sup>th</sup> century (Carlson and Shepherd, 2007) and therefore these species have had time to spread to available suitable habitat (e.g., are not new introductions), effects of violating the equilibrium assumption of species distributions made by statistical species distribution modeling techniques (Gallien et al. 2012) are less than if these models were based on novel introductions.

We chose the Kenai Peninsula and Prince of Wales Island areas within the coastal ecoregions as focal areas. Here, we created local models at a 30-m resolution, incorporating anthropogenic factors, land cover, hydrology, and topography specific to each location. Criteria for focal area selection considered areas with contrasting but representative population density, infrastructure, and climate in two geographically distinct locations with sufficient GIS layer availability. The Kenai Peninsula in south-central Alaska is approximately 24,338 km<sup>2</sup>, with a population of 55,400 in 2010. The area is one of the most

densely populated in the state, with a well-developed infrastructure and strong tourism industry. Additionally, partially climate-driven spruce bark beetle outbreaks on the Kenai over the past 20 yr (ACIA, 2005; Berg and Anderson, 2006) have increased opportunities for nonnative species establishment by decreasing forest cover by over 60%. Prince of Wales Island in southeastern Alaska, at approximately 6674 km<sup>2</sup>, the majority of which is National Forest land, contains the highest road density in the state due to historic and active logging within it. Approximately 13.4% of the island's forests have been harvested (U.S. Forest Service Tongass National Forest, 2007); the human population is approximately 6,000.

We obtained location data from the Alaska Exotic Plant Information Clearinghouse (AKEPIC, 2010), a database that aggregates spatial nonnative plant species data in Alaska. We extracted presence locations for five problematic invasive species (Canada thistle [*Cirsium arvense* (L.) Scop.], white sweetclover [*Melilotus albus* Medik.], reed canarygrass [*Phalaris arundinacea* L.], spotted knapweed [*Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek], and a knotweed complex [Japanese knotweed, *Polygonum cuspidatum* Sieb. & Zucc; Sakhalin knotweed, *Polygonum sachalinense* F. Schmidt ex Maxim.; & Bohemian knotweed, *Polygonum ×bohemicum* (Chrtek & Chrtková) Zika & Jacobson] in southern Alaska (Carlson et al., 2008). Absence data were extracted from the AKEPIC database to use as background locations in Maxent, using a Negative Database Tool (developed by the USDA Forest Service, Alaska Region, and HDR Alaska, Inc.) in which sites were thoroughly surveyed but the focal species were not observed. We were originally interested in modeling these five species, nested in two local areas within two regions: coastal and interior. However, only one of the five species had data for the interior region and only three species for both local areas within the coastal region. Thus, we limit our discussion to these three species in two areas within the coastal region to allow for comparisons and to minimize confusion. The other models (coastal models for spotted knapweed and the knotweed complex and an interior model for white sweetclover) are included and described in the Supplemental Material.

**Environmental Layers.** For climate data we used products created specifically for Alaska by the Scenarios Network for Alaska Planning (SNAP, 2010) as 2 km grid cells (Supplemental Material 1). SNAP contains historical climate downscaled from Climate Research Unit data, and we calculated average precipitation and temperature for the most recent 20-year period available, 1987 to 2006, to match the climate conditions during the sampling. The future climate projections are a five-model composite, derived from the top five International Panel on Climate Change's GCMs tested for Alaska climate space (Walsh et al., 2008) for 2030 with two different emission scenarios

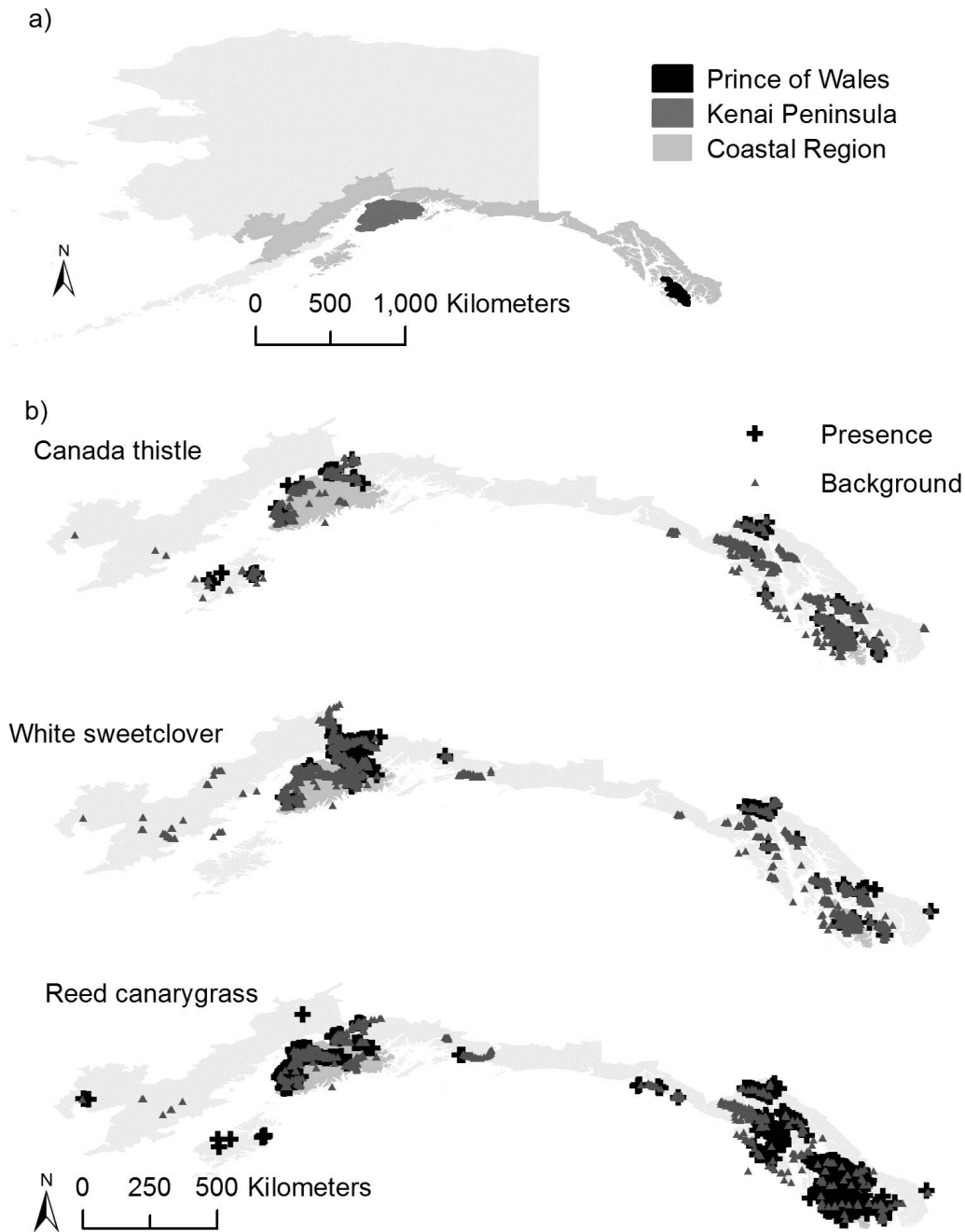


Figure 1. Within Alaska (a) the regional and local scale study areas and (b) the point locations for the three focal species.

representing the two extremes in the range of possibilities (B1 representing an integrated and environmentally and socially conscious world and A2 representing a divided, less ecologically-minded world; Table 2). For all climate data, we derived bioclimatic variables following Hijmans (2006) using average monthly temperature rather than minimum and maximum temperature because minimum and maximum were not available.

For the fine scale models we were interested in anthropogenic effects and fine scale environmental features.

Predictors included distance from anthropogenic features (roads and trails for Kenai and Prince of Wales; urban areas and utilities for Kenai only; and recreation areas for Prince of Wales only), distance from water and wetlands, land cover type, and elevation (see Supplemental Material 1). Anthropogenic features chosen were based on characteristics of and data availability for the specific locality.

**Modeling.** We used the maximum entropy modeling program Maxent (Phillips et al., 2006; Phillips and Dudik,

Table 1. Input and model performance for three invasive species at three locations in coastal, Alaska, the average AUC values for the test data (and the training data (if the jackknife approach was used) and the independent (Indep.) test data AUC), and the threshold value using the 10 percentile training presence rule (and the minimum training presence (MTP) rule when indicated).

Model	Region	Sample size	Background points	Regularization value	Test AUC (Train)	Threshold values
Canada thistle	Coastal	88	1060	2	0.72 (0.79)	0.276 (0.126 MTP)
Reed canarygrass	Coastal	1024	1617	2	0.57 (0.60)	0.39929 (0.212 MTP)
White sweetclover	Coastal	236	1308	5	0.755 (0.778)	0.201 (0.077 MTP)
Canada thistle	Kenai	10	434	1	0.71 (0.88) (Jackknife)	0.332 (MTP)
Reed canarygrass	Kenai	657	1173	1	0.74 (0.76)	0.282
White sweetclover	Kenai	54	991	2	0.85 (0.94)	0.30
Canada thistle (with roads)	Prince of Wales	22	2950	1	0.86 (0.94) (Jackknife)	0.081 (MTP)
Canada thistle (without roads)	Prince of Wales	22	2950	1	0.77 (0.88) (Jackknife)	0.067 (MTP)
Reed canarygrass	Prince of Wales	549 (reduced)	2577	1	0.55 (0.64) Indep.	0.53
White sweetclover	Prince of Wales	7	1015	1	0.63 (0.80)	0.294 (MTP)

2008) to develop our species distribution models within the Software for Assisted Habitat Modeling (SAHM) framework, which is a software application to facilitate modeling (Morissette et al., 2013). This technique is suitable when true absence data are not available, works well with both small and large numbers of locations (Wisiz et al., 2008), and has performed well when compared with other techniques (Elith et al., 2006). Maxent requires both presence locations for a species and background locations to characterize the available environment. For background locations we followed the targeted background approach (Phillips et al., 2009), using records from AKEPIC that reported other exotic species, but not the species of interest, by collectors who were familiar with the target species and had recorded those species at other locations. We used the auto setting for features, allowing Maxent to choose the feature types to use. For four of the species, we withheld 30% of the data for testing and ran 25 replicates using the subsample method (Table 1; Supplemental Material 3). With these options, a different random 30% was withheld 25 times. For species with less than 25 presence records (see

Table 1, Supplemental Material 3), we used the jackknife approach following Pearson et al. (2007).

We ran each model 25 times, varying the regularization value from 1 to 10. To control for over-fitting as our location data suffered from clustering, we then used the ENMTools software program to select the optimum regularization value for each iteration (Warren and Seifert, 2011), and took the average optimum value to use in our model runs (see Table 1).

We used the SAHM CovariateCorrelationAndSelection module to examine correlations among the climate predictors. This tool uses the Pearson, Spearman, and Kendall coefficients to examine correlations, and we removed any with a value greater than  $\pm 0.7$ . We selected variables based on knowledge of the species' ecology.

**Analyses.** To assess model performance we examined receiver operating characteristic area under the curve (AUC) values as calculated by Maxent (Fielding and Bell, 1997). AUC values range between 0.5 and 1, with values between 0.5 to 0.7 being relatively poor, those between 0.7

Table 2. The percent of the coastal Alaska region classified as suitable using the 10 percentile training presence threshold rule (10P) and the minimum training presence threshold rule (MTP) for each species under current climate conditions and predicted future conditions for 2030 using the B1 emissions scenario and the A2 emissions scenario, with the percentage ignoring any locations with novel environments. The percent of the coastal region classified as having novel environmental conditions for each scenario is also included.

Scenario	Canada thistle			White sweetclover			Reed canarygrass		
	10 P	MTP	% novel	10 P	MTP	% novel	10 P	MTP	% novel
Current	44.6 (51)	64.7 (73.6)	20.3	52 (53.7)	92.1 (92.9)	8.7	25 (30.3)	72.3 (83.9)	17.8
2030 B1	51.4 (57.6)	65.5 (72.7)	22.5	31 (31.7)	87 (89.1)	12.3	25.5 (31.9)	72 (83.7)	23.8
2030 A2	60.3 (65)	77.2 (86.1)	38	50.4 (50.3)	93.4 (93.8)	11.8	28.3 (32.1)	74.1 (84)	19.2

and 0.9 being useful, and those above 0.9 indicating relative high accuracy when assessed with a completely independent data set (Swets, 1988). The AUC values from Maxent are different from the traditional AUC in that we have background locations to compare presence locations to rather than actual absence.

We used the multivariate environmental similarity surface (MESS) analysis within Maxent to identify locations outside the range of the environments used to generate the model (i.e., locations of extrapolation; Elith et al., 2010). These values are determined by comparing the minimum and maximum value from the presence and background points for each environmental predictor to each location the model is being projected to. If the value for any predictor used in the model falls outside the range, that location has a novel environment and thus we have less certainty about predictions there.

We compared changes in suitability with predicted climate change both visually and by calculating the percent of the coastal region classified as suitable under two different threshold rules. The rules included the 10 percentile training presence and the minimum training presence thresholds. The 10 percentile training presence threshold assigns probabilities to each presence location and then selects the value that will misclassify the 10% of the presence points with the lowest predicted values. In contrast, the minimum training presence threshold value classifies all presence locations used to develop the model correctly. By allowing some locations to be misclassified one has more conservative predictions of suitable habitat, acknowledging that some presence locations may be in marginal habitat on the edge of the range, as we included no information about abundance or population trends at presence locations.

To examine differences in predictions spatially at the regional and local scale we also discretized the predictions to define locations as either suitable or unsuitable. For species' models with more than 25 presence locations we used the 10 percentile training presence threshold. For species' models with less than 25 presence locations, however, we used the minimum training presence threshold (Table 1) because we did not want to misclassify any locations when we had a very small number of them (e.g., for white sweetclover on Prince of Wales Island one of only seven locations would be misclassified using the 10 percentile method). The two discretized models for each locality (regional and local) were then added together to highlight locations predicted as suitable by both, only suitable regionally, only suitable locally, or unsuitable by both.

## Results and Discussion

**Regional Models.** At the regional scale, the model for Canada thistle performed marginally well (AUC = 0.72), as did the white sweetclover model (AUC = 0.76). The

reed canarygrass model performed poorly for the region (AUC = 0.57). Poor performance of all reed canarygrass models indicates that we may be missing an important variable controlling its distribution, that we were missing important environmental gradients in the sampling, or that the species is a generalist which lacks specific habitat characteristics. These regional models predict an increase in area of suitable habitat for most species through 2030, particularly under the more extreme A2 emissions scenario (Table 2; Figure 2). The A2 scenario always had the greatest percentage of suitable habitat, both when areas with novel environments were excluded or included in the analysis and with both threshold rules. The B1 scenario results indicate an increase in percentage of suitable habitat, with the exception of white sweetclover for the 2030 B1 scenario where habitat noticeably decreased (Table 2). Additionally, there was an increase in mean elevation of suitable habitat with the future climate scenarios (Table 3). A substantial portion of the coastal region was classified as having novel environments (>20% for Canada thistle, >17% for reed canarygrass, and >8% for white sweetclover), and this proportion increased under future climate scenarios. This result underscores the uncertainty inherent in climate change research. Also, while climate change projections can highlight locations that in the future will have environments similar to where species exist today and may be useful as early detection sites, areas of decreasing suitability do not necessarily indicate that established populations would no longer persist as these models only estimate empirical relationships rather than mechanistic ones between species locations and current climate (Araújo and Peterson, 2012).

The distribution of each species was driven by different variables, although some common patterns emerged (Supplemental Material 2a). Precipitation variables were commonly more important in our models than temperature-driven variables. The most important precipitation variables included a temperature component (warm season or cold season precipitation) for the three regional models, but temperature-only related variables were not the most important. However, annual mean temperature was the second greatest contribution for the knotweed complex (Supplemental Material 2) and maximum temperature of the warmest month was the second greatest contribution for Canada thistle. Canada thistle distribution was driven by precipitation of the warmest quarter (general negative trend) followed by maximum temperature of the warmest month (general positive trend) and precipitation seasonality (sharp decrease with leveling off when interactions considered). The regional model for white sweetclover had precipitation seasonality (initial positive trend followed by leveling off) as most important, followed by precipitation of the warmest quarter (general negative trend) and topographic slope (general positive trend).

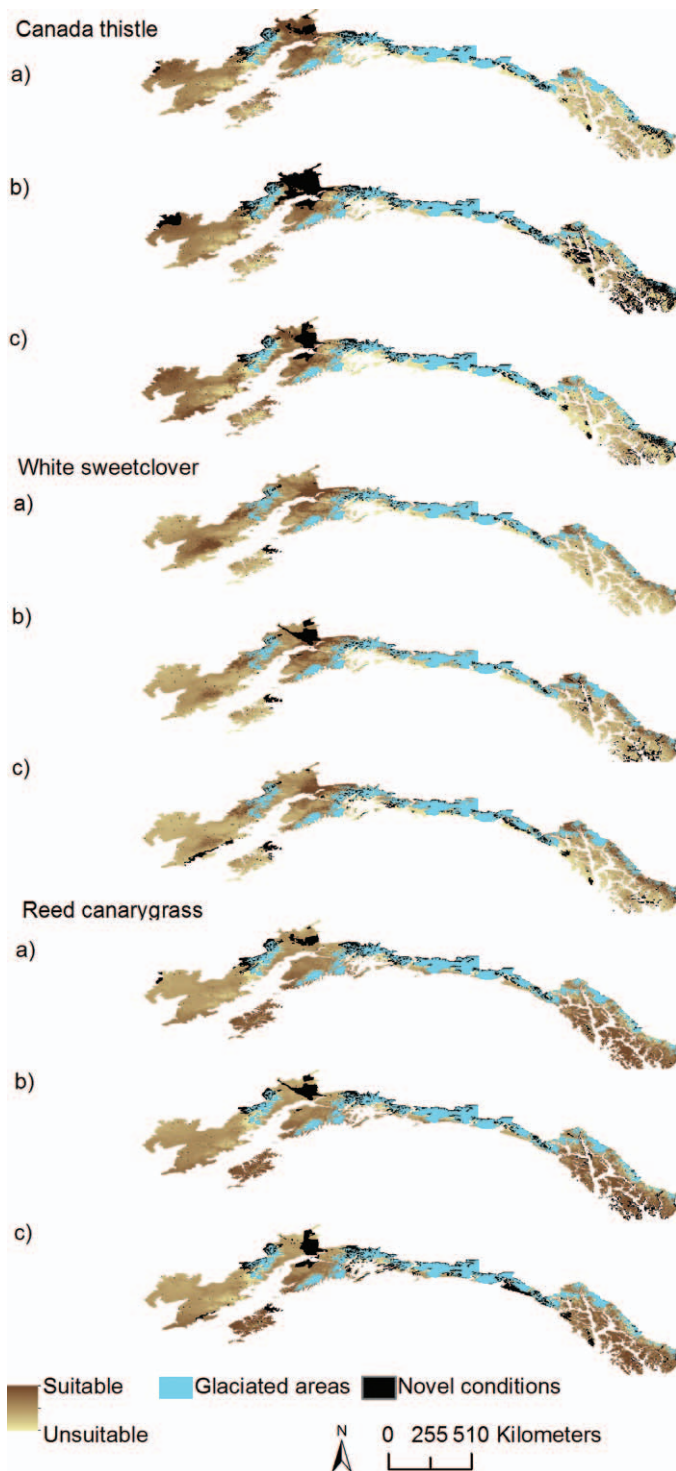


Figure 2. Habitat suitability under (a) current climate conditions, (b) predicted climate for 2030 with an A2 emissions scenario, and (c) predicted climate for 2030 with a B1 emissions scenario for Canada thistle, white sweetclover, and reed canarygrass. In all maps the grey transparent overlay indicates locations with novel environments according to the multivariate environmental similarity surface.

Increased habitat suitability for Canada thistle was associated with higher temperatures and timing of precipitation, while precipitation variables were most important in white sweetclover and reed canarygrass. Species response to differing temperature is likely associated with unknown or unrecorded biotic or abiotic factors correlated with temperature, or with differences in ecophysiology. For example Canada thistle seed germination is substantially greater at 25–30°C, with bolting and reproduction largely a function of summer temperatures (Amor and Harris, 1974; Bakker, 1960; Moore, 1975). Alaska is at the northern limit of Canada thistle's known distribution and tends to be associated with warmer microsites. While our results for Canada thistle suggest that summer precipitation and maximum temperatures are most important in this region of Alaska, winter temperatures may control the northern distribution of high density populations in Canada (Moore, 1975), and different aspects of temperature likely control the northern distribution of this species in coastal and continental locations.

The lack of importance of temperature variables in white sweetclover models may be related to the lack of presence or background locations at high elevation, and the species' distribution extending northward of the coastal region. By extending the model scope northward we anticipate that temperature variables would be more important predictors for this species. In fact, preliminary models of white sweetclover in the interior of the state suggested that temperature during the warmest month was an important variable in the model (Supplemental Material 2a).

Growth of reed canarygrass is related to tiller development that can occur during warm periods in winter or early spring (Hoveland et al., 1974) and growth may relate to higher temperatures when not accompanied by reduced soil moisture (Ge et al., 2012). Additionally this cool-season grass is preferentially associated with wetland and riparian habitats, in locations with high annual or seasonal precipitation, which may explain why precipitation variables are important in our models. The poor performance of the coastal region model, which only included climate factors, indicates that climate may not be an important driver within the coastal spatial extent for reed canarygrass. Due to the paucity of locations of reed canarygrass northward of the coastal region, expansion of the model northward might identify a suspected bottleneck in temperature for establishment of reed canarygrass.

Despite the lack of temperature drivers identified for some species, our hypothesis of increase in suitable habitat under future climate was supported for all species for at least one future emissions scenario. However increases were minor and Canada thistle was the only species with an increase greater than two percent. Also, the mean elevation of suitable habitat did increase, indicating that within the coastal region these

Table 3. Mean elevation in meters of areas of coastal Alaska classified as suitable using the 10 percentile (10P) training presence and the minimum training presence (MTP) for each species under current climate conditions and predicted future conditions for 2030 using the B1 emissions scenario and the A2 emissions scenario.

		Canada thistle		White sweetclover		Reed canarygrass	
		10P	MTP	10P	MTP	10P	MTP
With novel	Current	219	303	524	524	254	293
	2030 B1	244	329	707	534	268	334
	2030 A2	287	353	567	525	266	301
Without novel	Current	182	253	470	447	252	281
	2030 B1	219	286	631	459	271	298
	2030 A2	260	316	538	474	274	299

species may be able to survive across a wider elevation range with changing climate. Additionally, using the target background approach here, we did not cover the full range of temperature and precipitation gradients in the coastal region as illustrated by the high percent of novel areas. Increasing the sample gradient might improve model performance and realism by detecting potential temperature thresholds.

**Local Models.** At the local scale, the models for Canada thistle performed marginally well (Kenai AUC = 0.71, Prince of Wales AUC = 0.86; Table 1). The white sweetclover model had mixed results at the local scale (Kenai AUC = 0.85; Prince of Wales AUC = 0.63). The reed canarygrass models performed poorly for Prince of Wales (AUC = 0.55) and marginally better for Kenai (AUC = 0.74). We subsampled the presence points for Prince of Wales as the number of presence locations exceeded that of background and the locations were heavily clustered. Again, poor performance of models (white sweetclover for Kenai and reed canarygrass for Prince of Wales) indicates that we may be missing an important variable controlling distribution, that we missed important environmental gradients in the sampling, or that the species is a generalist at these locations. At the local level, reed canarygrass is generally

considered to be a habitat specialist associated with wetland and riparian areas (see Lavergne and Molofsky, 2004); however, in this region it commonly occurs across a broader range of habitats, including mesic roadsides and forest edges, encompassing a diverse spectrum of land cover classes, reducing its predictability (Evangelista et al., 2008). The influence of roadside occurrences and off-road data is exemplified in the difference in local model performance between Kenai (moderate) and Prince of Wales (poor). Prince of Wales has the highest density of roads in Alaska, with a single comprehensive road survey for nonnative species conducted by the Forest Service and contracted consultants between 2005 and 2007. The Kenai Peninsula has far fewer roads, with an extensive set of trail, river, and road surveys to detect this species conducted by the Forest Service, the Park Service, the US Fish and Wildlife Service, the Kenai Watershed Forum, and contracted consultants starting in 2003 and continuing to the present (Bella, 2011). Studies indicate that past location data for invasive species may result in poor projections of future scenarios because invasive species are not in equilibrium with their environment (Jones, 2012), therefore an iterative modeling approach incorporating new location data is important (Crall et al., 2013).

Table 4. Percent of the specified location (Kenai Peninsula or Prince of Wales Island) classified as suitable after applying either the 10 percentile training threshold or minimum training presence threshold (see Table 1) to the regional and local models for each of the three species. Regional and local includes locations suitable according to both models, regional only means the regional model was suitable and the local was not, and local only means the local model was suitable and the regional was not.

	Canada thistle			White sweetclover		Reed canarygrass	
	Kenai	Prince of Wales (with roads)	Prince of Wales (without roads)	Kenai	Prince of Wales	Kenai	Prince of Wales
Climate & local	17.1	10.9	42.0	29.9	34.5	15.6	5.1
Climate only	51.1	58.3	27.1	50.7	64.3	58.7	1.9
Local only	6.9	2.9	16.9	9.4	0.2	5.5	87.4
Unsuitable	25.0	27.9	13.9	10.0	1.1	20.1	5.6
Total climate	<b>68.2</b>	<b>69.2</b>	<b>69.2</b>	<b>80.6</b>	<b>98.7</b>	<b>74.3</b>	<b>7.0</b>
Total local	23.9	13.8	58.9	39.3	34.7	21.2	<b>92.5</b>



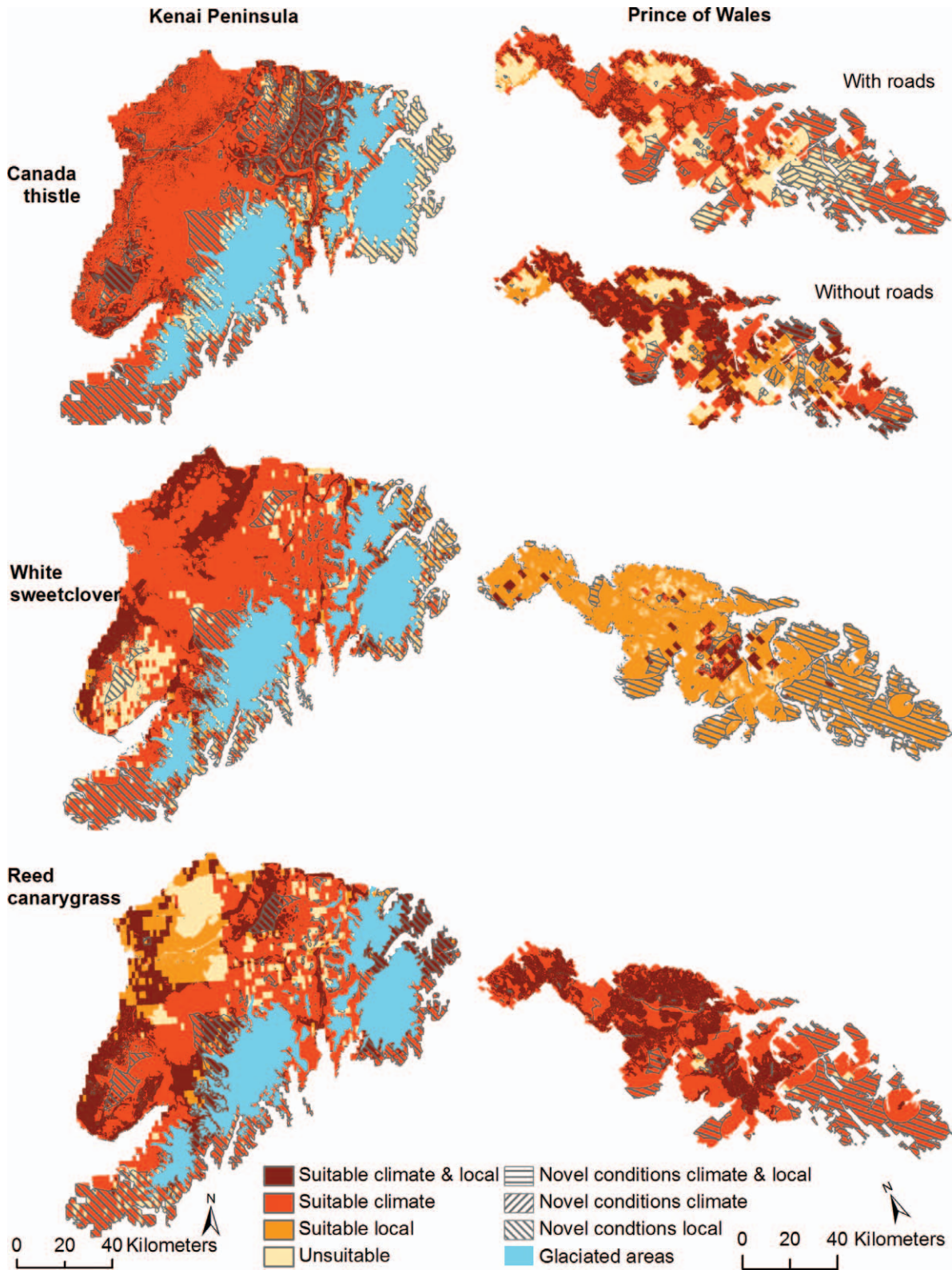


Figure 3. Habitat suitability at the local scale including Kenai and Prince of Wales for each of the three species, with suitable and unsuitable defined using the threshold values in Table 1.

Similarly, clustering samples in one year may result in diminished model performance as the location data from those years may poorly predict recorded locations in other years. Thus sustained, moderate and expanding survey efforts like those on the Kenai Peninsula may play an important role in model performance as it may better record data of an invasive species reaching equilibrium in a locale. Expansion of survey effort from roads to other habitats may play an important role in model performance within Prince of Wales, as climate and temperature lacks strong variability within this region of Alaska.

Some common patterns emerged again for the local scales models (Supplemental Material 2a). Distance to anthropogenic features was associated with habitat suitability for all three species at the local scale for both areas, but the type of anthropogenic feature differed among species and between locations (Supplemental Material 2b and 2c). Other predictors also varied by species and location. Differences were apparent in primary explanatory variables between Kenai Peninsula and Prince of Wales local models for some species. For example, distance to wetland, land cover, and utility line distance drove the Kenai Peninsula model for Canada thistle; however roads, recreation areas, and elevation were the contributing predictors for Prince of Wales. Similarly, the white sweetclover Kenai Peninsula model was driven by elevation, distance to water, and distance to utilities with trail distance barely contributing, while the Prince of Wales Island model had distance to trails as most important, followed more distantly by elevation and then land cover with distance to water not contributing to the model.

**Cross-scale Examination.** As predicted, most of the local models refined the predictions within the area defined as suitable in the regional models rather than included suitable habitat beyond the area defined as suitable in the regional model. This held true with six of seven models having a greater percent of suitable habitat defined by a regional model compared to a local model (Table 4 and Figure 3). The exception is reed canarygrass (Figure 3c) where almost all of Prince of Wales was suitable locally (92%) and only 5% was suitable climatically. However, neither of these two reed canarygrass models performed well. For Canada thistle on the Kenai Peninsula excluding roads (Figure 3a), percent area of climate suitability was only slightly greater than local model suitability (69.2% compared to 58.9%), although the more restrictive model including roads followed a more divergent pattern (local 13.8%).

The Prince of Wales models differed between which model, local or regional, was limiting based on the inclusion or exclusion of the distance from roads predictor variable for Canada thistle. This suggests that factors at both scales are important, and highlights the importance of identifying factors that may be more restrictive such as road

corridors, river corridors or trails. All three species have cosmopolitan distributions when considered at a global scale, but are restricted to a limited subset of habitats within their ranges. This suggests that while the modeled species have broad climatic tolerances, local scale models may have greater capacity to identify suitable and unsuitable habitat.

Locations with consistent predictions across scales (i.e., coastal and local model predictions for a location are both suitable or both unsuitable) are areas with greatest certainty about the potential for species establishment. The ensemble model approach has often been used to produce a more robust model than individual ones across different initial conditions, model classes, model parameters and boundary conditions (Araújo and New, 2007; Roura-Pascual et al., 2009), whereas in this case we are creating an ensemble of two different scales. Locations where models at both scales indicate high-risk of potential establishment based on high suitability values across scales are more appropriate targets for current control and monitoring efforts than locations identified by a model that considers factors operating at a single scale. Confidence in models could be improved by sampling in locations of novel environment (i.e. high uncertainty; Crall et al., 2013; Scheffer et al., 2001), especially where models indicate novelty. These cross-scale predictions could also provide information about timing of establishment. The local scale models can be thought of as predicting near term establishment and distribution, while longer term trends in distribution may be driven by climate, especially related to the future climate scenarios at the coastal scale.

Future work could examine the impact of the two thresholds, minimum training presence and 10 percentile, used for generating binary maps of the results for comparison. Additionally, studies coupling plant performance and population dynamics with climate and habitat variables in natural populations or in newly established populations subjected to current and predicted future climates (e.g., Reshetnikov and Ficetola, 2011) would be invaluable in understanding critical predictors of distribution.

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