MAXENT MODELING OF CLIMATE CHANGE EFFECTS ON SIX SPECIES OF NORTH AMERICAN SPRUCE

Rather than stick to the parameters of the assignment, I chose to look evaluate the effect of climate change on the future distribution of North American six spruce species—Engelmann, Picea engelmannii; white, P. glauca; black, P. mariana; blue, P. pungens; red, P. rubens; and Sitka, P. sitchensis—using MaxEnt (Phillips et al. 2006, Elith et al. 2011). Two other North American spruce species (Brewer's spruce, *P. breweriana*; and Chihuahua spruce, *P.* chihuahuana) were excluded because the small number of grid cells they were present in (19 for Chihuahua spruce and two for Brewer's of a total grid of nearly 104,000 cells) made a valid test all but impossible (Table 1). Total grid cells occupied for the other species ranged from 275 for blue spruce to 38,165 for black spruce (Table 1).

The six species used can be grouped by preferred environment. White and black spruce favor continental lowlands; Engelmann and blue spruce are found nearly exclusively in subalpine environments; and red and Sitka spruce are found in a mix of coastal, lowland, and subalpine environments (Table 1).

Because of the scope of my project in terms of spatial extent and resolution, I could not use the climate change scenario data provided. Instead, I downloaded downscaled data—based on the 19 bioclimatic variables (Hijmans et al. 2005) we used in the original MaxEnt analysis—from the Climate Change Agriculture and Food Security Web site (Ramirez and Jarvis 2008). The time period covered by the two scenario A1b and A2a datasets I obtained is 2070-2099.

For each of the six species in this analysis, I originally ran MaxEnt using all 19 bioclimatic variables and selected a subset of five variables based on analysis of response curves, variable contributions, and jackknife results in order to weed out redundant (correlated) variables while still retaining a subset that contributes to an understanding of the species' distributions. The response curves were initially used to group variables according to similarities in behavior. Afterward, the variable contribution table and jackknife results were consultant to determine which variable out of a particular grouping should be incorporated into each species' MaxEnt model (Table 2).

Afterward, three different MaxEnt runs were performed on each species: first, a model of the species' contemporary environmental niche using the five selected variables; followed by a model using the A1b scenario, and a third run involving the A2a scenario.

Results: White and Black Spruce

MaxEnt does a rather poor job of modeling the climatic envelope for white and black spruce. The receiver operating characteristic (ROC) curve AUC values are 0.607 and 0.603 for the five-variable models for white and black spruce, respectively. The AUC values for the climate change scenarios are 0.590 for white spruce and 0.587 for black spruce under both A1b and A2a scenarios (Table 3).

For the two predominantly lowland species—white and black spruce—the primary

bioclimatic variable influencing their contemporary distribution was mean annual temperature, followed by mean temperature of the warmest quarter and annual temperature range (Table 4a).

The results suggest that the suitable climate envelope for both white (Figure 1) and black (Figure 2) spruce is much broader than their current distributions—with room for expansion both north and south of their current range in North America, as well as throughout the boreal zone. Lawrence (2012) discusses these results in more detail. MaxEnt predicts a loss of suitable climate conditions south of white spruce's current range, but a substantial expansion of suitable range to the north through the Arctic and North Atlantic region under both the A1b (Figure 3) and A2a (Figure 4) scenarios. A similar result was obtained for black spruce (Figure 5 for scenario A1b; Figure 6 for scenario A2a).

Results: Engelmann and blue spruce

MaxEnt does an excellent job of modeling the climatic envelope for the exclusively subalpine species, Engelmann and blue spruce. The receiver operating characteristic (ROC) curve AUC values are 0.891 for the five-variable models for Engelmann spruce, and 0.988 percent for blue spruce. The AUC values for the climate change scenarios are 0.872 for Engelmann spruce and 0.985 for blue spruce under both A1b and A2a scenarios (Table 3).

Both are subalpine species and their ranges substantially overlap, thus it should be little surprise that the climatic variables that play a significant role in influencing their geographic distribution are largely the same as noted in Lawrence (2012). Mean annual temperature, mean diurnal temperature range, temperature seasonality, and mean temperature of wettest quarter are included in both species five-variable model, though the relative importance varies for both (Table 4b). The species differ in that mean temperature of the coldest quarter is included in the Engelmann spruce model, while precipitation seasonality is included in the blue spruce model.

These differences may shed light on the reasons why Engelmann spruce is a common treeline species in the Rockies, while blue spruce often grows better under more mesic conditions that its Rocky Mountain neighbor.

For Engelmann spruce, MaxEnt predicts additional suitable climate conditions throughout the Great Basin and Sierra Nevada, and north and west along the Gulf of Alaska (Figure 7). Blue spruce has a much smaller suitable climate envelope: in addition to its current range, it could potentially expand north into the Canadian Rockies (Figure 8). As with white and black spruce, MaxEnt predicts that under the two climate models, Engelmann spruce will lose suitable conditions in the south of its current range, but would gain suitable conditions to the north in western Alask (Figure 9 for scenario A1b; Figure 10 for scenario A2a). Blue spruce, however, will not find room to expand, as much of the area it could potential expand into now will become unsuitable for its growth under both scenario A1b (Figure 11) and A2a (Figure 12).

Results: Red and Sitka spruce

As with the exclusively subalpine species, MaxEnt does an excellent job of modeling the climatic envelope for red and Sitka spruce. The receiver operating characteristic (ROC) curve AUC values were 0.938 for the five-variable models for both species. The AUC values for the climate change scenarios are 0.926 for red spruce and 0.925 for Sitka spruce under both A1b and A2a scenarios (Table 3).

The five-variable model for red spruce includes four variables shared with the other species: mean annual temperature with all but Sitka spruce; mean diurnal temperature range with Engelmann and blue spruce; annual temperature range with white and black spruce, and precipitation seasonality with all but Engelmann spruce (Table 4c). The only variable unique to the red spruce model was isothermality. Likewise, the only variable unique to the Sitka spruce

model was mean temperature of driest quarter (Table 4c). In addition to precipitation seasonality, it shared three more variables with other species' models: mean temperature of wettest quarter with Engelmann and blue spruce; mean temperature of warmest quarter with white and black spruce; and mean temperature of coldest quarter with Engelmann spruce.

As pointed out by Lawrence (2012), red spruce already occupies much of what the MaxEnt results suggest is its environmental envelope, with potential for expansion into the Great Lakes region and northeastward into Newfoundland and Labrador (Figure 13). Suitable climate conditions for Sitka spruce occur to the east of its current range—across the Great Basin into the Rocky Mountains (Figure 14). The MaxEnt runs for both climate change scenarios A1b (Figure 15) and A2a (Figure 16) suggest a potential northwestward expansion of red spruce into the James Bay region of Ontario and Quebec. As with blue spruce, Sitka spruce faces a likely contraction of its potential range (Figure 17 for scenario A1b; Figure 18 for scenario A2a).

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Table 1. Number of grid cells present (out of a possible total of 103,897) and preferred geographic zones occupied by the eight species of North American spruce.

	Number	
Species	of Grid Cells	Preferred Geographic Zones
Black spruce	38,165	Subarctic; Continental Lowlands
Blue spruce	275	Subalpine
Engelmann spruce	3,145	Subalpine
Red spruce	1,627	Subalpine; Coastal Lowlands
Sitka spruce	1,582	Coastal Lowlands; Subalpine
White spruce	37,470	Subarctic; Continental Lowlands

Table 2. Variables selected for the MaxEnt modeling of climate change effects on the distribution of Engelmann spruce (PCEN), white spruce (PCGL), black spruce (PCMA), blue spruce (PCPU), red spruce (PCRU), and Sitka spruce (PCSI).

Variable Name	BioVar	PCEN	PCGL	PCMA	PCPU	PCRU	PCSI
Mean Annual Temperature	bio1	X	X	X	X	X	
Mean Diurnal Range	bio2	X			X	X	
Isothermality	bio3					X	
Temperature Seasonality	bio4	X			X		
Min Temperature							
of Coldest Month	bio6		X	X			
Temperature Annual Range	bio7		X	X		X	
Mean Temperature							
of Wettest Quarter	bio8	X			X		X
Mean Temperature	bio9						
of Driest Quarter							X
Mean Temperature							
of Warmest Quarter	bio10		X	X			X
Mean Temperature							
of Coldest Quarter	bio11	X					X
Precipitation Seasonality	bio15		X	X	X	X	X

Table 3. MaxEnt Receiver Operating Characteristic curve AUC values based on training data for the MaxEnt models of North American spruce distributions now and under the A1a and A2a climate change scenarios for the late twenty-first century.

Species	Contemporary	A1b	A2a
White spruce	0.607	0.590	0.590
Black spruce	0.603	0.587	0.587
Engelmann spruce	0.891	0.872	0.872
Blue spruce	0.988	0.985	0.985
Red spruce	0.938	0.926	0.926
Sitka spruce	0.938	0.925	0.925

Table 4a. Analysis of variable contributions to the MaxEnt models for white and black spruce.

	White	spruce	Black spruce		
	Percent	Permutation	Percent	Permutation	
Variable	contribution	importance	contribution	importance	
Mean Annual Temperature	88.1	58.1	82.8	51.6	
Min Temperature of Coldest Month	7.0	0.0	11.8	0.0	
Temperature Annual Range	0.5	17.3	0.6	21.3	
Mean Temperature					
of Warmest Quarter	2.7	16.6	2.3	16.2	
Precipitation Seasonality	1.7	8.0	2.5	11.0	

Table 4b. Analysis of variable contributions to the MaxEnt models for Engelmann and blue spruce.

	Engelma	nn spruce	Blue spruce		
	Percent	Permutation	Percent	Permutation	
Variable	contribution	importance	contribution	importance	
Mean Annual Temperature	59.3	69.1	34.3	64.3	
Mean Diurnal Range	7.2	5.6	40.7	19.5	
Temperature Seasonality	4.1	13.8	5.6	11.3	
Mean Temperature of Wettest Quarter	12.5	0.8	1.1	0.6	
Mean Temperature of Coldest Quarter	17.0	10.7			
Precipitation Seasonality			18.3	4.4	

Table 4c. Analysis of variable contributions to the MaxEnt models for red and Sitka spruce.

	Red spruce		Sitka spruce	
	Percent	Permutation	Percent	Permutation
Variable	contribution	importance	contribution	importance
Mean Annual Temperature	37.2	41.1	_	_
Mean Diurnal Range	2.2	4.4	_	
Isothermality	1.0	13.3		
Annual Temperature Range	0.2	2.0	_	
Mean Temperature of Wettest Quarter		_	54.0	46.2
Mean Temperature of Driest Quarter			2.6	39.9
Mean Temperature				
of Warmest Quarter			5.8	11.9
Mean Temperature				
of Coldest Quarter			37.0	0.5
Precipitation Seasonality	59.5	39.3	0.7	1.5

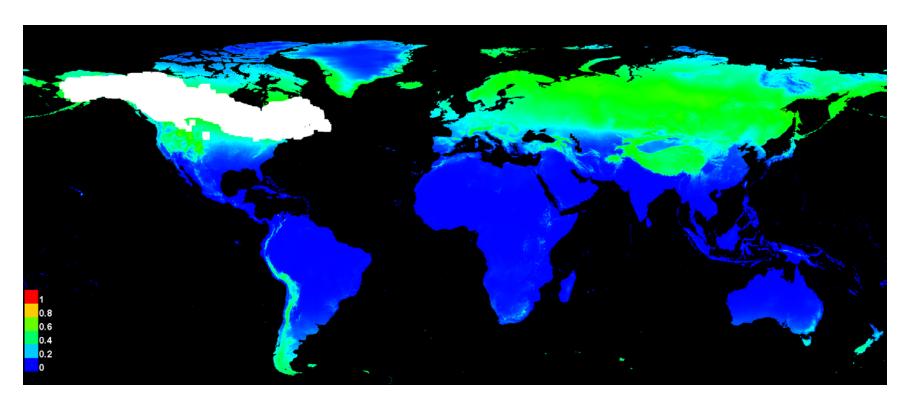


Figure 1. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of white spruce (shades of green and light blue).

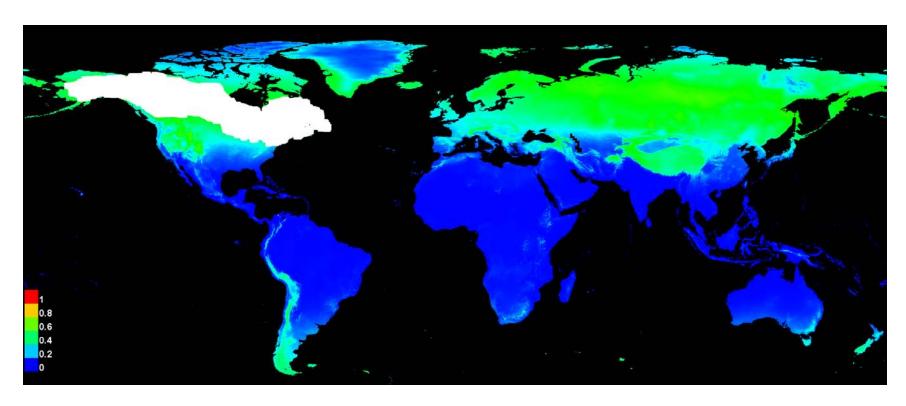


Figure 2. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of black spruce (shades of green and light blue).

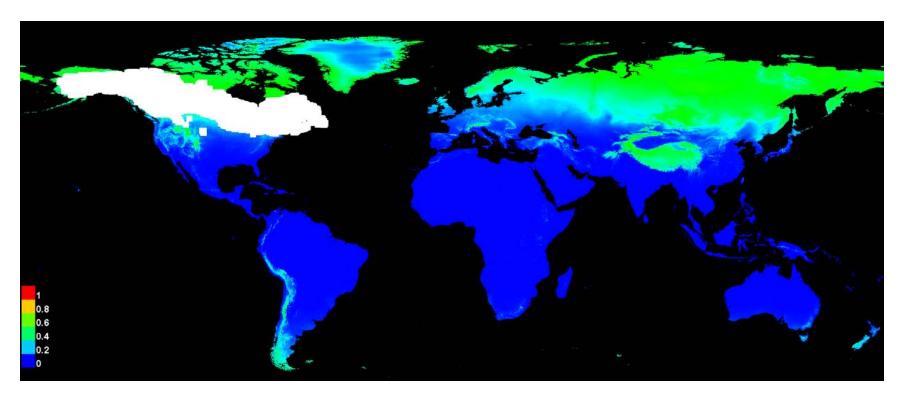


Figure 3. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of white spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

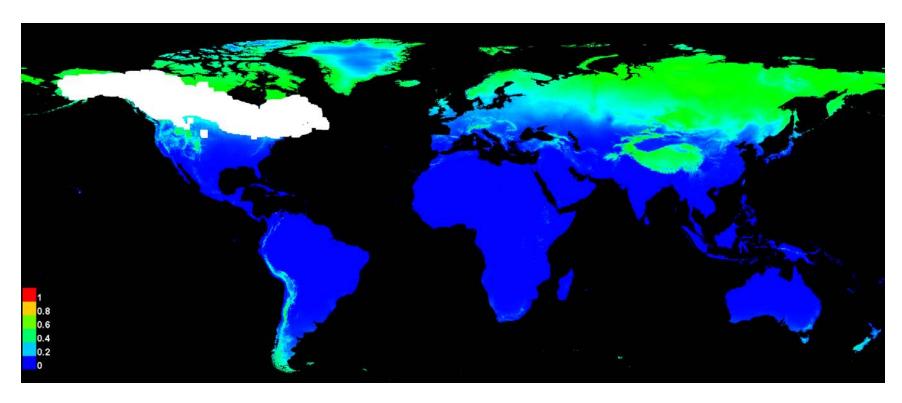


Figure 4. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of white spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.

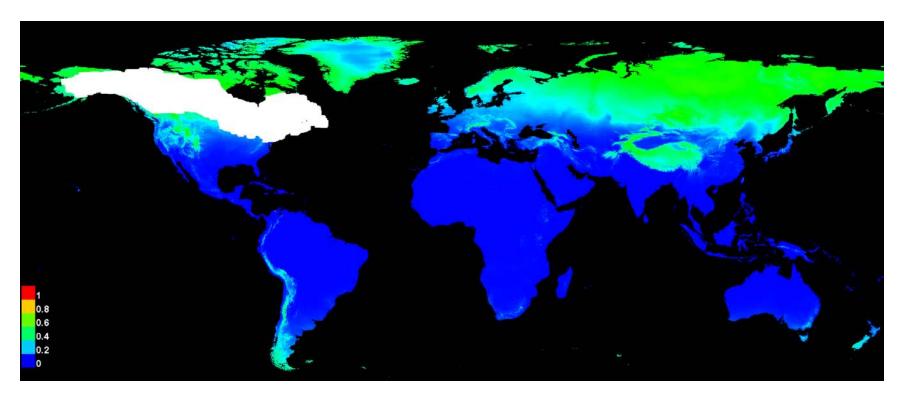


Figure 5. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of black spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

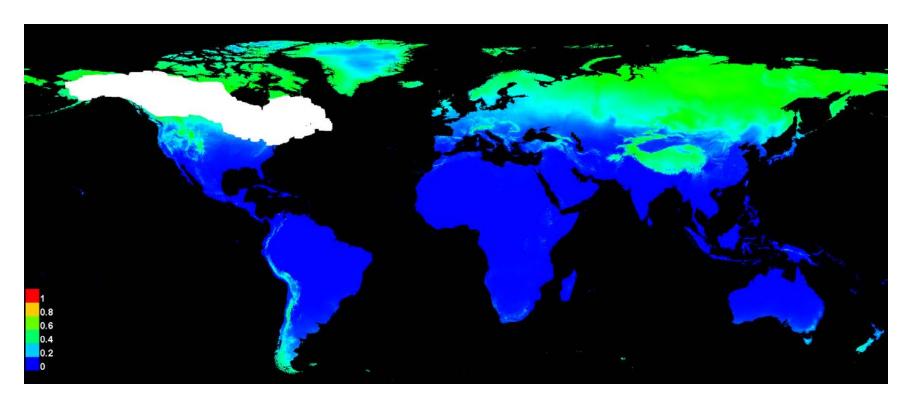


Figure 6. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of black spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.

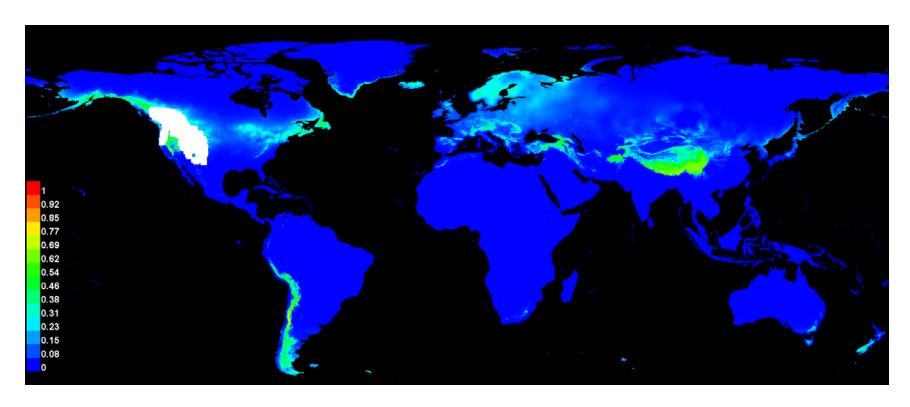


Figure 7. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of Engelmann spruce (shades of green and light blue).

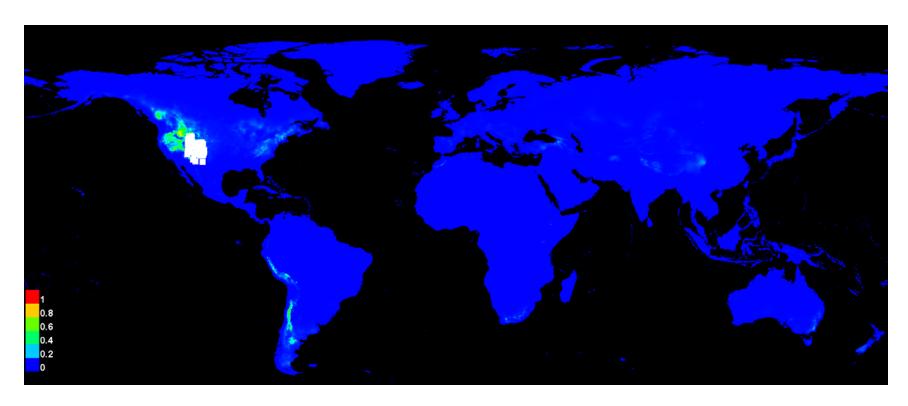


Figure 8. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of blue spruce (shades of green and light blue).

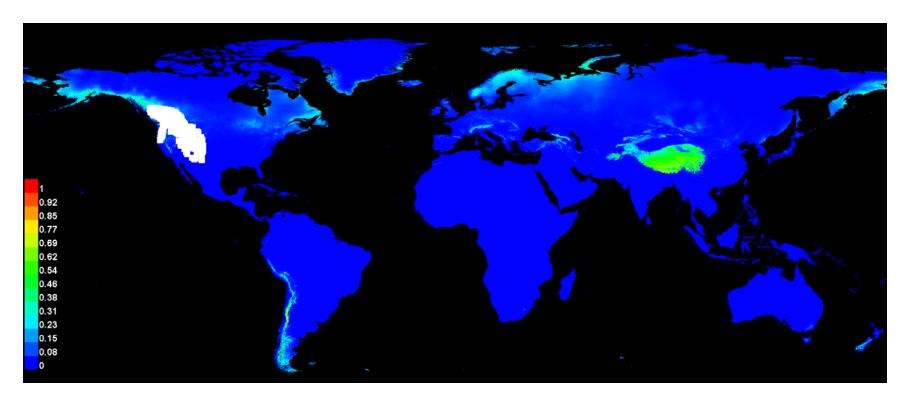


Figure 9. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of Engelmann spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

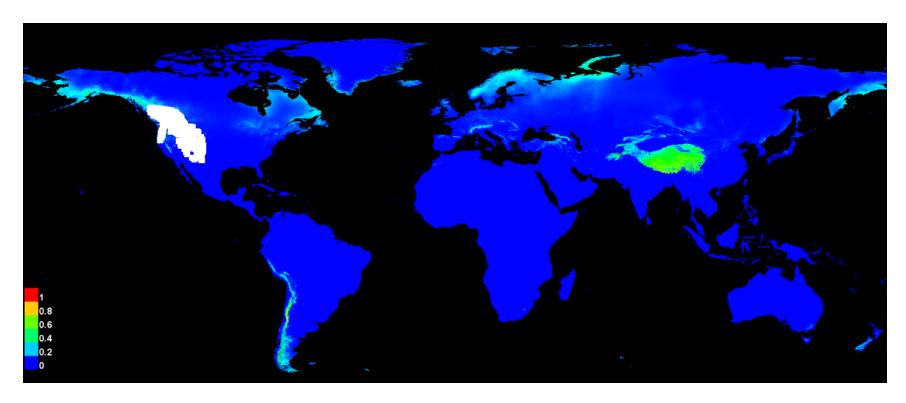


Figure 10. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of Engelmann spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.

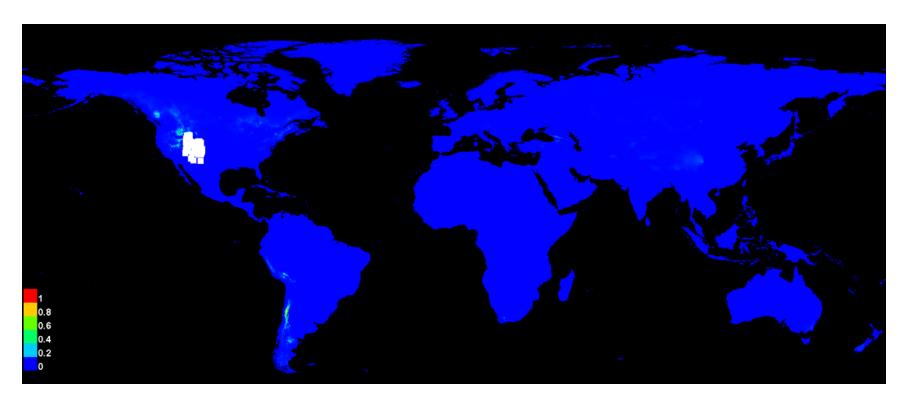


Figure 11. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of blue spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

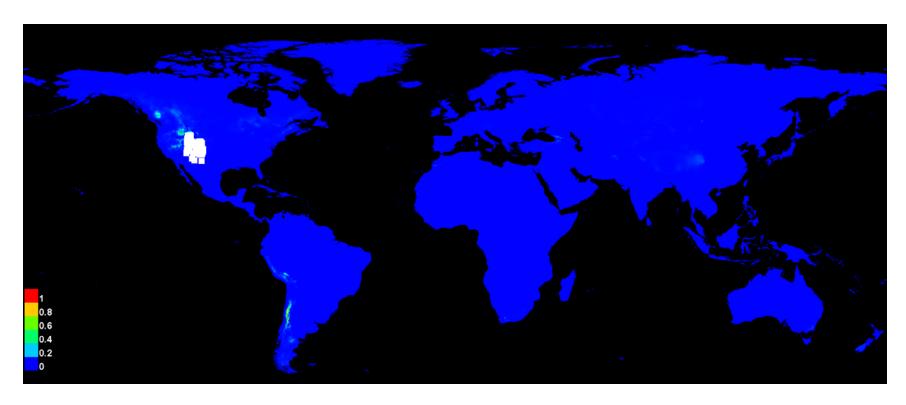


Figure 12. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of blue spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.

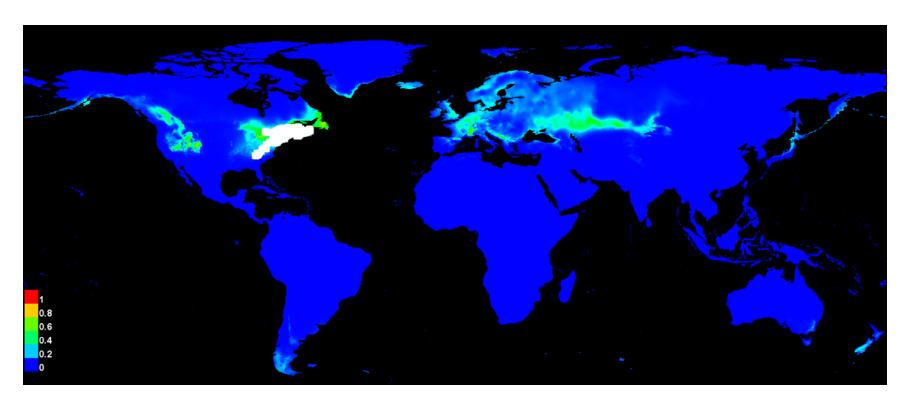


Figure 13. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of red spruce (shades of green and light blue).

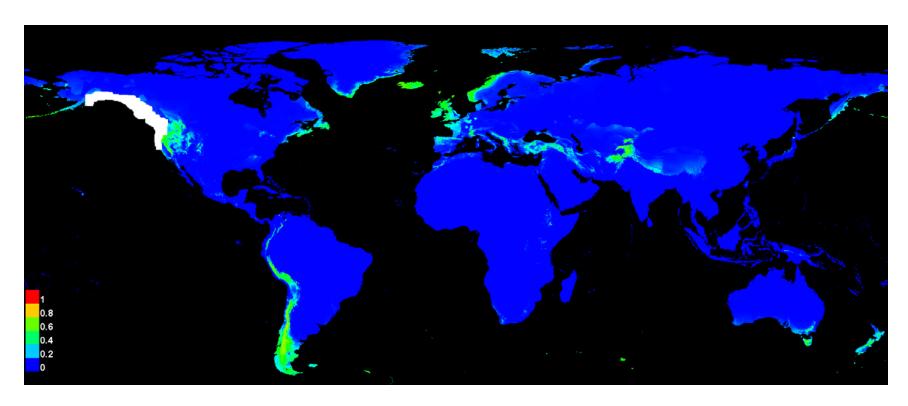


Figure 14. Current distribution (white) and MaxEnt prediction of areas where climate conditions are suitable for the establishment of Sitka spruce (shades of green and light blue).

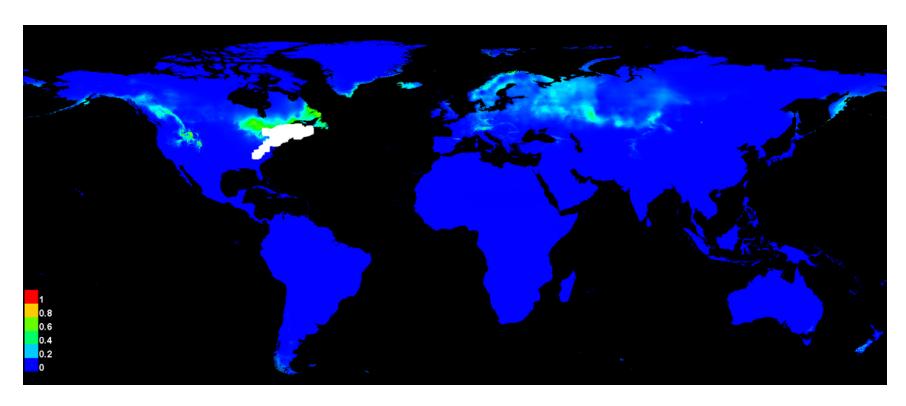


Figure 15. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of red spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

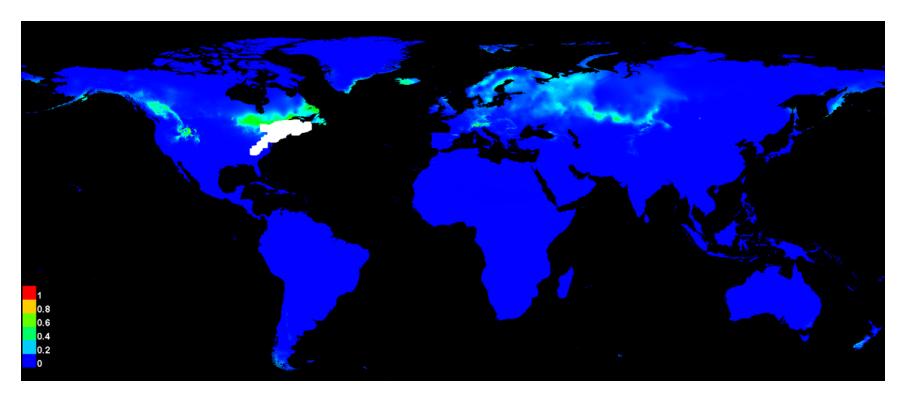


Figure 16. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of red spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.

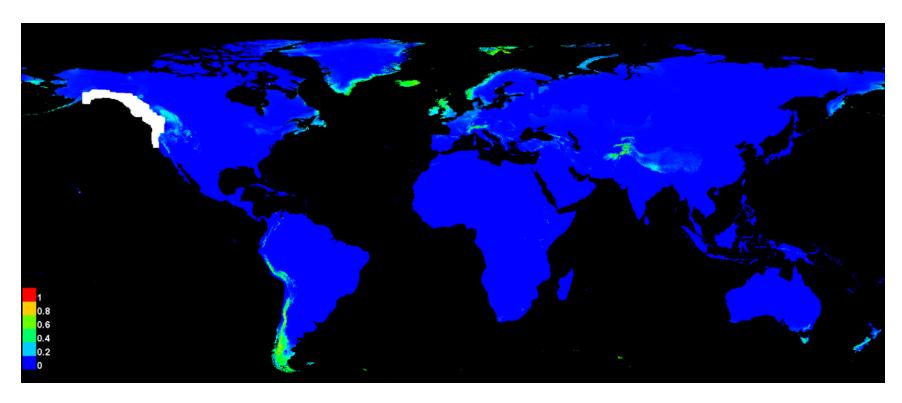


Figure 17. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of Sitka spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A1b.

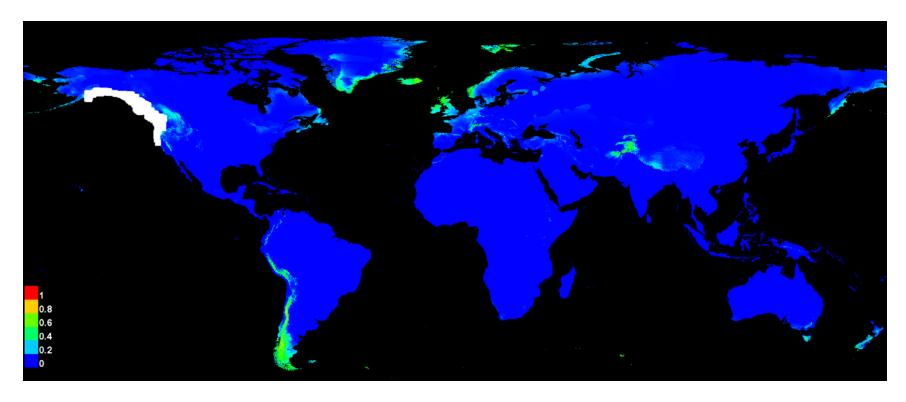


Figure 18. Predicted distribution (white) and MaxEnt prediction of areas where climate conditions will be suitable for the establishment of Sitka spruce (shades of green and light blue) in the latter twenty-first century under IPCC climate change scenario A2a.