Ecological Niche Modeling of North American Glacial Refugia for *Juncus biglumis* (Juncaceae)

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The contemporary distribution of arctic-alpine plants is largely the product of both climate and glaciation history (Stewart et al. 2016). The cool climate of the early Pleistocene allowed a more widespread distribution of these species than exists today (Marret al. 2012). During the Last Glacial Maximum (LGM; approximately 21,000-18,000 years ago (Beatty and Provan 2011)), two major ice sheets covered Canada: the Cordilleran Ice Sheet covered southern Alaska and nearly all of British Columbia, and the Laurentide Ice Sheet covered the rest of Canada (Shafer et al. 2010). During multiple glaciation periods throughout the Pleistocene, cold-adapted plant species were able to survive in ice-free areas of suitable habitat, called “glacial refugia” (Waltari et al. 2007; Shafer et al. 2010). These areas provided sources for recolonization following glacial retreat, resulting in the biogeographical distributions that we see today (Tremblay et al. 1999; Waltari et al. 2007).

Initial theories of post-glacial recolonization suggested a single refugial region for plant species. For example, in 1937 Eric Hultén proposed that the region of Beringia, the land bridge between northwestern North America and eastern Siberia that formed due to low sea levels during glaciation, acted as a single glacial refugium for North America during the Pleistocene (Hultén 1937, cited in Tremblay and Schoen 1999; Beatty and Provan 2011). Contrary to this simplistic view of recolonization patterns, several recent studies have indicated a more complex refugial scenario in North America, including multiple refugia and nonlinear rates of dispersal resulting in disjunct areas of occupied habitat (Beatty and Provan 2011; Stewart et al. 2016).

The focal species of this study, *Juncus biglumis*, is a circumpolar species that occurs in a variety of cool, moist habitats, including wet gravel, open rocky alpine slopes, and periglacial habitats (Hermann 1975; Brooks 2000; Marr et al. 2012). Within North America, the distribution of *J. biglumis* can be divided into three main regions corresponding with proposed glacial refugia (Schonswetter et al. 2006; Marr et al. 2012). The northwestern distribution (western Canada and Alaska) was influenced by the northwestern margin of the CIS, while the northeastern distribution (eastern Canada) was moderated by the Laurentide Ice Sheet. Schonswetter et al. (2006) presented evidence for two separate *J. biglumis* lineages within North America: one in western Canada and one in northeastern Canada. The third region, located in the Central Rockies of the western United States, represents a disjunct ice-free region of suitable habitat to the south of the CIS (Marr et al. 2012). Marr et al. (2012) hypothesized that this southern population was a result of the region's glacial legacy. Despite sampling gaps in central Canada (Schonswetter et al. 2006), these factors create a distinct distribution pattern comprised of three extents: a northwestern region in British Columbia, the Northwest Territories, and the Yukon, Alaska; a northeastern region in Nunavut, Quebec, and Newfoundland and Labrador; and a disjunct southern population at high elevations in Colorado, Wyoming, and Montana (Figure 1).

Locating glacial refugia and understanding distributional patterns has significant ecological implications for predicting future vegetation changes (Waltari et al. 2007). As the climate warms, cold-adapted species are expected to see major shifts in suitable habitat and may become restricted to climate refugia (Keppel et al. 2012). Although multiple studies have found evidence of glacial refugia (Beatty and Provan 2011; Pellissier et al. 2016; Stewart et al. 2016) and have investigated the concept of climate change refugia (Ashcroft et al. 2009; Keppel et al. 2012; Olson et al. 2012), few studies have made species-specific connections between past glacial refugia and future climate refugia. This study fills that research gap by comparing ecological niche models at regional and continental scales for both current and future climate conditions. Combined with

Table 1: Analysis variables (WorldClim 2017)

Variable Code	**Description**
alt	Altitude
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (mean of monthly (max temp – min temp))
BIO3	Isothermality (BIO2/BIO7)*100
BIO4	Temperature Seasonality (standard deviation * 100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (max temp of warmest month – min temp of coldest month)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (coefficient of variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

previous phytogeographical studies of *J. biglumis* survival via glacial refugia, this study will link the past to the future. The aim is to determine the primary bioclimatic drivers of suitable habitat in North America for this arctic-alpine species.

METHODS

Occurrence data

Occurrence records for *J. biglumis* were downloaded from two online herbaria databases: (i) SEINet and (ii) the Consortium of Pacific Northwest Herbaria (CPNWH). These collections are not comprehensive and do not represent the entire extent of the species, but they do provide an appropriate coverage of its North American distribution. Georeferencing is the process of assigning coordinates to an occurrence record based on locality information included on the specimen label. Although many records had been previously georeferenced, the majority were lacking coordinates. I georeferenced those records using Google Maps in tandem with the GEOLocate online software to find the radius of coordinate uncertainty. The EarthPoint website and Google Earth software (version 7.3.0.3832) were used to georeference records with township-range information. The compiled dataset of occurrence records was screened for redundancy and precision. Duplicate or redundant occurrences (i.e., within 1 km of another occurrence) were removed. The final dataset included 342 records across northwestern US (Colorado, Montana, and Wyoming), Alaska, and Canada.

Environmental variables

A suite of 20 variables was used in this analysis. To characterize contemporary climate conditions (average of 1970-2000), a suite of 19 bioclimatic variables were downloaded from the WorldClim online database. The bioclimatic variables are derived from monthly temperature and precipitation data (Table 1). In addition to those 19 variables, altitude data was downloaded in eight 30° x 30° tiles spanning the North American distribution of *J. biglumis*. All data were downloaded at a spatial resolution of 30 arc-seconds.

Bioclimatic data representing future climate conditions (2070, average of 2061-2080) were also downloaded from WorldClim. This data is generated by the Coupled Model Intercomparison Project (CMIP5) of the World Climate Research Programme (WCRP). The CMIP5 provides a set of general circulation models (GCMs) that can be used to test hypotheses about future climate conditions (Taylor et al. 2012). After testing 25 of the CMIP5 models, Watterson et al. (2014) found that the Max Planck Institute Earth System Model at low resolution (MPI-ESM-LR) performed the best for North America. The representative concentration pathway (RCP) 8.5 was selected, which represents an upper extreme scenario of emissions typically considered to be a "business as usual" projection (Taylor et al. 2012). Thus, future climate data was downloaded at a 30 arc-second resolution for the year 2070 from the MPI-ESM-LR model for the RCP8.5 emissions scenario.

The data were divided into three extents corresponding with phylogeographical patterns (south, northwest, and northeast) using R (version 3.3.3) within the RStudio graphical user interface (version 1.0.136). While the southern extent was a simple bounding box, the northwest and northeast extents were more complex. I cropped those extents using shapefile polygons created in QGIS (version 2.18.3).

Pearson's correlation coefficient

I applied a Pearson's correlation coefficient test to the current climate data for each of the three extents. The correlation tables were then manipulated in Microsoft Excel to eliminate strongly correlated variables. To achieve this, I first identified all correlation coefficients with an absolute value greater than 0.8 and colored these cells red. The variable(s) with the greatest number of red cells were eliminated first. The remaining red cells were recounted and the variable(s) with the next greatest number of red cells were eliminated. This iterative process was repeated until each variable had 3 or fewer red cells. Finally, I compared the remaining variables from each extent and selected the ones that were present in at least 2 of the tables. The following 8 variables were selected: altitude, mean diurnal range (BIO2), isothermality (BIO3), minimum temperature of coldest month (BIO6), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), mean temperature of driest quarter (BIO9), and precipitation seasonality (BIO15).

Environmental Niche Modeling (ENM)

One approach to understanding the drivers of species distributions is through environmental niche modeling (ENM). ENM provides a way to link ecological variables to species occurrence points. Although there are multiple methods, the maximum entropy method (MaxEnt) has proved to be particularly useful (Phillips et al. 2005; Waltari et al. 2007). Using a list of occurrence points and a set of raster layers as inputs, MaxEnt randomly selects background points, extracts values from the input environmental variables at both background and known occurrence points, then compares the variables between the two (Merow et al. 2013). Thus, the predicted habitat suitability will differ if MaxEnt is trained at a regional extent versus a continental extent. Using the smaller, regional extent is a better method for examining landscape-scale processes, while the larger extent is more appropriate for continental-scale patterns (Merow et al. 2013). I used the MaxEnt software (version 3.4.1; Phillips et al.) to produce models for the three regional extents as well as the full continental extent, under both current and future climate conditions.

Principal Components Analysis (PCA)

Principal components analysis (PCA) is a statistical method of analyzing groups of variables and summarizing their impact on the variance within a dataset. PCA has been used extensively in environmental modeling and biotic community analysis (Janžekovič and Novak, 2012). Using the ggbiplot package in R, I conducted a PCA analysis for each extent under both time frames using the full suite of 20 variables (19 bioclimatic plus altitude).

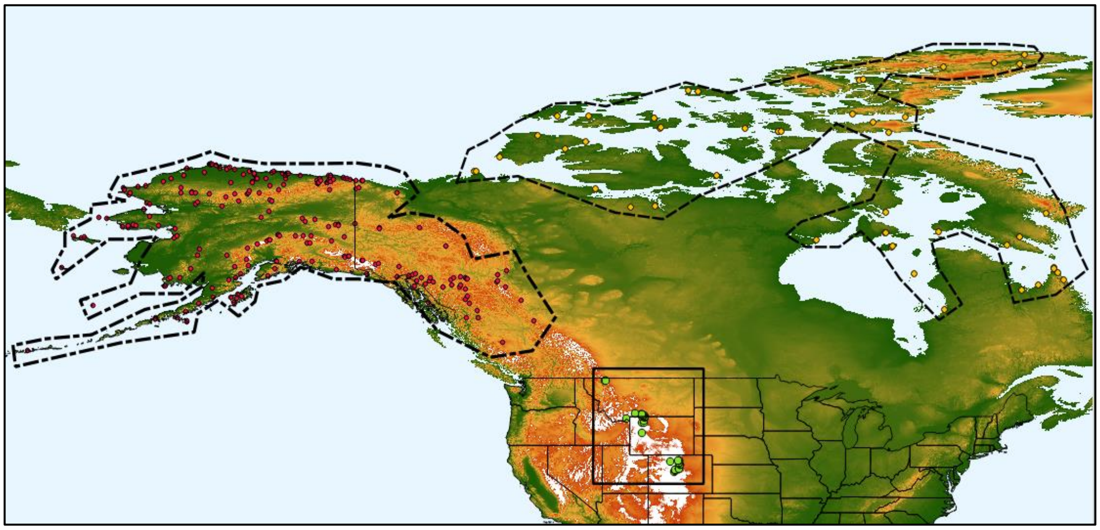

Figure 1: Map of North American distribution of *Juncus biglumis* displayed against altitude. The dashed-dotted line and red points denotes the northwestern population, the dotted line and yellow points denotes the northeastern population, and he solid line and green points denotes the southern population.

RESULTS

Current climate

Within the southern extent, MaxEnt showed the highest probability of suitable habitat for *J. biglumis* occurring in a northwest-to-southeast swath of high elevation, including the Lewis Range in Glacier National Park; the Wind River Range, Beartooth Plateau, and the Bighorn Mountains in northern Wyoming; and the Mosquito and Front Ranges in central Colorado (Figure 3). Altitude was the most important variable (56.6%), and the mean temperature of the wettest quarter (BIO8) was of secondary importance (18.3%; Table 2). The response curves supported this result, showing that occurrence of *J.*

biglumis peaks at higher elevations (> 4000 m) (Appendix A). Principal component analysis (PCA) of the initial suite of 20 variables (19 bioclimatic, plus altitude) revealed a grouping pattern (Figure 2). The majority of the precipitation variables (BIO12 through BIO19) were grouped toward the upper-right side of the plot, while the majority of the temperature variables were grouped toward the lower-right side of the plot.

While the southern distribution of *J. biglumis* was restricted to high elevations, suitable habitat in the northwestern extent was predicted to span a much larger elevational range (Figure 3). In Alaska, for example, there was an equally high probability of occurrence along the coast as in higher-elevation areas (e.g., Brooks Range of northern Alaska). The two most important variables, mean temperature of the wettest quarter (BIO8; 41%), and precipitation seasonality (BIO15; 12.9%; Table 2), occupied distinct areas of the PCA biplot (Figure 4).

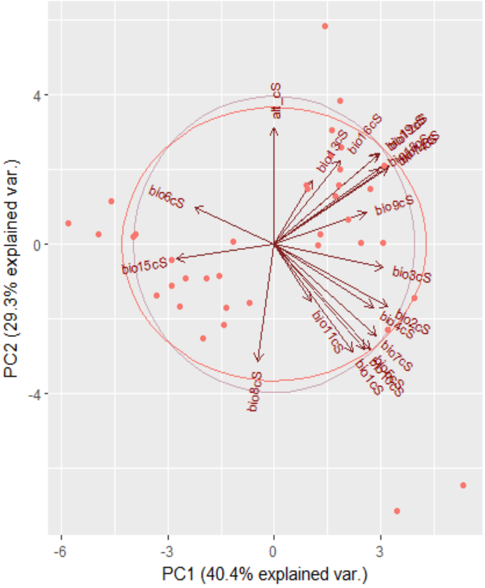

Figure 2: PCA biplot for the southern extent of *Juncus biglumis* distribution in North America showing correlation (circle) and spatial niche (ellipse). Arrows point in the direction of increasing variable values and arrow length corresponds to magnitude of model variance attributed to that variable.

Table 2: Percent contribution of model variables. Highest contributing variables in bold; secondary variables italicized.

	Current				Future			
	South	**NW**	**NE**	**Full**	**South**	**NW**	**NE**	**Full**
alt	**56.6**	7.2	**57.0**	10.2	**50.6**	12.9	**59.9**	10.8
BIO2	4.9	11.8	10.3	6.6	0.0	0.8	0.2	1.5
BIO3	0.9	4.3	1.8	2.0	0.0	6.2	1.9	6.9
BIO6	0.1	2.0	2.3	9.5	6.5	11.7	0.9	2.7
BIO7	14.1	11.6	*16.4*	*14.5*	*26.9*	9.4	*27.3*	6.0
BIO8	*18.3*	**41.0**	9.2	**39.9**	10.8	**37.6**	7.2	**41.4**
BIO9	2.8	9.3	0.0	11.0	1.1	7.5	0.1	*21.0*
BIO15	2.3	*12.9*	2.9	6.3	4.1	*13.9*	2.5	9.7

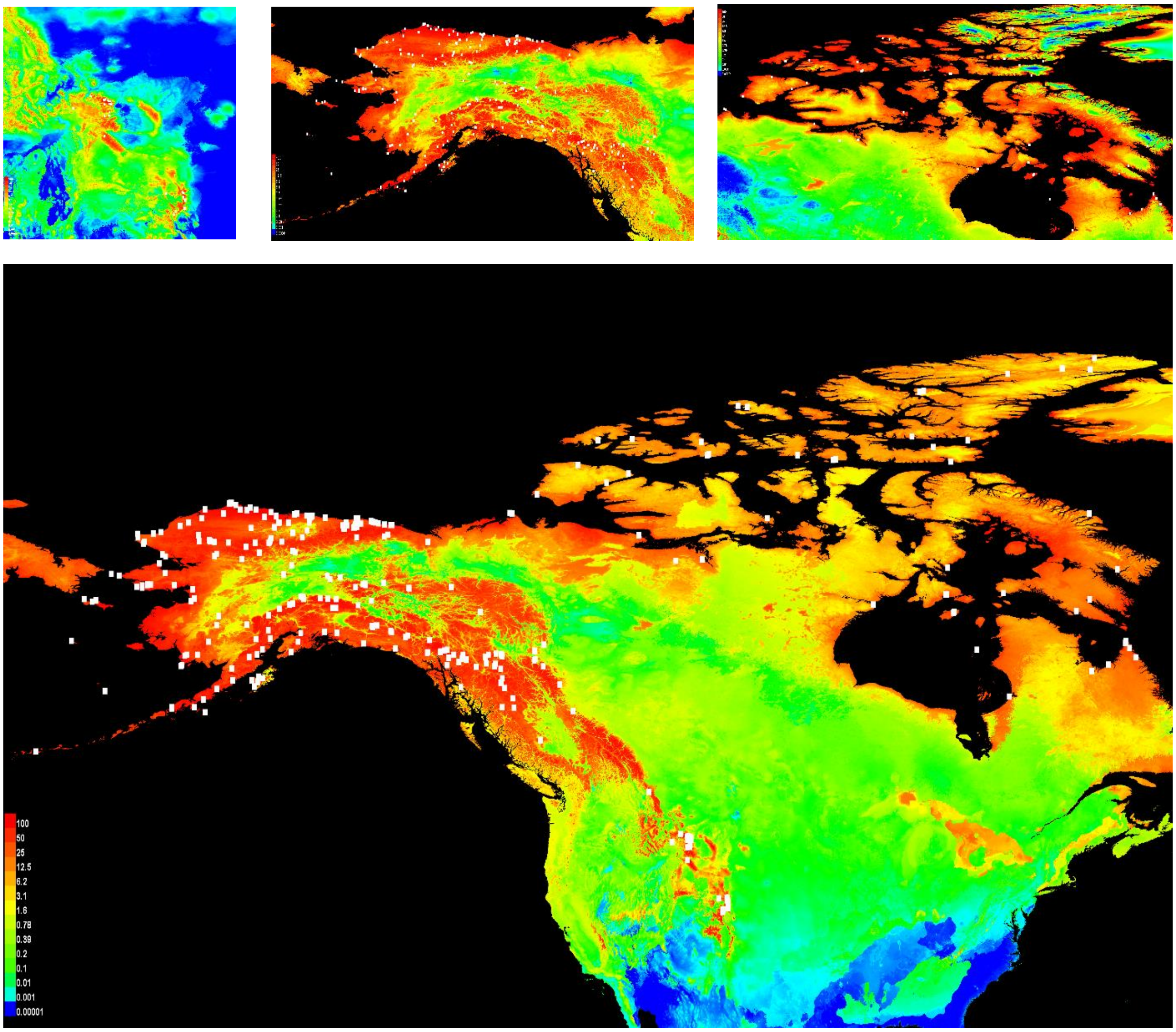

Figure 3: MaxEnt heatmaps of suitable habitat for *Juncus biglumis* for each extent. Clockwise from top left: (i) southern extent, (ii) northwestern extent, (iii) northeastern extent, and (iv) full continental extent. Warm colors indicate high probability of occurrence, cool colors indicate low probability of occurrence.

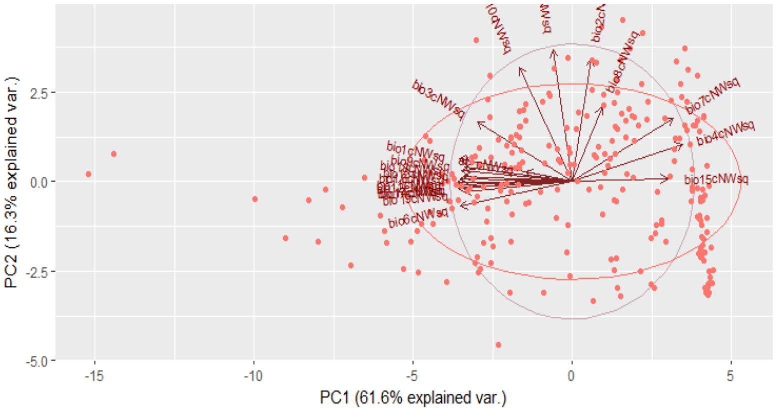

Figure 4: PCA biplot for the northwestern extent of *Juncus biglumis* distribution in North America. The spatial niche (red ellipse) is more correlated with PC1 than PC2 due to the strong association between PC1 and the majority of the variables.

In the northeastern extent, the highest occurrence probabilities were located along the shorelines of the northern Canadian islands (Figure 3). Notably, the areas at the highest elevations (e.g., Arctic Cordillera) had the lowest probability of occurrence within this extent. The response curve for altitude, which was the most important model variable, reinforced this finding: *J. biglumis* abundance peaked at 0 m elevation and was absent above 1000 m (Appendix C). The response curve for the second most important variable, annual temperature range (BIO7), indicated a preference for lower temperature fluctuations (Appendix C). This trend is echoed by the response curve for mean diurnal temperature range (BIO2), which was the third most important variable for this extent (10.3%; Table 2, Appendix C). The PCA biplot showed the precipitation variables (except precipitation seasonality, BIO15) clustered and positively correlated with PC1 (Figure 5).

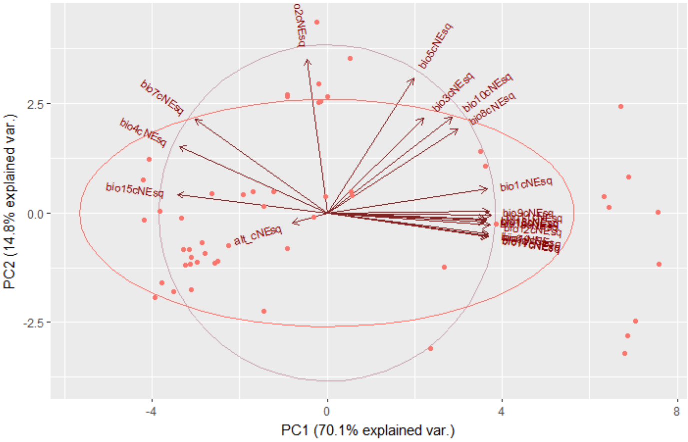

Figure 5: PCA biplot for the northeastern extent of *Juncus biglumis* distribution in North America.

MaxEnt analysis trained at the full continental extent revealed large-scale patterns of occurrence. The highest probabilities of occurrence were located in northwestern Alaska and the Rockies (Figure 3). There were also widespread areas of secondary importance in the Canadian islands north of the Arctic Circle. It is important to note that the MaxEnt heatmap showed areas of suitable habitat in the Sierra mountains of California, the Cascade mountains of the Pacific Northwest, the mountain ranges of central Nevada, and even as far south as the southernmost Sangre de Cristo mountains in New Mexico – areas with no occurrence records of *J. biglumis*. The two most important variables, mean temperature of the wettest quarter (BIO8) and annual temperature range (BIO7), occupied distinct areas of the PCA biplot, and thus contributed unique variance to the model (Figure 6).

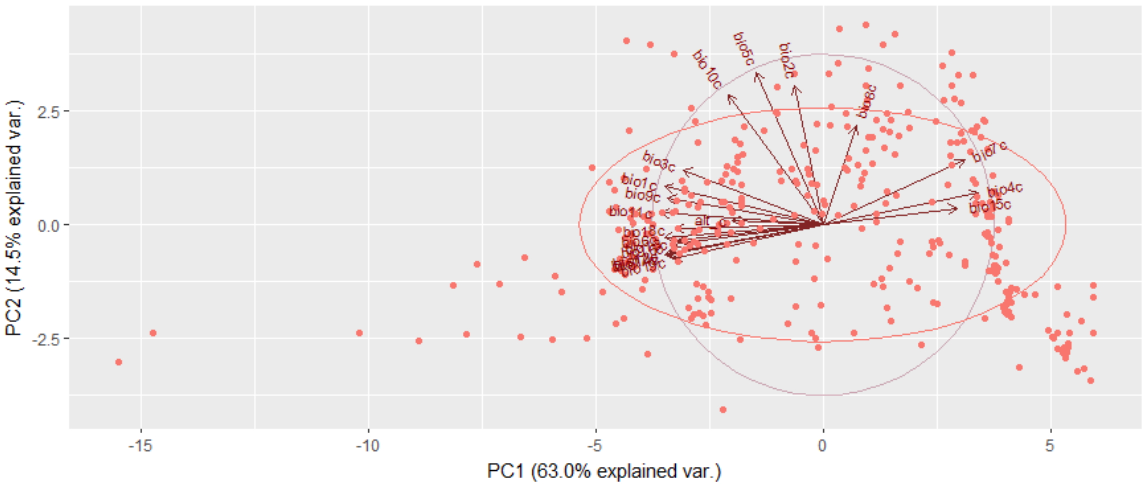

Figure 6: PCA biplot for the full continental extent of *Juncus biglumis* distribution in North America.

Future climate

The predicted shifts in suitable habitat did not follow a singular direction of change (i.e. shifts could not be explained solely in terms of increasing altitude or latitude). This phenomenon is shown in Figure 11 as a map of the changes in variable values (i.e., future values minus current values) rather than the absolute values of future occurrence probability.

Within the mountainous terrain of the southern extent, suitable habitat was predicted to decrease in some high-altitude areas as it became restricted to higher, cooler elevations, while other upland areas experienced an increase in suitable habitat (Figure 11). The most important variable for the southern extent in the future was altitude (50.6%; Table 2). Assuming altitude will not undergo significant changes within the next half century, however, it is more relevant to examine changes in the bioclimatic variables. Annual temperature range (BIO7) was the most important bioclimatic variable (26.9%; Table 2), and the corresponding response curve indicates that *J. biglumis* occurrence peaks at a lower annual temperature range (i.e., less fluctuations in temperature across the year; Appendix E). The PCA biplot showed two main groups of variables: the precipitation variables were positively correlated with PC1 while most of the temperature variables were negatively correlated with PC1. Notably, altitude was also positively correlated with PC1 and thus positively correlated with the precipitation variables (i.e., high-altitude occurrence points tend to experience high values for the correlated precipitation variables; Figure 7).

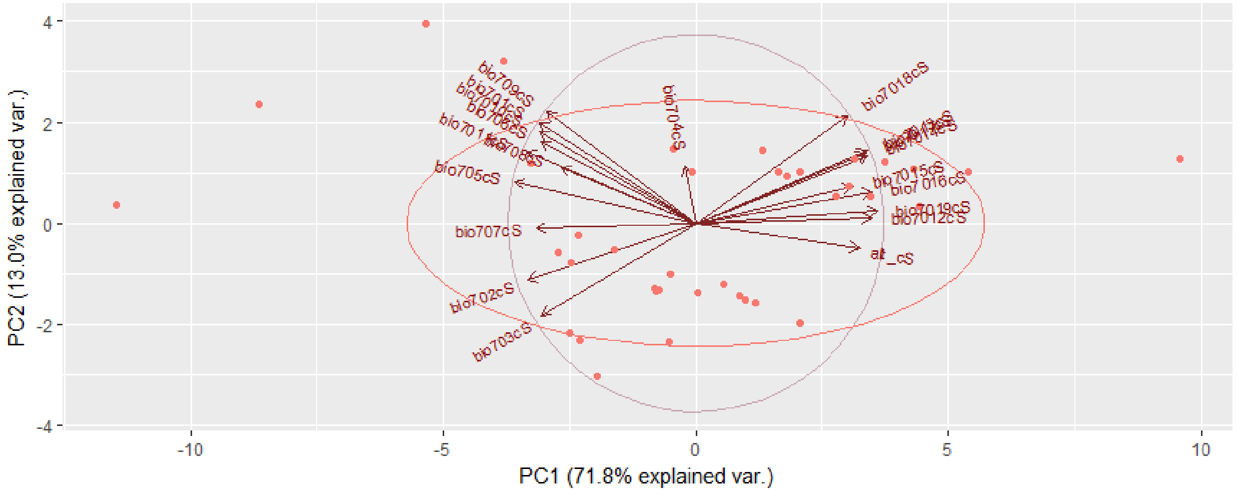

Figure 7: PCA biplot for the southern extent of *Juncus biglumis* distribution in North America under future climate conditions.

Like the southern extent, *J. biglumis* distribution in the northwestern region was predicted to decrease both in low-lying areas (e.g., the Yukon Delta in western Alaska) and in high-elevation areas (e.g., the Brooks Range of northern Alaska; Figure 11). The most important variables to the MaxEnt model were mean temperature of the wettest quarter (BIO8; 37.6%) and precipitation seasonality (BIO15; 13.9%; Table 2). The response curve for BIO8 showed a preference for mid-range temperatures (~ 5 °C); the curve dropped to zero at the upper end of the plot (~15 – 25 °C; Appendix F). The BIO15 response curve indicated a preference for high values of precipitation seasonality. Both BIO8 and BIO15 occupied distinct regions of the PCA biplot, and therefore contributed unique variance to the model (Figure 8).

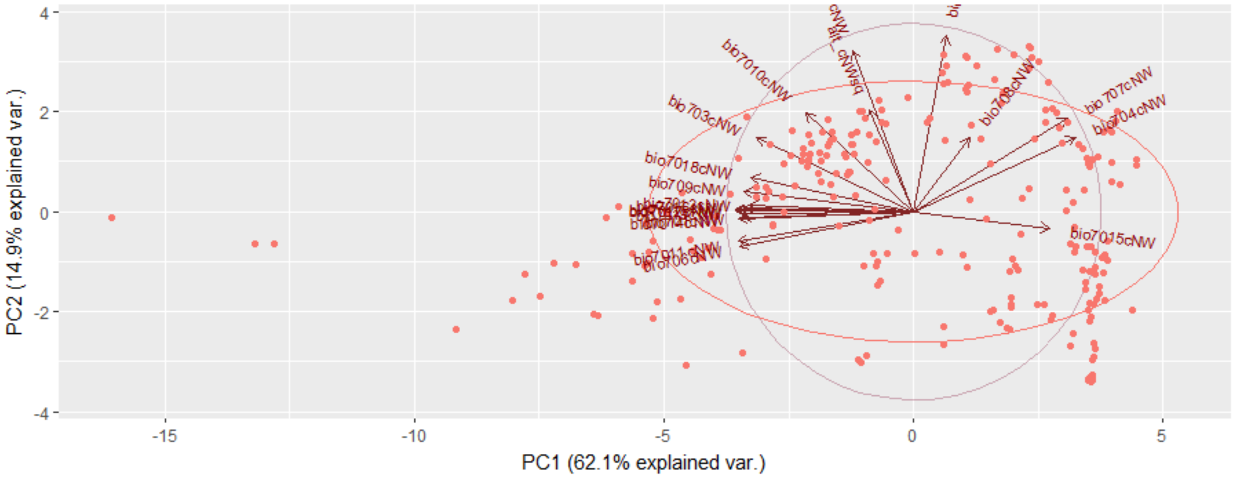

Figure 8: PCA biplot for the northwestern extent of *Juncus biglumis* distribution in North America under future climate conditions.

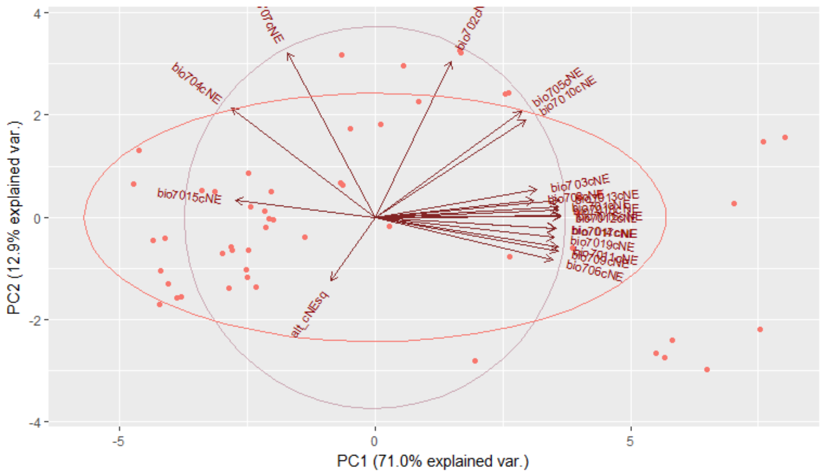

Figure 9: PCA biplot for the northeastern extent of *Juncus biglumis* distribution in North America under future climate conditions.

Many islands in the northeastern extent were predicted to experience an increase in suitable habitat at inland locations and a decrease along the coast (e.g., Baffin Island, Banks Island; Figure 11). Altitude was the most important variable to the MaxEnt model (59.9%), but the most important climatic variable was annual temperature range (BIO7; 27.3%; Table 2). Both altitude and BIO7 were strongly dominant in the MaxEnt model (Table 2) and also represented distinct variance as shown by the PCA biplot (Figure 9).

The shift in suitable habitat within the full continental extent was predicted to be similar to that shown within the individual extents. Alaska and northwestern British Columbia were predicted see the most dramatic shifts overall (Figure 11). The response curves for the two most important variables – mean temperature of the wettest quarter (BIO8; 41.4%) and mean temperature of the driest quarter

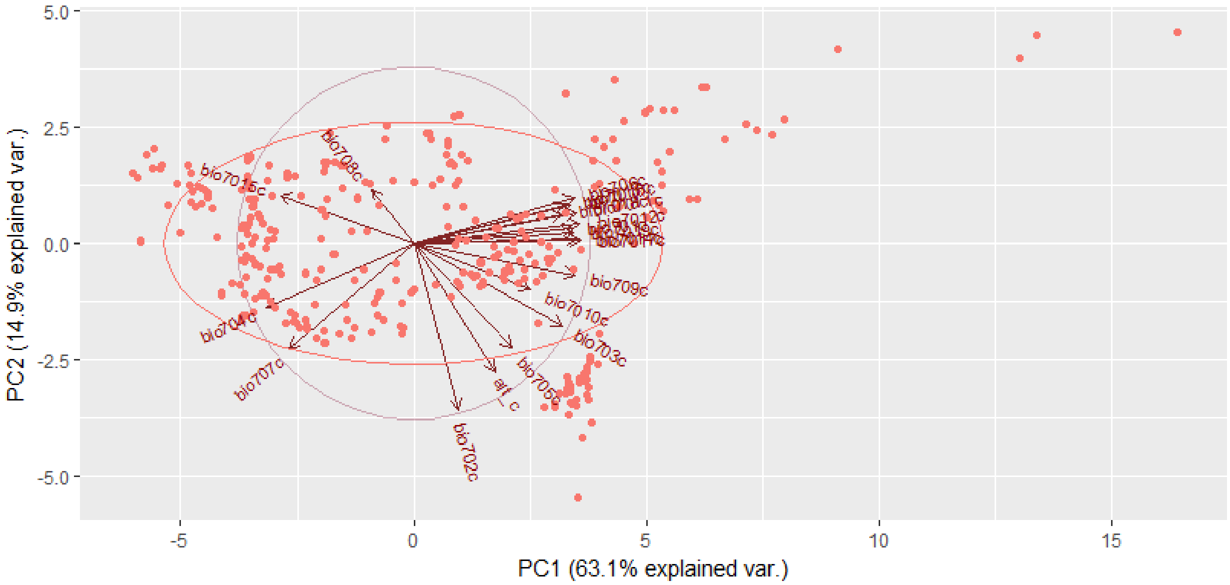

Figure 10: PCA biplot for the full continental extent of *Juncus biglumis* distribution in North America under future climate conditions.

(BIO9; 21.0%; Table 2) – showed that *J. biglumis* occurrence was predicted to peak at approximately 10.0 °C (Appendix H). The PCA biplot revealed strong correlations among precipitation variables, which were positively correlated with PC1 (Figure 10).

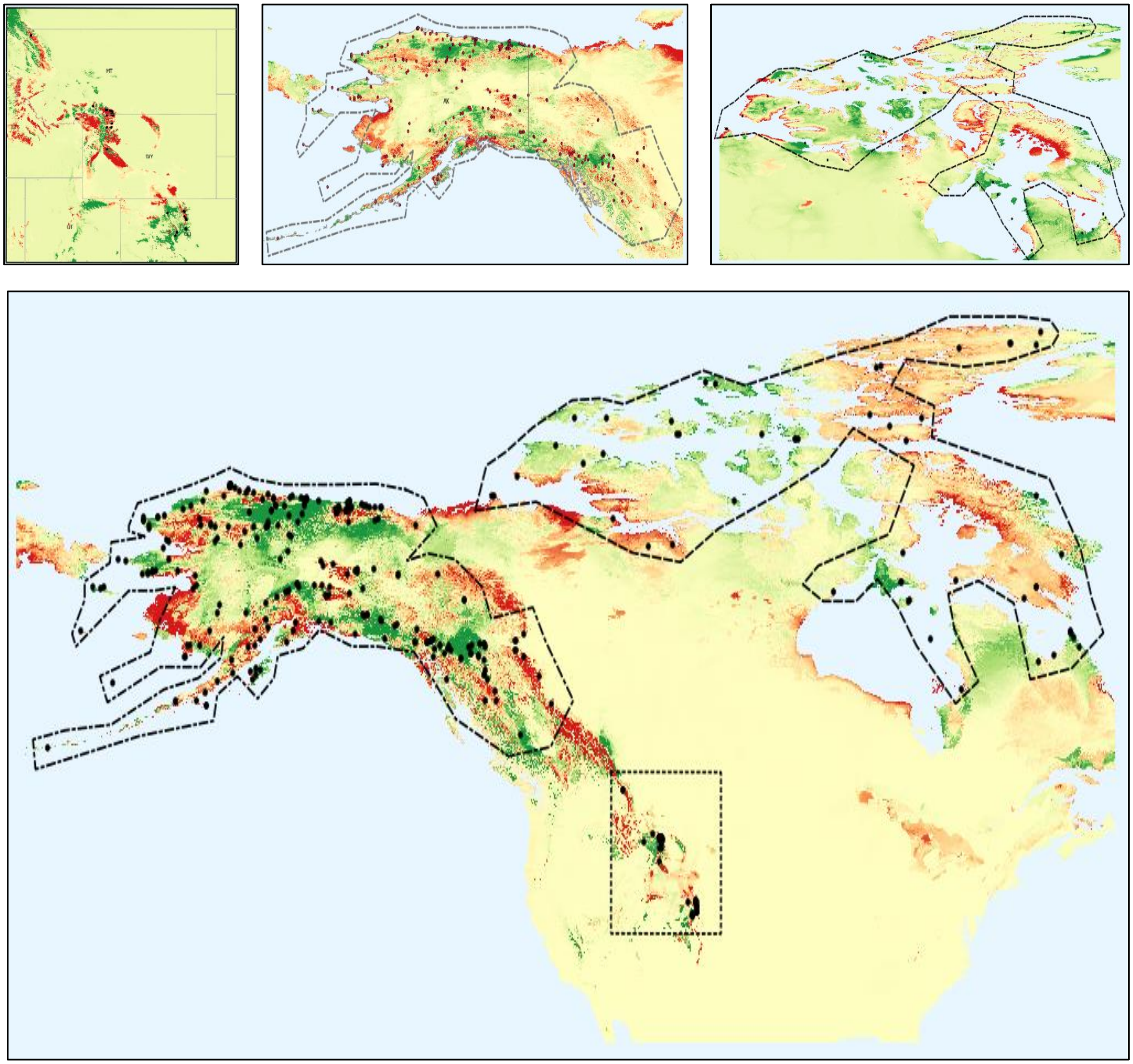

Figure 11: Maps displaying the change in suitable habitat for *Juncus biglumis* from present to 2070. Clockwise from top left: (i) southern extent, (ii) northwestern extent, (iii) northeastern extent, and (iv) full continental extent. Red indicates areas with a decrease in suitable habitat, green indicates areas with an increase in suitable habitat.

DISCUSSION

The environmental niche model for *J. biglumis* indicated that suitable habitat for the arctic-alpine rush species tends to be located at high elevations south of Arctic Circle and low elevations (i.e., sea level) north of Arctic Circle. In the current climate, *J. biglumis* prefers cold, wet winters and cool, dry summers, with low variation in both annual and diurnal temperature but high variation in annual precipitation. Under future climate conditions, the species is predicted to occupy habitat at lower altitudes (< 2000 m), and is expected to exhibit an increase in both annual and diurnal temperature variation, decreased annual precipitation seasonality (i.e. less variation in precipitation across the year), as well as a 5°C increase in both the minimum temperature tolerance (BIO6) and the mean wet season temperature (BIO8).

Current climate

The two variable groups revealed by the PCA biplot of the southern region can be interpreted to represent precipitation and temperature. PC1 is approximately equally correlated to both groups and therefore PC1 corresponds to a measure of climate for the region. Within the northwestern extent, a slightly complicated ecological niche is shown by comparing the response curves for annual temperature range (BIO7) and precipitation seasonality (BIO15; Figure 12): occurrence probability appears to increase as precipitation seasonality increases, but occurrence decreases as annual temperature range increases. This indicates that the species prefers relatively uniform temperatures throughout the year, with variations in precipitation across the year. The positive correlation of PC1 with both precipitation seasonality (BIO15) and temperature seasonality (BIO4) indicates that PC1 can be interpreted as a "seasonality" component (Figure 8). Variables that are placed near each other on a PCA biplot are

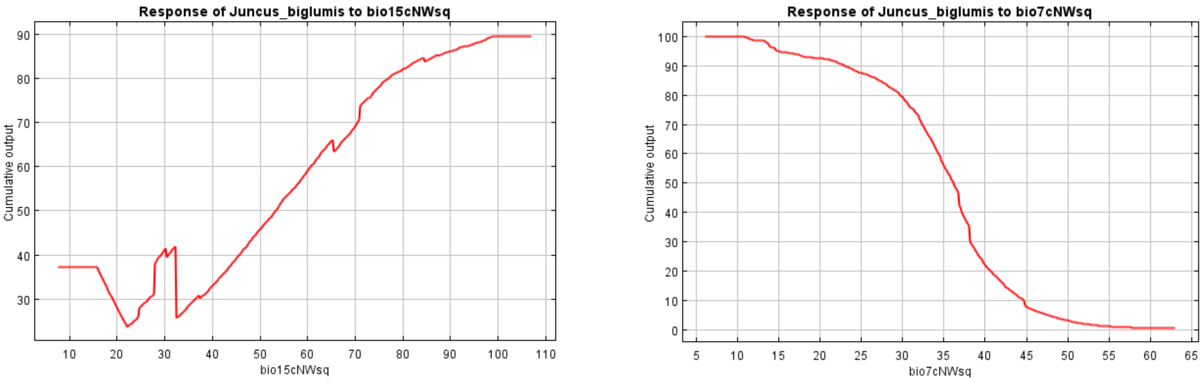

Figure 12: Response curves for Juncus biglumis occurrence compared to annual temperature range (BIO7; left) and precipitation seasonality (BIO15; right) for the northwestern extent under current climate

strongly correlated with each other. For example, occurrence points in the northwestern extent with high annual mean temperatures (BIO1) tend to have high annual precipitation (BIO12) and high maximum temperature of the warmest month (BIO5). All but two of these highly correlated variables (BIO6 and BIO9) were eliminated by the Pearson's correlation coefficient test, which provides validation to the elimination procedure. The northeastern extent represents the northernmost extreme of the species' range. The PCA biplot here can be interpreted such that occurrence points with high annual precipitation (BIO12) are likely to have low temperature seasonality (BIO4) and low annual temperature range (BIO7; Appendix C).

Future climate

Within the southern extent, the suitable habitat for *J. biglumis* will experience a decrease in variation of both annual precipitation and annual temperature, and an increase in the average temperature for both the wet season and the dry season (Appendix E). The climate for the suitable habitat within the northwestern extent appears to remain relatively unchanged. The only variable with significant differences between the two time periods is the mean temperature of the driest quarter (BIO9). This variable increases significantly: under current climate conditions, *J. biglumis* occurrence peaks between -27 °C and -10 °C, but in 2070, it will peak between -19 °C and 13 °C (Appendix F). This indicates that the species will occupy habitat in the northwestern region with a much warmer dry season. Similarly, few changes in bioclimatic changes were found within the northeastern region. The variables with significant differences were precipitation seasonality (BIO15), annual temperature range (BIO7), and mean temperature of the wettest quarter (BIO8). Both the annual variation in precipitation and temperature are expected to decrease, while the average temperature of the wet season is expected to increase (Appendix G).

Limitations

The suite of bioclimatic variables selected for this analysis could have been reduced. Although several variables consistently performed well (e.g., altitude, BIO8) others had consistently low contribution percentages (BIO2, BIO3) (Table 2). The low-performing variables also had little effect on the model when omitted, according to the jackknife plots of every extent. Thus, the model would have performed just as well without them. If I were to do this analysis again, I would remove BIO2 and BIO3, and perhaps consider including an absolute measure of temperature or precipitation, such as annual mean temperature (BIO1).

Merow et al. (2013) recommend that users consider the ecological basis for choosing the extent when running MaxEnt. As seen in the continental extent for both current and future climates, the suitability heatmap indicated areas that *J. biglumis* should theoretically currently occupy and can be expected to occupy in the future (e.g., the Cascade Mountains of the Pacific Northwest). Those areas, however, are likely not within the dispersal capacity of the species due to a lack of continuous habitat from its current range to the coastal area (Marr et al. 2012). This analysis might be improved by adjusting the MaxEnt settings for selecting background points, so that only the range of potential habitat is available (Merow et al. 2013).

Similarly, assumptions about sampling procedures will affect the construction of the model. Unless input adjustments are made, MaxEnt assumes a uniform likelihood that any point within a given extent can be sampled (Merow et al. 2013). This assumption, however, does not match the reality that sampling bias is frequently present in the collection of herbaria specimens. Merow et al. (2013) recommend accounting for sampling bias in occurrence datasets as often as possible when using MaxEnt. Because little was known about sampling procedures for all occurrence records used in this study, it was not feasible to account for sampling bias.

Future research

This research contributes to the body of literature addressing arctic-alpine plant species' response to climate change and the concept of future climate change refugia. Future research should further investigate the altitude-latitude link by including a latitude variable or exploring the connection between high-altitude/low-latitude and low-altitude/high-latitude habitat. Future research should also be directed towards developing an understanding the drivers of habitat change at a fine spatial scale. Understanding the characteristics of climate refugia, both for individual taxa as well as biological communities, has significant implications for conservation of cold-adapted species.

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