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Integrating ensemble species distribution modeling and statistical phylogeography to inform projections of climate change impacts on species distributions

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**INTEGRATING ENSEMBLE SPECIES DISTRIBUTION MODELING AND
STATISTICAL PHYLOGEOGRAPHY TO INFORM PROJECTIONS
OF CLIMATE CHANGE IMPACTS ON SPECIES DISTRIBUTIONS**

By

Brenna R. Forester

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

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MASTER'S THESIS

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Brenna R. Forester

April 23, 2012

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A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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Brenna R. Forester
April 2012

ABSTRACT

Species distribution models (SDMs) are commonly used to forecast climate change impacts on species and ecosystems. These models, however, are subject to important assumptions and limitations. By integrating two independent but complementary methods, ensemble SDMs and statistical phylogeography, I was able to address key assumptions and create robust assessments of climate change impacts on species' distributions while improving the conservation value of these projections.

This approach was demonstrated using *Rhodiola integrifolia*, an alpine-arctic plant distributed at high elevations and latitudes throughout the North American cordillera. SDMs for *R. integrifolia* were fit to current and past climates using eight model algorithms, two threshold methods, and between one and three climate data sets (downscaled from general circulation models, GCMs). This ensemble of projections was combined using consensus methods to create a map of stable climate (refugial habitat) since the Last Interglacial (124,000 years before present).

Four biogeographic hypotheses were developed based on the configuration of refugial habitat and were tested using a statistical phylogeographic approach. Statistical phylogeography evaluates the probability of alternative models of population history given uncertainty about past population parameters, such as effective population sizes and the timing of divergence events. The multiple-refugia hypothesis was supported by both methods, validating the assumption of niche conservatism in *R. integrifolia*, and justifying the projection of SDMs onto future climates.

SDMs were projected onto two greenhouse gas scenarios (A1B and A2) for 2085 using climate data downscaled from five GCMs. Ensemble and consensus methods were used to illustrate variability across these GCMs. Projections at 2085 showed substantial losses of climatically suitable habitat for *R. integrifolia* across its range. Southern populations had the greatest losses, though the biogeographic scale of modeling may overpredict extinction risks in areas of topographic complexity. Finally, past and future SDM projections were assessed for novel values of climate variables; projections in areas of novel climate were flagged as having higher uncertainty.

Integrating molecular approaches with spatial analyses of species distributions under global change has great potential to improve conservation decision-making. Molecular tools can support and improve current methods for understanding species vulnerability to climate change, and provide additional data upon which to base conservation decisions, such as prioritizing the conservation of areas of high genetic diversity in order to build evolutionary resiliency within populations.

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Introduction

Anthropogenic climate change is impacting ecosystems worldwide, generating a global signal of climate-induced range shifts and phenological responses crossing all ecosystems and taxonomic groups (Hughes 2000; Parmesan and Yohe 2003; Root et al. 2003; Parmesan 2006, 2007; Chen et al. 2011). Forecasting impacts on species distributions has important conservation implications, as scientists and managers try to determine the best strategies for preserving habitat for imperiled species and maintaining ecosystem functioning. Species distribution models (SDMs) have become one of the most accessible and widely used tools to develop these forecasts (Franklin 2009; Zimmermann et al. 2010).

Correlative SDMs are based on the principle that climate constrains species' distributions within their biogeographic and evolutionary history (Woodward 1987; Webb and Bartlein 1992). They are created by extracting a relationship between a species' observed distribution and climate and environmental variables. That relationship can then be projected onto models of current climate to determine the geographic distribution of climatically suitable habitat. Predictive distributions are created by projecting that same relationship onto models of past or future climate.

SDMs are also known as niche models, reflecting their foundation in the fundamental and realized niche concepts first described by Hutchinson (1957). There is a growing literature dedicated to understanding which parts of the niche are being modeled with SDMs (Araújo and Guisan 2006; Kearney 2006; Soberón 2007, 2010; Colwell and Rangel 2009), however this debate is far from consensus. I favor the interpretation of Soberón (2007, 2010) who recognizes three primary factors affecting the distribution of species: (1) the spatial distribution of favorable environmental conditions, (2) the biotic environment, including

predators, competitors, facilitators, etc., and (3) the dispersal capability of the species. He terms the first of these factors the Grinnellian niche (operating at broad geographic scales), the second the Eltonian niche (operating at local scales), while the third introduces the potential for metapopulation structure and source-sink dynamics. In this interpretation, SDMs at biogeographic scales are representations of the Grinnellian niche (niche as habitat rather than function), which interacts at finer scales with both the Eltonian niche and dispersal capability/source-sink dynamics. Because of these interactions, correlative SDMs based on climate variables potentially model both Hutchinson's realized niche (Hutchinson 1957) and sink habitats that are accessible because of dispersal capabilities.

Under this framework, SDM output at biogeographic scales is best described as the distribution of climatically suitable habitat for a species, rather than a representation of a species' niche. While the inclusion of occurrence records from sink populations will introduce error in correlative models, the assumed small number of these records relative to source records and the coarse scale (and broad extent) of modeling are generally thought to minimize their contribution to overall error rates (Franklin 2009).

Despite their widespread use, SDMs have many technical limitations, including problems handling historical demographic signals, biotic interactions, and changing combinations of climate variables, and theoretical assumptions, such as species-climate equilibrium and niche conservatism (Jackson et al. 2009; Wiens et al. 2009). Furthermore, recent papers have argued that SDMs provide only a starting point for understanding species' responses to climate change and planning adaptive management strategies to conserve biodiversity (Franklin 2010; Scoble and Lowe 2010; Dawson et al. 2011).

One proposal for the improvement of SDMs is to integrate phylogeography, which examines the current geographic distribution of genetic variation within and between populations to infer demographic history and how paleoclimatic events may have impacted population divergence (Avice 2000). For example, Pleistocene glacial cycles generated periods of expansion and contraction of species ranges, leaving a genetic fingerprint on current populations (Davis and Shaw 2001). The geographic distribution of current genetic variation depends on how species responded to these climate oscillations, the number, location, and size of refugia, the connectivity among populations, dispersal capabilities, and rates of recolonization (Hewitt 2000).

Phylogeography is most often used to determine the impact of Pleistocene glacial cycles on genetic variation within species or among groups of species, including the identification of migration barriers, long-term refugia (areas where species persist for at least an entire glacial-interglacial cycle), and suture zones (regions where lineages that were isolated in the past now meet) (Scoble and Lowe 2010). Phylogeographers have started to use SDMs to generate paleodistribution models, with which they develop spatially explicit biogeographic hypotheses which can be tested using statistical phylogeographic methods (Carstens and Richards 2007; Richards et al. 2007). Statistical phylogeography evaluates the probability of alternative models of population history given uncertainty about past population parameters, such as effective population size. The outcome of these efforts includes an improved understanding of the mechanisms creating patterns of biodiversity, as well as the patterns and timing of divergence and speciation events (Hugall et al. 2002; Knowles et al. 2007; Waltari et al. 2007; Dépraz et al. 2008; Chan et al. 2011).

Ecologists looking to model future impacts of climate change on species distributions can integrate phylogeographic approaches to address one of the fundamental problems with SDM projections: the assumption that these models can accurately project species distributions over time. For many reasons, an SDM that performs well on current data cannot be presumed to perform well on projected climate data (Heikkinen et al. 2011), though this assumption is routinely made. Reciprocal inferences derived from SDMs and statistical phylogeography can be used to provide support for a model's ability to accurately project distributions over time.

Phylogeographic analyses can help address other important SDM assumptions and limitations, including niche conservatism and dispersal capability. Niche conservatism is the tendency of a species to retain its climatic niche over time (Wiens et al. 2010). This is a fundamental assumption of projecting SDMs, since projection of a labile species-climate relationship into the future (or past) would be inappropriate. Dispersal capability is another limiting factor; SDM projections usually assume either unlimited dispersal or none at all. In some cases, the differences between these projections can be significant, contributing to uncertainty (for example, Thomas et al. 2004; Engler and Guisan 2009). Phylogeographic analyses can provide a species-specific metric of dispersal capability with which SDM projections can be constrained.

Finally, the detection of refugia and past barriers to dispersal has important conservation applications. Long-term refugia tend to be geographic locations with high levels of allelic diversity (Stewart et al. 2010). Locating past barriers can result in the identification of suture zones, which have been shown to support high levels of

diversification and speciation (Hewitt 1996; Moritz et al. 2009). Including these locations in conservation planning can help build evolutionary resiliency within populations, mediating extinction risks (Klein et al. 2009; Sgro et al. 2011).

Only a few studies have used the combination of SDMs and phylogeography to both understand the impact of paleoclimatic events on species distributions and assess future climate change impacts (Cordellier and Pfenninger 2009; Galbreath et al. 2009). These authors typically employ accessible and user-friendly approaches to species distribution modeling, such as Maxent modeling software (Phillips et al. 2006; Phillips and Dudik 2008) and interpolated climate data from WorldClim (Hijmans et al. 2005). However, the growing literature devoted to improving SDMs has indicated that the two greatest sources of uncertainty in SDM projections are the choice of model algorithm and the general circulation model (GCM) used for climate forecasting (Diniz-Filho et al. 2009; Buisson et al. 2010). For this reason, the use of a single model algorithm and a single GCM to project changes in species' distributions has been critiqued (Nogués-Bravo 2009).

A recent approach to addressing this uncertainty is ensemble modeling combined with consensus projections, for example, taking the mean of projections, or using a model “voting” approach (Araújo and New 2007; Marmion et al. 2009). Ensemble modeling is based on the idea that different combinations of initial conditions, model algorithms, and GCMs represent alternate possible states of the system being modeled (Araújo and New 2007). When these are combined using consensus methods (such as the mean of all models), they can form a more accurate projection, outperforming single models (Marmion et al. 2009; Grenouillet et al. 2011). This assumes that the included models meet some standard of

“good” performance, since increased accuracy would not be expected simply by combining poor models (Araújo et al. 2005).

Ensemble modeling and consensus projections are particularly well-suited to temporal and spatial projection of SDMs. Research has indicated that single models that have the best performance on current data will not necessarily provide the most accurate future projections, and that consensus projections can more effectively model observed range shifts (Thuiller 2004; Araújo et al. 2005). Furthermore, some algorithms are better at extrapolation modeling, where variables are outside the range used to build the models (Marmion et al. 2009; Heikkinen et al. 2011). While projection of SDMs onto these “novel climates” is discouraged (Fitzpatrick and Hargrove 2009; Elith et al. 2010), it is usually unavoidable since novel combinations of temperature and precipitation are highly likely over forecast periods (~100 years) on the spatial scale of most SDM studies (Williams et al. 2007). Detecting areas of non-analog climates and indicating larger levels of uncertainty in those areas is essential to producing robust projections of climate change impacts.

Another important component of improving SDMs (ensemble or otherwise) is incorporation of an ecological understanding of how the environment shapes patterns of species distributions. The selection of biologically appropriate, functionally-relevant predictor variables has been emphasized by many authors (for example, Guisan and Zimmermann 2000; Austin 2002; Lookingbill and Urban 2005; Austin and Van Niel 2011). For example, these include “plant-relevant variables” such as radiation, temperature and soil moisture, as opposed to their “physical proxy variables” like aspect, elevation and topographic convergence (Lookingbill and Urban 2005). Unfortunately, selection of

ecologically relevant predictors is not addressed by many SDM practitioners. Part of this is a consequence of the easy availability of pre-calculated gridded predictor variables (for example, the 19 bioclimatic variables that make up the online WorldClim database (Hijmans et al. 2005)), as well as an assumption that the model algorithm will choose the most important predictive variables. This last assumption is particularly problematic, since including multiple correlated predictors (for example, mean temperatures for each month) can result in serious errors, including a bias for autocorrelated variables and coarse-scale over fine-scale predictors (Franklin 2009).

In this study, I combined ensemble modeling and consensus projections with statistical phylogeographic analyses to assess past and future climate change impacts on the geographic distribution of an alpine-arctic plant. Alpine and arctic species have responded to climate oscillations throughout their evolutionary history. However, the speed of anthropogenic climate change will challenge species responses through migration, dispersal, and genetic adaptation, by shifting habitat conditions more rapidly than in the past (Davis and Shaw 2001). Alpine species, with distributions defined by steep climatic gradients, are being disproportionately impacted by these changes (Nogués-Bravo et al. 2007; Lenoir et al. 2008; Engler et al. 2009; Dirnbock et al. 2011). In alpine and arctic systems, these range shifts will likely result in increasingly fragmented and reduced habitat as species move higher in elevation and latitude. The consequence for many local populations will be extirpation as they run out of high elevation and high latitude habitat.

For this analysis, I modeled the distribution of suitable habitat for *Rhodiola integrifolia* Raf. (Crassulaceae), roseroot or king's crown. *R. integrifolia* is a succulent,

perennial alpine-arctic specialist. It has a widespread, patchy distribution at high altitudes and latitudes throughout the North American Cordillera, from the Sierra Nevada Mountains in California, east to the Rocky Mountains, and north to the alpine tundra of Alaska and Siberia (Clausen 1975). Habitats include rocky slopes, alpine meadows and arctic tundra, with plants rooting in rock crevices or in shallow soil and gravel (Clausen 1975). This species reproduces by wind-dispersed seeds and can also propagate vegetatively at the root stock (Clausen 1975). I chose this species for analysis because of its widespread spatial distribution and climatic restriction to alpine and arctic areas.

The purpose of this research was to illustrate how the integration of ensemble SDMs and phylogeography can yield robust assessments of climate change impacts on species' distributions and provide additional information important for conservation. These reciprocally inferential approaches were used to model the effect of past and future climate change on the geographic distribution and genetic variability of *R. integrifolia*. My objectives were to:

1. Develop a model of climatically stable refugial areas in western North America for *R. integrifolia* over the last 124 kya (kya, thousand years ago).
 - a. Determine the geographic distribution of climatically suitable habitat using an ensemble modeling approach at four time periods: current, mid-Holocene (6 kya), Last Glacial Maximum (21 kya), and Last Interglacial (124 kya).
 - b. Establish the locations of potential refugia (areas of stable climate) over the past 124 kya.
 - c. Assess the impact of novel values of climate variables on this refugial model.

2. Evaluate the level of agreement between the SDM refugial model and empirical genetic data using a statistical phylogeographic approach.
 - a. Develop biogeographic hypotheses (models of population history) based on the geographic distribution of potential refugial habitat.
 - b. Test these alternate hypotheses using statistical phylogeography; determine which hypothesis is best supported by the genetic data.
 - c. If phylogeographic analyses and SDM projections disagree, assess the potential for dispersal barriers, lack of niche conservatism, and/or modeling errors.
 - d. If phylogeographic analyses and SDM projections agree, the ability of the SDMs to project over time and changing climates is supported; SDMs can be projected onto future climates.

3. Assess the impact of future climate change scenarios on the geographic distribution of climatically suitable habitat for *R. integrifolia* in western North America.
 - a. Project the impact of future climate change on suitable habitat using multiple general circulation models and greenhouse gas scenarios.
 - b. Assess the impact of novel values of climate variables on future projections.

Statistical phylogeography in combination with ensemble SDMs has great potential for improving our understanding of how species will respond to ongoing climate change.

Including molecular approaches allows us to better understand how species have responded to past climate fluctuations and plan more effective conservation strategies for the future.

Methods

Spatial and temporal scales

The spatial extent of this analysis was the North American Cordillera, extending from approximately 30°N to 80°N, and -180°W to -99°E. This extent includes the entire latitudinal distribution of *R. integrifolia* and a large part of its longitudinal distribution, an important means of minimizing bias in model projections (Barbet-Massin et al. 2010).

Spatial resolution was 0.5°. This relatively coarse pixel size was chosen to balance “resolution with realism” (Daly 2006) when downscaling climate data from general circulation models (GCMs). At scales finer than 0.5°, complex physiographic factors impact climate, including elevation, terrain features, cold air drainage, and coastal influences (Daly 2006). It is very difficult to account for these impacts when interpolating climate data from GCMs (typically generated at 2 to 3° resolution) to resolutions finer than 0.5°. Furthermore, coarse spatial resolutions minimize the effects of biotic interactions and source-sink dynamics, which typically occur at finer scales (Pearson and Dawson 2003; Soberón 2010). The tradeoff with this approach is that resolution is lost in complex terrain, such as mountain ranges, since the 0.5° pixel size averages climate over these heterogeneous areas. This must be taken into consideration when interpreting results.

Past, current and future distribution models were created for *R. integrifolia* (see below). Paleodistributions were created for the Mid-Holocene (6 kya), the Last Glacial Maximum (LGM, 21 kya), and the Last Interglacial (LIG, 124 kya). Current distributions were based on mean climatology from 1971-2000. Future distributions were based on mean

climate values projected for 2071-2100 (hereafter referred to as “2085”) under two greenhouse gas scenarios.

Occurrence records

Georeferenced occurrence records for *R. integrifolia* (including ssp. *integrifolia*, ssp. *procera*, and ssp. *neomexicana*) and its taxonomic synonyms were collected from six online herbarium databases: Arctos (<http://arctos.database.museum/>), the Oregon Flora Project (www.oregonflora.org), the Consortium of California Herbaria (www.ucjeps.berkeley.edu/consortium), the Rocky Mountain Herbarium (www.rmh.uwyo.edu), the University of British Columbia Herbarium (www.beatymuseum.ubc.ca/herbarium), and the University of Washington Herbarium (www.washington.edu/burkemuseum/collections/herbarium). Records were plotted on topographic maps in ArcMap (ESRI 2010) and visually inspected for obvious georeferencing errors. Georeferencing was evaluated and modified, if needed, on a subset of the records, yielding 554 total records. For modeling, one record was used per pixel, producing a final data set of 269 records (Figure 1a).

Phylogenetic analysis of all *R. integrifolia* subspecies by DeChaine et al. (*in prep*) showed a deep divergence (dating to approximately 500 kya) between the clade located in Colorado and New Mexico (currently represented as *R. integrifolia* ssp. *integrifolia*, ssp. *procera*, and ssp. *neomexicana*) and all other populations of *R. integrifolia*. Because of this deep divergence and the limitation of SDM paleodistributions to the LIG, records from Colorado and New Mexico were excluded from this analysis. Additionally, this analysis did not include ssp. *leedyi*, a relict subspecies confined to cold air seeps located along dolomite cliffs in Minnesota and New York. The extremely small range and microhabitat

specialization of this subspecies is not conducive to the spatial scale used in this analysis. The *leedyi* subspecies is included in the phylogenetic analysis (DeChaine et al. *in prep*).

Climate data and interpolation

Eight climate models were used in this analysis, covering five time periods (Table 1). When available, monthly global data were accessed for the following variables: total precipitation rate, mean surface air temperature, maximum surface air temperature, and minimum surface air temperature. Standard deviations of climate variables were also calculated. Detailed information on climate data sets and processing are available in Appendix A.

Anomalies were calculated for past and future climate data. Absolute anomalies (past-present and future-present) were calculated for temperature variables, while relative anomalies were calculated for precipitation (past/present and future/present). Anomalies were interpolated globally to a 0.5° pixel size using ordinary cokriging in ArcMap (ESRI 2010). CRU TS 2.1 climate data were used as the secondary cokriging dataset. The “Optimize Model” setting was used for each layer (minimizing the mean square error), and the search neighborhood for the climate layer was set to 12 maximum and 2 minimum neighbors with semiaxes settings of 20. The CRU dataset was set to a search neighborhood of 5 maximum and 2 minimum neighbors, with semiaxes set to 20. These settings were chosen to minimize error rates. Interpolated anomalies were applied to CRU climate data to create the final normalized climate layers for each time slice. Negative precipitation values were set equal to zero. Cokriging root mean square errors are reported in Appendix B. The

LGM ice layer is from Dyke et al. (2003) and corresponds well with the coarse ice sheet data provided with the LGM climate models (not shown).

Table 1: Climate data used to model the distribution of suitable habitat for *R. integrifolia*.

Time period	Model	Reference	Source
Current (1971-2000)	CRU TS 2.1	Mitchell and Jones 2005	University of East Anglia Climatic Research Unit
Mid Holocene (6 kya)	CCSM 3	Otto-Bliesner et al. 2006	Paleoclimate Modelling Intercomparison Project Phase 2 (Braconnot et al. 2007)
	HadCM3 UBRIS	Gordon et al. 2000	
	MIROC 3.2	K-1 model developers 2004	
Last Glacial Maximum (21 kya)	CCSM 3	Otto-Bliesner et al. 2006	Bristol Research Initiative for the Dynamic Global Environment
	HadCM3	Gordon et al. 2000	
	MIROC 3.2	K-1 model developers 2004	
Last Interglacial (124 kya)	HadCM3	Gordon et al. 2000	Coupled Model Intercomparison Project Phase 3 (Meehl et al. 2007)
	BCCR BCM 2.0	www.bjerknes.uib.no	
	CSIRO Mk3.5	Gordon et al. 2002	
	HadGEM1	Johns et al. 2006	
	IPSL CM4	Marti et al. 2009	
Future (2071-2100)	MIROC 3.2	K-1 model developers 2004	World Data Center for Climate, Hamburg, Germany

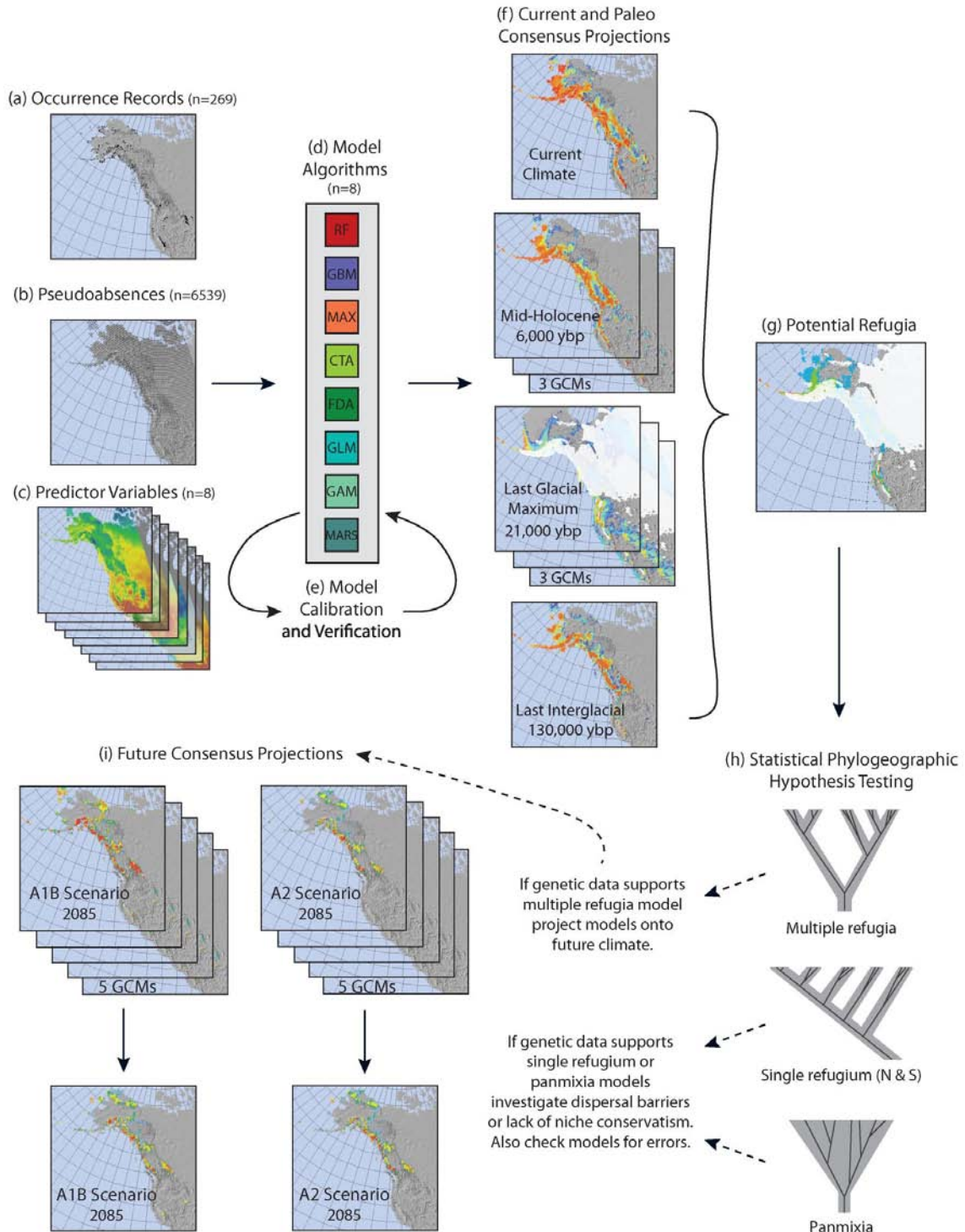


Figure 1: Methods for ensemble species distribution modeling of refugial areas for *R. integrifolia* since the Last Interglacial (a-g); use of the refugial model to develop biogeographic hypotheses for phylogeographic analysis (h); projection of verified models onto future climate, using an ensemble of GCMs (i).

Predictor variables

In this study, 60 potential predictor variables were calculated that are relevant to plant life generally and alpine species in particular. These included growing degree days, chilling period, seasonal snowpack, and annual and seasonal indices of precipitation and temperature. Snowpack was calculated using methods developed by Lutz and colleagues (2010). Recent research has shown that including measures of extreme climate events, as opposed to just climate variability, can greatly improve the prediction of species distributions, especially at range limits (Zimmermann et al. 2009). To incorporate measures of climate extremes, the standard deviations of temperature and precipitation were calculated, based on methods used by Zimmermann and colleagues (2009). Unfortunately calculation of actual evapotranspiration and water deficit, which account for the seasonal timing of water supply and energy input (Stephenson 1998) could not be calculated due to a lack of required inputs from paleoclimate data sets.

Of the 60 calculated predictor variables, the most relevant were identified using the randomForest package (Liaw and Wiener 2002) in R (R Development Core Team 2011). Random forest is an ensemble modeling approach based on classification and regression trees; it builds multiple trees using random subsets of the observations and predictor variables and then averages (regression) or tallies (classification) them. Random forest incorporates measures of variable importance that are increasingly being used for variable selection in a wide variety of applications because of their flexibility (e.g. variables are assessed both independently and using a multivariate approach among variables, Strobl et al. 2008). However, correlation between predictor variables can impact random forest variable

importance measures, so recommendations to address this problem by Strobl and colleagues (2008) were followed, including using multiple values of *mtry* (the number of variables randomly sampled at each split) as well as a large number of trees (5000). Absences were chosen at random to equal the number of presence records. Random forest was run 100 times with 5000 trees at the following values of *mtry*: 5, 10, 20, 30, 40, 50, 55, and 60. Gini importance and mean decrease accuracy scores were output and averaged over 100 runs for each value of *mtry*. Variables were chosen based on variable importance scores as compared across *mtry* values. Spearman's correlation was used to remove variables that were correlated at rho values greater than $|0.8|$. Of the 60 potential predictor variables, eight were chosen for modeling (Figure 1c, Results: Table 2).

Species distribution modeling and evaluation

Modeling was conducted using the BIOMOD package (Thuiller et al. 2009) in R and Maxent, v. 3.3.3 (Phillips et al. 2006; Phillips and Dudik 2008). Nine model algorithms were run, representing three types of analysis: (1) regression methods, including generalized linear models (GLM), generalized additive models (GAM), and multivariate adaptive regression splines (MARS); (2) classification methods, including classification tree analysis (CTA) and flexible discriminant analysis (FDA); and (3) machine learning methods, including artificial neural networks (ANN), generalized boosted models (GBM, also called boosted regression trees), random forest (RF), and maximum entropy (Maxent). All models except Maxent were run using BIOMOD.

GLMs were run with a binomial error distribution with logit link and were fitted with

linear and quadratic terms; stepwise AIC criteria were used for model selection. GAMs were run with a binomial error distribution with logit link and were fitted with nonparametric smoothing splines (four degrees of smoothing). MARS models were fit with a maximum interaction degree of two on the forward stepwise pass, with backward stepwise pruning of these models based on generalized cross-validation. CTA models were run with 50 cross-validations. FDA was run using the MARS regression method for optimal scaling. ANN models used five cross-validation runs. GBM models were run using a Bernoulli distribution (logistic regression for binary data), 5000 trees, and five cross-validation runs. RF models were run with 750 trees and an *mtry* value of four.

Independent validation data are required to assess the predictive performance of models. In the absence of independent data, data partitioning can be used to assess model stability and the sensitivity of the model results to initial conditions (Araújo and Guisan 2006; Thuiller et al. 2009). Data were partitioned using the heuristic reported in Fielding and Bell (1997): $[1 + (p - 1)^{1/2}]^{-1}$, where p is the number of predictor variables. This corresponded to a calibration data set using 70% of the original data, with 30% reserved for verification. For models run in BIOMOD, ten data partitions were run for each model using random selections (with replacement) for calibration and verification (Figure 1e). Because the removal of presence records has a negative effect on model projections, final consensus models were built using 100% of the available data (Araújo et al. 2005).

Maxent was run twice. The first run included ten bootstrapped replicates using a random test percentage of 30% of the sample records and the random seed setting (ensuring different random partitions for testing and training). These runs were used to calculate test

statistics (AUC and sensitivity, see below). The second run used all of the presence records to train the model; this run was used in model ensembles. In both runs, the number of maximum iterations was 500 and the convergence threshold was 0.00001 (following recommendations by Phillips and Dudik 2008).

For all models, the entire background of the study area was used to create pseudo-absence points (6539 background points, Figure 1b). The entire area was chosen to ensure complete sampling of environmental conditions in the study area. By training the model on a broad combination of predictor variables, climatic extrapolation is minimized when projecting onto different climates. For all models, background records were weighted to maintain the number of presence records equal to the number of background records (prevalence = 0.5). Weighting pseudo-absence records to maintain equal prevalence has been found to maximize model performance using simulated species distributions (Barbet-Massin et al. 2012).

The area under the curve of the receiver operating characteristic (AUC, Fielding and Bell 1997) and sensitivity (also known as true positive fraction) were used to assess model accuracy and stability. When using true absence data, AUC quantifies the ability of a model to discriminate presence from absence (Fielding and Bell 1997). When using pseudo-absence data, AUC instead determines if the model can classify presence records more accurately than random prediction (Phillips et al. 2006). AUC is a threshold-independent measure with values that range from 1 (perfect classification) to 0.5 (no better than random).

Maxent uses a slightly different approach to calculating AUC compared to BIOMOD, which may result in marginally inflated AUC values. Sensitivity was calculated to compare

all models using identical methods. Sensitivity is a threshold-dependent measure; it requires that probabilistic output be converted to presence/absence data in order to calculate the proportion of observed occurrences that are correctly predicted (true positives / (true positives + false negatives)). To convert probabilities to presence/absence, the mean probability value across model output was used; this is a simple threshold method that has been shown to be robust in threshold comparisons (Liu et al. 2005). Because high sensitivity can be achieved simply by predicting suitability across large parts of the study area, sensitivity values must be tested for statistical significance. An exact one-tailed binomial test was used to calculate the probability of obtaining sensitivity values by chance. Significant tests ($p < 0.05$) indicate that the model is classifying presence better than a random expectation, given the proportion of pixels predicted present (Anderson et al. 2002).

Evaluation statistics were averaged across the ten cross-validation runs and used to assess the internal consistency of the models, and determine if models should be removed from the consensus analysis. Models with mean AUC and mean sensitivity > 0.7 were determined to be useful and were kept in the consensus analysis (Figure 1d). Model projections were also inspected individually to ensure they were ecologically realistic. Evaluation statistics were calculated for the current consensus model (an ensemble of 16 binary models, see below) to compare the performance of the consensus model against the single models.

Paleodistributions and the refugial model

Models for *R. integrifolia* were projected onto current climate and models of past climate, including three GCMs each for the Mid-Holocene and LGM, and one GCM for the LIG (Figure 1f). Model output is probabilistic, indicating the probability of suitable habitat in a given pixel. These probabilities were converted to presence/absence predictions in order to assess the presence or absence of suitable habitat across all time slices in each pixel. Two thresholds were used: a threshold that minimizes the absolute value of sensitivity minus specificity (minSeSp), and the mean probability value across model output (mean). Both of these methods have been shown to perform well in threshold comparisons (Liu et al. 2005).

For each time period (current, Mid-Holocene, LGM, and LIG), consensus probability maps were created, indicating the percentage of models showing the presence of suitable habitat at each pixel. For the current and LIG, these consensus probabilities were composed of 16 models: eight model algorithms (one algorithm was discarded, see Results) using each of two threshold methods (minSeSp and mean). For the Mid-Holocene and LGM, consensus probabilities each consisted of 48 models: eight model algorithms using two threshold methods for three GCMs. The consensus probability map for each time period was converted to a binary map based on four thresholds: 30, 50, 70, and 90% probability of suitable habitat. Maps based on these thresholds for each time period were stacked to show agreement on suitable habitat across all four time slices. The final refugial map therefore indicates pixels classified as suitable habitat across all four time slices, based on the four thresholds of suitable habitat for each time period: 30, 50, 70 and 90%. The LGM ice layer (Dyke et al. 2003) was overlaid (to exclude potential suitable habitat under the ice sheet) to

create a final map of potential refugial habitat for *R. integrifolia* since the Last Interglacial (Figure 1g).

Biogeographic hypothesis development and testing

Biogeographic hypotheses consist of models of population history that indicate the branching patterns, timing of divergence events, and effective population size (N_e) of populations of a species. Generally, hypotheses should contain enough parameters to distinguish between alternate models, but be simple enough to be addressed with the genetic material available and method of analysis employed (Knowles 2004). Alternate biogeographic hypotheses for *R. integrifolia* were based on the configuration of potential refugia as identified by the refugial model:

1. Panmixia (no genetic differentiation between populations).
2. Northward colonization from a southern refugium after the LGM.
3. Southward colonization from a northern refugium after the LGM.
4. Colonization from multiple refugia (north and south).

The fourth hypothesis was tested using two divergence times and two levels of N_e .

Hypotheses are presented in more detail in Results.

Alternative biogeographic hypotheses were tested using a statistical phylogeographic approach (described below) to determine the extent to which the empirical genetic data supported each hypothesis (Figure 1h). Statistical phylogeography evaluates the probability of alternative models of population history given uncertainty about past population parameters, such as effective population sizes (N_e) and the timing of divergence events. The

genetic data set employed for this study was analyzed by Dr. Eric DeChaine (WWU, Biology Department) using coalescent simulations (see below). The coalescent is a model of population genetics that takes into account the stochasticity of the genetic process when modeling different mechanisms of population history within a species (Rosenberg and Nordborg 2002).

Agreement between the biogeographic hypothesis supported by the SDMs (hypothesis 4) and the genetic data would corroborate the ability of the SDMs to effectively project the distribution of suitable habitat over time. Agreement would also support niche conservatism in *R. integrifolia*. A lack of agreement between the SDM and the genetic data could occur for several reasons, including a lack of niche conservatism in the species, barriers to dispersal (areas indicated as suitable habitat by the SDMs but not actually occupied by the species), and/or errors in the SDMs or genetic analyses.

Statistical phylogeography (contributed by E. DeChaine)

The sampling scheme and molecular approaches are described in detail elsewhere (DeChaine et al. *in prep*). In brief: (i) genomic DNA was extracted from individuals of *R. integrifolia* sampled throughout their range; (ii) five anonymous nuclear loci were sequenced for each individual; (iii) phylogenies were estimated for each locus in Garli v. 0.951 (Zwickl 2006) and used as ‘observed’ trees for testing the models of divergence based on hypotheses developed from the SDMs; and (iv) population genetic parameters (i.e., TMRCA, N_e) were estimated in BEAST v. 1.6.2 (Drummond and Rambaut 2007) and LAMARC v. 2.1.6 (Kuhner 2006).

Coalescent simulations of genealogies constrained within models of population divergence were performed with MESQUITE 2.75 (Maddison and Maddison 2011). Each population model is comprised of the tree topology, estimates of effective population size for each population, and time (in generations) given as branch lengths. Four models were tested: (1) panmixia, (2) recent colonization of the north from the south, (3) recent colonization of the south from the north, and (4) colonization from northern and southern refugia. Gene trees were simulated by constraining the coalescence of lineages within the topology, branch lengths, and N_e for a given model. This yielded 1000 simulated gene trees within each model of divergence, over a range of branch lengths (times).

The expected distribution of discordance between gene trees and the population model was measured by deep coalescences (*DC*; Maddison 1997) by counting the number of extra gene lineages per population, assuming incomplete lineage sorting accounts for all discordance. The *DC* from the observed gene trees were averaged across loci ($DC = 18.8$) and compared with the null distribution from the simulations to test statistically whether the observed tree could have been generated under the expected distribution for the population model. If the observed *DC* did not fit the expected distribution ($\alpha = 0.05$) for a given model, that model was rejected. If the observation fell within the expected distribution for a model of population divergence, that model was accepted as a possible scenario that could have led to the distribution of genetic variation observed today.

Future projections

Models for *R. integrifolia* were projected onto models of future climate, including two greenhouse gas scenarios (A1B and A2) for each of five downscaled GCMs for 2085

(Figure 1i). This time period was chosen as it represents the maximum temporal coverage of future projections provided by the IPCC. The A2 (“business as usual”) scenario is considered a high-range scenario by the IPCC, with an average temperature increase of 3.4°C by 2100 (Meehl et al. 2007). The A1B scenario is a mid-high scenario involving eventual atmospheric CO₂ stabilization, with an average temperature increase of 2.8°C by 2100 (Meehl et al. 2007). Lower emissions scenarios (B1 and B2) were not considered in this analysis, since recent projections indicate that current global emissions are on track to surpass these more conservative scenarios (Sokolov et al. 2009).

As with the paleodistribution model, probabilistic output was converted to presence/absence predictions using two thresholds: minimizing the absolute value of sensitivity minus specificity, and the mean probability value. Consensus probability maps for each greenhouse gas scenario consist of a total of 80 models (8 algorithms using 2 threshold methods for 5 GCM projections). These maps indicate the percentage of models showing the presence of suitable habitat, truncated at 50% and more of the models indicating suitable habitat.

Novel values of climate variables

Analysis of the spatial distribution of novel values of climate variables was conducted using Maxent, v. 3.3.3 (Phillips et al. 2006; Phillips and Dudik 2008). For each climate data set, Maxent calculates a multivariate environmental similarity surface (MESS), which indicates how similar a point is to a set of reference points across multiple predictor variables (Elith et al. 2010, especially Appendix S3). Negative values indicate that at least one predictor variable is outside the range used to train the model (the reference set).

Combinations of predictor variables that are within the range of the reference set can be distinguished by low positive values (indicating unusual climatic environments) and high positive values (indicating common climatic environments). MESS values are determined by the variable that has a value most different from the reference set (the most dissimilar variable, MoD). MESS and MoD maps were created for each past and future climate data set, with the reference set being current climate conditions.

MESS maps were simplified to binary values by setting all negative values equal to one (novel values), with zero and positive values equal to zero (not novel). Binary MESS maps were combined for all paleodistribution climate layers (LIG, three 21k GCM layers, three 6k GCM layers) creating a single map indicating the number of GCMs with novel values of climate variables. For each of the two future climate scenarios (A1B and A2), binary MESS maps were combined (five GCM layers per scenario) to form single maps indicating the number of climate layers with novel values. Each of these maps was combined with its respective consensus projection (refugial, A1B, and A2 models) to determine which areas were subject to projections based on novel values of climate variables.

Area calculations

In order to calculate area from raster layers, raster data was projected using the following settings: coordinate system: North America Albers Equal Area Conic; geographic transformation: NAD83 to WGS84_1; resampling technique: nearest neighbor assignment; output cell size: 50,000 meters. Areas were calculated to determine changes in available habitat under future climate change scenarios.

Results

Climate data interpolation

Interpolation errors were reported as root mean square error (RMSE), which quantifies the difference between predicted and measured values (reported in Appendix B). RMSE can be sensitive to outliers (Hernandez-Stefanoni and Ponce-Hernandez 2006), but is considered one of the better measures of overall model performance (Willmott 1982). Small values of RMSE indicate good agreement between predicted and measured values.

Overall RMSE values for temperature climate variables were small, with 91% of 636 RMSE values less than one, and only four RMSE values greater than three (Appendix B, Tables B1-B4). Temperature climate variables from GCM data were surface air temperature, maximum surface temperature, minimum surface temperature, and the standard deviation of minimum surface temperature.

Values of RMSE for total precipitation rate were more variable, with 77% of 204 RMSE values less than one, and 11% of values greater than three (Appendix B, Table B5). Adjustments made to precipitation data with very large RMSE are detailed in Appendix B. Generally, the higher variability of GCM data for precipitation in comparison to temperature is expected. GCMs can quite accurately simulate seasonal temperatures, since the large scale factors controlling temperature (insolation patterns and the configuration of continents) are well understood (Randall et al. 2007). Factors controlling precipitation are more numerous and complex, and can be difficult to evaluate at large scales (Randall et al. 2007). While GCM ensembles (model means) show skill at global simulations of annual mean precipitation, individual models can show “substantial precipitation biases” (Randall et al.

2007). These biases may account for the larger RMSE errors found in precipitation vs. temperature variable datasets. They also illustrate why SDMs should be based on more than one GCM data set.

Predictor variables

Of the 60 calculated predictor variables, eight were chosen to model suitable habitat for *R. integrifolia* (Table 2). These variables correspond to climatic factors that are relevant to alpine and arctic plants, including measures of spring snowpack, summer temperatures, and summer temperature variability, as indexed by standard deviation (Körner 2003).

Table 2: Predictor variables used to model the distribution of suitable habitat for *R. integrifolia*.

Variable	Description
Annual temperature range	maximum temperature of the warmest month – minimum temperature of the coldest month, calculated per pixel
Isothermality	a measure of temperature seasonality; mean diurnal range / annual temperature range
Summer minimum temperature	mean of minimum temperatures for June, July and August
Standard deviation of summer minimum temperature	mean of standard deviations of minimum temperatures for June, July and August
Cumulative spring snowpack	sum of snowpack for March, April and May
Annual precipitation range	precipitation of the wettest month – precipitation of the driest month, calculated per pixel
Precipitation of the driest month	precipitation of the driest month, calculated per pixel
Mean spring precipitation	mean of precipitation for March, April and May

Model evaluation and selection

Models with mean AUC and mean sensitivity > 0.7 were considered useful and were included in the consensus projections. All models met these guidelines (Table 3), indicating that the models can classify presence records more accurately than random prediction. All binomial tests of sensitivity scores were significant ($p < 0.05$).

Variability across training data sets is illustrated in boxplots of sensitivity and AUC scores across the 10 cross-validation runs (Figure 2a and 2b). FDA and MARS had the lowest sensitivity scores and showed high variability in response to random pulls of training data. Despite this, both algorithms performed well according to AUC scores, and visual inspection of predictions indicated reasonable distributions, so both were retained in the final analysis. Variability across training data pulls supports building final models using 100% of the available data (Araújo et al. 2005). Inspection of model output showed that ANN probability values were much lower than other models, ranging from 3% to 27%. This problem could not be resolved, so the ANN model was removed from further analyses.

Table 3: Mean AUC and sensitivity of 10 cross-validation runs on test data for nine single models and the final consensus model (does not include ANN). The maximum value for each test statistic is indicated with bold font.

Model	AUC	Sensitivity
ANN	0.834	0.887
CTA	0.791	0.901
FDA	0.854	0.749
GAM	0.859	0.958
GBM	0.866	0.979
GLM	0.850	0.946
MARS	0.852	0.778
MAX	0.888	0.959
RF	0.872	0.949
Consensus	0.909	0.948

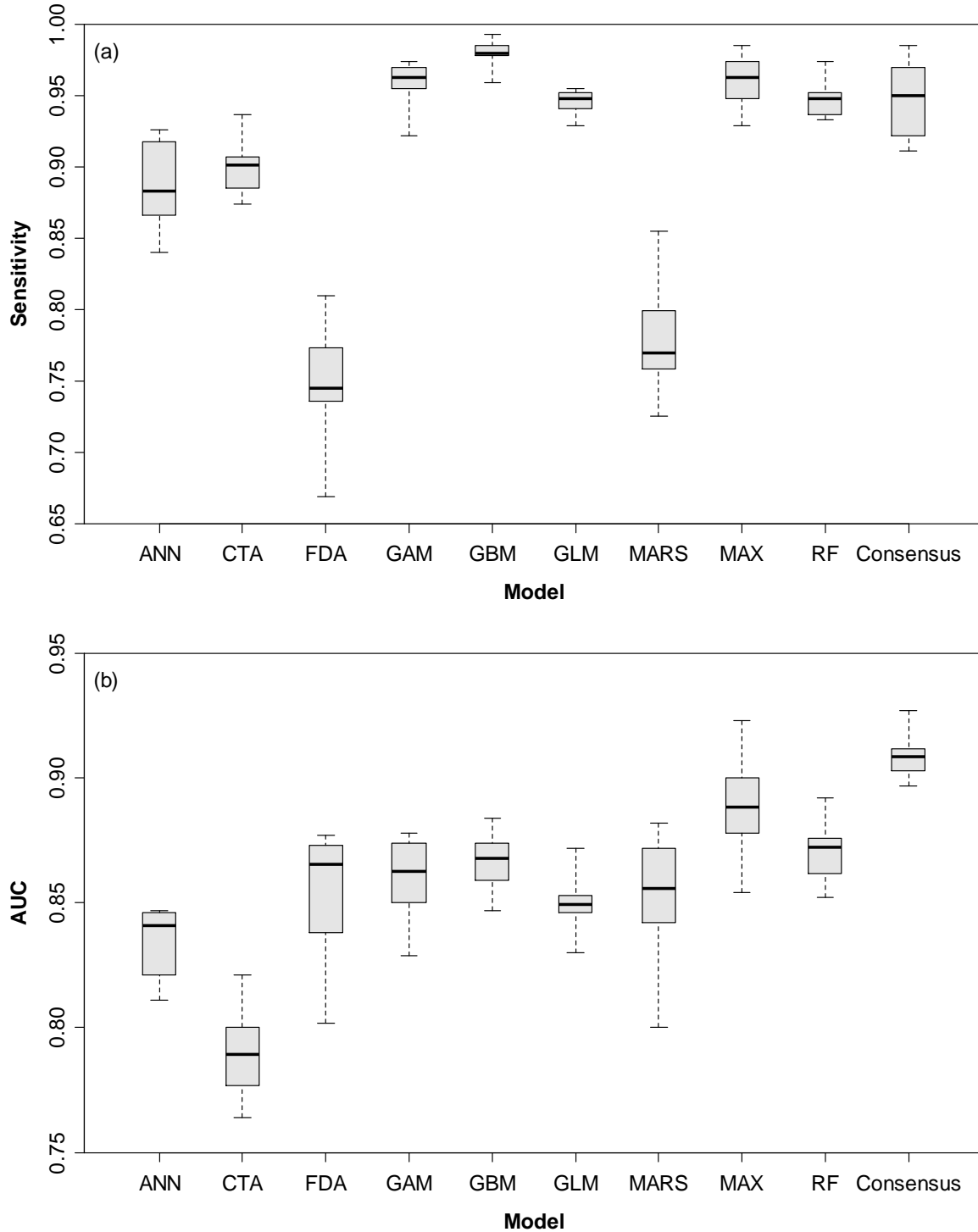


Figure 2: Boxplots for sensitivity (a) and AUC (b) scores for 10 cross-validation runs on test data. The boxes represent the range of half of the scores, with the median represented by the black line. The whiskers represent the minimum and maximum score values. The consensus model does not include ANN. Note difference in y-axis scaling between (a) and (b).

Refugial model, biogeographic hypotheses, and phylogeographic results

The refugial model shows potential refugial habitat to the north, south, and west of the LGM ice sheet (Figure 3). South of the ice sheet, the strongest support for refugial areas is found in the Oregon Cascades, Klamath, and Sierra Nevada Mountain ranges. North of the ice sheet, the strongest support for refugial habitat is located in the Aleutian Islands and southwest Alaska.

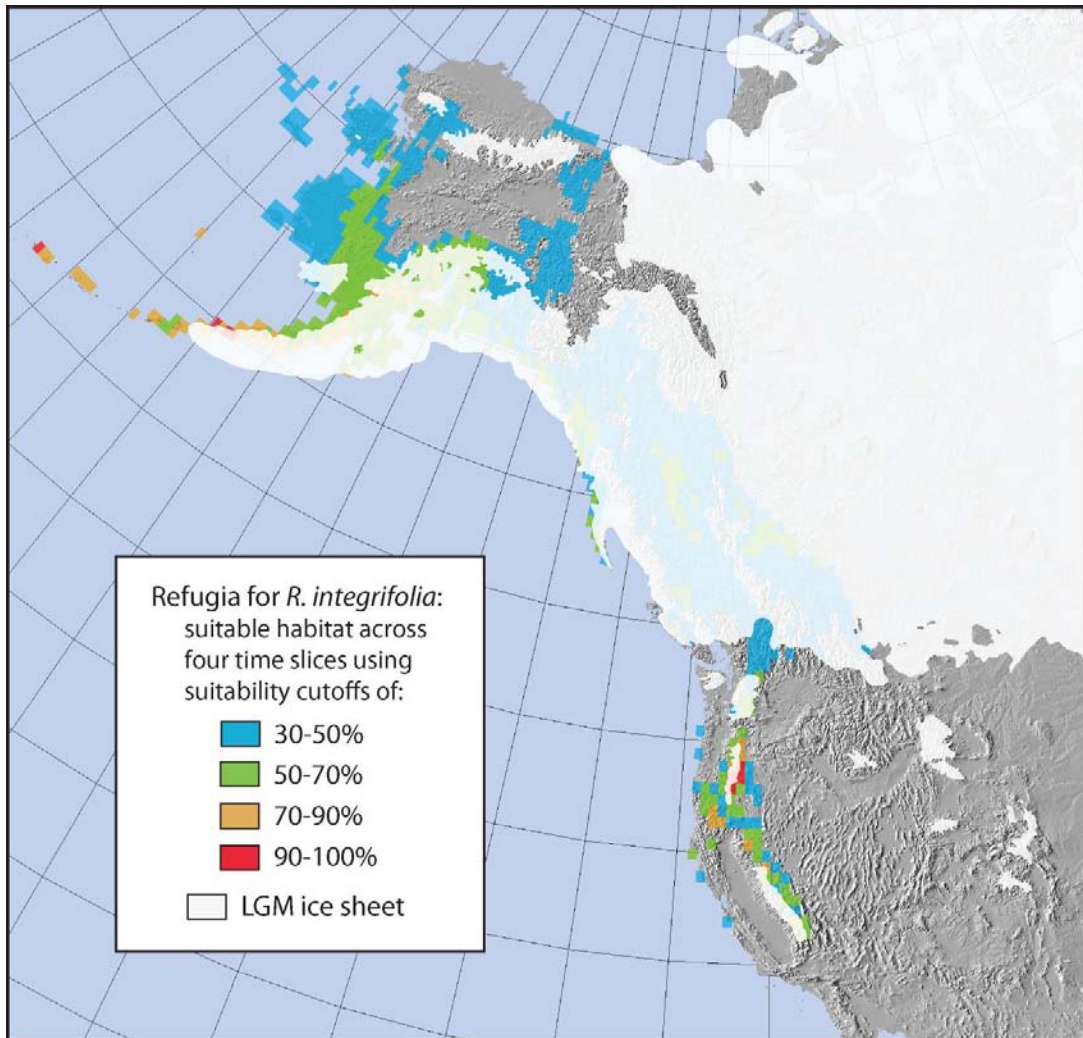


Figure 3: Consensus refugial model indicating areas of suitable habitat for *R. integrifolia* across four time slices: current conditions, mid-Holocene, LGM, and LIG. Ice sheet layer is from Dyke et al. 2003.

Potential coastal refugia in Haida Gwaii and the Alexander Archipelago (west coast of British Columbia and Alaska) are indicated as well. The presence of exposed land in this area during the LGM (now under water) likely provided additional habitat during the LGM (Shafer et al. 2010, and references therein). Unfortunately, a test of this west coast refugium could not be included in this analysis due to a lack of *R. integrifolia* tissue samples from that region. However, previous examination of the distribution of *R. integrifolia* haplotypes has provided support for a refugium in Haida Gwaii (Guest 2009).

Based on the configuration of refugial habitat in the SDM model and the availability of genetic samples, four alternate biogeographic hypotheses (Figure 4) were tested for *R. integrifolia* using a statistical phylogeographic approach:

1. Panmixia: no genetic differentiation between populations. This represents a null hypothesis that an individual has an equal probability of being found anywhere in its geographic range.
2. Northward colonization from a southern refugium after the LGM. This population model is defined by expansion out of a southern refugial area, likely in the southern Oregon Cascades or Sierra Nevada Mountains. This hypothesis predicts decreasing genetic diversity with increasing latitude, and lineage coalescence dating to, or prior to, the LGM. This model was parameterized with 90% of N_e located in the south and 10% of N_e located in the north.
3. Southward colonization from a northern refugium after the LGM. This population model is defined by expansion out of a northern refugial area, likely centered in southwestern Alaska. This hypothesis predicts increasing genetic diversity with

increasing latitude, and lineage coalescence dating to, or prior to, the LGM. This model was parameterized with 90% of N_e located in the north and 10% of N_e located in the south.

4. Colonization from multiple refugia (north and south). This population model is defined by expansion out of northern and southern refugial areas after the LGM. This hypothesis predicts no relationship between latitude and genetic diversity, and lineage coalescence dating prior to the LGM. This model was parameterized with a range of values of N_e (50,000 to 500,000) and two population divergence times: the LGM and mid-Pleistocene (Illinoian Glacial Period, 120-180 kya).

The SDM refugial model would be best supported by the multiple refugia hypothesis.

Genetic support for the single refugium or panmixia models would not invalidate the SDM projections, but would not exclude other possible explanations, such as mistakes in the modeling process, barriers to dispersal, or a lack of niche conservatism.

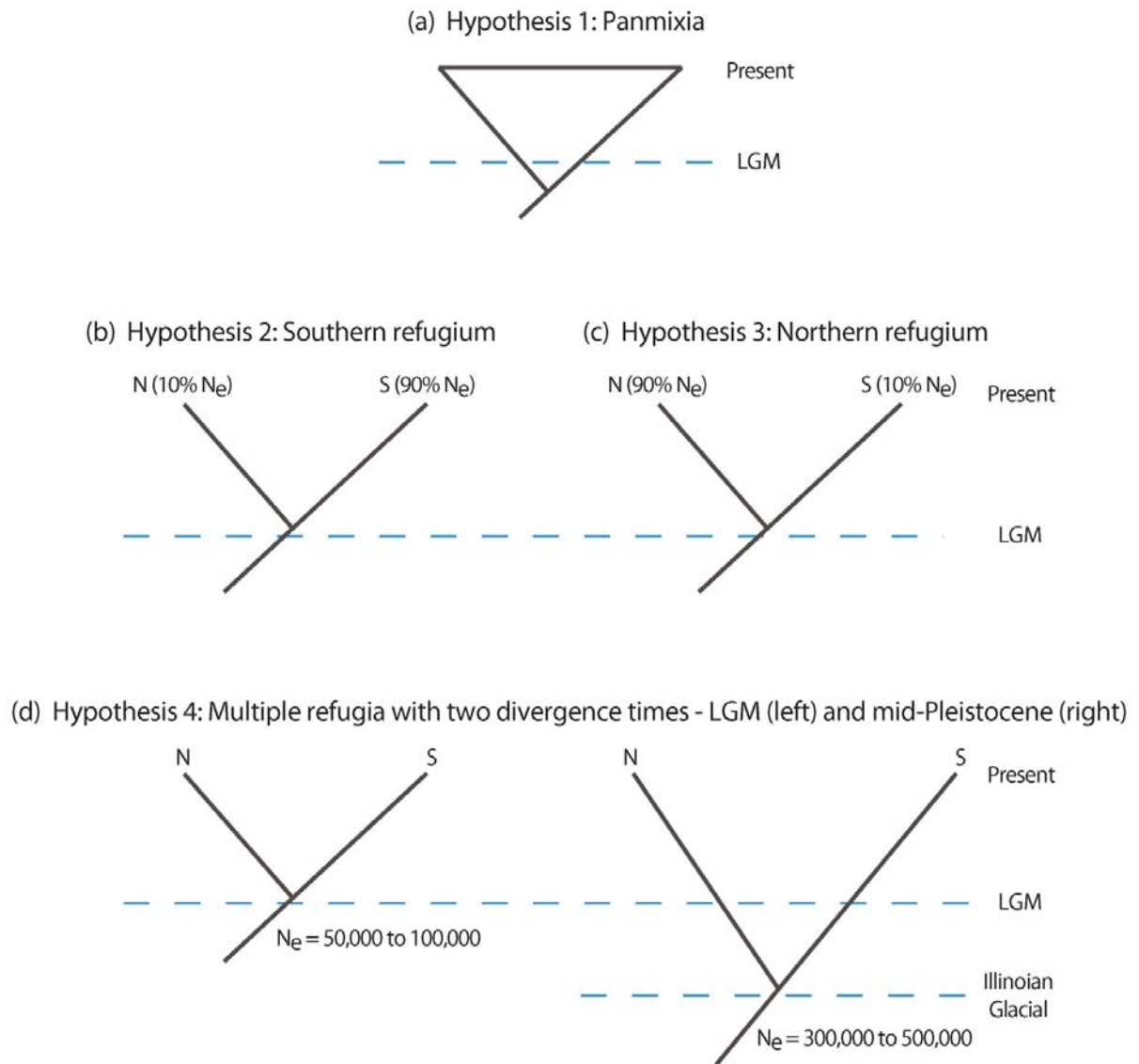


Figure 4: Biogeographic hypotheses tested using statistical phylogeography. Each hypothesis represents a different model of effective population sizes (N_e) and divergence times: (a) panmixia; (b) northward colonization from a southern refugium; (c) southward colonization from a northern refugium; (d) colonization from northern and southern refugia with divergence at the LGM (left) and Illinoian Glacial Period (right).

The first three biogeographic hypotheses (panmixia and colonization from single refugia) were not supported by the genetic data; the observed number of deep coalescences did not meet the expected distribution for these population models ($\alpha = 0.05$). The multiple refugia hypothesis was supported ($p < 0.05$), meaning the observed number of deep coalescences fell within the expected distribution for this model of population divergence. The currently observed distribution of genetic variation for *R. integrifolia* can therefore be explained by a model of population divergence in which northern and southern clades diverged at or prior to the LGM. Divergence between these clades is supported both at the LGM (where $N_e = 50,000$ to $100,000$) and the mid-Pleistocene (Illinoian Glacial where $N_e = 300,000$ to $500,000$). Additional phylogenetic analyses has further explored the timing of this divergence (DeChaine et al. *in prep*).

Future projections

With phylogeographic support for the multiple refugia hypothesis, niche conservatism in *R. integrifolia* was demonstrated across the modeled time period. Furthermore, the ability of the SDMs to accurately project the climate-habitat relationship through time was supported. Reciprocal inferences from both the refugial model and genetic data support the use of the SDMs to assess future climate change impacts.

SDMs were used to project the geographic distribution of suitable habitat for *R. integrifolia* in 2085 using five GCMs and two climate change scenarios. Consensus projections were truncated at values of 50% or more of the models predicting suitable habitat. Future consensus probability maps (Figure 5b and 5c) are based on five GCM

projections for each scenario (A1B and A2), and represent the consensus output from 80 models (eight model algorithms using two cutoff methods for each of five GCMs).

Projections for the A1B and A2 scenarios did not differ substantially, with both indicating a significant reduction in suitable habitat (63 to 67%) by 2085 (Table 4, Figure 5d and 5e). Both projections show a northward latitudinal shift in suitable habitat, with habitat losses represented by upward elevational shifts and/or contractions of suitable habitat (Figure 5d and 5e). Relative to habitat loss, habitat expansion was minimal, with the largest gains in the Brooks Range and north coast of Alaska. Both scenarios show dramatic loss of habitat in the southern part of the range, including the Sierra Nevada, Cascade, and Northern Rocky Mountains.

Though not explicitly quantified in this analysis, there were considerable differences across the five GCM projections for both the A1B and A2 scenarios. To illustrate these differences, projections from the five separate GCM projections and the final consensus projection for the A2 scenario are presented in Figure 6.

Table 4: Changes in climatically suitable habitat for *R. integrifolia* from current conditions to future climate scenarios for 2085.

	A1B Scenario	A2 Scenario
Loss	63%	67%
Stable	25%	22%
Gain	12%	11%

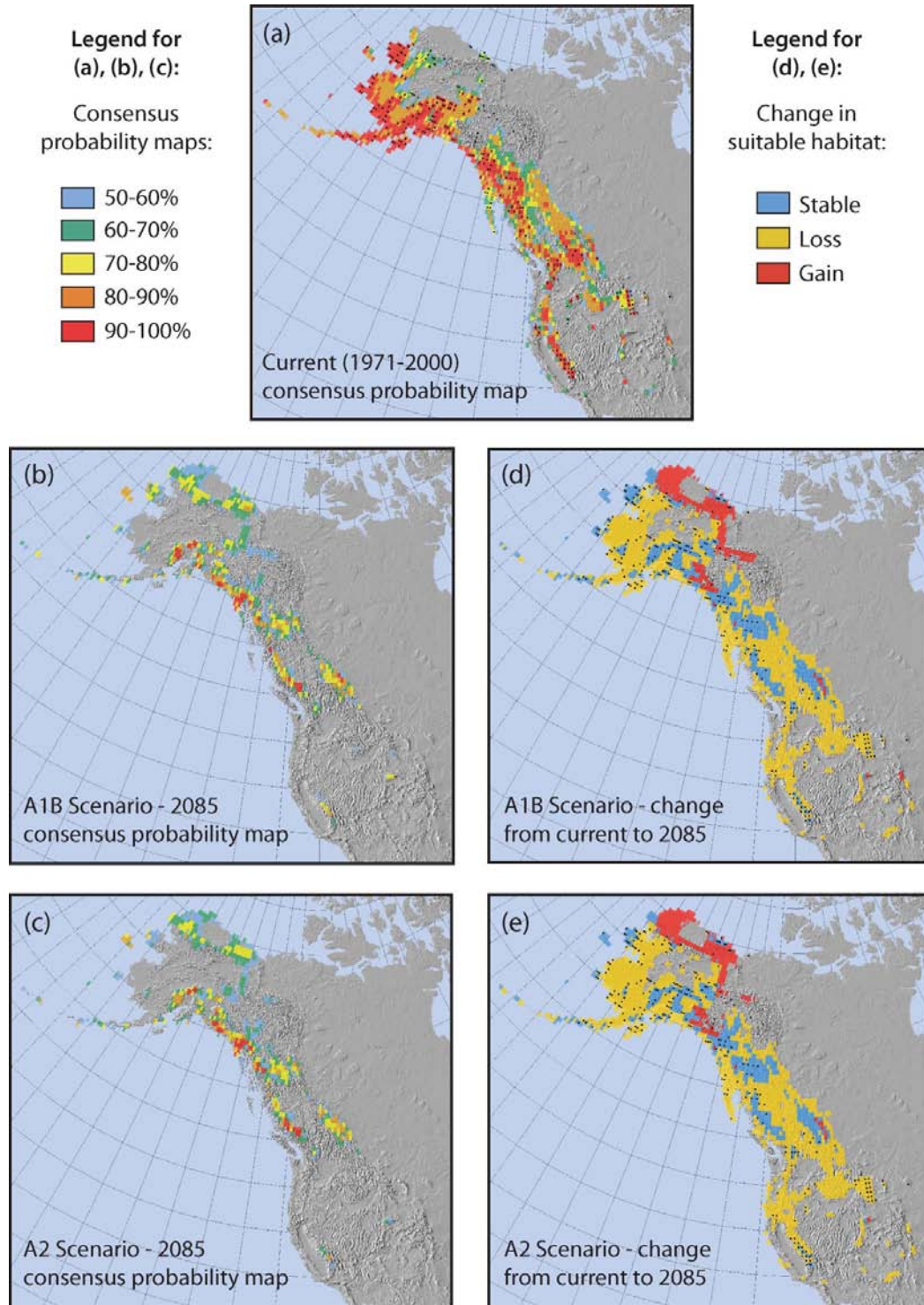


Figure 5: Current (a), A1B scenario (b), and A2 scenario (c) consensus probability maps. Change in suitable habitat from current to future for the A1B (d) and A2 (e) scenarios, based on a cutoff of 50% of the models indicating suitable habitat; black dots (a, d, e) indicate pixels with current populations of *R. integrifolia* (based on herbarium searches).

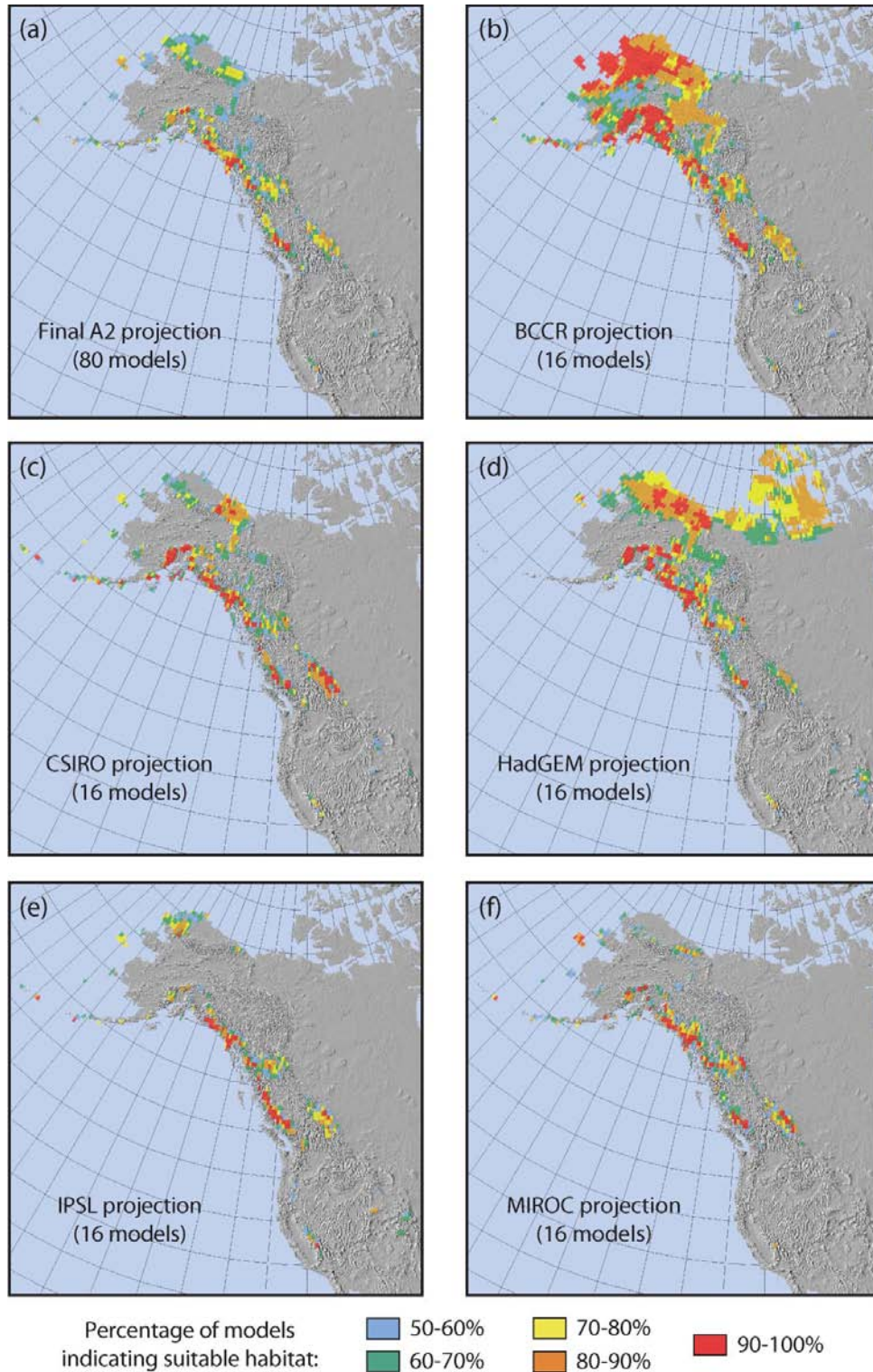


Figure 6: Comparison of projections across five GCMs (b-f) and the final consensus projection (a) for the A2 scenario at 2085. Projections are truncated at 50% of the models indicating suitable habitat.

Novel values of climate variables

For the refugial model, novel values of climate variables were present mainly to the north of the LGM ice sheet (Figure 7). In this area, suitable habitat and novel climate variables coincided for one to two of the seven GCMs. The most dissimilar variables (MoDs) north of the ice sheet were the standard deviation of summer minimum temperature (tmnSD.JJA) and annual temperature range, both of which were found in climate data from the LGM. For two of the GCMs (CCSM 3 and MIROC 3.2), novel values did not overlap north of the ice sheet.

South of the LGM ice sheet, the main MoDs were tmnSD.JJA and annual temperature range (again, all in the LGM data sets). The southern Rockies were of particular note, with all three LGM climate data sets indicating summer minimum temperature as the MoD. Overall, novel values of climate variables were more extensive in LGM climate data, compared to mid-Holocene and LIG data sets. This is not surprising, given the large differences between LGM and current climate.

For both the A1B and A2 projections, the overlap of future novel values of climate variables with projected suitable habitat is limited mainly to northwestern Alaska (Figure 8a and 8b). For both scenarios and across all GCMs, the MoD in this area is tmnSD.JJA. In both scenarios, there is at least one GCM that does not have novel values in this region. Future consensus projections do not show a gain of suitable habitat along the arctic coast; however novel values of climate variables in this region indicate that this is an area of uncertainty in model projections, and the potential for climatically suitable habitat in this region should not be dismissed.

In both future projections, the areas to the north (arctic coast) and south (northwestern Mexico) with high novel climates but no predicted habitat suitability have consistent MoDs. In the arctic, the MoD is tmnSD.JJA, while in Mexico the MoD is summer minimum temperature. These areas have novel climate values for these variables across all five GCMs, which is not surprising given that these regions represent the extremes of temperature variables in the climate data used to train the models. Coastal novel values are mainly contributed by annual precipitation range; this is consistent across both scenarios and all GCMs.

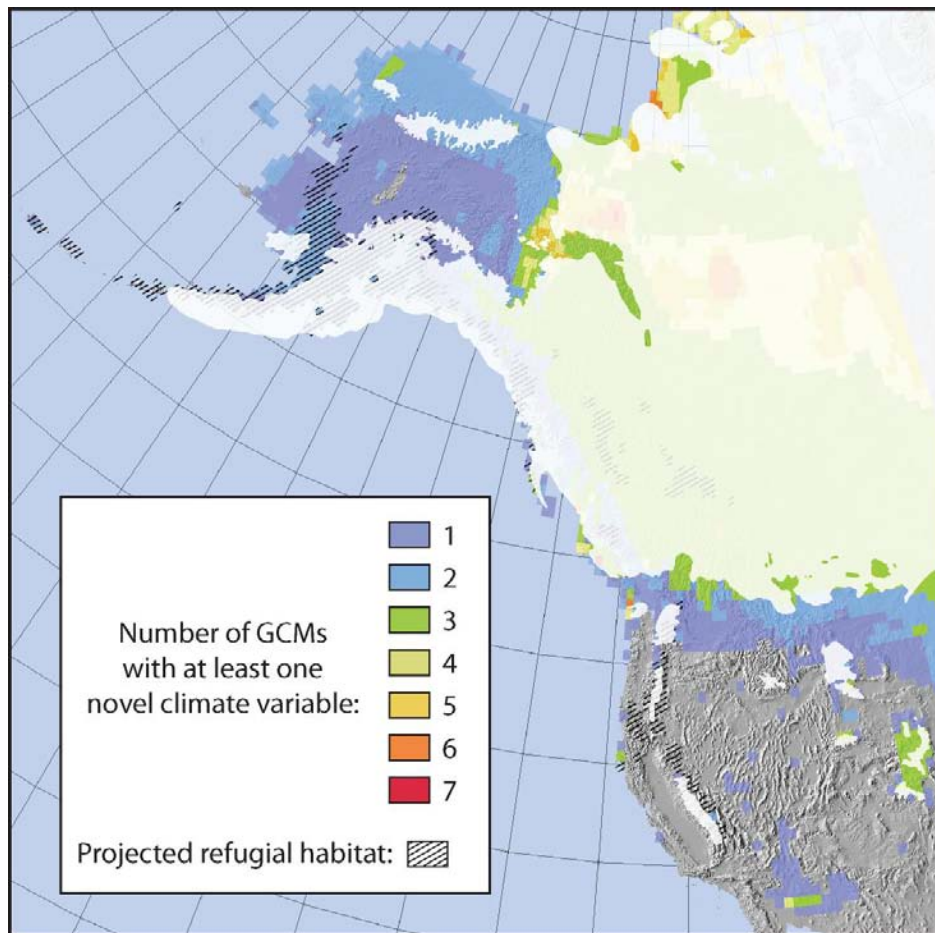
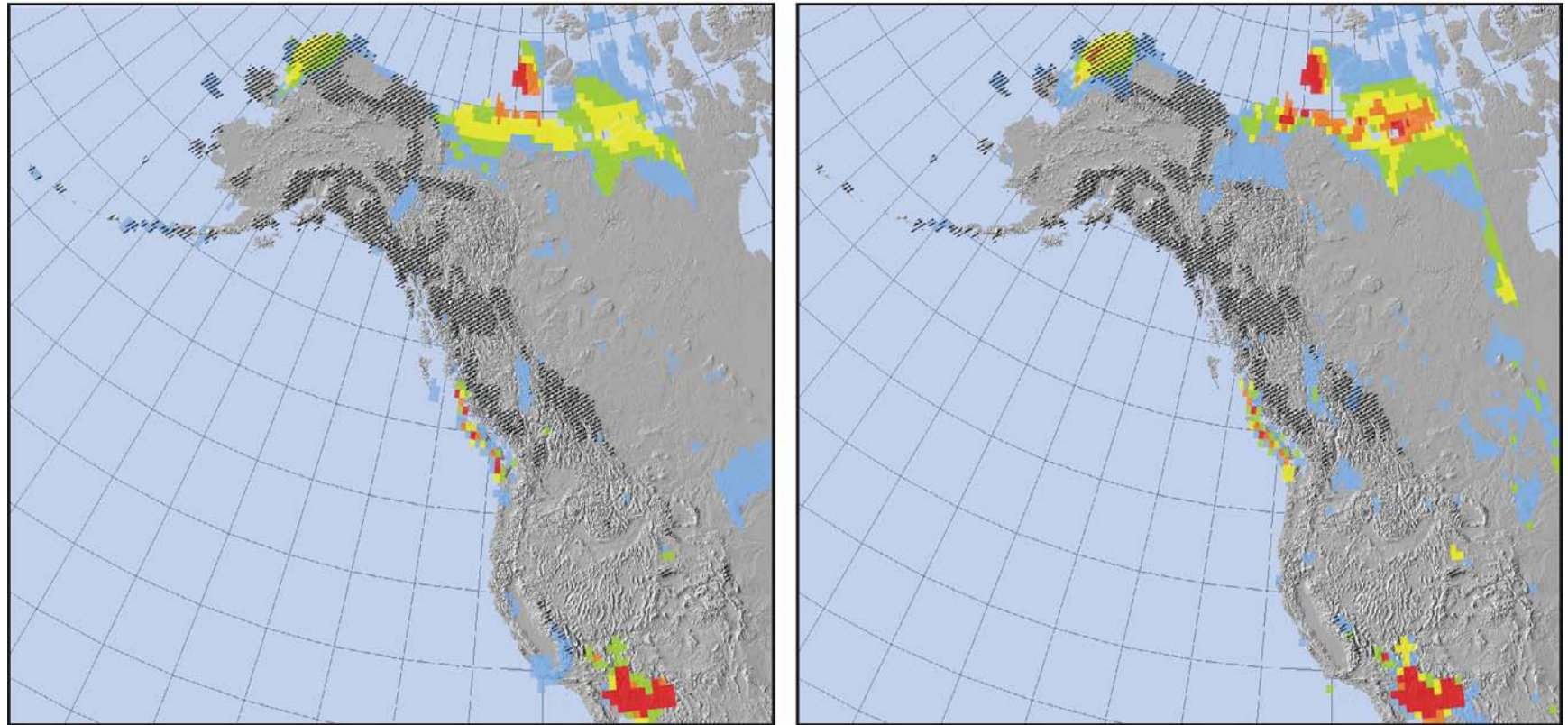


Figure 7: Geographic distribution of novel values of climate variables over seven GCMs used to project the refugial consensus map. Color scale indicates the number of GCMs indicating at least one climate variable is outside the range of the current climate data. Hatched areas represent projected refugial habitat (50% probability across all time slices). Ice sheet layer is from Dyke et al. 2003.

(a) A1B Scenario

(b) A2 Scenario




Legends: Number of GCMs with at least one novel climate variable: 1 2 3 4 5 Projected suitable habitat: 

Figure 8: Geographic distribution of novel values of climate variables for the A1B scenario (a) and the A2 scenario (b). Color scale indicates the number of GCMs indicating at least one climate variable is outside the range of the current climate data. Hatched areas represent projected suitable habitat.

Discussion

Biogeographic hypothesis testing and niche conservatism

There is agreement between the refugial model, developed using SDMs, and the phylogeographic analysis, conducted using simulations and empirical genetic data. Support for the same hypothesis from these two independent data sets strengthens the inferences from each, and indicates that there are two main lineages of *R. integrifolia* (north and south) that have persisted at least since the LIG, and likely since the mid-Pleistocene.

The match between refugia identified by the SDMs and the phylogeographic analysis supports niche conservatism in *R. integrifolia*, and justifies projection of the SDMs onto future climates. This finding of niche conservatism is consistent with previous work on plant responses to Quaternary climate change. Plants have a rich late-Quaternary paleoecological record in North America and Europe due to an abundance of palynological analyses. Research in this area, supported by phylogenetic work, has generally agreed that the fundamental response of most temperate plant taxa to Quaternary climate changes was migration, rather than adaptation (Huntley 1991; Prinzing et al. 2001; Ackerly 2003). Niche conservatism should not be assumed for all plants however; rapid adaptive capacity has been found for specific traits in some species (for example, changes in flowering time of *Brassica rapa*, an annual plant studied in southern California, in response to climate fluctuations, Franks et al. 2007).

The use of static SDMs to project future distributions is only appropriate for species where the climate-distribution relationship is stable. Though niche conservatism is usually assumed (or not addressed at all) in most SDM studies, genetic analyses have shown the

potential for rapid adaptation in some taxa, especially insects (Parmesan 2006; Reusch and Wood 2007) and invasive species (Broennimann et al. 2007). Additionally, a study of 23 mammal species suggested a lack of niche conservatism in five, though other explanations could not explicitly be ruled out (Martinez-Meyer et al. 2004). For some species evolutionary responses will be more nuanced, with adaptation occurring at species range limits, especially “trailing-edge” populations (Ackerly 2003; Hampe and Petit 2005; Parmesan 2006). With this diversity of species-specific responses to climate change, it is important to test the assumption of niche conservatism before projecting species distributions into the future, since projection of species with labile niches would lead to erroneous results. Especially for studies modeling at fine resolutions (e.g. 1-km pixel sizes), the potential for rapid adaptation at species range limits should give modelers pause, in addition to other concerns at these fine scales, such as changing biotic interactions and potential errors in climate data downscaling.

It is important to note that phylogeographic support for the alternate hypotheses of a single *R. integrifolia* refugium to the south or north of the LGM ice sheet would not have invalidated the SDM refugial model. The SDMs in this study model the distribution of climatically suitable habitat, but habitat suitability should not be equated with habitat occupation. In this case, phylogeographic support for a single refugium model could have multiple explanations, including: (1) long-term barriers to dispersal, such as sufficiently large distances between habitat patches during the LIG that prevented colonization of climatically suitable habitat; (2) adaptation (niche evolution or a lack of niche conservatism); (3) errors in SDMs or climate data; and (4) errors in the phylogeographic modeling. One previous study

disentangled these explanations, finding support for niche evolution in a land snail (genus *Candidula*) (Pfenninger et al. 2007) and further illustrating that the assumption of niche conservatism in SDM studies should be tested.

Additionally, support for the multiple-refugia hypothesis is limited to the context of the four models tested in this study. These models represent relatively simplistic hypotheses regarding the structuring of genetic diversity in this widely distributed species. Given the results of the SDMs, more sophisticated hypotheses could be tested in the future, including the potential for cryptic refugia (e.g. a west coast refugium) and “refugia within refugia” (isolation within major refugia, Shafer et al. 2010).

An interesting result of the refugial modeling was the indication of suitable habitat in the Alexander Archipelago and Haida Gwaii, to the west of the LGM ice sheet (Figure 3a). The presence of ice-free refugial areas on the west coast of British Columbia during the LGM has been established in previous studies (Warner et al. 1982; Cook et al. 2006; Shafer et al. 2010, and references therein), indicating that much of this suitable habitat was likely ice-free. Unfortunately, genetic samples were not available from *R. integrifolia* populations in this area, preventing a test of this west-coast refugial hypothesis. The presence of this refugium is supported, however, by previous analyses of haplotype distributions for *R. integrifolia* (Guest 2009). This illustrates how models derived from SDMs can be used to not only develop biogeographic hypotheses but also direct appropriate sampling strategies to better target specific phylogeographic questions. A test of this west coast hypothesis would contribute to our understanding of the role of cryptic refugia in structuring current patterns of genetic diversity, as well as improve estimates of dispersal and recolonization rates after the

LGM. Additionally, because refugia harbor high levels of genetic diversity (Hewitt 1996), confirmation of a west coast *R. integrifolia* clade would lend support to efforts to recognize and conserve the unique biota of these islands (Cook et al. 2006).

Future projections: the value of ensemble methods and genetic data, and a few caveats

Future projections of habitat suitability for *R. integrifolia* show substantial losses of climatically suitable habitat across the range. Overall differences between greenhouse gas scenarios were minimal (Figure 5, Table 4), while differences in projections across GCMs were quite large (Figure 6). This indicates that less focus should be placed on modeling alternate scenarios, with more effort directed toward sampling different GCM projections. This coincides with previous work by Buisson et al. (2010), who found that up to 19% of uncertainty in future model projections was due to the choice of GCM alone. Differences in model algorithms accounted for even more of the uncertainty in future projections (29% to 51%), while greenhouse gas scenarios explained little of the variability (less than 10%).

In the southern part of the range, there is an almost complete loss of climatically suitable habitat. Habitat persists at greatly reduced levels in the Sierra Nevada Mountains in both the A1B and A2 scenarios, while only the A1B scenario retains any suitable habitat by 2085 in the Northern Rocky Mountains. The central and northern parts of the range also show large losses of suitable habitat. Habitat gains in southeast Alaska may facilitate population connectivity (Figure 5d and 5e) between central and northern populations. The development of climatically suitable habitat in the Brooks Range of Alaska may also allow for population expansion in that area.

Dispersal estimates are lacking in most SDM studies; projections usually assume either unlimited dispersal, representing an optimistic scenario where species can colonize all climatically suitable habitat, or no dispersal, representing a more conservative scenario in which species can only persist in areas of stable climate. The difference between projections using these alternate scenarios can be significant, contributing to uncertainty (for example, Thomas et al. 2004; Engler and Guisan 2009). Phylogeography can provide a species-specific metric of dispersal capability with which SDM projections can be constrained, although these metrics are dependent upon the hypotheses tested (e.g. migration rates can be overestimated if cryptic refugia are not included, Shafer et al. 2010). However, even rough estimates of dispersal capability have been shown to greatly reduce this component of projection uncertainty in SDMs (Engler and Guisan 2009).

Although phylogeographic analysis can provide a dispersal metric, an assessment of dispersal capacity for *R. integrifolia* was outside the scope of this analysis. Based on future projections, however, it appears unlikely that dispersal limitations will prevent colonization of newly suitable habitat, since these areas are near currently established populations. Biotic interactions and/or fine-scale climate variability (which are not addressed at the coarse scale of this analysis) may prove to be greater determinants of successful population expansion. An additional component of dispersal capability is the potential for populations to maintain gene flow. Southern populations (Sierra Nevada and Rocky Mountains) are geographically isolated, so dispersal between these populations is highly unlikely. The more closely located west coast and southern Alaskan populations, however, have the potential to maintain gene flow, since many of these populations are separated by only one or two pixels (approximately

50 to 100 km). Additional genetic analyses would allow an assessment of the potential for increased connectivity or isolation of populations under future climates.

The ability to identify past refugia is an important benefit of phylogeography. Because glacial-interglacial refugia tend to harbor high levels of allelic diversity (Hewitt 1996; Stewart et al. 2010), these regions have implications for conserving the genetic structure of current and future populations. The refugial model indicates discrete southern refugia in the southern Oregon Cascades, Klamath, and Sierra Nevada Mountain ranges (Figure 3a). Populations in the Oregon Cascades are predicted to be extirpated by 2085, though the potential for persistence in microclimate refugia should not be discounted (see below). The Sierra Nevada population is likely to persist but will be further isolated under both future climate change scenarios. The persistence of these populations will be important to the maintenance of overall levels of genetic diversity in this species. Further analysis of genetic data can corroborate this interpretation, by providing indices that quantify neutral genetic diversity within these populations. Overlap between northern (Alaskan) refugia and future distributions of suitable habitat are not as clear; further analysis of relative levels of genetic diversity within and between populations in Alaska would be helpful to better understand the potential genetic impacts of population losses, especially in southwestern Alaska and the Aleutian Islands. Additionally, populations currently located in the Alexander Archipelago and Haida Gwaii are forecast to lose all suitable habitat under both future scenarios. This should encourage efforts to assess the genetic support for this region as a cryptic refugia for *R. integrifolia*, and a possible area of unique genetic diversity for the species.

Although these projections appear dire, it is important to recognize that the coarse grain of this biogeographic analysis can overpredict the loss of climatically suitable habitat. Especially in mountainous regions, coarse SDMs are likely to underestimate the potential for suitable habitat under future climate change (Randin et al. 2009; Barbet-Massin et al. 2010). At landscape to local scales topography has important impacts on the distribution of alpine plants. This is mainly due to the influence of topography on the distribution of microclimate refugia in mountainous terrain (Dobrowski 2010). In these areas of topographic complexity, climate patterns at fine scales are influenced by spatially varying elevation relationships, terrain barriers, terrain-induced climate transitions, cold air drainage patterns, inversions, and coastal effects (Daly 2006). Because coarse climatic data average out these complexities, the most likely outcome is underestimation of potential habitat, though one study has shown the opposite effect (Trivedi et al. 2008).

This suggests some important limitations in the use of SDMs to predict climate change impacts. First, modelers need to balance “resolution with realism” (Daly 2006) when downscaling projections from GCMs, although the improved availability of regional climate models may help with this limitation (at least for future climate projections). The common use of gridded climate data that are interpolated to ~1-km pixel sizes from very large scale GCM runs (e.g. 2 by 3°) should be questioned. A second consideration is that at fine (landscape to local) scales, climatic controls over species distributions breaks down. Biotic interactions, range dynamics, demographic processes, topography and microclimate are extremely important. At these scales, the use of SDMs alone is not suitable; SDMs

integrated with mechanistic models is a more appropriate approach (for example, Keith et al. 2008; Brook et al. 2009).

Predictor variable selection and SDMs

The importance of using predictor variables in correlative SDMs that are biologically appropriate and functionally-relevant to the species being modeled has been stressed by many authors (for example, Guisan and Zimmermann 2000; Austin 2002; Lookingbill and Urban 2005). Less commonly emphasized is how the selection of appropriate variables interacts with scale (both extent and pixel size); for example, climate-related variables are most applicable at global to regional scales, with topography, land use and soil type more relevant at landscape to site-level scales (Pearson and Dawson 2003). As mentioned above, biotic interactions and source-sink dynamics also become extremely important at landscape and site-level scales. Unfortunately, many SDM studies still rely exclusively on pre-calculated biogeographic-scale abiotic variables (e.g. WorldClim data), even when modeling at fine spatial scales. Difficulties in compiling gridded data sets (e.g. workload, access, feasibility) will prevent many SDM practitioners from using ecologically-based, scale-appropriate predictor variables. On the other hand, the removal of highly correlated predictor variables is becoming more common in SDM studies. This is a positive development, since highly correlated variables can cause serious prediction errors in some model algorithms (Franklin 2009). Overall, ecologists using SDMs need to be aware of these limitations and plan the scale (extent and grain) of their studies based on what is logistically feasible and ecologically appropriate.

In this study, the final choice of predictor variables clearly relates to the ecology and distribution of alpine and arctic plants at biogeographic scales. Spring snowpack, summer temperatures, and summer temperature extremes (as indexed by standard deviation) are particularly relevant to alpine-arctic plants (Körner 2003). These factors interact, especially at the beginning of the growing season when the start of plant growth is triggered by photoperiod, temperature, and snowpack depth (Körner 2003). Plants must strike a balance between warming temperatures, diminishing snowpack, and the potential for extreme cold events that could cause frost damage to sensitive tissues (Inouye 2008). Research on herbaceous plants and shrubs in the alpine has shown that the negative impact of early season low-temperature events on bud mortality outweighed the positive effects of longer growing seasons (Inouye 2008; Wipf et al. 2009). Reduced snowpack in spring resulted in increased exposure of leaf and flower buds to early spring frost events, reducing seed production and impacting demographic recruitment (Inouye 2008).

Methods to select relevant predictor variables from a potentially large, correlated list of possibilities have not been addressed specifically in the SDM literature. In this study, the random forest algorithm was successfully used to select the most relevant predictor variables for *R. integrifolia*, while controlling for the highly correlated nature of these predictors (Strobl et al. 2008). To my knowledge, this multivariate approach to variable selection has not been used in SDM studies. It should be considered, as it provides a simple and intuitive method to filter highly correlated predictors and select the most species-relevant variables.

Ensemble modeling and novel climates

In addition to support from genetic analyses, species distribution projections were made more robust through the use of an ensemble and consensus approach to modeling. The consensus model of current *R. integrifolia* distribution had a higher predictive capacity based on AUC scores than any of the single SDMs alone (Figure 2b, Table 3), and was among the highest scoring based on sensitivity scores (Figure 2a, Table 3). This is in agreement with previous work indicating that consensus models outperform individual models, providing more robust projections of habitat distribution (Marmion et al. 2009; Grenouillet et al. 2011). The use of multiple model algorithms in studies that project species distributions is also supported by recent work showing that models with the highest accuracy on current climate data may not be the best at projecting onto new areas or climate conditions (Heikkinen et al. 2011).

The ensemble and consensus approach also allows a spatial depiction of agreement across model algorithms, by showing areas of consensus among models and areas of disagreement. Current and future projections for *R. integrifolia* (Figure 5) show the percentage of models “voting” for suitable habitat for a given pixel. Areas of agreement are regions of greater confidence in the model projections, while areas of disagreement (e.g. at the low end of the 50% cutoff) indicate areas of lower confidence. The combined output of model algorithms, threshold methods and GCM conditions helps delimit a range of uncertainties associated with projecting the distribution of suitable habitat (Araújo and New 2007). For example, rather than basing an analysis spanning 124 kya on the output from one model algorithm and one GCM projection, I combined output from 8 model algorithms on

anywhere from one to five GCMs. Using this ensemble and consensus approach, my final maps indicate agreement across many model projections (from 16 to 128 models). As each of these indicates possible states of the system being modeled, this approach allows for greater confidence in model output, especially when projecting across temporal scales.

Despite its advantages, ensemble modeling should be used with caution. Naïve use of model algorithms can result in poor parameterization and poorly performing models. Ensemble approaches also greatly magnify the work-load associated with modeling species distributions. Despite these drawbacks, ensemble approaches appear to be an effective way to create robust projections that include a depiction of variability and uncertainty.

As mentioned above, the use of multiple GCMs is an especially important component of the ensemble approach when projecting species distributions. I found substantial variability across the five GCMs used for future projections (Figure 6). By combining these projections and showing areas of consensus and disagreement among models, I can indicate areas of higher and lower confidence in projected distributions. This analysis only takes a small sample of available projections; the IPCC's Fourth Assessment Report included 23 GCMs. However, most SDM studies use one or at most two GCMs for future projections; there is certainly room for improvement in this component of projecting climate change impacts. Modelers are limited by the availability of interpolated climate data from these GCMs, and so often focus their efforts on including multiple greenhouse gas scenarios, despite the fact that these contribute very little to sampling the variability in future projections (Buisson et al. 2010).

Novel climate variable analysis also illustrates why it is important to use multiple GCMs. While GCMs can sometimes be spatially coherent in their novel climates across variables (e.g. different GCMs predicting areas of novel climate in similar locations based on the same variable), many times GCMs differ in their spatial prediction of novel values of climate variables. For example, in the A1B and A2 projections, areas of novel climate are seen in the northwestern part of Alaska and along the arctic coast (Figure 8a and 8b). For both scenarios, there are GCMs without novel values in these regions. If this were an area of potential conservation concern, those GCM projections without novel values could be individually inspected to avoid the uncertainties associated with projecting models onto novel climates.

For future projections, most of the novel values of climate variables are found at the latitudinal limits of the projected study area. This is expected, since these regions represent the extremes of temperature variables in the climate data used to train the models. In both paleoclimatic and future climate data sets, the possibility of encountering novel climates is minimized by training the current model on the entire latitudinal range of the species, ensuring that all current values and combinations of climate variables are included in creation of response curves.

The very real possibility of projecting SDMs onto novel climates is frequently mentioned in the literature, but rarely addressed. The MESS analysis included with the most recent versions of Maxent is an excellent tool to help modelers consider the impact of novel values of climate variables on their projections. This technique, however, does not consider novel *combinations* of climate variables. This analysis is equally important because models

are trained not only on the values of the variables, but on their correlation with each other; novel combinations of variables force algorithms to make predictions outside the range of variability used to train them. Relatively simple methods can be used to assess novel combinations of climate variables, such as standardized Euclidean distance (Williams et al. 2007), and other multivariate approaches (Saxon et al. 2005; Elith et al. 2010).

Unfortunately, these are not yet part of the mainstream in SDM studies, and user-friendly tools have not been created to automate the process (although see Zurell et al. 2012 for a recent contribution to addressing this problem). For example, in this study, testing for novel combinations of climate variables was not a component of the original study plan, so necessary variables (e.g. standard deviation of interannual variability of climate variables) were not calculated when climate data were compiled.

Applications and conservation strategies

In this analysis, I have examined some of the advantages and limitations of using SDMs to assess the impact of climate change on species distributions. It is essential that users understand the limitations of these models, including the importance of using a scale appropriate to the data and question being asked. While SDMs provide an indication of a species' potential exposure to climate change (Dawson et al. 2011), they do not account for demographic and/or adaptive responses, or the influence of changing community interactions. Due to these limitations, integrating complementary methods, such as genetic analyses and/or mechanistic and demographic models, will be the best approach to developing robust conservation strategies under global change.

In this study, SDMs were coupled with phylogeographic analyses, providing a more comprehensive assessment of climate change impacts that addresses both exposure and past responses to climate change, as well as identification of areas of potentially high genetic diversity (past refugia). Genetic analyses can also provide measures of neutral (and increasingly, adaptive) genetic diversity, population differentiation, and dispersal capability. The use of molecular data to improve conservation responses to global change will continue to increase as the costs of obtaining genetic data decline. The explicit incorporation of “evolutionary resilience” (Sgro et al. 2011) in conservation planning has become feasible with rapid developments in sequencing and analytic tools. These approaches are especially important for proactive conservation actions since research indicates that wild populations are more susceptible to extinction in the absence of genetic variation (Spielman et al. 2004).

I agree with Dawson and colleagues (2011) that efforts to conserve biodiversity and improve ecosystem functioning need to move beyond predictions of climate change impacts and toward an integrated effort to address solutions. SDMs will be only one component of that effort. Practitioners should continue to develop a more sophisticated understanding of the advantages, limitations and appropriate uses of SDMs, while working with colleagues to incorporate alternate and complementary analyses. This integrated approach will be the most effective way to develop robust conservation strategies for species and ecosystems in the face of the interacting stressors of climate change, land-use change, habitat destruction, invasive species, pollution, and other anthropogenic influences.

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Appendix A: Climate data processing

When available, global monthly layers were downloaded from climate databases for the following four climate variables: total precipitation rate (pr), surface (2m) air temperature (tas), maximum surface temperature (tasmax), and minimum surface temperature (tasmin). Current climate data are based on a 30-year mean (1971-2000). Mid Holocene (6 kya) and LGM (21 kya) climate data are 100-year means, except as indicated below. LIG (124 kya) climate data are 30-year means. Future climate data are 30-year (2071-2100) or 29-year (2071-2099) means.

All monthly climate data files for pr, tas, tasmin, and tasmax were plotted as histograms and inspected visually for problems. All models passed this inspection except specific months in two future climate models for variable pr (see Future Data below).

Current Data:

CRU TS 2.1 model (Mitchell and Jones 2005): Global monthly values for all four variables representing current global climate (mean of 1971-2000) were downloaded from the Climate Research Unit TS 2.1 model. The native resolution of this data is 0.5°. Standard deviations of the four variables were calculated by taking the standard deviation of monthly data over 30 years (1971-2000). These standard deviations were used in variable selection (see main text). For past and future climate data, standard deviations were calculated for tasmin alone, since this variable was chosen during variable selection.

Paleoclimate Data for Mid-Holocene (6 kya) and Last Glacial Maximum (21 kya):

These data were downloaded from the Paleoclimatic Modelling Intercomparison Project Phase 2 (PMIP 2) database (Braconnot et al. 2007). I would like to acknowledge the international modeling groups for providing their data for analysis, the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) for collecting and archiving the model data, and individual members of the modeling groups who assisted with questions. The PMIP 2 Data Archive is supported by CEA, CNRS and the Programme National d'Etude de la Dynamique du Climat (PNEDC). Data were downloaded from the database between 1/15/2011 and 2/26/2011. More information is available at <http://pmip2.lsce.ipsl.fr/>.

CCSM 3 model (Otto-Bliesner et al. 2006): Global monthly values for all four variables were downloaded from the PMIP 2 database for 0, 6, and 21 kya. The native resolution of this data is 2.8125° . The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 100 years. Some CCSM precipitation anomalies showed extreme values (e.g. $3e14$); to correct for these extremes, the 0.5th and 99.5th quantiles of the CCSM precipitation anomalies were changed to the closest (lowest or highest) value prior to interpolation.

HadCM3 UBRIS and HadCM3 models (Gordon et al. 2000): The 6 kya and 21 kya data from this model were produced on different computers using different compilers, so are treated separately; each time slice (6 and 21 kya) has its own 0 kya set from which anomalies were calculated (Michel Crucifix, *pers. comm.*, February 2011). The native resolution of the 6 and 21 kya datasets is 3.75° (longitude) x 2.5° (latitude).

For 6 kya data, global monthly values for all four variables were downloaded from the PMIP 2 database. The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 100 years. For 21 kya data, global monthly values for pr and tas were downloaded from the PMIP 2 database. Monthly data for tasmin and tasmax were not available for the 21 kya model run, so daily tasmin and tasmax data (over 20 years) were downloaded. These data were processed to create 20-year mean monthly data sets for tasmin and tasmax. The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 20 years.

MIROC 3.2 model (K-1 model developers 2004): Global monthly values for all four variables were downloaded from the PMIP 2 database for 0, 6, and 21 kya. The native resolution of this data is 2.8125°. The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 100 years.

Paleoclimate Data for the Last Interglacial (124 kya):

I would like to acknowledge the assistance of Dr. Joy Singarayer in obtaining access to these data.

HadCM3 model (Gordon et al. 2000): Global monthly values for pr and tas were downloaded from the Bristol Research Initiative for the Dynamic Global Environment (BRIDGE) database for 0 and 124 kya. The native resolution of this data is 3.75° (longitude) x 2.5° (latitude). Model data for tasmin and tasmax were not available. Assuming similar variability in temperature between the LIG and current interglacial conditions, offsets between current (CRU) mean temperature (tas) and minimum and maximum temperature

(tasmin and tasmax) were calculated. These offsets were applied to LIG mean temperature values to create LIG tasmin and tasmax data sets. The standard deviation of tasmin was therefore identical to that for the current period.

Future Data:

These data were downloaded from the Coupled Model Intercomparison Project Phase 3 (CMIP 3) database (Meehl et al. 2007), and the World Data Center for Climate's CERA database (Hamburg Germany). Scenarios downloaded include 20C3M (simulation of 20th century climate), A1B, and A2.

BCCR BCM 2.0 model (www.bjerknes.uib.no): Global monthly values for all four variables were downloaded from the CERA database for the 20C3M, A1B, and A2 scenarios. The native resolution of this data is 2.8125° and the model has been run through 2099 (29-year mean). The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 29 years.

CSIRO Mk3.5 model (Gordon et al. 2002): Global monthly values for all four variables were downloaded from the CMIP 3 database for the 20C3M, A1B, and A2 scenarios. The native resolution of this data is 1.875° and the model has been run through 2100 (30-year mean). The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 30 years.

HadGEM1 model (Johns et al. 2006): Global monthly values for pr and tas were downloaded from the CERA database for the 20C3M, A1B, and A2 scenarios. The native resolution of this data is 1.875° (longitude) x 1.24° (latitude) and the model has been run

through 2099 (29-year mean). The exception is the A2 scenario, which has been run through November 2099. In order to maintain the full 29-year mean, A2 means were calculated from December 2070 through November 2099.

Monthly data for tasmin and tasmax were not available, so daily data were downloaded. These data were processed to create 29-year mean monthly data sets for tasmin and tasmax. The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 29 years.

Visual inspection of histograms for monthly data indicated non-climatic patterns in the A2 January pr file. The problem was not resolved by working back through the data file, so an A2 January pr file was produced for the HadGEM1 data set by averaging the A2 January pr files from the other four future data sets.

IPSL CM4 model (Marti et al. 2009): Global monthly values for pr and tas were downloaded from the CMIP 3 database for the 20C3M, A1B, and A2 scenarios. The native resolution of this data is 3.75° (longitude) x 2.5° (latitude) and the model has been run through 2100 (30-year mean).

Monthly data for tasmin and tasmax were not available, so daily data were downloaded from the CERA database. These data were processed to create 30-year mean monthly data sets for tasmin and tasmax. The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 30 years.

Visual inspection of histograms for monthly data indicated non-climatic patterns in the A1B March, November, and December pr files as well as the A2 November and December pr files. The problems were not resolved by working back through the data files,

so alternate pr files were produced by averaging the appropriate pr files from the other four future data sets.

MIROC 3.2 model, run 1 (K-1 model developers 2004): Global monthly values for all four variables were downloaded from the CERA database for the 20C3M, A1B, and A2 scenarios. The native resolution of this data is 2.8125° and the model has been run through 2100 (30-year mean). The standard deviation of tasmin was calculated by taking the standard deviation of monthly data over 30 years.

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Appendix B: Interpolation Errors

Interpolation errors are reported as root mean square error (RMSE), which quantifies the difference between predicted and measured values. It can be sensitive to outliers (Hernandez-Stefanoni and Ponce-Hernandez 2006), but is considered one of the better measures of overall model performance (Willmott 1982). Small values of RMSE indicate good agreement between predicted and measured values.

For temperature climate variables, all RMSE values were small. Values of RMSE for surface air temperature (Table B1), maximum surface temperature (Table B2), minimum surface temperature (Table B3), and the standard deviation of minimum surface temperature (Table B4) are presented below. Of these RMSE values, 9% (57 values) had errors greater than 1, and less than 1% (4 values) had errors greater than 3. Of the errors greater than 1, all but one were found in 21 kya data sets.

Values of RMSE for total precipitation rate were more variable (Table B5). Of the 204 RMSE values for precipitation, 23% (47 values) were greater than 1, 11% (22 values) were greater than 3, and 7% (14 values) were greater than 10. Some of these had values much larger than 10 (see Table B5). Precipitation datasets with RMSE values greater than 10 were inspected visually using histograms and mapped monthly data. Six of these 14 monthly datasets were found to have non-climatic patterns: HadGem1 A2 January; IPSL CM4 A1B March, November, and December; and IPSL CM4 A2 November and December. Problems with these files were not resolved by working back through the data files, so alternate precipitation files for these months were calculated by averaging the monthly precipitation files from the remaining four future data sets in each case (see Appendix A). The remaining

datasets with RMSE values greater than 10 were within normal precipitation ranges for the study area and were not altered.

References:

Hernandez-Stefanoni JL, Ponce-Hernandez R (2006) Mapping the spatial variability of plant diversity in a tropical forest: Comparison of spatial interpolation methods. *Environmental Monitoring and Assessment* 117:307-334

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Table B1: Values of RMSE for surface air temperature. Values greater than 3 are shaded grey.

Model	Time	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
CCSM 3	6 kya	0.063	0.062	0.060	0.051	0.055	0.053	0.099	0.124	0.092	0.081	0.073	0.069
	21 kya	0.520	0.306	0.332	0.321	0.280	0.278	0.259	0.327	0.309	0.302	0.492	0.509
HadCM3 UBRIS	6 kya	0.268	0.299	0.310	0.284	0.234	8.270	0.348	0.395	0.356	0.324	0.307	0.265
HadCM3	21 kya	2.735	2.501	2.299	2.058	1.742	1.968	2.058	1.853	1.858	2.232	2.656	2.907
	LIG	0.428	0.468	0.483	0.415	0.328	0.411	0.632	0.617	0.479	0.434	0.462	0.393
MIROC 3.2	6 kya	0.100	0.094	0.088	0.071	0.075	0.070	0.084	0.111	0.152	0.148	0.123	0.101
	21 kya	0.857	0.666	0.755	0.679	0.617	0.591	0.605	0.607	0.626	0.630	0.833	0.844
BCCR BCM 2.0	A1	0.210	0.198	0.239	0.269	0.328	0.351	0.356	0.294	0.231	0.245	0.224	0.219
	A2	0.217	0.215	0.272	0.310	0.352	0.393	0.411	0.346	0.275	0.271	0.240	0.239
CSIRO Mk 3.5	A1	0.162	0.158	0.141	0.151	0.222	0.257	0.217	0.108	0.092	0.143	0.173	0.175
	A2	0.187	0.178	0.150	0.177	0.259	0.259	0.222	0.116	0.084	0.149	0.185	0.199
HadGEM1	A1	0.315	0.358	0.381	0.348	0.319	0.343	0.313	0.296	0.236	0.251	0.263	0.283
	A2	0.340	0.377	0.402	0.376	0.354	0.377	0.314	0.311	0.254	0.266	0.278	0.303
IPSL CM4	A1	0.230	0.224	0.204	0.199	0.242	0.226	0.234	0.186	0.173	0.191	0.248	0.244
	A2	0.234	0.226	0.208	0.196	0.244	0.217	0.240	0.198	0.173	0.193	0.242	0.237
MIROC 3.2	A1	0.166	0.178	0.190	0.179	0.153	0.154	0.146	0.161	0.212	0.196	0.176	0.162
	A2	0.168	0.181	0.195	0.196	0.168	0.168	0.166	0.175	0.213	0.197	0.175	0.160

Table B2: Values of RMSE for maximum surface temperature. All values were less than 3.

Model	Time	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
CCSM 3	6 kya	0.163	0.181	0.219	0.247	0.197	0.220	0.345	0.433	0.266	0.172	0.158	0.158
	21 kya	0.905	1.069	1.036	1.040	1.034	1.086	1.200	1.132	0.985	0.893	0.892	0.885
HadCM3 UBRIS	6 kya	0.395	0.422	0.445	0.471	0.433	0.370	0.460	0.551	0.570	0.480	0.460	0.421
HadCM3	21 kya	2.440	2.344	2.162	1.945	1.755	2.106	2.360	1.934	1.853	2.148	2.530	2.754
	LIG	--	--	--	--	--	--	--	--	--	--	--	--
MIROC 3.2	6 kya	0.095	0.100	0.107	0.094	0.107	0.101	0.123	0.131	0.148	0.131	0.109	0.097
	21 kya	0.542	0.508	0.478	0.555	0.602	0.582	0.592	0.554	0.495	0.469	0.508	0.729
BCCR BCM 2.0	A1	0.207	0.198	0.246	0.279	0.334	0.311	0.363	0.300	0.241	0.246	0.219	0.213
	A2	0.213	0.216	0.280	0.308	0.357	0.392	0.421	0.352	0.292	0.272	0.235	0.232
CSIRO Mk 3.5	A1	0.141	0.133	0.117	0.101	0.215	0.227	0.214	0.160	0.083	0.114	0.144	0.147
	A2	0.164	0.145	0.123	0.107	0.226	0.236	0.223	0.125	0.087	0.120	0.153	0.165
HadGEM1	A1	0.353	0.381	0.408	0.372	0.368	0.398	0.363	0.319	0.269	0.248	0.267	0.301
	A2	0.358	0.397	0.441	0.438	0.417	0.328	0.352	0.348	0.331	0.336	0.342	0.335
IPSL CM4	A1	0.286	0.283	0.293	0.341	0.349	0.373	0.400	0.363	0.268	0.260	0.293	0.288
	A2	0.324	0.297	0.300	0.365	0.389	0.405	0.406	0.337	0.292	0.272	0.295	0.316
MIROC 3.2	A1	0.170	0.174	0.209	0.235	0.228	0.204	0.194	0.212	0.226	0.191	0.162	0.161
	A2	0.187	0.193	0.221	0.256	0.238	0.224	0.221	0.226	0.237	0.199	0.165	0.170

Table B3: Values of RMSE for minimum surface temperature. Values greater than 3 are shaded grey.

Model	Time	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
CCSM 3	6 kya	0.302	0.302	0.300	0.277	0.220	0.192	0.201	0.279	0.354	0.333	0.372	0.302
	21 kya	1.629	1.775	1.611	1.346	1.212	1.125	1.123	1.301	1.407	1.603	1.581	1.538
HadCM3 UBRIS	6 kya	0.363	0.355	0.403	0.412	0.378	0.314	0.375	0.437	0.440	0.453	0.401	0.374
HadCM3	21 kya	3.001	2.775	2.585	2.374	1.978	2.073	2.275	2.060	2.152	2.511	3.098	3.929
	LIG	--	--	--	--	--	--	--	--	--	--	--	--
MIROC 3.2	6 kya	0.120	0.115	0.101	0.089	0.081	0.067	0.083	0.144	0.196	0.170	0.154	0.121
	21 kya	1.020	0.980	0.961	0.889	0.725	0.704	0.715	0.755	0.822	0.818	0.905	0.988
BCCR BCM 2.0	A1	0.221	0.207	0.242	0.275	0.324	0.337	0.350	0.287	0.230	0.249	0.235	0.231
	A2	0.229	0.224	0.273	0.306	0.339	0.342	0.403	0.341	0.275	0.277	0.252	0.253
CSIRO Mk 3.5	A1	0.207	0.207	0.197	0.227	0.226	0.277	0.145	0.140	0.102	0.214	0.220	0.216
	A2	0.235	0.233	0.209	0.250	0.230	0.261	0.150	0.111	0.139	0.222	0.237	0.247
HadGEM1	A1	0.423	0.470	0.503	0.458	0.403	0.477	0.370	0.360	0.331	0.338	0.344	0.362
	A2	0.414	0.462	0.504	0.517	0.467	0.380	0.378	0.374	0.377	0.406	0.393	0.390
IPSL CM4	A1	0.308	0.305	0.285	0.315	0.367	0.356	0.435	0.337	0.305	0.294	0.344	0.324
	A2	0.347	0.314	0.301	0.330	0.365	0.372	0.367	0.330	0.329	0.324	0.358	0.353
MIROC 3.2	A1	0.206	0.227	0.232	0.199	0.172	0.149	0.149	0.189	0.266	0.238	0.216	0.198
	A2	0.208	0.228	0.234	0.210	0.187	0.161	0.163	0.210	0.264	0.238	0.219	0.197

Table B4: Values of RMSE for the standard deviation of minimum surface temperature. All values were less than 3. This variable was only calculated for summer (June-July-August) minimum temperatures.

Model	Time	Jun	Jul	Aug
CCSM 3	6 kya	0.135	0.133	0.152
	21 kya	0.278	0.256	0.297
HadCM3 UBRIS	6 kya	0.272	0.271	0.283
HadCM3	21 kya	0.825	0.759	0.696
	LIG	--	--	--
MIROC 3.2	6 kya	0.041	0.039	0.059
	21 kya	0.123	0.126	0.136
BCCR BCM 2.0	A1	0.146	0.112	0.085
	A2	0.158	0.105	0.126
CSIRO Mk 3.5	A1	0.056	0.060	0.050
	A2	0.060	0.061	0.051
HadGEM1	A1	0.169	0.169	0.178
	A2	0.173	0.183	0.171
IPSL CM4	A1	0.158	0.177	0.171
	A2	0.175	0.175	0.174
MIROC 3.2	A1	0.063	0.063	0.090
	A2	0.071	0.066	0.088

Table B5: Values of RMSE for total precipitation rate. Values greater than 10 are shaded light grey. Precipitation files shaded dark grey showed non-climatic patterns and were replaced (see text).

Model	Time	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
CCSM 3	6 kya	0.069	0.073	0.068	0.075	0.085	0.090	0.231	0.469	0.173	0.062	0.068	0.056
	21 kya	0.116	0.129	0.112	0.126	0.130	0.126	0.158	0.139	0.101	0.077	0.088	0.106
HadCM3 UBRIS	6 kya	0.131	0.150	0.143	0.202	0.127	0.131	1.422	2.643	0.387	0.158	0.119	0.126
HadCM3	21 kya	0.320	0.305	0.227	0.205	0.412	1.383	2.366	3.236	2.755	2.336	0.584	0.371
	LIG	0.333	0.389	0.457	0.209	0.552	0.372	11.75	6.083	4.188	0.593	0.304	0.270
MIROC 3.2	6 kya	0.035	0.035	0.043	0.027	0.027	0.041	0.046	0.054	0.039	0.045	0.068	0.031
	21 kya	0.114	0.125	0.088	0.045	0.058	0.197	0.438	0.175	0.091	0.054	0.056	0.056
BCCR BCM 2.0	A1	2.013	0.516	0.246	0.165	0.287	0.140	1.987	0.307	1.095	3.295	1.842	1.213
	A2	1.720	1.513	0.481	0.145	0.214	4.247	1.073	0.792	0.724	1.065	0.441	6.964
CSIRO Mk 3.5	A1	0.459	0.234	0.102	0.078	0.100	0.787	0.560	0.388	1.284	0.141	0.123	0.172
	A2	0.269	0.170	0.215	0.088	0.120	0.345	0.466	0.747	0.418	0.124	0.116	0.372
HadGEM1	A1	1.709	33.51	0.207	0.086	0.096	0.095	2.001	0.553	3.840	0.128	0.697	4.897
	A2	76.49	132.5	0.138	0.091	0.116	0.131	1.962	1.364	1.276	0.148	0.348	248.1
IPSL CM4	A1	156.0	0.732	4041.4	0.176	0.085	0.138	1.870	0.691	0.251	1.028	78.13	12572.4
	A2	18.77	42.72	44.01	0.157	0.087	0.174	1.238	0.377	0.305	1.009	76.02	14973.0
MIROC 3.2	A1	0.095	0.116	0.083	0.055	0.062	0.082	0.074	0.075	0.070	0.070	0.079	0.078
	A2	0.306	0.173	0.087	0.058	0.080	0.073	0.091	0.079	0.075	0.089	0.103	0.122