

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

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ABSTRACT

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

Location North American cordillera.

Methods This approach was demonstrated using the arctic-alpine plant *Rhodiola integrifolia* (Crassulaceae). SDMs were fitted to current and past climates using eight models, two thresholds and one to three climate data sets. These projections were combined to create a map of stable climate (refugia) since the Last Interglacial (124,000 kya). Five biogeographic hypotheses were developed based on the configuration of refugia and tested using statistical phylogeography. Projection of SDMs into the future was contingent on agreement across approaches; future projections (to 2085) used five climate data sets and two greenhouse gas scenarios.

Results A multiple-refugia hypothesis was supported by both methods, confirming the assumption of niche conservatism in *R. integrifolia* and justifying the projection of SDMs onto future climates. Future projections showed substantial loss of climatically suitable habitat. Southern populations had the greatest losses, although the biogeographic scale of modelling may overpredict extinction risks in areas of topographic complexity. Past and future SDMs were assessed for novel values of climate variables; areas of novel climate were flagged as having higher uncertainty.

Main conclusions 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 the vulnerability of species to climate change and provide additional data upon which to base conservation decisions, such as prioritizing the conservation of areas of high genetic diversity to build evolutionary resiliency within populations.

Keywords

Arctic-alpine plants, climate change, conservation, ensemble modelling, phylogeography, species distribution models.

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INTRODUCTION

Anthropogenic climate change is impacting ecosystems world-wide, generating a global signal of climate-induced range shifts and phenological responses crossing all ecosystems and taxonomic groups (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 imperilled species and maintaining ecosystem functioning. Species distribution models (SDMs) have become one of the most widely used tools to develop these forecasts. SDMs have many limitations, however, including difficulty handling historical demographic signals, biotic interactions and changing combinations of climate variables, as well as theoretical assumptions, such as species–climate equilibrium and niche conservatism (Jackson *et al.*, 2009; Wiens *et al.*, 2009). Furthermore, SDMs provide only a starting point for understanding species responses to climate change and planning adaptive management strategies to conserve biodiversity (Franklin, 2010; Dawson *et al.*, 2011).

One proposal for the improvement of SDMs is to integrate phylogeography (Scole & Lowe, 2010), which examines the current geographic distribution of genetic variation within and between populations to infer demographic history and how palaeoclimatic events have impacted population divergence (Avice, 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 and long-term refugia. Phylogeographers have started using SDMs to develop spatially explicit biogeographic hypotheses that can be tested using statistical phylogeographic methods (Richards *et al.*, 2007). 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 (Chan *et al.*, 2011).

Ecologists looking to model future impacts of climate change on species distributions can integrate phylogeography to address one of the fundamental assumptions of projecting SDMs: niche conservatism, or the tendency of a species to retain its climatic niche over time (Wiens *et al.*, 2010). Because SDMs are built using the climatic niche defined by the present distribution of a species, projecting that niche onto palaeoclimate data indicates where the species would have been distributed in the past given no change in its climatic niche (i.e. assuming niche conservatism). An independent data source, such as a fossil record or phylogeographic data that shows a similar palaeodistribution argues in favour of niche conservatism for that species. A mismatch may indicate niche evolution, barriers to dispersal or errors in the modelling process. Additionally, phylogeography allows for the detection of refugia and past barriers to dispersal which have important conservation applications. Long-term refugia tend to maintain high levels of allelic diversity (Keppel *et al.*, 2012), while past barriers can result in suture zones, which

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

Only a few studies have used the combination of SDMs and phylogeography to both understand the impact of palaeoclimatic events on species distributions and assess future climate change impacts (Cordellier & Pfenninger, 2009; Galbreath *et al.*, 2009). These authors typically employ accessible and user-friendly approaches to SDMs, such as Maxent modelling software (Phillips & 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 criticized (Nogués-Bravo, 2009).

A recent approach to addressing this uncertainty is ensemble modelling combined with consensus projections. Ensemble modelling is based on the idea that different combinations of initial conditions, model algorithms and GCMs represent alternate possible states of the system being modelled (Araújo & 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, because increased accuracy would not be expected simply by combining poor models (Araújo *et al.*, 2005). Ensemble modelling 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 modelling, where variables are outside the range used to build the models (Marmion *et al.*, 2009; Heikkinen *et al.*, 2012). While projection of SDMs onto these ‘novel climates’ is discouraged (Fitzpatrick & Hargrove, 2009; Elith *et al.*, 2010), it is usually unavoidable because 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-analogue climates and indicating larger levels of uncertainty in those areas is essential to producing robust projections of climate change impacts.

In this study, we combined ensemble modelling and consensus projections with statistical phylogeographic analyses to assess past and future climate change impacts on the geographic distribution of an arctic-alpine plant, *Rhodiola integrifolia* Raf. (Crassulaceae). This species, which includes a relict subspecies listed as threatened under the U.S.

Endangered Species Act, has been the subject of a recent phylogeographic analysis indicating the presence of cryptic species lineages (E.G. DeChaine & B.R. Forester, unpublished data). Determining how past climate change has influenced the diversification of these lineages can help us understand how anthropogenic climate change will impact their persistence.

Our objectives were: (1) to develop a model of climatically stable refugial areas in western North America for *R. integrifolia* over the last 124 kya (kya, thousand years ago), (2) to evaluate the level of agreement between the SDM refugial model and empirical genetic data using a statistical phylogeographic approach, and (3) assuming agreement between the SDMs and phylogeographic analyses, to assess the impact of future climate change scenarios on the geographic distribution of climatically suitable habitat for *R. integrifolia* in western North America.

METHODS

Study species and occurrence records

Rhodiola integrifolia, roseroot or king's crown, is a perennial arctic-alpine succulent characteristic of wet meadows and rocky slopes with a widespread, patchy distribution at high altitudes and latitudes throughout the North American cordillera (see Fig. S2, in Supporting Information). It reproduces by wind-dispersed seeds and also propagates vegetatively at the root stock, indicating either widespread or limited dispersal, respectively (Clausen, 1975). A recent analysis showed a deep divergence between two phylogenetic clades dating to ~700 kya (E.G. DeChaine & B.R. Forester, unpublished data). The Beringian clade ranges from arctic Alaska south to the Sierra Nevada and the Central Rocky Mountains and includes microenvironments in the north-east, while the Rocky Mountain clade is based solely in the Southern Rocky Mountains. In this analysis, we focused on the larger of the clades (the Beringian), excluding *R. integrifolia* ssp. *leedyi*, whose confinement to microclimate refugia in the north-east makes its inclusion inappropriate for the spatial scale of this analysis. Occurrence records for *R. integrifolia* and its taxonomic synonyms were collected from online herbaria; georeferencing was evaluated for accuracy.

Scaling, climate data and predictor variables

The spatial extent of analysis was 30°N to 80°N and 99°W to 180°W. This 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). Palaeodistributions 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 to 2000. Future distributions were based on mean climate values projected for 2071–2100 (hereafter referred to as '2085') under two greenhouse gas scenarios (A1B and A2).

Eight climate models were used (Table 1). Data from GCMs were interpolated to 0.5° using ordinary cokriging in Arc-Map (Environmental Systems Resource Institute (ESRI), 2010). Sixty predictor variables were calculated; the most relevant were identified using the randomForest package (Liaw & Wiener, 2002) in R (R Development Core Team, 2012) and a modified approach from Strobl *et al.* (2008). Methods for climate data processing and variable calculation and selection are provided in Appendix S1.

Species distribution modelling and evaluation

Modelling was conducted using the BIOMOD package (Thuiller *et al.*, 2009) in R and Maxent, v. 3.3.3 (Phillips *et al.*, 2006; Phillips & Dudik, 2008). Nine algorithms were run: generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), flexible discriminant analysis (FDA), artificial neural networks (ANN),

Table 1 Climate data used to model the distribution of suitable habitat for *Rhodiola integrifolia*; kya = thousand years ago.

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

generalized boosted models (GBM), random forest (RF) and maximum entropy (MAX). Model parameterizations are provided in Appendix S2.

One presence record per pixel was used for a total of 269 records (Fig. 1a). The entire background of the study area was used to create pseudo-absence points (Fig. 1b), ensuring complete sampling of environmental conditions and minimizing extrapolation when projecting onto different

climates. Background records were weighted to maintain equal prevalence; this has been found to maximize model performance (Barbet-Massin *et al.*, 2012). Data partitioning (70% training, 30% verification) was used to assess model stability and sensitivity to initial conditions because independent data were not available. Ten partitions were run for each model using random selections with replacement (Fig. 1e). Final consensus models were built using 100% of the available

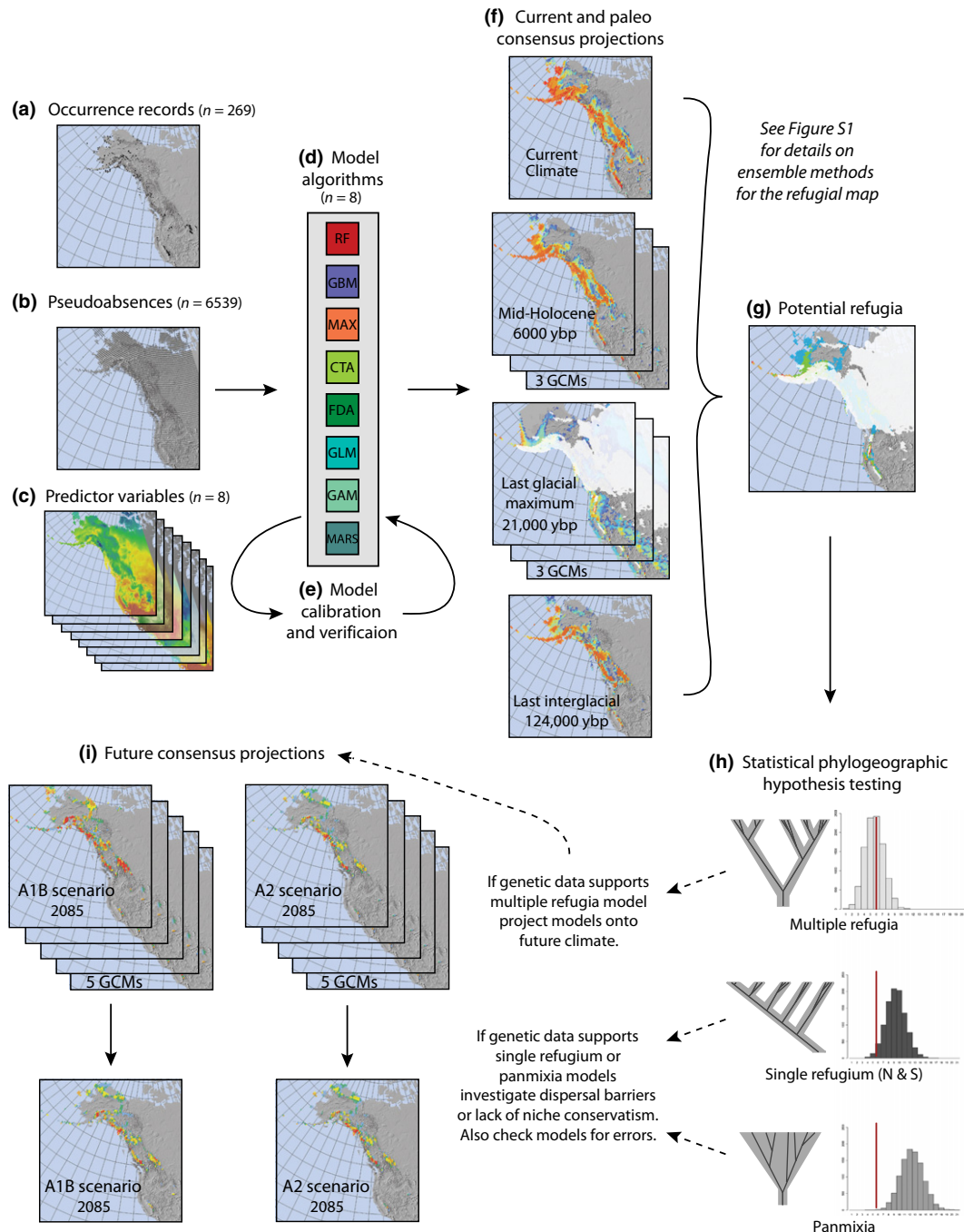


Figure 1 Methods for ensemble species distribution modelling of refugial areas for *Rhodiola integrifolia* since the Last Interglacial (a–g); use of the refugial model to develop biogeographic hypotheses for phylogeographic analysis (h); projection of verified models onto future climate, using an ensemble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

data, because the removal of presence records has a negative effect on model projections (Araújo *et al.*, 2005).

The area under the curve of the receiver operating characteristic (AUC, Fielding & Bell, 1997) and sensitivity were used to assess model accuracy and stability (see Appendix S2 for details). Evaluation statistics were averaged across ten cross-validation runs. Models with mean AUC and mean sensitivity > 0.7 were determined to be useful and were kept in the consensus analysis (Fig. 1d,e).

Palaeodistributions and the refugial model

Models for *R. integrifolia* were projected onto current and past climates (Fig. 1f). To assess suitable habitat across time, probabilistic output was converted to presence/absence using two thresholds: minimizing the absolute value of sensitivity minus specificity (minSeSp), and taking the mean probability value across model output (mean). Both of these methods perform well in threshold comparisons (Liu *et al.*, 2005). For the current and LIG, this resulted in 16 models each: eight algorithms (one algorithm was discarded, see Results) using two thresholds. For the Mid-Holocene and LGM, this produced 48 models each: eight algorithms using two thresholds for three GCMs.

Refugia are defined as pixels that are classified as suitable habitat across all four time periods. For each time slice, individual models were combined to create one map showing the percentage of models indicating presence of suitable habitat in each pixel based on four thresholds: 30, 50, 70 and 90% probability of suitable habitat. Each pixel was assessed for agreement across the four time slices at each threshold, resulting in a final consensus refugial map indicating pixels classified as suitable habitat across all four time slices (a schematic of these methods is provided in Fig. S1). The LGM ice layer (Dyke *et al.*, 2003) was overlaid to exclude potential suitable habitat under the ice sheet (Fig. 1g).

Biogeographic hypotheses

Biogeographic hypotheses are models of population history that indicate branching patterns, timing of divergence events and effective population size (N_e) of populations of a species. Hypotheses should contain enough parameters to distinguish between alternate models, but be simple enough to be addressed with the genetic material available (Knowles, 2004). Alternate biogeographic hypotheses for *R. integrifolia* (Fig. S2) were based on the configuration of refugia as identified by the refugial model (see Results, Fig. 3).

1. Panmixia. This is a null hypothesis that an individual has an equal probability of being found anywhere in its geographic range, such that divergence between the north and south is effectively at present.
2. Northward colonization from a southern refugium after the LGM. This model is defined by expansion out of a southern refugium 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 in the south and 10% of N_e in the north.

3. Southward colonization from a northern refugium after the LGM. This model is defined by expansion out of a northern refugium based in south-western 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 in the north and 10% of N_e in the south.

4. Colonization from multiple refugia with divergence after the LGM. This model is defined by expansion out of northern and southern refugia after the LGM. This hypothesis predicts no relationship between latitude and genetic diversity, and lineage coalescence dates to the LGM.

5. Colonization from multiple refugia with divergence during the mid-Pleistocene. This model is defined by expansion out of northern and southern refugia during the mid-Pleistocene. This hypothesis predicts no relationship between latitude and genetic diversity, and lineage coalescence dating to the Illinoian Glacial Period, 120–180 kya.

Statistical phylogeographic analysis

Biogeographic hypotheses were tested using statistical phylogeography to determine the extent to which the empirical genetic data supported each hypothesis (Fig. 1h). We used the following protocol: (1) genomic DNA was extracted from individual *R. integrifolia* sampled throughout their range, (2) five anonymous nuclear loci were sequenced for each individual, (3) phylogenies were estimated for each locus in Garli v. 0.951 (Zwickl, 2006) and used as 'observed' trees for testing models of divergence based on hypotheses developed from the SDMs; and (iv) population genetic parameters (i.e. N_e) were estimated in LAMARC v. 2.1.6 (Kuhner, 2006).

Coalescent simulations of genealogies constrained within models of population divergence were performed with MESQUITE 2.75 (Maddison & Maddison, 2011). Each population model is comprised of the tree topology, relative estimates of N_e for each population and time (in generations) given as branch lengths. Gene trees were simulated by constraining the coalescence of all sampled lineages within the topology, branch lengths and relative N_e for a given model. This yielded 10,000 simulated gene trees within each model of divergence, over a range of times (branch lengths). Given the uncertainty in estimating N_e , we tested each model using a range of values (10,000, 100,000, 300,000, 500,000, 700,000 and 1,000,000).

To test the fit of our observed data to a model, we generated an expected distribution of discordance between gene trees and the population model, measured by deep coalescences (DC; Maddison, 1997). DCs are 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 and compared with the null distribution from the simulations to test whether the observed tree could have been generated under

the expected distribution for the population model (Fig. 1h and 4). If the observed *DC* did not fit the expected distribution for a given model ($P < 0.05$), that model was rejected. If the observation fell within the expected distribution for a model ($P > 0.05$), that model was accepted as a possible scenario that could have led to the distribution of genetic variation observed today.

Future projections and novel climates

Models for *R. integrifolia* were projected onto future climate, including two greenhouse gas scenarios for each of five GCMs for 2085 (Fig. 1i). Probabilistic output was converted to presence/absence using two thresholds (minSeSp and mean). Consensus probability maps used 80 models (eight algorithms, two threshold methods and five GCMs). These maps indicate the percentage of models showing the presence of suitable habitat, truncated at 50% or more of the models indicating suitable habitat.

Analysis of the spatial distribution of novel values of climate variables was conducted using the program Maxent, v. 3.3.3 (Elith *et al.*, 2010). For each climate data set, Maxent calculates a multivariate environmental similarity surface, which indicates how similar a point is to a set of reference points across multiple predictor variables. Surfaces for palaeo- and future climates were reclassified and combined to indicate the number of GCMs with novel values of climate variables.

RESULTS

Predictor variables and model evaluation and selection

Eight predictor variables were chosen to model suitable habitat for *R. integrifolia* (Table 2). All models met the guideline of mean AUC and mean sensitivity > 0.7 (Table 3). Variability across cross-validation runs (Fig. 2) supports building final models using 100% of the data. FDA and MARS had the lowest sensitivity scores and showed high variability in response to random pulls of training data. Both performed well based on AUC, however, so were retained in the ensemble. ANN probabilities were much lower than other models, so it was removed from the ensemble.

Refugial model and biogeographic hypotheses

The consensus refugial model showed a high level of support for multiple refugia since the LIG (Fig. 3). Both north and south of the LGM ice sheet, there were pixels classified as suitable habitat with 90–100% agreement across the four time slices, indicating that at least 118 of 128 models classified those pixels as suitable habitat (Fig. S1). This provides very strong support for a two refugia hypothesis (north and south of the LGM ice sheet).

Additionally, each of the 128 binary models (Fig. S1) were inspected for the presence of suitable habitat to the north

Table 2 Predictor variables used to model the distribution of suitable habitat for *Rhodiola 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

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. See text for model abbreviations.

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

and/or south of the LGM ice sheet. Of the 128 models, 122 (95%) had pixels classified as suitable habitat both north and south of the ice sheet. Only six models (5%) did not have suitable pixels in both the north and south. These six models used the same combination of RF and the minSeSp threshold applied to the three GCMs of the Mid-Holocene and LGM. These models had a very small number of suitable pixels overall indicating that, in this case, the RF/minSeSp threshold combination may be too conservative.

At the 50% level, the consensus refugial model showed potential refugia to the north, south and west of the LGM ice sheet (Fig. 3). South of the ice sheet, the strongest support (70% and greater) was found in the Oregon Cascades, Klamath

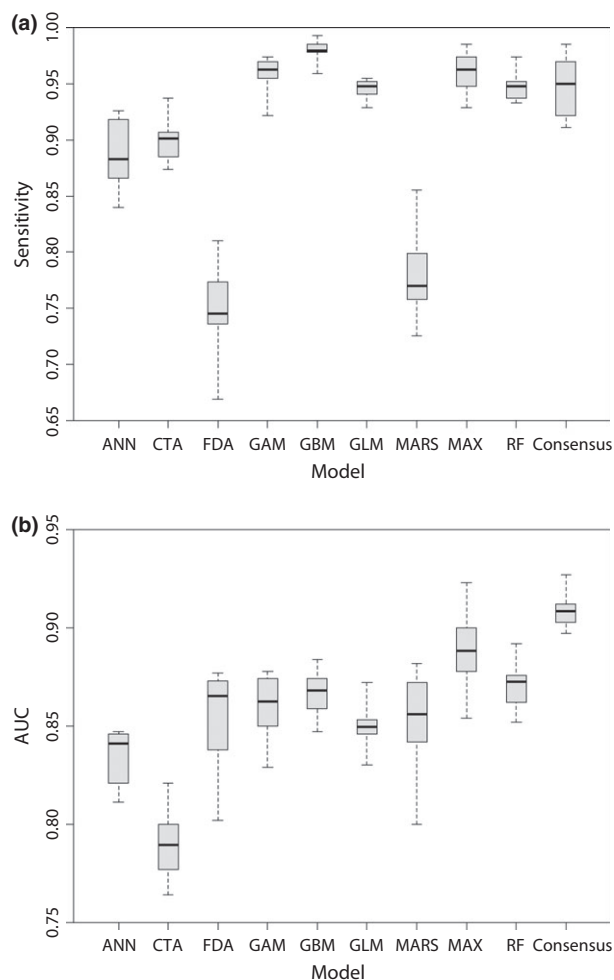


Figure 2 Boxplots for sensitivity (a) and AUC (b) scores for 10 cross-validation runs on test data. The boxes represent the range of half of the scores, with the median represented by the black line. The whiskers represent the minimum and maximum score values. The consensus model does not include ANN.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

and Sierra Nevada Mountain ranges, while north of the ice sheet refugia were found in the Aleutian Islands and south-west Alaska. Coastal refugia in Haida Gwaii and the Alexander Archipelago (west coast of British Columbia and Alaska) were also indicated at a 50% level. Based on the configuration of refugial habitat in the SDM model and the availability of genetic samples, five alternate biogeographic hypotheses were tested (Fig. S2 and Methods). Because the consensus refugial model shows a high level of support for multiple refugia since the LIG, phylogeographic support for hypothesis 4 or 5 would best corroborate niche conservatism in *R. integrifolia*. Support for alternative hypotheses is considered in the discussion.

Statistical phylogeographic analysis

The first three hypotheses were not supported by the phylogeographic analysis; the average observed number of deep

coalescences ($DC = 9.8$) did not meet the expected distribution for the population models at $\alpha = 0.05$ ($P < 0.0001$ for each model across all estimates of N_e). Likewise, the recent (LGM) hypothesis of divergence between northern and southern refugia (hypothesis 4) was also rejected ($P < 0.0001$ across all estimates of N_e). The only model that was supported was that of a mid-Pleistocene divergence between northern and southern refugia (hypothesis 5). For this model, the observed number of deep coalescences fell within the expected distribution for $N_e = 500,000$ ($P = 0.5387$, Fig. 4a) and $N_e = 700,000$ ($P = 0.0805$, Fig. 4b) with a lower bound near $N_e = 300,000$ ($P = 0.0347$, Fig. 4c); all other estimates of N_e yielded P -values < 0.0001 . Overall, the northern population has a much larger effective population size ($N_e = 15,750,000$) relative to the southern population (centred in the Sierra Nevada Mountains, $N_e = 68,000$), as estimated in LAMARC.

Future projections

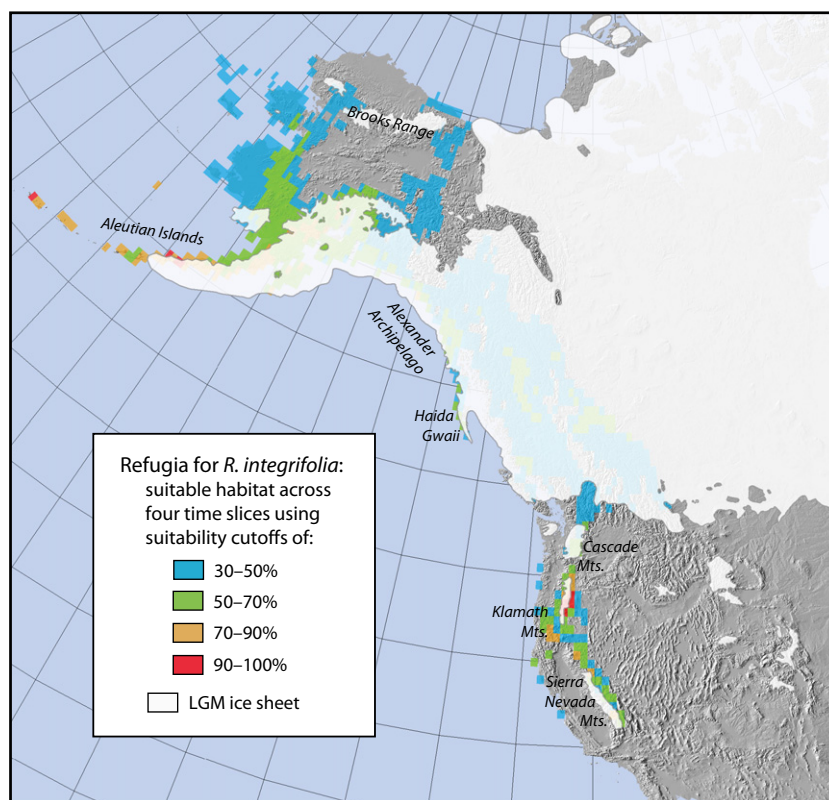
The match between refugia identified by the SDMs and phylogeographic analysis supports niche conservatism in *R. integrifolia* across the modelled time period. This stable climate-distribution relationship was therefore used to assess future climate change impacts on the distribution of suitable habitat. Projections for the A1B and A2 scenarios at 2085 did not differ substantially, with both indicating a significant reduction in suitable habitat (63% to 67%) by 2085 (Table 4, Fig. 5d,e). Both projections show a northward latitudinal shift in suitable habitat, with habitat losses represented by upwards elevational shifts and/or contractions of suitable habitat (Fig. 5d,e). 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. Although not explicitly quantified in this analysis, there were considerable differences across the five GCM projections for both the A1B and A2 scenarios (Fig. 6).

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 (Fig. 7a), where suitable habitat and novel climate variables coincided for one to two of the seven GCMs, both from the LGM. For two of the GCMs novel values did not overlap north of the ice sheet. South of the ice sheet all novel values came from the LGM data; the southern Rockies were of particular note, with summer minimum temperature from all three LGM GCMs being outside the training range. The presence of novel values in LGM data is not surprising given the large differences between LGM and current climate.

For both future scenarios, the overlap of novel values of climate variables with projected suitable habitat is limited mainly to north-western Alaska (Fig. 7b,c), where there is at least one GCM that does not have novel values. Future consensus projections do not show a gain of suitable habitat

Figure 3 Consensus refugial model indicating areas of suitable habitat for *Rhodiola integrifolia* across four time slices: current conditions, mid-Holocene, Last Glacial Maximum (LGM) and Last Interglacial. Major features are labelled. Ice sheet layer is from Dyke *et al.*, 2003. Map projection: North America Albers Equal Area Conic.



along the arctic coast; however, novel values of variables in this region indicate that this is an area of uncertainty in model projections, so the potential for climatically suitable habitat in this region should not be dismissed.

DISCUSSION

Niche conservatism and biogeographic hypothesis testing

The use of static SDMs to project future distributions is only appropriate for species where the climate-distribution relationship is stable. Although niche conservatism is usually assumed (or not addressed at all) in SDM studies, previous research has shown the potential for rapid adaptation (e.g. Berlocher, 2000; Broennimann *et al.*, 2007; Franks *et al.*, 2007). For many species evolutionary responses will be nuanced, with adaptation occurring at range limits, particularly trailing-edge populations (Ackerly, 2003; Hampe & Petit, 2005; Parmesan, 2006). Especially for studies modelling at fine resolutions (e.g. 1-km pixel sizes), the potential for rapid adaptation at range limits should give modellers pause, in addition to other concerns at fine scales, such as changing biotic interactions and potential errors in climate data downscaling.

We addressed the assumption of niche conservatism for *R. integrifolia* by using two complementary methods, SDMs and phylogeography. In this study, both analyses supported the same multiple-refugia hypothesis, supporting niche conservatism in *R. integrifolia* and justifying projection of the

SDMs onto future climate data. This finding of niche conservatism is consistent with previous palynological and phylogenetic research on plant responses to Quaternary climate change which has generally agreed that the fundamental response of most temperate plant taxa to Quaternary climate changes was migration, rather than adaptation (Prinzinger *et al.*, 2001; Ackerly, 2003). Additionally, phylogeographic analysis has a role in resolving taxonomic uncertainty prior to the use of SDMs, because improperly grouped (or separated) clades can impact assessments of niche conservatism.

It is important to note that phylogeographic support for the alternate hypotheses of panmixia or a single *R. integrifolia* refugium to the south or north of the LGM ice sheet would not necessarily have invalidated the refugial model, but inference concerning the mechanisms at work would be less straightforward. For example, areas modelled as climatically suitable may not have been occupied by the species due to long-term barriers to dispersal. Alternatively, if range expansion after the LGM was accompanied by niche expansion, the climate niche of *R. integrifolia* would have changed between the current and pre-LGM time periods, resulting in a mismatch between the palaeodistribution models and the phylogeographic analyses. This case has been demonstrated in *Candidula* land snails (Pfenninger *et al.*, 2007) 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 five models tested. These models represent relatively simple hypotheses regarding the

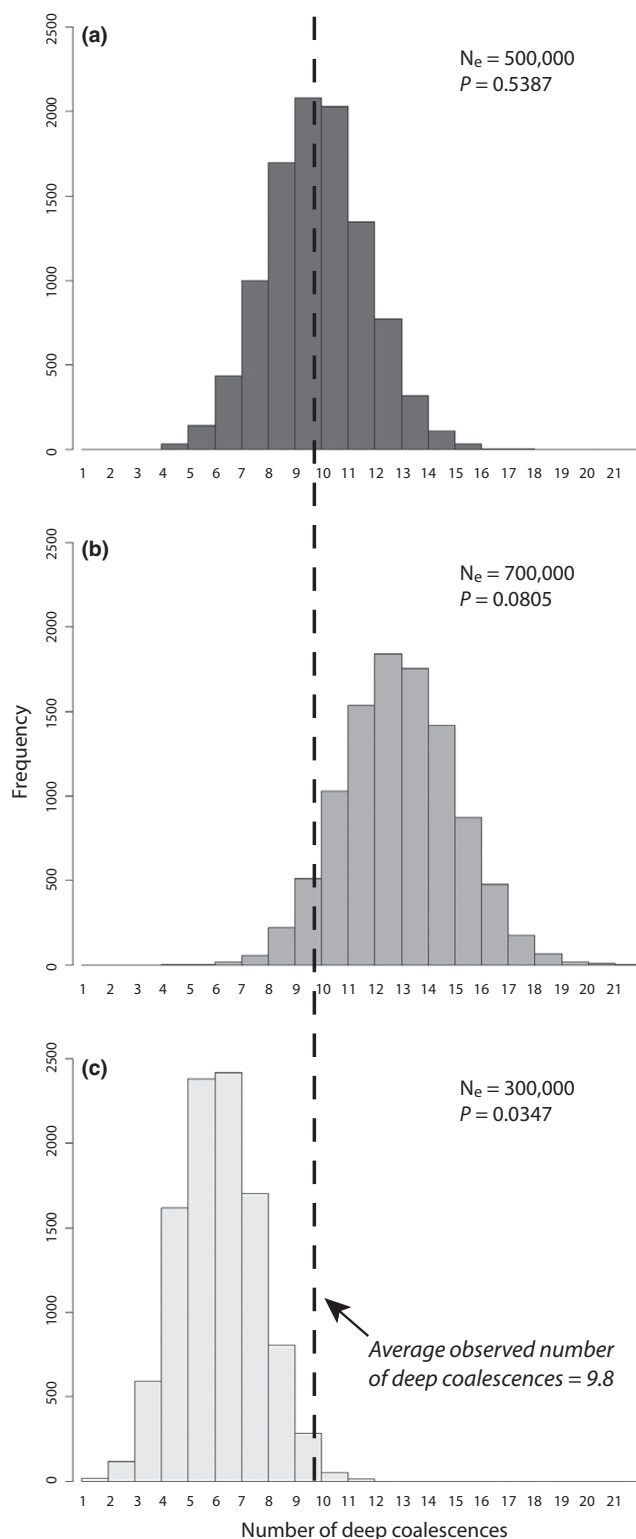


Figure 4 Tests of biogeographic hypotheses comparing the average observed number of deep coalescences ($DC = 9.8$) with a null distribution of DC values from simulated genealogies constrained within models of population divergence and effective population sizes (N_e). Models with $P > 0.0001$ are illustrated here; all three are models of hypothesis 5, a mid-Pleistocene divergence between northern and southern refugia. The most highly supported model was for (a) $N_e = 500,000$ ($P = 0.5387$), bounded by the models for (b) $N_e = 700,000$ ($P = 0.0805$) and (c) $N_e = 300,000$ ($P = 0.0347$).

structuring of genetic diversity in this widely distributed species. Given the results of the SDMs, more sophisticated hypotheses could be tested with additional genetic data. For example, an interesting result of the refugial modelling was the indication of suitable habitat in the Alexander Archipelago and Haida Gwaii, to the west of the LGM ice sheet

(Fig. 3). The presence of this cryptic refugia in coastal British Columbia has been established in previous studies (Warner *et al.*, 1982; Cook *et al.*, 2006; Shafer *et al.*, 2010; and references therein). Unfortunately, we did not have genetic samples from this area, preventing a test of this west-coast refugial hypothesis. The presence of this refugium has been

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

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

supported, however, by an analysis 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, 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 (Fig. 5, Table 4), while differences in projections across GCMs were quite large (Fig. 6). This indicates that less focus should be placed on modelling alternate scenarios, with more effort directed towards sampling different GCM projections (Buisson *et al.*, 2010).

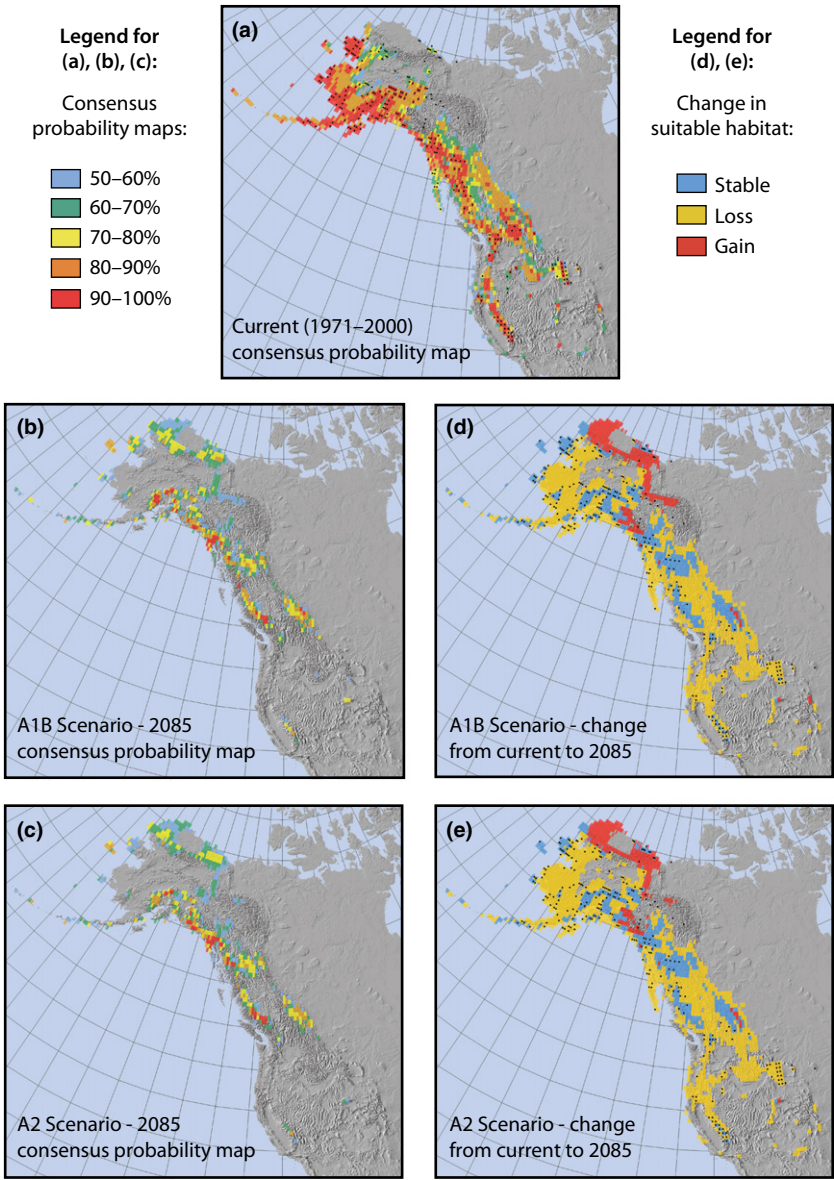


Figure 5 Current (a), A1B scenario (b) and A2 scenario (c) consensus probability maps. Change in suitable habitat from current to future for the A1B (d) and A2 (e) scenarios, based on a cut-off of 50% of the models indicating suitable habitat; black dots (a, d, e) indicate pixels with current populations of *Rhodiola integrifolia* (based on herbarium searches). Map projection: North America Albers Equal Area Conic.

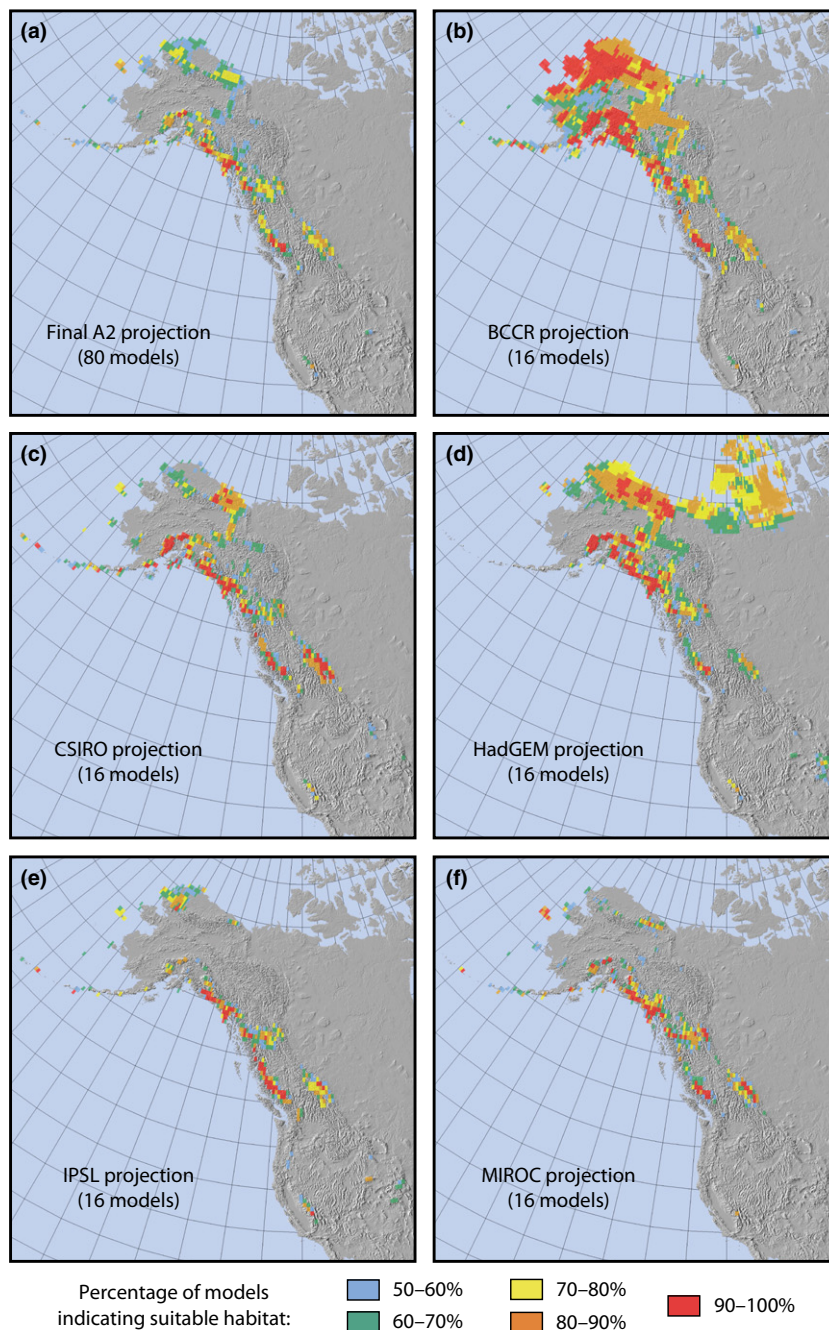


Figure 6 Comparison of projections of suitable habitat for *Rhodiola integrifolia* across five general circulation models (b–f) and the final consensus projection (a) for the A2 scenario at 2085. Projections are truncated at 50% of the models indicating suitable habitat. Map projection: North America Albers Equal Area Conic.

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 habitat losses, including complete loss of habitat in the Alexander Archipelago and Haida Gwaii. Habitat gains in south-east Alaska may facilitate population connectivity between central and northern populations, while the development of climatically suitable habitat in the Brooks Range of Alaska may allow for population expansion (Fig. 5d,e).

The identification of past refugia is an important benefit of combining phylogeography and SDMs. Because glacial–interglacial refugia tend to harbour high levels of allelic diversity, these regions have implications for conserving the genetic variability of current and future populations. The refugial model indicates discrete southern refugia in the southern Oregon Cascades, Klamath and Sierra Nevada Mountain ranges (Fig. 3). Populations in the Oregon Cascades are predicted to be extirpated by 2085, although 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

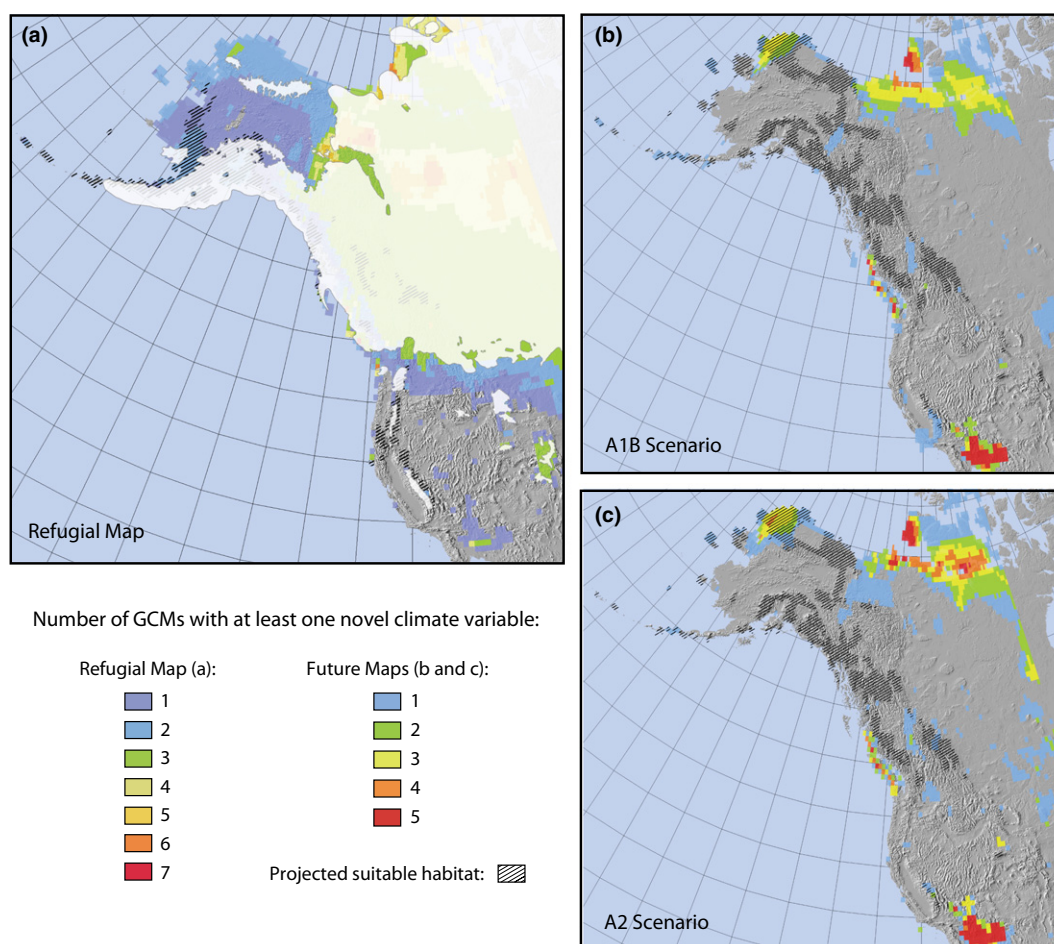


Figure 7 Geographic distribution of novel values of climate variables for the refugial map (a), A1B future scenario (b) and A2 future scenario (c) for *Rhodiola integrifolia*. Colour scales represent the number of general circulation models (GCMs) with at least one climate variable outside the range of the current climate data (out of seven total GCMs for the refugial map, and five for the future scenarios). Hatched areas represent projected suitable habitat. Ice sheet layer in (a) is from Dyke *et al.*, 2003. Map projection: North America Albers Equal Area Conic.

scenarios. The persistence of these populations will be important to the maintenance of overall levels of genetic diversity in this species, because phylogeographic analyses indicate that these populations represent genetically distinct lineages.

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, mainly due to its influence on the distribution of microclimate refugia in mountainous terrain (Dobrowski, 2011). 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 climate data average out these complexities, the most likely outcome is underestimation of potential habitat, although 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, modellers need to balance 'resolution with realism' (Daly, 2006) when downscaling projections from GCMs, although the increasing availability of regional climate models may help with this limitation (at least for future climate projections). The common use of climate data that are interpolated to ~1-km pixel sizes from very large scale GCMs (e.g. 2 by 3°) should be questioned. A second consideration is that at fine (landscape to local) scales, climatic controls over species distributions break down. Biotic interactions, source-sink 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 (e.g., Brook *et al.*, 2009).

Ensemble modelling and novel climates

In addition to support from genetic analyses, projected species distribution were made more robust through the use of an ensemble and consensus approach. The consensus model of current *R. integrifolia* distribution had a higher predictive capacity based on AUC scores than any of the single SDMs alone (Fig. 2b, Table 3) and was among the highest scoring based on sensitivity scores (Fig. 2a, Table 3). This is in agreement with previous research indicating that consensus models outperform individual models, providing more robust projections of habitat distributions (Marmion *et al.*, 2009; Grenouillet *et al.*, 2011). Additionally, the use of multiple algorithms in studies that project species distributions is essential because 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.*, 2012).

The ensemble and consensus approach also allows a spatial depiction of agreement across model algorithms, by showing areas of consensus (higher confidence) and disagreement (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 & New, 2007). Despite its advantages, ensemble modelling should be used with caution. Naïve use of model algorithms can result in poor parameterization and poorly performing models. Ensemble approaches can also magnify the work-load associated with modelling species distributions. Despite these drawbacks, ensemble approaches are an effective way to create robust projections that include a depiction of variability and uncertainty.

The use of multiple GCMs is an especially important component of the ensemble approach when projecting species distributions. We found substantial variability across the five GCMs used for future projections (Fig. 6). 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. Modellers 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 (Fig. 5d,e, Table 4, Buisson *et al.*, 2010).

Novel climate 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 north-western part of Alaska and along the arctic coast (Fig. 7b,c). For both scenarios, there are GCMs without novel values in these regions. If this were an area of conservation concern, those GCM projections without novel values could be individually

inspected to avoid the uncertainties associated with projecting models onto novel climates. Overall, novel climates can be minimized in SDMs 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 the creation of response curves.

Applications and conservation strategies

Efforts to conserve biodiversity and improve ecosystem functioning need to move beyond predictions of climate change impacts and towards an integrated effort to address solutions (Dawson *et al.*, 2011). With their focus on quantifying exposure of species to climate change, SDMs will be only one component of these efforts. Practitioners should continue to develop a more sophisticated understanding of the advantages, limitations and appropriate uses of SDMs, while working with colleagues to incorporate complementary analyses. Integrating molecular approaches such as phylogeography has great potential to improve conservation decision-making by providing a more comprehensive assessment of climate change impacts that addresses both exposure and past responses to climate change, as well as identifying areas of potentially high genetic diversity. 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 and other anthropogenic influences.

ACKNOWLEDGEMENTS

B.F. would like to thank Wilfried Thuiller for assistance with modelling questions and Gavin Schmidt, Joy Singarayer and Michel Crucifix for facilitating climate data access. B.F. was funded through the Western Washington University Research and Sponsored Programs Research Fund and Huxley College Small Grants for Graduate Research. E.D. was funded by the National Science Foundation (ARC – 0714232) and Western Washington University (Summer Research Grant and Project Development Award).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Method for developing the consensus refugial model from an ensemble of 128 individual models.

Figure S2 Biogeographic hypotheses tested using statistical phylogeography.

Appendix S1 Climate data and predictor variables.

Appendix S2 Species distribution model parameterization and evaluation.

BIOSKETCH

Brenna R. Forester is currently a PhD student in the Landscape Ecology Lab at Duke University. She works across disciplines to better understand how species will respond to global change, and to develop appropriate conservation strategies. Her current research uses spatial and molecular analyses to explain the relative capacity of species to disperse and/or adapt in response to anthropogenic stressors. This research was part of her Master's Degree Thesis at Western Washington University.

Editor: Brendan Wintle