**Predicting species distribution of Sierra Nevada butterflies in response to climate change**

**Joel Scheingross**

**Abstract**   The conservation and management of biodiversity utilizes knowledge of the geographical distribution of species and the environmental changes that threaten species. Distributional modeling has been used to predict species ranges from limited data and the effects of environmental change. This study develops distributional models for two species of rare, alpine butterflies that are endemic to the Sierra Nevada, California and are important candidates for conservation. Two distinct modeling techniques (BIOCLIM and MAXENT) are compared to predict distributions for each butterfly based on bioclimatic variables averaged over 1950-2000 and future conditions based on a scenario of doubling atmospheric $CO_2$. Results are compared by examining accuracy of prediction (with AUC and Kappa statistics) and spatial overlap of models. Both modeling techniques yield high prediction accuracy with similar values of AUC and Kappa for the study species.  This suggests BIOCLIM and MAXENT are both valid modeling approaches for alpine organisms. Future climate models show the most suitable habitat moving towards areas of higher elevation and an overall reduction in alpine habitat within the Sierra Nevada. Such shifts in geographic distribution may have important implications for ongoing efforts to monitor and conserve alpine species.

**Introduction**

The 20th century witnessed a significant increase in Earth's average surface temperature, rising sea levels, and greater frequencies and intensities of extreme weather events (IPCC, 2001). Even with efforts to curb fossil fuel emissions, climate scientists predict these trends will continue throughout the 21st century (IPCC, 2001). These changes could pose a significant threat to global biodiversity. As early as 1924, Joseph Grinnell noted that sudden environmental changes could lead to species extinction (Grinnell, 1924). A number of recent studies have documented poleward shifts in species distribution, and other changes in population structure and abundance that can be explained by a warming climate (Parmesean and Yohe 2003; Root *et al* 2003).

Species that live along a steep climate gradient, as in alpine ecosystems, are particularly at risk from global warming. Warmer temperatures can cause habitat fragmentation (Thomas *et al.* 2004), which in turn can lead to the loss of population genetic diversity and dwindling resources. Boggs and Murphy (1997) predict that rising temperatures will increase habit fragmentation and lead to population decline for montane butterflies. Roland *et al* (2000) noted that rising treelines in the Rocky Mountains (due in part to climate warming) has acted to reduce the ability of butterflies to move between meadows at high-elevation. Furthermore, Shapiro (1996) has suggested that recent climate variation has contributed to changes in the distribution and total number of butterflies in the Sierra Nevada.

While dynamic distributions are natural, it is unlikely that species will be able to adapt on the timescale of current climate change (Pearson 2005). Already, climate change has been seen to play a part in species distribution shifts (Root *et al*. 2003). Thomas *et al* (2004) use the species-area power-law relationship and future climatic scenarios to predict a large number of species extinctions as a result of climate change over the next 50 years. Because the species-area relationship predicts extinction with reductions in habitat size, alpine species are particularly at risk.

Core areas of alpine habitat must be preserved in order to minimize the effects of global warming on alpine communities. However, determining where these preserves should be located can be difficult, especially as climate change can cause shifting species distributions. Ecological niche modeling has been used to predict current and future species distributions, and provide recommendations of habitat conservation (Graham *et al*. 2004). Such models correlate species

presence data with environmental variables (e.g. temperature, precipitation, and elevation) to project a species distribution over a larger landscape. These models have been used extensively to predict butterfly distribution. Beaumont and Hughes (2002) use models comparing current and future distributions of Australian butterflies to identify species most vulnerable to climate change. Similarly, Berry *et al.* (2002) explore the impacts of climate change on 54 species and 15 habitats in the United Kingdom using a niche modeling technique. Their models showed species in montane habitats to be most affected by climate change, and even predicted the loss of all suitable climate space for the mountain ringlet butterfly, *Erebia epiphron* Knoch. These techniques have yet to be applied to alpine butterflies in North America.

This study focuses on the effects of climate change on two endemic species of butterfly within California's Sierra Nevada range; the Sierra Green Sulfur (*Colias behrii* Edwards) and Sierra Nevada Parnassian (*Parnassius behrii* E.). Records from natural history collections (dating from 1890 – 1990) and field surveys (2003 – 2006) are used to build ecological niche models for these butterflies. BIOCLIM, a simple, bioclimatic envelope modeling technique, and MAXENT, a machine learning method based on the principle of maximum entropy, are used to predict distribution for each species of butterfly under current and future climates.

Data from these models are used to test the efficiency of the modeling programs through the evaluation of the area under the Receiving Operator Curve (AUC) and Kappa. Based on the findings of Elith *et al* (2006) MAXENT can be predicted to have higher AUC and Kappa values than BIOCLIM. In testing the response of the species to a future climate scenario, southeast shifts towards higher elevations in the Sierra Nevada range are expected. Synthesis of datasets for both species will identify key areas of habitat to be preserved for the study species and the alpine community as a whole.

## Methods

**Study system:** The Sierra Nevada mountain range stretches approximately 1050 kilometers from southern California near Bakersfield to near the California-Oregon border. The range increases in elevation moving southward, reaching its highest point at Mount Whitney (4419 m).

Two species of butterflies were chosen for this study because they are endemic to a small range of insular habitat in the Sierra Nevada and they are considered to be potentially threatened. The Sierra Green Sulfur (*Colias behrii* Edwards) is found in Hudsonian Zone meadows, where

*Salix* spp. (Salicaceae) and *Vaccinium cespitosum* Michaux (1803) serve as hostplants (Scott 2001). *Salix* is present throughout wet habitats in the Sierra Nevada while *Vaccinium cespitosum* is limited to wet meadows in the alpine zone (S. Schoville, personal communication). *C. behrii's* adult flight period is from late July to mid August (Scott 2001). The Sierra Nevada Parnassian (*Parnassius behrii* E.) occurs on talus slopes in the alpine zone and *Sedum roseum/lanceolatum* (Crassulaceae) serve as its hostplant (Scott 2001). *P. behrii* adults emerge in June and are present through August (Scott 2001).

**Data Collection:** *Natural history collections:* Observed sightings of hostplants for the two butterfly species were taken in January, 2007 from the SMASCH database, provided by the Consortium of California Herbaria (Table 1). Butterfly records from natural history museums (Table 2) were compiled to develop historical occurrence data for both species. For each specimen, all identification label data (date and locality of collection, collector, and any additional data present) were recorded verbatim. In addition, published records from *Yosemite Butterflies* (Garth and Tilden 1963) and *The Yosemite Butterflies* (Davenport 2001) were incorporated. The locality of each specimen was transformed into latitude and longitude coordinates (WGS 84 datum) using National Geographic TOPO! California software (2002). In order to reduce error in historical locations, several criteria were followed. Records were only included for place names that could be isolated into a single 7.5-minute USGS quadrangle or, in the event of a place name with multiple listings, alternative locations were eliminated based on predetermined biological criteria (Table 3). Once place location was determined, areas meeting two or more biological criteria were identified as probable localities. This method allows predictions within 1 km$^2$ of actual occurrence for most records. However, when a place name occurred at a scale in which the error exceeds 1 km$^2$, but the habitat is biologically equivalent at that scale, records were placed at the center of the named place.

Table 1: Hostplant records collected from the SMASCH database.

|  | *Sedum lanceolatum* | *Sedum roseum* | *Vaccinium cespitosum* |
|---|---|---|---|
| Total Records | 24 | 40 | 50 |
| Unique Localities | 21 | 35 | 49 |

Table 2: Records collected from natural history collections.  Unique localities refer to the number of records restricted to distinct 1 km$^2$ grid cells; these were the records used for modeling.

| Natural history collection | Number of records of *C. behrii* | Number of records of *P. behrii* |
|---|---|---|
| Bohart Museum of Entomology (UC Davis) | 64 | 87 |
| California Academy of Sciences | 550 | 77 |
| Essig Museum of Entomology (UC Berkeley) | 265 | 92 |
| Los Angeles Natural History Museum | 735 | 92 |
| Oakland Natural History Museum | 17 | 7 |
| San Diego Natural History Museum | 138 | 26 |
| Smithsonian Institution | 115 | 22 |
| Total | 1884 | 403 |
| Unique Localities | 110 | 68 |

Table 3: Biological criteria for georeferencing historical data

| | *C. behrii* | *P. behrii* |
|---|---|---|
| Elevation bounds (m) | 2490 - 3764 | 2490 - 3820 |
| Habitat bounds | Requires meadow habitat, near lake and streams, on slopes with 0-30 degree aspect | Requires semi-moist talus slopes and outcrops, near snowmelt and small creeks, on slopes with 15-45 degree aspect |
| Confirmed sighting of host plant | *Vaccinium caespitsoum* (Ericaceae) | *Sedum roseum/lanceolatum* (Crassulaceae) |

*Current collection*: Butterflies were collected in the Sierra Nevada in July and August of 2003-2006.  Field surveys employed walking transects and sites were selected with the aid of topographic maps, with preference given to sites above 2900m that included alpine meadows and talus slopes.  For both species of butterfly, sampling started in the late morning and continued through the early evening; butterflies were visually detected, captured, and identified.  A GPS (Garmin eTrex Vista) was used to determine the locality of all collections within <20m error.

**Modeling:** Models were made using BIOCLIM and MAXENT.  BIOCLIM (Nix, 1986) is a commonly used modeling program which relates climatic parameters (i.e. temperature, precipitation, moisture, etc.) to species presence data to predict areas within which an organism can survive (Beaumont *et al*. 2005).  BIOCLIM examines the minimum and maximum values a species occurs at for each climatic variable within the model.  The program uses these values to construct a climatic envelope (the total hyper-dimensional volume constrained by the minimum and maximum values of all variables included) within which a species is likely to be found.  BIOCLIM was run in DIVA-GIS, available for free download at http://www.diva-gis.org.  MAXENT (Phillips *et al*, 2006) uses presence-only data to predict the distribution based on the theory of maximum entropy.  The program attempts to find a probability distribution of occurrence that is closest to uniform while still subject to environmental variables.  MAXENT

takes into account the background environment and is based on complex statistics, while BIOCLIM is one of the original, and arguably the most simple, technique (Elith *et al* 2006). Use of these techniques should maximize differences in ecological niche models allowing for a more comprehensive view of potential species distributions.

Models were made to compare current and projected future distribution based on a worst-case climate change scenario. Current environmental climate data was taken from the Worldclim data set (Hijmans *et al.*, 2005) at 30 arc-second (approximately 1 km$^2$ grid cells) resolution. Prediction of future climate, based on a doubling of atmospheric carbon dioxide levels, was available for download from the Worldclim data set at 30 arc-second resolution. This data was produced by Worldclim based on models made by Govindasamy's *et al*. (2003) CCM3 global circulation model interpretation.

Table 4: Variables used in all modeling techniques.

| Variables |
| --- |
| Altitude |
| Annual Mean Temperature |
| Annual Precipitation |
| Isothermality |
| Max Temperature of Warmest Month |
| Maximum Temperature of August |
| Maximum Temperature of July |
| Maximum Temperature of June |
| Maximum Temperature of May |
| Maximum Temperature of September |
| Mean Diurnal Range |
| Mean Temperature of Driest Quarter |
| Mean Temperature of Wettest Quarter |
| Minimum Temperature of August |
| Minimum Temperature of Coldest Month |
| Minimum Temperature of July |
| Minimum Temperature of June |
| Minimum Temperature of May |
| Minimum Temperature of September |
| Precipitation of August |
| Precipitation of Driest Month |
| Precipitation of Driest Quarter |
| Precipitation of July |
| Precipitation of June |
| Precipitation of September |
| Precipitation of Warmest Quarter |
| Precipitation of Wettest Month |
| Precipitation of Wettest Quarter |

| |
| --- |
| Precipitation Seasonality |
| *Sedum lanceolatum* (*P. behrii* only) |
| *Sedum roseum* (*P. behrii* only) |
| Temperature Annual Range |
| Temperature Seasonality |
| *Vaccinium cespitosum* (*C. behrii* only) |

Many of the climate variables in the Worldclim dataset have the potential to be correlated with one another (e.g. maximum and minimum temperature). Including many correlated variables can lead to statistical bias and model over-prediction (i.e. modeling an overly small distribution by placing too many restrictions on where a species can occur). The number of variables was minimized by selecting only those which were deemed biologically relevant to alpine species (Table 4).

Additionally, locations of hostplants were used in creating models. Because sufficient distribution maps for these species do not exist, confirmed sightings (Table 1) were used to create niche models of the hostplants in MAXENT. The resulting rasterized predicted distribution from these models was added as an environmental layer to the butterfly prediction models. In order to maximize the

accuracy of the hostplant models, all methods described above were applied to variable selection of hostplants.

All models were tested for their accuracy in predicting species distributions. 25% of all presence records and 75 absence points (generated from field surveys and literature review) were set aside to be used in evaluating model performance. This evaluation data was compared with model output to test if models correctly predicted a presence or absence at the location of the evaluation presence/absence data. In order to avoid bias associated with withholding 25% of presence records from model building, all models were repeated 25 times (i.e. 25 runs of BIOCLIM for *C. behrii*, 25 runs of MAXENT for *C. behrii*, etc) with different, randomly selected presence points withheld in each run.

Kappa (Cohen 1960), a statistical measure of agreement, and the area under the Receiver Operating Characteristic curve (AUC) were used to examine model accuracy in each of the 25 runs per model. AUC is similar to the Mann-Whitney U test and compares the likelihood that a random presence site will have a higher predicted value in the model than a random absence site (Elith *et al.*, 2006). An AUC value of 0.5 implies the model predicts species occurrence no better than random and a value of 1.0 implies perfect discrimination. Kappa compares the ratios of true positives, false positives, true negatives, and false negatives in a model prediction and can be calculated with testing data described above.

Model outputs give pixel values in percents and percentiles, where higher values are more suitable habitat. These models do not specify at what output values pixels become suitable habitat. This can be tested for using Maximum Kappa (max Kappa) which is the threshold of model prediction at which true positives and negatives are maximized while false positives and negatives are minimized. Max Kappa thus defines the value above which all points can be considered suitable habitat. Max Kappa was calculated for each of the 25 runs of a model to make binary rasters showing areas of suitable habitat (value=1) and areas of unsuitable habitat (value=0). These 25 binary rasters were summed to make a final distribution for each model. In this final distribution, pixels could take on values of 0 to 25; a value of 0 means that none of the 25 runs predicted the pixel as suitable habitat, while a value of 25 means all runs predicted the pixel as suitable habitat. This technique allowed comparison between BIOCLIM and MAXENT. Total area and geographic extent of suitable habitat were then directly compared between modeling techniques for each species. This technique could not be used for the future climate

predictions as there are no true absences or presences to test; instead, the future climate trials were averaged over rasterized model outputs. This allowed comparisons between species modeled under the same technique, but did not allow direct comparison of modeling approaches. Finally, areas of suitable habitat overlapping between species, models, and climate conditions were considered to identify core areas for conservation.

**Results**

   **1950-2000 averaged climate:** Both modeling methods yielded high values of AUC and max Kappa (Table 5). MAXENT had significantly higher AUC (p<.001, paired t-test) and max Kappa (p<.001, paired t-test) values than BIOCLIM for *C. behrii*, MAXENT values were not significantly higher than BIOCLIM for *P. behrii* (AUC p=0.13, max Kappa p=0.07, paired t-tests).

Table 5: AUC and max Kappa values for butterfly models.

| Species | Model | Mean AUC $\pm$ Standard Deviation | Mean max Kappa $\pm$ Standard Deviation |
|---------|-------|-----------------------------------|------------------------------------------|
| *C. behrii* | BIOCLIM | $0.87 \pm 0.04$ | $0.69 \pm 0.07$ |
|  | MAXENT | $0.93 \pm 0.02$ | $0.76 \pm 0.04$ |
| *P. behrii* | BIOCLIM | $0.87 \pm 0.05$ | $0.72 \pm 0.09$ |
|  | MAXENT | $0.89 \pm 0.03$ | $0.75 \pm 0.05$ |

   Visual comparison of MAXENT and BIOCLIM outputs (Figs. 1 and 2) shows differences in geographical distributions between the modeling approaches, with MAXENT generally predicting larger areas of suitable habitat than BIOCLIM. For *C. behrii*, MAXENT's distribution extends further into the western and northern Sierra Nevada than BIOCLIM, and also includes scattered locations in the White Mountains and greater Lake Tahoe area (Fig. 1). *P. behrii* occurs across a larger area than *C. behrii*, but the same trends hold with MAXENT extending distributions into the western Sierra Nevada and White Mountains (Fig. 2). Additionally, MAXENT identifies a small amount of area around Mt. Shasta and the Trinity Alps (not shown) as potentially suitable habitat which BIOCLIM ignores. All colored areas are defined in at least one of the trials as suitable habitat, warmer colors imply the area was considered suitable habitat by multiple trials. The abundance of red area (Figs. 1 and 2) shows that majority of suitable habitat was consistently determined by all trials.
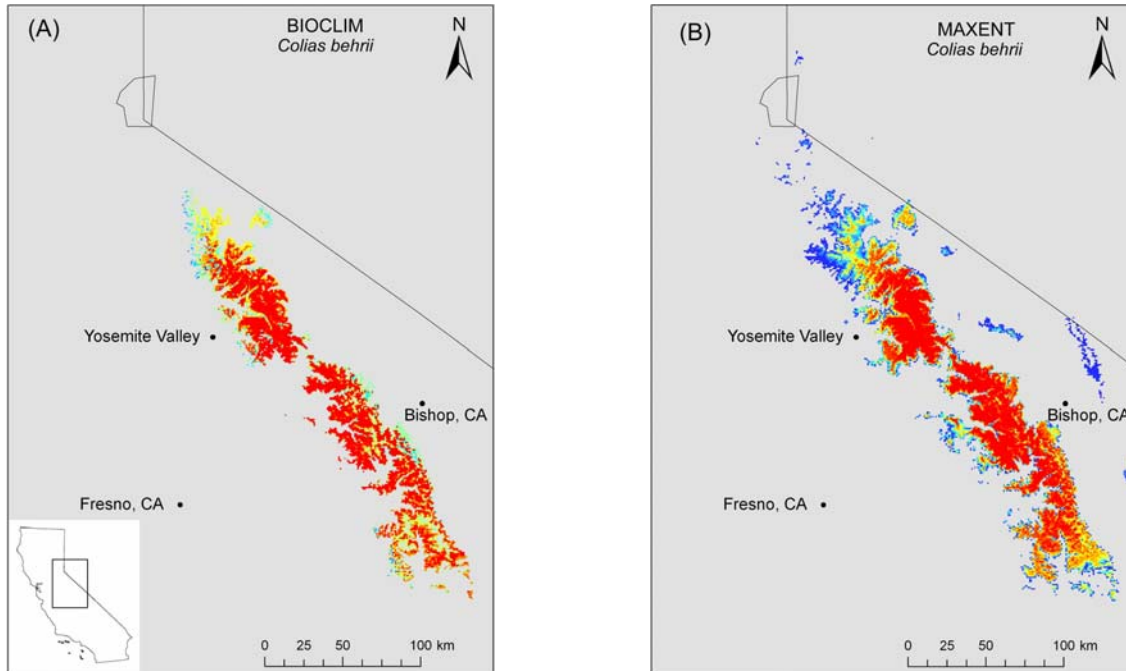
Figure 1: Distributions of *C. behrii* as predicted by (A) BIOCLIM and (B) MAXENT. Images were made by calculating max Kappa in each of the 25 trials. If a pixel in the model was above max Kappa (i.e. suitable habitat) it was given a value of 1. These values were summed across all 25 rasters to create the distribution shown. Warmer colors indicate multiple trials classified the grid above max Kappa; for example, red areas have a value of 25, indicating all 25 trials classified that area above max Kappa while dark blue areas have a value of 1 indicating only 1 of the 25 trials found that pixel to be suitable habitat.
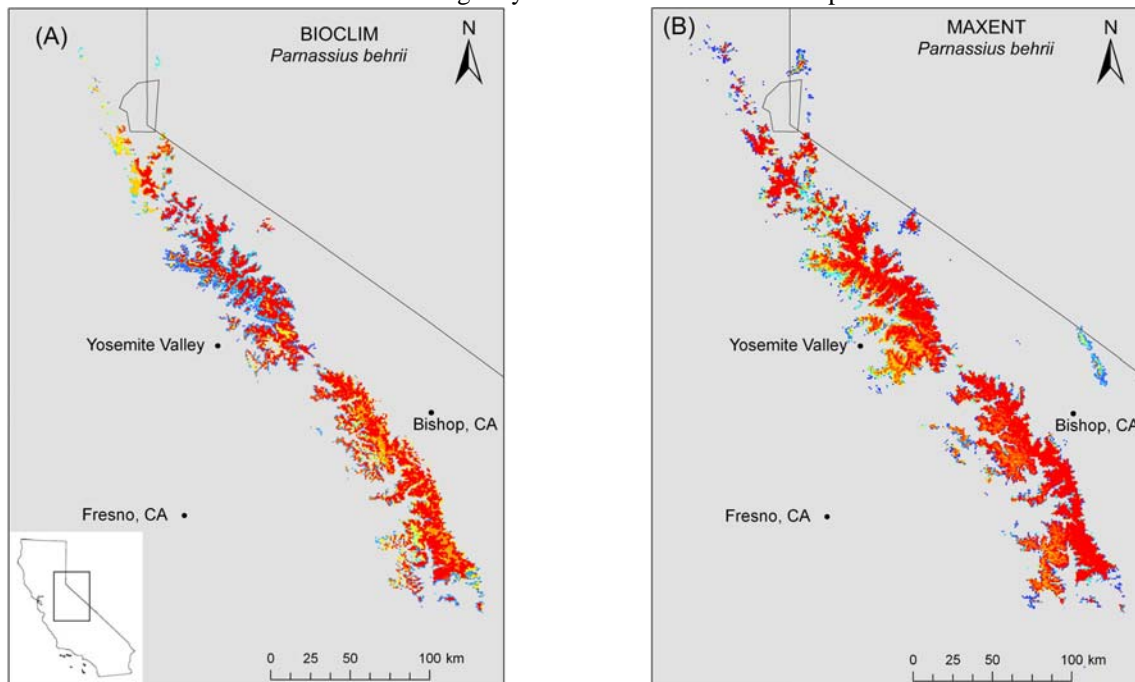


Figure 2: Distributions of *P. behrii* as predicted by (A) BIOCLIM and (B) MAXENT. Images were made with the same methods described in Figure 1. MAXENT additionally predicts a scattering of low values of suitable habitat in the Trinity Alps and Mount Shasta area (not shown as it is highly unlikely butterflies could migrate from the Sierra Nevada to these areas).

  **Future Climate:** BIOCLIM predicts the complete extinction of both *C. behrii* and *P. behrii* under the future climate scenario (images not shown). Under the double $CO_2$ scenario, MAXENT predicts suitable areas for *C. behrii* in the southeast Sierra and White Mountains (Fig. 3a and 3b). A similar geographic displacement toward the southeast Sierra and White Mountains is seen for *P. behrii*, but the suitability of the habitat decreases across the range (Fig. 4a and 4b). Analysis of distributions for the Sierra Nevada and White Mountains shows a large drop in total available habitat above MAXENT's 50% threshold for *P. behrii* while *C. behrii* habitat remains similar between the two climatic scenarios (Fig. 5). Additionally MAXENT highlights areas outside of the Sierra Nevada as potential habitat for both species under a double CO2 scenario, but gives this area low prediction values (Figs. 3c, 3d, 4c, and 4d).
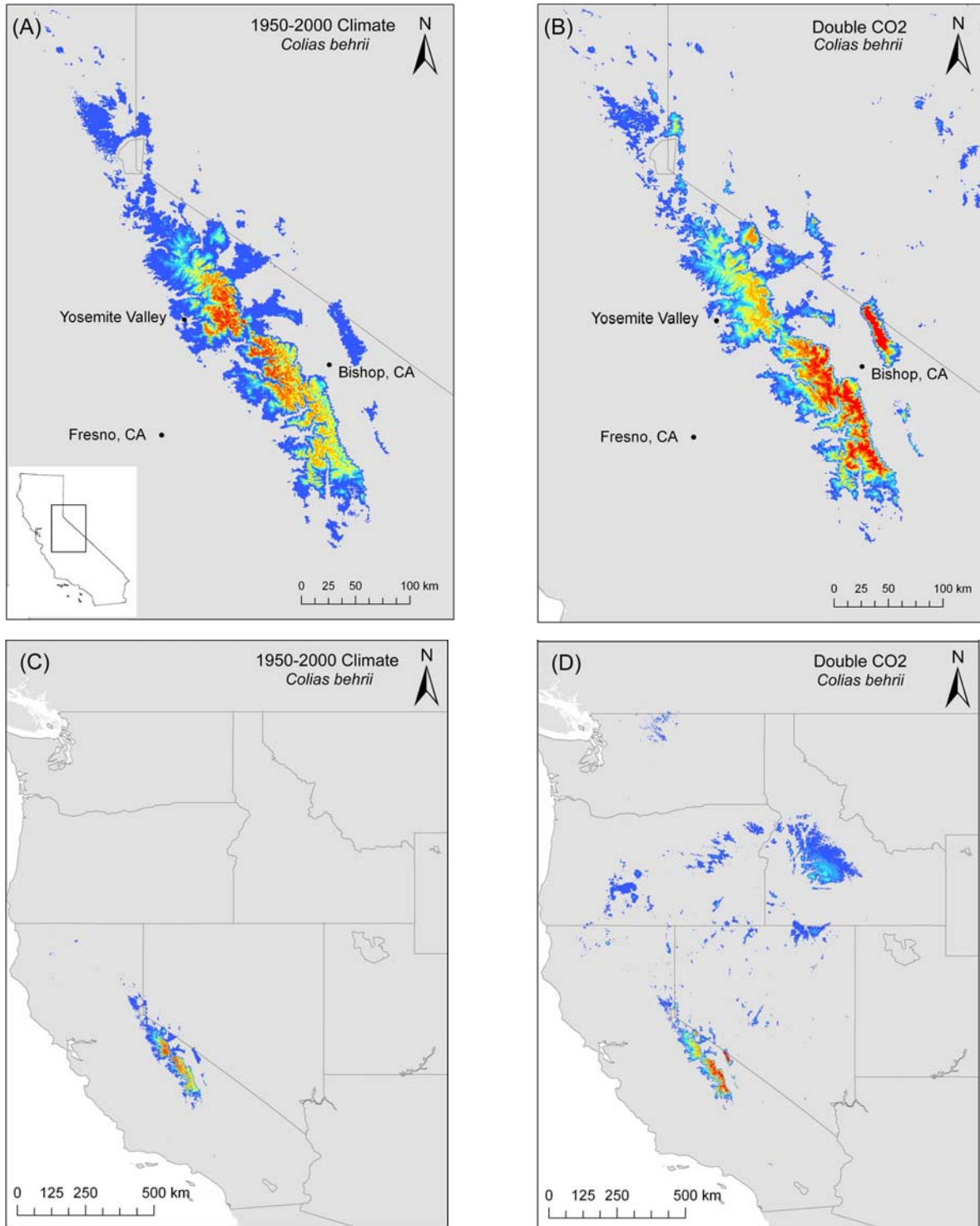
Figure 3: Distributions of *C. behrii* as predicted by MAXENT under (A and C) 1950-2000 averaged climate and (B and D) a double $CO_2$ emission scenario. These figures are based on the MAXENT scaling system, warmer colors indicate more suitable habitat, but, because max Kappa cannot be calculated with future climate scenarios (there are no present or absence points to test with), suitable habitat cannot be clearly distinguished from unsuitable habitat in these images.
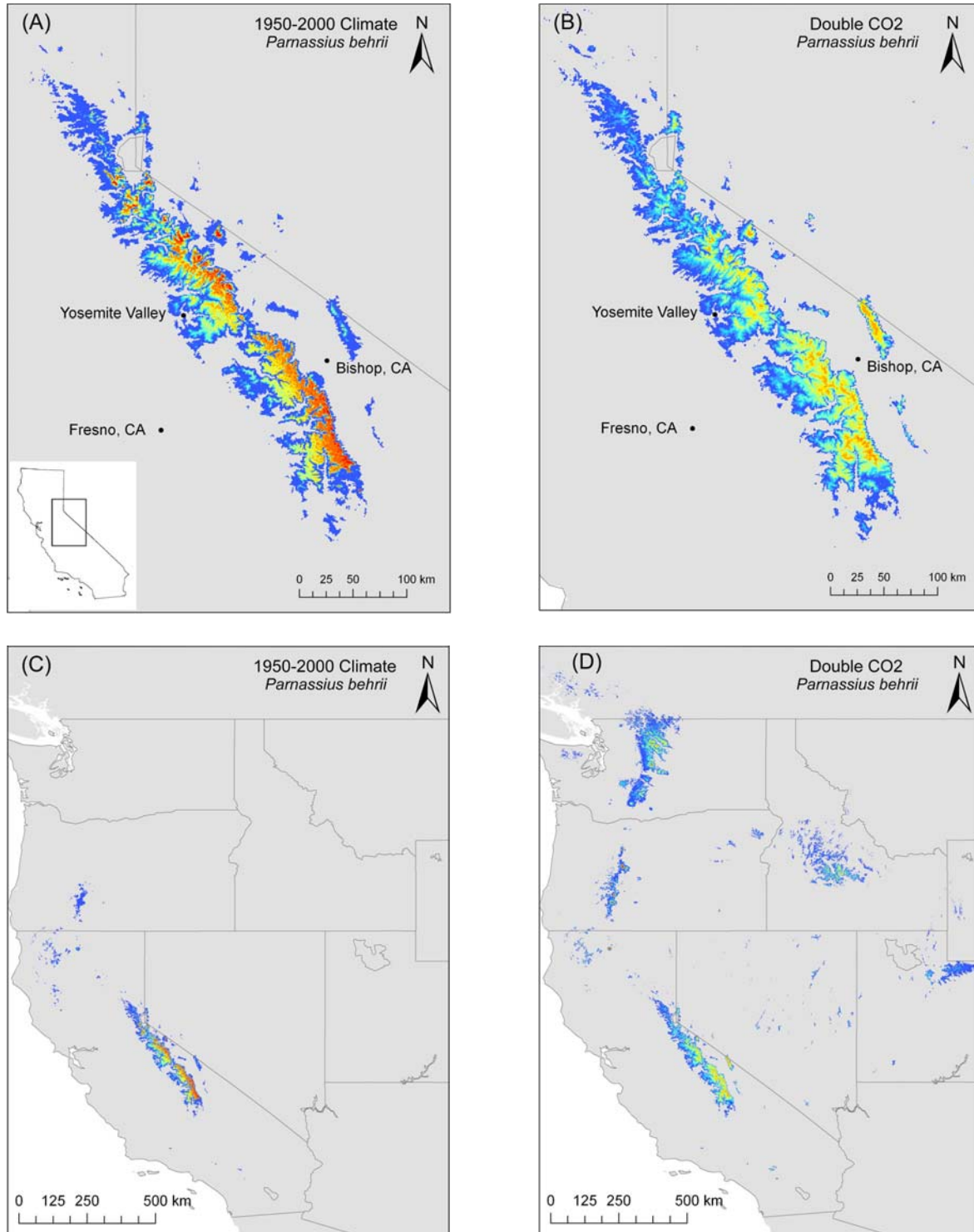
Figure 4: Distributions of *P. behrii* as predicted by MAXENT under (A and C) 1950-2000 averaged climate and (B and D) a double $CO_2$ emission scenario.  Warmer colors indicate more suitable habitat.  These figures were generated with the same methods as those in figure 4.
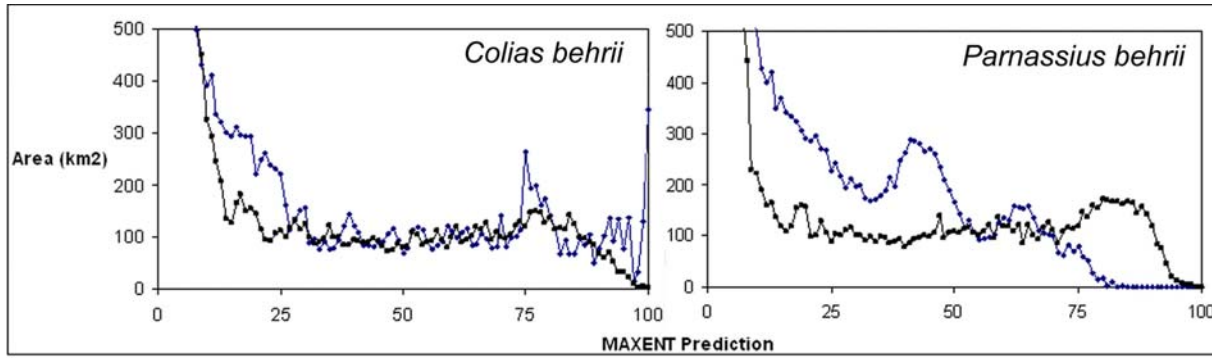
Figure 5: Comparisons of 1950-2000 averaged climate (black line) and double $CO_2$ emission scenario (blue line) predictions within the Sierra Nevada and White Mountains under MAXENT for *C.* and *P. behrii*. The x-axis shows the MAXENT prediction value, higher numbers indicate more suitable habitat and correspond with warmer colors in figures 4 and 5. The y-axis shows the area of habitat classified at each of these MAXENT prediction values.

Overlap of these species' occurrence allows generalizations about alpine butterflies and alpine insects in general. An average of all modeling approaches for both species shows a concentration of diversity in eastern Yosemite National Park under the current climate. This concentration shifts southeast to higher elevation in Sequoia and Kings Canyon National Parks under the double $CO_2$ scenario (Fig. 6).
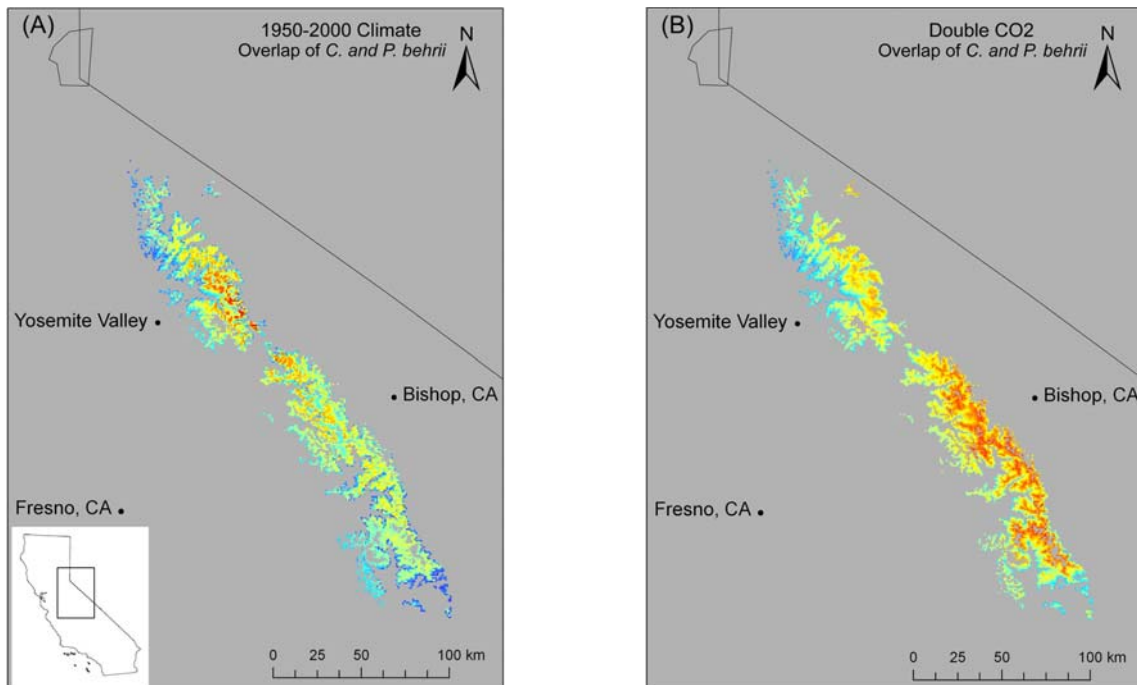


Figure 6: Comparisons of overlap of between *Colias behrii* and *Parnassius behrii* for (A) 1950-2000 averaged climate and (B) a double $CO_2$ emission scenario. Images show the average of *C.* and *P. behrii* predictions restricted to the area where both species occur on the 1950-2000 climate. Warmer colors indicate increased likelihood of co-occurrence.

**Discussion**

    MAXENT and BIOCLIM were used to create species distribution models for two species of alpine butterflies endemic to the Sierra Nevada. Models were made with both 1950-2000 averaged bioclimatic data and a double atmospheric $CO_2$ concentration scenario. Under 1950-2000 climate, both models predicted distributions within the Sierra Nevada and exhibited high AUC and max Kappa values. MAXENT predicted slightly higher values than BIOCLIM, but this difference was only significant for *C. behrii*. Under the double $CO_2$ scenario BIOCLIM predicted the loss of all suitable habitat for both species, while MAXENT showed a general displacement into areas of higher elevation (in the southeast Sierra Nevada). MAXENT additionally highlights potentially suitable habitat in areas outside of the Sierra Nevada (figs. 3 and 4); while it is unlikely Sierra Nevada butterflies can migrate to these areas, it is possible similar species exist in these regions.

    BIOCLIM has performed poorly when compared to MAXENT (Elith *et al*, 2006), but the two techniques performed similarly for alpine butterflies under 1950-2000 averaged climate examined here. AUC and max Kappa values under current climate conditions were not significantly different for *P. behrii* and were similar (yet significantly different) for *C. behrii*. These AUC and max Kappa values are much larger than those reported by Elith *et al* (2006) in their averaging of multiple species across different regions. This implies that these modeling methods are more powerful in alpine areas than other habitats. The differences between BIOCLIM and MAXENT under the 1950-2000 averaged climate are small enough that both techniques can be considered equally valid approaches for modeling alpine organisms.

        However, some differences are evident when comparing predictions under future climate. BIOCLIM predicts extinction while MAXENT shows rising temperature driving alpine organisms to higher elevations. Because area at higher elevations is finite and butterflies are unlikely to migrate outside the Sierra Nevada range through lowland habitat, the MAXENT models suggest a loss of suitable habitat and population decline will result from increased warming. It is easy to imagine that if $CO_2$ concentrations increase beyond a single doubling, available habitat at high elevations will continue to decrease and MAXENT will eventually predict a complete extinction within the Sierra Nevada. From this perspective, the MAXENT and BIOCLIM future climate distributions are quite similar; each predict extinction, but disagree

on the $CO_2$ concentration above which the species will go extinct. Because model performance cannot be tested under future scenarios, it is not possible to say which modeling approach is superior. However, it can be noted that BIOCLIM is more sensitive than MAXENT in predicting changes in distributions based on climate warming for alpine butterflies.

As both modeling techniques predict alpine butterflies to be negatively affected by climate warming, prospects for conservation should examined. The results shown here suggest the southeast Sierra Nevada appears to be the most important area to protect, and the eastern Yosemite region appears to be an important area to monitor for ongoing effects of climate change. Persistence in the southeast Sierra Nevada is likely as both species already occur within this region and therefore, do not need to disperse great distances. However, future climate models show a movement away from eastern Yosemite, so that monitoring of this area can serve as a proxy for the species response to climate change. Both butterfly species clearly exhibit shifts towards higher elevation with the onset of warming (Figs. 3, 4, and 6); this trend is likely to hold for most alpine species and suggests preservation of high elevation habitats should benefit all alpine organisms. In order to build upon these findings, future studies should compare additional alpine species and examine their responses with more realistic climate models.

## Acknowledgements

## References

Beaumont, L.J. and L. Hughes. 2002. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. Global Change Biology **8**: 954-971.

Beaumont, L.J., L. Hughes, M. Poulsen. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. Ecological Modelling **186**: 250-269

Berry, P.M., T.P. Dawson, P.A. Harrison, and R.G. Pearson. 2002. Modelling potential impacts

of climate change on the BIOCLIMatic envelope of species in Britain and Ireland. Gloabal Ecology and Biogeography **11**: 453-462.

Boggs C. L., D. D. Murphy. 1997. Community composition in mountain ecosystems: Climatic determinants of montane butterfly distributions. Global Ecology and Biogeography Letters **6**:39-48.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educ. Psyschol. Meas. **20**: 37-46.

Elith, J., Graham, C. H., Anderson, R. P., Dudı´k, M., Ferrier, S., Guisan, A., Hijmans, R. J., Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T., Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Sobero´n, J., Williams, S., Wisz, M. S. and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**: 129-151.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology **41**: 263-274.

Garth, J. S., and T. W. Tilden. 1963. Yosemite Butterflies: An ecological survey of the butterflies of the Yosemite sector of the Sierra Nevada, California. Journal of Research on the Lepidoptera **2**: 1-96.

Govindasamy, B., P. B. Duffy, and J. Coquard. 2003. High-resolution simulations of global climate, part 2: effects of increased greenhouse cases. Climate Dynamics **21**: 391–404.

Graham C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology & Evolution **19**:497-503.

Grinnell, J. 1924. Geography and evolution. Ecology **5**: 225-229

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis, 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**: 1965-1978.

Intergovernmental Panel on Climate Change. 2001 Sep. 24. Summary for policymakers. <http://www.ipcc.ch/pub/un/syreng/spm.pdf>. Accessed 2006 Apr. 15.

Leathwick, J.R., J. Elith, and T. Hastie. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling **199**: 188-196.

Nix, H. 1986. A biogeographical analysis of Australian Elapid snakes. In: Longmore, R. (Ed.), Snakes: Atlas of Elapid snakes of Australia. Bureau of Flora and Fauna, Canberra, p. 4-10.

Parmesan C., G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature (London) **421**: 37-42.

Pearson, R.G. 2005. Climate change and the migration capacity of species. Trends in Ecology and Evolution **21**: 111-113.

Phillips, S.J., R.P. Anderson, and R.E. Schapired. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**: 231-259.

Roland J., N. Keyghobadi, and S. Fownes. 2000. Alpine Parnassius butterfly dispersal: Effects of landscape and population size. Ecology (Washington D C) **81**:1642-1653.

Root T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature (London) **421**:57-60.

Scott, J.A. 2001. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA.

Shapiro, A. M. 1996. Status of butterflies. Pages 743-757 *in* Sierra Nevada Ecosystem Project: final report to congress, volume II. Assessments and scientific basis for management options. University of California, Centers for Water and Wildland Resources, Davis, CA.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. Siqueria, A. Grainger, L. Hannah, L. Hughes, B. Huntly, A.S. van Jaarsveld, G.F. Midgley, L. Miles, M.A. Ortega-Huerta, A.T. Peterson, O.L. Phillips, and S.E. Williams. 2004. Extinction risk from climate change. Nature (London) **427**: 145-148.