Assessing the Impact of Climate and Snowpack on the Distribution of Amphibian Species in Sierra Nevada

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ABSTRACT

Amphibian biodiversity decline is a severe global problem. With 22 out of 69 species at conservation risks, climate change is a key environmental factor for the decline in California. Snowpack is closely related to the life history of amphibians but its impact on species range remains unknown. To model current and future species distribution of amphibians in Sierra Nevada (SN) using Maxent, I assembled species occurrence data of 10 species from the Museum of Vertebrate Zoology, bioclimatic data from WorldClim, and snowpack data from Cal-Adapt. I evaluated the model performance and projected future species range in 2050 and 2070 under the climate change scenarios of RCP4.5 and RCP8.5. Overall, the model fitted strongly for 8 species and computed high model contributions from average snow water equivalence, precipitation seasonality, mean diurnal temperature range, and annual precipitation. Projections gave 1 species maintaining, 2 species expanding, and 7 species losing their ranges, including 2 species shrunk inconsistently under the four future scenarios. Comparing the two climate change scenarios with different limiting novel predictors and values, amphibians in general lost larger suitable habitat range under RCP8.5. Specifically, *Hydromantes platycephalus* would bear the highest risk of extinction even under RCP4.5 in 2050 so that requires immediate conservation and research attention. I concluded snowpack as an important environmental predictor in future studies of amphibian distribution, high-elevation endemic species and species of Plethodontidae as the most susceptible groups to climate change, and RCP4.5 being more bearable than RCP8.5 for amphibians in SN.

KEYWORDS

climate change, Maxent, Plethondontidae, high-elevation endemic species, RCP

INTRODUCTION

Amphibians worldwide are facing a severe problem of biodiversity decline including in California. With 42 salamander species and 27 frog and toad species, as many as 9 salamander and 13 frog and toad species face conservation risks in California (Thomson et al. 2016). Multiple factors are driving the problem including habitat destruction, alteration and fragmentation (Dodd Jr and Smith 2003), introduced species (Kats and Ferrer 2003, Lannoo et al. 1994, Vredenburg 2004), over-harvest (Jennings and Hayes 1985), infectious disease (Cheng et al. 2011, Seimon et al. 2015), and climate change (Araújo et al. 2006, Ochoa-Ochoa et al. 2012). Research have been constantly studying the impacts of each factor on amphibian biodiversity decline while many questions still remained obscure.

Global evaluation of climate change indicates both direct and indirect effects on amphibian biodiversity decline. Direct effects of climate change relate to the ectothermic thermal regulation and aquatic reproduction phase of amphibians (Carey 2003). Their permeable skin, biphasic lifecycle and unshelled eggs make them extremely sensitive to small changes in temperature and moisture, which determines their body temperature and the rate of biochemical, cellular and physiological process (Carey 2003, Rome et al. 1992, Shoemaker et al. 1992, Stebbins and McGinnis 2012). Indirect effects refer to the situation where climate change leads to amphibian mortalities by manipulating other threatening factors including change in phenology of breeding, emergence and enhancement of infectious disease, shrinking in ranges size, reduction in body size, change in hydrology and fire regime, and shifts in vegetation type (Carey 2003, Li et al. 2013, Thomson et al. 2016). The indirect effects of climate change on amphibian decline are drawing more and more attention with a growing number of research in these years.

Based on current studies, climate change indirectly drives the decline of amphibian biodiversity in California. The snowpack in Sierra Nevada (SN) serves as a source of water supply to replenish mountainous streams and lakes for amphibian habitats in summer (Ishida et al. 2018). Observations and projections predict a future with a warmer winter and spring temperature, more precipitation falling as rain and less as snow, reduced amounts of accumulated snow after the wet season, and earlier snowmelt in early spring (Cayan et al. 2008). Reduction would be most prominent in low-middle (1,000 to 2,000m, 60-93% loss) and middle elevation (2,000 to 3,000m, 25-79% loss) sites (Cayan et al. 2008). The northern and central region of SN is lower in elevation compared to the southern region, which infers a more serious future snow loss to take place in the central and northern part in the future. Sensitive to climate warming, the reducing size of snowpack is presumptive to become another factor linked to amphibian biodiversity decline.

To better understand the extent and scale of the issue in SN in the 21st century, I examine how the distribution of Sierran amphibian population might shift with the change of climate and snowpack under two representative concentration pathways (RCP) 4.5 and RCP8.5 emission level (Table 1, Moss et al. 2010).

Table 1: Comparison between RCP4.5 and RCP8.5

Name	Radiative Forcing	CO_2 Concentration (ppm)	Pathway	Model followed
RCP 4.5	Stabilized at approximately 4.5W/m^2 after 2100	Stabilized at approximately 650 CO2-Equivalent after 2100	Stabilized, no overshoot	GCAM
RCP 8.5	Higher than 8.5W/m^2 in 2100	Higher than 1370 CO2-Equivalent in 2100	Rising	MESSAGE

I ask the following questions: (1) How well would the model perform given current climate and snowpack conditions? (2) How would species response under projected future climate and snowpack levels (RCP4.5 or RCP8.5 and 2050 or 2070)? (3) How would the two RCP scenarios influence the projection on suitable habitat? I expect: (1) model will show reasonable to good discrimination for all ten species. The average snowpack level and annual precipitation will have greater contribution to the model than other variables. (2) for all four projection scenarios, suitable habitats will shrink for high-elevation endemic species and will shift or expand for species present in low elevation areas. (3) suitable habitats will have more dramatic changes under RCP8.5 than RCP4.5.

METHODS

Sierra Nevada (SN) region

To define the geographic bounds of my study site, I used Sierra Nevada Conservancy (SNC) boundary to define the study area. California Public Resource Code (PRC) Section 33302 (CA Pub Res Code § 33321 (2018)) defines and describes the SN Region as including the entire area of the following counties: Alpine, Amador, Butte, Calaveras, El Dorado, Fresno, Inyo, Kern, Lassen, Madera, Mariposa, Modoc, Mono, Nevada, Placer, Plumas, Shasta, Sierra, Tehama, Tulare, Tuolumne, and Yuba. The SNC boundary meets the area of SN Region defined above. It locates between 35.0 and 42.0º N, 117.7 and 122.2 º W in California and has a peak elevation of 4,418 meters high. The north and central areas are lower in elevation compared to the south. The region exhibits a Mediterranean climate pattern for the foothills and a mountain climate for the highlands.

Study species

To cover a wide range of Sierran amphibian, I chose 10 species (*Ambystoma macrodactylum, Taricha sierrae, Batrachoseps gregarius, Hydromantes platycephalus, Anaxyrus boreas, Anaxyrus canorus, Rana muscosa, Rana sierrae, Rana cascadae,* and *Rana boylii*) and summarized their information on life history, conservation status, abundance, and range in SN (Appendix A) (AmphibiaWeb 2018, Stebbins and McGinnis 2012). Of these are three Endangered (*Anaxyrus canorus, Rana muscosa* and *Rana sierrae*) and two Nearly Threatened species (*Rana cascadae* and *Rana boylii*) on the Red List.

In addition, I selected the group to represent a wide variation in distribution and life history. *Anaxyrus canorus, R. sierrae* and *H. platycephalus* are endemic to SN. *Anaxyrus boreas* are present throughout California except for the majority of desert areas and the central high Sierra because *A. canorus* are present in the latter. *A. macrodactylum* and *R. cascadae* are present only in northern SN where *B. gregarious* and *H. platycephalus* are absent. In terms of breeding, all 10 species are aquatic reproducers except *H. platycephalus*, a terrestrial reproducer. The breeding time of *A. macrodactylum, A. boreas, R. muscosa, R. sierrae,* and *R. cascadae* are dependent on the timing of snowmelt or ice-melt. The larvae of *A. macrodactylum, A. canorus, R. cascadae* and *R. sierrae* overwinter before transforming.

Species occurrence data

To obtain data of species presence locality, I collected historical occurrence data using specimen records in the Museum of Vertebrate Zoology (Arctos 2018). Museum specimens have more accurate data on coordinates and collection dates than observations. I removed occurrences without coordinates or collection years. I checked environmental outliers and geographical errors with DIVA-GIS (Hijmans et al. 2005, Hijmans et al. 2012) and QGIS (Hijmans et al. 1999) respectively.

Environmental data

To obtain environmental data, I collected current and future bioclimatic (BV) and Snow Water Equivalent (SWE) variables. I unified their geographic bounds to the geographical boundary of SN and cell size of 0.01 using ArcGIS (ESRI 2018). All future data were averages of the year range from 2041 to 2060 for 2050 and from 2061 to 2080 for 2070. Along with the two RCP levels, I chose the Global Climate Models (GCMs) of HadGEM2-ES for interpolations and projections of BV and SWE.

Climate data

I selected 7 BV from WorldClim (Hijmans et al. 2005): (1) annual mean temperature (BV1); (2) mean diurnal temperature range (BV2); (3) maximum temperature of the warmest month (BV5); (4) minimum temperature of the coldest month (BV6); (5) annual precipitation (BV12); (6) precipitation seasonality expressed as coefficient of variation across months (BV15); and (7) precipitation of the driest quarter (BV17). These bioclimatic variables were selected because they have low correlations with each other , represent the general trend, range, and seasonality of climatic variations and are closely related to the physiological limits of amphibian species (Graham and Hijmans 2006, Hijmans and Graham 2006). For current data, I used the current conditions of version 1.4 which interpolated observed data to represent the time period from 1960 to 2000 approximately (Hijmans et al. 2005).

Snowpack data

To account for the projected advance of snowmelt in future scenarios, I collected monthly averages of SWE data in January, February and March in addition to April, which is usually chosen to represent the size of spring snowpack in western United States (Bohr and Aguado 2001, Cayan et al. 2008, Pierce et al. 2008). The original data were downloaded from Cal-Adapt (Geospatial Innovation Facility, 2018). To reduce the correlation, I computed the 4-month mean and range of SWE for each year and calculated the average from 1950 to 2005 for current scenario using ArcGIS. The range was estimated by subtracting the value in January from March.

Data analysis

To predict species ranges, I chose Maxent, a maximum entropy modelling method, which has been increasingly used in species distribution modelling (Phillips et al. 2006, Phillips et al. 2018). With presence only data, Maxent uses machine learning to make prediction on current species distribution, to evaluate predictor response over the given environmental gradient, and to make projections based on trained environmental variables (Phillips et al. 2006, Phillips et al. 2018).

Model performance evaluation

To identify responsive species and the key climate and snowpack variables, I ran Maxent to make prediction of current distribution using current BV and SWE with species occurrence data under model settings of 6 replicates and 30% random test. I evaluated the training and test values of Area Under Curve (AUC) for all species and left out species with AUC lower than 0.5. I considered the remaining species suitable for the modeling method and reran the model, if needed, to test the model fitness using AUC (Swets 1988). I determined key environmental variables for the responsive species through Jackknife tests, response curves and permutation importance. At last, I used the value of the most efficient modeling threshold for each species to make binary maps of their predicted current range.

Species response projection

To estimate the distributions of the 10 species in the future, I used the future BV and SWE values to make projection of their distribution under the 4 future scenarios under model setting of replicates of 10. Using the same type of threshold but corresponding projection values, I made binary maps for their projected suitable habitat range. By comparing the change in range from current to future and classifying it as maintaining, expanding, shrinking or shifting, I concluded species that would be facing a more severe conservation risk than the other species because of warming climate and shrink in snowpack. Bringing in information on life history, I proposed potential explanations for species response at group-level and family-level.

Comparison between RCP4.5 and RCP8.5

To compare the impacts of RCP4.5 and RCP8.5 on suitable habitat, I compared the three of out of four classifications of habitat change (maintaining, expanding or shrinking) between RCP4.5 and RCP8.5. For range shrinking, I evaluated the level of shrinking by visually comparing the future range size to current range size, taking range shift into account. To further discuss abnormal changes in range that life history could not justify between the two RCP scenarios, I evaluated the inconsistent range change with limiting novel predictors, i.e., predictors being outside the current range, and response curve to propose model level explanations. The map of the limiting novel predictors showed the most novel predictors at each point. The pointwise novel values on the novel value maps reflect how novel future predictors would be. The negative values with red color represent the level of deviation for the minimal novel predictors, while the positive values with blue color represent values fallen within the current range of predictors (Phillips 2017).

RESULTS

Species occurrence data

Summarizing the species occurrence data collected from MVZ through Arctos, I assembled a total of 8041 observations in California and 4814 in SNC. From the latter, I omitted a total of 1650 observations existing outside of the time interval (1950-2000, N=1587), or being considered as environmental outliers (N=63) according to the result of DIVA-GIS species distribution modeling. The 1650 omitted observations took up 34.275% of total assembled observations in

SNC (N = 4814). At last, 3164 observations were included in the prediction model which summed 403 occurrence points for the 10 species (Table 2).

Table 2: Species occurrence. I counted the number of occurrence for each species after removing temporal and environmental outliers and geographical errors.

Species	Number of Occurrence (N)
A. macrodactylum	25
B. gregarius	89
H. platycephalus	30
T. sierrae	3
A. boreas	82
A. canorus	27
R. boylii	58
R. cascadae	9
R. muscosa	11
R. sierrae	69
Total	403

Model Performance

Maxent modeling resulted in all species having training and test AUC greater than 0.5 with training AUC higher than test AUC (Figure 1). 8 out of the 10 species have both AUC above 0.75 while the other 2 species have training AUC between 0.75 and 0.9 and test AUC below 0.75. Training and test AUC are both above 0.90 for *A. macrodactylum, B. gregarious, H. platycephalus, A. canorus,* and *R. sierrae.*

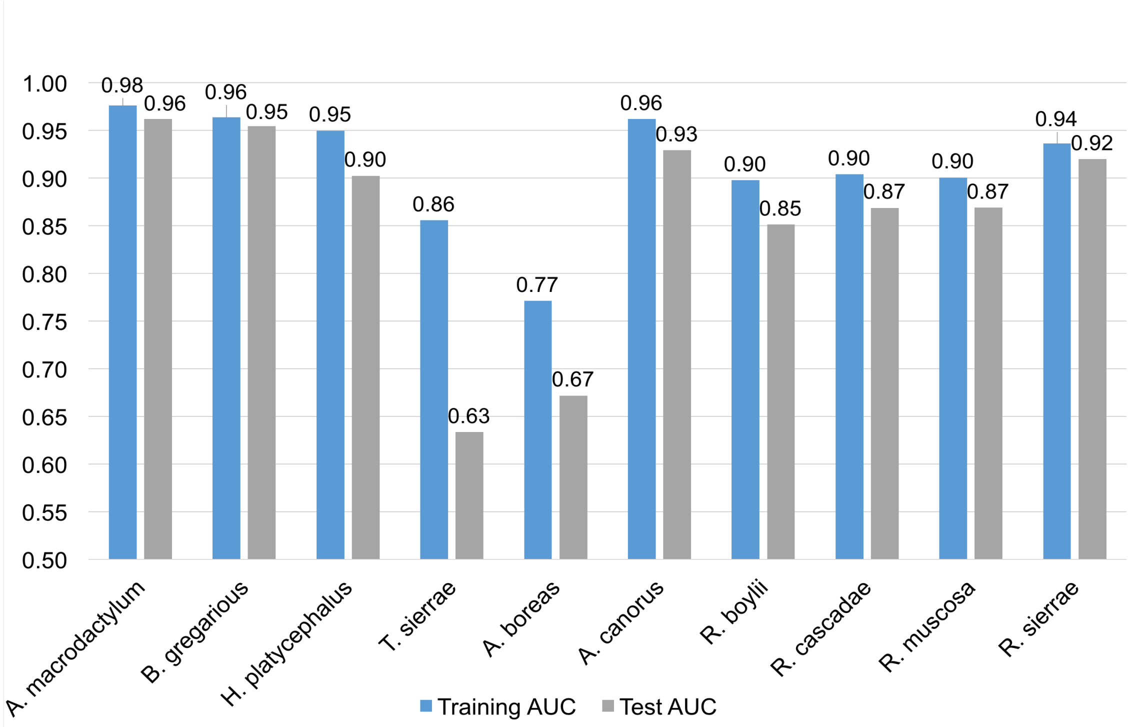


Figure 1: AUC of the predicted current amphibian distribution.

Using permutation importance to evaluate the contribution of predictors, I determined each environmental variable had different level of contribution to the models of different species (Table1). Overall, precipitation seasonality (BV15), average snow water equivalence (SWE_avg), and mean diurnal temperature range (BV2) had the three highest total contributions to the 10 models. In addition, annual precipitation (BV12) and precipitation seasonality (BV15) contributed to the model for all 10 species but BV12 was at lower permutation importance. However, annual mean temperature (BV1) had the lowest contribution to both the total value and the number of species, 6 out of 10, for the models. Minimum temperature for the coldest month (BV6) also only contributed to 6 models.

Not all species relied on all 9 environmental predictors to make prediction. *Batrachoseps gregarious*, *A. boreas*, *R. boylii*, and *R. sierrae* relied on the contribution of all 9 environmental predictors where the predictors were most evenly contributed to the model of *A. boreas* (Table 3). Contrarily, the model of *R. muscosa* was only dependent on 3 out of the 9 predictors with 85.83% from mean diurnal temperature range and was the only species whose model did not rely on either average or range of snow water equivalence. For the other eight species, annual precipitation (BV12) and precipitation of the driest quarter (BV17) were the key predictors for *A.*

macrodactylum. Maximum temperature of the warmest month (BV5) and precipitation seasonality (BV15) were the key predictors for *R. sierrae.* Precipitation seasonality (BV15) was the key predictor for both *B. gregarius and R. boylii*. The average of snow water equivalence (SWE_avg) was the key predictor for *H. platycephalus, A. canorus,* and *R. cascadae*. Minimum temperature for the coldest month (BV6) was the key predictor for *T. sierrae.*

Table 3: Permutation importance of environmental predictors. Average permutation importance (%) of the 9 environmental predictors in the current distribution. BV1=annual mean temperature, BV2=mean diurnal temperature range, BV5=maximum temperature of the warmest month, BV6=minimum temperature for the coldest month, BV12=annual precipitation, BV15=precipitation seasonality, BV17=precipitation of the driest quarter.

Species	**BV1**	**BV2**	**BV5**	**BV6**	**BV12**	**BV15**	**BV17**	**SWE_avg**	**SWE_range**
A. macrodactylum		**0.83**	**1.45**	**5.68**	**47.51**	**0.35**	**43.02**	**0.56**	**0.61**
B. gregarius	**7.07**	**1.81**	**0.52**	**5.84**	**1.62**	**53.62**	**25.01**	**3.15**	**1.36**
H. platycephalus	**6.71**	**0.16**	**4.17**		**5.54**	**21.21**	**8.91**	**30.38**	**22.92**
T. sierrae		**7.71**		**57.48**	**7.00**	**8.78**		**15.70**	**3.33**
A. boreas	**3.33**	**13.42**	**7.48**	**9.32**	**16.94**	**18.96**	**8.49**	**4.61**	**17.44**
A. canorus	**3.93**	**18.02**	**11.86**		**7.45**	**0.23**	**1.44**	**55.66**	**1.40**
R. boylii	**11.27**	**2.18**	**11.30**	**3.86**	**0.89**	**49.25**	**1.40**	**17.92**	**1.93**
R. cascadae					**16.97**	**1.54**	**34.27**	**37.25**	**9.97**
R. muscosa		**85.83**			**9.79**	**4.38**			
R. sierrae	**0.66**	**7.55**	**36.46**	**12.01**	**0.96**	**31.65**	**2.04**	**6.45**	**2.21**
Total	**32.95**	**137.52**	**73.25**	**94.20**	**114.67**	**189.97**	**124.59**	**171.68**	**61.17**

Species response under four future scenarios

Binary maps of the 10 species under future scenarios presented patterns of maintaining, expanding, shrinking, or shifting for the projected suitable habitats when compared with current binary maps. Eight species had consistent direction of response under all four projection scenarios. Among the eight, *R. muscosa* maintained its range while *R. boylii,* and *T. sierrae* expanded their suitable range. *Rana boylii* not only expanded its range but also shifted to a high elevational area. The shift for *R. boylii* is most evident under RCP 8.5 in 2070 while expansion is most apparent under RCP in 2050. *Taricha sierrae* expanded their range along SN foothill.

The projected range shrank for *A.macrodactylum, H. platycephalus, A. boreas, A. canorus,* and *R. cascadae*. *Hydromantes platycephalus* was close to extinction for all four scenarios. *A. boreas* almost disappeared from low elevation areas to the west of SN and shifted to higher elevation areas or areas to the east of SN.

Batrachoseps gregarius and *R. sierrae* responded inconsistently under four projection scenarios. *B. gregarius* expanded its suitable habitat along SN foothills under RCP 8.5 in 2050 and had it shrunk under the other scenarios. Under RCP 4.5, *R. sierrae* expanded to higher elevation areas in 2050 and shrank back to current range size in 2070. Under RCP 8.5, *R. sierrae* shrank its range in both 2050 and 2070 by shifting to higher elevation areas.

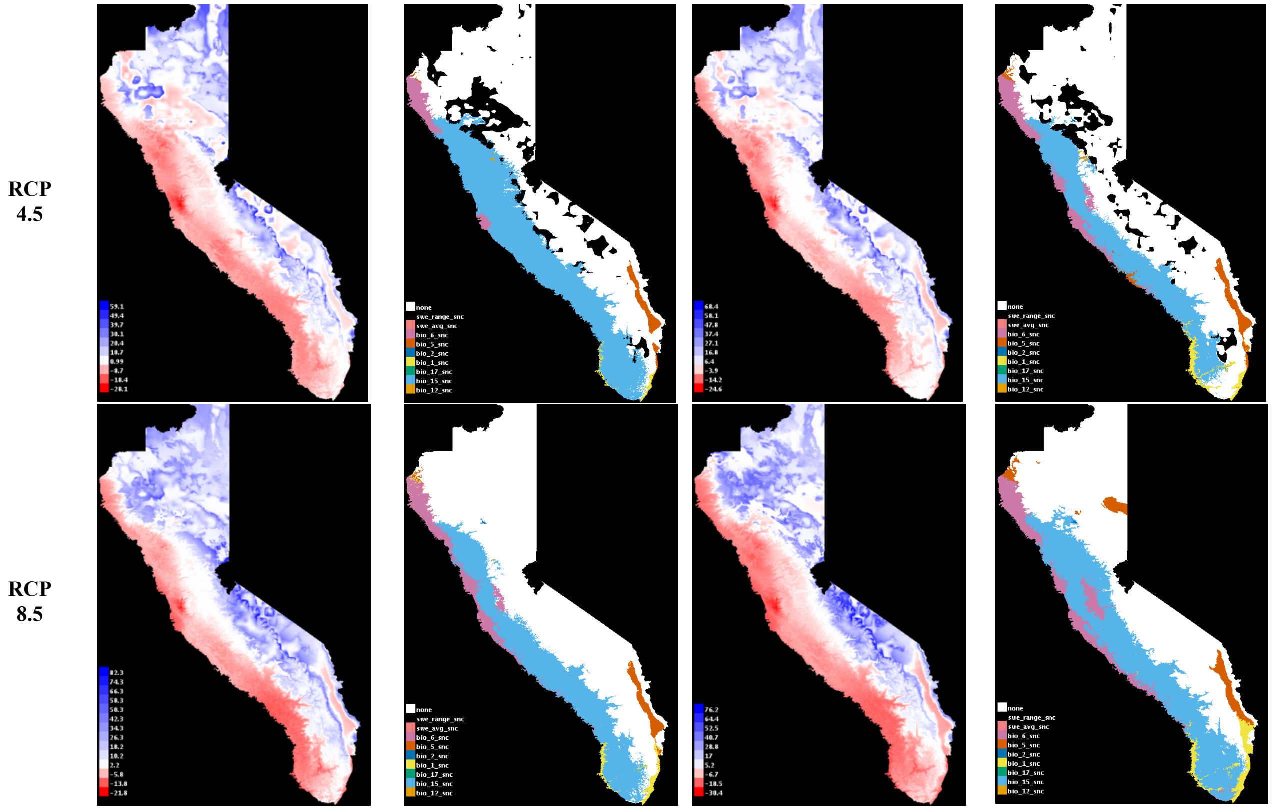
Influence of RCP 4.5 and RCP 8.5 on suitable habitat

Species in general lost more areas of suitable habitat under RCP8.5 than RCP4.5 if not maintained the same or increased. The pattern was most evident for *A. macrodactylum, A. canorus, R. cascadae* and *R. sierrae* where more severe reduction in range size occurred under RCP8.5 than RCP4.5 regardless of the averaged time period (Appendix C). *Hydromantes platycephalus* had severe reduction and fragmentation of range under all scenarios which were evenly close to extinction. *Batrachoseps gregarius* was in better situations under RCP8.5 than RCP4.5 in both 2050 and 2070. For *A. boreas*, habitat shrinking under RCP4.5 in 2050 and 2070 was more apparent than under RCP8.5 in 2070 while the most critical case was under RCP8.5 in 2050. The toads seemed to be disappeared in the west of SN under RCP8.5 and occupied more areas in the northeast of SNC in 2070.

I found different limiting novel predictors with different values under the four future scenarios (Table 4). Under RCP4.5, the limiting novel predictors were annual mean temperature (BV1) around the northern boundary, maximum temperature of the warmest month (BV5) to the east of SN, minimum temperature of the coldest month (BV6) and precipitation seasonality (BV15) along the foothill of SN up to Mount Shasta, and range of snow water equivalence (SWE_range) scattered through high SN regions. Under RCP 8.5, the limiting predictors were mostly the same except that there was no limiting effect of range of snow water equivalence (SWE_range). In 2070, precipitation seasonality (BV15) expanded to high-elevation areas in Placer County while maximum temperature of the warmest month (BV5) also had effect in the north.

Table 4: Limiting novel predictors and novel values under projection. I summarized the limiting novel predictors and novel values at each point in SNC under the four future scenarios.

2050		2070	
Point-wise Novel Value	**Limiting Novel Predictors**	**Point-wise Novel Value**	**Limiting Novel Predictors**



The region with the most negative novel values located along the SN foothill up to Mount Shasta. The negative novel values were most narrowly distributed on the point-wise novel value maps under RCP 4.5 in 2070, followed by under RCP 8.5 in 2050, then RCP 4.5 in 2050, with RCP 8.5 being most different from the current variable ranges.

DISCUSSION

Identifying the strengths and limitations of the studied models and interpreting the future projections of suitable habitat ranges are critical for understanding the conservation risks the wildlife are facing. I found the species distribution models highly fitted for all amphibians except *A. boreas* and *T. sierrae* and affirmed the important contribution from snowpack. Future projections of suitable habitat ranges were related to the life history of amphibians and pointed to two most susceptible groups in face of climate change, high-elevation endemic species and salamanders from the family Plethodontidae. The warmer climate scenario, RCP8.5, would put more pressure on amphibians, though there were exceptional species that might maintain or expand their ranges.

Model performance

Model fitness

The model fitted quite well for some important species in California, including the endangered and endemic species. With both training and test AUC greater than 0.85, the models were reliable for *A. macrodactylum, B. gregarius, H. platycephalus, A. canorus, R. muscosa, R. sierra, R. cascadae,* and *R. boylii*. Especially for *A. marcodactylum, B. gregarious, H. platycephalus, A. canorus,* and *R. sierrae,* with both AUC greater than 0.90, the models were highly reliable with good discrimination (Swets 1988). Even though the occurrence data were not abundant for *R. muscosa* (N=11) and *R. cascadae* (N=9), the model fitness was high and reliable. Among the 8 species, *A. canorus, R. muscosa* and *R. sierrae* are the only 3 endangered species (Baillie et al. 2004) in the selection while *A. canorus, H. platycephalus* and *R. sierrae* are the only 3 high-elevation endemic species. The high fitness of the above models ensured high confidence in the interpretation for the predictors, predicted distribution and projected suitable habitat.

The number of occurrence data points, coverage of the environmental gradient, and selection methods of environmental predictors limited the model fitness for *T. sierrae* and *A. Boreas,* which had test AUC under 0.75, being classified as poor discrimination (Swets 1988). In addition, the difference between training and test AUC were much greater than the that for other species.

On the one hand, the selected area of analysis might also limit the fitness of the model. *A. boreas* are habitat generalists which are only absent in the desert and central high SN, which is occupied by *A. canorus*, in California (Goebel et al. 2009). The model only covered SN region which exhibits mountainous environment. It excluded the coastal and Central Valley areas which represent the warmer and drier environmental conditions suitable for *A. boreas*. The environmental gradients were truncated where only half of the unimodal species response curve was covered. This situation could have been offset by choosing the most suitable feature class in Maxent (Merow et al. 2013), while I simply used the default setting for all 10 species to compare the modeling output among species. Therefore, choosing complete modelling region and narrowing down the feature class of the model to the most descriptive only may help improve model performance.

On the other hand, the number of available occurrence points might impact the fit of the model. The model for *T. sierrae* integrated only 3 occurrence points, which is much lower than the number of occurrence points used in the model for the other species. In addition, *T. sierrae* was identified as a subspecies of *T. torosa* before 2007 (Kuchta 2007). The occurrence data used in the research ranged from 1950 to 2000 when the species had not been identified as an individual species. Although the records before 2007 in MVZ had been updated before I assembled the data, the collecting for *T. sierrae* during field trip might be biased by the number of *T. torosa* collected. In terms of Maxent, test AUC reflects the model's predictive power (Phillips 2017), that is the ability to make projections into other geographical areas or time periods. The test score would not be strong if training sample failed to represent the environmental conditions of most suitable habitat range. Therefore, the limited occurrence points underrepresented the environmental conditions that were suitable for the living of *T. sierrae,* dropped the value of test AUC, and lowered the model's ability to make projections for *T. sierrae*. Future studies can do sampling to collect presence and absence data for modeling but the process can be both time and resource consuming.

Besides, verifying the identification of museum specimen requires time, labor and professional experience. Due to the above three limitations, I did not check museum specimens to verify the identification for *T. sierrae* or the other 9 species used in the analysis, which might reduce the model quality. Reliable museum records lead to reliable modeling outcomes while museum need enough funding and resources to keep records fully updated. Therefore, an alternative method is to provide natural history museums with financial and professional support to timely update specimen information. This option will also benefit future research in long term.

Last but not least, the selection process of environmental predictors is as important as the process of collecting data, defining the studied area and choosing feature class. The study did not perform any analysis, such as correlation analysis, principle component analysis (PCA), clustering algorithm or other dimension reduction methods to minimize correlation among predictors, to minimize the correlation among predictors, which has been highly recommended as to enhance model performance (Merow et al. 2013, Phillips et al. 2017). This study built predictors by learning from previous research and did test runs. The method was feasible and could give strong AUC for some species. However, the model might fit better if I selected predictors using any correlation minimizing method. Future studies should use one of above analysis method to minimize correlation of the predictors to generate fitter models.

Dimensions of Key Predictors

The model included predictors across the dimensions of annual trends, seasonality and extreme environmental conditions. Among the top four key environmental predictors, three of them described annual trend (i.e. mean snow water equivalence, mean diurnal temperature range, and annual precipitation) while one of them described seasonality (i.e. precipitation seasonality). Although the only variable referring to seasonality was about precipitation, it had the highest total permutation importance and contributed to all ten species. However, precipitation seasonality did not always have greater influence than annual precipitation for each individual species which in general usually respond to different climate factors with heterogeneity (Rowe et al. 2014, Rubidge et al. 2012, Tingley et al. 2012). Therefore, no consistent inference could be made on the relative importance of annual trend and seasonality for precipitation for all ten species.

However, some key life history events of amphibians are seasonal and precipitation-related (Table 5) which might support and explain the high overall contribution of precipitation seasonality to the model. *Taricha sierrae* and *B. gregarius* aestivated in the summer to avoid high temperature or getting dry while *H. platycephalus* reduce their surface activities in summer. *Batrachoseps gregarius, H. platycephalus, A. boreas, A. canorus, R. cascadae, R. muscosa* and *R. sierrae* hibernate through the winter and emergence at the time of snowmelt or ice-melt (Bradford 1983, Briggs 1987, Sherman and Morton 1993). The breeding time of all amphibians, except unknown for *H. platycephalus*, is triggered by snowmelt, ice-melt, or seasonal rainfall (Corn 2003, Sherman and Morton 1993) . Metamorphosis of larvae is signaled by increasing temperature and pond drying in summer or fall for *A. macrodactylum, T. sierrae, H. platycephalus, A. boreas, A. canorus* and *R. sierrae* (Smith-Gill and Berven 1979). The seasonal activities of hibernation, aestivation, breeding, and metamorphosis and reliance on snow, ice, and pond water support and explain the importance of precipitation seasonality to all models.

Table 5: Selected important life history of 10 species. The selected life history features, hibernation/aestivation, breeding time, and metamorphosis, are seasonal events and closely related to precipitation seasonality.

Species **Life History**	***Ambystoma macrodactylum***	***Taricha sierrae***	***Batrachoseps gregarius***	***Hydromantes platycephalus***	***Anaxyrus boreas***
Hibernation/ Aestivation	Larvae overwinter when water temperatures drop and surface ice form.	Aestivation occurs in underground retreats from July to early fall.	Presumably go underground to avoid extreme temperatures of winter and summer.	Surface activities are reduced in the summer. Hibernation may occurs at high elevations when snow accumulates.	Hibernation observed beneath or near large boulders along a spring-fed brook.
Breeding time	January and February in lowlands. May, June, and probably July in higher mountains after snow melts.	From December to May, dependent on elevation, local site conditions, and seasonal rainfall.	Coincides with the start of the rainy season from mid-November to early January. It can be later at higher elevation sites.	Unknown	January to July. Can depend on the timing of snowmelt. Later spawning occur at high elevations.
Metamorphosis	Larvae above 2500m transform during the second summer. Those at lower elevations take 3-4mo. The timing can be triggered by temperature and pond drying.	Occurs in late summer or early autumn. Takes about 2 weeks. May be triggered by pond drying in some waters and other undetermined factors.	Developmental time range from 65 days to 73 days in lab (Jockusch and Mahoney 1997).	Hatching probably occurs in the fall (Stebbins and mcginnis 2012) and has been found in early summer (Adams, 1942).	Dependent on the temperature of water. Duration is longer at high elevation. Occurs between mid-May and late-September in California.

Species **Life History**	***Anaxyrus canorus***	***Rana cascadae***	***Rana boylii***	***Rana muscosa***	***Rana sierrae***
Hibernation/ Aestivation	Hibernate from late September or early October before snowing to May or June when snowmelt recharges breeding pools (Sherman and Morton 1993).	Hibernates through snowy winter. Re-emergence in March coinciding with ice-melt (Briggs 1987).	Unknown.	Became inactive for winter when temperature drop freezing or below (Bradford 1983).	Only active for 3 months a year. May spend 6-9 months beneath ice-covered waters.
Breeding time	2-4 wk in May to July, depending on the depth of snowpack and time of melting (Sherman and Morton 1993).	Early April to mid-July at higher elevations when ice begins to melt in the breeding pools.	Mid-March to early June when streams are sufficiently charged and sediment is being transported.	After ice-melt when high stream flows subside. Range from April at low elevation to June–July at high elevation.	Late May, June, and July. May begin before meadows are free of snow and ice still present in parts of streams.

Metamorphosis	Tadpoles metamorphosed in 52-63 days at one location. Many larvae overwinter and transform the following summer.	Takes about two and a half to three months for metamorphosis. Sometimes overwinter.	Take place over a few days.	Fast larval development.	Rapid embryo development and larval growth driven by elevated water temperatures. Larvae overwinter and may not transform until third or fourth larval year.

The predictor with the second highest total permutation importance was average snow water equivalence from January to April. Besides, the range of snow water equivalence (SWE_range) was the limiting novel predictors scattered through high SN region. Both snowpack variables contributed to or limited the prediction or projection to the majority of the 10 amphibians. The importance of snowpack can not only be explained by model performance, but also be supported by life history of amphibians. One key duty for snowpack is to refill the temporal pools, streams, or other breeding sites, from late raining season in lowlands to early summer on high SN (Table 5, 6). Annually, the refill triggers a new circle of breeding, providing water bodies for the breeding, depositing of eggs, and living of larvae (Bradford 1983, Briggs 1987, Corn 2005, Sherman and Morton 1993). Sherman and Morton 1993 linked the decreased spring snow depths to low tadpole survival. The average of snowpack reflected the yearly average total storage of snow-water after the winter while the range of snowpack reflected how much is melt in the winter. The melting of snowpack in the winter coincided with the breeding of amphibians living in lowlands, while the snowpack mean implicated how much potential water might be refilling the transient pools for highland-species. Therefore, snowpack mean and range are both indispensable predictors for the distribution of amphibians.

Table 6: Additional snowpack-related life history activities. The breeding and reproduction of some amphibians rely on snowpack to refill temporal pools.

Species **Life History**	***Anaxyrus boreas***	***Anaxyrus canorus***
Breeding sites	Ponds, slowly flowing streams, lakes, canals, and reservoirs.	Water-filled loblollies, meandering streams, and shallow meadow snowmelt pools.
Breeding migration	Migrate in large numbers after hibernation.	Migrate 150-230 m at Tioga Pass (Kagarise Sherman, 1980). Males: stay at breeding ponds for 1-2 weeks. Females: stay for only a few days.
Egg deposition	Occurs after snowmelt when breeding ponds are refilled. Eggs are deposited in shallow water.	Deposit in shallow pools less than 7.5 cm deep.

Although both snowpack variables are important, average snow water equivalence had more influence than its corresponding seasonality for all ten species except *A. macrodactylum* and *A. boreas*. For *A. macrodactylum*, the contributions from snowpack mean and range were both relatively close to zero. For *A. boreas*, the model fitness was not as reliable with test AUC below 0.75 and with significant difference between training and test AUC. The relatively consistent trend between mean and variance of snowpack variables suggested that amphibians might rely more on the contribution of mean than variance of snowpack if the factor matters. For example, for the Columbia spotted frog, changes in mean snowpack had larger influence than changes in its variance on their viability (McCaffery et al. 2012). However, in Maxent, the contribution of each predictor also depends on the selection of studied species and the other predictors in the model (Elith et al. 2011). New selections of predictors, such as bringing in other variables or using a subset of the variables to combine with others, might influence the trend. In this way, although the snowpack average appeared to be more important than variance for snowpack in terms of the distribution of amphibians, I realize further studies to better understand the importance of annual trend and seasonality of snowpack.

Species response with habitat loss

High-elevation endemic species

Hydromantes platycephalus, R. sierrae and *A. canorus* are high-elevation endemic species in SNC. Their projected habitat range shifted towards higher altitude areas with *H. platycephalus* approaching extinction. However, as an exception, the range of *R. sierrae* did not change under RCP 4.5 in 2050.

In general, high-elevation endemic species face multifactor challenges under a warming climate. Endemic species live in unique or restricted environment, having small or declining population size with low reproduction rate, and being more susceptible to new species interactions (Işik 2011, Malcolm et al. 2006). High-elevation species accommodate to cooler mountainous environment but they can only adapt to climate change by moving up to areas with higher altitude, which will narrow their habitat range (Corn 2005, Lenoir et al. 2008, Rowe et al. 2014, Sandel et al. 2011). Climate change would also cause habitat shifting for other species, including competitors and predators. It might also enhance the dispersal and infection rate of infectious disease and parasites (Bosch et al. 2018). Therefore, high-elevation endemic species would face greater ecological stress.

For *H. platycephalus, R. sierrae* and *A. canorus*, larval development and community composition might influence their survival and distribution in SNC (Table 7). The larvae of both *R. sierrae* and *A. canorus* overwinter (Matthews and Preisler 2010, Sherman and Morton 1993) which means they take a relatively long time before transforming into adults. In contrast, *R. boylii, R. muscosa* and *T. sierrae,* the only three species which would not have their suitable habitat shrunk under all four scenarios, have rapid larval development. The larvae of *R. boylii* can transform into adult form within a few days. For species that slowly transform into maturity, climate change would accelerate the metamorphosis of their larvae and might damage the function of their immune system (Gervasi and Foufopoulos 2008), making them more susceptible to infectious disease, parasite, and agrochemicals. Therefore, climate change might impact the distribution of the endemic species by increasing the risks of underdeveloped immune system.

Table 7: Selected Important Life History for High-Elevation Endemic Species. The selected life history features, current habitat types, food sources for adults and larvae, and metamorphosis, might limit the adaptation of the high-elevation endemic species to climate change.

Species **Life History**		***Hydromantes platycephalus***	***Anaxyrus canorus***	***Rana sierrae***
Habitat		Found in moist fissures in granite outcrops or cliff faces. Habitat downslope from melting snowfield.	Prefer open area with low vegetation, good illumination, good soil moisture, and patches of willows at high elevations. Prefer denser forest cover at lower elevations.	Chaparral belt, coniferous forests, high mountain meadows. Sunny river banks, creeks, meadow streams, isolated pools, and lake shore.
Food	**adult**	Small arthropods.	Insects, centipedes, other invertebrates.	Arthropods.
	larva	Unknown.	Unknown. Presumably algae and other suspended materials.	Unknown. Presumably herbivorous and detritivores.
Metamorphosis		Hatching probably occurs in the fall (Stebbins and mcginnis 2012) and has been found in early summer (Adams, 1942).	Tadpoles metamorphosed in 52-63 days at one location. Many larvae overwinter and transform the following summer (Sherman and Morton 1993).	Rapid embryo development and larval growth driven by elevated water temperatures. Larvae overwinter and may not transform until third or fourth larval year (Matthews and Preisler 2010).

In addition, the community composition of the high-elevation areas would change and elevate the competition for *H. platycephalus, R. sierrae* and *A. canorus*. The three species might experience new interactions with *R. boylii* which might compete for habitat and preys. *Rana boylii* currently live in the SN foothills and were projected to expand their range to higher altitude areas. As the other three species, they occupy the same habitat types of forest streams, rivers with sunny banks, and shallow creeks and feed on the same food sources of arthropods, insects, and snails (Table 7). The expansion of *R. boylii* into the high-elevation communities might increase the competition for food among the four species, reshape their distribution and narrow down the habitat range of each species.

Species of the Family Plethodontidae

The two species from the family of Plethodontidae, *B. gregarius* and *H. platycephalus*, were more sensitive to climate change than species from the other family groups (Appendix B). Plethodontid salamanders lack lungs so that they rely solely on cutaneous respiration (Ruben and Boucot 1989). This physiological constraint limits individuals to cool and moist habitat (Farallo and Miles 2016, Spotila 1972). Therefore, warming climate will drive individuals to areas with higher latitude or altitude where the environmental conditions are more suitable.

Batrachoseps gregarius lost the majority of their habitat with some individuals dispersing to the east side of SN under RCP 4.5. Under RCP 8.5, the degree of habitat loss was not as severe as under RCP 4.5. The majority of the habitat range shifted to higher latitude areas with a small portion dispersed to the east SN. However, the dispersal ability of Plethodontidae is limited (Marsh et al. 2004, Pacini and Harper 2008). Even though the climate and snowpack conditions would be suitable, *B. gregarius* might not spread to the northwest area of SNC as projected.

Hydromantes platycephalus was the only species that is predicted to go extinct in the study even though it is currently classified as Least Concern on the IUCN Red List (Baillie et al. 2004). Given a training AUC of 0.95 and a test AUC of 0.90, the projection was reliable, which inferred a potential steep decline with a high mortality rate even under RCP 4.5. *Hydromantes platycephalus* is also a member of the high-elevation endemic species. Plethodontidae restricted to high-elevation areas are far more vulnerable to climate change than those widespread in lower altitude areas (Farallo and Miles 2016). The synergistic effects of being in both threatened groups made the fate worse for *H. platycephalus*. If an endemic species were extinct, there would be no strategy to bring it back. In this way, *H. platycephalus* deserves more and timely research and conservation attention.

However, the situation might not be as pessimistic as projected because Plethodontid salamanders can move vertically through borrows under soil or crevices between rock sediments to shelters where the environment is cooler and moister than the dry and hot surface (Farallo and Miles 2016, Liang et al. 2017). The model did not cover the availability of underground retreats for the two species. Nevertheless, retreating to suitable microhabitat is only a temporal solution. Species usually retreat to refugia during summer and winter months and have to be active during breeding seasons (Ashton and Ashton 1978). If the overall climate became too stressful for the living of the two species, there would be intensive intraspecific and interspecific competition as well as other ecological stressors (Urban Mark C. et al. 2012, Walther et al. 2002). Therefore, utilization of underground retreats could mitigate the harm of climate change in the short-term but might not be the long-term solution for the thriving of Plethodontidae.

RCP4.5 and RCP8.5

Predicted expansion for R. boylii and B. gregarius under RCP8.5 in 2050

Rana boylii and *B. gregarius,* currently occupying the region of SN foothills, were projected to have habitat ranges wider under 2050 of RCP8.5 along the foothill than the other three scenarios (Appendix C). This expansion was different from expectation where 2070 of RCP8.5 was the most preferable for expanding species (*Rana boylii*) while 2050 of RCP4.5 was the most preferable for shrinking species (*B. gregarius*). However, the projection might be dependable since the both training and test AUC for both species were high.

Precipitation seasonality and minimum temperature of the coldest month were the limiting novel variables along SN foothill from the southmost point to the westmost point of SNC for all four scenarios. The two species, *R. boylii* and *B. gregarius*, also received the two highest contributions from precipitation seasonality. Although precipitation seasonality seemed to influence their abnormality, the condition might be more complicated. In 2070, as expected, RCP8.5 had precipitation seasonality more distant to the current range than RCP4.5. In 2050, RCP4.5 (45.969-96.936) had more distinct precipitation seasonality than RCP8.5 (39.992-93.944) than current (35.988-83.954). However, precipitation seasonality might not have contributed to the expansion for *B. gregarius.* Based on prediction response curve, the variable covered the whole unimodal distribution under current scenarios. Values outside of the current range of values should not make much difference (Phillips 2017). However, the range of current precipitation seasonality only covered the lower half of the complete environmental gradient of *R. boylii* and stopped at high probability of presence on the upper edge. Values falling outside the upper edge during projection would be considered the same as the value at the upper boundary (Phillips 2017), which might be much lower in reality. This incompleteness of environmental gradient might bias the projection towards habitat expansion for *R. boylii* along the foothill under RCP8.5 in 2050.

The expansion for *B. gregarius* and *R. boylii* might be caused by minimum temperature of the coldest month even though the permutation contributions were much lower than those of precipitation seasonality. The predictor exhibited linear response curves instead of unimodal distribution for both species with relatively high probability of presence at both ends, especially for *R. boylii*. Therefore, values both outside and within the current range of values would be projected as highly possible to be present. As stated above, this setting would bias projection to expansion in foothill as well as in Mount Shasta.

Climate change and conservation

Comparing the two climate change scenarios, RCP4.5, the more modest carbon emission scenario relating to less extreme climate change, was unsurprisingly more bearable for most declining species than RCP8.5. Out of the seven declining species, *A. macrodactylum, A. canorus, R. cascadae, R. sierrae* would experience more serious habitat shrinking under RCP8.5 than RCP4.5 for both 2050 and 2070. Among the four, *A. canorus* and *R. sierrae* were listed as Endangered on the IUCN Red List (Baillie et al. 2004) but, surprisingly, neither would face the risk of extinction based on projection. This result might be caused by the data processing method where all predictors were averaged over 20 years for 2050 and 2070 respectively. The values of the predictors failed to reflect the conditions in the extreme years when sharp decline could take place (Bradford 1983). Therefore, this adjustment might underestimate the impacts of climate change in the future.

There were three declining species did not support RCP4.5 as a better emission pathway. For *H. platycephalus*, RCP4.5 and RCP8.5 were both threatening and risked extinction. For *B. gregarius* and *A. boreas*, the models showed better situations under RCP8.5 especially in 2050. The conditions for *B. gregarius*, as mentioned above, were complicated and need further studies to account for other relevant biological and ecological factors. For *A. boreas*, the model suggested slightest reduction in 2070 of RCP8.5 but showed apparent range shift towards northeast. Although the range size might not change much under the scenario, its position moved towards higher latitudes. However, the model was also not as strong so that it might mislead to a weak conclusion on habitat range change. Further studies with wider geographic coverage would give better understanding of the distribution change for the habitat generalist under the situation of climate change.

Climate change has been linked to the decline of many species globally (Moritz and Agudo 2013, Thomas et al. 2004). With an accelerating rate of extinction resulting from global warming regardless of taxonomic groups (Urban 2015). Climate scenarios are closely related to climate policy, market supply and demand, and energy and land use. RCP8.5 is a non-climate policy scenario which also includes large uneconomic coal resources into projection (Ward et al. 2012). RCP4.5 has some climate policies with low emissions reference (van Vuuren et al. 2011). This scenario is not only more bearable for amphibians but also encourages changes in energy systems, shifts to high-efficiency technology, and expansion of forest land (Thomson et al. 2011). Policies following RCP4.5 will not be as stringent as RCP2.6 yet still can push forwards establishment of a sustainable socioeconomic system that protects the long-term development of our society as well as the living of wildlife and supply of natural resources.

Limitations and future directions

The design of the study could be improved in four ways. First, some models had poor discrimination due to the availability and limitation of museum data records. Museums require funding to support the timely update of data since taxonomy is constantly updating (Komárek and Mareš 2012, Stümpel and Joger 2009). Efforts and resources invested into museum data, such as identification checked by visiting experts, will efficiently help future research in a long term. Second, the predictors used in the study can be further optimized in the future. A better model might also consider species interactions, vegetation type, proximity to watershed, as well as conditions of microhabitat. It should also use methods such as correlation analysis, principle component analysis (PCA), clustering algorithm to select predictor with minimized correlation. Third, future studies on individual species should select the most appropriate feature class or use more representative current habitat range to cover wider environmental gradient to improve the performance of the model. Last but not least, the model for habitat generalists should cover wider geographic region to capture most environmental conditions suitable for their survival.

Conclusion

First, snowpack influences the suitable habitat range for amphibians and contributes highly to the species distribution models. Before the study, there was evidence showing the importance of snowpack to the life history of amphibians but few research linking snowpack and amphibian decline. The result showed that snowpack mean had high contribution to the species distribution models while snowpack variance was one of the limiting novel variables under RCP 4.5. Future studies should take into account the impact of snowpack as one key environmental predictor for the distribution of amphibians.

Second, by comparing the ten different species, I inferred that the life history of species could have crucial influence on the ability to adapt to climate change. All three species which would not lose habitat range in the future have rapid metamorphosis rate. The rapid larval development might prevent them from damaging their immune system due to accelerated transformation. Future studies could use experimental design to test if rapid metamorphosis rate could benefit amphibians from the impact of climate change.

Third, by comparing species over their current distribution range, I found high-elevation endemic species to be more vulnerable to climate change. Species of this group are limited in suitable habitats and can only move to higher altitude areas when facing climate change. Endemic species are also ecological landmarks for a region. They also have unique positions in the regional wildlife community. The loss of endemic species cannot be retrieved by any strategies. Therefore, endemic species could be prioritized in conservation and research attention and efforts to mitigate their decline.

Fourth, I found Plethodontidae to be the family group that is most susceptible to a warming climate. However, the inference needs studies on more Plethodontid salamanders from different geographic areas to evaluate and refine. The method of comparing species from different families can give more ecological implications than studying a single species. The common trends among all families suggests general information for all amphibians while the differences among families with consistent trends within each family suggest specific inferences for each family. Especially for species modelling, selecting related species would give ecological implications benefiting the direction of future studies.

Fifth, the range of amphibians' point to the potential change in community composition. There will be new species interactions among the ten species as well as other competitors, predators, and preys. The interactions might be neutral, beneficial or stressful for different species. In addition, there might also be new overlapping between human activities and amphibians. Therefore, there is need for long-term monitoring of amphibians' distribution.

Lastly, climate change would alter the distribution for most species while RCP4.5 is more bearable than RCP8.5. *H. platycephalus* was the only species that might face extinction even under RCP4.5 and need timely conservation and research attention. Regulations and conservation strategies following RCP4.5 would benefit most studied amphibians as well as promoting the development of low-carbon energy sources, high-efficiency technology, and a sustainable socioeconomic system.

ACKNOWLEDGEMENTS

I thank my mentors Patina K. Mendez and Michelle S. Koo, and the Museum of Vertebrate Zoology for their help with developing and shaping the research. I thank Claudia Ruslim, Colette Cameo Christensen, Kavya Niranjan, Matt Li, and Yujing Wu for their support.

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APPENDIX

Appendix A. Life history table of the 10 studied species

Species / **Life History**	***Ambystoma macrodactylum***	***Taricha sierrae***	***Batrachoseps gregarius***	***Hydromantes platycephalus***	***Anaxyrus boreas***
Conservation status	Least concern (IUCN status)	Least concern (IUCN status)	Least concern (IUCN status)	Least concern (IUCN status)	Least concern (IUCN status)
Abundance	Difficult to determine	Stable in its current home range	Locally abundant	No indication of decline.	Known to be declining in CO, NM, WY, and UT.
Range in SN / (including elevation)	From Tuolumne county northward across the northern SN.	Throughout SN. Found up to about 2000 m.	Elevation is between 300 and 1800m. Mostly in southern SN Foothills.	Endemic to SN. Mostly in central SN and southern SN.	Throughout SN except the central High SN. Elevation up to 3600m.
Habitat	Arid grassland, sagebrush, dry woodland, coniferous forests, alpine meadows, barren rocky shores	Woodlands, grassland and chaparral	Examples including mesic areas, oak forests, mixed conifers, xeric annual grassland	Found in moist fissures in granite outcrops or cliff faces. Habitat downslope from melting snowfield (amphibiaweb).	Grassland, woodland, and meadows in forest areas
Longevity (years of age)	~ 10	> 20 (estimated)	Unknown	> 3 (estimated)	> 9
food adult	Insects, centipedes, earthworms, snails, and slug	Earthworms, snails, slugs, arthropods. Occasionally cannibalize	A variety of small invertebrates.	Small arthropods	Arthropods and worms. Probably adult cannibalism.
larva	Small aquatic invertebrates	Aquatic insect larvae; scavenge.	A variety of small invertebrates.	Unknown	Filamentous algae, detritus; scavenge
Hibernation/ Aestivation	Larvae overwinter when water temperatures drop and surface ice form.	Aestivation occurs in underground retreats from July to early fall.	Presumably go underground to avoid extreme temperatures of winter and summer.	Surface activities are reduced in the summer. Hibernation may occurs at high elevations when snow accumulates.	Hibernation observed beneath or near large boulders along a spring-fed brook
Age/Size at reproductive maturity	1-3 years of age	3 years of age	Males: mean 35.9mm svl Females: mean 42.5mm svl	Estimated ~2.5 years of age	4-6 years of age.
Breeding time	January and February in lowlands. May, June, and probably July in higher mountains after snow melts.	From December to May, dependent on elevation, local site conditions, and seasonal rainfall.	Coincides with the start of the rainy season from mid-November to early January. It can be later at higher elevation sites.	Unknown	January to July. Can depend on the timing of snowmelt. Later spawning occur at high elevations.

location	Ponds, lakes, seeps, and transient pools.	Ponds, lakes, streams, and reservoirs.	Unknown	Terrestrial reproduction. Likely to be in moist or wet cavities or crevice	Ponds, slowly flowing streams, lakes, canals, and reservoirs.
migration	Often migrate across snow in early spring.	Begin in January and February. Typically 6-8wk.	Unknown	Unknown and unlikely	Migrate in large numbers after hibernation.
Egg deposition	Deposit in shallow water, on the bottom, or attached to objects in water before complete ice-out.	Favors rocky beds, covers, and attachment sites.	Eggs are in temporary communal nests beneath covers.	Has not been observed.	Occurs after snowmelt when breeding ponds are refilled. Eggs are deposited in shallow water.
Metamorphosis	Larvae above 2500m transform during the second summer. Those at lower elevations take 3-4mo. The timing can be triggered by temperature and pond drying.	Occurs in late summer or early autumn. Takes about 2 weeks. May be triggered by pond drying in some waters and other undetermined factors.	Developmental time range from 65 days to 73 days in lab (Jockusch and Mahoney 1997).	Hatching probably occurs in the fall (Stebbins and mcginnis 2012) and has been found in early summer (Adams, 1942).	Dependent on the temperature of water. Duration is longer at high elevation. Occurs between mid-May and late-September in California.

Species / **Life History**	***Anaxyrus canorus***	***Rana cascadae***	***Rana boylii***	***Rana muscosa***	***Rana sierrae***
Conservation status	Endangered (IUCN status)	Near threatened (IUCN status)	Near threatened (IUCN status)	Endangered (IUCN status)	Endangered (IUCN status)
Abundance	Dramatic decline (Sherman and Morton 1993)	Documented decline	Historic population loss on the western slope of the SN	Once numerous but is on the brink of extinction in Southern California now	Dramatic decline
Range in SN/(including elevation)	Endemic to SN. Elevation: 1460-3630m. Has been disappeared from more than 50% of its historic range (Stebbins and McGinnis 2012).	Lassen peak areas in northern SN.	Throughout SN Foothills. Elevation up to 1830m.	Once throughout SN but now close to extinction.	Endemic to SN. Only ranid found in the highlands of SN. Has disappeared from about 95% of its historic range.
Habitat	Prefer open area with low vegetation, good illumination, good soil moisture, and patches of willows at high	Small streams, ponds, and lakes in coniferous forests	Forest streams and rivers with sunny, sandy and rocky banks, deep pools, and	Clear pools and Streams (Stebbins and McGinnis 2012)	Chaparral belt, coniferous forests, high mountain meadows. Sunny river banks, creeks, meadow streams,

		elevations. Prefer denser forest cover at lower elevations.		shallow creeks.		isolated pools, and lake shore.
Longevity (years of age)		> 15 for female, >12 for male. (Sherman and Morton 1993)	> 5	Unknown	Unknown	Unknown
food	**adult**	Insects, centipedes, other invertebrates.	Poorly known. Probably consume invertebrates and is cannibalism	Terrestrial arthropods with a variety of insects, snails.	Arthropods; cannibalism.	Arthropods
	larva	Unknown. Presumably algae and other suspended materials	Benthic feeders.	Algae, diatoms, detritus; scavenge	Unknown. Presumably herbivorous and detritivores	Unknown. Presumably herbivorous and detritivores
Hibernation/ Aestivation		Hibernate from late September or early October before snowing to May or June when snowmelt recharges breeding pools (Sherman and Morton 1993).	Hibernates through snowy winter. Reemergence coincide with ice-melt (Briggs 1987).	Unknown	Became inactive for winter when temperature drop freezing or below (Bradford 1983).	Only active for 3 months a year. May spend 6-9 months beneath ice-covered waters.
Age/Size at reproductive maturity		Females: 4–6 years of age. Males: 3–5 years of age.	Males: 2-3 Females: 4 years of age.	Uncertain	~ 3-4 years of age. Females: 45–50 mm SVL. Males uncertain.	Uncertain
Breeding	**time**	2-4 wk in May to July, depending on the depth of snowpack and time of melting (Sherman and Morton 1993)	Early April to mid-July at higher elevations when ice begins to melt in the breeding pools.	Mid-March to early June when streams are sufficiently charged and sediment is being transported.	After ice-melt when high stream flows subside. Range from April at low elevation to June–July at high elevation.	Late May, June, and July. May begin before meadows are free of snow and ice still present in parts of streams.
	location	Water-filled loblollies, meandering streams, and shallow meadow snowmelt pools.	Temporary and permanent static waters with silt/mud substrates, lack of fish, low UV-B transmission.	Streams and rivers	Streams or lakes	Streams or lakes
	migration	Migrate 150-230 m at Tioga Pass (Kagarise Sherman, 1980).	No extensive breeding migration.	Modest movements along stream corridors.	No distinct breeding migration.	No distinct breeding migration.

	Males: stay at breeding ponds for 1-2 weeks. Females: stay for only a few days				
Egg deposition	Deposit in shallow pools less than 7.5 cm deep.	Shallow pools and lake shoreline sites. Warm water with no severe wave action. Not attached to support structures	Eggs attached to stones in stream beds or to vegetation	Under banks or attach to rocks, gravel, or vegetation in streams or lakes .	Under banks or attach to rocks, gravel, or vegetation in streams or lakes. Be in or connected to deep permanent lakes and ponds (preferably more than 2.5m deep).
Metamorphosis	Tadpoles metamorphosed in 52-63 days at one location. Many larvae overwinter and transform the following summer.	Takes about two and a half to three months for metamorphosis. Sometimes overwinter.	Take place over a few days	Fast larval development	Rapid embryo development and larval growth driven by elevated water temperatures. Larvae overwinter and may not transform until third or fourth larval year.

Appendix B. Binary maps of current and future species range by family

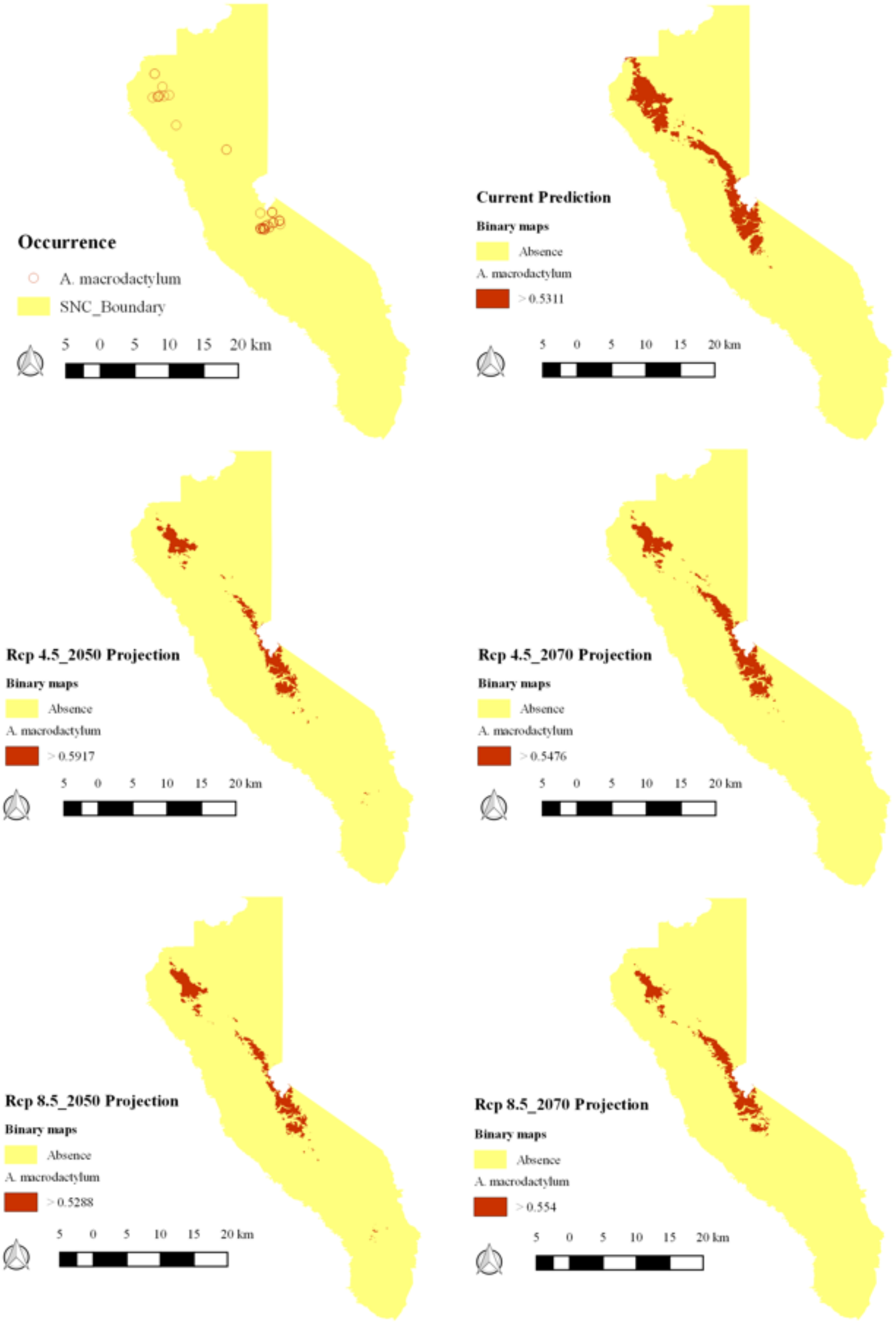


Figure I. Current and future binary range for Ambystomatidae (*A. macrodactylum*)

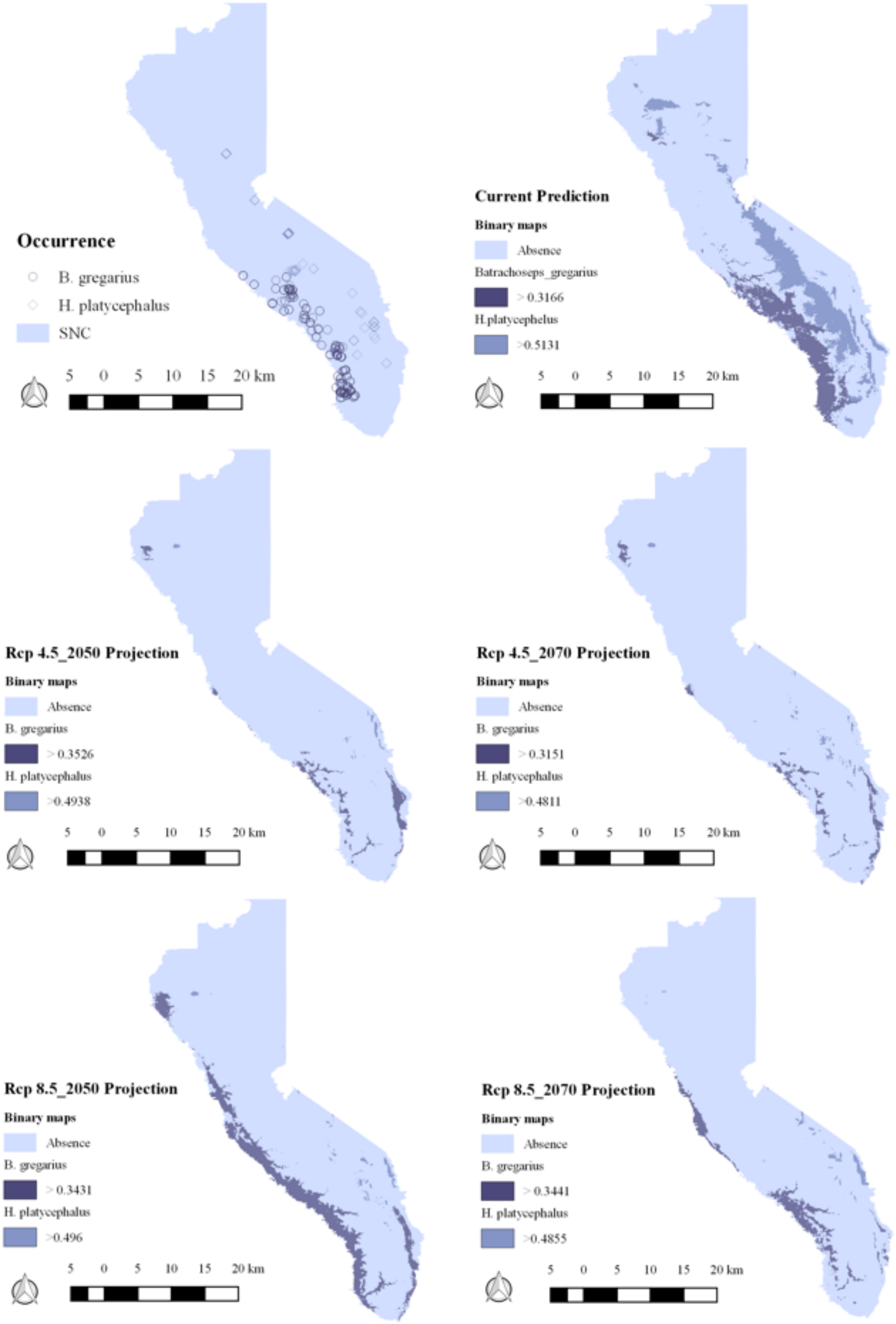


Figure II. Current and future binary range for Plethodontidae (*B. gregarius, H. platycephalus*)

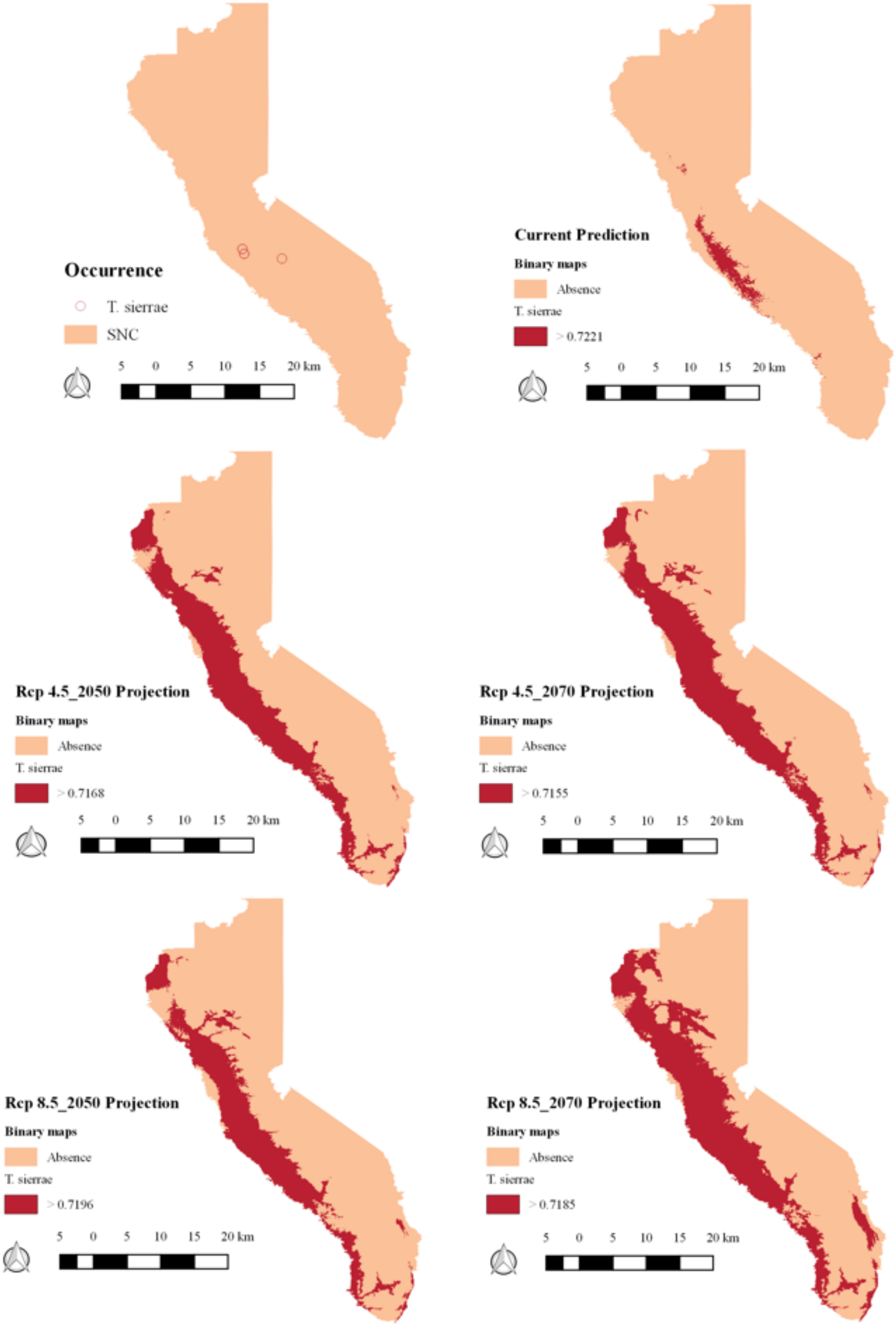


Figure III. Current and future binary range for Salamandridae (*T. sierrae*)

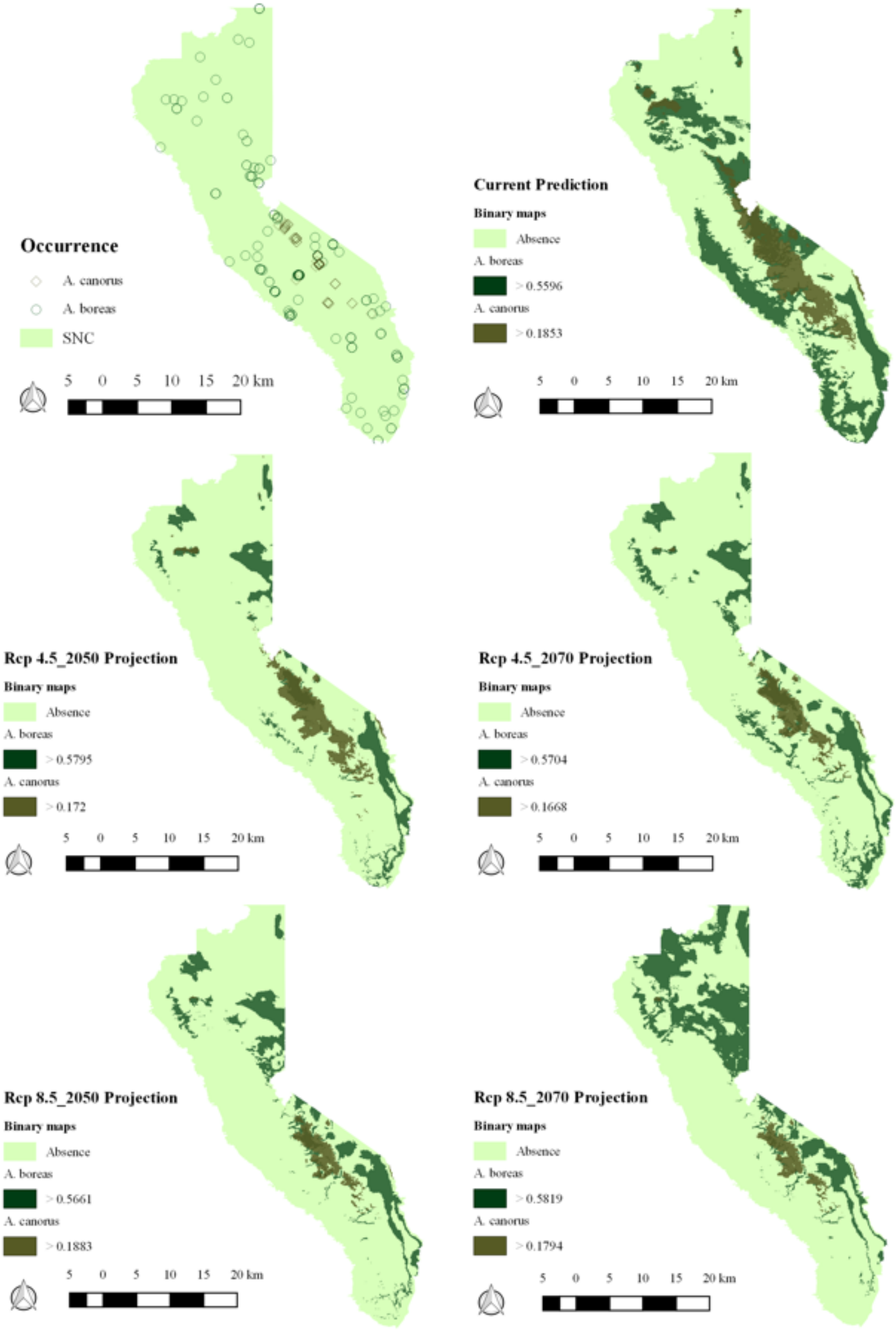


Figure IV. Current and future binary range for Bufonidae (*A. boreas and A. canorus*)

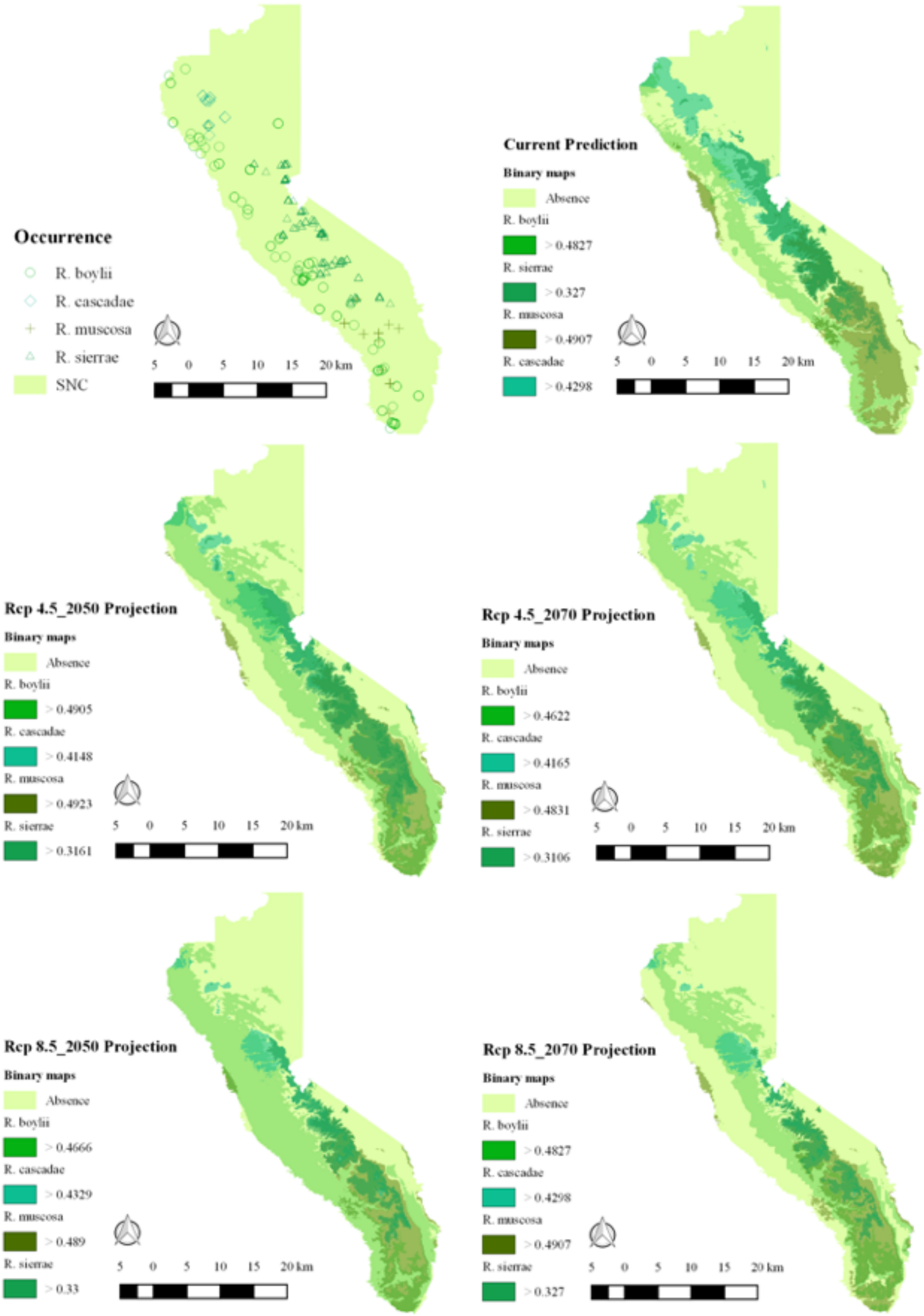
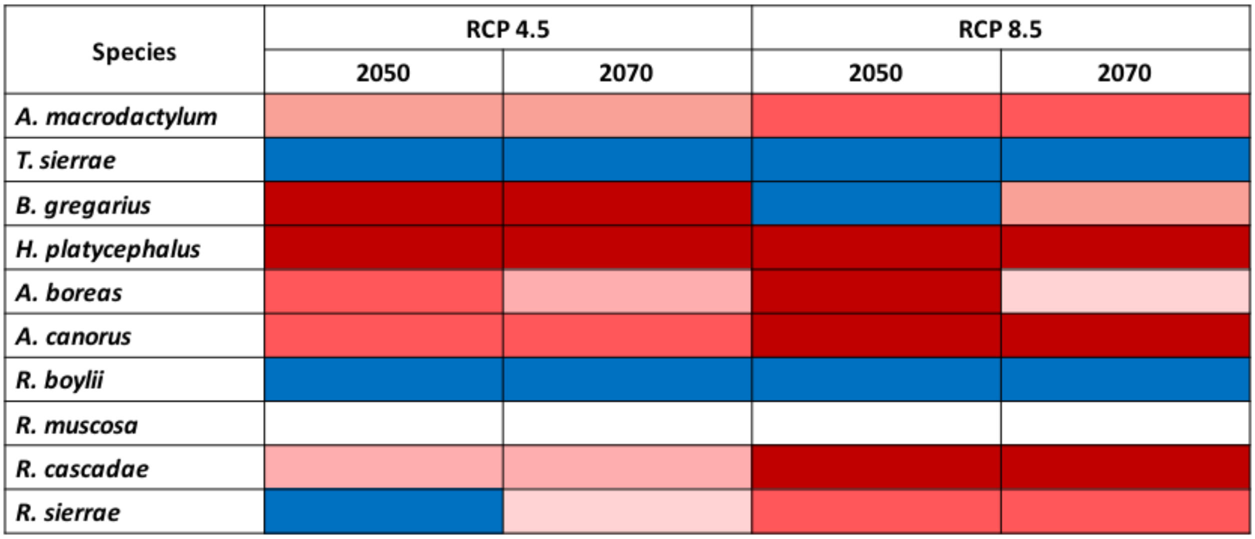


Figure V. Current and future binary range for Ranodae (*R. boylii, R. cascadae, R. muscosam R. sierrae*)

Appendix C. Direction of range change under RCP4.5 and RCP8.5. The blue box represents habitat expansion, white box for species maintaining their range, and red box for habitat loss. I classified the degree of habitat shrinking and used darker color representing more severe habitat loss.



Species	RCP 4.5		RCP 8.5	
	2050	2070	2050	2070
A. macrodactylum	🟥	🟥	🟥	🟥
T. sierrae	🟦	🟦	🟦	🟦
B. gregarius	🟥	🟥	🟦	🟥
H. platycephalus	🟥	🟥	🟥	🟥
A. boreas	🟥	🟥	🟥	🟥
A. canorus	🟥	🟥	🟥	🟥
R. boylii	🟦	🟦	🟦	🟦
R. muscosa	⬜	⬜	⬜	⬜
R. cascadae	🟥	🟥	🟥	🟥
R. sierrae	🟦	🟥	🟥	🟥