

**Predicting the Distribution of *Pomacea canaliculata* in California  
Under Current and Future Climate Scenarios**

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**ABSTRACT**

*Pomacea canaliculata*, a freshwater snail native to South America, has become an invasive species in California since being unintentionally introduced in the 1990s, threatening local ecosystems, agricultural areas, native organisms, and humans. Climate change is predicted to promote the expansion of invasive species within California. Knowledge of the areas at risk of invasion by *P. canaliculata* and the environmental factors vital to their distribution, is important for preventing their spread and establishment in new areas of California under climate change conditions. In this study, I predicted suitable areas and bioclimatic variable importance for *P. canaliculata* by using Maximum entropy species distribution modeling under five different climate scenarios: current climate averaged from 1981-2010, climate under SSP1-2.6 from 2041-2070, SSP5-8.5 from 2041-2070, SSP1-2.6 from 2071-2100, and SSP 5-8.5 from 2071-2100. I found that the range of *P. canaliculata* is not at its full potential in California under current climatic conditions, and that their range is expected to increase under all climate change scenarios but greatest under SSP5-8.5 from 2071-2100. The most important bioclimatic variables were temperature seasonality (68.9%), mean daily mean air temperature of the coldest quarter (22.1%), and mean daily maximum air temperature of the warmest month (6.8%). These results indicate that *P. canaliculata* may expand more northward and further across coastal regions of California under all climate change scenarios. This supports the widespread view that decreasing greenhouse emissions is the most efficient method in controlling the expansion of invasive species.

**KEYWORDS**

species distribution modeling, Maximum entropy, climate change, invasive species, dispersal risk

## INTRODUCTION

Climate change has been shown to play an important and complex role in the expansion of invasive species worldwide. Climate change is the long-term change in local, regional, and global weather patterns (NASA 2021). Shared Socioeconomic Pathways (SSPs) are scenarios of globally projected socioeconomic changes and the subsequent increases in greenhouse gasses, world population, world population growth, average global temperature, and other global social and environmental changes (Masson-Delmotte et al. 2021). There are four potential SSP scenarios (1, 2, 3, and 5), which are associated with five radiative forcings (1.9, 2.6, 4.5, 7.0, and 8.5 watts per square meter), to create five combined SSP and radiative forcing scenarios: SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5. These combined scenarios range from low (1-2.6) to high (5-8.5) regarding future concentrations of greenhouse gasses in the atmosphere and subsequent impacts of climate change (Masson-Delmotte et al. 2021). For example, the scenario SSP1-2.6 is expected under low greenhouse gas emissions if carbon dioxide emissions are cut to net zero around the year 2075, resulting in an increase in temperature of 1.8 degrees Celsius between 2081-2100, and a peak and decline in population to about 7 billion people by 2100 (Table 1). In California specifically, under all SSP models, climate change is predicted to increase annual temperatures, slightly decrease precipitation, reduce snowpack in the Sierra Nevada mountains, and increase temperature extremes in both magnitude and frequency (Hayhoe et al. 2004). Many studies predict that climate change will accelerate the spread of invasive species globally in the future through its varying impacts on climate and ecosystems (Hellmann et al. 2008, Mainka and Howard 2010). In California, invasive plant and animal species are expected to spread to new areas and outcompete native organisms under the predicted drier and hotter climate change conditions (Renteria et al. 2021, CDFW 2022, Wolf et al. 2016). With climate change accelerating invasions worldwide, it will become increasingly important to track invasive species distribution and prevent their spread into vulnerable areas.

Species distribution modeling (SDM) has been widely used to predict potentially suitable areas for invasive species in the present and future, in order to aid in the early detection of invasive species and with decisions regarding their management. SDMs can be especially

valuable for anticipating the spread of invasive species under the different SSP scenarios of climate change. Species distribution models are able to predict invasive species' distributions by investigating the relationship between observations of species occurrence and the environmental variables that contribute to a species' reproduction and survival (Václavík and Meentemeyer 2009). Policy makers and government officials can then utilize SDM predictions to enact measures that prevent the spread of invasive species to vulnerable areas (Fournier et al. 2019). Preventing the spread of invasive species into new areas is thought to be the most effective way of preventing and controlling economic and environmental costs associated with invasions (Finnoff et al. 2007). However, predicting suitable areas of invasive species is species dependent, and thus species distribution models must be created with an individual species' life history and habitat preferences in mind.

*Pomacea canaliculata*, channeled apple snails, are a species of freshwater snail native to South America that were unintentionally introduced to California in the 1990s, where they have since become an invasive species, threatening native organisms, local agriculture, and human health. The first population of *P. canaliculata* in California was observed in 1997 in Lake Miramar within the San Diego County, and has since become an invasive species in several other areas of the state including the Contra Costa, Riverside, San Diego, Los Angeles, and Kern counties (Howells et al. 2006). The snails have become devastating agricultural pests of rice in Southeast Asia, which raises the concern that *P. canaliculata* may become a pest to California's rice fields if they spread to agricultural areas (Brito and Joshi 2016). *P. canaliculata* pose a threat to human health because they have the potential to carry the rat lungworm parasite, which causes eosinophilic meningitis in humans (Liu et al. 2018). They also have the potential to compete with native freshwater snail species, and significantly alter native freshwater ecosystems (Rawlings et al. 2007). The risks associated with the invasive *P. canaliculata* pose a threat to the people and organisms of California, and thus it is important to track their current and potential future distribution in order to inform management decisions and prevent their expansion to vulnerable areas.

To better understand climate change impacts on *Pomacea canaliculata* and the areas of California that are vulnerable to its invasion, I examined how the distribution of *P. canaliculata* is predicted to change under several different climate scenarios. I had the following objectives: (1) to predict the possible present distribution of *P. canaliculata* in California under current

climatic conditions, (2) to predict the future distribution of *P. canaliculata* in California under SSP 1-2.6 and 5-8.5 from 2041-2070 and 2071-2100, and (3) to identify the environmental variables utilized in the species distribution modeling that are most important in predicting the distribution of *P. canaliculata*. I hypothesize that (1) *P. canaliculata* will expand in range when modeled under current climate conditions, (2) the range of *P. canaliculata* will expand under all future climate change projections, but greatest under RCP 8.5 from 2071-2100, (3) and that maximum and minimum temperature, as well as annual precipitation will prove to be the most important bioclimatic variables in the species distribution models.

**Table 1. SSP scenarios and their predicted effects on climate and population.** Sourced from the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (Masson-Delmotte et al. 2021).

| SSP Scenario | Greenhouse Gasses                                                                                           | Estimated Warming (2041-2060) in °C | Estimated Warming (2081-2100) in °C | World Population in 2100 (in billions) | Socioeconomic Scenario                                                                                                                                                                 |
|--------------|-------------------------------------------------------------------------------------------------------------|-------------------------------------|-------------------------------------|----------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1-1.9        | CO <sub>2</sub> emissions cut to net zero around 2050                                                       | 1.6                                 | 1.4                                 | 7                                      | High income and reduced inequalities, environmentally-friendly technology and lifestyles. Low challenges to mitigation and high adaptive capacity.                                     |
| 1-2.6        | CO <sub>2</sub> emissions cut to net zero around 2075                                                       | 1.7                                 | 1.8                                 | 7                                      | Same as above.                                                                                                                                                                         |
| 2-4.5        | CO <sub>2</sub> emissions remain around current levels until 2050, then fall but not reach net zero by 2100 | 2.0                                 | 2.7                                 | 9                                      | Medium income and technological progress. Gradual reduction in inequality. Medium challenges to mitigation and medium adaptive capacity.                                               |
| 3-7.0        | CO <sub>2</sub> emissions double by 2100                                                                    | 2.1                                 | 3.6                                 | 13                                     | Low income and continued inequalities, material-intensive consumption and production, and slow rates of technological change. High challenges to mitigation and low adaptive capacity. |
| 5-8.5        | CO <sub>2</sub> emissions triple by 2075                                                                    | 2.4                                 | 4.4                                 | 7                                      | High income, reduced inequalities, resource-intensive production and consumption. High challenges to mitigation, and high adaptive capacity.                                           |

## METHODS

### Study Site

To complete the analysis for this study, I collected the data from the state of California. The geographic bounds of my study site are the state lines of California (Figure 1). California has a total land area of 423,967 square kilometers (USCB 2010). The highest elevation is 4,418 meters on Mount Whitney, and the lowest in Death Valley at 86 meters below sea level (USGS 2021). It is one of the few areas on earth where five major climate types are located within close proximity of each other: desert, cool interior, highland, steppe, and mediterranean climates (CDFW 2003). This diversity in climate types, elevation, precipitation levels and temperatures, creates a diversity of habitat types and subsequently a diversity of organisms (both native and nonnative) that exist in California (CDFW 2003). Channeled Apple Snails, *Pomacea canaliculata*, were unintentionally introduced to California in the late 1990s, most likely through the aquarium trade, with the first population observed in 1997 (Howells et al. 2006). I chose California as my study area due to the widespread presence of *P. canaliculata*, and the absence of morphologically similar non-native apple snail species (such as *P. insularum* and *P. haustrum*), which are present in the Southeastern United States. The lack of similar species prevents misidentifications by citizen scientists.



**Figure 1. Map of the United States with the state of California highlighted in blue.** Created using ArcGIS Pro and a shapefile of California from the UC Berkeley GeoData Repository.

## Species Occurrence Data

To determine the current and future predicted distribution of *P. canaliculata*, I collected geo-referenced species occurrence data from the iNaturalist and Nonindigenous Aquatic Species (NAS) online databases. From the iNaturalist database, I collected 393 geo-referenced occurrence data for *P. canaliculata* in California (iNaturalist 2021), all sourcing from citizen science observations. iNaturalist is a joint initiative of the California Academy of Sciences and the National Geographic Society. Citizens can input photo observations of plant and animal organisms, which other users verify or reject. Figure 2 shows three examples of photo observations of *P. canaliculata* from iNaturalist users in California (Figure 2). An observation records an individual's encounter with an organism at a particular time and location (iNaturalist 2021). From the NAS database, I collected 10 geo-referenced occurrence data. The NAS database is a central repository for spatially-referenced presence and distribution data of nonindigenous aquatic species, run by the US Geological Survey (NAS 2021). Occurrence data from both databases were in the form of longitude and latitude locations of observations of species. I downloaded a total of 403 data from the NAS and iNaturalist databases, which I combined and formatted into a comma-separated values (CSV) file using Excel (Microsoft Corporation 2018) to prepare for use in the Maximum Entropy modeling program. There were 19 duplicate coordinates within the collected iNaturalist data, which were deleted when running the model, reducing total data points to 384.



**Figure 2. Images of *Pomacea canaliculata* taken from iNaturalist observations in California.** (a) two *P. canaliculata* interacting underwater, (b) *P. canaliculata* shell, and (c) pink *P. canaliculata* egg clutches.

## Climate Data

To include data on California's present and future climate conditions, I obtained climate data from the CHELSA website (<https://www.chelsa-climate.org>). CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas) is an online database of global weather and climate data of high spatial resolution (Karger et al. 2017, Karger et al. 2018). I collected 19 bioclimatic variables with 1km resolution in raster format from the CHELSA website for three climate scenarios: current climate conditions, and future climate conditions under the SSP1-2.6 and SSP5-8.5 global climate models (GCMs) as outlined under the IPCC's Sixth Assessment Report. For SSP1-2.6 and SSP5-8.5, I collected data for two time periods each, from 2041-2070 and 2071-2100. The 19 bioclimatic variables are derived from the monthly temperature and rainfall values to generate more biologically meaningful variables. The bioclimatic variables represent annual trends, seasonality, and extreme or limiting environmental factors (Karger et al. 2017, Karger et al. 2018). The bioclimatic raster data had to be trimmed to the state of California using ArcGIS Pro 2.8's "Extract by Mask" tool, and converted to ESRI ASCII (American Standard Code for Information Interchange) format using ArcGIS Pro 2.8's "Raster to ASCII" tool. ArcGIS Pro is a professional desktop GIS software used to explore, visualize, and analyze geographic data (ESRI 2021).

## Species Distribution Modeling

To predict the potential distribution of *Pomacea canaliculata* under current and predicted future climate conditions, I used Maximum Entropy species distribution modeling, called Maxent for short (Phillips et al. 2022). Maxent is a machine-learning algorithm that estimates species occurrences by finding the probability distribution that has maximum entropy (meaning that it is closest to uniform), while taking into account constraints of environmental conditions at known occurrence sites (Gomes et al. 2018). Maxent is appropriate for this study because it is used for modeling species geographic distributions with presence-only occurrence data and environmental data, and my occurrence data is presence-only data. Maxent has consistently outperformed other presence-only species distribution modeling methods and thus is currently the most commonly used method in scientific literature for modeling the distribution of species

with presence-only data (Phillips et al. 2006). To run Maxent, I input both the species occurrence data (in CSV format) and the 19 bioclimatic variable data (in ASC format) into the Maxent program that I ran using Java Runtime. A total of five models were run for the current and future climate scenarios, and the climatic data had to be replaced before each run with the appropriate climate data. The logistic output format of Maxent provides a potential species distribution map, which provides predicted presence probabilities between 0 and 1. The settings used for each Maxent run are in the appendix (Appendix A). To evaluate model performance of Maxent, I used the area under the receiver operating curve (AUC) to determine if the model performed better than at random. If an AUC value is greater than 0.5, then the model has the discrimination capacity to differentiate between positive and negative class, which indicates good model performance.

To create habitat suitability maps for each climate scenario, I input the ASC file from each Maxent run into ArcGIS Pro 2.8 and used the “Copy Raster” tool to convert the ASC files to raster files. I then divided the contents of the potential distribution areas into four categories of habitat suitability, including unsuitable areas (0-0.25), low suitable areas (0.25-0.50), suitable areas (0.50-0.75), and highly suitable areas (0.75-1.0) using the “Classify” tool under “Symbology” (Xin et al. 2021).

### **Variable Contribution**

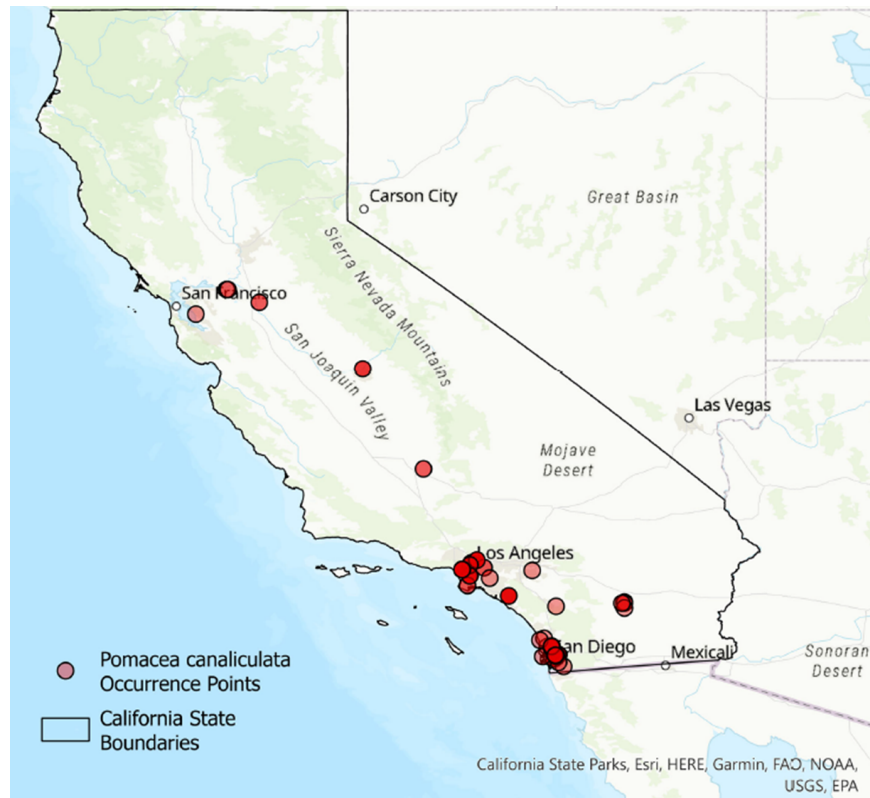
To determine which of the 19 bioclimatic variables used for Maxent were the most important in predicting the distribution of *Pomacea canaliculata* in California, I used the analysis of variable contribution output from the Maxent model. The analysis of variable contribution is a natural output of the Maxent model, and includes both percentage contribution and permutation importance. I used the permutation importance output because this measure depends only on the final Maxent model, not the path used to get there. Permutation importance works by randomly permuting the values of a variable among the training points and measuring the resulting decrease in training AUC. A large decrease indicates that the model heavily depends on that variable, meaning that the variable is important in predicting the distribution of a species.



## RESULTS

### Data Collection

I found that *Pomacea canaliculata* were widely distributed across the state of California, with areas of high density. My occurrence data for *P. canaliculata* consists of 384 data points throughout California, after deleting 19 duplicate coordinates (Figure 3). *P. canaliculata* are now found in the Contra Costa, Riverside, San Diego, Orange, Los Angeles, and Kern counties in California. They are concentrated in the San Diego and Los Angeles areas (Figure 3).



**Figure 3. *Pomacea canaliculata* occurrence data in California.** Red points represent occurrence data from the iNaturalist database. Opaque red points represent overlapping points.

## Predictive Accuracy of the Maxent Model

I found that the AUC (area under the receiver operating curve) value for each climate scenario was much greater than 0.5, which indicated excellent performance of the Maximum Entropy model in predicting suitable habitats of *P. canaliculata* under both current and future predicted climate conditions (Table 2). The AUC of the test data for each model was 0.980, and the AUC of the training data for each model was 0.975. In Maxent, the test data was used to assess the model accuracy, and the training data was used to create the predictive model. The graph of the AUC values for all of the climate models is in the appendix (Appendix C).

**Table 2. Predictive accuracy of the Maxent model.** Estimated by AUC values of both test and training data.

| Climate Conditions       | AUC of Test Data | AUC of Training Data |
|--------------------------|------------------|----------------------|
| Near current (1981-2010) | 0.980            | 0.975                |
| 2041-2070 SSP1-2.6       | 0.980            | 0.975                |
| 2041-2070 SSP5-8.5       | 0.980            | 0.975                |
| 2071-2100 SSP1-2.6       | 0.980            | 0.975                |
| 2071-2100 SSP5-8.5       | 0.980            | 0.975                |

## Contribution of Bioclimatic Variables

I derived the contribution of each bioclimatic variable for modeling the predicted habitat of *P. canaliculata* using the “Analysis of Variable Contribution” output of the Maximum Entropy model (Table 3). I identified three variables that contributed the most to the habitat modeling of *P. canaliculata*. These variables were temperature seasonality (bio 4) which contributed 68.9% permutation importance, mean daily mean air temperatures of the coldest quarter (bio 11) which contributed 22.1%, and mean daily maximum air temperature of the warmest month (bio 5) which contributed 6.8% (Table 2). The mean monthly precipitation amount of the coldest quarter contributed the remaining 2.1% to the Maxent model. Jackknife tests conducted by Maxent, produced graphs of the gain of training and test data for each bioclimatic variable. These

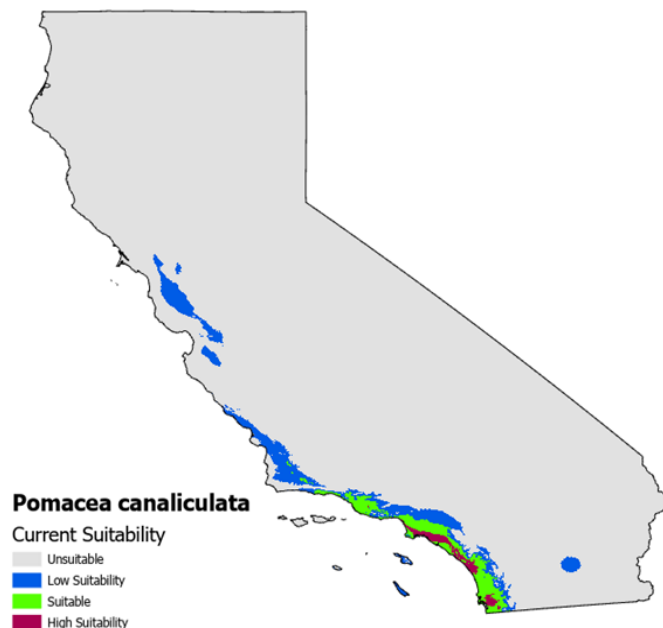
jackknife test graphs present a different method of analyzing variable importance and are in the appendix (Appendix B).

**Table 3. Permutation importance and percent contribution of bioclimatic variables.** Includes the 19 bioclimatic variables used in the Maxent model, sourced from CHELSA.

| Variable Code | Bioclimatic Factor                                       | Permutation Importance (%) | Percent Contribution (%) |
|---------------|----------------------------------------------------------|----------------------------|--------------------------|
| Bio4          | Temperature seasonality                                  | 68.9                       | 44                       |
| Bio11         | Mean daily mean air temperatures of the coldest quarter  | 22.1                       | 26.9                     |
| Bio5          | Mean daily maximum air temperature of the warmest month  | 6.8                        | 16.5                     |
| Bio19         | Mean monthly precipitation amount of the coldest quarter | 2.1                        | 1                        |
| Bio7          | Annual range of air temperature                          | 0                          | 4.7                      |
| Bio8          | Mean daily mean air temperatures of the wettest quarter  | 0                          | 2.1                      |
| Bio10         | Mean daily mean air temperatures of the warmest quarter  | 0                          | 1.5                      |
| Bio1          | Mean annual air temperature                              | 0                          | 1.4                      |
| Bio9          | Mean daily mean air temperatures of the driest quarter   | 0                          | 1.1                      |
| Bio2          | Mean diurnal air temperature range                       | 0                          | 0.3                      |
| Bio12         | Annual precipitation amount                              | 0                          | 0.3                      |
| Bio15         | Precipitation seasonality                                | 0                          | 0.3                      |
| Bio3          | Isothermality                                            | 0                          | 0                        |
| Bio6          | Mean daily minimum air temperature of the coldest month  | 0                          | 0                        |
| Bio13         | Precipitation amount of the wettest month.               | 0                          | 0                        |
| Bio14         | Precipitation amount of the driest month                 | 0                          | 0                        |
| Bio16         | Mean monthly precipitation amount of the wettest quarter | 0                          | 0                        |
| Bio17         | Mean monthly precipitation amount of the driest quarter  | 0                          | 0                        |
| Bio18         | Mean monthly precipitation amount of the warmest quarter | 0                          | 0                        |

## Potential Distribution Under Current Climate Conditions

By performing a Maximum entropy species distribution model under near current climate conditions, I found that the model predicted an expansion in the range of *P. canaliculata* (Figure 4). The model predicted that under current climate conditions (averaged from 1981-2010), the suitable habitat for *P. canaliculata* has the capacity to expand to the San Clemente and Santa Catalina islands offshore of California (although these areas are shown to be low suitability for *P. canaliculata*), to more northern regions of California such as the San Pablo Bay Wildlife Area (low suitability), and to coastal areas between San Diego and Los Angeles such as Huntington Beach, Santa Ana, San Clemente, and Oceanside (these coastal regions have high suitability). Coastal regions between Oceanside and San Diego are expected to be suitable. *P. canaliculata* also has the capacity to expand to slightly more inland areas than their present distribution, such as inland of Los Angeles like the cities of West Covina, Pomona and Corona. *P. canaliculata* are also expected to expand more inland of the San Diego region. The raw map output of Maxent for the current climate is in the appendix (Appendix A).



**Figure 4. Predicted habitat distribution of *Pomacea canaliculata* in California under near current climate conditions.** Map was created using Maxent and ArcGIS Pro. High suitability is defined as 0.75 and above, suitable is between 0.5 and 0.75, low suitability is between 0.25 and 0.5, and unsuitable is 0.25 and below.

## **Predicted Distribution Under Future Climate Conditions**

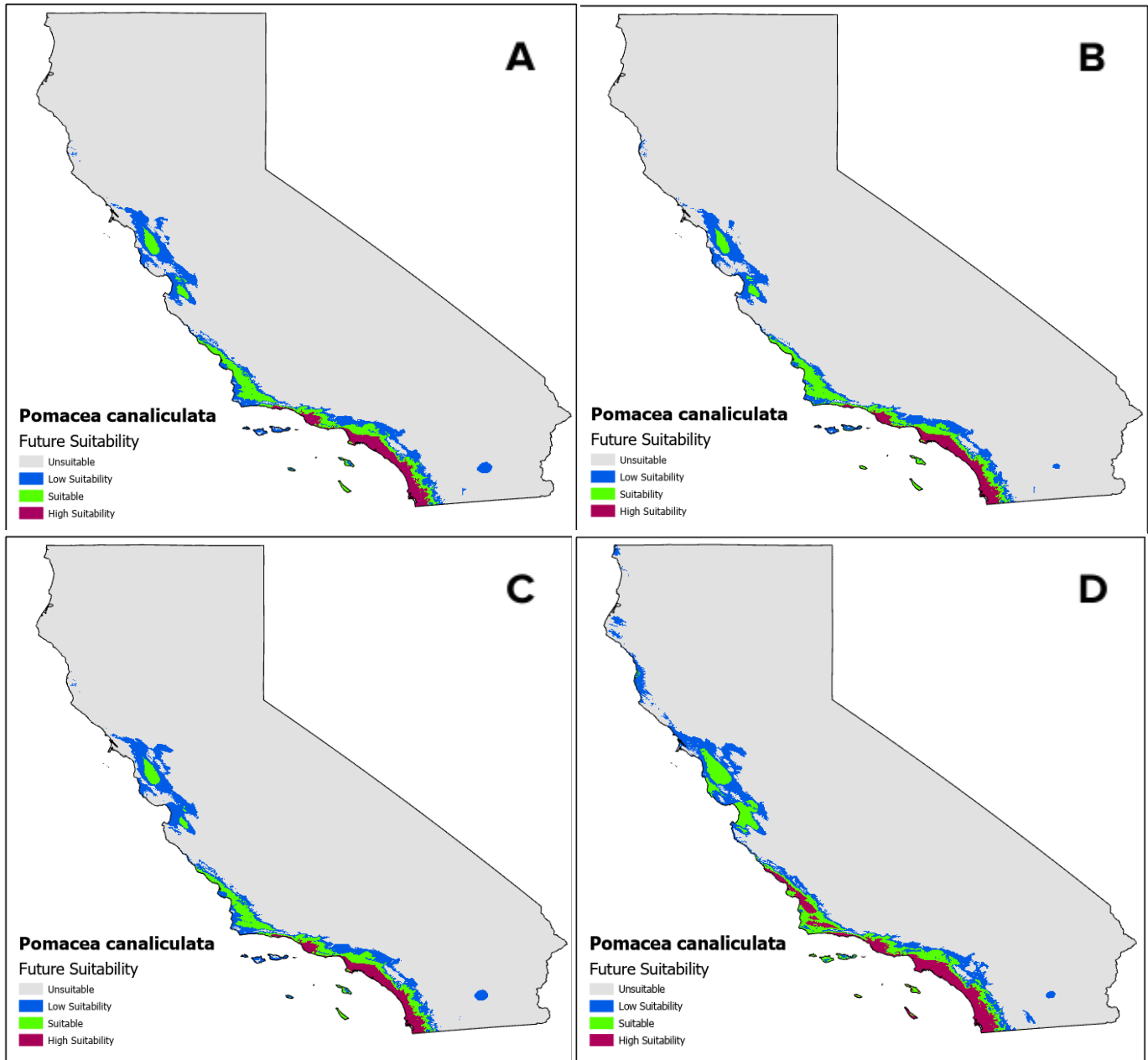
I found that under all future climate scenarios, the predicted suitable habitat for *P. canaliculata* would expand much greater than under current climate conditions averaged from 1981-2010 (Figure 4 and Figure 5). The raw map outputs from Maxent for all future climate change scenarios are in the appendix (Appendix A). The greatest expansion was shown under SSP5-8.5 in the time range of 2071-2100. This was much more than under SSP5-8.5 from 2041-2070, which predicted the least amount of predicted suitable area of all of the climate scenarios I analyzed (Figure 5).

The trends seen within these future climate change scenarios are similar to those seen under current climate conditions, just more exaggerated, with suitable conditions predicted to expand more northward, slightly more inland, and further along the coast between Square Black Rock and Tijuana River Valley Park (the lower half of California). All of the climate change scenarios have very similar predicted suitability maps when compared to each other, but differ in the suitability of the offshore islands, the area of low suitable habitat in coastal and inland northern California, the area of low suitable habitat in inland southern California, and the area of highly suitable habitat in southern California.

In SSP5-8.5 from 2041-2070, with the least predicted expansion, there is slightly less predicted suitable area than under SSP1-2.6 from 2041-2070. There is slightly less northward and inland predicted expansion in both the San Francisco Bay region and near Los Angeles. However, in both scenarios in the 2041-2070 time range, the offshore islands are predicted to be less suitable than under current climate, and the coast between Los Angeles and San Diego is predicted to be highly suitable.

In SSP5-8.5 from 2071-2100, with the greatest predicted expansion, all of the islands off of southern California are predicted to be suitable for *P. canaliculata*, with most having suitable habitat, and San Clemente island having both suitable and highly suitable areas. Coastal areas of high suitability are expected to expand under this climate scenario between Los Angeles and San Diego, and between Square Black Rock and Santa Barbara. Low suitability coastal areas are expected to expand northward, and suitable areas in the San Francisco Bay area region are expected to expand inland more so than any other climate scenario analyzed. Another area of great interest is the Salton Sea (roughly indicated in the bottom right of California in each

suitability map by a blue circle), which has low suitability for each climate scenario but has the greatest area under SSP1-2.6 from 2041-2070 and least under SSP5-8.5 from 2041-2070.



**Figure 5. Predicted future habitat suitability of *P. canaliculata*.** (A) predicted habitat suitability from 2041-2070 under SSP 1-2.6, (B) predicted habitat suitability from 2041-2070 under SSP 5-8.5, (C) predicted habitat suitability from 2071-2100 under SSP 1-2.6, (D) predicted habitat suitability from 2071-2100 under SSP5-8.5.

## DISCUSSION

Identifying areas of California that are susceptible to invasions by *P. canaliculata* and the factors that determine their spread is critical for preventing their spread and establishment in new areas. I found that the suitable habitat of *Pomacea canaliculata* is predicted to expand under all climate scenarios, both current and future, but is expected to expand the greatest under the most pessimistic climate change scenario, with the highest rate of greenhouse gas emissions, SSP5-8.5 from 2071-2100. The Maxent model identified three critical bioclimatic variables; temperature seasonality, mean daily mean air temperatures of the coldest quarter, and mean daily maximum air temperature of the warmest month, which is consistent with other similar habitat modeling studies of *P. canaliculata*. The findings of my study can be used to predict areas that are at risk of invasion by *P. canaliculata* in the present and the future under several different climate scenarios, and by extension, assist invasive species managers in preventing their spread.

### Contribution of Bioclimatic Variables

The analysis of variable contribution output from the Maxent modeling showed that temperature seasonality (bio 4), mean daily mean air temperatures of the coldest quarter (bio 11), and mean daily maximum air temperature of the warmest month (bio 5) were the variables that contributed most to the suitable habitat modeling of *P. canaliculata*, which suggests that temperature may affect the growth, survival, and reproduction of *P. canaliculata*. These results were expected because many previous studies on invasive *P. canaliculata* have shown that temperature is important for their distribution. A study that predicted the distribution of *P. canaliculata* under climate change regimes using Maxent in China, supports my findings by showing that maximum temperature in the coldest month was a critical climate variable to their model (Yin et al. 2022). This variable is slightly different from the mean daily mean air temperatures of the coldest quarter variable from my study, but comparable in that it involves the coldest air temperatures over the course of a year. My results are further supported by a study done by Matsukura et al. in 2009, which found that indirect chilling injury is a factor in the death of *P. canaliculata* at low temperatures (Matsukura et al. 2009). Temperature has proven to be one of the most important, if not the most important, biological factors limiting the spread of *P.*

*canaliculata* and other species of apple snails because it is a key determinant of their activity levels. Lower temperatures cause lowered activity levels (Bae et al. 2021, Heiler et al. 2008, Seuffert et al. 2010). For example, *P. canaliculata* at the southernmost extreme of its native range, in Argentina, has been shown to remain inactive for several months due to low winter temperatures, and low winter temperatures in southern Japan has shown to cause high winter mortality (Hayes et al. 2015). *P. canaliculata* are occasionally subject to temperatures near freezing in the southernmost limit of their native range but they cannot tolerate freezing. A Maxent study on *P. canaliculata* in Florida found that mean daily maximum air temperature of the warmest month (bio 5) was the most critical to their Maxent model, which supports my result of this variable being significant to the habitat distribution of *P. canaliculata* (Reilly 2017). This is logical because significantly warm temperatures (above 30°C) can also cause lowered activity levels and inhibit the viability and production of eggs in *P. canaliculata* (Seuffert et al. 2010, Seuffert and Martín 2017).

Other studies have found different critical variables for their *P. canaliculata* Maxent models besides the coldest and warmest temperatures. A study done by Yu et al. in 2018 on *P. canaliculata* in China, found that the influence of annual mean air temperature, average annual precipitation, and precipitation seasonality were the most critical in the model. Additionally, researchers in Florida showed that *P. canaliculata* is negatively correlated with annual precipitation, with this and the maximum temperature of the warmest month being the most critical to their species distribution model (Reilly 2017). These differences in critical variables between other studies and my own may be due to the difference in study locations and the associated differences in climate, with California being about 6 °C cooler than Florida on average and about 10 °C warmer than China on average, and each location having distinct temperature and precipitation patterns throughout the year (NOAA 2022). In addition, many of these studies used bioclimatic variables from the WorldClim website, while I used data from the CHELSA website. Both sources have the same 19 bioclimatic variables but source their climate change data from different scientific papers, which may have caused differences in the variable data and thus variable importance (Eyring et al. 2016, Karger et al. 2017). Temperature, precipitation, and other climate variables may be helpful in determining areas at risk of *P. canaliculata* invasion; this information can be used for managing their distribution.



## **Predicted Distribution Under Current Conditions**

My study shows that the current distribution of *P. canaliculata* is predicted to expand under current climatic conditions, which suggests that *P. canaliculata* has the capacity to invade new areas of California which currently contain suitable habitats but have yet to be invaded. *P. canaliculata* may spread to new suitable areas within California via many methods including release by aquarium owners, movement across land, floating in water currents and floods, crawling upstream, the accidental movement by people through agricultural goods, and even traveling by being attached to birds (CDFW 2022). *P. canaliculata* has been shown to tolerate temperatures of 13-37°C, and many areas of California experience these temperatures nearly year round (Reilly 2017). The winter season in California averages 10°C across the state, and *P. canaliculata* can go dormant at temperatures between 10-17.5°C (Estebenet and Martin 2002), but this is still above the limit that *P. canaliculata* can survive, which is at or below freezing or 0°C (NOAA 2022; Hayes et al. 2015; Matsukura et al. 2009; Reilly 2017). Many existing studies show similar results in the areas of study having suitable areas which have yet to be invaded. In Argentina, many regions that have yet to be colonized, are suitable for the establishment of *P. canaliculata* and thus it is likely that this species will continue to establish new populations and spread to these suitable areas (Seuffert and Martín 2017). Further, *P. canaliculata*'s invasive range throughout Asia is continuing to expand, causing concern for damage to invaded wetland agricultural systems and many scientists warn that their capacity for causing damage should not be underestimated (Brito and Joshi 2016). *P. canaliculata*, even before the future effects of climate change, has the capacity to expand in range within California, which is important for invasive species managers to consider.

## **Future Predicted Distribution Under Climate Change Scenarios**

Maxent modeling predicts that the distribution of suitable habitat for *P. canaliculata* is expected to expand greatly under future climate change scenarios, showing that climate change will assist in their expansion to new areas by shifting currently non-suitable areas to suitable areas in the future through changes in temperature, precipitation, and other climatic factors. This is consistent with the results of studies that focus on the global effects of climate change, which

predict that the environmental changes that accompany climate change such as increases in temperature and changes in precipitation will allow many terrestrial and freshwater species (not including coldwater) to expand northward and more inland (Mainka and Howard 2010; Rahel and Olden 2008). Climate change is predicted to increase the likelihood of invasive species becoming established, by eliminating cold temperatures and subsequent winter hypoxia that currently serve to prevent their survival (Rahel and Olden 2008). The results of my study are supported by many others that have modeled the habitat suitability of *P. canaliculata* under the influence of climate change, in areas where they are considered invasive. In the Patagonia region of South America, climate change driven increases in precipitation give *P. canaliculata* a high probability of expanding their range in Patagonia by invading into northern Patagonia (Darrigran et al. 2011). Similarly, in China with climate change, there is expected to be a trend of expansion and northward movement of *P. canaliculata* in the future (Yin et al. 2022). One study analyzed the worldwide invasion of *P. canaliculata* and found that climate change in the future may promote its global invasion (Lei et al. 2017). The expansion of *P. canaliculata* under climate change may increase damages on local environments and native species.

Maxent produced surprising results for the climate change scenarios under the first time range, from 2041-2070. My hypothesis was that the scenario with the least predicted greenhouse gas emissions, SSP1-2.6, would have the least predicted overall suitable area in California for *P. canaliculata*, under all time ranges because it has a lower predicted temperature increase than under SSP5-8.5. This hypothesis was supported for the later time range of 2071-2100, but it was not supported for the first time range of 2041-2070 because the scenario with the highest predicted greenhouse gas emissions, SSP5-8.5 seemed to have the least amount of predicted suitable area. This result is surprising because it is not seen in any other studies that used Maxent or other species distribution modeling software to predict suitable habitat for *P. canaliculata* under future climate change conditions (Lei et al. 2017; Yin et al. 2022; Yu et al. 2018). However, SSP1-2.6 seems to only have a higher amount of low suitable area, while SSP5-8.5 from 2041-2070 seems to have the most moderately suitable area. Similar results were found in Lei et al. 2017, in which their SSP1-2.6 and SSP5-8.5 scenarios in the 2050s only visually differed by the amount of suitable habitat that could be gained, with more suitable habitat expected to be gained under SSP5-8.5, while the stable suitable habitats and suitable habitat loss visually have approximately the same area in both scenarios (Lei et al. 2017). Additionally, my

visual analysis is most likely subject to mistakes since the differences between the scenarios are slight and difficult to discern with the naked eye. I suspect that the differences between the overall suitable land area under SSP1-2.6 and SSP5-8.5 from 2041-2070 are so slight that using my visual analysis approach was not enough to determine the subtle differences between their suitable areas accurately. A more in depth analysis, by calculating the suitable areas of each suitability category for each scenario, would most likely provide clarification on the differences between the climate change scenarios in the time range between 2041-2070.

### **Predicted Distribution Under Current and Future Climate Scenarios**

The distribution of *Pomacea canaliculata* is predicted to expand under all climate scenarios, both current and future, but is expected to expand most under the climate change scenario with the highest predicted greenhouse gas increases. Shared socioeconomic pathway (SSP) 5-8.5 is expected to have the highest greenhouse gas emissions and subsequently the highest increase in global temperatures, with temperatures expected to rise by 4.4°C by 2100 (Masson-Delmotte et al. 2021) and carbon dioxide concentrations in the atmosphere are expected to reach 1135.2 parts per million, which is almost three times the current atmospheric concentration of 419 ppm (Meinshausen et al. 2020). Climate change is expected to change the ecological impacts of invasive species on their invaded environments by enhancing their competitive and predatory effects on native species (Rahel and Olden 2008). These and other impacts will increase in intensity as climate change alters temperature and precipitation regimes worldwide, with the most pessimistic climate change scenarios (such as SSP5-8.5) having the most impacts from invasive species. Thus, the most effective way to slow down the expansion of *P. canaliculata* in California, and worldwide, would be for the world to follow the two lowest SSP paths with the lowest predicted greenhouse gas emissions and lowest global temperature increases, SSP1 or SSP 2 (Yin et al. 2022).

On smaller scales, invasive populations of *P. canaliculata* in California can be managed by using tactics proven to be effective in controlling their populations in agricultural areas, such as hand-picking and removing eggs and adult snails. This tactic is improved by attracting *P. canaliculata* with jackfruit skin, tapioca leaf, or spinach (Salleh et al. 2012). Other tactics include lowering the water level below the height of the snails' shells, using tobacco waste, and using

ducks as biological controls (Salleh et al. 2012). Many managers use chemical controls such as molluscicides as a last resort due to their unintended effects on local mollusks, but this tactic is useful and effective in low doses when necessary (Litsinger and Estano 1993).

### **Limitations and Future Directions**

My study has a few limitations that may affect the accuracy of its results, with most arising from the use of Maxent. Maxent has the possibility of over-fitting, which limits the capacity of the model to generalize well to independent data; however the “regularization multiplier” parameter within the program addresses this by generating a less localized prediction of species distribution (Phillips and Dudík 2008). I used a higher regularization multiplier than the default to address this. Maxent may also underestimate the probability of a species’ occurrence within areas of observed presence, while overestimating it in areas beyond their known extent (Gomes et al. 2018). Additionally, similar to other species distribution models, Maxent has the assumption that the presence-data are an independent sample from the species’ unknown probability distribution of occurrence over the study area. This assumption is most likely not met in my study due to the sampling bias introduced by my data sourcing from citizen scientists on the iNaturalist website taking photos and identifying *P. canaliculata* in areas easily accessible to people, such as parks, recreational areas, and regions near cities and densely populated regions. There are also the assumptions of niche stability and the study species being at equilibrium, which are commonly violated when modeling invasive species because they are not at equilibrium with their invaded environment (Gallien et al. 2012).

There are also limitations that arise from my choice to use species occurrence data from iNaturalist. There were several observations from the exact same coordinates, which I chose to delete, and these duplicates lowered the amount of data I was able to use within my model. iNaturalist compiles photos and associated species identifications from citizen scientists, who may incorrectly identify the species or possibly take photographs and identify the same snail or clutch of eggs as someone that has already entered it into the database, which may overestimate the number of *P. canaliculata* in an area. Additionally, many photograph observations that I analyzed were of the egg clutches of *P. canaliculata*, not the snails themselves, which may overestimate the number of snails in the area since these are large and bright pink in color,

probably attracting the attention of many people walking past the area, and each snail lays several hundred eggs every few weeks.

There are many possible future studies that can be done to expand the research done on *P. canaliculata* invasions and their impacts. Specifically, the results of my study would benefit from corroboration, in which other researchers could repeat my study several times in the future, in order to track the snails' current distribution and expansion and keep up with the most accurate and current climate change modeling. Additionally, comparing the expansion possibility of *P. canaliculata* in several different areas would prove to be informative studies; such as comparing the snails' distributions in Hawaii, California, Florida, China, Argentina, and other areas where they are invasive. Comparing their distributions in different areas across the world could provide more insight into their habitat preferences and the biological variables which are critical to their survival. Another important study would be to compare the success of management strategies used by each different area which has invasive *P. canaliculata*, which could help inform the best methods of managing their expansion.

### **Broader Implications**

My study may assist in informing invasive species managers by drawing attention to the areas of California which are at high risk of invasion by *P. canaliculata* under the current climate and under future predicted climate change scenarios. My study indicates that *P. canaliculata* may expand into more northward and inland regions of California under all of the climate scenarios I studied, and most profoundly under the most severe scenario of climate change in the latest time range. The areas at risk, especially areas shown in my results to have highly suitable habitat for *P. canaliculata*, could be carefully observed and management policies could be implemented to prevent the snails' spread into these areas.

Additionally, the results of this study further support the overarching theory that environmental changes, such as increases in precipitation and temperature brought about by climate change, will increase the range of many invasive species. This corroborates many researchers' and scientists' views that the most efficient method in controlling the expansion of invasive species is following a less severe climate path with less greenhouse gas emissions and more sustainable practices.

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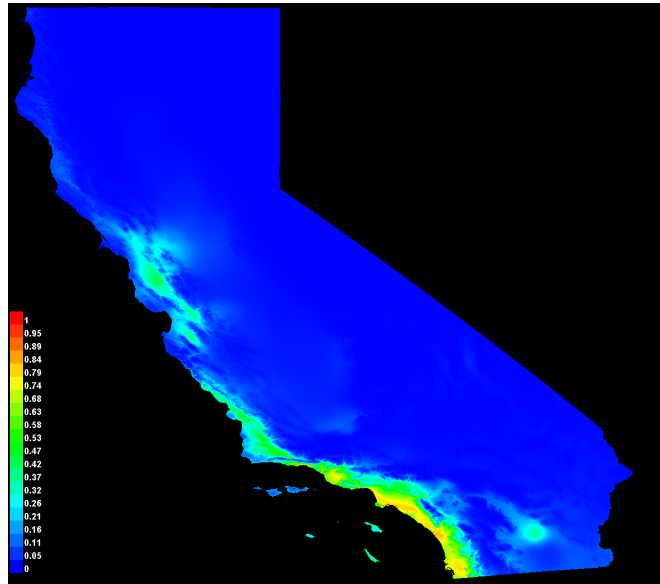
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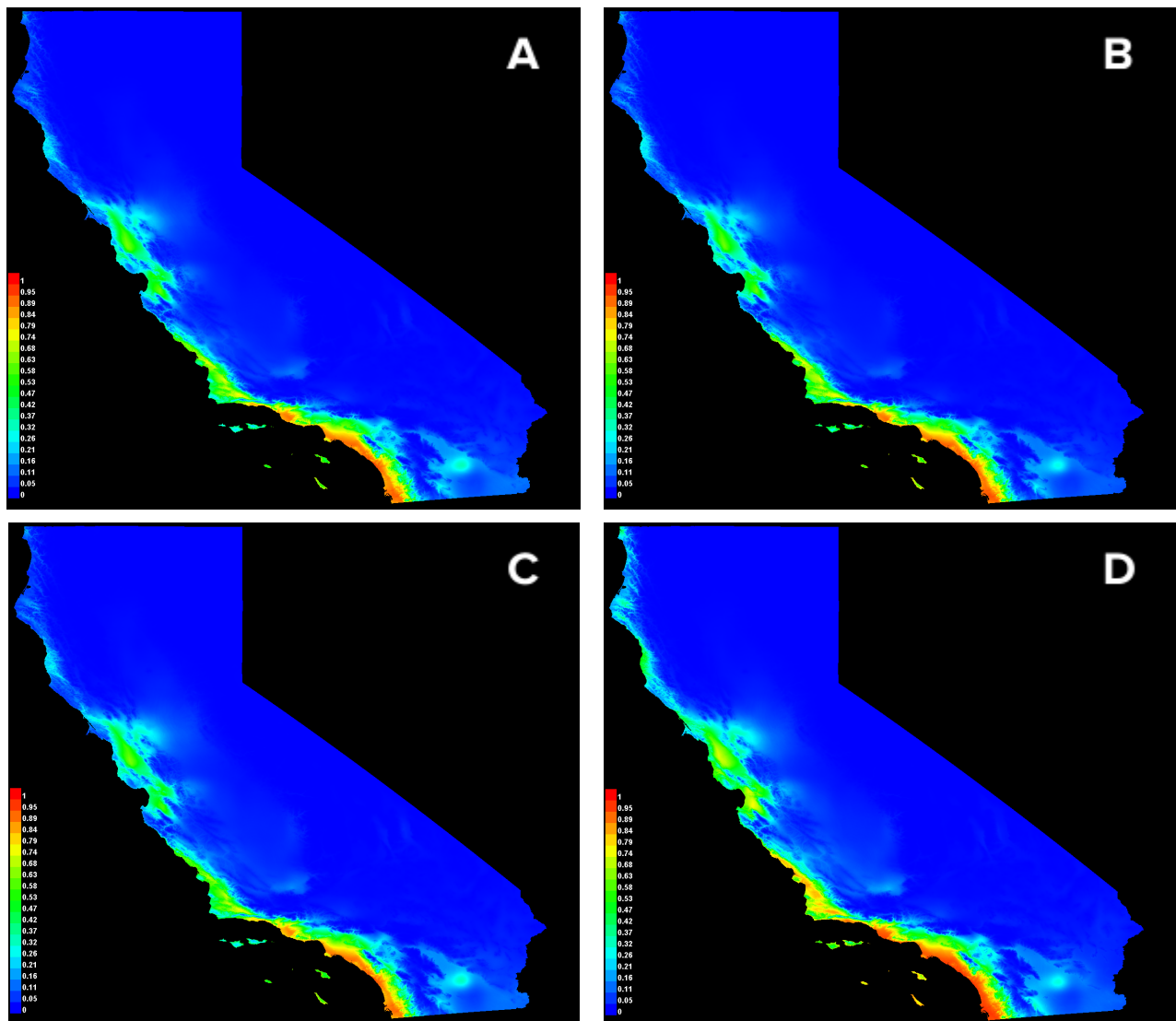
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**APPENDIX A: Maxent Raw Maps and Settings**

**Figure A1. Raw map output of Maxent for current climate.** Climate data averaged from 1981-2100.

**Table A1. Maxent settings used for the model.** Using Maxent version 3.4.4.

| Setting Label                                | Value or Setting Used |
|----------------------------------------------|-----------------------|
| Number of Occurrence Points Used for Testing | 25%                   |
| Adjust Sample Radius                         | -7                    |
| Regularization Multiplier                    | 25                    |
| Remove Duplicates                            | No                    |
| Output Format                                | Logistic              |
| Create Jackknife Tests                       | Yes                   |



**Figure A2.** Raw map output of Maxent for future climate scenarios. (A) SSP1-2.6 from 2041-2070, (B) SSP5-8.5 from 2041-2070, (C) SSP1-2.6 from 2071-2100, and (D) SSP5-8.5 from 2071-2100.

### APPENDIX B: Jackknife Tests

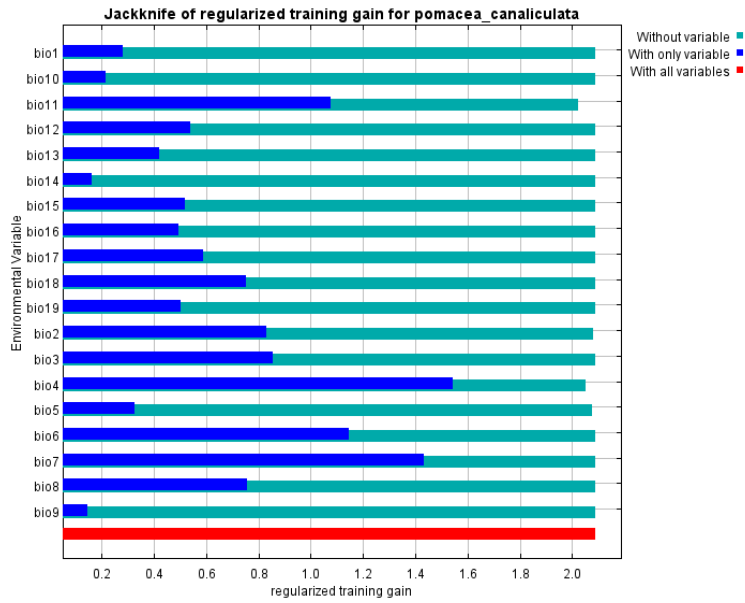


Figure B1. Jackknife test of regularized training gain for all climate models. Produced by Maxent.

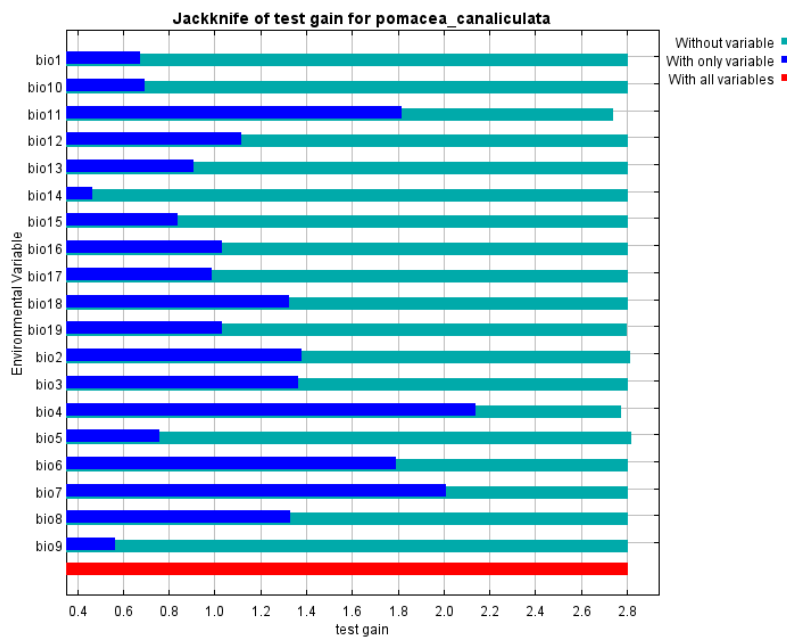


Figure B2. Jackknife test of test gain for all climate models. Produced by Maxent.

### APPENDIX C: AUC Graph

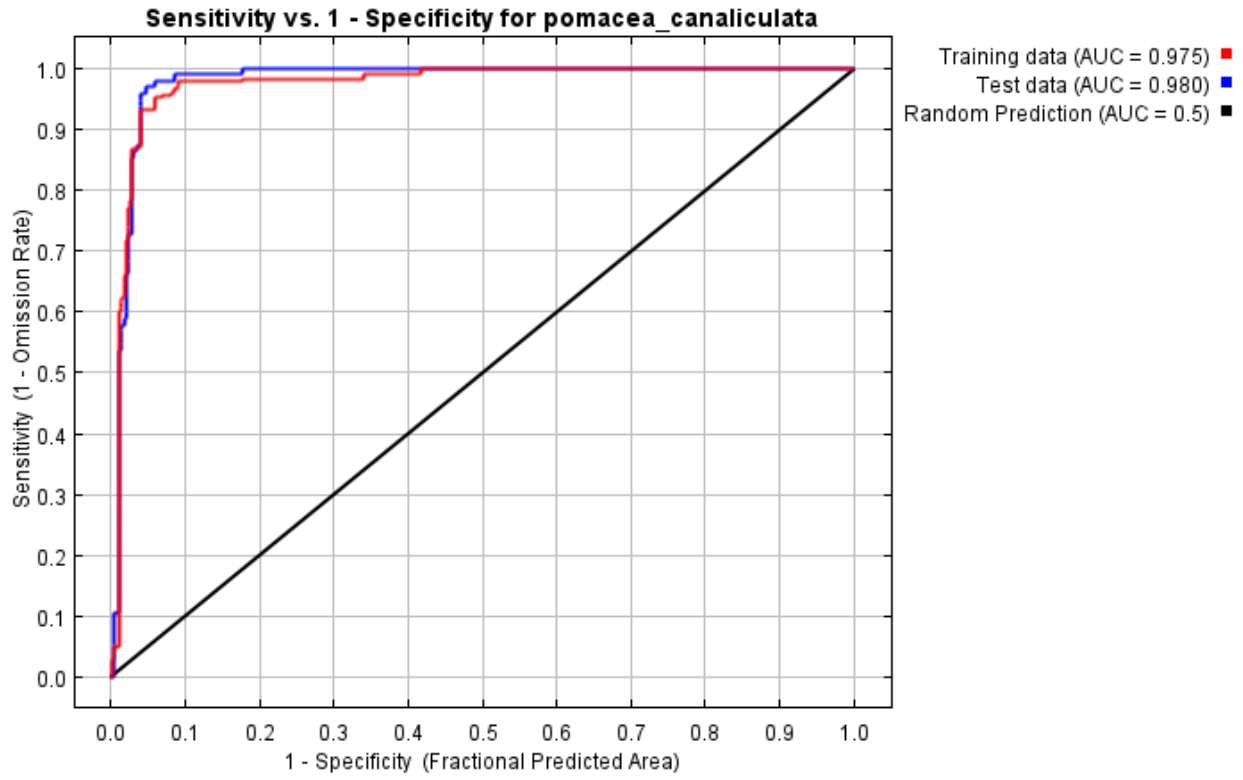


Figure C1. AUC graph for all climate models. Produced by Maxent version 3.4.4.