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Projecting the Impacts of Climate Change on Species Occupying Aquatic Habitats in Southern California

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**Publication Date**

2019

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Los Angeles

# Projecting the Impacts of Climate Change on Species Occupying Aquatic Habitats in Southern California

A dissertation submitted in partial satisfaction of the requirements for the degree

Doctor of Environmental Science and Engineering

by

Jennifer Beth Taylor

2019

# ABSTRACT OF THE DISSERTATION

# Projecting the Impacts of Climate Change on Species Occupying Aquatic Habitats in Southern California

by

Jennifer Beth Taylor

Doctor of Environmental Science and Engineering

University of California, Los Angeles, 2019

Professor Richard F Ambrose, Chair

Climate change will impact aquatic habitats in southern California through novel precipitation and temperature regimes, as well as higher sea levels. The dense urbanization of southern California has already drastically reduced the extent of these habitats through land conversion to hardscapes and harbors, which makes them more vulnerable to changing conditions. These aquatic habitats support several native species listed under the federal and/or state Endangered Species Acts, which means management of these habitats for species protection is not simply a moral or environmental issue, but an issue with legal and economic implications. In this research we evaluate the impacts of climate change on riparian and coastal salt marshes and the species that depend on those habitats. Species occurrence data is combined with hydrology, temperature, water level, and precipitation data to model species distributions. We use projections from climate models to predict future stream conditions, which are used in the species distribution models to predict changing habitat suitability with climate change. We project that streams in the region will become hotter by an average of 3°C, with more intense warming occurring in high elevation streams. We also project that streamflow conditions will become more extreme with approximately one additional storm each year, a larger magnitude of high flow, and an increased duration of dry- or low-flow conditions. We project that riparian species in high elevations will lose suitable habitat due to temperature increases, but that species in low elevations will gain suitable habitat driven by both streamflow and temperature. We find that an endangered salt marsh bird has habitat associations which may make it particularly vulnerable to climate change. First, it uses the entire marsh, which suggests that the rapid loss of upper marsh habitat projected due to sea level rise, could exacerbate conditions for the bird despite nesting in the low marsh. Second, breeding population is generally negatively associated with high streamflows, suggesting that additional storms from the watershed could decrease breeding pairs. This research can be used in climate change planning to prioritize vulnerable habitats and species for additional protection, restoration, and/or monitoring efforts.

The dissertation of Jennifer Beth Taylor is approved.

Mark Andrew Gold

Thomas Welch Gillespie

Dennis P Lettenmaier

Eric D Stein

Richard F Ambrose, Committee Chair

University of California, Los Angeles

2019

I dedicate this dissertation to:

my mom, Anita, for her work in industrial hygiene,

my dad, Marc, for teaching me about environmentalism,

my nana Esther and Big Al for their never-ending support, and

to Ben, for your encouragement and love.

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Chapters two through four (the three core chapters) in this dissertation are a version of co-authored manuscripts that are currently in preparation for submission to peer reviewed journals.

Chapter 2: Taylor, Jennifer B., Stein, Eric D., Beck, Marcus, Flint, Kelly, Ambrose, Richard F. (In Prep). Modeling future changes to the hydrological and thermal regime of unaltered streams in southern California due to projected changes in climate.

Chapter 3: Taylor, Jennifer B., Stein, Eric D., Beck, Marcus, Ambrose, Richard F. (In Prep). Modeling the impact of climate change modeled alterations of streamflow and stream temperature on the distribution of riparian species in southern California.

Chapter 4: Taylor, Jennifer B., Stein, Eric D., Ambrose, Richard F. (In Prep). Light-footed Ridgway's rail nesting habitat and the relationship of streamflow, precipitation, and marine water level on the number of annual breeding pairs.

Chapters 2 and 3 were funded by the Los Angeles Regional Water Quality Control Board, Region 4. Chapter 4 was partially funded by the National Oceanic and Atmospheric Association (NOAA) Ecological Effects of Sea Level Rise program. The PI's of these three projects were Eric Stein and Richard Ambrose. The co-authors on these three papers assisted with research direction and different parts of the modeling tasks. My portion of the work included data collection and compilation, model development, and manuscript writing. In each chapter, I acknowledge the individuals who contributed to that manuscript. In this section I want to thank the people who contributed above and beyond to my dissertation as a whole.

I first want to thank my advisor Dr. Richard Ambrose and my supervisor Dr. Eric Stein for their willingness to work with me as a student and dedicate a large portion of their time toward helping me develop research and science communication skills. I am a better scientist thanks to the countless conversations with them about creative ways to approach problems, their incredible attention to detail with method development and data analysis, and their infinite reminders of the need to consider application of findings beyond not only the field of study to the broader scientific context, but also beyond the world of scientific research and into the realms of management, policy, and governance.

I next want to thank Dr. Marcus Beck, Dick Zembal and Carolyn Lieberman for the incredible amount of time they spent helping me with different aspects of this work. Marcus not only helped with the many modeling tasks that this research entailed, but he helped me develop my own interest in data science and contributed greatly toward my becoming proficient in data management, analysis, and visualization. My first two chapters would not have been nearly as thorough without Marcus's contributions. Dick not only spent many hours with me in the field, but he was incredibly generous in his willingness to teach me about salt marsh ecology, nest searching methods, and Light-footed Ridgway's rails. He also allowed us to use many years of his data on Light-footed Ridgway's rail breeding data. For his generosity and time, I am grateful. Finally, Carolyn Lieberman similarly donated multiple early mornings in the field with me to collect data. She not only made the work fun, but without her expertise in surveying I would not have been able to collect the data that we needed. My third chapter would not have been possible without Dick or Carolyn.

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### Publications

Taylor, J. B., Stein, E. D., Beck, M., Flint, K. & Ambrose, R. F. (In preparation). Modeling future changes to the hydrological and thermal regime of unaltered streams in southern California due to projected changes in climate.

Taylor, J. B., Stein, E. D., Beck, M., & Ambrose, R. F. (In preparation). Modeling the impact of climate change modeled alterations of streamflow and stream temperature on the distribution of riparian species in southern California.

Taylor, J. B., Stein, E. D., & Ambrose, R. F. (In preparation). Light-footed Ridgway's rail nesting habitat and the relationship of streamflow, precipitation, and marine water level on the number of annual breeding pairs.

### Presentations

Rising sea levels and habitat suitability for the Ridgway's rail and Belding's Savannah sparrow in southern California coastal salt marshes. Coastal Wetland Workshop. University of California, Los Angeles, 2019.

The impact of climate change on the distribution of riparian and riverine species in southern California. Biology Department seminar. California State University, Los Angeles, 2019.

Managing streamflow to support aquatic species in consideration of climate change and new water management practices. State of the Los Angeles River Watershed Symposium. Los Angeles, CA, poster, 2018.

Feeling the squeeze: A GIS analysis of southern California rocky intertidal habitats. University of California, Los Angeles Institute of the Environment and Sustainability Annual Gala, poster, 2017.

Can the anthropogenic addition of sediment help coastal wetlands survive sea level rise? University of California, Los Angeles Earth Now: Earth 2050, poster, 2016.

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# Chapter 1 Introduction to streams and salt marshes in southern California

Global climate change will impact ecosystems across the world. Sensitive habitats, due to their rarity or vulnerability, may require management intervention to increase their resiliency toward new conditions. As an example, suitable habitat zones for a particular species may shift to higher elevations in response to warming temperatures (Benito et al., 2011; Domisch et al., 2011), but if anthropogenic or natural barriers prevent shifting, the habitat extent decreases and the species becomes more vulnerable. Riparian zones and coastal salt marshes are two habitats which are especially vulnerable to climate change because of habitat loss and fragmentation from anthropogenic developments (Faber et al., 1989; Stein et al., 2014), and because they are maintained by processes that are predicted to change, such as temperature, precipitation, and sea level. Resource and wildlife agencies already engage in management of these habitats, which support threatened and endangered species, but changing climate conditions will necessitate innovative approaches. This dissertation explores the relationships between climate and species habitat suitability and develops projections about the impact of climate change on species occupying different niches in aquatic habitats.

Southern California is one of five Mediterranean climate zones around the world where species throughout the watershed, headwaters to estuary, endure rather extreme conditions. Characteristic of Mediterranean climates, annual rainfall in southern California is episodic and mostly occurs in just a few storms during the winter months, which are followed by dry summers (Zedler, 1982). Total streamflow can vary drastically from year to year and the timing of high- and low-flows are consistent with the annual patterns of precipitation (Gasith & Resh, 1999).

Streamflow serves many functions that support wildlife habitat, such as geomorphic forcing and hydraulic habitat maintenance through sediment mobilization and deposition, and vegetation scour or seedling recruitment through floodplain wetting. Another function of streamflow is supporting and cuing life history phases of riparian and riverine species, such as spawning and migration, triggered by events such as the timing or magnitude of a peak flow (e.g. Poff et al., 1997; Yarnell et al., 2015).

Streamflow also impacts the estuary and salt marsh at the base of the watershed. Large precipitation events and associated flood flows have a large impact on the salt marsh despite their rarity (Zedler, 1982). Annual sediment discharge from rivers varies considerably, but most sediment is delivered during a few intense storms (Warrick & Farnsworth, 2009). Salt marsh habitat is impacted from the marine front as well as the watershed front. Inundation by tides, from twice daily to just a few times a year depending on elevation, creates a continuum of habitat including deep and shallow subtidal, mudflat, salt marsh, and upland/riparian. The frequency of inundation within the salt marsh drives the vegetation composition. Coastal salt marsh elevation is maintained by transgression inland with rising sea levels, accretion of organic matter through vegetative root growth (Nyman et al., 2006; Kirwan & Guntenspergen, 2012), accretion of inorganic sediment from ocean tides and waves (Reed, 1989; Stoddart et al., 1989; Rosencranz et al., 2016), and accretion of inorganic sediment delivered from fluvial sources.

Anthropogenic activity has resulted in differing levels of habitat change from the headwaters in the coastal mountains to the estuary by the Pacific Ocean. The headwaters and small tributaries in the mountains are in a mostly natural state, which changes as the stream enters the valley floor. At this transition, the channel is converted from a natural stream to an engineering conduit managed for resource extraction, flood control, urbanization, agriculture, and flood/debris control (Mount, 1995). In many estuaries the stream is naturally disconnected from the ocean by a sand bar for much of the year except during high tides or high streamflows. Construction activities have further decreased the tidal prism by adding in aggregate materials for roads or other infrastructure, and concrete channeling. In other locations, the estuary is surrounded by a coastal salt marsh. Most coastal salt marshes in southern CA, like the urbanized streams, are walled in on all sides by infrastructure, homes, and general city living. Marsh transgression is largely stifled due to the urbanization surrounding the marsh boundaries, in addition to steep upland terrain in many locations (Thorne et al., 2018). Accretion of inorganic sediments in many marshes is also largely disrupted: Approximately 80% of sediment flux to the Southern California Bight comes from rivers, which are largely dammed, followed by coastal bluff/cliff erosion, which are often armored, atmospheric sources, and anthropogenic dumping and discharges (Warrick & Farnsworth, 2009). Due to the dominance of fluvial sediment inputs for salt marshes, disruptions to river systems such as dams, rerouting, channelizing, and land use change can have massive impacts on the sediment budget. In some cases, such as the Seal Beach National Wildlife Refuge, the removal of fluvial inputs, in addition to other factors, has resulted in a sediment deficit (Rosencranz et al., 2016). In other cases, such as the Tijuana River National Estuarine Research Reserve, poorly planned developments in the watershed has resulted in a massive sediment surplus (Taniguchi et al., 2019). In either case, rivers are large drivers of salt marsh elevation stability and channel or watershed modification is impactful.

From headwaters to coast, watersheds in southern California exist on a spectrum of engineering ingenuity, but all stream reaches succeed in supporting wildlife and providing city dwellers a taste of nature. Species inhabiting riparian and riverine areas in Mediterranean climate zones are exposed to the seasonal cycles of flooding and drying (Gasith & Resh, 1999), and have adaptions which allow them to persist, either by their ability to find refuges when needed (Robson et al., 2013) or because the individual or the community displays resistance or resilience to the disturbance (Hershkovitz & Gasith, 2013). For example, there is evidence that fish native to regions with seasonal flooding are tolerant of the disturbance (Lafferty et al., 1999) and better able to survive than similar fishes from regions without flashy seasonal floods (Greenfield et al., 1970; Castleberry & Cech, 1986). The ability to survive in flashy streams also gives native species an advantage over nonnative species, unaccustomed to the large seasonal swings, which might otherwise outcompete them (Meffe, 1984) or predate them (Miller et al., 2012).

In response to the degradation and fragmentation of riparian habitat (and other stressors like invasive species or water quality), wildlife are listed as threatened, endangered, or sensitive in a variety of niches throughout the watershed: cold water fishes and amphibians in the mountains (e.g. Santa Ana speckled dace (*Rhinichthys osculus* ssp.) and southern mountain yellow-legged frog (*Rana muscosa*)), warm water fishes, amphibians, and riparian birds in river valleys (e.g. unarmored threespine stickleback (*Gasterosteus actileatus williamsoni*), arroyo toad (*Anaxyrus californicus*), and least Bell's vireo (*Vireo bellii pusillus*)), anadromous fishes that require connectivity of the entire watershed (e.g. southern California steelhead (*Oncorhynchus mykiss irideus*) and Pacific lamprey (*Entosphenus tridentatus*)), salt marsh birds (e.g. light-footed Ridgway's rail (*Rallus obsoletus levipes*)), and estuarine fishes (e.g. tidewater goby (*Eucyclogobius newberryi*)). It is estimated that 95-97% of riparian areas have been eliminated in southern California (Faber et al., 1989). Similarly, estuaries have been converted to marinas by dredging and urban land by filling, and remaining natural land is often harmed by recreational use (Zedler, 1982). Since 1850 there has been a 75% reduction in salt marsh habitat (Stein et al., 2014).

Throughout the watershed climate change will pose an additional threat from rising sea level, increasing air temperature and changing precipitation regime which drives streamflow. These three forces, marine, climatic, and watershed, can impact estuarine and riparian habitats in many ways. Sea level rising at a more rapid rate, driven by melting glaciers, melting ice caps, and thermal expansion (IPCC, 2014), that surpasses the marsh accretion rate, will convert lower marsh zones to subtidal habitats and upper marsh zones to lower marsh zones. In addition to driving sea level rise on the coast, higher air temperature will increase stream temperature and evaporative losses from streamflow. Precipitation changes alter the streamflow regime which can drive geomorphic changes in the river and salt marsh. Precipitation can also alter the salinity dynamics of the salt marsh (Noe & Zedler, 2001).

This dissertation explores the relationship between habitat characteristics and the distribution of species in riverine, riparian, and salt marsh habitat in southern California. Using global climate model (GCM) projections, species – habitat relationships are used to make projections about species vulnerability to climate change. Chapter 2 starts by quantifying riparian and riverine habitat characteristics and projecting future changes using data from locally downscaled climate models. Habitat characteristics include streamflow and stream temperature metrics, which we model using precipitation and air temperature predictions, respectively. Chapter 3 explores the impact of projected riparian and riverine changes on native species, which are designated as sensitive, threatened, or endangered, that occupy unique habitat niches in the watershed. We focus on six species that occupy cool high elevation streams, mid elevation streams, warm low elevation streams, quiet edgewater pools, dense scrubby riparian vegetation, and slow streams with deep pools – habitats that occur in southern California and may be impacted differently by climate change. Chapter 4 explores the salt marsh, at the base of the watershed, and investigates the association between salt marsh characteristics, climate, and water level, and an endangered salt marsh resident bird.  Chapter 5 concludes by discussing the vulnerability of southern California aquatic wildlife, the role of environmental and wildlife management, and modeling innovations for future studies.

# Chapter 2 Modeling future changes to the hydrological and thermal regime of unaltered streams in southern California due to projected changes in climate

## *Abstract*

Stream habitats have been degraded or destroyed worldwide due to anthropogenic modifications for flood control, water resources, and/or land use. Climate change will further alter stream habitats through precipitation and air temperature changes. Species that occupy stream habitats are often sensitive to streamflow and stream temperature, which drives the need for stream habitat projections to inform wildlife management. In this study, we project the change in streamflow and stream temperature characteristics for six watersheds in southern California from baseline (2010) to future year 2100 using projections from three global climate models (GCMs). Unlike other studies that focus on regional trends, we model stream habitat at the National Hydrography Dataset (NHD) reach scale to provide a detailed map of projected change. Stream temperature is projected to increase in all the stream reaches that we modeled across the three GCMs. The projected average increase in rolling 7-day mean, maximum, and minimum temperature is 3.13°C, 2.59°C, and 2.73°C, respectively, across all the stream reaches by year 2100, under the business as usual scenario for carbon emissions RCP 8.5. The highest elevation sub-watersheds are projected to have the largest relative increase in stream temperature. There is more disagreement between the three GCM's streamflow projections, but in general there is a trend toward more extreme hydrology. Most streams are projected to have larger high flow magnitudes and more storm events. However, streams are projected to be more uniform in their low- and no-flow periods, i.e. perennial and ephemeral streams trend toward intermittent stream types. Overall, we project most streams will become drier for a greater portion of the year, despite the additional storms. With regional mapping of future streamflow and stream temperatures, species and habitat conservation measures can be spatially prioritized in regions that remain suitable, or restoration can be planned in areas that decrease in suitability for target species.

## *Keywords*

Climate change, riparian habitat, ecohydrology, stream temperature modeling, hydrologic modeling, conservation planning

## *Web supplemental data*

The results of the hydrologic and stream temperature modeling are available for viewing and download at https://sccwrp.shinyapps.io/flowecology/

## *Acknowledgements*

I thank the Los Angeles Regional Water Quality Control Board, Region Four, for funding this project. I thank Alex Hall, Jerry H-Y. Huang, and Neil Berg, at the University of California, Los Angeles, for letting us use their downscaled air temperature and precipitation global climate model output for baseline conditions and future projections. I am very grateful for Kelly Flint and Marcus Beck for contributing to different modeling tasks in this study.

## *Introduction*

Ecologically relevant streamflow and temperature regimes support biological communities. Important characteristics of a streamflow regime include flow variability, the timing, magnitude, frequency, and duration of events (Poff et al., 1997), and in many cases, deviation from ‘reference’ conditions (Carlisle et al., 2017). Certain characteristics of streamflow are critical for sustaining a population (Yarnell et al., 2015), such as flows that breach an estuary for anadromous fish. Ecohydrological relationships have been described for many species including fish (Poff & Allan, 1995; Patterson et al., 2017), birds (Sidle et al., 1992), amphibians (Kupferberg, 1995), and vegetation (Mahoney & Rood, 1998; Stromberg et al., 2007). Important characteristics of a stream temperature regime often includes the magnitude and duration of maximum and minimum temperatures. The importance of maximum stream temperatures has been demonstrated for riverine fishes (e.g. Matthews & Berg, 1997; Sloat & Osterback, 2013; Wenger et al., 2011). Streamflow and temperature needs depend on an organism's life history and environmental niche.

Disruption of these regimes can be detrimental to riparian and riverine species. Climate change will alter streamflow and stream temperature regimes through new precipitation and air temperature patterns in different ways across the landscape. Climate models project increases in air temperature of 2-5°C (Cayan et al., 2012) and more intense and frequent extreme precipitation events (Polade et al., 2017; Gershunov et al., 2019).

Wildlife conservation requires an understanding of the habitat that species use and knowledge of where those habitats occur. There is growing consensus that spatial prioritization for species conservation programs must consider the projected impacts of climate change on habitats (see review: Jones et al., 2016). Species restoration and conservation projects can benefit if future habitat projections are available because this allows for prioritization of locations based on future habitat suitability (Loyola et al., 2013), as opposed to limiting the scope of a restoration project to areas where species currently occur. Additionally, future habitat projections can highlight streamflow or temperature regimes that become less common which may prompt monitoring of species occupying those habitats, even if the populations are currently stable.

To assess future stream habitat changes we need a method for modeling streamflow and temperature across the landscape, which is difficult because these characteristics are monitored sparsely in natural areas. Statistical and physical methods have been developed for modeling streamflow characteristics in ungauged areas (Vogel et al., 1999; Sanborn & Bledsoe, 2006) and for modeling stream temperature (Stefan & Preud'homme, 1993; Mohseni et al., 1998). However, these methods are typically either detailed and focus on specific stream segments or catchments, or, low-resolution models for large areas exploring general trends. Local management and restoration projects typically occur at a small scale, less than 1 km stream length (Bernhardt et al., 2005), and endemic species may occupy just a few watersheds, which highlights the need for small scale focused models. However, the domain covered by resource management agencies can be quite large, covering multiple watersheds, which highlights the need for regional habitat characterization to inform spatial prioritization of projects within a jurisdiction. Therefore, it can be beneficial to have detailed stream projections mapped, using future climate projections, over a large extent so restoration or conservation projects can be prioritized and implemented.

Modeling a large region at the stream reach scale presents a challenge for both stream temperature and streamflow. Typically, physically based models require large data inputs and are time intensive, which makes them difficult to use for multiple watersheds (e.g. Marks et al., 1999; Mohseni & Stefan, 1999; Jayakrishnan et al., 2005). Alternatively, statistical models can be applied over a large region because they are less computationally and data intensive, but they are often of low resolution (Vogel et al., 1999). A challenge for both methods is that precipitation and air temperature data may be sparsely available across a region and not at a scale that captures microclimates in topographically diverse regions like southern California- the focus of this study.

In this study we use multiple modeling approaches and data sets in innovative ways to model stream-reach scale temperature and streamflow metrics in current and future climate scenarios to provide managers with data that will help them further characterize species' habitat needs and spatially prioritize streams for conservation or restoration. We model streamflow throughout the landscape using a joint method of physically based ensemble modeling (Sengupta et al., 2018) and statistical extrapolations of hydrologic metrics. By using an ensemble of physically based streamflow models, different physical relationships between rainfall and runoff can be modeled, and the statistical extrapolations only occur within similar watersheds. We model stream temperature metrics using statistical methods.

Our goals are to describe the current streamflow and stream temperature regimes of a subset of major watersheds in southern California, and to model future conditions using climate change projections. The baseline modeling allows for wildlife managers to assess biological needs using historical or contemporary species distributional data, and the future modeling supports analysis of species' vulnerabilities to climate change. We model the stream conditions at a high resolution so that managers can have a better understanding of where conditions will change, and by overlaying this information with species distributional data, they can better decide what areas to target for conservation. For example, the expectation that streamflow and temperature regimes remain favorable toward certain amphibians may warrant restoration dollars put toward invasive species removal. However, a projection that stream temperature will exceed the tolerance of certain fishes may suggest not investing in invasive species removal at that location, or combining invasive species removal with riparian tree planting to maintain acceptable temperatures.

## *Methods*

### Overview

We used a series of models to characterize the hydrologic and thermal regimes of streams in southern California. Using downscaled precipitation data for baseline water years 1982 through 2014 we conducted hydrologic modeling in a selection of sub-watersheds. We calculated flow metrics from the streamflow time series data, such as number of high flow events, that describe the hydrologic regime. We developed a random forest model to extrapolate the flow metrics to the remaining sub-watersheds in the region for three baseline time periods (1993, 2010, and 2014 which represent wet, moderate, and dry water years, respectively). We then used future precipitation projections from three GCMs and the business as usual carbon emission scenario RCP 8.5 to model the flow metrics in future year 2100. We developed a multivariate linear regression model for stream temperature using air temperature data from the same baseline time period and twenty-one water temperature gauges in the region that report continuous measurements. We used the model to predict weekly stream temperature values at all streams within the region for baseline years and future years using air temperature projections from the same GCMs and carbon emission scenario. Using the weekly stream temperature data, we calculated thermal metrics, such as maximum seven-day maximum stream temperature. Ultimately, we produced data layers with spatially explicit streamflow metrics and stream temperature metrics for the baseline and future time periods.

### Study region

The focus of this study is on natural and semi-natural streams in six major watersheds in Los Angeles and Ventura counties in southern California, southwestern United States (Figure 2-1). Urbanization and flood control measures dominate the lower regions of the major watersheds in the study area; consequently, factors other than climate change, such as waste water discharge, dam operation, and dry/wet weather runoff, exert much greater influence on stream habitat than climate change effects. Therefore, we limited our focus to the mainly unaltered sub-watersheds where changes in climate will drive changes in streams, and ultimately, impact the riparian fauna.

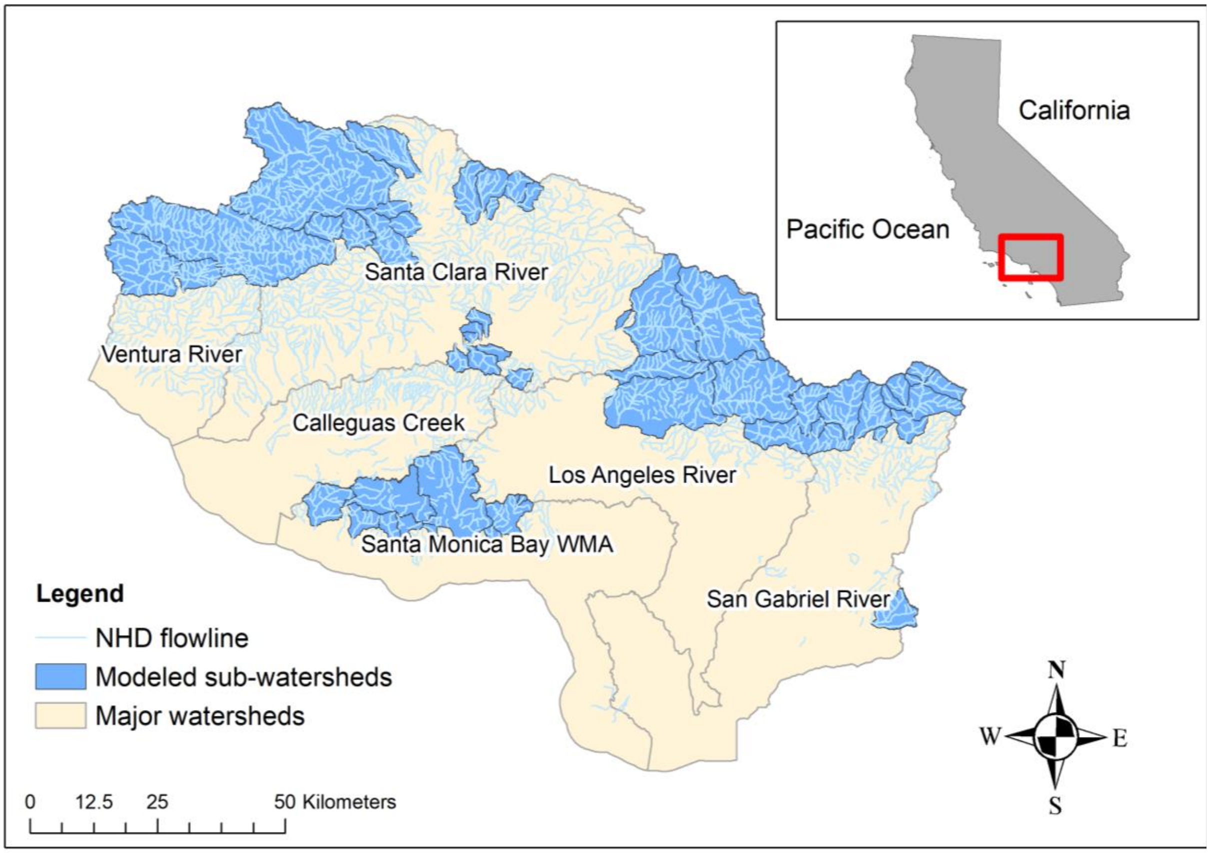

Figure 2-1: Map showing the study region's major watersheds and the sub-watersheds that were modeled with HEC-HMS. NHD flowlines show the streams included in the analysis after removing those with alterations like dams.

To determine which streams were considered urbanized (for *exclusion* in our study), we hierarchically clustered stream reaches using the National Hydrography Dataset (NHD) stream reach designation as our spatial unit (https://www.usgs.gov/core-science-systems/ngp/national-hydrography). Clustering was based on four U.S. EPA StreamCat data sets (Hill et al., 2016) (Table 2-1). We cut the dendrogram at the point where we identified major divisions between

NHD stream reaches and produced five clusters. With this method, there was one cluster that represented the minimally altered stream reaches (low or no dams, low impervious surface area, low urban space of any kind, and low road density) in the region, which we included in our study.

Table 2-1: Data used for clustering. 'W's refers to watershed defined as the entire basin that ultimately runs through that pour point. 'Cat' refers to catchment defined as the basin portion upstream until the next confluence. For more information on these variables refer to https://www.epa.gov/national-aquatic-resource-surveys/streamcat (Hill et al., 2016).

| Data | Variable | Description |
|---|---|---|
| Dams_Region18 | DamDensWs | Density of georeferenced dams within watershed (dams/ square km) |
| Dams_Region18 | DamNrmStorWs | Volume all reservoirs per unit area of watershed (cubic meters/square km) |
| ImperviousSurfaces2011_CA | PctImp2011Cat | Mean imperviousness of anthropogenic surfaces (NLCD 2011) within catchment |
| NLCD2011_Region18 | PctUrbOp2011Cat | % of catchment area classified as developed, open space |
| NLCD2011_Region18 | PctUrbLo2011Cat | % of catchment area classified as developed, low-intensity land use |
| NLCD2011_Region18 | PctUrbMd2011Cat | % of catchment area classified as developed, medium-intensity land use |
| NLCD2011_Region18 | PctUrbHi2011Cat | % of catchment area classified as developed, high-intensity land use |
| RoadDensity_Region18 | RdDensCat | Density of roads from 2010 within catchment (km/square km) |

To further ensure that these watersheds were not hydrologically altered, we excluded watersheds with major dams that change the hydrology by damming water in reservoirs. We did not remove all other types of dams, of which there are likely many, like silt dams or recreational dams, because of the lack of data and their lessor impact on hydrology. Many of the streams included in this study are mountainous because the streams in the lowlands have been impacted by urbanization.

### Climate scenarios

The three global climate models (GCMs) used in this analysis were CanESM2, CCSM4, and MIROC5, from the Coupled Model Intercomparison Project Phase 5 (CMIP5, https://cmip.llnl.gov/cmip5/ (Taylor et al., 2012)). The reason these were chosen was because they capture a large amount of the variation among CMIP5 GCMs in projections of future climate (Berg & Hall, 2015; Walton et al., 2015) and they performed well in modeling atmospheric rivers hitting

California (Goldenson, 2018). Additionally, these three GCMs were among the ten models selected as the best for planning in California based on global and southwestern USA historical performance and on their ability to capture California's climate variability (DWR, 2015). It is important to note that the projections of future climate from the CMIP5 data set represent uncertain futures, not realities, from a range of different forcing scenarios to allow for studies of future impacts or conditions (Emori et al., 2016). Therefore, while the three CMIP5 models that we used cover a large amount of the variability in future projections for changing precipitation and air temperature, there are other CMIP5 models, which predict different future climates that are equally possible (Figure 2-2). It is important to remember when interpreting our results that they do not represent the entire range of outcomes projected from climate models.

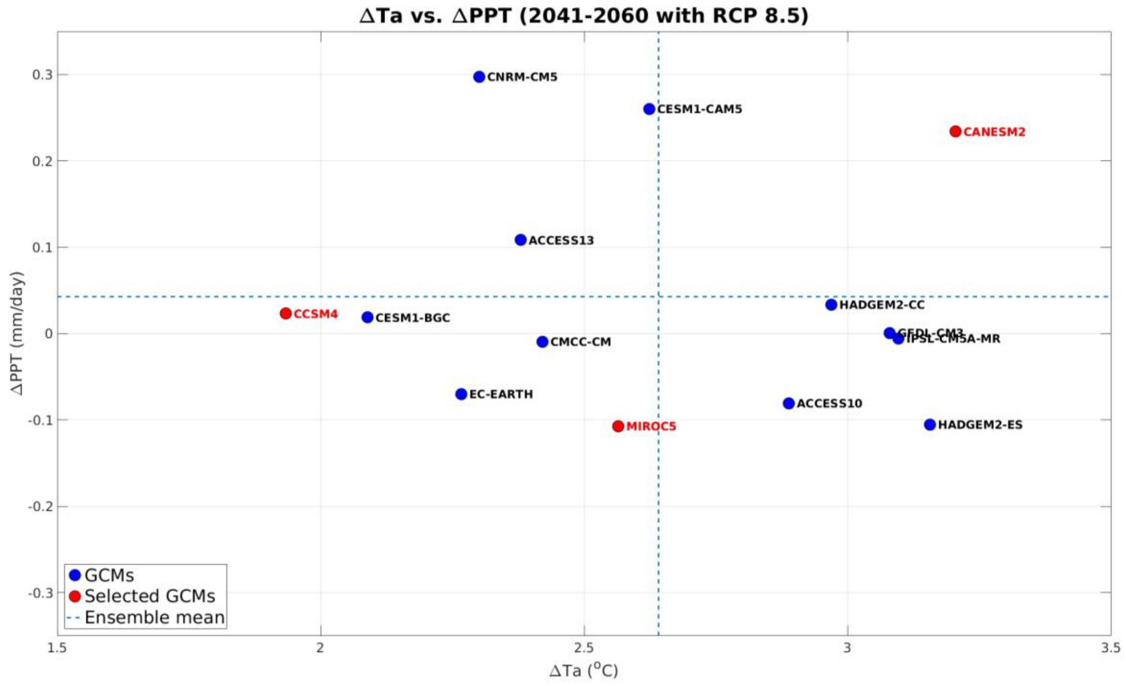

Figure 2-2: Average projected changes in air temperature (Ta, x-axis) and precipitation (PPT, y-axis) for mid-century from models in the CMIP5 ensemble that were found to be historically accurate for southern California (DWR, 2015; Gershunov et al., 2019). Blue dotted lines show ensemble means for air temperature and precipitation. The models in red are the three used in our analysis. Figure: Jerry H-Y. Huang, UCLA, printed with permission.

We modeled stream conditions for three baseline water years (Oct. through Sep.) selected based on the precipitation magnitude. Year 1993 was selected as a wet year, year 2010 as a moderate year, and year 2014 as a dry year. The future year that we modeled for end of century was year 2100, which is projected to be a moderate precipitation year.

### Watershed modeling

Within our region of unaltered stream reaches there are only two United States Geological Survey (USGS) flow gages; the majority of flow gages are in streams that are channelized, below a dam, or dominated by anthropogenic runoff. This is not enough streamflow data to be representative of the entire study region, which meant physically based modeling needed to be done in strategic locations so that flow could be extrapolated to each NHD stream reach in the region. We conducted hydrologic modeling using the Army Corps rainfall-runoff model, Hydrologic Engineering Center – Hydrologic Modeling System (HEC-HMS) (http://www.hec.usace.army.mil/software/hec-hms/) in ungauged watersheds, outlined in Figure 2-1. We selected watersheds that had a high density of species observation data, were geographically distributed across the region, and that represented diverse geologies and watershed areas for regional statistical extrapolation of flow metrics. We wanted to model watersheds with a high density of biological surveys to ensure that areas with biological data were most accurately modeled. We tried to ensure modeled watersheds included igneous, metamorphic, sedimentary, and unconsolidated bedrock by referring to the California geology shapefile, varying elevations, and varying watershed areas.

To model streamflow in ungauged watersheds we directly applied a regional ensemble model approach, which was calibrated and validated with flow gages in southern California in a region that encompasses the six watersheds in our study domain (Sengupta et al.,2018). The ensemble models were originally developed so that ecohydrological studies could be carried out in southern California streams that have long-term biology data, but no long-term streamflow data. The ensemble model includes 26 HEC-HMS models that attempt to be collectively representative of the variety of hydrologic conditions across southern California. They calibrated the 26 models with flow data from USGS flow gages and precipitation data from national, state, and local databases. Validation was performed to investigate model transferability (i.e. to use the model for flow modeling at different sites), as well as validating each model with 10 years of testing data withheld from the calibration data set. They used random forest models to determine which of the 26 models from the ensemble model set should be assigned to an ungauged watershed according to land cover and soil criteria: Mean imperviousness, road density, National Land Cover Database (NLCD) urban, agricultural, and developed open space land use, and soil erodibility. *Using the same random forest method they used, we mapped 68 ungauged watersheds back to their 26 gauged watersheds for the set of model parameters*. See Sengupta et al., (2018) for a full description of the ensemble model approach, flow gages used in calibration, and validation performance.

Once assigned to a gauged watershed, rainfall, watershed area, time of concentration (Tc), Storage Coefficient, and percent impervious area are the only additional watershed-specific parameters that the model requires. Watershed area was calculated using ESRI ArcMap software. Tc values were estimated using the Kirpich Method and Storage Coefficient was calculated as 0.6Tc, which is consistent with methodology used in development of the ensemble models. Percent impervious area was derived from the NLCD 2011 Percent Developed Imperviousness data set using ESRI ArcMap software. The NLCD 2001 to 2006 and NLCD 2006 to 2011 Percent Developed Imperviousness Change data sets were referenced to confirm that developed land area had remained relatively consistent through the portion of study period for which NLCD data is available.

Precipitation time series for each model were derived from a 90-meter, gridded precipitation data set (Berg et al., 2015; downscaled by Huang & Hall, 2018). This is a modeled data set that was originally validated against three observational data sets with reasonably high correlations. The average $R^2$ value between the modeled precipitation and one of the data sets (National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center (CPC) 0.25° × 0.25° daily U.S. unified precipitation) was 0.82. The precipitation data set consisted of a continuous, 3-hourly time series spanning water years 1982-2014 for the entire study region. Gridded precipitation values were averaged over each watershed to produce a 3-hourly time series for each watershed. The resulting precipitation time series were used as input into the HEC-HMS models. Each HEC-HMS model was run at an hourly time-step, consistent with development of the ensemble models. The hourly streamflow time series were averaged into daily average flow values in post-processing, resulting in a daily streamflow time series spanning water years 1982-2014 for each watershed at its downstream terminus.

### Flow metric calculation

Flow-ecology studies have shown that patterns of streamflow are important to wildlife (Yarnell et al., 2015), not necessarily the daily flow magnitude produced by the HEC-HMS models. Therefore, we calculated flow metrics that drive species habitat suitability, which describe aspects of the flow regime from the model-derived streamflow time series (Table 2-2). These metrics were selected based on their ability to describe the hydrological pattern and based on what we know from the literature to be important to the life history stages of various riparian species. As an example, streamflow recession influences recruitment of riparian vegetation which require that roots maintain contact with water (Mahoney & Rood, 1998); streamflow magnitude impacts fish inhabiting shallow water habitats like riffles (Patterson et al., 2017); and flood timing and frequency impact birds that nest in early successional riparian habitats (Kus, 1998). Relationships

Table 2-2: Streamflow metrics. Script used for calculation and definition came from Konrad et al., 2008 except for the last three variables in the table which we calculated separately. Timeframe refers to the number of years of flow data used in the calculation, measured back in time, from the dates in this analysis: 1993, 2010, 2014, and 2100.

| Variable | Pattern | Definition [units] | Timeframe |
|---|---|---|---|
| Qmean | Magnitude | [ft$^3$/s] mean Q for the period of analysis | 3,5 10, all |
| QmeanMedian | Magnitude | [ft$^3$/s] median annual mean Q | 3,5 10, all |
| Qmax | Magnitude | [ft$^3$/s] median annual maximum daily Q | 3,5 10, all |
| Qmin | Magnitude | [ft$^3$/s] median annual minimum daily Q | 3,5 10, all |
| QmeanIDR | Variability | [ft$^3$/s] Interdecile range of mean Q | 3,5 10, all |
| QmaxIDR | Variability | [ft$^3$/s] Interdecile range of maximum Q | 3,5 10, all |
| QminIDR | Variability | [ft$^3$/s] Interdecile range of minimum Q | 3,5 10, all |
| Qmed | Magnitude | [ft$^3$/s] median daily Q | 3,5 10, all |
| HighNum | Frequency | [events/year] number of events > high flow threshold. | 3,5 10, all |
| LowNum | Frequency | [events/year] number of events <= low flow threshold. | 3,5 10, all |
| HighDur | Duration | [days/event] - longest consecutive days > the high flow threshold | 3,5 10, all |
| LowDur | Duration | [days/event]- longest consecutive days <= the low flow threshold | 3,5 10, all |
| NoDisturb | Duration | [days] - longest number of consecutive days between the low and high flow threshold | 3,5 10, all |
| Hydroperiod | Duration | [% of years] - fraction of period of analysis with Q | 3,5 10, all |
| FracYearsNoFlow | Frequency | [% of years] - fraction of years with at least one no-flow day | 3,5 10, all |
| Mednoflowdays | Frequency | [days/year]- median annual number of no-flow days | 3,5 10, all |
| RecessMaxLength | Duration | [days] Maximum length of Q recession | 3,5 10, all |
| R10D.5 | Variability | [ft$^3$/day] - Median 10-day recession rate for low flow year | 3,5 10, all |
| R10D.9 | Variability | [ft$^3$/day] - 90% percentile 10-day recession rate for low flow year | 3,5 10, all |
| R10D4D | Variability | [ft$^3$/day] - 10-day recession rate starting after 4 days of recession | 3,5 10, all |
| BFR | Variability | [ft$^3$/day] - Base flow recession. | 3,5 10, all |
| SFR | Variability | [ft$^3$/day] - Storm flow recession. | 3,5 10, all |
| MaxMonth | Timing | [1= Jan] - month of maximum mean monthly Q | 3,5 10, all |
| MinMonth | Timing | [1= Jan] - month of minimum mean monthly Q | 3,5 10, all |
| Max Month Q | Magnitude | [ft$^3$/s] - maximum mean monthly Q | 3,5 10, all |
| Min Month Q | Magnitude | [ft$^3$/s] - minimum mean monthly Q | 3,5 10, all |
| Q01-Q99 | Magnitude | [ft$^3$/s] - Q quantiles | 3,5 10, all |
| Oct - Sept | Magnitude | [ft$^3$/s] - Mean Q in the 12 months preceding a specific date | 1 |
| RBI | Variability | [unitless] Richards-Baker flashiness Index. | 3,5 and 10 |
| Twoyr, fivyr, tenyr | Timing | [days] - Number of days from a specific date to a storm. | all |

of these metrics with riparian species are explored in a companion analysis (Taylor et al., In Prep). All processing for the streamflow metrics was completed in RStudio (RStudio Team, 2016).

### Regional streamflow metric extrapolation

The streamflow metrics from the 68 HEC-HMS modeled watersheds were extrapolated to all NHD reaches in the study region using a random forest model. Two types of variables were included in the random forest: static predictors (Table 2-3), which included watershed characteristics, and variable predictors, which included precipitation metrics. Static predictor variables were derived from the StreamCat database. We removed variables that did not vary across the NHD stream reaches in our region; for example, percent of the watersheds classified as lithology type 'water' did not vary much across stream reaches and was removed. The variable predictors were derived from the baseline precipitation data and we calculated the same metrics that were calculated for streamflow (Table 2-2), such as 'fraction of the year with no *precipitation'*.

Table 2-3: Static predictor variables used in the flow metric extrapolation. All variables have been joined to the NHD stream reach data and are available from the EPA StreamCat. A brief definition is given, for more information refer to the source column.

| Variable | Source | Definition |
|---|---|---|
| Ws/CatPctFull | EPA StreamCat | % of the watershed/ catchment that is covered by the landscape layer. |
| Ws/CatAreaSqKm | EPA StreamCat | Watershed area (km$^2$) at NHDPlus stream segment outlet or area of NHDPlus catchment (km$^2$) |
| Cluster of NHD reach | This analysis | |
| Dam presence | This analysis | Presence of dam in watershed |
| PctImp2011Cat | ImperviousSurfaces2011_CA | |
| ElevWa/Cat | Elevation_Region18 | Mean watershed/catchment elevation (m) |
| HydrlCondWs/Cat | GeoChemPhys3_Region18 | Mean lithological hydraulic conductivity (micrometers per second) content in surface or near surface geology within watershed/catchment |
| PctNonCarbResidWs | Lithology_Region18 | % of watershed area classified as as lithology type: non-carbonate residual material |
| PctAlluvCoastWs | Lithology_Region18 | % of watershed area classified as as lithology type: alluvium and fine-textured coastal zone sediment |
| Precip8110Ws/Cat | PRISM_1981_2010 | 30-year normal mean precipitation (mm): Annual period: 1981-2010 within the watershed/catchment |
| Tmax8110Ws/Cat | PRISM_1981_2010 | 30-year normal maximum temperature (C°): Annual period: 1981-2010 within the watershed/catchment |
| Tmean8110Ws | PRISM_1981_2010 | 30-year normal mean temperature (C°): Annual period: 1981-2010 within the watershed |

| | | |
|---|---|---|
| Tmin8110Ws | PRISM_1981_2010 | 30-year normal minimum temperature (C°): Annual period: 1981-2010 within the watershed |
| RckDepWs/Cat | STATSGO_Set2_Region18 | Mean depth (cm) to bedrock of soils within watershed/catchment |
| WtDepWs/Cat | STATSGO_Set2_Region18 | Mean seasonal water table depth (cm) of soils within watershed/catchment |
| OmWs | STATSGO_Set2_Region18 | Mean organic matter content (% by weight) of soils within watershed |
| PermWs | STATSGO_Set2_Region18 | Mean permeability (cm/hr) of soils within watershed |
| PctUrbOp2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as developed, open space land use |
| PctUrbMd2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as developed, medium-intensity land use |
| PctBl2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as barren |
| PctDecid2011Cat | NLCD2011_Region18 | % of catchment area classified as deciduous forest |
| PctConif2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as evergreen forest |
| PctShrb2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as shrub/scrub |
| PctGrs2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as grassland/herbaceous |
| PctHay2011Ws/Cat | NLCD2011_Region18 | % of watershed/catchment area classified as hay |
| PctOw2011Ws | NLCD2011_Region18 | % of watershed area classified as open water |
| PctIce2011Ws | NLCD2011_Region18 | % of watershed area classified as ice/snow |
| PctMxFst2011Ws | NLCD2011_Region18 | % of watershed area classified as mixed deciduous/evergreen forest |
| PctCrop2011Ws | NLCD2011_Region18 | % of watershed area classified as crop |
| PctWdWet2011Ws | NLCD2011_Region18 | % of watershed area classified as woody wetland |
| PctHbWet2011Ws | NLCD2011_Region18 | % of watershed area classified as herbaceous wetland |

Four random forest models were created for each flow metric based on January, April, July, and October data from 1982 to 2014 to account for seasonal variation in flow. January represents the part of the water year when most precipitation falls in this region (snow in the mountains and rain near the coast). April is the end of the wet season when streams would be flowing near their maximum. July represents the summer months when streams may still have water but are drying out. Finally, October is the start of the next water year when conditions are often dry.

Two models were created with 75% of the data for training, for each flow metric-month combination, where the first used *all* static and variable predictors and the second used only the top ten most important predictors from the first model. Variable importance was evaluated by determining the increase in model error after excluding each predictor. The final model for each metric-month combination was based on overall performance on a validation data set that was a random selection of 25% of the observations from the complete data set. Overall performance was assessed using root mean squared errors and R-squared values comparing the observed flow metrics and those predicted from each model for the validation data set (see Appendix S-2-1 for the random forest performance). Flow metrics were then extrapolated to all stream reaches using the best performing model for each metric-month combination.

To predict the flow metrics for the projected conditions in year 2100, the random forest extrapolation was repeated using the same static predictors, but with the future precipitation data from three GCMs instead of the current precipitation. Some of the static variables like land cover may change; however, because our region includes only the unaltered watersheds predominantly in mountainous areas, many of which are protected, we do not anticipate substantial change in future years. Other anthropogenic changes to streamflow from water use and discharge practices will largely be important in the streams that we excluded from our study, i.e., the lowland altered streams.

### Water temperature modeling

Twenty-one stream sites in southern California (Figure 2-3) were lumped together to develop a statistical model using air temperature to predict maximum, minimum, and mean stream temperature. Stream sites were included where continuous (not spot measurements) stream temperature data was available during the summer months, May through September, when warm water temperatures can be harmful to riparian species. Refer to Table 2-4 for the length of the stream temperature record and a short description of the site. This infers that streams we included were perennial or maintained water in disconnected pools throughout the summer. Some of the stream temperature data loggers reported maximum, minimum, and mean temperature. In the remainder of sites, the mean stream temperature was not reported so we calculated the mid-range, in lieu of the mean, with the maximum and minimum stream temperature values. Although different metrics, the mid-range and the mean values, in the sites that report both, are similar ($r^2$=0.99), but at high stream

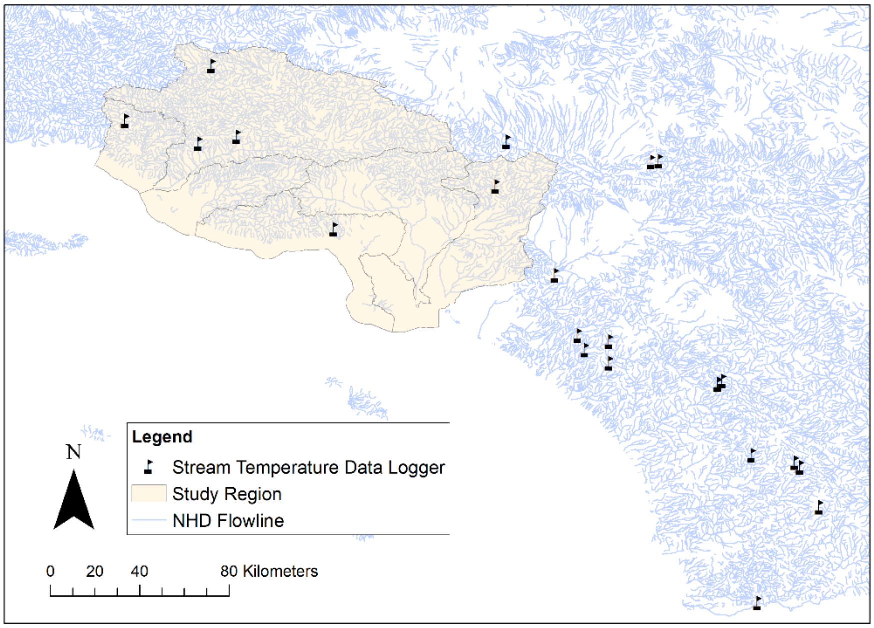

Figure 2-3: Locations of stream temperature loggers with the study region shown for reference.

Table 2-4: NHD stream reach COMID's that had stream temperature loggers and were included in the air temperature to water temperature model. All streams were relatively to completely unaltered unless noted in the description. * after NHD reach means the air temperature data was Livneh et al., (2015), otherwise it was Walton et al., (2015). SMC: Southern CA Stormwater Monitoring Coalition. SWAMP: Surface Waters Ambient Monitoring Program

| NHD Reach | Start | End | Days | Stream Temp Data | Stream name and short description |
|---|---|---|---|---|---|
| 17573647* | 4/30/1969 | 1/15/1971 | 625 | USGS | Santa Paula Creek ~ 6km from Santa Clara river. |
| 17574397* | 11/8/1966 | 9/6/1978 | 4320 | USGS | Tributary to Sespe creek ~6km to Santa Clara River. |
| 20325695* | 4/2/2013 | 12/31/2013 | 273 | SMC | Tributary to Tijuana River, San Diego county |
| 20329578* | 4/3/2013 | 12/31/2013 | 272 | SMC | Temescal creek, San Diego county |
| 20329654* | 4/10/2008 | 7/16/2008 | 97 | SMC | Santa Ysabel Creek, San Diego county |
| 20329758* | 4/11/2008 | 7/9/2008 | 89 | SMC | San Diego River in San Diego county |
| 20332588* | 4/25/2013 | 8/1/2013 | 98 | SMC | Cold Stream, San Diego county |
| 20348295* | 4/4/2013 | 12/31/2013 | 271 | SMC | Tributary to San Juan Creek, Orange county |
| 20348331* | 4/28/2008 | 7/3/2008 | 66 | SMC | Tributary to San Juan Creek, Riverside county |
| 20348471* | 4/23/2008 | 6/24/2008 | 62 | SMC | San Juan Creek, Orange County. |
| 20348769* | 4/4/2013 | 10/20/2013 | 199 | SMC | Tributary to San Mateo Creek, San Diego County. |
| 22549515* | 4/8/2008 | 6/14/2008 | 67 | SMC | Arroyo Seco Creek, Riverside County. |
| 22550557* | 4/3/2013 | 8/13/2013 | 132 | SMC | Tributary to Arroyo Seco creek, Riverside county. |
| 22563116* | 2/2/1968 | 12/31/2013 | 16769 | USGS | Santa Ana River below Prado Flood Control Basin. Altered. |
| 22658309* | 12/1/2006 | 12/31/2013 | 2587 | USGS | Deep creek, San Bernardino county. |
| 22660257* | 2/28/2007 | 12/31/2013 | 2498 | USGS | West Fork Mojave River. Altered. |
| 22684930* | 1/18/1962 | 3/9/1979 | 6259 | USGS | Big Rock Creek, LA county. |
| 17567207 | 5/14/2014 | 9/30/2014 | 139 | SWAMP | Lockwood creek, tributary to Piru creek. |
| 17585800 | 5/28/2014 | 7/29/2014 | 62 | SMC | Matilija creek, Ventura county. |
| 20365115 | 5/20/2014 | 7/31/2014 | 72 | SMC | Coastal creek, Santa Monica Bay. |
| 22524629 | 5/6/2014 | 9/30/2014 | 147 | SWAMP | Bear Creek, tributary to west fork San Gabriel. |

temperatures, the mid-range value exceeds the mean value and the variance around the mean value increases (see Appendix S-2-2 for a mid-range and mean stream temperature comparison). Therefore, monitored stream temperature data was only used if it reported maximum and minimum temperature, or sub-daily reporting, so that we could calculate the maximum, mean, and minimum temperatures. If sub-daily values were reported, the maximum was the maximum value reported and the minimum was the minimum value reported.

Of the twenty-one sites with stream temperature loggers, one of them is in a heavily altered channel. To determine whether to include that site we regressed the stream temperature time series against the air temperature time series at each site. The slope and intersect coefficients of the altered site were within the range of the other twenty sites so we included it in the stream temperature model. Our reason for wanting to be inclusive of sites is because our model domain is large so the more sites we can include in the training data, the more likely the characteristics of the sites being modeled are contained in those training sites.

Two gridded air temperature data sets were used; one from a regional model (Walton et al., 2015) and one from a state-wide data set of historical observations downloaded at https://cal-adapt.org/data/ (Livneh et al., 2015). The regional model was validated against 24 station measurements and a previous version of the Livneh data set from 2013, and in both cases, there were strong correlations suggesting the model captured spatial and temporal trends. The model preformed particularly well in the summer months when compared to station measurements, with an $R^2$ value of 0.93, which is important because in this analysis we include the summer months only. The regional air temperature was modeled mean air temperature at daily increments of 90m resolution from water year 1982- 2014 calculated from 3-hourly temperature observations. The statewide air temperature data consists of observed daily maximum and minimum air temperature values from 1950 -2013 with approximately 6km pixels. We averaged the maximum and minimum temperatures over the 6km scale, to get daily mid-range air temperature, so it would be comparable to the modeled data set. Again, we combined mid-range and mean values. The mid-range air temperature data was paired with the mid-range stream temperature data.

For every day of the stream temperature record, daily air temperature was extracted from the appropriate air temperature data set for the correct date and location. Stream temperature was summarized as running 7-day average, minimum, and maximum temperatures, which have been found in the literature to have a more linear relationship with air temperature than daily data (Stefan & Preud'homme, 1993). For the air temperature which is a time series of daily means, we used the 7-day running maximum-mean, mean-mean, and minimum-mean values. The three stream temperature metrics were modeled using the air temperature metrics, watershed area, A ($km^2$), and watershed elevation, E (m) as predictor variables with a multiple linear model using 75% of the data and saving 25% for validation (see Appendix S-2-3 for model performance). We included watershed area and elevation to account for some of the differences in model coefficient and slope between small headwater streams and higher order streams where drivers like shading and discharge differ. These models were used to calculate the mean, minimum, and maximum daily stream temperature for water years 1982 through 2014 for every reach within the study region. Six stream temperature metrics were calculated from the predicted values that are reported in the literature to be ecologically relevant (Table 2-5) (e.g. Sloat & Osterback, 2013; Welsh et al., 2001). For example, maximum temperatures can surpass critical thresholds for survival. Residuals were sufficiently normal suggesting the use of a linear model was appropriate. Final models below:

$$eq. 1: 7\ day\ mean\ water \ = \ 7.16 + \ 0.6078\ (7\ day\ mean\ air) + 0.0003\ (A)$$

$$eq. 2: 7\ day\ max\ water \ = \ 20.93 + \ 0.5455\ (7\ day\ max\ mean\ air) - 0.0059\ (E) \ - 0.0006\ (A)$$

$$eq. 3: 7\ day\ min\ water \ = \ 6.64 + \ 0.4815\ (7\ day\ min\ mean\ air) - 0.0003\ (E) + 0.0006\ (A)$$

Table 2-5: Stream temperature metric definitions. The months included in calculating these metrics are May through September.

| Temperature Pattern | Metric | Definition |
|---|---|---|
| Magnitude | Minimum 7-day minimum | [°C] The minimum value of a rolling 7-day minimum |
| | Maximum 7-day maximum | [°C] The maximum value of a rolling 7-day maximum |
| | Maximum 7-day average | [°C] The maximum value of a rolling 7-day average |
| Variability | Maximum 7-day range | [°C] The maximum difference between the rolling 7-day maximum and minimum. I.e. the largest temperature swing within a 7-day period. |
| | Mean 7-day range | [°C] The average difference between the rolling 7-day maximum and minimum. I.e. the average temperature swing within a 7-day period. |
| Frequency | Number of 7-day maximums > 30°C | [days] The number of 7-day rolling averages that are greater than 30°C |

Future stream temperature metrics were calculated for each of the GCMs using the same regression models, but with mean air temperatures derived from the downscaled climate projections at a 3-hourly model output (Walton et al., 2015). As discussed above, the mean values are similar to the mid-range values, except at high temperatures the mean values tend to be slightly lower. This suggests that predictions for high temperature streams could be more conservative (i.e. slightly lower temperatures).

### *Results*

Some characteristics of streamflow and stream temperature change strikingly from the baseline years and some show little change. The general trend for streamflow is an increase in flashiness due to a greater number of storms, more rapid recessions, and larger flows in the wet season. There is also a trend toward more uniformity across streams in metrics that relate to no- and low-flow durations. In the future, the large and small values for duration of low flows and fraction of time with no flows are lost to more central values. Stream temperatures are projected to increase; more so for maximum and average temperatures compared to minimum temperatures.

### Stream temperature projections

Table 2-6: The change in temperature metrics, across GCM's, from baseline year 2010 to future year 2100. The mean shows the average change for each metric and the range shows the minimum and maximum change values.*unit is days.

| Variable | Mean (°C) | Range (°C) |
|---|---|---|
| Max 7- day Max | 2.59 | 0.91-4.86 |
| Max 7-day Mean | 3.13 | 1.30-5.33 |
| Min 7-day Min | 2.73 | 1.48-4.10 |
| Max7- day Rng | 0.49 | -1.78-1.92 |
| Number of 7-day maximums >30°C | *53 | *0 -146 |

Across GCM's, and from baseline to year 2100, regional mean stream temperatures are projected to increase the most, followed by maximum temperatures, and finally minimum temperatures (Table 2-6). There is an average addition of 53 days where stream temperatures exceed 30°C. The overall ranking of major watersheds, based on maximum stream temperature, remains consistent in the future (Table 2-7). For example, in the baseline years, Calleguas Creek had the highest median maximum 7-day maximum temperature and it is projected to have the highest in the future as well. However, there is an overall greater projected increase in minimum temperatures in three of the four mountainous watersheds compared to the two coastal watersheds. At the sub-watershed scale, we see greater warming in

Table 2-7: Median values of stream temperature metrics for the baseline (years 1993, 2010, and 2014) and future year 2100 (three GCMs) by watershed. Number in parentheses shows the percent increase from baseline.

| Watershed | Scenario | Max 7-day Mean (°C) | Max 7-day Max (°C) | Min 7-day Min (°C) | Max 7-day Rng (°C) | Max 7-day Max >30 (day) |
|---|---|---|---|---|---|---|
| Coastal Watersheds | | | | | | |
| Calleguas Creek | Baseline | 21.70 | 33.90 | 12.8 | 20.60 | 81 |
| | Future | 24.46 (13%) | 36.89 (9%) | 14.73 (15%) | 20.35 (-1%) | 146 (80%) |
| Santa Monica Bay WMA | Baseline | 20.48 | 32.65 | 12.49 | 19.54 | 49 |
| | Future | 23.06 (13%) | 35.29 (8%) | 14.40 (15%) | 18.82 (-4%) | 143 (192%) |
| Mountainous Watersheds | | | | | | |
| Los Angeles River | Baseline | 22.27 | 29.82 | 11.53 | 16.46 | 2 |
| | Future | 25.24 (13%) | 32.62 (9%) | 14.05 (22%) | 17.16 (4%) | 77 (3750%) |
| San Gabriel River | Baseline | 22.15 | 29.73 | 11.56 | 16.54 | 1 |
| | Future | 24.89 (12%) | 32.37 (9%) | 14.23 (23%) | 17.11 (3%) | 63 (6200%) |
| Santa Clara River | Baseline | 22.21 | 28.88 | 10.44 | 16.10 | 0 |
| | Future | 25.43 (14%) | 31.87 (10%) | 12.90 (24%) | 17.61 (9%) | 50 (NA) |
| Ventura River | Baseline | 22.32 | 31.41 | 12.50 | 17.82 | 30 |
| | Future | 24.84 (11%) | 34.17 (9%) | 14.49 (16%) | 18.51 (4%) | 109 (236%) |

the upper elevation regions (Figure 2-4), particularly in the Santa Clara watershed. The highest elevations in the Santa Clara watershed, Ventura watershed, Los Angeles watershed, and the San Gabriel watershed are projected to maintain temperatures below 30°C, which may be an important ecological refuge for certain species. Therefore, while warming is projected to be more pronounced for minimum, maximum, and average temperatures in high elevations, they may maintain temperatures below biologically harmful levels, meaning native fishes could still be able to inhabit those areas, although the total area of suitable habitat in that region decreases. See Appendix S-2-4 and Appendix S-2-5 for more results of the temperature modeling.

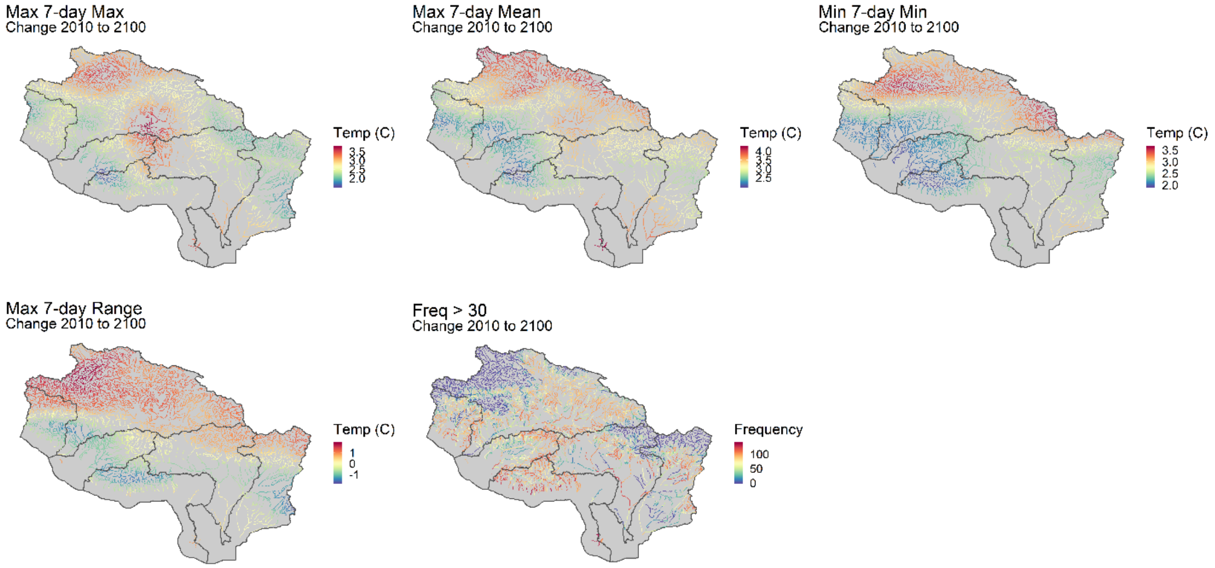

Figure 2-4: Change in the five-temperature metrics from baseline year 2010 to 2100. Change calculated as 2100 value minus 2010 value. The value in 2100 is the average of the values modeled based on the three GCM's.

All of the stream reaches that we modeled are projected to have higher maximum 7-day average, maximum 7-day maximum, and the minimum 7-day minimum temperatures from the baseline year, 2010, to future year 2100 (Figure 2-5). However, the magnitude of increase varied among the three GCMs. The maximum and average stream temperatures are projected to increase the most based on CanESM2, average increases of 3.6°C and 4.3°C, respectively, and almost double the increases compared to CCSM4, 1.9°C and 2.5°C, and MIROC5, 2.2°C and 2.5°C (Figure 2-5 panel A and B). The minimum temperatures increase more based on MIROC5 (3.2°C), followed by CanESM2 (2.6°C), and then CCSM4 (2.3°C) (Figure 2-5 panel C). The maximum 7-day range and the frequency of days when the maximum 7-day maximum is above 30°C are similar between GCM's (Figure 2-5 panel D and E).

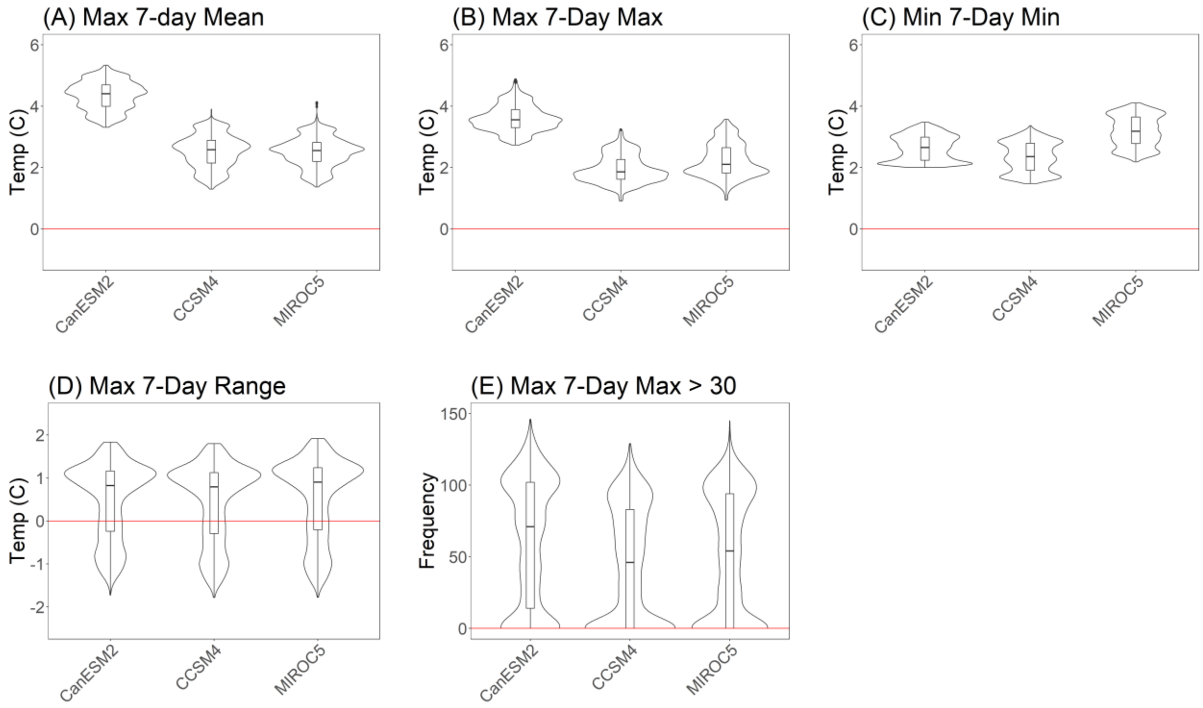

Figure 2-5: The distribution of the change in stream temperature metrics from baseline year 2010, to future year, 2100 for the NHD stream reaches. Change calculated as 2100 value minus 2010 value. The x-axis shows which GCM is being used, and the y-axis shows the change in temperature (°C). The outer violin plot shows the distribution of streams, represented by the width of the violin. The inner box plot shows the descriptive statistic locations which include the median, the 25th and 75th percentiles, and either 1.5*the inter-quartile range at the upper and lower end, or the highest and lowest value. Points beyond the 'whiskers' represent outliers.

### Streamflow projections

Streamflow metric projections suggest that future flows will have a higher frequency of more intense storms, with longer periods between storms during which there is low- or no- flow (Table 2-8). The flow metric projections for each stream reach generally trended in a similar direction (positively or negatively) from the baseline year and the magnitudes of deviation minorly varied between GCMs. However, CanESM2 and CCSM4 were more similar and showed greater deviation from the baseline, whereas MIROC5 showed less change from the baseline (Figure 2-6). See Appendix S-2-4 and Appendix S-2-5 for more results of the flow metric modeling.

Table 2-8: The change in flow metrics, across GCM's, from baseline year 2010 to future year 2100. The mean shows the average change for each metric and the percent greater than 0 (Pct>0) shows the percent of stream reaches that had a positive change from baseline. Pct>0 also shows the level of agreement between streams in the direction of the change from the baseline year. A pct>0 value near 1 or 0 indicates that there was high agreement and the values across stream reaches increased or decreased, respectively. A more central value indicates streams responded differently to climate change across the region.

| Variable | Mean | Pct>0 |
|---|---|---|
| Q99 | 46.98 | 0.98 |
| SFR | -0.065 | 0.18 |
| Hydroperiod | -0.08 | 0.24 |
| LowDur | 65.08 | 0.73 |
| HighNum | 1.05 | 0.94 |

There was less regional consistency in projections for the flow metrics than the temperature metrics because certain streams increase, and others decrease, in value. The 99th percentile flow (Q99) is projected to increase for almost all stream reaches (Figure 2-6 panel A) with similar distribution of increases across GCM's. The magnitude of the increase varies only slightly between GCM's– average increases of 57.20cfs (CanESM2), 39.31cfs (CCSM4), and 44.42cfs (MIROC5). The variance of the magnitude of the increase between streams is large, but most streams increase in discharge less than approximately 50cfs. Storm flow recessions in

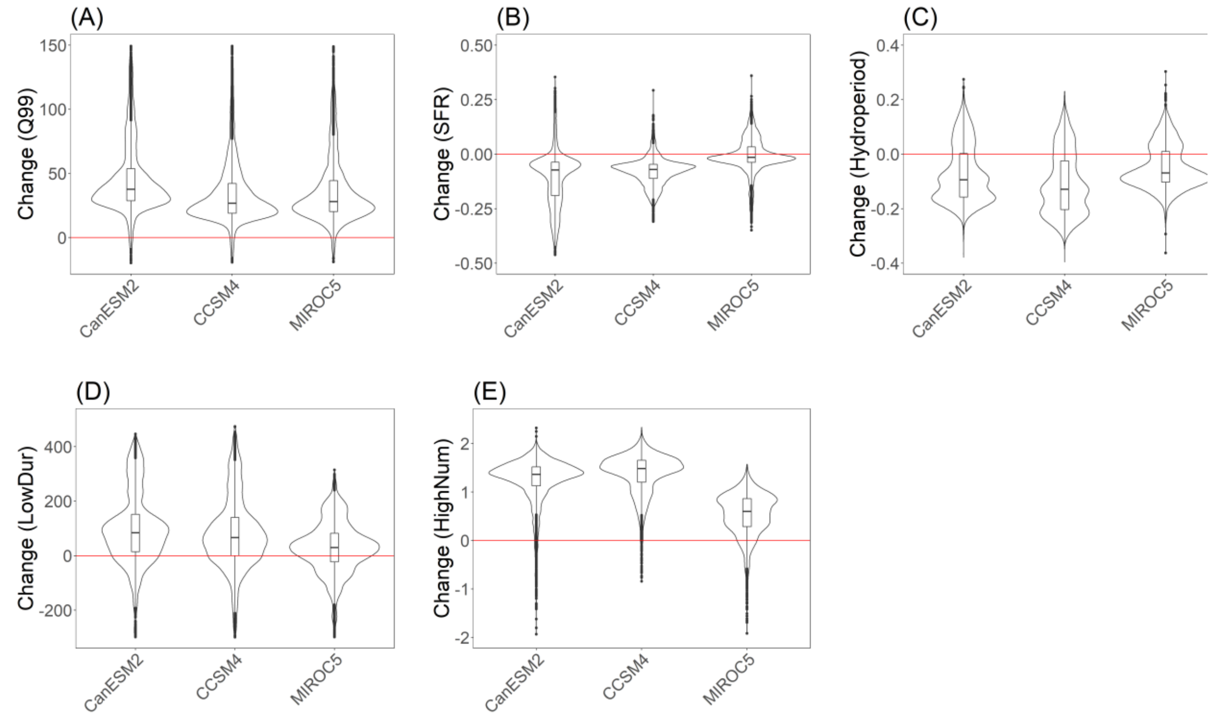

Figure 2-6: The change in flow metrics from baseline year 2010, to future year, 2100. The x-axis shows which GCM is being used, and the y-axis shows the change in flow metric (units vary). Positive outliers for panel (A) go up to 473cfs and negative outliers for panel (D) go through -552 days but were cut off here to see the distribution of most of the data. Full range of values for all variables is shown in the maps in Figure 2-8.

general change little from baseline, but are projected to become more rapid, i.e. decrease in value, across most stream reaches for CanESM2 (average of -0.10) and CCSM4 (average of -0.08), but for MIROC5 the recessions change very little from baseline (average of -0.01) (Figure 2-6 panel B). However, though the change appears small, the importance will vary depending on the local ecology – for example, amphibian eggs can become stranded and vegetation roots can lose contact with groundwater if recession is too rapid. Hydroperiod is projected to decrease for 72.74%-79.70%% of streams (Figure 2-6 panel C). The duration of the year with low flow shows the most varied projections among the flow metrics, in that the direction of the trend differs for a large proportion of streams, but on average the low flow duration is projected to increase (Figure 2-6 panel D). For CanESM2 and CCSM4, 78.12% and 74.14%, respectively, of streams are projected to have an increase in low flow duration, and under MIROC5, 65.60% of streams are projected to increase in low flow duration. Combined with the projections for hydroperiod, this suggests streams will be drier for more of the year. The number of storm events increases for most of the streams in the region, but the distribution varies across GCM (Figure 2-6 panel E). The increase is greater for CanESM2 and CCSM4, which have an increase of approximately 1.23 and 1.38 storms, respectively, than MIROC5, which has an increase of approximately 0.53 storms.

By comparing the projected streamflow metrics in year 2100, a moderate year, with the baseline wet, dry, or moderate year, we can determine what future year ‘types’ will look like. The future moderate year has a higher 99th percentile flow, more rapid recessions, and more storms than the baseline wet, moderate, and dry year (Figure 2-7 panel A, B, and E). The average projected duration of low flow in the future moderate year is similar to the baseline dry or moderate year, although there is a large reduction in the spread of the values (Figure 2-7 panel D). This suggests that future moderate winters will be like baseline wet winters, and future moderate

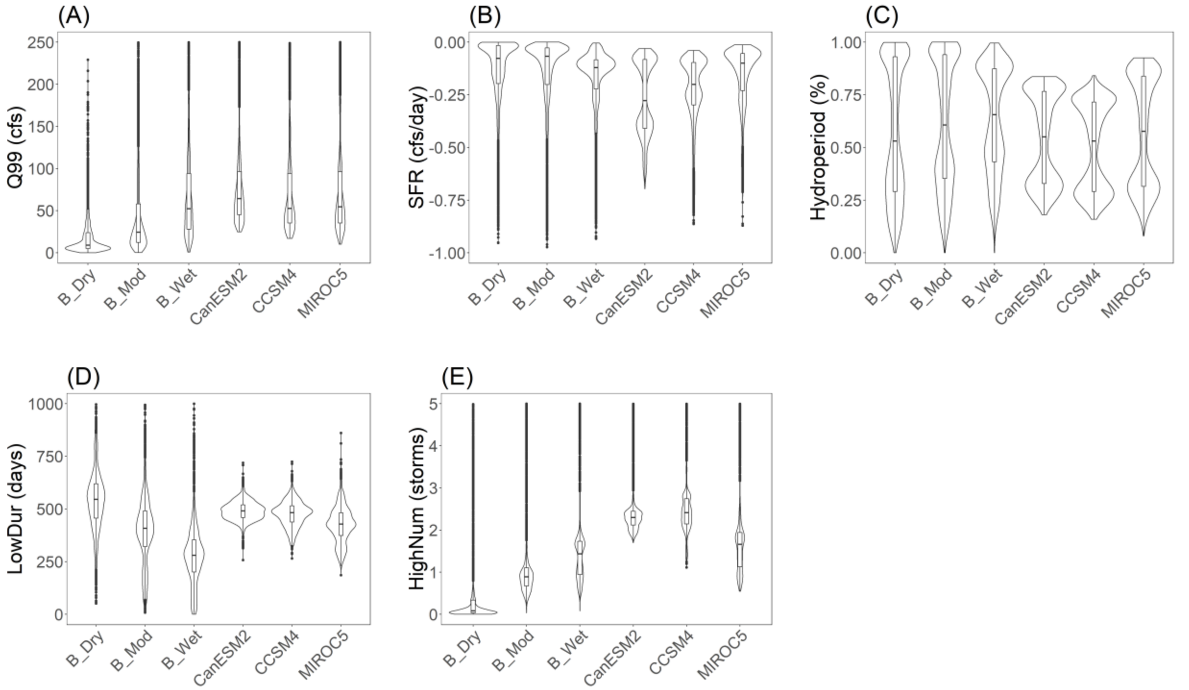

Figure 2-7: Violin plots showing the trend of five streamflow metrics in the three baseline years and year 2100 based on each of the three GCMs.

summers will be more like baseline dry summers. Interestingly, hydroperiod is unlike any of the baseline years (Figure 2-7 panel C). While there currently is a bimodal distribution in hydroperiod for all year types, the bimodal distribution is accentuated in the future and there is a compression of stream types – in the baseline years, through the distribution shifted in response to year type, there were streams with hydroperiod values from 0-1. In the future year, we project a loss of streams with high and low hydroperiods, suggesting there will be no perennial streams, and no ephemeral streams.

While the trends in streamflow metrics are similar across major watersheds, the magnitudes of change differ (Table 2-9). In the future moderate year, the 99th percentile flow (Q99) in the mountainous watersheds is projected to increase an average of 2.34 times the baseline moderate year. In contrast, compared to the baseline moderate year, the Q99 in the two coastal watersheds

Table 2-9: Median values of 3-year stream flow metrics for the baseline and future (bold) years by watershed.

| Year | Watershed | GCM | Q99 | SFR | Hydroperiod | LowDur | HighNum |
|---|---|---|---|---|---|---|---|
| | | | Coastal Watersheds | | | | |
| 1993 | Calleguas Creek | B_Wet | 26.05 | -0.36 | 0.37 | 384 | 2.76 |
| 2010 | | B_Mod | 10.76 | -0.36 | 0.31 | 487 | 2.49 |
| 2014 | | B_Dry | 6.19 | -0.33 | 0.27 | 560 | 1.49 |
| **2100** | | **Future** | **38.64** | **-0.37** | **0.28** | **485** | **3.29** |
| 1993 | Santa Monica Bay WMA | B_Wet | 18.85 | -0.31 | 0.23 | 401 | 2.95 |
| 2010 | | B_Mod | 9.05 | -0.31 | 0.17 | 484 | 2.74 |
| 2014 | | B_Dry | 6.11 | -0.30 | 0.13 | 550 | 1.83 |
| **2100** | | **Future** | **35.31** | **-0.36** | **0.24** | **466** | **3.59** |
| | | | Mountainous Watersheds | | | | |
| 1993 | Los Angeles River | B_Wet | 54.49 | -0.07 | 0.73 | 254 | 0.94 |
| 2010 | | B_Mod | 23.52 | -0.04 | 0.72 | 356 | 0.86 |
| 2014 | | B_Dry | 7.16 | -0.03 | 0.63 | 467 | 0.06 |
| **2100** | | **Future** | **55.55** | **-0.12** | **0.62** | **470** | **1.89** |
| 1993 | San Gabriel River | B_Wet | 61.66 | -0.06 | 0.79 | 363 | 1.10 |
| 2010 | | B_Mod | 23.77 | -0.03 | 0.75 | 525 | 0.75 |
| 2014 | | B_Dry | 7.24 | -0.03 | 0.71 | 748 | 0.05 |
| **2100** | | **Future** | **56.98** | **-0.11** | **0.66** | **535** | **2.03** |
| 1993 | Santa Clara River | B_Wet | 72.51 | -0.12 | 0.80 | 256 | 1.63 |
| 2010 | | B_Mod | 31.78 | -0.05 | 0.78 | 387 | 0.92 |
| 2014 | | B_Dry | 10.77 | -0.05 | 0.76 | 523 | 0.07 |
| **2100** | | **Future** | **70.10** | **-0.12** | **0.69** | **458** | **2.16** |
| 1993 | Ventura River | B_Wet | 87.49 | -0.21 | 0.53 | 271 | 1.57 |
| 2010 | | B_Mod | 37.97 | -0.11 | 0.46 | 422 | 0.94 |
| 2014 | | B_Dry | 14.65 | -0.15 | 0.43 | 590 | 0.10 |
| **2100** | | **Future** | **91.49** | **-0.29** | **0.39** | **460** | **2.36** |

is projected to increase by 3.59 and 3.90 times in the future moderate year. To put this in perspective, the *moderate* future year Q99 is very similar to the values in the baseline *wet* year in the mountainous watersheds, whereas it is a 48% and 87% increase from the baseline wet year for the two coastal watersheds. All watersheds are projected to have higher flows, but the driest watersheds will see the largest relative increase in large stream flow magnitudes. Coastal watersheds are projected to get flows larger than in all the baseline years, but the future flows in mountainous watersheds will be similar to baseline wet conditions. The projected change in hydroperiods (fraction of period of analysis with flows) does not show the same trends in the mountainous versus coastal watersheds. Instead, we project an average decrease from the baseline moderate year to the future moderate year of an average of 12% for all watersheds except the Santa Monica Bay where we project a 41% increase in hydroperiod, a large increase in a region that has many ephemeral streams. Across all watersheds, the number of large events is projected to increase from the moderate baseline year to the moderate future year. In the mountainous watersheds, we project an average of 2.4 times the number of storm events in the moderate baseline year, compared to an increase of 1.3 times the number of storm events in the coastal watersheds. The number of days with low flow similarly is different between the two types of watersheds. In the coastal watersheds, we project a slight decrease in low flow days from the baseline to future moderate year (-2 and -18 days), whereas in the mountainous watersheds there are increases in the number of low flow days from +10 to +114 days. The review by Garssen et al., (2014) found an increase in drought of 30 days or more to be harmful to riparian vegetation. Finally, the projected change in SFR, from baseline to future moderate year, is a small increase in recession rate (i.e. a lower value) in the coastal watersheds, and a large increase in recession rate in the mountainous watersheds.

At the sub-watershed scale, the future trends are not as consistent as the temperature metrics. In the high elevation sub-watersheds, hydroperiod is projected to decrease and the number of storms is projected to increase (Figure 2-8). However, in the coastal streams of Santa Monica Bay and Ventura, hydroperiod is actually projected to increase which could make these streams, many of which were intermittant or ephemeral, potential habitat for anadromous, or other native, fishes which managers are attempting to recover. Duration of low flow is projected to increase the most in major tributaries in the mountainous watersheds which are also projected to increase the most in storm flow magnitude; this increases the range of conditions that organisms will be exposed to in these areas. Recessions are projected to be more rapid at intermediate elevations, but show little change at the highest elevation sub-watersheds.

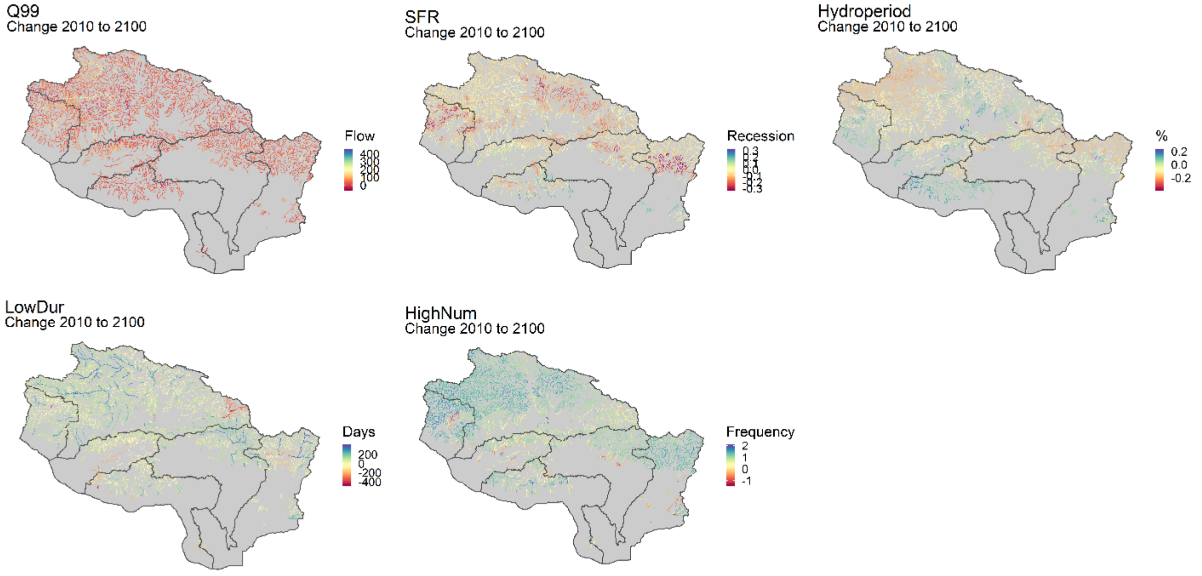

Figure 2-8: Change in five flow metrics from baseline year 2010 (moderate year) to future year 2100 (moderate year). Change calculated as 2100 value minus 2010 value. Future year is the average of the values modeled based on the three GCM's. Note for SFR, negative numbers mean more rapid recession.

## *Discussion*

In this study we find that there will be substantial changes to stream hydrology and stream temperatures in the relatively natural mountains and foothills of the Los Angeles region, which support endemic and widespread species alike. Summertime stream temperatures are projected to increase regionally, with the largest increases of 3-4°C occurring in the mountains. For all major watersheds, by 2100, median maximum 7-day maximum temperatures are projected to be 31°C to 38°C, which is comparable to the temperature ranges that were found along the Los Angeles River and lower tributaries in 2016 (Mongolo et al., 2017). This suggests that many of the less impaired watersheds in this study will have summertime temperatures similar to the channelized and shade free conditions in the lower Los Angeles region, although some sub-watersheds in the highest elevations will maintain temperatures below 30°C.

The increase of mountain stream temperatures will impact ecology. Stream temperature influences the distribution of fishes, often driven by upper thermal tolerances, by creating a habitat gradient from the cool high grade mountain streams to warm lowland rivers (Cech et al., 1990). Maximum stream temperatures have also been found to be related to the distribution of benthic macroinvertebrates that have traits predisposing them toward cool temperatures (Poff et al., 2010). In the northern part of their range, rainbow trout (*Oncorhynchus mykiss*), a native fish to the West Coast of the United States, have a thermal threshold of 25°C (Cech et al., 1990), however, in the southern part of their range, this study area, they occur in temperatures approaching 30°C (Sloat & Osterback, 2013). Other studies have found that the southern limit of a range is due to a thermal limit (Jones et al., 2009). Our results projected many streams to have maximum temperatures exceeding 30°C. Given the likely adaptation to warmer water temperatures already displayed by southern California rainbow trout, further thermal stress may be detrimental - due to, for example, lower food consumption and growth as temperatures approach lethal temperatures (Myrick & Cech, 2000) - , particularly if there is no cooler water refugia available. Alternatively, warmer water has been found to facilitate invasion by warm water fishes (see review: Rahel & Olden, 2008), which already are widespread in the lowland portions of these watersheds; their further movement to high elevation areas would further imperil the remaining native fishes through competition or predation.

These changes in stream temperature could be further amplified if more fires occur, which is expected with climate change (Westerling et al., 2006). Among other chemical impacts, fires increase stream temperatures by burning down riparian vegetation, which removes shading (Mahlum et al., 2011; Beakes et al., 2014; Koontz et al., 2018), and the immediate impact of heating the water during the fire (Hitt, 2003). Canopy cover has been shown to be more important than air temperature and streamflow in driving stream temperature (Wondzell et al., 2018), and by not considering decreased canopy cover due to fire, we may have underestimated future stream temperatures in reaches that currently have dense tree cover.

The major hydrologic trend we projected is for streams to spend a larger portion of the year dry or flowing below the low flow threshold, but for storm flows to be larger and more frequent. The exception is the Santa Monica Bay, where hydroperiod increases. For many metrics, the change will be most prominent in high elevations, which are projected to have the largest decrease in hydroperiod and the largest increase in storm frequency. In many ways, this future hydrologic regime resembles an amplified version of the current regional climate, where most rain occurs in a few winter storms and the summers are long and dry. Our results, and other studies, find the magnitude of very large flood events to increase toward the end of the century (Das et al., 2013;

Knowles et al., 2018). Additionally, studies have projected the timing of flows will shift earlier in the year creating wetter winters and drier springs and summers (Knowles et al., 2018).

Flow patterns in the riparian corridor drives the distribution of vegetation (Amlin & Rood, 2001; Dixon, 2003). Increased drought, particularly greater than 30 additional days of drought, has been shown to be negatively related to riparian plant biomass and riparian seedling survival (see review: Garssen et al., 2014). Our results project the duration of low flows to be extended in the future by an average of 65 days and that hydroperiods decrease suggesting that riparian plants may shift away from water loving plants like willow (*Salix* spp.), which can reduce nesting area for birds that use scrubby riparian plants like the endangered least Bell's vireo (*Vireo bellii pusillus*). Alternatively, it is not clear how native fishes and amphibians will respond to some of our projections. Species native to southern California in many ways are acclimated to periodic high flows and long droughts (e.g. Castleberry & Cech, 1986; Fisher et al., 2018) whereas invasive fishes and amphibians are not. Additional storm flows of higher magnitude, increased duration of low flows, and decreased hydroperiod (lower water permanence), may favor native species over invasive species (Riley et al., 2005). However, it is also possible that species native to the region are already tolerating conditions near their limits and further deviation from normal could lead to extirpations or extinctions (Filipa et al., 2013).

Changes in streamflow that we project could be exacerbated if more winter precipitation falls as rain and if snow melts earlier in the year (Knowles et al., 2018). The southern California mountains, which surround the urban areas in Los Angeles, get snow in the wintertime. The models we used in this analysis were trained with contemporaneous data, meaning the rain to snow fraction is implicit in the model. End of century snow fall is predicted to be less than 50% of baseline snow fall at low elevations, less than 70% of snowfall at mid-elevations, and little change to the highest elevations (Sun et al., 2016). This could mean even higher flows in the winter and lower flows earlier in the spring than what our models projected, i.e. even lower hydroperiod. Similarly, flows could be less due to increased evaporation from higher temperatures.

### Policy applications

Climate change is widely acknowledged in national, state, and local policy planning as a stressor that will exacerbate many if not all challenges including water, health, and the environment. Studies that quantify climate change can be used in planning in a hands-on manner. The California Water Action Plan 2016 Update (California Natural Resources Agency et al., 2016) acknowledges that climate change will exacerbate most conditions, such as droughts, water supply, and flow regime, but it does not lay out a framework for incorporating climate change projections into the actions laid out in the plan. For example, plans are discussed for enhancing fish migration through barrier removal, fish passageways, and flow enhancements. Studies like this one could be used to help prioritize locations that are projected to maintain suitable conditions within the region and suitable conditions in reaches that provide connectivity through the watershed to promote anadromy, recolonization, and gene flow. Similarly the United States Environmental Protection Agency's (U.S. EPA) Healthy Watersheds Initiative (EPA, 2011), acknowledges that healthy watersheds can help build resiliency toward the impacts of climate change, but passively consider climate change a future stressor in vulnerability assessments. The HWI uses six watershed categories to assess the health of a watershed including (1) landscape condition, (2) habitat, (3) hydrology, (4) geomorphology, (5) water quality, and (6) biological condition (EPA, 2012). Resiliency to climate change, based on studies like this, that project stream hydrology or temperature changes, could be used as an additional watershed health assessment category. That may allow protections, such as with the Wild and Scenic Rivers Act (1968), to be proactively used on rivers projected to maintain high suitability for sensitive or recreationally important species.

The Instream Flow Program, managed by the California Department of Fish and Wildlife (CDFW), determines the amount of flow that should stay in a stream to support ecological needs. This protects stream biology from human diversion of too much flow for other purposes. The program prescribes water use limits based on data collected in current conditions that relate, for example, the relationship of flow and depth or wetted perimeter. With this program, biological streamflow needs can be quantified in the same way as human needs, such as cooling water or irrigation water, are quantified. However, it is important that the flow amounts allocated to other uses not only consider flow availability today, but the flow availability in future years. Studies that document changing flow magnitudes can help managers determine which streams should be allocated more conservatively by considering future flows, or perhaps should not be allocated from at all, versus the streams projected to maintain sufficient flows and can be allocated for other uses. Alternatively, flow allocation review dates could be set based on periods where stream conditions are projected to change so that diversions can be re-evaluated periodically.

There are many other examples of ways that climate change planning can be incorporated into environmental and water related policies. It is important that agencies involved in planning move beyond acknowledging the threat of climate change and begin using projections in decision making.

## *Conclusions*

The goal of this study was to develop a method for modeling streamflow and stream temperature at a high resolution, over multiple watersheds, to help managers plan for wildlife conservation. By projecting future stream conditions, managers can either prioritize locations for restoration projects considering future habitat suitability, or they can proactively plan restoration projects in areas that lose suitability but currently host native species. For example, if certain stream temperatures are projected to exceed the thermal limit of the fish assemblages that occur there, extensive riparian tree planting can be implemented to minimize temperature increases. We project stream temperature to increase regionally, in many locations above thermal limits of freshwater fishes, but certain headwaters are projected to maintain maximum temperatures at levels which native fish can endure. We project the regional hydrology to become drier overall but with more frequent storms. This could strand more fish and amphibians, and vegetation could transition to upland species. There may be a tradeoff between streamflow and temperature that managers will need to consider when planning refuge habitats. While high elevation regions do increase the most, relatively, in stream temperature, they still maintain the coolest temperatures in the region. However, these areas are projected to have longer low- and no-flow periods. Alternatively, the Santa Monica Bay streams are unique in that streams are projected to have flow for a longer duration throughout the year, but temperatures there are very warm. Managers can use these types of projections to plan restoration or conservation activities, and to determine where to initiate monitoring programs to track changing conditions.

### *Supporting Information*

More information is provided on modeling performance and results: Flow metric modeling performance (Appendix S-2-1), stream temperature mid-range and mean value comparison (Appendix S-2-2), stream temperature modeling performance (Appendix S-2-3), median values of temperature and streamflow metrics by watershed and year (Appendix S-2-4), and maps showing the distribution of temperature and streamflow metrics for baseline year 2010 and future year 2100 for each GCM (Appendix S-2-5).

## Appendix S-2-1: Flow metric random forest performance

The random forest models performed well for each flow metric, with $R^2$ values mostly above 0.8, except monthly flows, two- and five-year storm, and the months of minimum and maximum flow. The random forest models for each flow metric generally performed better with the entire suite of predictor variables. For each variable, the prediction $R^2$ was better for the longer timeframes, i.e. the prediction for the 'all year' timeframe was perfect for every variable whereas the predictions for the 3, 5, and 10 year were less accurate. Therefore predicting flow characteristics over a long period is more accurate with this method than attempting to predict the flow regime over just a few years – not surprising given that in Mediterranean regions, total stream flow can vary drastically from year to year (Gasith & Resh, 1999).

Table S-2-1: Flow metric random forest performance.

| Flow Metric | Time Frame | Cal RMSE | Val RMSE | Cal $R^2$ | Val $R^2$ |
|---|---|---|---|---|---|
| R10D.5 | 3 | 0.00 | 0.00 | 0.98 | 0.99 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| R10D.9 | 3 | 0.00 | 0.00 | 0.99 | 0.99 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| HighNum | 3 | 0.02 | 0.02 | 0.96 | 0.95 |
| | all | 0.00 | 0.01 | 1.00 | 1.00 |
| Q90 | 3 | 0.11 | 0.36 | 0.96 | 0.96 |
| | all | 0.02 | 0.01 | 1.00 | 1.00 |
| LowNum | 3 | 0.03 | 0.05 | 0.94 | 0.95 |
| | all | 0.00 | 0.01 | 1.00 | 1.00 |
| Qmean | 3 | 0.08 | 0.27 | 0.96 | 0.96 |
| | all | 0.00 | 0.01 | 1.00 | 1.00 |
| Hydroperiod | 3 | 0.00 | 0.00 | 0.94 | 0.95 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |

| | | | | | |
|---|---|---|---|---|---|
| Q75 | 3 | 0.04 | 0.18 | 0.95 | 0.94 |
| | all | 0.01 | 0.01 | 1.00 | 1.00 |
| SFR | 3 | 0.00 | 0.00 | 0.93 | 0.93 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q50 | 3 | 0.04 | 0.14 | 0.95 | 0.94 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| tenyr | all | 5.42 | 27.33 | 0.96 | 0.97 |
| FracYearsNoFlow | 3 | 0.00 | 0.01 | 0.92 | 0.92 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q99 | 3 | 0.50 | 3.74 | 0.93 | 0.93 |
| | all | 0.06 | 0.12 | 1.00 | 1.00 |
| QmeanIDR | 3 | 0.13 | 0.32 | 0.92 | 0.92 |
| | all | 0.02 | 0.02 | 1.00 | 1.00 |
| QmeanMEDIAN | 3 | 0.03 | 0.21 | 0.90 | 0.91 |
| | all | 0.00 | 0.01 | 1.00 | 1.00 |
| Qmed | 3 | 0.03 | 0.11 | 0.93 | 0.92 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q95 | 3 | 0.28 | 1.20 | 0.89 | 0.91 |
| | all | 0.01 | 0.03 | 1.00 | 1.00 |
| MedianNoFlowDays | 3 | 0.32 | 2.83 | 0.90 | 0.91 |
| | all | 0.24 | 0.20 | 1.00 | 1.00 |
| MinMonthQ | 3 | 0.04 | 0.10 | 0.92 | 0.92 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Qmin | 3 | 0.05 | 0.13 | 0.90 | 0.89 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q25 | 3 | 0.03 | 0.09 | 0.93 | 0.91 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| LowDur | 3 | 0.67 | 5.03 | 0.86 | 0.86 |
| | all | 0.95 | 0.86 | 1.00 | 1.00 |

| | | | | | |
|---|---|---|---|---|---|
| BFR | 3 | 0.00 | 0.00 | 0.84 | 0.85 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| NoDisturb | 3 | 0.32 | 6.13 | 0.87 | 0.87 |
| | all | 0.86 | 0.85 | 1.00 | 1.00 |
| MaxMonthQ | 3 | 0.09 | 0.78 | 0.82 | 0.85 |
| | all | 0.00 | 0.01 | 1.00 | 1.00 |
| Q05 | 3 | 0.03 | 0.09 | 0.87 | 0.86 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| QminIDR | 3 | 0.05 | 0.22 | 0.83 | 0.82 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q10 | 3 | 0.02 | 0.09 | 0.87 | 0.86 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Q01 | 3 | 0.03 | 0.08 | 0.87 | 0.85 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| R10D4D | 3 | 0.00 | 0.01 | 0.78 | 0.79 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| HighDur | 3 | 1.65 | 6.05 | 0.79 | 0.80 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Qmax | 3 | 1.37 | 6.04 | 0.76 | 0.79 |
| | all | 0.03 | 0.03 | 1.00 | 1.00 |
| QmaxIDR | 3 | 0.90 | 54.82 | 0.78 | 0.74 |
| | all | 0.55 | 0.30 | 1.00 | 1.00 |
| May | all | 0.07 | 0.27 | 0.88 | 0.87 |
| Apr | all | 0.17 | 0.36 | 0.85 | 0.86 |
| RecessMaxLength | 3 | 2.57 | 10.15 | 0.72 | 0.71 |
| | all | 0.29 | 0.27 | 1.00 | 1.00 |
| Jun | all | 0.06 | 0.28 | 0.87 | 0.84 |
| Jan | all | 0.69 | 1.31 | 0.81 | 0.83 |
| Mar | all | 0.32 | 1.78 | 0.77 | 0.83 |
| RBI | 3 | 0.01 | 0.01 | 0.70 | 0.71 |

| | | | | | |
|---|---|---|---|---|---|
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Jul | all | 0.05 | 0.28 | 0.86 | 0.82 |
| MinMonth | 3 | 0.03 | 0.12 | 0.68 | 0.68 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |
| Feb | all | 0.44 | 1.81 | 0.79 | 0.78 |
| Aug | all | 0.15 | 0.38 | 0.73 | 0.75 |
| Oct | all | 0.14 | 0.33 | 0.73 | 0.74 |
| Sep | all | 0.14 | 0.34 | 0.72 | 0.74 |
| Nov | all | 0.13 | 0.30 | 0.72 | 0.73 |
| Dec | all | 0.05 | 0.43 | 0.69 | 0.67 |
| twoyr | all | 13.56 | 21.00 | 0.66 | 0.65 |
| fivyr | all | 12.14 | 60.23 | 0.61 | 0.62 |
| MaxMonth | 3 | 0.06 | 0.11 | 0.53 | 0.55 |
| | all | 0.00 | 0.00 | 1.00 | 1.00 |

## Appendix S-2-2: Mid-range and mean comparison

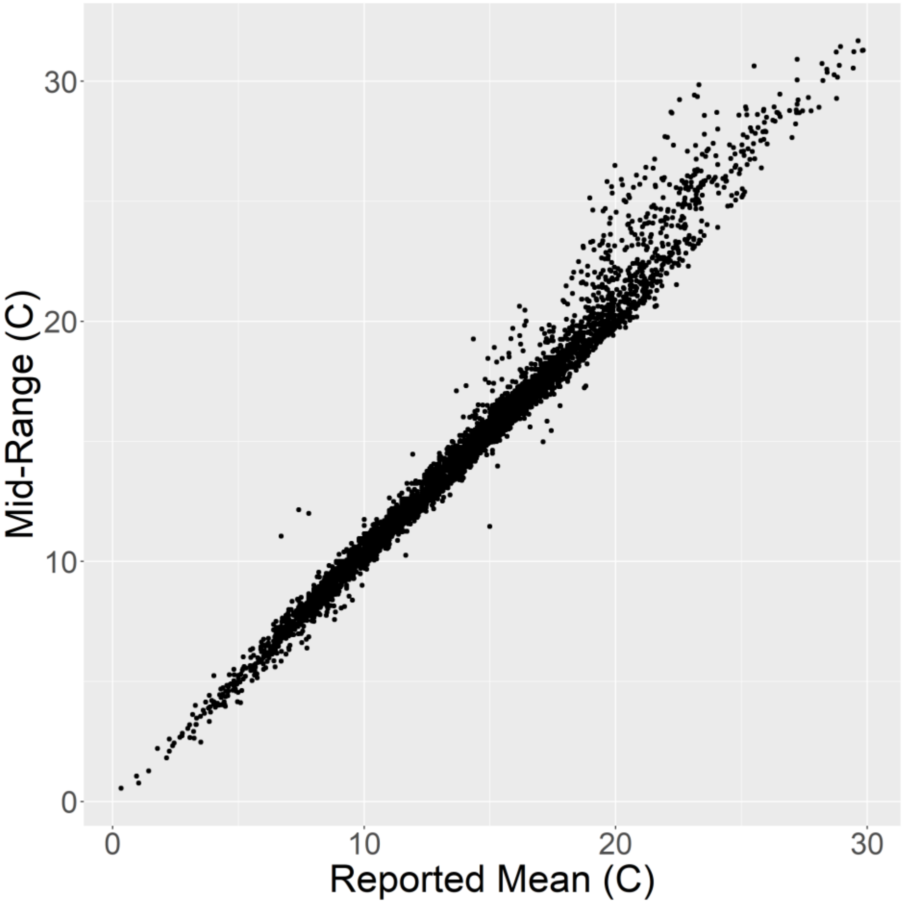

Figure S-2-1: The relationship between stream temperature mean and stream temperature mid-range calculated at sites that reported the mean, maximum, and minimum stream temperatures. Note the strong relationship, but the increase in variance at high temperatures. Additionally, the mid-ranges tend to be higher than means at the high temperatures.

### Appendix S-2-3: Stream temperature modeling performance

Results of the stream temperature model performance. The linear model that predicted rolling seven-day averages, minimums, and maximums performed well with root mean square errors (RMSE) approximately 10% of the range of the values (Table S-2-2, Figure S-2-2). Residuals of each model were sufficiently normal to ensure that a linear regression was appropriate (Figure S-2-3). The model for average and minimum temperatures performed better than the maximum temperature, perhaps because at very hot air temperatures evaporative cooling becomes important and the linear relationship flattens creating an ‘S’ shaped curve, i.e. an increase in air temperature leads to less of an increase in stream temperature. (Mohseni & Stefan, 1999).

Table S-2-2: Stream temperature model performance.

| Model | RMSE (°C) | NSC (unitless) | Testing data range (°C) |
|---|---|---|---|
| Average | 2.14 | 0.63 | 10.27 - 30.89 |
| Min | 2.21 | 0.69 | 4.10 - 25.00 |
| Max | 3.33 | 0.47 | 13.30 - 42.05 |

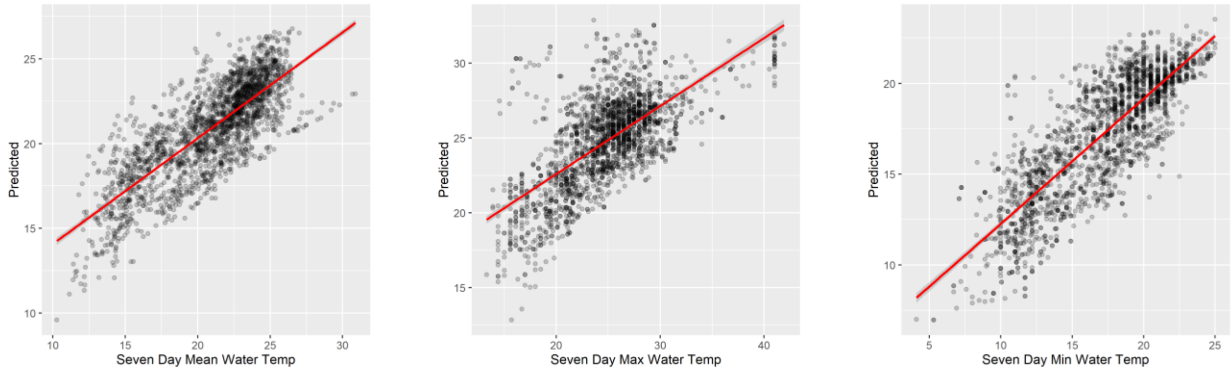

Figure S-2-2: Observed stream temperature metrics (x-axis) versus predicted stream temperature metrics (y-axis).

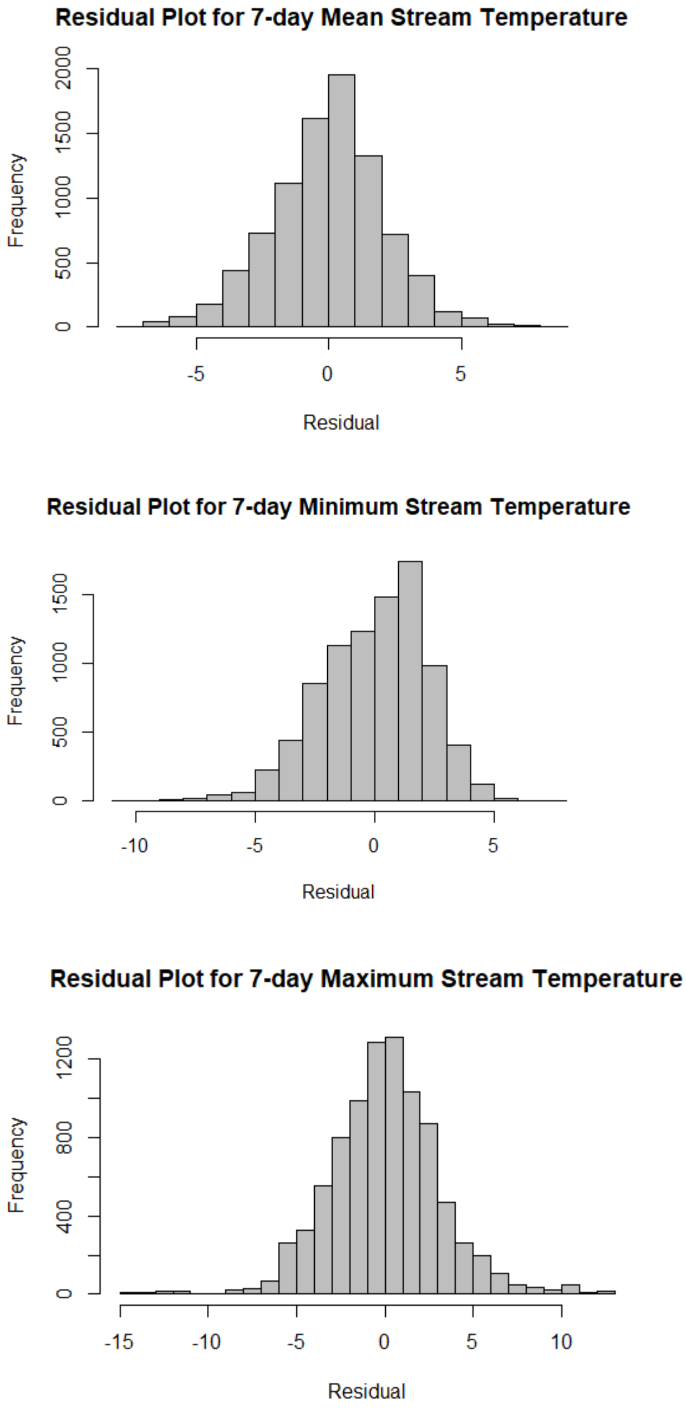

Figure S-2-3: Residual plots for seven day mean (top), minimum (middle), and maximum (bottom) models used on the testing data.

## Appendix S-2-4: Median streamflow and temperature metrics

Table S-2-3: Median streamflow metric values by watershed, in baseline and future years.

| Year | Watershed | GCM | Q99 | SFR | Hydroperiod | LowDur | HighNum |
|---|---|---|---|---|---|---|---|
| 1993 | Calleguas Creek | B_Wet | 26.05 | -0.36 | 0.37 | 384 | 2.76 |
| 2010 | | B_Mod | 10.76 | -0.36 | 0.31 | 487 | 2.49 |
| 2014 | | B_Dry | 6.19 | -0.33 | 0.27 | 560 | 1.49 |
| 2100 | | CanESM2 | 45.79 | -0.43 | 0.29 | 506 | 3.51 |
| 2100 | | CCSM4 | 34.02 | -0.41 | 0.27 | 469 | 3.59 |
| 2100 | | MIROC5 | 36.12 | -0.27 | 0.27 | 479 | 2.78 |
| 1993 | Los Angeles River | B_Wet | 54.49 | -0.07 | 0.73 | 254 | 0.94 |
| 2010 | | B_Mod | 23.52 | -0.04 | 0.72 | 356 | 0.86 |
| 2014 | | B_Dry | 7.16 | -0.03 | 0.63 | 467 | 0.06 |
| 2100 | | CanESM2 | 65.28 | -0.16 | 0.62 | 485 | 2.14 |
| 2100 | | CCSM4 | 50.42 | -0.13 | 0.6 | 477 | 2.26 |
| 2100 | | MIROC5 | 50.91 | -0.08 | 0.63 | 447 | 1.28 |
| 1993 | San Gabriel River | B_Wet | 61.66 | -0.06 | 0.79 | 363 | 1.1 |
| 2010 | | B_Mod | 23.77 | -0.03 | 0.75 | 525 | 0.75 |
| 2014 | | B_Dry | 7.24 | -0.03 | 0.71 | 748 | 0.05 |
| 2100 | | CanESM2 | 67.93 | -0.13 | 0.65 | 529 | 2.37 |
| 2100 | | CCSM4 | 49.87 | -0.12 | 0.65 | 546 | 2.34 |
| 2100 | | MIROC5 | 53.15 | -0.08 | 0.68 | 529 | 1.38 |
| 1993 | Santa Clara River | B_Wet | 72.51 | -0.12 | 0.8 | 256 | 1.63 |
| 2010 | | B_Mod | 31.78 | -0.05 | 0.78 | 387 | 0.92 |
| 2014 | | B_Dry | 10.77 | -0.05 | 0.76 | 523 | 0.07 |
| 2100 | | CanESM2 | 74.14 | -0.14 | 0.68 | 482 | 2.32 |
| 2100 | | CCSM4 | 67.26 | -0.15 | 0.64 | 476 | 2.45 |
| 2100 | | MIROC5 | 68.91 | -0.08 | 0.75 | 417 | 1.72 |
| 1993 | Santa Monica Bay WMA | B_Wet | 18.85 | -0.31 | 0.23 | 401 | 2.95 |
| 2010 | | B_Mod | 9.05 | -0.31 | 0.17 | 484 | 2.74 |
| 2014 | | B_Dry | 6.11 | -0.3 | 0.13 | 550 | 1.83 |
| 2100 | | CanESM2 | 44.85 | -0.44 | 0.26 | 504 | 3.86 |
| 2100 | | CCSM4 | 31.7 | -0.38 | 0.24 | 434 | 3.84 |
| 2100 | | MIROC5 | 29.38 | -0.26 | 0.21 | 459 | 3.07 |
| 1993 | Ventura River | B_Wet | 87.49 | -0.21 | 0.53 | 271 | 1.57 |
| 2010 | | B_Mod | 37.97 | -0.11 | 0.46 | 422 | 0.94 |
| 2014 | | B_Dry | 14.65 | -0.15 | 0.43 | 590 | 0.1 |
| 2100 | | CanESM2 | 91.61 | -0.37 | 0.4 | 483 | 2.37 |
| 2100 | | CCSM4 | 92.43 | -0.27 | 0.38 | 486 | 2.81 |
| 2100 | | MIROC5 | 90.42 | -0.24 | 0.4 | 410 | 1.9 |

Table S-2-4: Median stream temperature metric values by watershed, in baseline and future years.

| Year | Watershed | GCM | Max 7-day Mean | Max 7-day Max | Min 7-day Min | Max 7-day Rng | Max 7-day Max >30 |
|---|---|---|---|---|---|---|---|
| 1993 | Calleguas Creek | B_Wet | 21.49 | 33.6 | 12.5 | 20.45 | 78 |
| 2010 | | B_Mod | 21.96 | 34.43 | 12.6 | 21.05 | 68 |
| 2014 | | B_Dry | 21.65 | 33.68 | 13.3 | 20.31 | 96 |
| 2100 | | CanESM2 | 25.77 | 38.06 | 14.71 | 20.39 | 147 |
| 2100 | | CCSM4 | 23.79 | 36.28 | 14.31 | 20.29 | 144 |
| 2100 | | MIROC5 | 23.83 | 36.33 | 15.16 | 20.38 | 147 |
| 1993 | Los Angeles River | B_Wet | 22.43 | 29.59 | 11.08 | 16.12 | 0 |
| 2010 | | B_Mod | 22.08 | 30.16 | 11.36 | 16.68 | 7 |
| 2014 | | B_Dry | 22.31 | 29.7 | 12.14 | 16.59 | 0 |
| 2100 | | CanESM2 | 26.46 | 33.68 | 13.91 | 17.16 | 103 |
| 2100 | | CCSM4 | 24.65 | 32.08 | 13.7 | 17.12 | 55 |
| 2100 | | MIROC5 | 24.61 | 32.11 | 14.54 | 17.2 | 73 |
| 1993 | San Gabriel River | B_Wet | 22.02 | 29.23 | 11.07 | 15.99 | 0 |
| 2010 | | B_Mod | 21.81 | 30.17 | 11.77 | 16.74 | 4 |
| 2014 | | B_Dry | 22.62 | 29.79 | 11.84 | 16.9 | 0 |
| 2100 | | CanESM2 | 26.01 | 33.44 | 14.11 | 17.1 | 87 |
| 2100 | | CCSM4 | 24.32 | 31.85 | 13.9 | 17.08 | 47 |
| 2100 | | MIROC5 | 24.35 | 31.81 | 14.68 | 17.16 | 54 |
| 1993 | Santa Clara River | B_Wet | 22.57 | 29.01 | 10.37 | 16.12 | 0 |
| 2010 | | B_Mod | 22.01 | 29.14 | 9.71 | 16.56 | 0 |
| 2014 | | B_Dry | 22.04 | 28.49 | 11.24 | 15.63 | 0 |
| 2100 | | CanESM2 | 26.67 | 32.77 | 12.75 | 17.59 | 71 |
| 2100 | | CCSM4 | 24.86 | 31.19 | 12.54 | 17.56 | 35 |
| 2100 | | MIROC5 | 24.77 | 31.66 | 13.42 | 17.68 | 44 |
| 1993 | Santa Monica Bay WMA | B_Wet | 20.38 | 32.35 | 12.32 | 19.33 | 52 |
| 2010 | | B_Mod | 20.29 | 33.04 | 12.3 | 19.86 | 28 |
| 2014 | | B_Dry | 20.77 | 32.56 | 12.86 | 19.44 | 66 |
| 2100 | | CanESM2 | 24.23 | 36.43 | 14.43 | 18.88 | 147 |
| 2100 | | CCSM4 | 22.41 | 34.67 | 13.98 | 18.78 | 139 |
| 2100 | | MIROC5 | 22.53 | 34.77 | 14.8 | 18.79 | 143 |
| 1993 | Ventura River | B_Wet | 22.53 | 31.16 | 12.3 | 17.91 | 31 |
| 2010 | | B_Mod | 22.13 | 31.77 | 12.2 | 17.84 | 13 |
| 2014 | | B_Dry | 22.3 | 31.3 | 13.01 | 17.71 | 47 |
| 2100 | | CanESM2 | 26.14 | 35.34 | 14.5 | 18.54 | 130 |
| 2100 | | CCSM4 | 24.15 | 33.52 | 14.07 | 18.45 | 85 |
| 2100 | | MIROC5 | 24.24 | 33.64 | 14.91 | 18.53 | 112 |

## Appendix S-2-5: Streamflow and temperature metrics spatial distribution by GCM

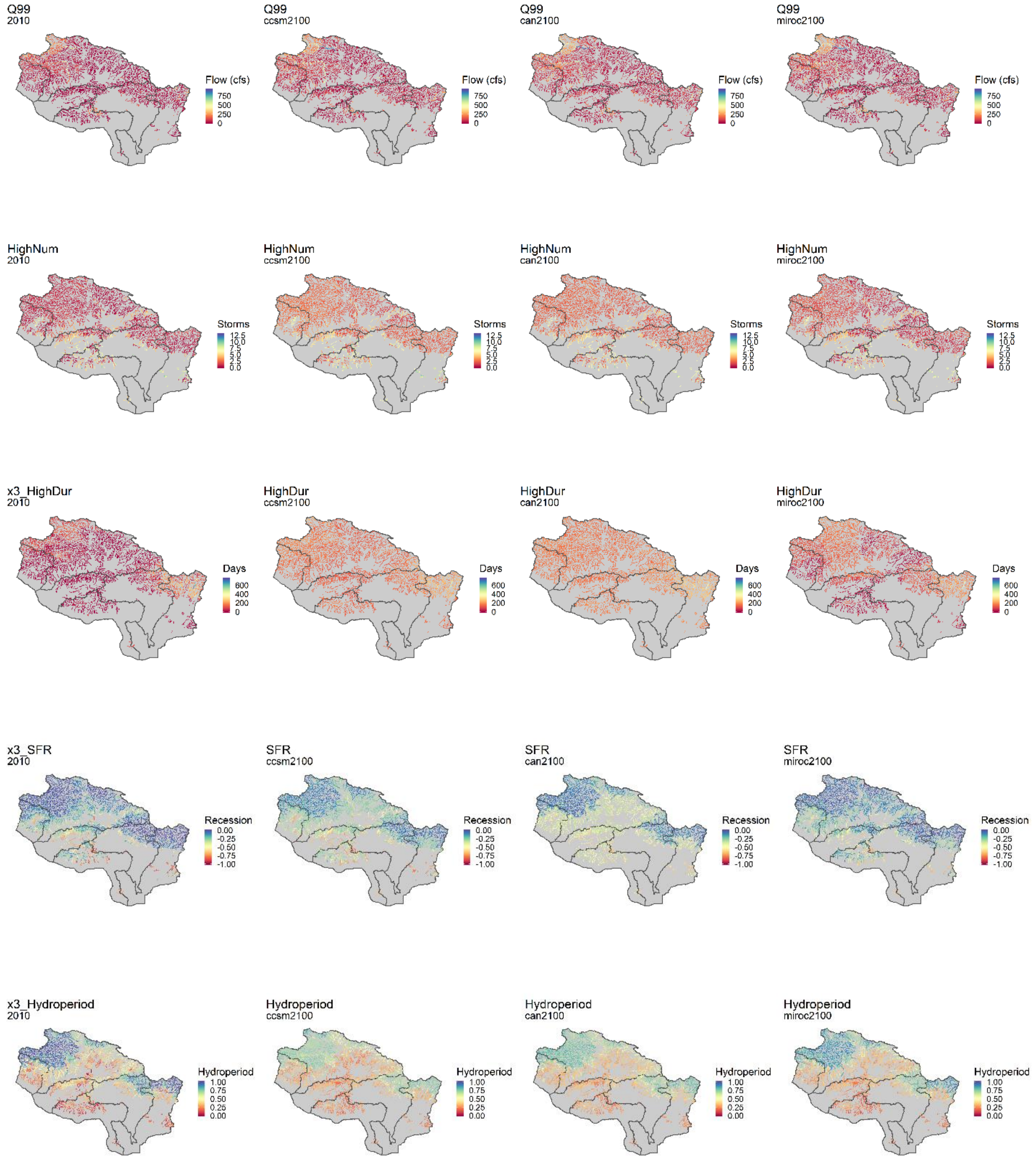

Figure S-2-4: Streamflow metric value distribution for baseline year 2010 and future year 2100, both moderate precipitation years, for the three GCMs. From the top row: Q99, HighNum, HighDur, storm flow recession, hydroperiod.

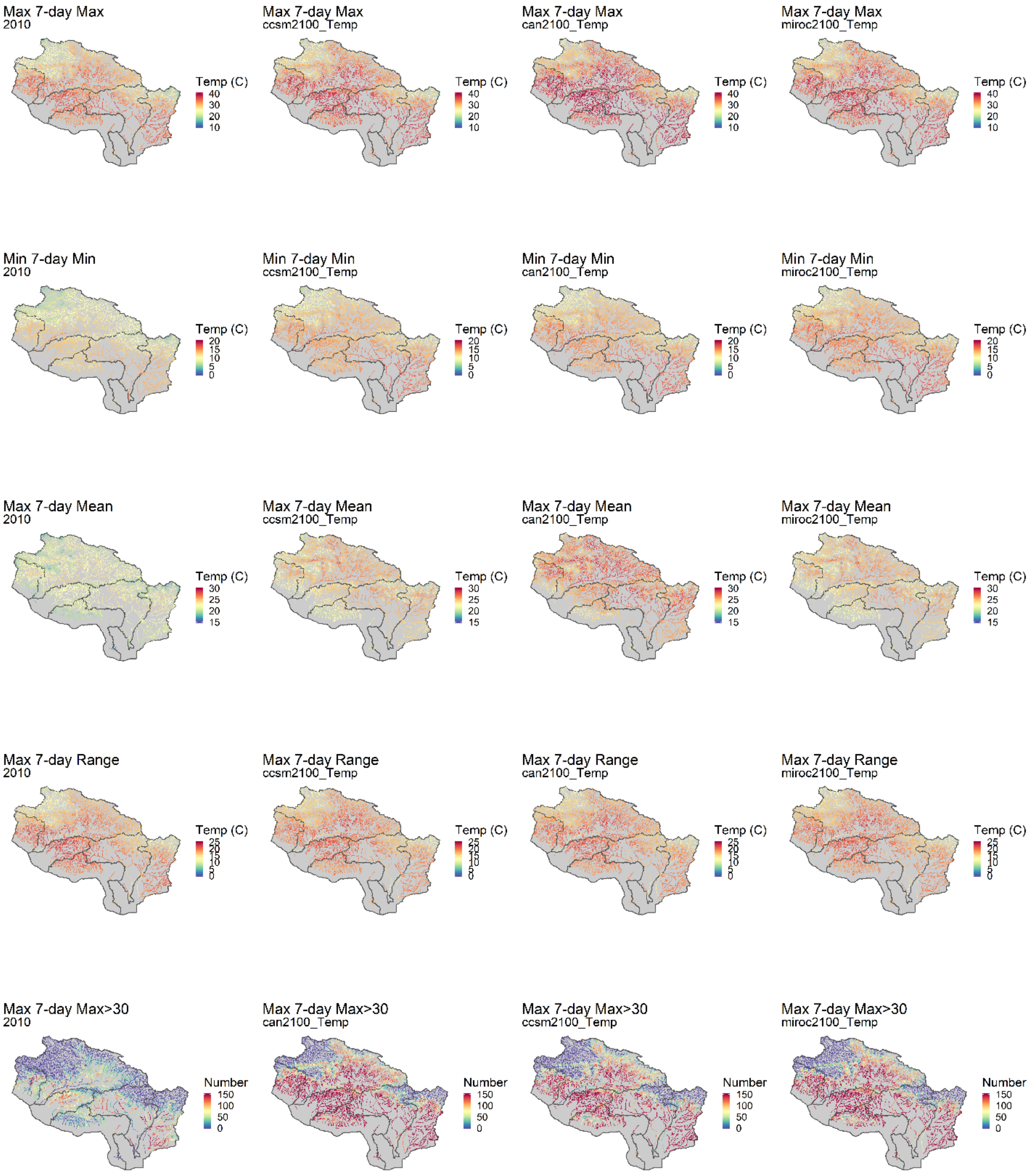

Figure S-2-5: Temperature metric values for baseline year 2010 and future year 2100, both moderate precipitation years, for the three GCM's. From the top row: maximum 7-day maximum flow, minimum 7-day minimum flow, maximum 7-day mean flow, maximum 7-day range, and number of maximum 7-day maximums greater than 30°C.

# Chapter 3 Modeling the impact of climate change induced alterations of streamflow and stream temperature on the distribution of riparian species in southern California

## *Abstract*

Species inhabiting riparian and riverine environments adapt to the habitat formed by physical drivers of the stream. Changing climate will alter this habitat through new precipitation and temperature regimes. Conservation of riparian species benefits from a projection of both future streamflow and stream temperature changes and species response to these changes. In this study, we assess the degree to which projected changes to streamflow and stream temperature in southern California will affect the probability of occurrence and spatial distribution of riparian species. We combine spatially and temporally explicit species occurrence data with streamflow and stream temperature time series, modeled from downscaled climate data, to predict and map habitat suitability in future years 2040 and 2100. This is a novel approach because we use stream-specific environmental predictors rather than general climatic conditions, and because we use environmental data from the time of species occurrence rather than long term trends. We project some species will have moderate to high reduction of suitable habitat while others have a moderate to high expansion of suitable habitat. The three species whose suitable habitat is projected to contract include arroyo toad (*Anaxyrus californicus*), western pond turtle (*Actinemys marmorata*), and coastal rainbow trout / steelhead (*Oncorhynchus mykiss irideus*). The contraction is largely due to warming stream temperatures. The three species whose suitable habitat is projected to expand include arroyo chub (*Gila orcuttii*), least Bell's vireo (*Vireo bellii pusillus*), and Santa Ana sucker (*Catostomus santaanae*), and the expansion is driven by combined streamflow changes and temperature increases. We discuss different interpretations for these findings, including the way the six species differ in their elevational preferences, environmental niche breadths, and endemicity levels. These findings can help managers spatially prioritize conservation efforts such as habitat restoration, habitat connectivity paths, or assisted migration in areas projected to remain suitable under climate change.

### *Keywords*

Species distribution modeling, climate change, environmental flows, ecohydrology, habitat conservation, riparian habitat

## *Web supplemental data*

Spatially explicit probabilities of species occurrence and relationships of species occurrence and environmental metrics are available for viewing and download at https://sccwrp.shinyapps.io/flowecology/

## *Acknowledgements*

We thank the Los Angeles Regional Water Quality Control Board, Region Four, for funding this project. We thank Alex Hall, Jerry H-Y. Huang, and Neil Berg, at the University of California, Los Angeles, for letting us use their downscaled air temperature and precipitation model output for baseline conditions and future projections. We thank Rosi Dagit, Mary Larson, Chris Medak, Chris Dellith, Johnathan Baskin, and Jeff Weaver for letting us species occurrence data collected by their agencies. Finally, we thank members of our technical advisory committee for their thoughtful comments throughout the study.

## *Introduction*

Species occupying stream habitats have a high extinction risk compared to terrestrial species due to habitat isolation and the resulting migration challenges within and between river networks (Poff et al., 2012). In the future, climate change is expected to be a leading cause of species extinction (Thomas et al., 2004; Urban, 2015). Riverine species will exhibit different levels of susceptibility to climate change depending on their environmental tolerances, capacity for adaptation, geographic range size, and their ability to migrate combined with the degree of connectivity of the watershed (Poff et al., 2012). Driven by precipitation and air temperature changes, both range contractions and expansions have been projected for riverine species through novel hydrology and stream temperature (Bond et al., 2011; Wenger et al., 2011). Streams in regions with Mediterranean climates are projected to be particularly affected by climate change due to their already extreme characteristics and repercussions for biota include range shifts, community changes and changes in life history (see review: Filipa et al., 2013). Changes in habitat due to climate change will be particularly felt in southern California where the active channels and riparian zones have been altered by over a century of resource extraction, flood control, urbanization, and agriculture (Mount, 1995), and, as a result, many species and communities are now endangered or threatened (Faber et al., 1989).

Ecohydrology studies are used to elucidate the key characteristics of streamflow that support riparian species (see reviews Bunn & Arthington, 2002; Poff et al., 1997). In Mediterranean regions, total streamflow varies drastically from year to year and often most of the precipitation falls in a few storm events (Gasith & Resh, 1999). Therefore, annual averages are less helpful for describing the annual hydrograph compared to temporally explicit streamflow metrics that describe attributes such as peak flows, recession rates, and timing of events which are essential for different phases of a species life history (Yarnell et al., 2015). Similarly, a stream's thermal regime drives species occupancy and range limits (Welsh et al., 2001; Poff et al., 2002). An assessment of the relationship between species range and streamflow and stream temperature can help develop projections of species occurrences with different future climate scenarios.

Species distribution models are common tools for studying the environmental tolerances of plants and animals (Araújo et al., 2019). One of the major uses of species distribution modeling is assessing the impact of global change on species habitat suitability through changing habitat condition (Guisan & Thuiller, 2005; Guillera-Arroita et al., 2015). A species distribution model uses environmental conditions, such as climatic or topographic data, to predict the distribution of a species globally or locally. There many kinds of models used in the literature including correlations derived from spatial relationships (Prasad et al., 2006; Elith et al., 2008; Wenger et al., 2011; Chee & Elith, 2012), hybrid models which combine process based mechanisms with spatial correlations (Rodríguez et al., 2019), and purely process based approaches (Kearney et al., 2008; Dunbar et al., 2012; Wilding et al., 2014).

In this analysis, we model the future distributions of a selection of sensitive and native riparian species in southern California with metrics that describe the hydrologic and thermal regime. We were able to leverage regionally downscaled climate modeling to use more riparian relevant predictor variables. We use temporally and spatially dynamic species distribution modeling to quantify biologically relevant streamflow and stream temperature metrics that are related to species occurrence. By doing this, we ensure that metric values were exhibited in years when the species was observed, which is especially important for short lived aquatic species in climatically extreme areas like southern California, where populations can surge or crash due to the local and recent climate conditions. This contrasts with many studies which use low resolution climate data related to a general knowledge of species presence in certain regions. We then predict how projected changes in streamflow and stream temperature under different climate change scenarios will impact probability of species occurrence.

This research addresses the following questions:

1. What are the key streamflow and stream temperature metrics that drive the distribution of native riparian or riverine species in southern California?
2. How are species distributions projected to change in future years (2040 and 2100) under novel streamflow and stream temperature regimes resulting from climate change?

## *Methods*

### Study region

The focus of this study is on natural and semi-natural streams in six major watersheds throughout Los Angeles and Ventura counties in southern California, southwestern United States (Figure 3-1), the same study region as Taylor et al., (In Prep). Streams in this region drain steep, geologically young mountains to the Pacific Ocean. These streams range from perennial to intermittent to ephemeral, and the riparian vegetation transitions with these designations from those with high water needs like willow and alder, to those with lower water needs like oak, sycamore, and walnut. There are fewer than ten native fishes in the region dependent on streams, and there are numerous amphibians, reptiles, and birds that have varying levels of dependence on streams. For a full profile of riparian areas in southern CA, see review by Faber et al., (1989). We limited our focus to the mainly unaltered watersheds, mostly in the mountains, where stream habitats and floodplains are still intact and changes in climate will be the leading impact on riparian habitat and fauna, rather than anthropogenic activities.

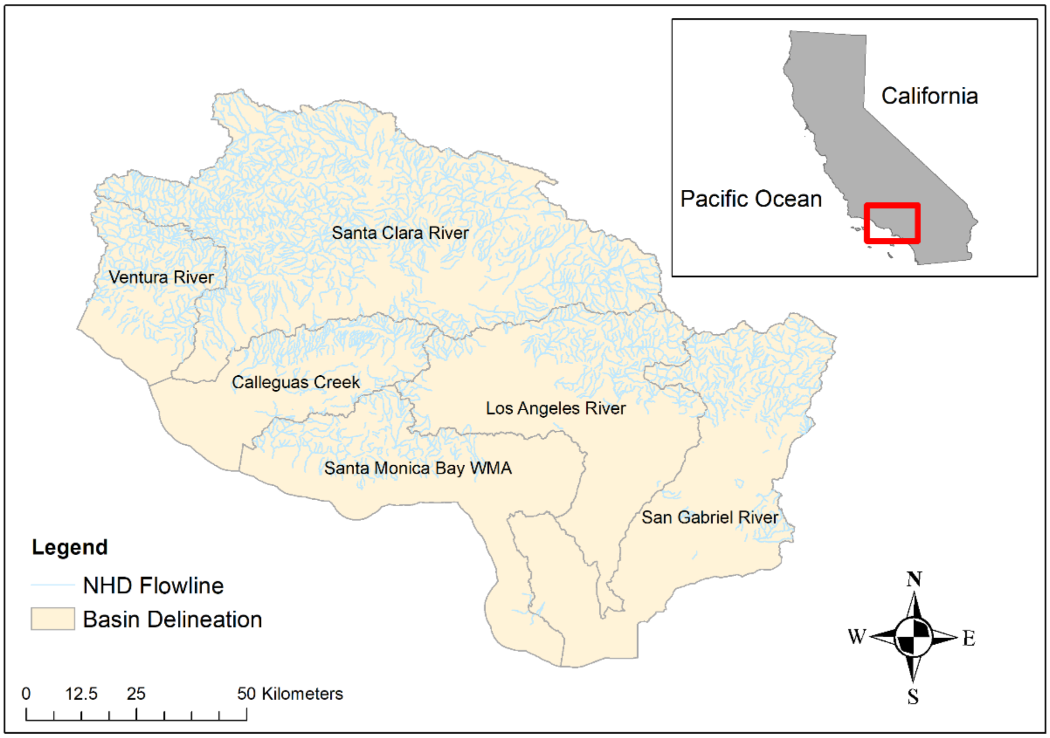

Figure 3-1: Extent of the study region with inset map showing location within California, USA. The flow lines shown are included in this analysis. Blank watershed spaces, such as the lower half of the Los Angeles River watershed, are areas with heavily altered streams and not included in this analysis. Flow line source: USGS national hydrography dataset (NHD).

### Species selection

Our study region covered a diverse landscape including high-grade mountainous streams, low-grade sluggish rivers, and perennial, intermittent, and ephemeral reaches. To select species to model, we used a method that combined the focal species concept described by Lambeck, (1997) and the trait-based approach described in (Olden et al., 2008). We grouped species based on their habitat preferences, which has been shown to be critical in determining which species can be encapsulated by the habitat of an umbrella species (Suter et al., 2002). We selected species that occupy, and therefore characterize, the spectrum of niches available in the region by using a clustering approach followed by a focal species selection, details explained below. This allows for a general understanding of how major groups of riparian-dependent species may respond to changing conditions, without needing to collect detailed occurrence data for all the native species.

However, it is important to note that the use of focal species, or other variations of focal species discussed in the literature, like umbrella or indicator species, will not represent all riparian species (e.g. Simberloff, 1998) and there has been limited validation of the concepts (Roberge & Angelstam, 2004).

We identified sixty-six riparian species in the study area by reviewing databases and reports (Appendix S-3-1). We included species that require stream or adjacent riparian habitat for at least one of their life history stages. Through a rigorous literature review and input from local biologists, we created a life history database for each species that listed habitat and behavioral characteristics that will likely be impacted by climate change, such as stream velocity, vegetation preference, and substrate type. For a complete list of variables see Appendix S-3-2. We separated the birds from the fish, amphibians, and reptiles because the birds were so different that we did not want their differences to mask the more nuanced differences within each group. We transformed the habitat and life history data for both groups, which were compiled as categorical data, to a numeric dissimilarity matrix for use in clustering. We used the function ‘daisy’ from the package “cluster” (Maechler et al., 2017) in RStudio (RStudio Team, 2016) with the distance metric set to “Gower” (as opposed to Manhattan or Euclidian) which calculates distance between categorical variables based on Gower distance (Gower, 1971). With this method, species that have identical habitat traits are characterized as identical (for example each species is 0% dissimilar from itself), and as there are more dissimilar traits between species (for example a preference for fast vs slow velocity), they are classified as more dissimilar from each other. With the habitat dissimilarity matrix, taxa were clustered using a hierarchical clustering method so we could cut the dendrogram where natural breaks appeared to occur, rather than predetermine the number of clusters. In each group, we cut the dendrogram to make five clusters of birds and five clusters combining fish, amphibians, and reptiles where breaks between clusters appeared natural. Clusters were modified and ultimately two additional clusters were made based on feedback from local expert biologists, which helped to ensure that our clusters represent the conditions in the field. The final twelve clusters are shown in Appendix S-3-1.

While we ultimately created twelve clusters to represent the different habitat characteristics of riparian species, we only selected five clusters to model. First, we did not model clusters that were composed entirely invasive species because there is no need to develop conservation programs for these clusters. Next, we did not model a cluster if the species were habitat generalists, such as dabbling ducks or herons, which use many parts of a stream. While massive changes in water availability would no doubt impact these habitat generalists, changes in flow or temperature will have little direct impact, although we do acknowledge that their prey would likely be impacted by stream changes. Additionally, habitat generalists have been found to relate poorly to focal species (Suter et al., 2002). From the five remaining clusters, focal species (Table 3-1) were selected as the most sensitive species in each cluster (Lambeck, 1997), the species more dependent on streams than other aquatic habitats, and finally, for modeling purposes, species with occurrence data from reliable surveys throughout the study region. In one cluster, two focal species were selected because they met all the criteria and are both of high management interest. We think this approach addresses some of the issues with the umbrella species concept because rather than trying to represent all species within a single umbrella based on a large habitat extent, we select focal species to represent only a subset of extant species that occupy a similar niche. Of the six focal species, the order of geographic range size (largest to smallest) is *O. mykiss irideus*, *A marmorata*, *V. bellii pusillus* (breeding only), *A. californicus*, *G. orcuttii*, and *C. santaanae.*

Table 3-1: Focal species for habitat modeling. Conservation status codes: SSC (California Species of Special Concern); FT (federally threatened); FE (federally endangered); ST (state threatened); SE (state endangered). Level of endemism codes: Low (west coast drainages of North America), Medium (central California through Baja California, Mexico), High (Los Angeles region only), CA (California).

| Common name | Scientific name | Life history stage | Habitat description | Conservation status | Mean (sd), and Max elevation based on our data | Level of endemism |
|---|---|---|---|---|---|---|
| Coastal rainbow trout / steelhead | *Oncorhynchus mykiss irideus* | All | Cool, swift, high gradient streams, coarse substrate, deep pools | FE (Steelhead) | 440(317), 1450m | Low: Alaska through southern CA |
| Western pond turtle | *Actinemys marmorata* | Juvenile / adult | Warm, low to mid gradient stream, deep pools | SSC | 246(168), 711m | Low: Washington to North Baja CA, Mexico |
| Least Bell's vireo | *Vireo bellii pusillus* | Breeding pair | Dense, 5-10 year successional stage, riparian vegetation | FE SE | 173(109), 400m | Medium: Central CA to Baja CA, Mexico |
| Arroyo toad | *Anaxyrus californicus* | Clutch | Temporary shallow backwater pools, sandy substrate | FE SSC | 426(196), 1061m | Medium San Luis Obispo county to Baja CA, Mexico |
| Arroyo chub | *Gila orcuttii* | All | Warm, sluggish, shallow, backwater or main channel, low to mid gradient streams | SSC | 345(184), 1153m | High: Santa Barbara to San Diego County |
| Santa Ana sucker | *Catostomus santaanae* | All | Warm to cool flowing water, coarse substrate, low to mid gradient stream | FT | 387(162), 808m | High: Los Angeles and Orange Counties |

### Species distribution data

We compiled the focal species observations within the study region from manuscripts, agency reports and standardized surveys, consulting firm memos, and unpublished raw data sets for the years 1981 through 2017 (Figure 3-2); a list of sources is shown in Appendix S-3-3. It is a

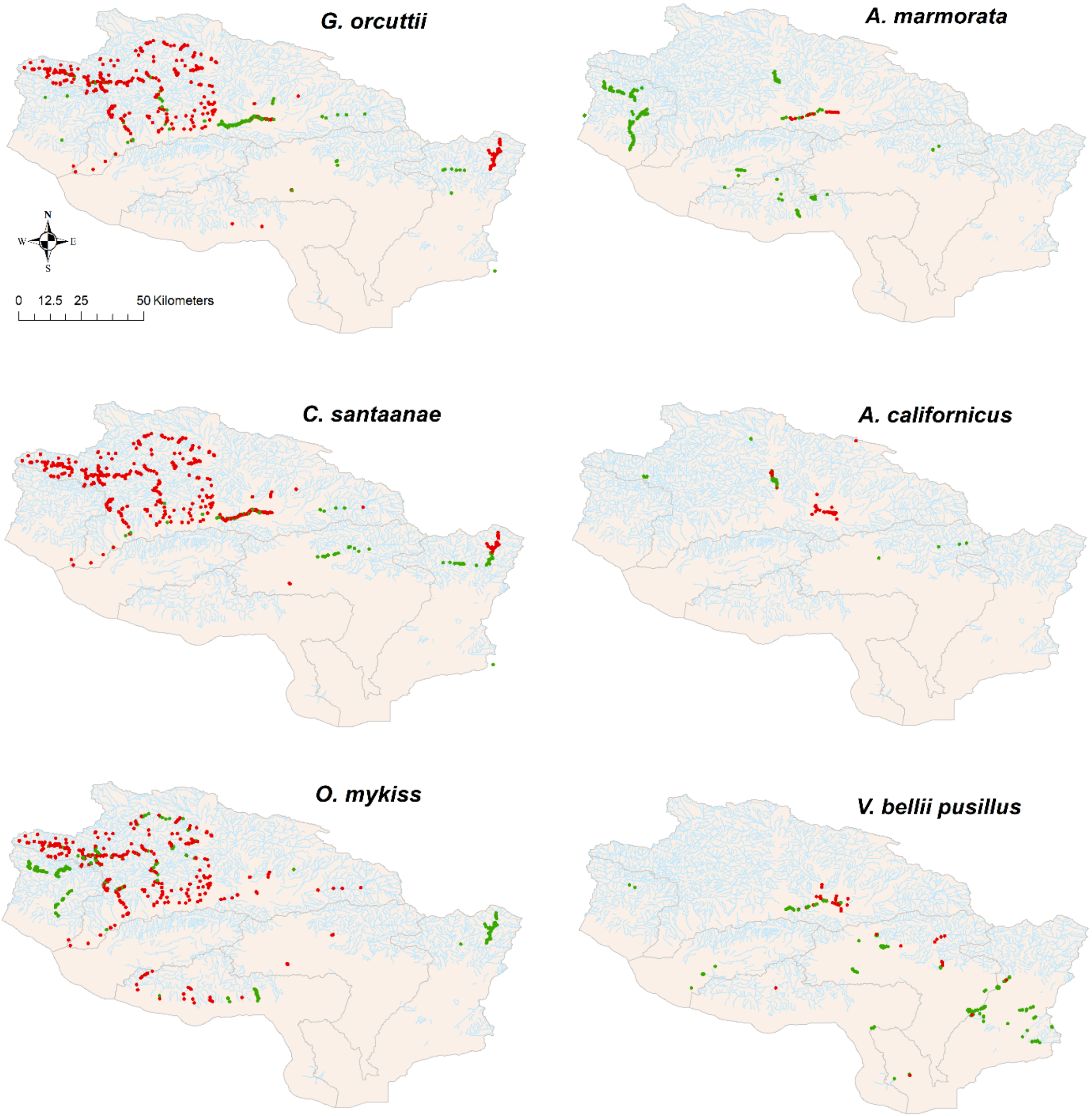

Figure 3-2: Species distributional data across the study region. Each point represents a unique survey. Red points denote species absence and green points denote species presence. Note: If a species observation point is shown in areas where there is no flowline, they are occurring along altered streams reaches and not included in this analysis unless a flow gauge is present in that stream reach, such as some of the points along the Santa Clara River.

limitation of this approach that data were not collected randomly across the entire region because we took advantage of the wealth of survey data that already exists. Species occurrence sources were only included if they reported occurrence location information at the National Hydrography

Dataset (NHD) reach scale (https://www.usgs.gov/core-science-systems/ngp/national-hydrography), and temporal information at the month scale. The NHD characterizes the drainage network in the United States and a reach is the length of stream between two confluences. Occurrences reported in the same stream reach or the same month were combined into a single data point to ensure that the analysis was not biased toward data rich streams. For example, if a surveyor reported an occurrence every 100m in a stream where they were seining for fish, we assigned that stream reach a single occurrence point, as opposed to an occurrence point at each seine location within the reach. We did this because different surveys reported occurrences at different scales which does not reflect the abundance of fish or habitat quality– rather it is an artifact of the sampling procedure. This addresses the issue of pseudo-replication (Hurlbert, 1984) where, in this scenario, detailed survey reporting in certain stream reaches would incorrectly augment the number of species occurrence data points in our model.

The data were minimally altered to get consistency across data sets. For example, sources reported record locations in different ways including coordinates, a stretch of stream marked by stream crossings or roads, or with maps. To compile the record location information, we used the following procedure:

1. A precise coordinate was always used when provided.
2. Stream segment locations were digitized at the beginning and end of the reach, or throughout the segment if multiple NHD stream reaches were surveyed.
3. Locations shown on a map were digitized by finding the location visually in Google Maps and recording the coordinates.

Species occurrence is recorded as presence or absence. If a total count or abundance was provided, a single ‘present’ point was recorded. Absence was assumed when a surveyor failed to find the species they were looking for or when a surveyor did not record the presence of a species in certain locations but did in others. In some cases, the surveyor was contacted to ensure a lack of species record could be considered an absence rather than a lack of reporting. It is important to acknowledge that survey techniques are limited in their ability to detect species 100% of the time (Lahoz-Monfort et al., 2014) and thus there is greater uncertainty in the absence data than the presence data. It is also important to note that species may be absent for many reasons and a limitation of this approach is we attribute absence data to streamflow and temperature conditions, as opposed to, for example, a dispersal limitation.

In our study, we combined the life history forms of *O. mykiss irideus* (coastal rainbow trout and steelhead), and all *aquatic* life history stages of each focal species into a single data set. We did this to be as inclusive of all data sets as possible because some surveys did not note life history stage. Additionally, in some locations it is not clear which life history form of *O. mykiss irideus* was observed. We therefore lumped all reports of either life history form of *O. mykiss irideus* and all life history stages of each focal species into a single presence and absence data set, even though life history stages can have different environmental preference (Welsh et al., 2001; Spina, 2007; Kaylor et al., 2019).

### Environmental data

This analysis investigated the impact of hydrological metrics that describe the pattern of streamflow and stream temperature on the distribution of species. Metrics included have been found to be biologically relevant for freshwater biota, such as high flows or maximum temperatures, and are also sensitive to climate conditions. Daily streamflow and stream temperature were modeled as described in (Taylor et al., In Prep). Briefly, gridded air temperature and precipitation data for three baseline years, a representative wet (1993), dry (2014), and moderate (2010) year, and two future years, 2040 (dry) and 2100 (moderate), were used to model streamflow and stream temperature metrics.

The two future years were modeled using three downscaled global climate models (GCM's) from the Coupled Model Intercomparison Project phase 5 (CMIP5) ensemble, which allows us to consider a range of possible, yet uncertain, future scenarios assuming Representative Concentration Pathway (RCP) 8.5 (an increase of 8.5 Watts/square meter of radiative forcing). According to IPCC (2014), RCP 8.5 represents the upper end of an emission scenario in which no efforts are taken to decrease greenhouse gas emissions, i.e., the business as usual scenario. The three GCM's include CanESM2, CCSM4, and MIROC5, which were among the ten highest rated models for planning in California based on global and southwestern USA historical performance, and based on their ability to capture California's climate variability (DWR, 2015). When compared to observed historical conditions, all three GCM's performed well with mean annual temperature predictions (the bias was within the range of the observed), but for precipitation, only CanESM2 had bias within the range of the observed data; the other two had bias above the range (Rupp et al., 2015). It is important to note that good historical modeling ability may not translate to future modeling accuracy, so it is best to capture as much variation as possible to determine the most likely future climate.

For the baseline and future years, daily flow time series were compiled either from flow gages or from HEC-HMS rainfall runoff modeling of a subset of watersheds using modeled precipitation data (see Taylor et al., In Prep for details). With the flow time series, hydrological metrics were calculated for each species' presence or absence record at the time and location of the biological survey to build models relating species occurrence to hydrologic metrics. Examples of hydrological metrics include hydroperiod, maximum flow, or number of storm events. Each metric was calculated for 3-, 5-, and 10-year time periods from when a species occurrence was observed. For a regional data layer of hydrological metrics for use in species presence or absence prediction, the hydrological metrics were modeled regionally (i.e. for every stream reach) using a random forest approach driven by physical basin characteristics and precipitation, resulting in a hydrological metric for each NHD stream reach for the baseline and future years.

Weekly stream temperature maximum, minimum, and mean were modeled using air temperature data that was either monitored or modeled for baseline and future years for each NHD stream reach using multiple linear regression (see Taylor et al., In Prep for details). From these stream temperature time series, stream temperature metrics were calculated, such as annual maximum seven-day maximum stream temperature or minimum seven-day minimum stream temperature, for each year and location that there was a species observation record (for building the species occurrence model) and for all other NHD reaches (for prediction). These environmental variables used in the species distribution modeling are unique from other studies using CMIP phase 3 or 5 future projections (e.g. Hof et al., 2011; Ochoa-Ochoa et al., 2012; Remya et al., 2015; Wright et al., 2016) because we use highly spatially and temporally explicit environmental metrics mapped to the actual species occurrence or absence point (as opposed to averaged values along a baseline time period and spatial grid cell) and we use stream condition variables instead of precipitation and air temperature variables.

### Biological modeling

We developed statistical models to predict probability of species occurrence (species distribution) using the stream temperature and streamflow metrics. The probability distribution of species occurrence varies within the region depending on the year and sub-watershed. A limitation of this approach is extirpation in one year will not impact the species range predicted for the following year – this is relevant in the event of an extreme period of drought, for example.

The streamflow and temperature metrics were tested for the strength of the relationship with each focal species presence or absence using simple logistic regression. The metrics that were found to be insignificant (P>0.05, except for *A. californicus* where we set the cutoff to P>0.2 because there were so few observations) were removed from the pool of metrics. Each species was analyzed separately; therefore, metrics vary by species. The remaining streamflow and stream temperature metrics were used to predict the species distribution with two separate models.

The first model was a random forest model using streamflow metrics as the predictor variables, which accommodated the large number of hydrological metrics that had significant univariate relationships with each species occurrence. Although the model was trained with a binary 'presence' or 'absence' outcome, we were able to convert this to probability of species occurrence by considering the percentage of time that a 'presence' outcome occurred out of the 500 trees that were produced. Validation of these random forest models was done using 25% of the data that had been removed from the training data (Table 3-2). Full confusion matrices are shown in Appendix S-3-4.

Table 3-2: The accuracy of the species distribution random forest model using the streamflow metrics on the validation data set. The low accuracy and high error rate of *A. californicus* is reflective of the low number of observations.

| | *O. mykiss irideus* | *A. marmorata* | *V. bellii pusillus* | *A. californicus* | *G. orcuttii* | *C. santaanae* |
|---|---|---|---|---|---|---|
| Validation data accuracy | 0.94 | 0.97 | 1.0 | 0.75 | 0.93 | 0.94 |
| Error rate | 7.29% | 5.63% | 6.12% | 32% | 15.73% | 8.47% |

The second model to predict species 'presence' and 'absence' was driven by stream temperature metrics. We used logistic regression modeling and a probability of occurrence was calculated from the log odds by: $P(occurrence) = \exp(\log \text{odds})/(1 + \exp(\log \text{odds}))$. Unlike with the random forest used for the streamflow metric driven model, regression modeling cannot include highly correlated independent variables. To minimize collinearity between the stream temperature metrics, we selected a subset of the six temperature metrics. We either selected the most significant predictor, or if multiple were significant on their own, we selected ones that represented maximum and minimum temperatures.

The two models for species occurrence, streamflow and temperature, resulted in two different predictive maps of species occurrence, which we treated as equally important variables that could both be the limiting environmental variable. To combine the results of the streamflow and temperature modeling, we selected the minimum value of the two models in each stream reach. For example, if the outcome of the streamflow model was 'P=0.60', and the outcome of the temperature model was 'P=0.78', then the final species occurrence probability was 'P=0.60'. A probability of zero, from either the streamflow or temperature model, would result in a 'P=0.0'

It is important to note that there are other drivers of species distribution, besides streamflow and stream temperature, that may change with climate change such as biotic competition (Davis et al., 1998) and barriers to dispersal such as dams, roads, or watershed connectivity (Davis et al., 1998; Araújo & Pearson, 2005). It is also important to note that we did not include the entire range of some of the species which underestimates the range of environmental tolerances (Sinclair et al., 2010). This may underestimate impacts of climate change for species toward the southern end of their range (*O. mykiss irideus* and *A. marmorata*) and potentially overestimate impacts of climate change for species at the mid- to northern end of their range (*A. californicus*). Similarly, as a migratory bird, *V. bellii pusillus* may have problems with climate change in other parts of their range or during migration that we do not consider (Zurell et al., 2018).

## *Results*

The six focal species have different relationships to the streamflow and temperature metrics, as expected (Table 3-3, Table 3-4, respectively). We found that although there was some similarity in the response among species to the baseline conditions, for example high suitability across species in the baseline wet year, there were large differences in the projected response to the future conditions. Though there are exceptions, species that occur in higher elevation sub-watersheds appear to be vulnerable to climate change, while those that occur in lower elevation sub-watersheds appear to either benefit or be unharmed by climate change. This suggests watershed position may be a useful first assessment of species vulnerability, and that different management approaches may be necessary for species depending on their position in the watershed.

### Species environment relationship

For a full account of each species association with the streamflow and stream temperature metrics, see Appendix S-3-5; we briefly summarize here.

There were significant relationships found between streamflow metrics and each of the focal species (Table 3-3). *Oncorhynchus mykiss irideus* was consistently associated with high flow magnitudes and more consistent flows, i.e. there was a negative relationship with storm events and drought events, and a positive association with hydroperiod. *Anaxyrus californicus* was associated with more rapid recessions, flashier flows, and no flow periods in the short term (3-year), but consistent flows in the stream reach over longer time periods (all-year). *Gila orcuttii* and *C. santaanae* were associated with flashiness, rapid recessions, storm events, and were negatively associated with hydroperiod (i.e. they occur in streams that do not flow for part of the year). Both *G. orcuttii* and *C. santaanae* had positive relationships with flow magnitude at the 3-year timeframe, but *C. santaanae* had negative relationships with flow magnitude at the all-year time frame. *Vireo bellii pusillus* had a positive relationship with flashy streams, fast recessions, and the frequency and recency of storms, but had a negative relationship with hydroperiod. *Vireo bellii pusillus* consistently had a negative relationship with flow magnitude. *Actinemys marmorata* was positively related to RBI, yet otherwise was associated with low flow magnitudes, and a long duration of low flows, and a low frequency of storms.

Table 3-3: Univariate logistic regression results for species presence or absence and a subset of the streamflow metrics. Sign refers to the direction of the coefficient. Significance codes: $p<0.001$ ***; $p<0.01$ **; $p<0.05$ * except for *A. californicus* where $P<0.2$ *.

| Timeframe | Flow Metric | *Category* | *O. myk* | *A. mar* | *V. b. pu* | *A. cal* | *G. orc* | *C. san* |
|---|---|---|---|---|---|---|---|---|
| all | R10D.5 | Flashiness | + *** | NS | - *** | NS | - *** | - *** |
| 3 | R10D.5 | Flashiness | + *** |  | - *** | NS | - *** | - *** |
| 3 | R10D.9 | Flashiness | + *** |  | - *** | - * | - *** | - *** |
| all | R10D.9 | Flashiness | + *** | - *** | - *** | NS | - *** | - *** |
| all | RBI | Flashiness | - *** | + *** | + *** | NS | + *** | + *** |
| 3 | RBI | Flashiness | - * |  | + *** | + * | + *** | + *** |
| all | FracYearsNoFlow | Duration | - *** | NS | + *** | - * | + *** | + *** |
| 3 | FracYearsNoFlow | Duration | - *** |  | + *** | + * | + *** | + *** |
| all | Hydroperiod | Duration | + *** | NS | - *** | + * | - *** | - *** |
| 3 | Hydroperiod | Duration | + *** |  | - *** | NS | - *** | - *** |
| all | RecessMaxLength | Duration | + *** | + * | - *** | NS | - *** | - *** |
| 3 | RecessMaxLength | Duration | + *** |  | - ** | - * | - *** | - *** |
| all | HighDur | Duration | + *** | - ** | NS | NS | NS | NS |
| 3 | HighDur | Duration | + *** |  | NS | NS | - * | + *** |
| all | LowDur | Duration | - *** | + ** | + ** | NS | + ** | + ** |
| 3 | LowDur | Duration | - *** |  | + *** | NS | NS | - * |
| all | NoDisturb | Duration | + *** | + * | - *** | NS | - *** | - *** |
| 3 | NoDisturb | Duration | + *** |  | - *** | NS | - *** | - *** |
| all | HighNum | Frequency | - ** | - *** | + *** | NS | + *** | + *** |
| 3 | HighNum | Frequency | - ** |  | + *** | NS | + *** | + *** |
| 3 | LowNum | Frequency | - *** |  | + *** | NS | + *** | + *** |
| all | LowNum | Frequency | - ** | NS | + *** | NS | + *** | + *** |
| 2 | storm | Timing | - *** |  | - ** | NS | - * | - *** |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 5 | storm | Timing | NS | | - * | + * | NS | - ** |
| 3 | Q01 | Magnitude | + *** | | - *** | NS | + ** | NS |
| all | Q01 | Magnitude | + *** | NS | NS | NS | - *** | NS |
| 3 | Q10 | Magnitude | + *** | | - *** | NS | + ** | NS |
| all | Q10 | Magnitude | + *** | NS | - *** | NS | NS | NS |
| 3 | Q75 | Magnitude | + *** | | - *** | NS | + * | NS |
| all | Q75 | Magnitude | + *** | - * | - *** | NS | + * | - * |
| 3 | Q99 | Magnitude | + *** | | NS | NS | + * | + * |
| all | Q99 | Magnitude | + *** | - *** | - * | NS | NS | - * |
| 3 | Qmed | Magnitude | + *** | | - *** | NS | + ** | NS |
| all | Qmed | Magnitude | + *** | - * | - *** | NS | + * | NS |
| 3 | Qmin | Magnitude | + *** | | - *** | NS | + ** | NS |
| all | Qmin | Magnitude | + *** | - * | - *** | NS | + ** | NS |
| all | QmaxIDR | Variability | + *** | - *** | NS | NS | NS | NS |
| 3 | QmaxIDR | Variability | + *** | | NS | NS | NS | NS |
| all | QmeanIDR | Variability | + *** | - *** | - *** | NS | NS | - * |
| 3 | QmeanIDR | Variability | + *** | | - ** | NS | NS | + * |
| 3 | QminIDR | Variability | + *** | | - ** | NS | NS | NS |
| all | QminIDR | Variability | + *** | NS | - ** | NS | NS | NS |

Stream temperature was found to be important for all six species although the relationships differed between species (Table 3-4). *Oncorhynchus mykiss irideus* and *A. californicus* had a strong preference for cooler temperatures whereas *G. orcuttii*, *C. santaanae*, and *V. bellii pusillus* were associated with warmer temperatures. The turtle *A. marmorata* was the only species to display a more complex relationship with stream temperature and was associated with warmer maximum temperatures but cooler minimum temperatures. In general, *A. californicus* was associated with streams that maintained the coolest maximum temperatures (<28.4°C), followed by *O. mykiss irideus* (<32.5°C). The two other fishes had maximum stream temperatures which were 25°C to 32.5°C, (*C. santaanae*) and greater than 27.5°C (*G. orcuttii*). Interestingly, *V. bellii pusillus* occurred only in streams that had a maximum 7-day maximum greater than 30°C, and as high as 34°C which could be mediated through the low elevations that support their preferred riparian vegetation for nesting, their insect prey relationship with stream temperature, or some other factor associated with warm water.  Overall, there is a spectrum of thermal associations showing the importance of warm and cool water habitat throughout the region.

Table 3-4: Logistic regression results from the species distribution model driven by stream temperature.

| Species | Variable | Coefficient (log odds) | Std. error (log odds) | P-value |
|---|---|---|---|---|
| *O. mykiss irideus* | Maximum 7-day maximum | -0.8189 | 0.2144 | 1.34e-4 |
| | Minimum 7-day minimum | -1.3128 | 0.1993 | 4.53e-11 |
| | Maximum 7-day range | 1.0909 | 0.1987 | 4.03e-08 |
| *A. marmorata* | Maximum 7-day maximum > 30°C | 0.05757 | 0.01775 | 0.00118 |
| | Minimum 7-day minimum | -0.70585 | 0.37377 | 0.05897 |
| *V. bellii pusillus* | Maximum 7-day maximum | 1.6718 | 0.4621 | 2.97e-4 |
| | Minimum 7-day minimum | 1.9528 | 0.4194 | 3.22e-06 |
| *A. californicus* | Maximum 7-day maximum | -0.7605 | 0.4577 | 0.0966 |
| *G. orcuttii* | Minimum 7-day minimum | 1.3972 | 0.2447 | 1.13e-08 |
| *C. santaanae* | Maximum 7-day Average | 0.4353 | 0.2566 | 0.0897 |

### Projected changes in species occurrence due to climate change

Compared to the moderate baseline year, 2010, *A. californicus*, *A. marmorata,* and *O. mykiss irideus* are projected to have a reduction in average probabilities of occurrence in response to the novel climate conditions in year 2100, whereas the other three species are projected to have increases in the probability of occurrence (Table 3-5).  The average probabilities of occurrence are projected to decrease by 40% for *A. californicus*, 67% for *A. marmorata,* and 6% for *O. mykiss irideus* - a much smaller reduction than the first two species and possibly not meaningful.  The magnitude of the projected impact on *O. mykiss irideus* could have been diminished because we included migration observations in the species occurrence data set from low elevations, as opposed to only including observations from their spawning grounds in the high elevation tributaries. On the other hand, the average probabilities of occurrence are projected to increase by 102% for *G. orcuttii*, 74% for *C. santaanae*, and 68% for *V. bellii pusillus*.

Table 3-5: Average probability of occurrence throughout the region in the baseline moderate year (2010) and in the future moderate year (2100) averaged across all GCMs.

| Species | Year | Mean | St. dev | Change |
|---|---|---|---|---|
| *O.mykiss irideus* | Baseline | 0.32 | 0.21 | ↓ |
| *O.mykiss irideus* | Future | 0.30 | 0.15 | |
| *A. marmorata* | Baseline | 0.76 | 0.17 | ↓ |
| *A. marmorata* | Future | 0.25 | 0.23 | |
| *V. bellii pusillus* | Baseline | 0.28 | 0.39 | ↑ |
| *V. bellii pusillus* | Future | 0.47 | 0.33 | |
| *A. californicus* | Baseline | 0.32 | 0.28 | ↓ |
| *A. californicus* | Future | 0.19 | 0.25 | |
| *G. orcuttii* | Baseline | 0.19 | 0.24 | ↑ |
| *G. orcuttii* | Future | 0.41 | 0.17 | |
| *C. santaanae* | Baseline | 0.19 | 0.11 | ↑ |
| *C. santaanae* | Future | 0.33 | 0.14 | |

There were three projected outcomes: species occurrence probabilities that decreased in response to the climate change conditions but were not as low as the dry baseline year probabilities of occurrence, species occurrence probabilities that decreased in response to the climate change conditions to levels lower than all three baseline years, and species occurrence probabilities that increased in response to the climate change conditions to levels greater than all three baseline years (Table 3-6). By 2100, probability of *O. mykiss irideus* occurrence is projected to drop toward the level in the dry baseline year. Probabilities of *A. californicus* and *A. marmorata* occurrences are projected to drop precipitously to levels below all the baseline year probabilities and are approximately four times below the moderate baseline year. The remaining three species are projected to respond favorably to new conditions. In the baseline years, the three fish species had the highest probabilities of occurrence during the wet year, 1993, followed by the moderate year, 2010, and the dry year, 2014. Two of the fishes, C. *santaanae* and *G. orcuttii*, are projected to respond favorably to climate change and the median probability of occurrence surpasses the wet baseline year. Probability of *V. bellii pusillus* occurrence is projected to increase beyond all three baseline years.

Table 3-6: The median probability of occurrence for each species in the three baseline years (wet,1993; moderate, 2010; and dry,2014) and the two future years (dry, 2040; moderate, 2100), for the three GCMs. The highest values of all the years is bolded. Future years include only the unaltered NHD reaches that were included in the baseline modeling, so the change in probability reflects the changing climate alone. The value in parentheses includes all NHD reaches, so the change in probability reflects both the changing climate, and the inclusion of stream reaches which applies only if the natural hydrology is restored.

| Year | GCM | *O.mykiss irideus* | *A. marmorata* | *V. bellii pusillus* | *A. californicus* | *G. orcuttii* | *C. santaanae* |
|---|---|---|---|---|---|---|---|
| Wet | baseline | **0.38** | **0.79** | 0.004 | 0.28 | **0.16** | **0.22** |
| Mod | baseline | 0.34 | **0.79** | 0.003 | 0.23 | 0.09 | 0.18 |
| Dry | baseline | 0.25 | 0.70 | **0.01** | **0.35** | 0.11 | 0.16 |
| 2040 | CanESM2 | **0.35** (0.33) | 0.48 (0.46) | **0.39** (0.48) | 0.13 (0.09) | **0.39** (0.43) | **0.29** (0.31) |
| | CCSM4 | 0.34 (0.33) | **0.71** (0.70) | 0.34 (0.44) | **0.17** (0.13) | 0.32 (0.35) | 0.22 (0.25) |
| | MIROC5 | 0.32 (0.31) | 0.56 (0.55) | 0.37 (0.49) | 0.13 (0.10) | 0.37 (0.40) | 0.28 (0.31) |
| 2100 | CanESM2 | 0.27 (0.24) | 0.03 (0.03) | 0.44 (0.52) | 0.02 (0.01) | **0.41** (0.45) | **0.36** (0.38) |
| | CCSM4 | **0.33** (0.30) | 0.23 (0.21) | 0.43 (0.53) | **0.07** (0.05) | 0.33 (0.36) | 0.29 (0.33) |
| | MIROC5 | 0.28 (0.26) | **0.24** (0.22) | **0.48** (0.55) | 0.05 (0.04) | 0.38 (0.42) | 0.30 (0.34) |

### Influence of streamflow versus temperature

In this analysis we combined the projected species occurrence probabilities from streamflow and temperature models, but it can be helpful for managers to determine the limiting variable. Figure 3-3 shows the distribution of projected occurrence probabilities for each species and timeframe, based on streamflow (black) and temperature (grey). Most surprising is that for all species except *V. bellii pusillus,* there was a similar negative response in the probability distributions for streamflow and temperature to the dry baseline year compared to the moderate and wet year, but in the future there is no common trend between the species. In the two future years, temperature is projected to be limiting for *A. californicus* and *A. marmorata*, and there is a clear streamflow limitation projected for *G. orcutii*.

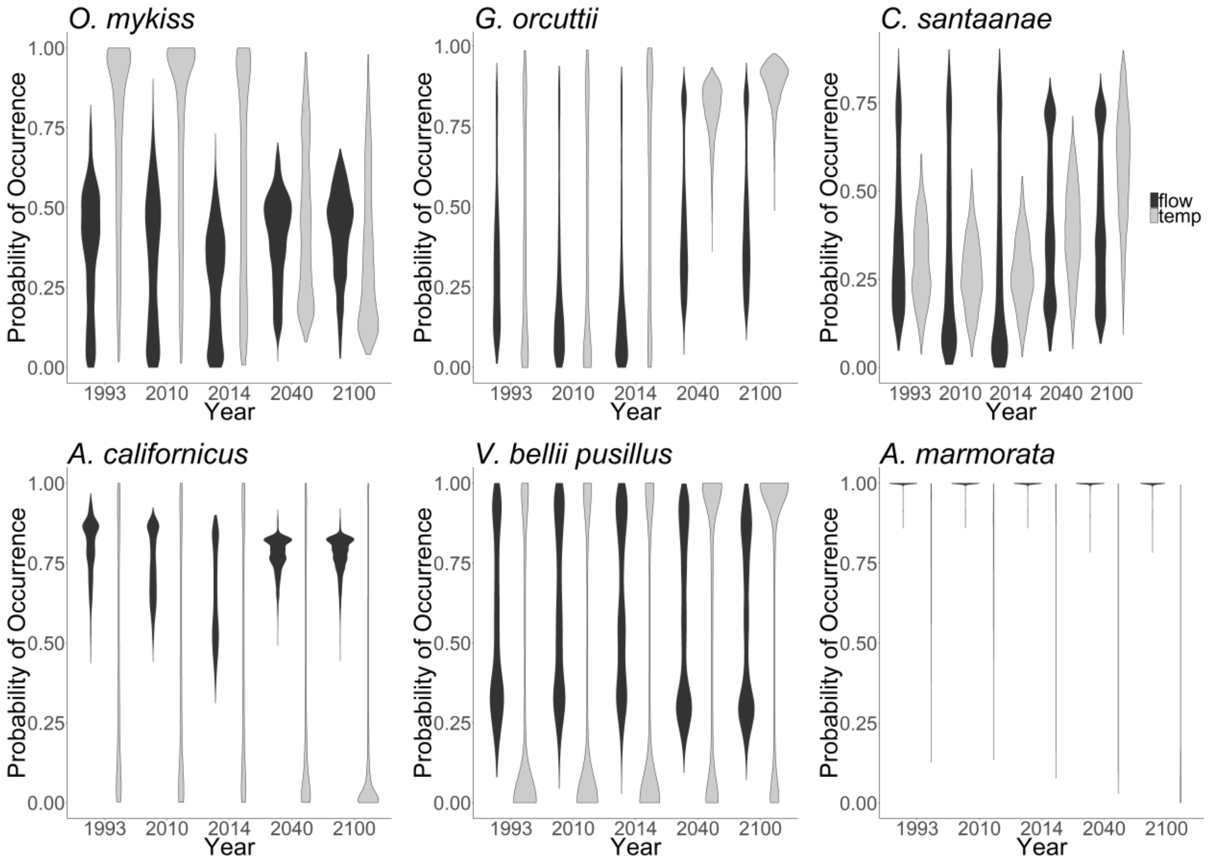

Figure 3-3: Violin plots show the probability distributions for each of the five years investigated. In the future years, all GCM values are included. The black violins are probabilities of occurrence driven by streamflow metrics and the gray violins are driven by the stream temperature metrics.

In the three baseline years, *O. mykiss irideus* has favorable probabilities of occurrence due to temperature (large grey point mass near one) but the distribution from streamflow (black) is lower (Figure 3-3). Projected probabilities due to streamflow and temperature are lowest in the dry baseline year 2014. In the two future years, projected probabilities of occurrence due to streamflow do not change much, although the distributions are less spread toward zero, but probabilities due to temperature decrease dramatically. In the three baseline years, *G. orcuttii* has a spread out and fairly uniform distribution of occurrence probabilities due to streamflow and temperature, but there is a larger point mass toward zero due to streamflow. In the future years, projected probabilities of occurrence due to temperature increase dramatically and the distribution becomes less spread out. Minimum probabilities of occurrence due to streamflow increase, but the distribution remains spread showing that streamflow is limiting for *G. orcuttii* in future years. *Catostomus santaanae* has a similar, though slightly decreasing, probability distribution in the three baseline years due to temperature, but the distribution due to streamflow decreases, despite the large spread in all three years. In the future years, the projected distribution due to temperature extends toward higher probabilities while the minimum values stay similar, and the distribution due to streamflow becomes slightly less spread out. The probability distribution for *A. californicus* modeled from temperature are consistent in the three baseline years, but the distribution from streamflow decreases in the dry year. In the future years, the projected probabilities due to temperature decrease dramatically (a large point mass forms toward zero), despite streamflows remaining favorable, showing that temperature is projected to be limiting. The probability distribution of *V. bellii pusillus,* is strongly limited by temperature in the baseline years indicated by the large grey point masses at zero, while projections due to streamflow are spread. Projected probabilities from streamflow do not change in the future year but the probabilities due to temperature increase dramatically. Finally, *A. marmorata* was unique in that probabilities of occurrence from streamflow were high in all baseline and future years, which meant that its distribution was limited by temperature. Probability of occurrence based on temperature is projected to decrease in 2040 and decrease more in year 2100 showing a major temperature limitation.

## Range changes

The projected range (stream reaches with high probabilities of occurrence) contracted from the baseline years to both future years for *A. californicus*, and *A. marmorata* (Figure 3-4). The reduction in range for *A. californicus* occurred in high mountain regions where there is a clear decrease in probability. Interestingly, the projected probabilities increase in low elevation regions, but are still quite low so we do not expect expansion into those areas. The reduction in range is clear for *A. marmorata* across the entire region which had favorable probabilities in the baseline years, but dropped precipitously in year 2100, except in the Santa Monica Mountain area which, surprisingly, had an increase in probability. The range for *O. mykiss irideus* is projected be similar to the baseline years.

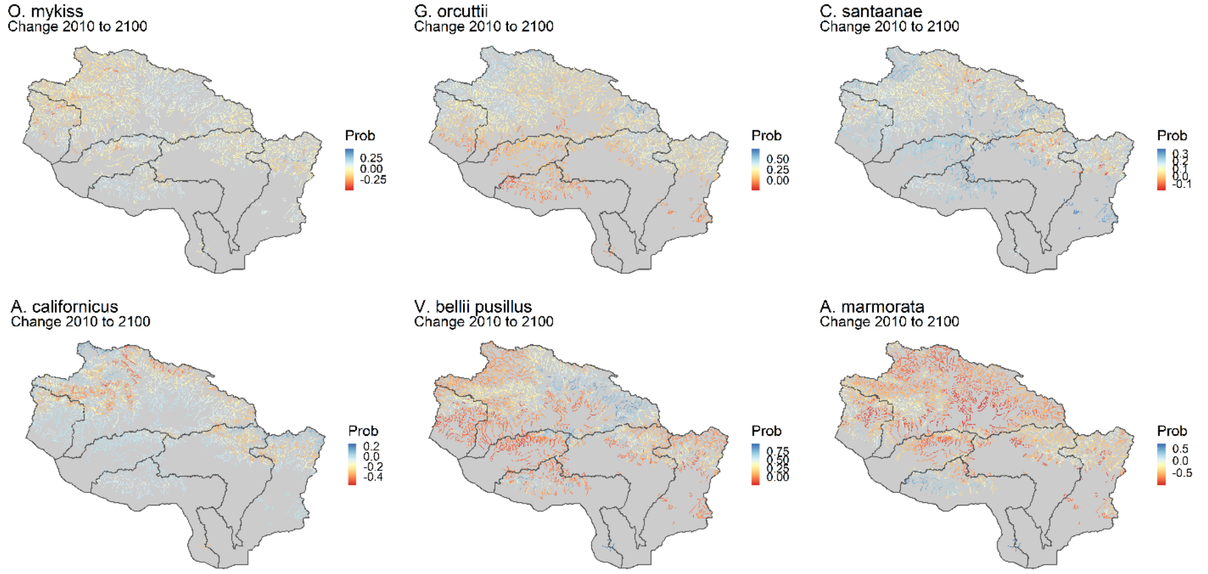

Figure 3-4: Change in probability of occurrence from 2010 to 2100 calculated as 2100 minus 2010. The 2100 value is the average values of the three GCMs. Note that the scale is different for each species.

The range for *G. orcuttii* is projected to extend to higher elevations than in the baseline year in all watersheds. Similarly, but less dramatically, the range of *C. santaanae* is projected to extend to regions in higher elevations, most notably in the upper Santa Clara River watershed. The range is also projected to include the Santa Monica Mountains, a region that historically did not support *C. santaanae*. The range for *V. bellii pusillus* is similarly projected to expand to higher elevations, particularly in the eastern areas of the Santa Clara River watershed. See Appendix S-3-6 and Appendix S-3-7 for maps showing the baseline range and the projected future ranges for each species.

### GCM comparison

Projections from the three GCMs, CanESM2, CCSM4, and MIROC5, showed similar trends across species and future years, except in year 2100 with CanESM2. The median probability for *A. marmorata*, in 2100, was substantially lower with CanESM2 (0.03), than CCSM4 (0.21) or MIROC5(0.22) (Table 3-6). While far less extreme, the 2100 CanESM2 model projected lower probabilities for *O. mykiss irideus* and *A. californicus* compared to the other two GCM's. These three species had populations in high elevation sub-watersheds which perhaps suggests that the three GCM's project similar changes in low regions but diverge from each other in high elevations.

## *Discussion*

### Species vulnerability patterns

Two characteristics emerged as potential risk factors of vulnerability to climate change: species that occur in high elevation sub-watersheds and species that have a small environmental niche breadth, regardless of the geographical extent of their range.

The two species that generally occurred highest in the watersheds (*O. mykiss irideus* and *A. californicus*) are projected to lose suitable habitat due to climate change whereas two of the species that mostly occur in low regions (*G. orcuttii* and *V. bellii pusillus*) are projected to gain suitable habitat due to climate change. An exception is *A. marmorata*, which occurs low in the watersheds but is projected to lose suitable habitat due to climate change. Other studies have found greater reduction in range size and risk of extinction for species in high elevation areas (Bomhard et al., 2005; Loarie et al., 2008). One reason could be that species which occur in cool high elevation areas are more vulnerable toward warming (Thuiller et al., 2005) which is also supported by our finding that both *O. mykiss irideus* and *A. californicus* were projected to be temperature limited in future years. As temperatures rise, the lower elevational limit moves up the mountain (Wilson et al., 2005; Dirnböck et al., 2011), resulting is less suitable habitat at moderate elevations which historically supported the species. Thuiller et al., (2005) found that species in very warm regions are less sensitive to warming and predicted that their range expands regardless of their rarity or niche breadth. Therefore, a replacement of high elevational species by lower elevational species is projected to occur at the transition between habitat types on the mountains, reducing the suitable habitat range of species occupying the highest elevations.

A decrease in habitat suitability at moderate elevations, which leaves just the highest elevations of a species range suitable, may start a negative feedback loop for additional habitat loss. River systems are connected longitudinally from headwaters to estuary and the anadromous life form of *O. mykiss irideus* migrate this length. A loss in suitability at moderate elevations could stifle recolonization by adults migrating up the watershed for spawning. Kaylor et al., (2019) found that trout populations in the highest headwaters, unlike the other streams in their study, did not rebound after a drought which they attributed to lack of connectivity at the upstream and downstream end of the reach. In our study, we cannot determine if the decrease in habitat suitability at the downstream end of a suitable reach would stifle trout migration (in which case connectivity would be impacted), because our *O. mykiss irideus* occurrence data combined spawning and migration observations. However, it is possible that the highest headwaters become isolated from the lower watersheds which would stifle recolonization for *O. mykiss irideus*, and potentially *A. californicus* as well depending on their migration ability.

Surprisingly, our results showed that the species highly endemic to the Los Angeles region in southern California (*G. orcuttii* and *C. santaanae*) were projected to have increased habitat suitability, whereas the species with larger ranges throughout western North America (*O. mykiss irideus* and *A. marmorata*) were predicted to have decreased habitat suitability. This finding is similar to Thuiller et al., (2006) who found endemic plants in Namibia were generally more resilient to climate change than widespread species. This could suggest that a large geographic range is associated with a negative response to climate change.

However, most studies of historic and future climate changes have alternatively found that endemic species were particularly harmed compared to more widespread species (see review: Isaac, 2009).

Historically, studies of climate warming during the Quaternary found that widespread species were able to inhabit regions of Europe that were frozen during the 'last glacial maximum' but that are currently suitable, whereas range restricted species to this day are limited to the areas suitable during that period for reptiles and amphibians (Araújo et al., 2008) and trees (Svenning & Skov, 2007). One explanation for this is that range restricted species are limited by dispersal and therefore cannot move into new territories as they become suitable (Graham et al., 2006). Considering future climate changes, this suggests that species with narrow geographic ranges may be more vulnerable than species with wider ranges because the former cannot disperse into new areas and will be at the mercy of the new climate conditions in the areas they currently inhabit. We did not account for dispersal limitations in our study (i.e. it was assumed that any habitat within the region was accessible should it become suitable), so this may be one reason why we did not see greater vulnerability of highly endemic species. We did not account for dispersal limitations because our study area is limited to six adjacent watersheds above all major dams, so, in general, dispersal, including the potential for assisted migration (see discussion below in "Species conservation") should not be an insurmountable barrier.

Like the historical studies of climate warming during the Quaternary, predicting the relative impact of *future* climate change on species, Zhang et al., (2017) found the species with the smallest geographic ranges to be the most vulnerable to future climate change compared to those with a larger geographic range. Similarly, in a meta-analysis of 131 studies, Urban ( 2015) also found that endemic species were more vulnerable to rising temperatures than non-endemic species and were more likely to become extinct. However, perhaps our finding is not contradictory with these historical and future findings of endemicity and range size and future climate change vulnerability. Within each focal species' geographic range, whether the full geographic range is widespread or restricted (highly endemic), the habitat generalists are projected to respond more favorably than habitat specialists (also suggested by Thuiller et al., (2005); Clavel et al., (2011); Poff et al., (2012)), which suggests a decoupling of geographic range size and environmental niche breadth, also shown in a study of *Gammarus* spp. (Gaston & Spicer, 2001) and a study of rattlesnakes (Waldron et al., 2006). Thompson et al., (1999) found weak relationships between *fundamental* niche breadth and range size in vegetation, but they did find a positive correlation between *realized* niche breadth and range size. The relationship between environmental niche breadth and geographic range is a hotly debated issue and many other studies have found a positive association between the two variables as reviewed in a meta-analysis of 64 studies by Slatyer et al., (2013). In our study however, the species with the smallest geographic range do not also have the most limited environmental niche. For example, although *A. californicus* has a larger geographic range than *G. orcuttii*, within its geographic range it occupies fewer habitat types. Therefore, despite high endemicity of *G. orcuttii,* their projected response to climate change is positive, possibly due to their wide environmental niche breadth within our study region.

Overall, the lack of dispersal limitation associated with endemics in this small study area, combined with the wide environmental niche breath, and warm stream temperature preferences of the highly endemic species in this study could explain why they were less vulnerable to climate change than the more widely dispersed species.

### Hydraulic-habitat explanations for hydrologic relationships

In this study we considered streamflow to be a major driver of stream habitat and used correlative modeling to determine habitat suitability. Streamflow as a driver of hydraulic habitat can offer a mechanistic explanation for the trends we observed. Following prolonged drought, which is indicative of how climate change may impact future habitats, there was a reduction in pool habitat and an associated decrease in trout populations (Dagit et al., 2017; Kaylor et al., 2019). This could explain why we observed *O. mykiss irideus* to be positively associated with hydroperiod and high flows which both contribute to maintaining pools.

While drought has been found to reduce the number of breeding pairs of *A. californicus* (Jennings & Hayes, 1994), Miller et al., (2012) found that the disturbance caused by alternating habitat drying and storm flows allowed *A. californicus* to occur without predators that required permanent surface water, such as the American bullfrog (*Lithobates catesbeianus*). *A. californicus* would only breed in the years when the conditions were suitable. However, if the drought lasted longer than the average lifespan of *A. californicus,* up to 6-8 years, than the population would not have a breeding opportunity and there would be significant reductions in the population (Fisher et al., 2018). This dynamic of needing surface water frequently enough to support breeding, but not consistently enough to support predators, could explain why we found that *A. californicus* was positively associated with no flow periods at the 3-year time frame but negatively associated with no flow periods at the all-year time frame.

### The use of focal species

In this analysis we selected species to model using a focal species approach. The idea was to allow our results to be applicable to other native species in the region that have similar behavior and habitat preferences as the focal species in their cluster. Interestingly, we modeled two species from the same cluster, *C. santaanae* and *A. marmorata* and got very different results in their projected distributions and their response to climate change. This is evidence of a caveat of correlative species distribution modeling –the model responds entirely to the observation points. In this case, observation points for the two species were compiled from separate agencies in separate watersheds, so even if they do occur together in some locations, it was not reflected in the data set. We suggest that in addition to the clustering, a cooccurrence analysis be completed as well, and a cluster would include those that cluster together based on life history traits and that co-occur within the study area. For many of our species clusters, there is co-occurrence with the focal species, but *C. santaanae* and *A. marmorata* was an extreme example where, due to the high endemicity of *C. santaanae*, there is no occurrence in the two watersheds where *A. marmorata* was largely surveyed – the Santa Monica Mountains and the Ventura River watershed – two watersheds that *C. santaanae* is absent from.

### Species conservation

Projecting future distributions of riverine species due to changing climates can help managers engage in proactive, rather than reactive, projects (Palmer et al., 2009). For example, investing in stream connectivity projects to connect populations from high and low elevation areas that are projected to be suitable will allow the lower population to migrate before becoming extirpated as the lower regions lose suitability.  Projections like these also aid with place-based management, which means developing plans tailored to a certain watershed's needs (Palmer et al., 2009). For example, a historical problem associated with the arroyo toad decline was recreation, such as off-road vehicle use, in breeding streams (U.S. Fish and Wildlife Service, 2014).  A place-based management approach could include more public forums about recreational use of streams during certain seasons and more transparency about when activities are encouraged or restricted.

Future conservation efforts can benefit from this study by incorporating spatial prioritization into management plans (Jones et al., 2016).  Knowledge of the preferred stream conditions of native species, and projections of where those conditions will persist in future years, can help managers target conservation and restoration projects to watersheds that maintain those favorable conditions (Loyola et al., 2013).  For example, managers may invest in riparian tree planting programs in stream reaches that are projected to maintain hydrology supportive of native fishes, to buffer against rising air temperatures and predation pressures.  We would recommend that resource managers begin monitoring in locations that are projected to support the three vulnerable species to assess for the presence of other stressors and opportunities to enhance the habitat.

In this analysis we assumed full migration capacity of all species in the future scenarios, meaning any new suitable habitat is considered possible regardless of overlap with the current range.  Other studies have often used two extreme dispersal scenarios, full or none, to determine future suitable habitat (e.g. Thuiller et al., 2006; Loarie et al., 2008; Gibson et al., 2010).  Rather than use this method, we simply delineated stream reaches that would be suitable for species occurrence which affords wildlife managers the most options in planning their conservation programs. Forecasts of suitable stream reaches that are not in the same watershed as current populations, or that are in the same watershed but separated by a barrier, help direct assisted migration programs or connectivity design in the event that species dispersal is limited naturally or due to anthropogenic barriers (Loss et al., 2011). In some cases, a separate watershed might be a better refuge for a species due to various practical reasons such as less reactional usage, and it could be helpful to project the suitability of separate watersheds.

In addition to local projects discussed above, state programs such as the California Department of Fish and Wildlife (CDFW) Landscape Conservation Planning can use studies like this one in future planning. Three initiatives within this program could use projections of future habitat suitability in their decision making: The Natural Community Conservation Act (NCCA), the Regional Conservation Investment Strategies program (RCIS), and Conservation or Mitigation Banking. The main goals of these three programs are to delineate an area of land for conservation or restoration, often in exchange for the destroying of habitat elsewhere, that is likely to be most appropriate for species or ecosystem success. For example, an NCCA puts aside large areas as conservation reserves in exchange for ecosystem or species loss during economic development activities. Future habitat suitability mapping can help inform decisions about *where* those areas for conservation should be. They can also help inform choices about the *types* of habitat to be included in the conservation areas based on projections of resilience of certain species in the future, such as making sure to include habitat used by species projected to lose habitat extent with additional climate change.

At the national level, environmental laws aimed at protecting natural resources could also use projections of species habitat suitability in their decision making. For example, the U.S. Fish and Wildlife Service Endangered Species Act (ESA) of 1973 bestows stringent habitat protections on species that are at risk of becoming extinct in the foreseeable future. Studies that project extent of suitable future habitat can be proactively used in deciding what species to list as threatened or endangered and provide protection to those species in advance of population declines. As directed by the ESA, habitat is designated as critical habitat which is protected from development or other activities that would result in a 'take' of the species. Critical habitat designations are static in nature whereas we know that suitable habitats will move in space in response to changing climatic conditions. This study can help with placing critical habitat boundaries in locations that account for both species' populations today, and the projected locations of habitat suitability in the future.

### *Supporting Information*

Additional information for the species clustering, model performance, and results: clustering analysis results (Appendix S-3-1), variables used in species clustering (Appendix S-3-2), sources used for the species observation data (Appendix S-3-3), performance of the random forest model of species occurrence using streamflow (Appendix S-3-4), detailed descriptions of species relationships with the streamflow and stream temperature metrics (Appendix S-3-5), baseline species range maps (Appendix S-3-6), and projected future species ranges (Appendix S-3-7).

## Appendix S-3-1: Species clusters

Table S-3-1: Riparian species (vertebrates) in the study area that were included in the clustering analysis. The last column, 'Cluster', shows how they grouped together. The bolded rows are the species which were selected as a cluster representative.

| Common name | Name | Group | Sensitive | Native | Cluster |
|---|---|---|---|---|---|
| African clawed frog | *Xenopus laevis* | Amphibian | | | 1 |
| American bullfrog | *Lithobates catesbeianus* | Amphibian | | Y | 1 |
| Baja California treefrog | *Pseudacris hypochondriaca hypochondriaca* | Amphibian | | Y | 1 |
| Western spadefoot | *Spea hammondii* | Amphibian | Y | Y | 1 |
| Red-eared slider | *Trachemys scripta elegans* | Reptile | | | 1 |
| Snapping turtle | *Chelydra serpentina* | Reptile | | | 1 |
| Western painted turtle | *Chrysemys picta bellii* | Reptile | | | 1 |
| Fathead minnow | *Pimephales promelas* | Fish | | | 1 |
| Golden shiner | *Notemigonus crysoleucas* | Fish | | | 1 |
| Western Mosquitofish | *Gambusia affinis* | Fish | | | 1 |
| Red shiner | *Cyprinella lutrensis* | Fish | | | 1 |
| Green Sunfish | *Lepomis cyanellus* | Fish | | | 1 |
| Two-striped garter snake | *Thamnophis hammondii* | Reptile | | Y | 2 |
| Texas spiny softshell | *Apalone spinifera emoryi* | Reptile | | | 2 |
| **Arroyo chub** | ***Gila orcuttii*** | **Fish** | **Y** | **Y** | **2** |
| Threespine stickleback | *Gasterosteus aculeatus* | Fish | Y | Y | 2 |
| California treefrog | *Pseudacris cadaverina* | Amphibian | | Y | 3 |
| California toad | *Anaxyrus boreas halophilus* | Amphibian | | Y | 3 |
| **Western pond turtle** | ***Actinemys marmorata*** | **Reptile** | | **Y** | **3** |
| **Santa Ana sucker** | ***Catostomus santaanae*** | **Fish** | **Y** | **Y** | **3** |
| California newt | *Taricha torosa* | Amphibian | Y | Y | 3 |
| California red-legged frog | *Rana draytonii* | Amphibian | Y | Y | 3 |
| Black bullhead | *Ameiurus melas* | Fish | | | 4 |

| | | | | | |
|---|---|---|---|---|---|
| Bluegill sunfish | *Lepomis macrochirus* | Fish | | | 4 |
| Brown bullhead | *Ameiurus nebulosus* | Fish | | | 4 |
| Largemouth bass | *Micropterus salmoides* | Fish | | | 4 |
| Tilapia spp | *Oreochromis* | Fish | | | 4 |
| Yellow bullhead | *Ameiurus natalis* | Fish | | | 4 |
| Common carp | *Cyprinus carpio* | Fish | | | 4 |
| Brown trout | *Salmo trutta* | Fish | | | 5 |
| Channel catfish | *Ictalurus punctatus* | Fish | | | 5 |
| **Coastal rainbow trout / steelhead** | ***Oncorhynchus mykiss irideus*** | **Fish** | **Y** | **Y** | **5** |
| Santa Ana speckled dace | *Rhinichthys osculus* | Fish | Y | Y | 5 |
| Mountain yellow-legged frog | *Rana muscosa* | Amphibian | Y | Y | 5 |
| **Arroyo toad** | ***Anaxyrus californicus*** | **Amphibian** | **Y** | **Y** | **6** |
| California least tern | *Sterna antillarum browni* | Bird | Y | Y | 7 |
| Spotted sandpiper | *Actitis macularius* | Bird | | Y | 7 |
| Black-necked stilt | *Himantopus mexicanus* | Bird | | Y | 7 |
| Bank swallow | *Riparia riparia* | Bird | Y | Y | 8 |
| Common yellowthroat | *Geothlypis trichas* | Bird | | Y | 8 |
| **Least Bell's vireo** | ***Vireo bellii pusillus*** | **Bird** | **Y** | **Y** | **8** |
| Lincoln's sparrow | *Melospiza lincolnii* | Bird | | Y | 8 |
| MacGillivray's warbler | *Geothlypis tolmiei* | Bird | | Y | 8 |
| Swainson's thrush | *Catharus ustulatus* | Bird | | Y | 8 |
| Willow flycatcher | *Empidonax traillii* | Bird | Y | Y | 8 |
| Wilson's warbler | *Cardellina pusilla* | Bird | | Y | 8 |
| Yellow warbler | *Setophaga petechia* | Bird | | Y | 8 |
| Yellow-billed cuckoo | *Coccyzus americanus* | Bird | Y | Y | 8 |
| Yellow-breasted chat | *Icteria virens* | Bird | Y | Y | 8 |
| Black-crowned night heron | *Nycticorax nycticorax* | Bird | | Y | 9 |
| Great blue heron | *Ardea herodias* | Bird | | Y | 9 |

| | | | | |
|---|---|---|---|---|
| Great egret | *Ardea alba* | Bird | Y | 9 |
| Green heron | *Butorides virescens* | Bird | Y | 9 |
| Pied-billed grebe | *Podilymbus podiceps* | Bird | Y | 9 |
| Snowy egret | *Egretta thula* | Bird | Y | 9 |
| Wilson's snipe | *Gillinago delicata* | Bird | Y | 9 |
| Cinnamon teal | *Anas cyanoptera* | Bird | Y | 10 |
| Mallard | *Anas platyrhynchos* | Bird | Y | 10 |
| Northern pintail | *Anas acuta* | Bird | Y | 10 |
| Song sparrow | *Melospiza melodia* | Bird | Y | 10 |
| Wood Duck | *Aix sponsa* | Bird | Y | 10 |
| Brown-headed cow bird | *Molothrus ater* | Bird | Y | 10 |
| Cooper's hawk | *Accipiter cooperii* | Bird | Y | 11 |
| Long-eared owl | *Asio otus* | Bird | Y | 11 |
| Red-shouldered hawk | *Buteo lineatus* | Bird | Y | 11 |
| American dipper | *Cinclus mexicanus* | Bird | Y | 12 |

## Appendix S-3-2: Variables used in clustering analysis

Table S-3-2: Variables used for grouping species

| Life history | Categories |
|---|---|
| General habitat | Main channel, backwater, riparian, wetland, variable |
| Foraging behavior | Dabble, dive, fly, run, stalk, swim |
| Vegetation preference | Aquatic, overhanging, scrub, woodland, none |
| Prey preference (birds only) | Fruit, seed, grain, plant, fish, bird/mammal, terrestrial invertebrate, aerial invertebrate, aquatic invertebrate, amphibian |
| Water velocity | Fast, medium, slow, NA |
| Preferred substrate | Fine, sandy/gravel, cobble, boulder, NA |
| Nest location | Submerged substrate, emergent vegetation, nest at the bottom of a channel, cavity within a channel, ground, tree, shrub, bank, variable, NA |
| Stream category | Permanent, temporary, NA |
| Stream depth (fish and herps only) | Shallow, average, deep |
| Stream temperature (fish and herps only) | Cool, warm, hot |

## Appendix S-3-3: Sources used for compiling the species distribution data

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## Appendix S-3-4: Performance of the random forest prediction of species occurrence using streamflow metrics.

Confusion matrices show the number of successes for each species. The first table shows the accuracy of predicting presence or absence on the training data and the second shows the accuracy for the testing data. The columns across the top (blue) are the numbers based on the species observation data and the rows (tan) show the model prediction. For example, in this first table, based on the observations, 32 arroyo chub were present. The model correctly identified 30 of them and mislabeled two as absent. Based on the observations 146 locations did not have arroyo chub present, and our modeled mislabeled one as being present. (A) arroyo chub; (B) *O. mykiss irideus*; (C) Santa Ana sucker; (D) western pond turtle; (E) arroyo toad; (F) least Bell's vireo.

(A) arroyo chub

| Training | Presence | Absence |
|---|---|---|
| Presence | 30 | 1 |
| Absence | 2 | 145 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 4 | 2 |
| Absence | 2 | 51 |

(B) *O. mykiss*

| Training | Presence | Absence |
|---|---|---|
| Presence | 78 | 0 |
| Absence | 5 | 342 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 18 | 2 |
| Absence | 6 | 115 |

(C) Santa Ana sucker

| Training | Presence | Absence |
|---|---|---|
| Presence | 23 | 0 |
| Absence | 0 | 163 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 10 | 1 |
| Absence | 1 | 50 |

(D) western pond turtle

| Training | Presence | Absence |
|---|---|---|
| Presence | 177 | 0 |
| Absence | 8 | 28 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 54 | 0 |
| Absence | 2 | 15 |

(E) arroyo toad

| Training | Presence | Absence |
|---|---|---|

| | | |
|---|---|---|
| Presence | 18 | 0 |
| Absence | 0 | 7 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 6 | 2 |
| Absence | 0 | 0 |

### (F) least Bell’s vireo

| Training | Presence | Absence |
|---|---|---|
| Presence | 28 | 1 |
| Absence | 0 | 20 |

| Testing | Presence | Absence |
|---|---|---|
| Presence | 9 | 0 |
| Absence | 0 | 7 |

## Appendix S-3-5: Species occurrence and streamflow / stream temperature associations

### *O. mykiss irideus*

*O. mykiss irideus* was negatively related to maximum 7-day maximum, maximum 7-day average, and minimum 7-day minimum temperatures. They occur in streams with maximum 7-day averages generally below 22°C, minimum 7-day minimums generally below 12.5°C, and that had few numbers of 7-day maximum temperatures greater than 30°C. There were no occurrences in streams that had a maximum 7-day maximum temperature above 32.5°C, a minimum 7-day minimum temperature above approximately 13.75°C, and 75% of presence observations had fewer than 29 instances when the maximum 7-day maximum was greater than 30°C (compared to the streams where 75% of absence instances had fewer than 63 instances of maximum 7-day maximum temperature greater than 30°C). Occurrence had a negative relationship with maximum 7-day range which might suggest an intolerance for large temperature swings. *Oncorhynchus mykiss irideus* occurrence was positively related to average and maximum flows, but negatively related to the number of high streamflow events. They occurred in streams with gradual recessions, perennial flows, and more days of no disturbance. This suggests that they favor consistent high flows with minimal disturbance.

### Arroyo Chub

Arroyo chub occurrence had a positive relationship with stream temperature, unlike *O. mykiss irideus*, and tended to occur in streams with a higher maximum 7-day maximum temperature. Most arroyo chub occurrences were in streams with a maximum 7-day maximum above 30°C and there were no occurrences in streams that had a maximum 7-day maximum less than 27.5°C. Aside from a single outlier, they did not occur in streams that had a minimum 7-day minimum temperature less than approximately 11°C and most minimum 7-day minimum temperatures were between 11°C and 15°C. Arroyo chub were not related to maximum 7-day temperature ranges (stream temperature variability). They tended to occur in flashy streams with a high number of high streamflow events with rapid recessions, and a high number of low flow events. T hey were positively related to minimum and maximum streamflow. Interestingly, they tended to occur in streams that did not have perennial streamflow which suggests that permanent pool refuges are important and that they can successfully recolonize intermittent reaches.

### Santa Ana Sucker

Santa Ana sucker showed less of a relationship with stream temperature than the other two fishes. This could be because they occur at low and high elevations and are thus more tolerant of warm and cool water temperatures than the other two which primarily occur at either high or low elevations. They occurred in streams with the maximum 7-day maximum temperature range from 25°C to 32.5°C. The only moderately significant temperature variables were maximum 7-day average stream temperature and minimum 7-day minimum stream temperature and they are both positively related to Santa Ana sucker occurrence. It is important to note that our species data for Santa Ana sucker was the most limited of the three fishes and was not representative of the entire region (e.g., there were no positive or negative observations in the Santa Monica mountains) and therefore this relationship is not as robust as the other two. The range of minimum 7-day minimum temperatures was like arroyo chub, and wider than *O. mykiss irideus*. Santa Ana sucker tended to occur in flashier streams, showing a preference for streams with a high number of high streamflow events, rapid recessions, and fewer no disturbance days. They also occurred in streams that had more recent two-year storms. Like arroyo chub, they tended to occur in intermittent streams, highlighting the importance of refuges.

### Arroyo Toad

Like *O. mykiss irideus*, arroyo toads were more likely to occur in cooler streams and none were observed in streams where the maximum 7-day maximum was greater than approximately 28.4°C - about 4°C lower than the threshold we observed for *O. mykiss irideus*. This is likely an artifact of their occurring in high elevation habitats within our region which have cooler water and this relationship may not hold in the southern portion of their range where they occur in lower more coastal streams. There was no relationship with temperature ranges or minimum temperatures. Like *O. mykiss irideus*, arroyo toads tended to occur in streams that had perennial flow, however, they were found in streams with fewer no disturbance days. This could be reflective of their dependence on periodic large flows for depositing coarse substrate and removing encroaching vegetation in their edgewater habitat. They occur in streams with rapid flow recessions. Generally, the relationships with the streamflow metrics were weaker than the other species likely due to the limited species data and the similarly of flow between the presence and absence data.

### Western Pond Turtle

Western pond turtle had the least consistent relationship with the temperature metrics. Their occurrence was positively related with the maximum 7-day maximum temperature and the number of 7-day maximums greater than 30°C. The range of maximum weekly maximum temperatures where turtles were observed was from approximately 29.5°C to 34°C, far higher than the three fishes and toad. However, occurrence was negatively associated with the maximum 7-day average and the minimum 7-day minimum stream temperatures. The minimum 7-day minimum temperature range was similar to arroyo chub and Santa Ana sucker. As expected, based on the temperature preferences, they were found in areas that had a large maximum 7-day temperature range. This could be that they occur in streams that can get very hot, but topographic or other environmental characteristics maintain cool minimum and average temperatures. The broad distribution of turtles within the study region combined with few absence observations yielded ambiguous streamflow preferences. However, they occurred in streams with median streamlow less than 30cfs, minimum streamflow less than 10cfs, Q75 less than 50cfs, and Q90 less than 100cfs.

### Least Bell's Vireo

Least Bell's vireo, unlike the other five species, have an indirect dependence on streamflow because while they do not have a life history phase where they live in the water, it supports their riparian habitat and insect food source. Although they nest in riparian vegetation alongside the stream, not in the water, they had a clear association with warmer streams. Least Bell's vireo were only found in streams that had a maximum 7-day maximum value *greater* than 30°C and were found in locations as high as 34°C, completely outside the range of the arroyo toad and largely outside the range of *O. mykiss irideus*. Similarly, they were found in areas with higher minimum temperatures- the lowest minimum 7-day minimum was approximately 12.5°C. There was no association with the maximum 7-day average. Least Bell's vireo occurred in intermittent streams that had a long duration of low flow. However, occurrence had a positive relationship with the number of high streamflow events, RBI, and a negative relationship with days since 10-, 5-, and 2-year storm. This suggests that although they tended to occur in streams that were intermittent with low flow magnitudes, they do select streams that get scouring flows. It also suggests that pools or groundwater seeps are vital to sustain their insect food source into the summer.

## Appendix S-3-6: Baseline species range

*Oncorhynchus mykiss irideus* and *A. californicus* had a high probability of occurrence in high elevation sub-watersheds and a very low probability of occurrence in the lower elevations, and *G. orcuttii* and *V. bellii pusillus* had a high probability of occurrence exclusively in the lower elevation portions of the major watersheds. The range of the low elevation species abutted the range of the high elevation species almost perfectly, suggesting an abrupt transition in habitat type. Because most of the low elevation sub-watersheds are heavily urbanized, much of the range of the low elevation species is not reflected in the baseline maps. While elevation and stream grade no doubt have a large role in this relationship as well, this is captured in our model through the relationship of both streamflow and temperature with elevation. *Catostomus santaanae* and *A. marmorata* had a wider distribution throughout the region than the other four species. Interestingly, *C. santaanae* had a relatively low probability of occurrence throughout the entire region and *A. marmorata* had a high probability of occurrence throughout the region.

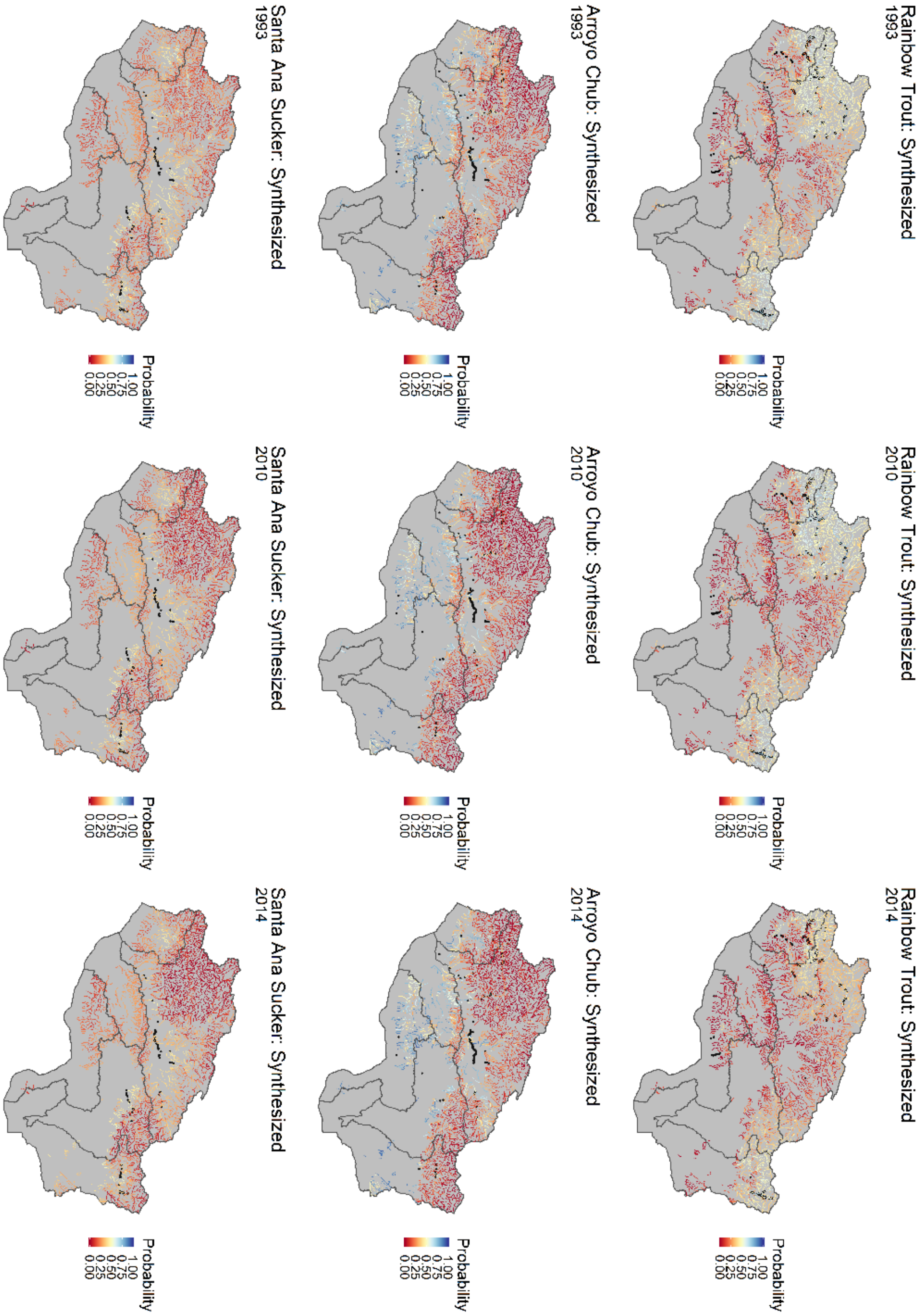


Figure S-3-1: Probability distributions of the six focal species for years 1993 (wet), 2010 (moderate), and 2014 (dry). Blue = probability of 1, and red = probability of 0. The black points show locations of species observation since 1981. Note that the species observation points are not from the same year as the prediction map but include all baseline observations.

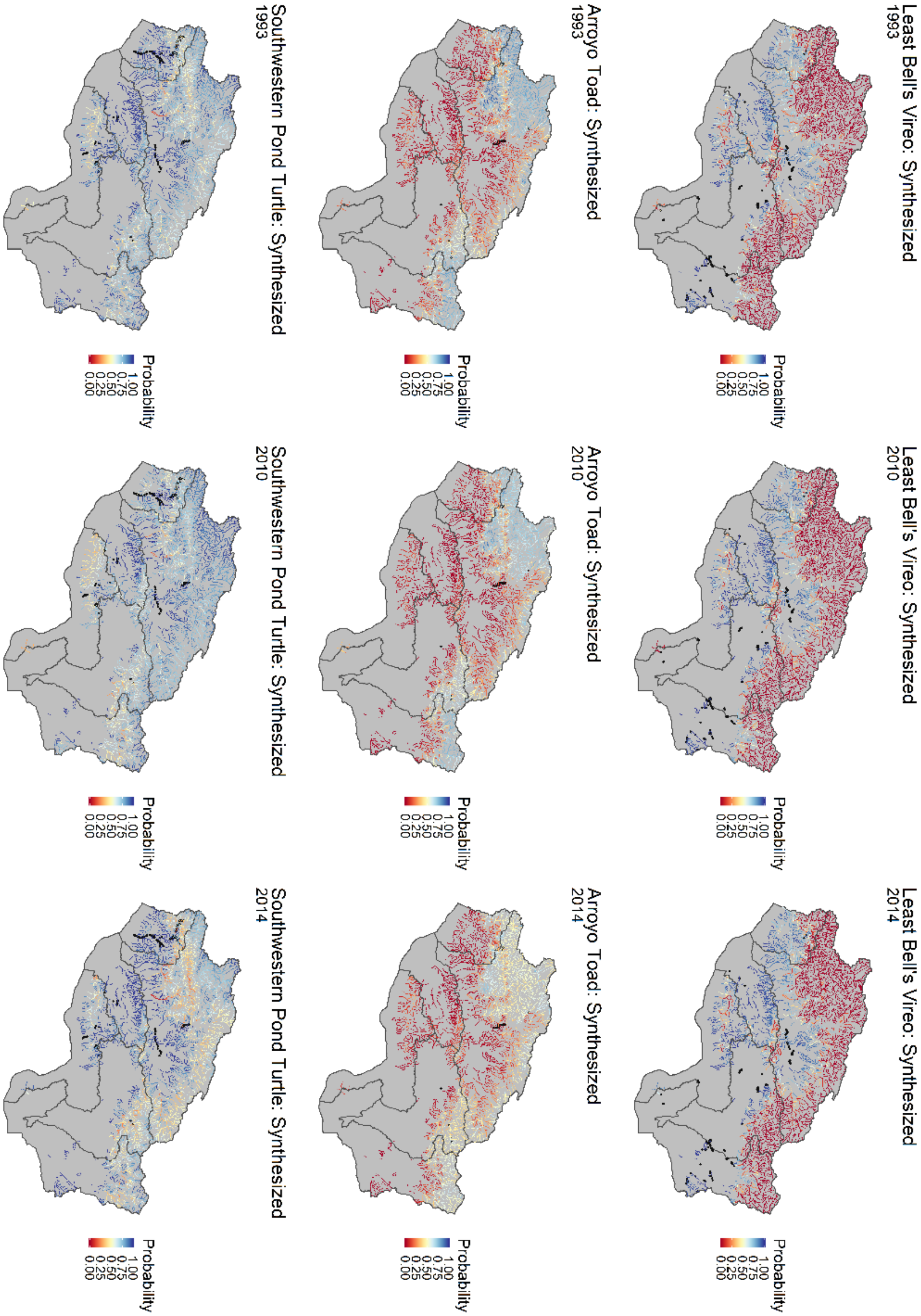
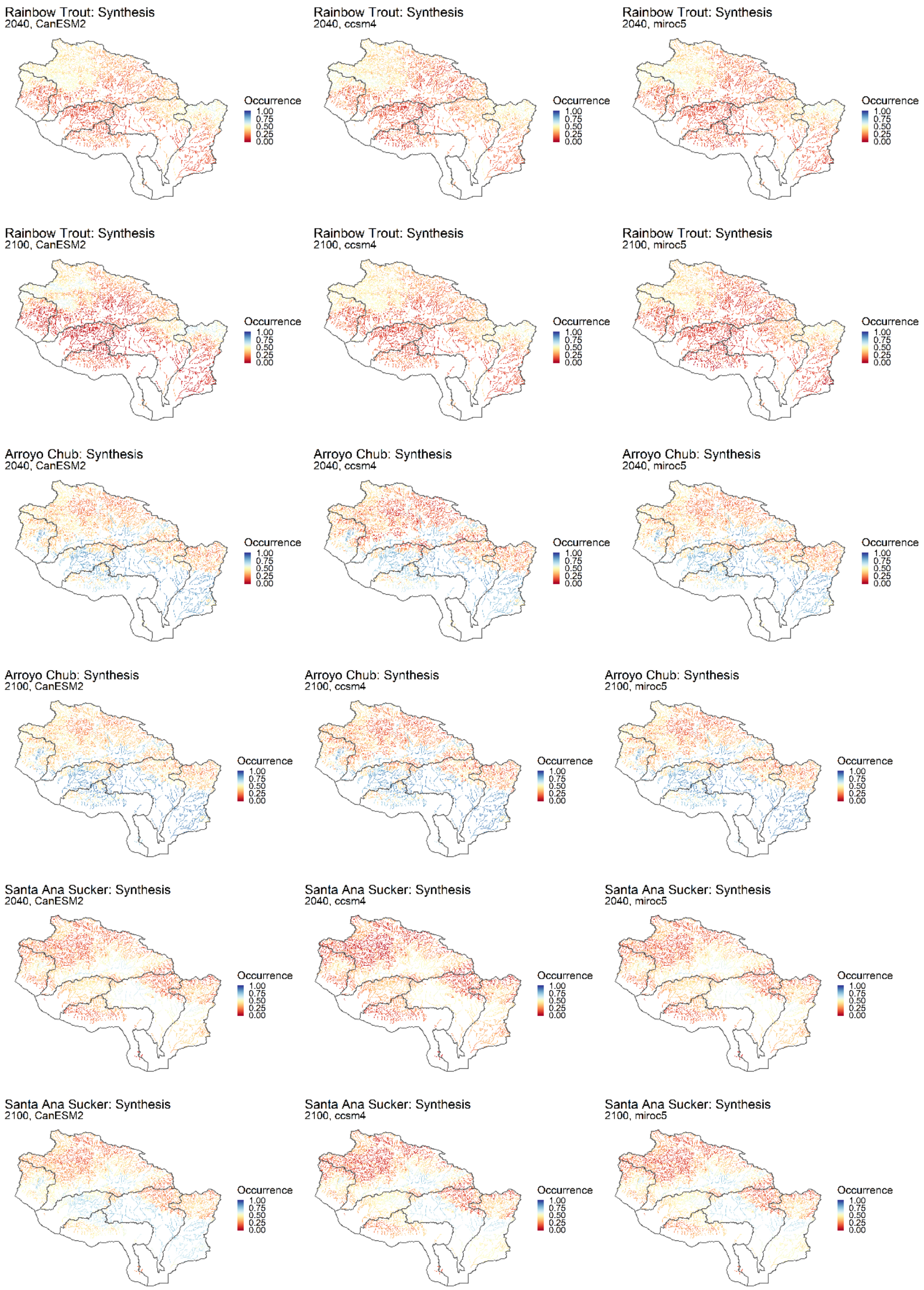


Figure S-3-1 continued.

## Appendix S-3-7: Projected future species range



Rainbow Trout: Synthesis
2040, CanESM2

Rainbow Trout: Synthesis
2040, ccsm4

Rainbow Trout: Synthesis
2040, miroc5

Rainbow Trout: Synthesis
2100, CanESM2

Rainbow Trout: Synthesis
2100, ccsm4

Rainbow Trout: Synthesis
2100, miroc5

Arroyo Chub: Synthesis
2040, CanESM2

Arroyo Chub: Synthesis
2040, ccsm4

Arroyo Chub: Synthesis
2040, miroc5

Arroyo Chub: Synthesis
2100, CanESM2

Arroyo Chub: Synthesis
2100, ccsm4

Arroyo Chub: Synthesis
2100, miroc5

Santa Ana Sucker: Synthesis
2040, CanESM2

Santa Ana Sucker: Synthesis
2040, ccsm4

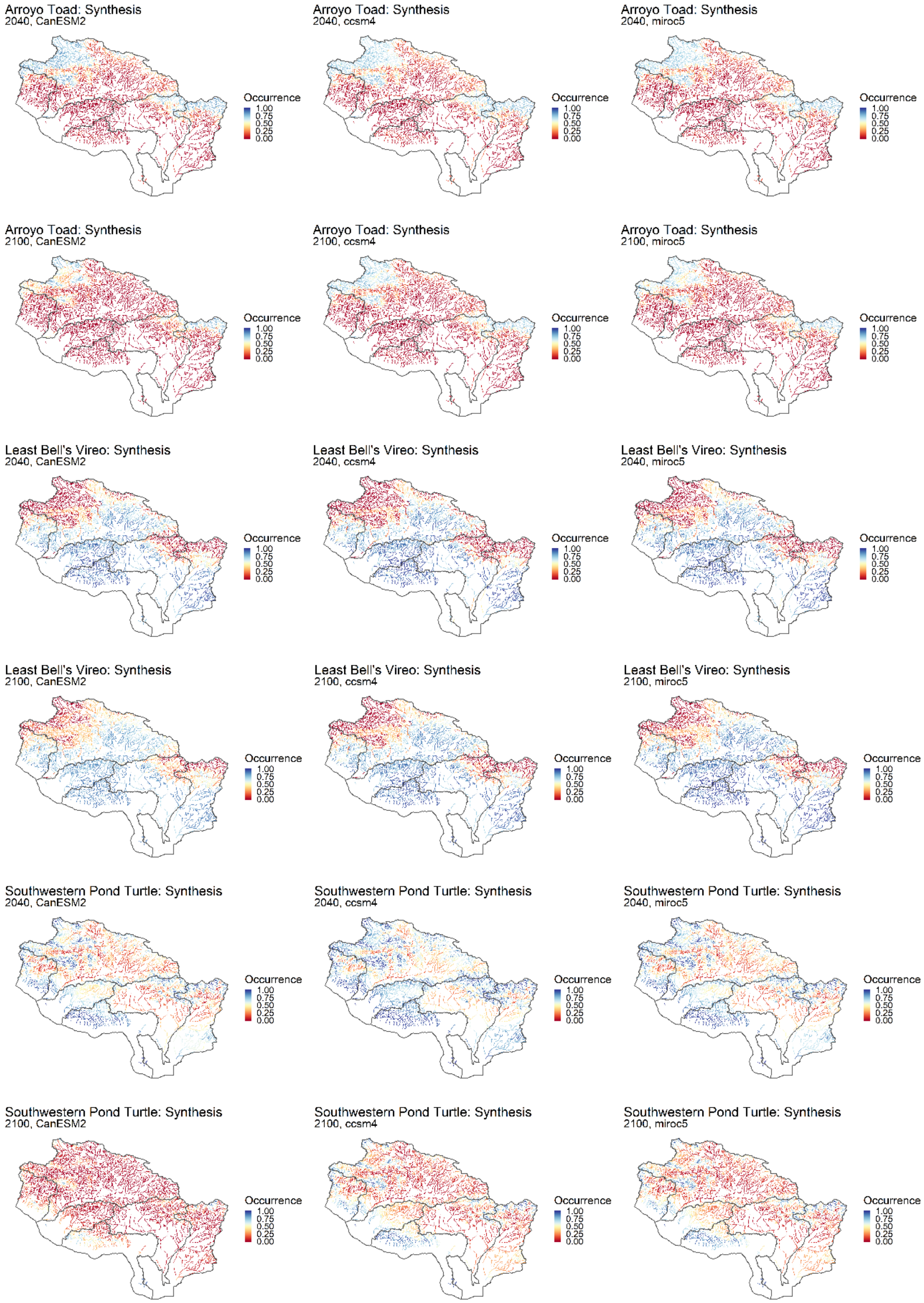
Santa Ana Sucker: Synthesis
2040, miroc5

Santa Ana Sucker: Synthesis
2100, CanESM2

Santa Ana Sucker: Synthesis
2100, ccsm4

Santa Ana Sucker: Synthesis
2100, miroc5

Figure S-3-2: Mapped predicted probability of occurrences in the two future years for each of the three GCM's. Unlike in the baseline maps, all streams are retained because conditions may change in the future. These results apply to future areas that do regain their natural hydrology. This shows where, under natural conditions, a species may occur.



Arroyo Toad: Synthesis
2040, CanESM2

Arroyo Toad: Synthesis
2040, ccsm4

Arroyo Toad: Synthesis
2040, miroc5

Arroyo Toad: Synthesis
2100, CanESM2

Arroyo Toad: Synthesis
2100, ccsm4

Arroyo Toad: Synthesis
2100, miroc5

Least Bell's Vireo: Synthesis
2040, CanESM2

Least Bell's Vireo: Synthesis
2040, ccsm4

Least Bell's Vireo: Synthesis
2040, miroc5

Least Bell's Vireo: Synthesis
2100, CanESM2

Least Bell's Vireo: Synthesis
2100, ccsm4

Least Bell's Vireo: Synthesis
2100, miroc5

Southwestern Pond Turtle: Synthesis
2040, CanESM2

Southwestern Pond Turtle: Synthesis
2040, ccsm4

Southwestern Pond Turtle: Synthesis
2040, miroc5

Southwestern Pond Turtle: Synthesis
2100, CanESM2

Southwestern Pond Turtle: Synthesis
2100, ccsm4

Southwestern Pond Turtle: Synthesis
2100, miroc5

Figure S-3-2 continued.

# Chapter 4 Light-footed Ridgway's rail nesting habitat and the relationship of streamflow, precipitation, and marine water level on the number of annual breeding pairs

## *Abstract*

This study aims to elucidate habitat characteristics and climatic conditions associated with the Light-footed Ridgway's rail (LFRR) nest placement and breeding population size to aid in management planning and increase LFRR resiliency toward projected changes in sea level, streamflow, and precipitation. The LFRR is a marsh obligate bird that nests and forages in low- to mid-elevation salt marsh vegetation. High water levels or large storms can trigger processes in the marsh like vegetation germination, but they can also flood nests or force birds to escape to upland areas. In this study we investigate marsh characteristics associated with LFRR nesting placement and we also explore the relationship between events from the watershed, ocean, and atmosphere on the annual breeding pair population. We find that most nests are in *Spartina foliosa* (Pacific cordgrass), as expected, but that *Schoenoplectus* spp. (bulrush) also supports nests and likely provides habitat of equivalent, if not better, quality. Surprisingly, upper marsh elevations and vegetation were just as important as lower marsh elevations and vegetations in the LFRR home range, which suggests that the entire marsh is important for these species, not just the nesting habitat. High streamflow magnitudes and durations are negatively associated with the annual breeding LFRR population. The number of breeding pairs in a certain year are positively associated with the number of high streamflow events during the previous decade, but negatively related to the number of high streamflow events in the previous year. These findings suggest tradeoffs between processes that maintain the marsh, like temporary salinity reduction, but cause

immediate harm to LFRR's, like nest flooding. These findings could be used to expand LFRR management programs, which currently focus on the nesting habitat, to include high marsh and even watershed level management.

### *Keywords*

Light-footed Ridgway's rail, salt marsh, habitat suitability, estuarine ecohydrology, sea level rise

### *Acknowledgements*

This work was partially funded by the National Oceanic and Atmospheric Association (NOAA) Ecological Effects of Sea Level Rise program. We thank Dick Zembal from Orange county water district for his help and expertise with nest searching and for letting us his maps showing the annual locations of breeding Light-footed Ridgway's rails. We thank Carolyn Lieberman, from the USFWS Carlsbad office, for her time and assistance in the field collecting nest site data, and for her expertise with RTK GPS surveying. We thank Susan Hoffman, Bernice Villanueva, Beth Sabiston, and Edward Owens for help in the field with nest searching. We thank Amber Jolly and Kyle Zolkin for the many hours they spent helping to georeference and digitize 8 years of survey data from hand drawn maps. We thank Karen Thorne from the USGS Western Ecological Research Center for letting us use her elevation and vegetation data from surveys in Upper Newport Bay. We thank Jeff Crooks, at the Tijuana River National Estuarine Research Reserve, for his help understanding and accessing the water level data collected in the estuary. Lastly, we thank all the individuals who have participated in the annual Ridgway's rail surveys at the salt marshes in southern California.

## *Introduction*

Managing for sensitive species in habitats at risk due to climate change requires understanding of all the processes that impact the species directly and indirectly so management and policy can address the correct problems. Endemic to southern California, USA, coastal marshes, the Light-footed Ridgway’s rail (*Rallus obsoletus levipes*), hereafter LFRR, is a non-migratory state and federally listed endangered salt marsh bird. Historical reasons for population decline and subsequent listing have been attributed to hunting (De Groot, 1927), predation (De Groot, 1927; Massey et al., 1984; Schwarzbach et al., 2006), nest flooding (Massey et al., 1984), egg contamination (Schwarzbach et al., 2006), and most importantly, habitat conversion and urbanization (De Groot, 1927; Wilbur, 1974). Salt marsh extent has decreased by 75% since the 1850s (Stein et al., 2014). Further land conversion of salt marsh habitats is unlikely due to habitat protections, but sea level rise threatens the resiliency of salt marshes through a process of coastal squeeze, which occurs when sea levels rise but habitats cannot transgress inland do to hardened shorelines (Doody, 2004; Torio & Chmura, 2013). The most extreme scenarios of sea level rise are projected to reduce salt marsh extent in southern California to non-existence (Thorne et al., 2018).

Since the late 1970’s, management of LFRR has been successful at rebuilding populations in many salt marshes. Efforts have included annual population censuses (e.g. Zembal et al., 2016), captive propagation programs (https://www.thelivingcoast.org/), artificial nest rafts (Overton et al., 2015), and marsh habitat restoration. These programs focus directly on LFRR’s and their nesting or foraging habitats which have been well studied (Massey et al., 1984; Zembal & Fancher, 1988; Zembal et al., 1989; Barton, 2016). The traditional nest patch has been described as *S. foliosa* with some stems taller than 60cm, and others taller than 90cm, in the low marsh (Zedler, 1993). Alternative nesting habitats include freshwater reeds, pickleweed, spiny rush, and tumbleweed (Massey et al., 1984, D. Zembal per. comm.). Upland habitat is used during high tides for protection and foraging.

These management programs do not consider external factors that directly cause LFRR mortality or indirectly impact the birds mediated through their impact on the salt marsh from the watershed, atmosphere, and sea (external meaning outside processes that act on the marsh). There is a lot of evidence that external processes drive salt marsh habitat maintenance or loss through physical or chemical processes (Table 4-1). The impact of relative marine water level is the most well studied external factor driving marsh plain stability. Dynamic feedback loops between primary productivity and higher relative water levels (to an optimum) maintain marsh surface elevations (Kirwan & Guntenspergen, 2012) with more sediment trapping and deposition on the marsh plain from the increased duration of settling time and the increased density of stems which trap the sediment (Kirwan & Murray, 2007). Other external processes contribute to marsh maintenance through influences on salinity, soil moisture, sediment delivery or scour which either stimulate or stifle vegetation growth.

The direct impacts of external processes on the LFRR have been observed (Table 4-1) although they have not been quantified. For example, there has been no quantification of the relationships between the number of LFRR breeding pairs and the duration of high-water levels, amount of winter precipitation, or frequency of stormflows from the watershed, which would assimilate the salt marsh processes and direct LFRR impacts. This would be especially helpful for managing marshes in southern California that drain urbanized watersheds and management policies on runoff, effluent conservation, suspended sediment concentration, and other variables are actively being developed. For example, quantifying the value of precipitation on the marsh

Table 4-1: Ways that external forces act on the salt marsh morphology or vegetation, and the impact external forces have on the LFRR directly with example references.

| Forcing | Impact to saltmarsh | Impact to LFRR |
|---|---|---|
| Water level | Sediment delivery (Rosencranz et al., 2016)<br>Optimum water level (depth of marsh) for marsh productivity (Morris et al., 2002)<br>Dynamic feedback: ↑ water level → ↑ biomass productivity → ↑ marsh plain sedimentation and ↑creek stability (Kirwan & Murray, 2007)<br>↑ water level too much → ↓ Vegetation → accretion rates decline (Kirwan et al., 2010)<br>↑ water level too much: soil hypoxia → ↓ vegetation (Morris et al., 2002)<br>Humped shaped relationship with root growth (Kirwan & Guntenspergen, 2012)<br>Vegetation specific relationship with above ground biomass (Kirwan & Guntenspergen, 2012)<br>↑ Sediment salinity with lower water levels (Morris, 1995) | Forces birds to upland – vulnerable to predation (Zembal et al., 1989) |
| Streamflow | Sediment delivery (Ward et al., 2003; Warrick & Farnsworth, 2009)<br>Vegetation scour /erosion (Massey et al., 1984)<br>↓Salinity: cordgrass germinate/expand (Zedler et al., 1986)<br>↓Salinity: changes fish/benthos (Nordby & Zedler, 1991) | Nest flooding and kill eggs/juveniles (Massey et al., 1984) |
| Precipitation | ↓Salinity: vegetation germinate/expand (Mahall & Park, 1976; Noe & Zedler, 2001)<br>↑ moisture: vegetation germination/expansion (Noe & Zedler, 2001)<br>Sediment mobilization (Mwamba & Torres, 2002) | ↓ Prey population, followed by rebound (Seapy, 1981) |

could help watershed managers alter the stream discharge to the marsh based on the amount of annual precipitation.

Despite the vast literature on marsh plain evolution there are not enough studies quantifying external factors as they relate to the LFRR populations, which can help management. Though anecdotal evidence exists (e.g. Massey et al., 1984) from surveys that occurred coincidently with large flooding events, no studies have quantified the relationship of external processes on higher trophic levels, like birds or mammals, over long time periods. Interestingly, the direct impacts to LFRR from external events may be harmful (scour, flooding, prey death, etc.) though the long-term impact on marsh habitat may be positive. For example, large storms have been observed to cause immediate population crashes (Massey et al., 1984), but also stimulate cordgrass colonization through decreased soil salinity and sedimentation (Ward et al., 2003). Longitudinal studies that can elucidate trends between external variables and LFRR breeding population can account for the direct impacts to LFRR mortality and indirect effects on the LFRR mediated by impacts on the salt marsh, even if the mechanisms and relative importance are not yet fully understood.

In this paper, our goals are to describe conditions that are associated with LFRR breeding to aid managers in planning. Our objectives are to document the habitat that the LFRR occupies in the marsh for breeding and the relationships between the annual breeding population and patterns of streamflow, precipitation, and water level. These relationships provide a foundation for studying the impact of external processes on higher trophic levels in salt marshes. We also explore the spatial patterns of LFRR nesting habitat and home range. We assess our results considering the projections of climate change to speculate positive or negative trends in future years.

## *Methods*

### Overview

In this study we used three separate analyses to characterize conditions that support LFRR, starting with a narrow analysis of the nest site to a broader analysis of external events. The first analysis focuses on the habitat in the close vicinity of the nesting site, where we collected data on marsh surface elevation and vegetation (nest site analysis). The second analysis models the home range habitat. We use multiple years of survey data that reported LFRR nesting location to investigate relationships between nest site selection frequency and marsh surface elevation and vegetation (home range analysis). The third analysis explores the relationship between external drivers from the atmosphere, watershed, and ocean and the annual population of breeding pairs (environmental analysis).

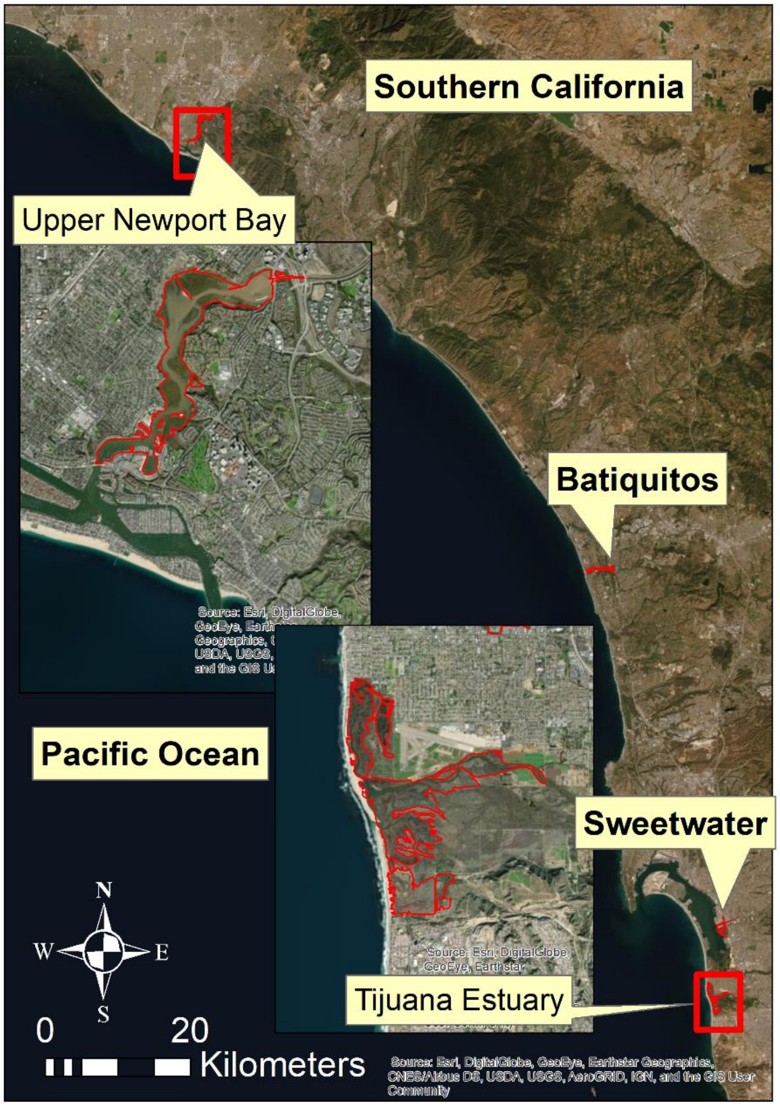


Figure 4-1: Study region in southern California, ranging from approximately Orange County in the north to San Diego County in the south. The two inset maps show the salt marshes where most data were collected for this study. The two other salt marshes, outlined in red, show where additional field data was collected.

### Study region

This analysis focused on a subset of coastal salt marshes in southern California, the only region that supports the LFRR (Figure 4-1). This region has a Mediterranean climate - long dry summers and cool wet winters - with most precipitation occurring in a few winter storms. The estuaries drain heavily urbanized watersheds. We used data from four salt marshes for the three different analyses in this study, from north to south: Upper Newport Bay (33.6463°N, -117.8862°W), Batiquitos Lagoon (33.0903°N, -117.2738°W), Sweetwater Marsh (32.6423°N, -117.1099°W), and the Tijuana Estuary (32.5514°N, -117.1161°W). Data for the nest site analysis was collected at all four salt marshes. LFRR data for the home range analysis was from historical and current surveys from Upper Newport Bay. The environmental analysis used data from Upper Newport Bay and Tijuana Estuary.

Upper Newport Bay drains an approximately 124 square mile watershed in northern Orange county (Trimble, 2003). It has a permanently open mouth due to the presence of two jetties on either side of the entrance channel and dredging in the lower bay which is a recreational harbor. The upper part of the bay is managed as an ecological reserve by the California Department of Fish and Wildlife and has approximately 752 acres of land including subtidal, mudflat, and salt marsh habitat. Two rivers empty into the upper bay: San Diego Creek and the Santa Ana Delhi channel. The upper bay is surrounded by steep coastal bluffs topped with residential housing and fresh water runoff from irrigation percolates through the bluffs and creates freshwater marsh habitat along the edges of the salt marsh. Channel erosion within the watershed historically occurred during development (Trimble, 1997) and led to the channelization of rivers and the construction of sediment basins within the marsh.

Batiquitos Lagoon is located in northern San Diego county and drains an approximately 52 square mile watershed (California Coastal Conservancy, 1987). There are six main habitat types: salt marsh, brackish marsh, sand/mudflats, subtidal, and riparian forest (California Coastal Conservancy, 1987). The lagoon had lost tidal connection due to development along the coast and in the watershed, but a large restoration project, completed in 1997, restored tidal action, dredged accumulated sediments, and created subtidal, intertidal mudflats, and salt marsh habitat, along with protected nesting areas (Walker et al., 1998). Two jetties were constructed at the mouth of the lagoon to maintain an open tidal inlet (Walker et al., 1998).

Sweetwater Marsh drains an approximately 230 square mile watershed in southern San Diego county. The marsh is part of the larger San Diego Bay National Wildlife Refuge, managed by the United States Department of Fish and Wildlife (U.S. FWS). Habitats in this marsh include mostly salt marsh and intertidal mud flat, but upland transition zone along with succulent scrub habitat occur as well.

Tijuana Estuary is at the southwestern corner of the United States and drains water from a 1,750 square mile watershed in Mexico (75%) and the US (25%) (http://trnerr.org/). The estuary is managed by the United States Department of Fish and Wildlife (U.S. FWS), California State Parks (https://www.parks.ca.gov), and the National Estuarine Research Reserve System under the National Oceanic and Atmospheric Association (NOAA). The reserve includes salt marsh vegetation, channels, mudflat, sand flats, and the upland includes riparian, coastal scrub and chaparral (Zedler et al., 1992). There is a sandbar at the mouth of the estuary that is typically open to the ocean, but does close rarely (Zedler et al., 1992). Historically, sewage discharge, vehicular transport, and residential development all negatively impacted the marsh (Zedler et al., 1992) and ongoing today is rapid development within the watershed that is contributing sediment build up (Taniguchi et al., 2019), trash and sewage to the marsh.

### Nest site analysis

We collected environmental data at LFRR nesting sites that were occupied in 2017 and 2018. In February 2018 we searched for nest site remains (from the 2017 breeding season) at freshwater marsh and salt marsh sites in Upper Newport Bay and recorded environmental data in a single marsh visit. The remainder of our collection efforts occurred in separate marsh visits to minimally disturb the LFRR: nest searching during the late spring and early summer of the 2018 breeding season, and nest site data collection in late 2018 summer after breeding season. In May and June of 2018, during active nesting season, we conducted four days of nest searching at Upper Newport Bay (5/18, 6/1, 6/6, 6/19), and one day of nest searching each at Tijuana Estuary (6/29), Batiquitos Lagoon (6/15), and Sweetwater marsh (5/31). An additional search at Sweetwater occurred on 7/27 during a marsh visit for a separate purpose. We focused our searches in sections of the marshes where LFRR have been observed nesting. In Upper Newport Bay we searched in both freshwater marsh and salt marsh, whereas in the other three marshes we exclusively searched in salt marsh habitat. The searching protocol included using sticks to gently inspect patches of tall and dense cordgrass, pickleweed, or bulrush. When a nest was observed, we used a hand-held GPS to record the coordinates, and then we moved away from that location to minimize disturbance to the LFRR. A marker (stick or dead reed found nearby) was placed outside the nesting patch to help locate it in the future.

In late August or September of 2018, after chicks hatched and adult LFRR were no longer defending their nests, we returned to the nests in each of the four marshes to collect data on vegetation and marsh surface elevation on the following dates: Upper Newport Bay (8/28, 8/29), Batiquitos Lagoon (8/31), Tijuana Estuary (9/7), and Sweetwater (9/8). Each site was found using navigation from an RTK-GPS, and at many sites we were able to confirm the location by the marker or the presence of nest remains (in some locations the marker or nest washed away). If we could not successfully re-locate a nest site with confidence, we did not take data at the site. If we came upon a nest site that we had not recorded earlier in the summer, we did take data. Elevation (datum NAVD88) was taken directly at the nest with an RTK GPS, and a 1m$^2$ quadrat was centered around the nest to take data on vegetation (Figure 4-2).

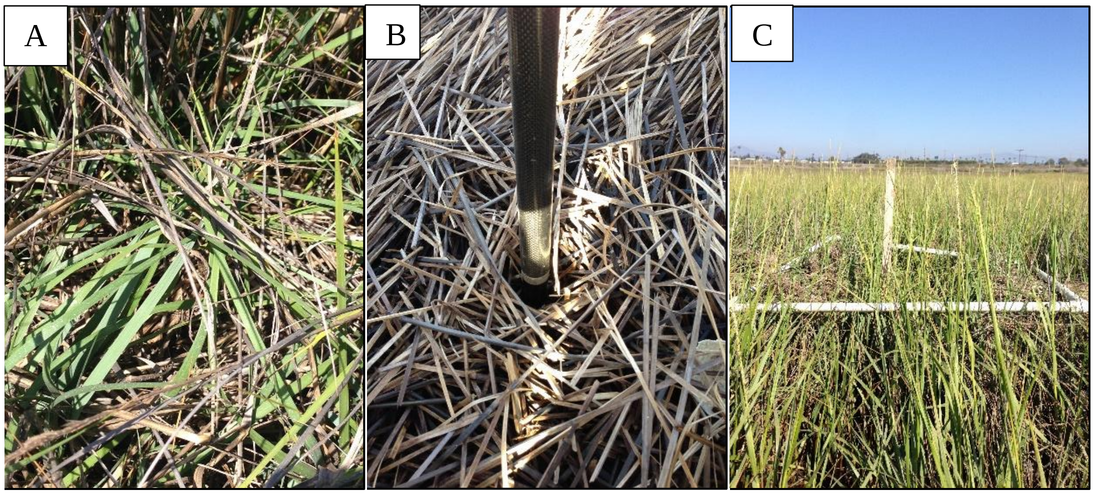


Figure 4-2: Photos from the field. (A) A nest that is being maintained during the breeding season. (B) Nest remains located after the breeding season showing the RTK-GPS taking elevation. (C) The 1m$^2$ quadrat surrounding a nest after the breeding season to collect data on vegetation.

Vegetation density and height has been shown to be important to LFRR nesting (Zedler, 1993) so we took data that addressed both characteristics (Table 4-2). In each quadrat, the tallest stem and the average stem height were recorded as is, i.e. we did not lengthen stems to be outstretched. Rather than count stems for density, we visually estimated the total plant cover of the plot which included all types of vegetation. To determine the respective vegetation species' cover in each quadrat we used cover classes and visual estimation which is commonly used in salt marsh studies (e.g. Wikum & Shanholtzer, 1978; Fox et al., 2012), largely following the Braun-Blanquet cover scale (Braun-Blanquet, 1932), but we included additional cover classes at the

Table 4-2: Nest environmental variables collected in the field and the definitions.

| Variable | Definition |
|---|---|
| Elevation (m) | Marsh surface elevation at nest (NAVD88) |
| Tallest stem (cm) | Tallest stem (as is) in 1m$^2$ quadrat |
| Average stem (cm) | The average height of 5 stems located at the center, and the intersection of the 0.2m mark on each side of the 1m$^2$ quadrat |
| Total cover (%) | By visual assessment, percentage of the 1m$^2$ quadrat that is covered with vegetation (0-100%), i.e. bare earth is not visible |
| Veg species cover (0, 1-5, 5-25, 25-50, 50-75, 75-99, 100) | Percentage of the 1m$^2$ quadrat that is covered with each vegetation species |
| Species richness | The number of vegetation species in each quadrat |

low and high end to more accurately represent the cover. To estimate the cover variables, we moved a meterstick along the side of the meter-long quadrat and estimated the cover within each 1/10th of the quadrat, and then summed the total. The two people in the field made cover class estimations independently and if we disagreed, we recounted.

The nest sites were clustered based on the environmental variables listed in Table 4-2. The thirteen vegetation species cover classes were collected as categorical data but we converted them to numeric data by taking the mid-range of each class (for example, the 5-25% class becomes 15) (Wikum & Shanholtzer, 1978). The other variables were all numeric and did not need any post processing. We used the 'dist' function from the stats package in RStudio (R Core Team, 2018) to calculate a distance matrix that represents the similarity of each nest site based on the environmental variables. We used the 'hclust' function, also from the stats package in RStudio, to run the hierarchical clustering. Hierarchical clustering is an agglomerative clustering technique where each site starts as its own cluster, and clusters get paired together based on their similarity until eventually there is only one total cluster made up of all the sites. This method produces a dendrogram that shows the grouping of nest sites. Higher up in the dendrogram, clusters get bigger and more inclusive of sites that are less similar. We cut the dendrogram at three clusters based on the location of natural breaks in the data. We calculated descriptive statistics (means and standard deviations) of the environmental variables within each cluster to describe different types of nesting sites.

### Home range analysis

The annual nesting sites used by LFRR were compiled from surveys from 2011 through 2018 for Upper Newport Bay (Zembal et al., 2016). The surveys employ 'evening clappering' call counts - the surveyor walks around the marsh at the start of breeding season and listens for LFRR calls from pairs vocally defending their nests or advertising for a mate. If no calls are heard, a recording of a LFRR call is played to elicit a response from a pair who thinks their territory is being intruded upon. The type of call indicates if the location is a nesting territory. The location of the call is marked by hand on a marsh map and while the nest is not physically located, studies have confirmed both that the number of vocalizations correspond with nest searches (Zembal & Massey, 1981) and that nests are near (~34m) to the LFRR call location (Bui et al., 2015). The 2011-2018 LFRR survey maps were georeferenced using ArcGIS version 10.6 (Esri Inc., 2017).

To account for limited accuracy, we put a buffer around each georeferenced point. We used the average distance between the 2018 *field* located nests (from the previous section) and the 2018 georeferenced *survey* data, but we only included survey data points that were within an area that has been reported as the higher end of the LFRR home range (1.66 ha, Zembal et al., 1989) – anything beyond this area we assumed was a pair nesting in a location that we did not find in the field. The average distance was 27m, which we used as the buffer distance surrounding each georeferenced point. This value is close to the 34m that Bui et al., (2015) found when comparing nest site and call location.

We used RStudio to partition the area of Upper Newport Bay, subtidal through upper marsh habitat, into approximately 0.40ha plots, which represents the average area per LFRR nest (R. Zembal per. comm.). Modeling at this scale prevents over predicting the carrying capacity of the marsh. In 2012, mapping was done for a portion of the marsh to collect data on vegetation and elevation (Thorne et al., 2018). We clipped the marsh surface to align with the mapped region and this included 200 plots (Figure 4-3). Each plot was assigned a percentage of years occupied, out of eight total years (2011-2018), depending on the number of years that a georeferenced LFRR survey point occurred in the plot (Table 4-3).

As mentioned above, marsh surface elevation data were obtained for Upper Newport Bay from a 2012 field survey of 1,037 points within the boundary outlined in Figure 4-3 (Thorne et al., 2018). We used these points to create an interpolated 5m$^2$ resolution raster of marsh surface elevation using inverse weighted distance in RStudio (RStudio Team, 2016). We clipped the raster surface to the dimensions of the marsh survey area to avoid erroneous values in the main channel or adjacent bluffs. For each of the 200 plots delineated as LFRR home range plots, we extracted the elevation values of all of the 5m$^2$ pixels that occurred in the plot using the 'extract' function in the raster package (Hijmans, 2018) in RStudio. For each plot, a series of elevation metrics were calculated based on the distribution of elevation values (Table 4-4). Three of the metrics we calculated described the percentage of the plot that fell within certain elevational ranges which were based on the nest site analysis data collected in the field. We used the minimum and maximum value of the LFRR nest

Figure 4-3: Plot of Upper Newport Bay divided into plots. The red outlines the area used in modeling.

Table 4-3: The number of years a plot was occupied over eight years within in the red outline in Figure 4-3.

| Years occupied | Number of plots |
|---|---|
| **0** | 20 |
| **1** | 22 |
| **2** | 26 |
| **3** | 16 |
| **4** | 22 |
| **5** | 18 |
| **6** | 34 |
| **7** | 28 |
| **8** | 14 |

site elevation which was 1.19m and 1.58m. There were actually three rail nests that were higher, but they fell into the next elevation range (1.58m to 1.95m) which was defined based on the elevation of nest sites collected for a different species that nests in the upper marsh for a separate study.

Table 4-4: Metrics calculated for each plot in Upper Newport Bay.

| Metric | Category | Definition |
|---|---|---|
| Mean (m) | Elevation | The mean elevation |
| Min (m) | Elevation | The minimum elevation |
| Max (m) | Elevation | The maximum elevation |
| 1.19m to 1.58m (%) | Elevation | Percentage of plot with elevations between 1.19m and 1.58m |
| 1.58m to 1.9m (%) | Elevation | Percentage of plot with elevations between 1.58m and 1.95m |
| >1.58m (%) | Elevation | Percentage of plot with elevations > than 1.58m |
| Mean (%) | Vegetation | The mean percent cover of each vegetation species |
| Max (%) | Vegetation | The maximum percent cover of each vegetation species |
| > 50% (%) | Vegetation | Percentage of percent cover for each species > 50% |

Vegetation surveys were also conducted at UNB, the same extent as the elevation surveys, from late November to early December 2012, in 248 locations (Thorne et al., 2018). Percent cover of different vegetation species within a quadrat was recorded. We used the same method for vegetation that we used for elevation, described above, to create an interpolated 5m$^2$ resolution raster of each vegetation species percent cover. For each of the 200 plots in the marsh, the values of the vegetation percent cover in each pixel were extracted and a series of metrics were calculated (Table 4-4).

To describe the relationship between the percentage of years a plot was occupied and the elevation and vegetation metrics we separated the 200 plots into training and testing data (75% and 25%, respectively) and used the training data to model the frequency of nesting occupancy using a multiple logistic regression model with eight weights - for each year 2011-2018 that there could have been a nesting bird. For this model, we used twelve variables: mean percent covers of

*S. folisa*, *J. carnosa*, *S. pacifica*, *D. spicata*, *B. maritima*, and *F. salina*, mean, maximum and minimum elevation (m), percentage of elevation between 1.19m and 1.58m, percentage of elevation greater than 1.58m, and the mean elevation squared because the data showed a quadratic relationship with elevation (Figure 4-6 in results). We added in 12 rows of observations that contained quasi-data for mean elevation values 0.0-0.5m (two rows for each) and zero percent occupancy. We did this because the elevation surveys were conducted to a minimum of 0.75m, likely because below this point is mostly mudflat with no vegetation and walking on the mud is difficult. However, because of this there were no values that show the low end of habitat suitability, which we rectified with the quasi zeros. Validation was performed on the testing data with root mean square error (RMSE) and the coefficient of determination, $R^2$. Comparing the predicted outcome (percent of years occupied) to the testing data had a RMSE of 0.22 and an $R^2$ of 0.73 with residuals normally distributed around zero.

### Environmental analysis

Whereas the previous two sections investigated spatial preferences of LFRR within the marsh based on habitat characteristics, this section explores the temporal trends of LFRR populations based on watershed, climatic, and marine forcing. We investigated the relationship between the annual breeding pair population and streamflow, precipitation, and water level metrics at Upper Newport Bay and Tijuana Estuary. See Appendix S-4-1 for the data sources in each section.

#### Water level

Tijuana Estuary water level data was downloaded from a logger in the Oneonta Slough managed by NOAA's National Estuarine Research Reserve System's (NERRS) National Monitoring Program. Water level data was recorded in Tijuana Estuary from 2010 to present, with methods to correct for differences in the measurement technique over time. At Tijuana Estuary, it was important to use water level data within the estuary because the sand bar at the mouth, whether open or closed, causes water level to be different from the coast. At Upper Newport Bay there is no long-term water level monitoring gage, so we used water level data from NOAA gage number 9410660 in the Los Angeles harbor. See Appendix S-4-2 for a comparison of water levels in Newport Bay compared to the NOAA gage for a period when a depth logger was deployed in the bay. Although the lower bay and anthropogenic modifications to the salt marsh do buffer some tidal action, it is managed as an open system and we think that local water level data is an acceptable proxy.

Water level metrics were calculated based on the ‘breeding year’, which goes from April of the previous year to March of the current year, when the annual bird surveys occur (Appendix S-4-3). This way LFRR survey data would be associated with water level data from the preceding 12 months. Each metric was calculated for four time periods in the breeding year: winter (Oct. – Mar.), summer (Apr. – Sep.), breeding season (Apr. – Aug.), and mating season (Feb. – Mar.). We chose to calculate metrics for breeding and mating periods because these are sensitive time periods when high water levels may be particularly harmful. For example, the breeding season would represent a time when nests need to be maintained and chicks could be emerging from the nest. We also calculated metrics for winter and summer season which are aligned with the growing season to see if there were times of year when high water is particularly helpful or harmful. As it turned out, breeding and summer time periods were very similar. For each period, we calcauted five metrics to describe the annual water level: maximum (m), mean (m), and duration of time the level exceeded 6ft, 6.5ft, and 7ft (hr).

### Streamflow data

Three streamflow time series were used for calculating metrics in Upper Newport Bay, all from the County of Orange, OC public works. There are two creeks that empty into Upper Newport Bay: San Diego Creek at the top of the marsh, and Santa Ana-Delhi about a third of the way down the marsh. A third, much smaller, creek empties into San Diego Creek just upstream of the marsh: Bonita Creek. The combined flow was used to calculate flow metrics for Upper Newport Bay. For the Tijuana Estuary, we used a discharge time series from the Tijuana River which is managed by the International Boundary & Water Commission (IBWC).

Flow metrics were calculated from the time series' by subsetting the data into 1-, 3- and 10-year periods that precede each survey year. We calculated metrics that describe the high flow magnitude, duration, frequency, and interannual variability (Konrad et al., 2008). High flow is defined as flow greater than the 90th percentile flow for that time series. Similarly, we calculate metrics that describe the low flow magnitude, duration, frequency, and interannual variability. Low flow is defined as flow less than the 10th percentile flow for that time series. We present the 1- and 10-year results for all metrics except interannual variability, where we report the 3- and 10-year results because that metric cannot be calculated for a single year. Like water level data, a breeding year was defined as April through March.

### Precipitation data

Precipitation data for Tijuana Estuary was acquired for years 2001 – 2019 at 15 minute increments from NOAA's National Estuarine Research Reserve System's (NERRS) National Monitoring Program. The Tijuana data was summed for total daily precipitation. Data for Upper Newport Bay was acquired from the ALRET system managed by the County of Orange, OC public works, for the location at San Diego Creek at Campus Drive and is recorded daily, for years 1990

– 2019. Years or seasons were excluded from analysis if missing data occurred for greater than 50% of the period. Four metrics were calculated from the daily precipitation: total precipitation seasonally (mm) and total duration of precipitation seasonally (days). Duration of precipitation refers to the length of time it was raining regardless of the intensity. Winter and Summer season were defined as Oct. – Mar. and Apr. - Sep., respectively. Seasonal precipitation was included because it can impact the growth structure of cordgrass, a critical structural component of LFRR nests (Zedler et al., 1986). Like the other metrics, a year was defined as April through March.

### Analysis

Streamflow, precipitation, and water level metrics were calculated, for each year of the LFRR survey data, for which there was sufficient historical monitoring of each variable. Streamflow and precipitation metrics were regressed against the breeding pair population using a simple linear mixed model. We used a mixed model in order to consider the random effects associated with the different marshes, in addition to the fixed effect of the external forcing metric. A mixed effect model is helpful for comparing data collected in different locations to account for the difference between the locations that are not otherwise included in the model. This was warranted because the two systems have important differences. The breeding population sizes differ – Upper Newport Bay has historically had a larger population of breeding pairs than Tijuana. The stream(s) enter the marshes at different angles so the flow of water and sediment over the vegetated marsh surface is different. Finally, other differences between the marshes that impact breeding populations include, among others, predator prevalence, upland habitat availability, and traffic exposure.

We analyzed the water level data in separate simple linear models for each marsh. We did separate models for this variable because the water level loggers are in different locations - one is directly in the marsh and the other is along the coast. Additionally, the two systems are different in their level of openness to tides, UNB is entirely open whereas Tijuana Estuary has a sandbar that dampens the tides. We felt that these differences were important enough that the relationship at each marsh may be different and lumping them into a single model would overlook these differences.

## *Results*

### Nest site analysis

Elevation ranges of the nests we located in the field were between 1.21m and 1.69m (NAVD88). Three types of sites were located and distinguished by cluster analysis (Figure 4-4). The most common were sites dominated by *S. foliosa* (Pacific cordgrass). *S. foliosa* dominated 62% (N=21) of the LFRR nests and 50% (N=17) of them had greater than 75% cover of *S. foliosa*. The second group included sites that had higher species richness and were at slightly higher elevations. Generally, the nests in this site were dominated by *S. pacifica* (pickleweed) and many sites also had *J. carnosa* (marsh jaumea) in high cover groups. The stem heights in this group were the lowest of the three groups (Table 4-5). The third group was dominated by *Schoenoplectus*

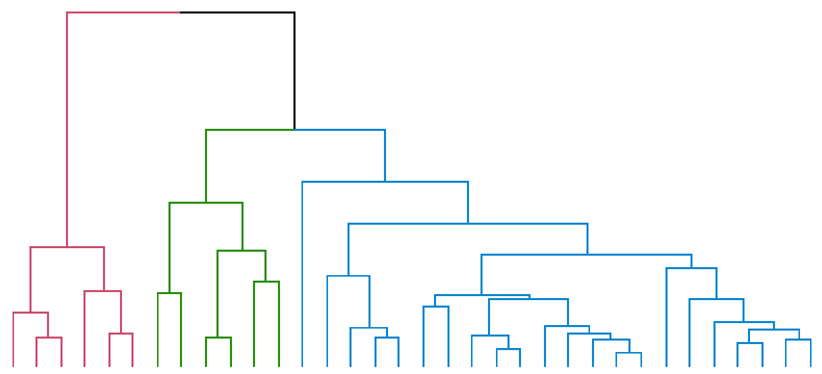


Figure 4-4: Groupings of the 34 nests located in the field based on elevation and vegetation metrics. Color indicates grouping based on hierarchical clustering. Red: sites dominated by *Schoenoplectus* spp.; green: sites dominated by *S. pacifica*; and blue: sites dominated by *S. folisa*. Table 4-5 describes each cluster.

Table 4-5: Characteristics of the clustered nest types. All values are averages within each cluster with standard deviation in parentheses. *n* is the number of nest sites in each cluster.

| **Cluster** | **Red** | **Green** | **Blue** |
|---|---|---|---|
| *n* | 6 | 6 | 22 |
| Stem avg (cm) | 113.67 (21.71) | 34.33 9 (11.50) | 54.82 (10.98) |
| Stem max (cm) | 162.33 (12.14) | 68.83 (17.29) | 95.45 (13.52) |
| Elevation (m) | 1.50 (0.08) | 1.52 (0.13) | 1.47 (0.09) |
| Total cover (%) | 90.83 (7.36) | 75.17 (18.76) | 74.95 (16.92) |
| *Spp.* rich (count) | 1.17 (0.41) | 4.67 (2.66) | 2.64 (1.05) |
| *S. foliosa* (%) | 0.00 (0.00) | 2.00 (1.55) | 63.48 (19.43) |
| *S. pacifica* (%) | 2.50 (6.12) | 52.42 (32.80) | 4.91 (5.75) |
| *Sch.*spp. (%) | 85.08 (12.22) | 0.00 (0.00) | 0.00 (0.00) |
| *J. carnosa* (%) | 0.00 (0.00) | 12.25 (13.96) | 6.14 (18.80) |

spp. (bulrush) and occurred around the marsh exterior. The nests in *Schoenoplectus* spp. had both the highest percent cover and the tallest stems of all the nest sites (Table 4-5). Other species that were present in low percent covers included *Batis maritima* (saltwort), *Frankenia salina* (Alkali Heath), *Salicornia bigelovii* (annual pickleweed), *Cuscuta salina* (dodder), *Limonium californicum* (sea lavender), *Distichlis spicata* (saltgrass), *Distichlis littoralis* (shoregrass), *Suaeda spp.* (seablite), and *Triglochin concinna* (arrow grass).

Species richness in a plot was negatively correlated with the tallest stem height (R = -0.62, P<0.001). Contrary to our expectation of a tradeoff between cover density and height, there was a positive relationship between total cover and average stem height (R=0.34, P=0.045).

### Home range analysis

In this analysis we compared the frequency of years (out of 8 total years) that a breeding pair occupied a plot with various elevation and vegetation metrics that differed between plots (Table 4-6). Of the vegetation metrics, frequency of plot occupancy was clearly positively related to the mean percent cover of *S. foliosa* (Figure 4-5 panel A) and the mean percent cover of *J.*

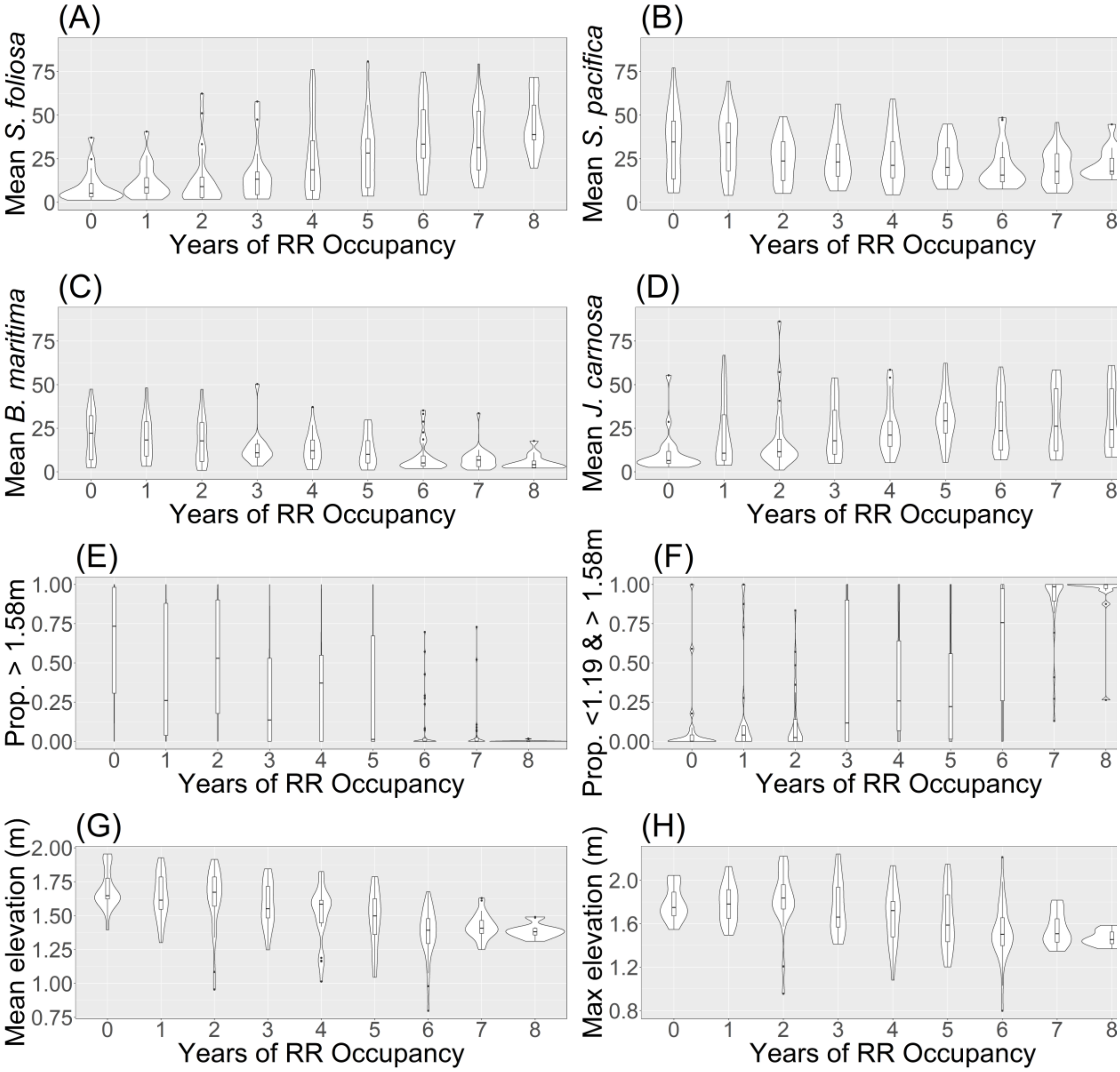


Figure 4-5: The frequency of LFRR occupancy and mean percent covers of vegetation or elevation metrics (not all the metrics are shown). The outer violin plots show the point density. The inner box plot shows the descriptive statistic locations which include the median, the 25th and 75th percentiles, and either 1.5*the inter-quartile range at the upper and lower end, or the highest and lowest value. Points beyond the 'whiskers' represent outliers.

*carnosa* (Figure 4-5 panel D). As expected, *S. folisa* was the most significant vegetation species and was positively related to more frequent LFRR site selection (P=0.0001, OR=1.03). Percent cover of *J. carnosa* in the plot was also positively associated with LFRR but to a lesser degree (P=0.0046, OR = 1.02). Frequency of plot selection decreased with mean cover of *B. maritma* – not surprising because *B. maritma* is a very low growing succulent that offers no nest building

Table 4-6: Results of the multivariate binomial regression with eight weights. Outcome variable is percent of year occupied. Elevation, elevation$^2$, and the mean percent covers of the major salt marsh vegetation types were used as predictors. *** p<0.001, **p<0.01, * p<0.05, NS p>0.05. Note the interpretation of odds ratio, for example, is a one meter increase in max elevation increases the odds of plot occupancy in any given year by 15.27 times.

| metric | Odds ratio (95% CI) | p-value |
|---|---|---|
| mean elevation (m) | 68.47 (0.38, 12332.79) | 0.1107 NS |
| mean$^2$ elevation (m$^2$) | 0.04 (0.01, 0.29) | 0.0012 ** |
| max elevation (m) | 15.27 (3.75, 62.14) | 0.0001 *** |
| min elevation (m) | 1.53 (0.50, 4.65) | 0.4572 NS |
| elevation 1.19m to 1.58m (%) | 4.51 (2.84, 7.17) | 0.0000 *** |
| elevation > 1.58m (%) | 2.96 (1.27, 6.88) | 0.0119 * |
| *S. folisa* (%) | 1.03 (1.01, 1.04) | 0.0001 *** |
| *J. carnosa* (%) | 1.02 (1.00, 1.03) | 0.0046 ** |
| *S. pacifica* (%) | 1.02 (1.00, 1.03) | 0.0265 * |
| *D. spicata* (%) | 1.02 (0.99, 1.05) | 0.1280 NS |
| *B. maritima* (%) | 0.97 (0.95, 0.99) | 0.0017 ** |
| *F. salina* (%) | 0.99 (0.97, 1.01) | 0.4743 NS |

material (Figure 4-5 panel C) (P=0.0017, OR=0.97). More surprising was that despite a negative trend displayed by the percent cover of *S. pacifica* when compared to the frequency of occupancy (Figure 4-5 panel B), in the model, *S. pacifica* was positively related to more frequent LFRR site selection (P=0.027, OR = 1.02). This suggests that when other variables are controlled for, the relationship with *S. pacifica* changes and LFRR are more likely to be in plots with higher percent covers of this species. We do not present results for the two freshwater grasses, cattails (*typha* spp.*)* or bulrush (*Schoenoplectus* spp.), even though we know that LFRR's nest in them, because the area sampled by Thorne et al., (2018) did not include sufficient coverage of those two species.

Elevation also had an important effect on the frequency of LFRR plot occupancy. We expected the frequency of plot occupancy to be positively related the proportion of the plot with surface elevation between 1.19m and 1.58m (Figure 4-5 panel F) because this is the elevation range that the birds build their nests in based on our field data, and this was confirmed (Table 4-6). The data show a negative relationship with the proportion of the plot with surface elevation greater than 1.58m, the mean elevation, and the maximum elevation (Figure 4-5 panels E, G, and H, respectively), but when controlling for other variables the multiple logistic regression had some unexpected results (Table 4-6). Percent of elevations greater than 1.58m, mean, and maximum elevation were all positively related to the frequency of LFRR site selection. This is interesting because while the other positive variables are associated with LFRR nesting site habitat elevation and vegetation, this suggests that upper marsh is also important in the home range. The positive relationships between high marsh elevation metrics and *S. pacifica*, suggest that LFRR use the whole marsh, not just the low marsh habitats typically associated with them. There is a significant quadratic relationship with mean elevation, where nesting likelihood is maximized at approximately a mean elevation of 1.25m, but goes to zero at approximately 0.5m and 2.0m (Table 4-6, Figure 4-6).

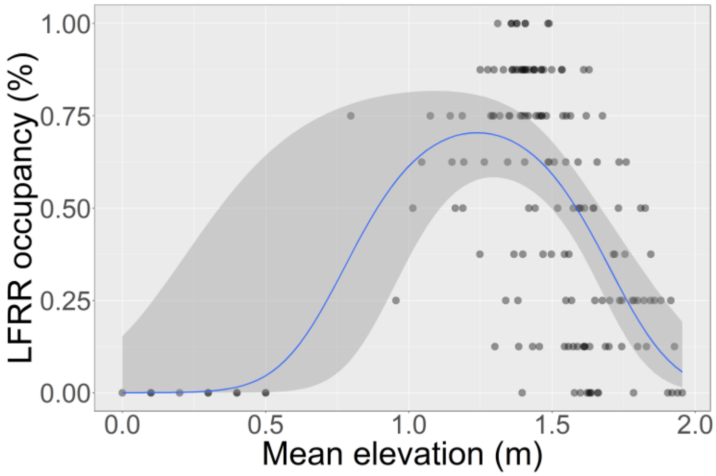


Figure 4-6: Quadratic relationship between the mean elevation and the percentage of years (out of eight) that LFRR occupied a plot. The trend line has a 95% confidence interval shaded around it.

### Environmental analysis

#### Streamflow

In this analysis we modeled a relationship with streamflow metrics to breeding population by using simple linear mixed models that included data from both marshes. We present results for each metric for low and high flows. We present results for these metrics calculated from the year and decade preceding the LFRR survey, but do not show results for the 3-year timeframe which is similar to the year. For the variability metrics, we do present results for the 3-year timeframe, instead of the 1-year timeframe, because these metrics are a measure of interannual variability and cannot be calculated within a single year.

There was a negative relationship with the frequency of high flow events in the year preceding the LFRR survey (P=0.10, N=64), but a positive relationship with the frequency of high flow events in the 10 years preceding the survey (P=0.08, N=58) (Table 4-7). On the other hand, the magnitude and duration of high flow events, at the 10-year timeframe, was negatively related to the population size (P<0.00, P<0.01, respectively, N=58). The high flow magnitude and duration in the year preceding the LFRR survey were not significant. This in some way challenged our expectations and in other ways supported them. We had anticipated that high flow events (magnitude, frequency, and duration) would be positively related to population size at the 10-year timeframe preceding the LFRR survey due to sediment deposition and freshwater influx, but negatively related at the 1-year timeframe due to direct impacts on LFRR's like nest scour and flooding. The frequency of high flow events was consistent with our prediction, but flow magnitude and duration variables were not. These relationships suggest that in general, LFRR breeding populations are highest in years that have minimal disturbance from the watershed.

Table 4-7: Relationship between key streamflow variables (for high and low flows) and LFRR population size. A negative arrow indicates a negative relationship and a positive arrow indicates a positive relationship. *** p<0.01, **p<0.05, ***** p<0.10, NS not significant.

| Flow Category | Flow | Timeframe preceding LFRR survey | Relationship |
|---|---|---|---|
| Magnitude | Low | year | ↓*** |
| | Low | decade | ↓** |
| | High | year | ↓ NS |
| | High | decade | ↓*** |
| Duration | Low | year | ↑** |
| | Low | decade | ↑** |
| | High | year | ↓ NS |
| | High | decade | ↓*** |
| Frequency | Low | year | ↑*** |
| | Low | decade | ↑*** |
| | High | year | ↓* |
| | High | decade | ↑* |
| Variability (flow range) | Low | 3 year | ↓*** |
| | Low | decade | ↓* |
| | High | 3 year | ↓ NS |
| | High | decade | ↓*** |

However, a higher frequency of high flow events at the decadal timeframe that are low in duration and magnitude appear to support of LFRR breeding populations.

Variability in low flow magnitude was negatively related to breeding population at the 3-year ($P<0.00$, $N=60$) and decadal ($P=0.10$, $N=58$) timeframe preceding the LFRR survey, and variability in high flow magnitude was negatively related to breeding population at the decadal timeframe ($P<0.01$, $N=58$). The high flow variability at the 3-year timeframe was not significant ($P=0.12$, $N=60$) but suggested a negative relationship with breeding population. Overall this suggests that consistent annual high and low flows are more favorable for breeding.

Precipitation

Breeding population did not have a statistically significant relationship with any of the precipitation metrics. Though not significant, there may be a positive relationship with the summer precipitation duration ($P=0.50$, $N=39$) and amount ($P=0.16$, $N=39$) but a negative relationship between the winter precipitation duration ($P=0.16$, $N=42$) and amount ($P=0.23$, $N=42$) (Figure 4-7). However, none of these relationships were statistically significant, so a future analysis with a larger sample size would be needed to determine if they are real.

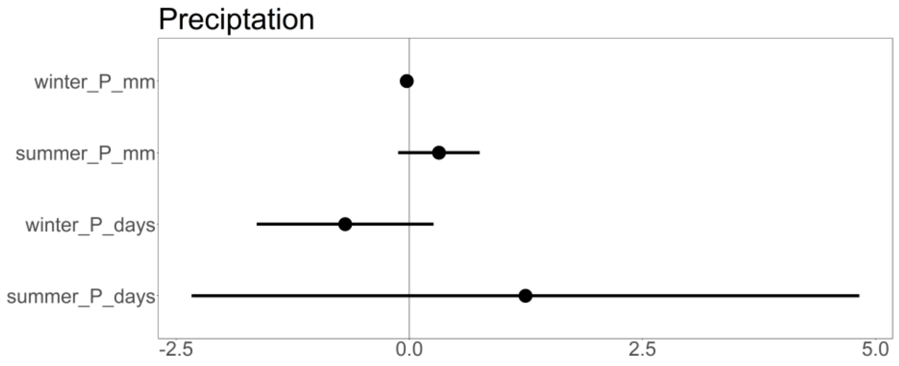


Figure 4-7: Summer and winter precipitation metrics. Winter_P_mm and summer_P_mm are the amount of rain in the winter and summer months, respectively. Winter_P_days and summer_P_days are the duration of the rain events (how many days there was rain) in the winter and summer months, respectively. The dot shows the estimated coefficient for the simple linear mixed model, i.e. a dot on the left side of zero means there is a negative relationship with breeding pair population and a dot on the right side of zero means there is a positive relationship with breeding pair population. Error bars show the 95% confidence interval, which cross zero for each variable showing non-significant results.

### Water level

We hypothesized that increased duration and height of high summer water level would be negatively correlated with the population due to direct impacts to LFRR such as nest flooding and predation in the upper marsh. There were few statistically significant results with the water level metrics, but we present results for five metrics in the summer or winter season. Metrics not presented were excluded because they are similar to others, for example, we do not present results for duration of time in the summer that level exceeded 6ft because the relationships are similar to the duration of time in the summer that level exceeded 6.5ft. Similarly, the relationships in the breeding season were quite similar to relationships in the summer season, as expected based on the overlap in dates.

In Upper Newport Bay (UNB), breeding pair population had a positive, though not significant, relationship with summer mean water level (Figure 4-8 panel UNB (A)) and the duration of time in the summer that level exceeded 6.5ft (Figure 4-8 panel UNB (C)) (P=0.10 and P=0.11, respectively, N=28). There was no relationship with the highest water level in the summer (Figure 4-8 panel UNB (B)). Though also not statistically significant, there was a positive relationship with the winter highest water level (Figure 4-8 panel UNB (D)) and the duration of time that water level in the winter exceeded 7ft (Figure 4-8 panel UNB (E)) (P = 0.18 and P=0.13, respectively, N=29).

In Tijuana Estuary (TE), breeding pair population had a negative relationship with the summer highest water level (Figure 4-8 panel TJ (B)) duration of water level during breeding season above 6.5ft (Figure 4-8 panel TJ (C)) (P=0.08 and P=0.04, respectively, N=8). There was no relationship between breeding pair population and the summer mean water level (Figure 4-8 panel TJ (A)). Though not significant, unlike the summer water level variables which had a

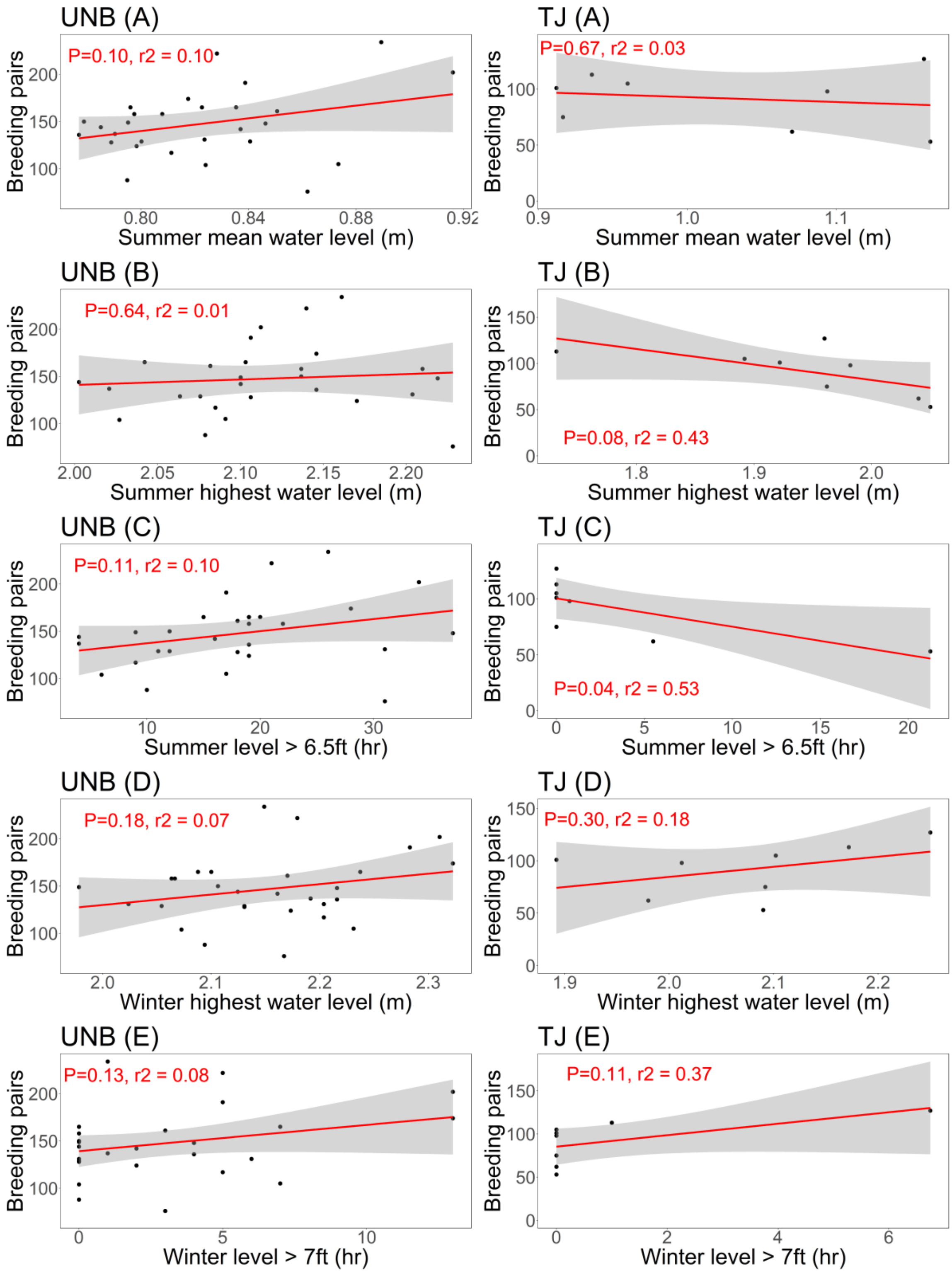


Figure 4-8: The relationships between water level metrics and the number of breeding pairs. Trend line is a linear model with a 95% confidence interval shaded around it. UNB: Upper Newport Bay. TE: Tijuana Estuary. Letters in parentheses refer to the panels used for referencing in the text.

negative relationship with the number of breeding pairs, the two winter water level variables, have a positive relationship with the number of breeding pairs (Figure 4-8 panel TJ (D) and TJ (E), respectively). Interestingly in TE, there was a negative relationship with breeding population and the duration of time that water level exceeded 6ft (P=0.18, N=8) and 6.5ft (P=0.27, N=8) in the mating season (Feb. and Mar.) (results not shown). This is interesting because though those two months are part of the winter season, which showed mostly positive relationships with breeding population, perhaps these months are unique, although the analysis needs to be repeated with a larger sample size to see if the effect it real.

### *Discussion*

Our studies document rather complex relationships between LFRR breeding sites and populations, and environmental characteristics. Breeding sites are associated with freshwater marsh and salt marsh, and lower marsh and upper marsh, which suggests that managers need to consider multiple endpoints for restoration or conservation projects. Breeding populations in some instances showed conflicting responses to precipitation (summer verse winter), water level (one marsh verse another) or streamflow (decadal verse annual frequency), which will likely complicate projections of climate change impacts on LFRR. Wildlife that depend on salt marshes are threatened because not only do they depend on the salt marsh vegetation surviving novel conditions, but they themselves and their prey need to survive the new physical or chemical conditions. Efforts to project the impact climate change on *Rallus* spp. often focus on sea level rise as the driving force behind habitat loss (Veloz et al., 2013; Zhang & Gorelick, 2014; Hunter et al., 2017; Rosencranz et al., 2018a). However, these other projected impacts of climate change will also contribute to the response salt marsh flora and fauna. We suggest that decadal and annual streamflow magnitude, precipitation timing, and water level impacts to upper marsh habitat extent (in addition to low marsh habitat extent) be included in studies that investigate the impact of climate change on salt marsh flora and fauna.

### Habitat conservation

Studies of salt marsh wildlife have generated recommendations for conservation such as the distance between habitat patches to support dispersal of the salt marsh harvest mouse (*Reithrodontomys raviventris*) (Bias & Morrison, 1999), maintaining upland habitat for the black Rail (*Laterallus jamaicensis*) protection during high tides (Evens & Page, 1986), maintaining upland for refuge during high tides and for sink populations of the marsh rice rats (*Oryzomys palustris*) (Kruchek, 2004), and further habitat and life history characterizations for the Florida salt marsh vole (*Microtus pennsylvanicus dukecampbelli*) (Hotaling et al., 2010). This type of information can be helpful for developing conservation plans that address climate change in the near term, such as ensuring presence of accessible upland and initiating monitoring, and longer term, such as designing corridor habitats (Thorne et al., 2012).

In this study we found that  majority of LFRR nests were in *S. folisa* and *Schoenoplectus* spp., and were similar to nests described in Massey et al., (1984) and Barton, (2016). Management efforts can help support these two habitats. *Spartina foliosa* distribution is driven by marsh surface elevation (Vogl, 1966; Zedler, 1977). While some studies have found that the atmospheric increase in $CO_2$ will help marsh elevation keep pace with sea level rise due to increased biogenic accretion (Langley et al., 2009), careful monitoring should be implemented and if accretion is not sufficient, techniques like sediment augmentation can be considered (Ford et al., 1999). In lieu of augmentation, distribution of sediment laden stream flow could be redirected over the salt marsh surface (Templet & Meyer-Arendt, 1988). *Schoenoplectus* spp. provided the tallest average stem heights and the highest percent cover. Maintaining freshwater input to the marsh, despite water conservation measures, could be one way to ensure *Schoenoplectus* spp. persists.

At the larger home range scale, we surprisingly found that in addition to low marsh elevations and vegetation, high marsh elevations and vegetation species were also positively associated with LFRR occupancy suggesting that high marsh has value as well, possibly for the same reason cited above, high tide refugia. Some studies are finding low marsh to be at less of a risk compared to the middle and upper marsh for moderate sea level rise projections (Kirwan et al., 2016; Thorne et al., 2018). This finding could erroneously lead to conclusions that LFRR habitat is safe based on their obvious low marsh preference for nesting and foraging, while overlooking the importance of higher zones during high tides when rails use the high marsh zone (Zembal et al., 1989) and predation pressures are the highest (Thorne et al., 2019). Management will likely need to engage in careful monitoring of marsh elevations to respond appropriately with projects that target the marsh zone that is submerging.

### Environmental analysis

Future climate projections show precipitation events to be more intense and more frequent despite disagreement about the total annual precipitation change (Das et al., 2013; Berg & Hall, 2015). This is projected to translate to novel riverine conditions including longer dry periods, more high stream flow events, increased maximum stream flow magnitudes, and more rapid return to baseflow following high stream flows (Taylor et al., In Prep.).

There may be a tradeoff between the negative impact on LFRR from more frequent storms and higher maximum stream flow, but positive effect on long term LFRR persistence through marsh maintenance. The positive impact of lowered soil salinity and increased soil moisture on salt marsh vegetation germination and zonation is well documented (Mahall & Park, 1976; Zedler et al., 1986; Callaway et al., 1990; Noe & Zedler, 2001). Moderate salinity levels are maintained through consistent tidal inundation (Callaway et al., 1990) and precipitation greater than 3cm has been found to lower soil salinity sufficiently for germination (Noe & Zedler, 2001). On the other hand, precipitation is also capable of substantial marsh sediment transport (Mwamba & Torres, 2002). Large storms can fill tidal creeks, close estuary mouths, and elevate the marsh plain (Zedler et al., 1992). These geomorphic or chemical changes can lead to invertebrate loss (Seapy, 1981; Nordby & Zedler, 1991) and changes in vegetation cover (Massey et al., 1984). In neither marsh did we find a significant impact of precipitation. However, there did appear to be a pattern suggesting a positive relationship between summer rain and breeding pair population but a negative relationship with winter rain and breeding pair population. This could reflect the tradeoff between the positive impacts of summer rain on marsh vegetation growth, and the harmful effects of sediment movement and marsh scour from large winter storms.

The negative relationship between the breeding pair population and high streamflow magnitudes, durations, and frequencies within the one-year timeframe suggests that immediate impacts of flooding from the watershed are harmful and trump the beneficial impacts of soil salinity reduction. However, we found that the frequency of large decadal floods, were positively related to breeding population count. Perhaps this reveals another tradeoff between the positive effect of freshwater on *S. folisa* germination and growth following sediment deposition, observed in Ward et al., (2003), when enough time has passed to create new LFRR habitat, but the negative impacts to LFRR directly following a storm.

### Management conclusions

Management for LFRR could occur at different spatial scales. In the salt marsh, habitat managers could implement restoration projects that support vegetation through sediment augmentation, vegetation planting, or freshwater runoff diversions. This would benefit nesting and home range habitat. Management actions that minimize direct harm to LFRR from external events could include upland space maintenance and access to upland via transition zones so birds can survive high tides. This may allow the positive impacts of external events on marsh maintenance to outweigh negative direct impacts on LFRR. At a larger spatial scale, watershed managers, such as stormwater agencies, could consider salt marsh species while setting flow requirements in effluent and stormwater programs. This could include a decadal large streamflow combined with efforts to minimize streamflow during other parts of the year through wastewater and stormwater capture and reuse. Precipitation and water levels cannot be managed like hydrology, but monitoring of these variables could be used to inform and predict annual rail populations.

## *Supporting Information*

Additional information is provided for the data sources of the environmental metrics (Appendix S-4-1), water level comparison for Newport Bay and Los Angeles harbor (Appendix S-4-2), and a conceptual layout of the breeding year (Appendix S-4-3).

## Appendix S-4-1: Data sources for streamflow, precipitation, and water level

Table S-4-1: Sources used for streamflow, precipitation, and water level. UNB: Upper Newport Bay, TJ: Tijuana Estuary. Dates refer to the years of data used – they are approximate because the days of data in a certain year may have excluded them from certain metrics.

| Variable | Marsh | Stream | Source | Dates |
|---|---|---|---|---|
| Streamflow | UNB | San Diego Creek | County of Orange, OC public works http://hydstra.ocpublicworks.com/web.htm | 1992-2018 |
|  | UNB | Bonita Creek |  |  |
|  | UNB | Santa Ana-Delhi |  |  |
|  | TJ | Tijuana River | International Boundary & Water Commission (IBWC), https://waterdata.ibwc.gov | 1980-2018 |
| Precipitation | UNB |  | County of Orange, OC public works http://hydstra.ocpublicworks.com/web.htm | 1990-2019 |
|  | TJ |  | NOAA's National Estuarine Research Reserve System's (NERRS) National Monitoring Program, Tijuana River, http://trnerr.org/ | 2005-2019 |
| Water level | UNB |  | NOAA Tides and Currents, LA harbor: CO-OPS_9410660, hourly data https://tidesandcurrents.noaa.gov | 1990 - 2019 |
|  | TJ |  | NOAA's National Estuarine Research Reserve System's (NERRS) National Monitoring Program, Tijuana River, 15 min, Oneonta Slough (OS) http://trnerr.org/ | 2010 - 2018 |

## Appendix S-4-2: Los Angeles harbor and Newport Bay water level comparison

We compared water level data (MSL) from measurements taken in Newport Bay in September/October of 2002 (33° 37.266' N, 117° 53.954' W) to the NOAA water level gage in Los Angeles (LA) harbor (Station ID: 9410660, 33° 43.2' N, 118° 16.4' W). There is a time lag of 7.083 hours which we calculated based on the difference between the times of highest water levels at the two sites.

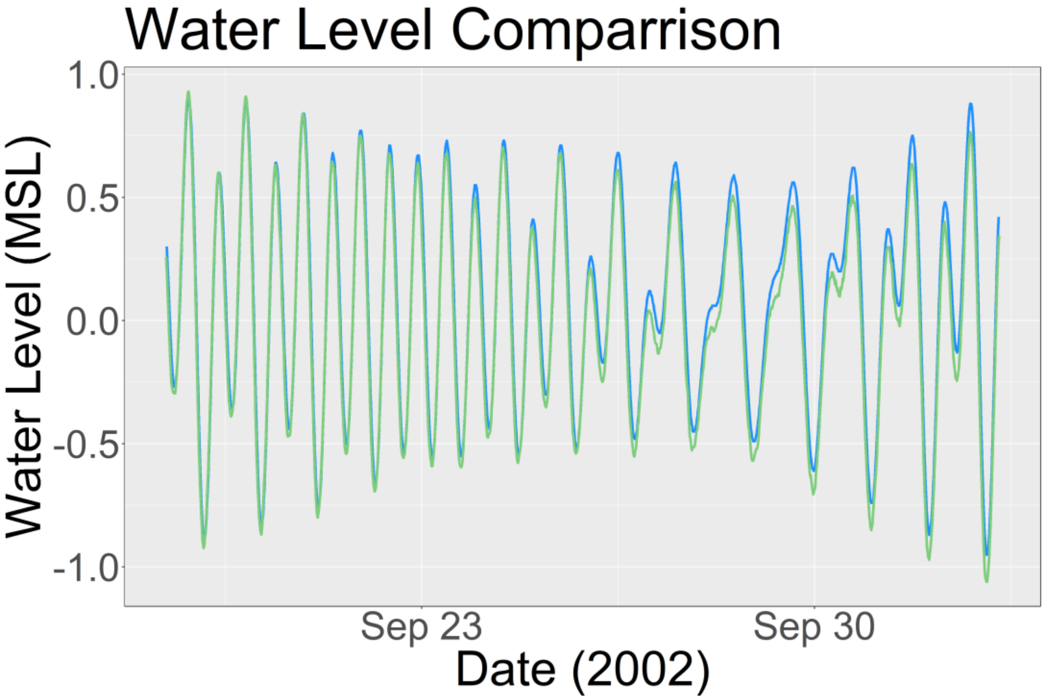


Figure S-4-1: Water level comparison after adjusting for the time lag. Green = Newport Bay, Blue = LA harbor

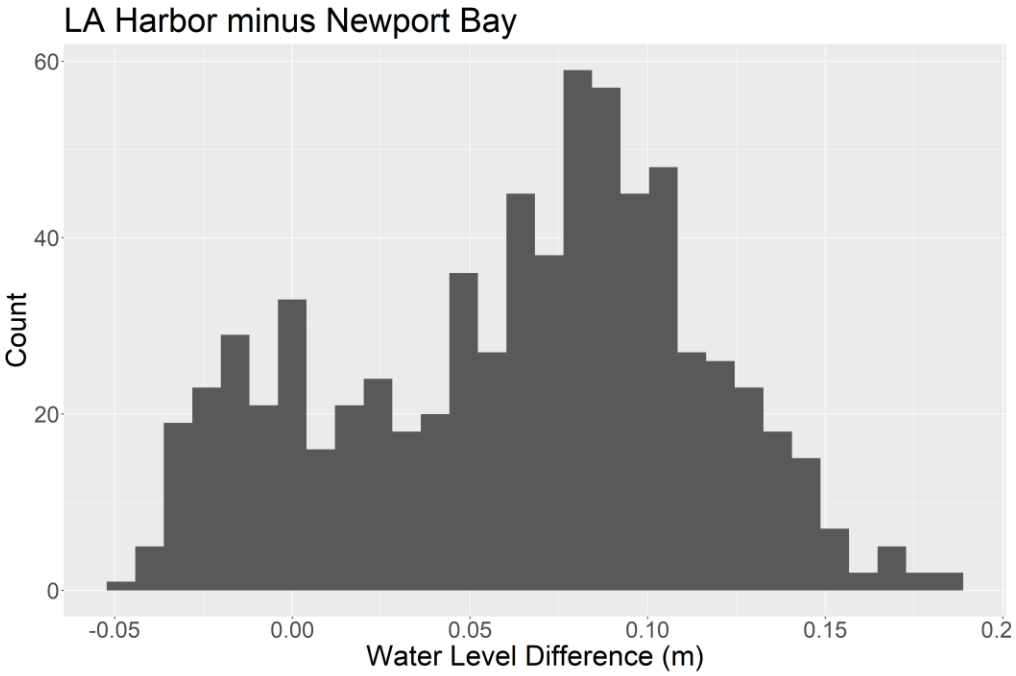


Figure S-4-2: Distribution of differences between the two gages every 30 minutes in meters.

Table S-4-2: Summary statistics of the water level time series for LA Harbor and Newport Bay.

| | LA harbor | Newport Bay |
|---|---|---|
| Min | -0.9500 | -1.060911 |
| 1st Qu. | -0.2900 | -0.337661 |
| Med | 0.0850 | 0.016089 |
| 3rd Qu. | 0.4100 | 0.345089 |
| Max | 0.9000 | 0.930089 |

## Appendix S-4-3: Breeding year example

The breeding year ends in March and metrics are calculated based on water levels in the previous 12 months. Green cells are part of the prior and next breeding year. Blue values show which months fall into each category which were used for calculating each metric. For example, summer maximum water level for breeding year 2000 is calculated by taking the max water level value that occurred during Apr – Sep of 1999.

| Calendar Yr | 🟩 1999 | 1999 | 1999 | 1999 | 1999 | 1999 | 1999 | 1999 | 1999 | 1999 | 2000 | 2000 | 2000 | 🟩 2000 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 🟩 Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | 🟩 Apr |
| Mating | 🟩 | | | | | | | | | | | 🟦 | 🟦 | 🟩 |
| Winter | 🟩 | | | | | | | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟩 |
| Summer | 🟩 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | | | | | | | 🟩 |
| Breeding | 🟩 | 🟦 | 🟦 | 🟦 | 🟦 | 🟦 | | | | | | | | 🟩 |

Figure S-4-3: Components of the breeding year.

# Chapter 5 Conclusion

In this dissertation I investigated the relationships between environmental and climatic variables and the distribution of vertebrates in aquatic habitats. We used these relationships to make projections about species vulnerability and distributional shifts based on climate change projections. The variables we used for riparian and riverine species occurrence predictions were streamflow and stream temperature, which were modeled from precipitation and air temperature data sets. The variables we used for coastal salt marsh species occurrence models were streamflow, precipitation, and water level from field monitored data. In the three chapters I explored how conditions in these habitats may change, described environmental – biological relationships, and developed biological projections for the future under projected climate conditions. In this chapter I will discuss the application of our results to other native riparian, riverine, and salt marsh species, potential management and policy responses to this research, and modeling innovations that can improve future analyses.

## *Implications of climate change for southern California native species*

We studied just seven native species occupying aquatic habitats in the coastal drainages in southern California. In this section I discuss how our results can be applied to other species.

We found that species that occupied high altitudinal river reaches were projected to have reduced habitat suitability due to stream temperature increases. Many, although not necessarily all, high-elevation species may have similar habitat constraints to the species we modeled. For example, the Santa Ana speckled dace (*Rhinichthys osculus*), the region's other native high elevation fish, may lose suitable habitat with climate change. Moyle et al., (2012) found *R. osculus* to be highly, borderline critically, vulnerable to climate change. Conversely, there is evidence that warmer temperatures in the mountains may positively impact the southern mountain yellow-legged frog (*Rana muscosa*), whose densities increased with both water and air temperature (Pope & Matthews, 2001). A positive impact of climate change was projected for *R. muscosa* in Wright et al., (2016) who projected an increase in mean habitat suitability under a selection of CMIP5 models compared to the other nine endangered reptiles or amphibians whose projected habitat suitability decreased across the state of California. Interestingly, *R. muscosa* occurrence was negatively correlated with *O. mykiss* presence so the decrease we projected in *O. mykiss irideus* may contribute to an increase in *R. muscosa* (Pope & Matthews, 2001) – a biotic interaction that we did not consider in our studies, but is certainly important. The American dipper (*Cinclus mexicanus*) is an aquatic bird that nests above mountain streams and forages in the stream for its prey. It is hard to know how warmer temperatures will impact this bird, but likely some of the impacts will be mediated through impacts on its invertebrate or fish prey.

Decreased hydroperiod and increased duration of low flows could potentially harm aquatic species that are living in perennial reaches of generally intermittent streams, such as the unarmored threespine stickleback (*Gasterosteus aculeatus williamsoni*), or species that occupy ephemeral pools in streams for part of their life cycle, such as the western spadefoot toad (*Scaphiopus hammondii*). For example, Morey, (1996) found that *S. hammondii* require 35 days for eggs to hatch and for larvae to develop. Pools that dry earlier result in total mortality. Once the 35-day threshold was reached, longer pool persistence allowed for greater fat storage in the larvae, which may increase fitness in their terrestrial life phase. A reduction in water permanence would of course decrease the time available for *S. hammondii* hatching and metamorphosis.

Some amphibians, such as the Western toad (*Anaxyrus boreas*) (Thompson, 2004) or California treefrog *(Pseudacris cadaverina*) (Cunningham, 1965; Harris, 1975), lay eggs in streams from late winter through summer. The timing is sensitive because egg laying and metamorphosis occur after the winter floods have passed but before the stream dries out and strands the eggs or larvae. An increase in winter storms combined with lengthened dryness may contract the length of time for the aquatic phase of the amphibian life cycle and make both flooding and stranding more common. Lengthened dry periods have been found to reduce breeding in *A. boreas* (Thompson, 2004; Pauly & Delaney, 2017). Overwintering locations for *P. cadaverina* have been documented in rock crevices near the stream but higher than the winter flood flows (Harris, 1975), which suggests that the timing and magnitude of winter flows could harm not just the eggs, but the adults as well. Predators of native amphibians, such as American bullfrog (*Lithobates catesbeianus*), require more perennial streams and may be further excluded from streams with lengthened dry periods. This could alleviate predation pressure on the native fishes and amphibians and offset some of the projected hydrologic or temperature stresses - another biotic interaction that we did not explore in our analysis.

For birds that nest and forage in riparian vegetation, impacts of changing stream conditions will be mediated through their prey and nesting vegetation. We projected that *V. bellii pusillus* will respond quite favorably to climate change, almost entirely due to temperature increases in higher elevation areas. The inherent assumption is that either their insect prey or vegetation preferences currently limit their elevational distribution, and that those elements will expand in response to climate change. Many studies have projected the impacts of climate change on riparian communities (see review by Perry et al., 2012). In a space for time substitution study, streams with longer durations of dry periods combined with increased storm events were associated with xeric plants with shorter canopies, as opposed to hydric pioneer species with tall canopies (Stromberg et al., 2010). A transition of this kind would harm nesting birds that rely on the dense riparian forest. Increased storm intensity was also found to be related to younger cohorts of hydric pioneer species due to increased disturbance and recruitment (Stromberg et al., 2010). It is hard to know how this would impact riparian birds that nest in trees at different successional stages. Perhaps birds that nest in very low shrubby sites would be less impacted, whereas birds that nest higher in the canopy would suffer from the reduction in tree height.

For birds that nest in river banks like the bank swallow (*Riparia riparia*) (Garrison, 1998) and the belted king fisher (*Megaceryle alcyon*) (Kimball et al., 2016), it is possible that the increase in flashiness combined with higher storm flow magnitudes will erode steeper banks and may actually augment breeding sites. However, this could also lead to more channelization, which is what destroyed their breeding sites initially (Garrison, 1998).

At the base of the watershed in the salt marsh, the Belding's savannah sparrow (*Passerculus sandwichensis beldingi*), like the LFRR, is a salt marsh obligate bird but it nests in upper marsh vegetation. Using species distribution modeling and marsh elevation, *P. sandwichensis beldingi* breeding and foraging habitat was projected to decline in southern California across all sea level rise scenarios, but particularly under moderate and high rates of sea level rise (Rosencranz et al., 2018b). It is possible that, like the LFRR, high stream flow events are negatively associated with breeding which would be projected to further decrease habitat suitability.

### *Management interventions*

The goal of developing species-environment relationships is to improve conservation or restoration programs which can improve projections for future habitat suitability. Species inhabiting streams and salt marshes may be positively impacted, negligibly impacted, and negatively impacted by climate change.  The species' I investigated in this dissertation are well studied, managed, and monitored, which means that in many cases sufficient species-specific knowledge exists to help translate these results into management action.  Programs can be designed to help specific species survive novel climates or to improve watershed features that can help species be more resilient to novel climates.

Management can aid a specific species that is projected to be vulnerable to climate change through different approaches, such as species translocations ("assisted migration") for animals (Hoegh-Guldberg et al., 2008) and plants (Williams & Dumroese, 2013) or habitat corridors to facilitate dispersal (Loss et al., 2011).  Assisted migration methods are helpful for species with limited mobility due to speed or distance limitations, like plants or amphibians, that are not projected to be able to move with the climate fast enough.  Perhaps these species can be translocated into locations projected to be suitable that they would not be able to get to on their own.  For animals that can disperse on their own, like fish, but where anthropogenic barriers such as dams have been constructed, building a dispersal route such as a fish passageway can allow them to migrate toward areas identified as suitable.  Often, a criticism of species distribution models is they do not account for dispersal limitations (Davis et al., 1998).  By accounting for management action, this limitation is less detrimental because managers can help ameliorate a dispersal limitation.

Other programs can be designed to enhance species resiliency toward climate change by improving habitat.  Projects can address drivers such as streamflow, stream temperature, sediment, or water chemistry to support species.  At a local level, to maintain thermal refuges, Kurylyk et al., (2015) suggest protecting natural cold water plumes through maintaining riparian vegetation, reducing groundwater and aggregate extraction, increasing thermal refugia through increased shading and reduced water mixing (debris upstream of tributary mouth or seep was found by Bilby, (1984) to naturally reduce mixing), or by creating new thermal refugia through groundwater pumping to certain reaches. Creating deep pools may not help as they were not been found to have cooler water in the deepest sections unless there was groundwater seepage (Bilby, 1984). At the watershed level, environmental flows and sediment dynamics can be restored through removal of roads and flow regulation (Beechie et al., 2010) and floodplain connectivity can be restored (Beechie et al., 2013). These watershed improvement projects can improve the outlook for species survival by alleviating other stressors present in the watershed.

In policy, habitat suitability projections can be used for delineating land in conservation programs and for making decisions about which species need protections. There are programs which provide compensation options for habitat destruction by restoring or conserving land elsewhere. For example, compensatory banking managed by the California Department of Fish and Wildlife (CDFW), the U.S. Army Corps of Engineers, and the U.S. Environmental Protection Agency (US EPA), helps ensure that if wetlands are lost during development activities, a comparable amount of wetland habitat is protected or even created elsewhere. Projections of climate change and species habitat suitability could be used to help decide where wetland habitat should be protected or created for the best chance of success.

Similarly, in the federal Clean Water Act, managed by the US EPA, waters of the United States are assigned ‘designated uses’ which then are assigned water quality goals that meet the criteria for that designated use. Designated uses can include human uses such as drinking water, recreation, or irrigation, but they also include the protection of fish and wildlife. Designated uses assigned for fish and wildlife can consider future stream suitability for various organisms. This would get a head start in achieving water quality improvements so that in future years the stream will already be managed for wildlife.

In addition to deciding where to place land restrictions, species are listed for protection, under the State or Federal Endangered Species Act, managed by CDFW or US EPA and National Marine Fisheries Service (NMFS), respectively.  Habitat suitability modeling could be used to project species vulnerability to climate changes.  The decision to list a species could consider projected habitat losses as well as current information on the status of populations and habitat quality.

### *Model innovations*

In this dissertation I took an interdisciplinary approach toward answering my research questions which involved assimilating multiple levels of modeling and data sets from different sources.  This approach used data and methods from climate modeling, hydrology, ecological theory, data sciences, and wildlife monitoring to help us address our complex questions.  There is room for improvement of many of our study methods in future projects.

In Chapter 2, we used a multivariate linear model to capture the relationship between stream temperature and air temperature throughout the study region.  In the future, it would be interesting to model a smaller area with a physically based temperature model to identify the cool water refugia in streams, characterized by Bilby, (1984), such as groundwater seeps, that are important in southern California streams during the summer (Matthews & Berg, 1997).  This would help differentiate sites that are prohibitively hot, and those that have enough refugia to allow survival through the hottest months.

Also in Chapter 2, we used three GCMs from the CMIP5 ensemble. Other studies that have used species distribution modeling combined with climate projections in CMIP3 or CMIP5 ensembles have used additional or fewer GCMs for different reasons. One study used a single model that performed well historically for their study region (Ochoa-Ochoa et al., 2012), another study used two models from CMIP5 because one preformed the best regionally for air temperature and the other performed the best regionally for precipitation (Remya et al., 2015), another study used seven CMIP5 models that could be compared to the CMIP3 ensembles (Wright et al., 2016), and finally another study used 14 models from the CMIP3 ensemble (Hof et al., 2011) to encompasses a range of plausible future climates. Other similar studies used two GCMs but do not provide a reason for their choice (Araújo et al., 2006; Milanovich et al., 2010).

The three models that we used were selected based on their historical performance and their variability in future projections (DWR, 2015; Rupp et al., 2015). It would be helpful to make additional projections of future stream conditions and habitat suitability using a larger sample size of GCMs from CMIP5 to better represent future uncertainty. A subset of GCMs shows only a small snapshot of all the plausible future scenarios – in fact, perturbing the physical parameters of just one of the GCMs from the CMIP3 ensemble created a new ensemble of future predictions that were fundamentally different from, not only the CMIP3 ensemble, but from the original model itself (McSweeney et al., 2012)!

We used correlative species modeling in Chapter 3 to relate spatial species occurrence data to georeferenced environmental conditions. Species distribution models have been used to map contemporary distributions for building range maps, finding suitable habitat for reintroduction or to search for yet unknown populations that may occur there (see review: Guisan & Thuiller, 2005). The increase in using species distribution modeling to support conservation decisions under future climate change conditions has been widely used but also criticized. Key issues from a policy and management perspective have been reviewed by Sinclair et al., (2010) and generally recognize the limitation of a species distribution model's ability to capture the true drivers of distributions, for biological or methodological reasons. They find that the use of statistical modeling is best with sufficient presence and absence data, good biological understanding of the target species to help with interpretation, and good communication of uncertainty.

One limitation of our method is that we made predictions based on future conditions that have a range of stream temperature and streamflow values that are not fully represented in the baseline training data (Sinclair et al., 2010). For example, a positive relationship with water temperature under current conditions does not mean a species will thrive under the projected hotter temperatures. A similar problem is that these models assume that constraints on the realized niche, such as biotic interaction, stay constant (Pearson & Dawson, 2003). By conducting our analysis in a temporally explicit manner with environmental scenarios from the past 30 years, we do expand the range of environmental conditions in the training data compared to a study using data from a single time period, but of course we do not include the full range of climate projections.

A future innovation to our methods would be to develop mechanistic relationships between a species and variables like streamflow, salinity, temperature, and water level. The distribution could then be modeled using the biophysical relationships that constrain the fundamental niche (Kearney et al., 2008; Kearney & Porter, 2009). However, it is challenging to accurately model physiological processes. Another option, is to combine correlative and mechanistic models which involve developing physiological relationships between the species and the environmental condition that includes the projected future environmental values (to avoid needing to extrapolate beyond the range of the data), and incorporating this relationship into the correlative species distribution model (e.g. Buckley et al., 2011; Rodríguez et al., 2019). The correlative portion of the model addresses the realized niche, which accounts for biotic and dispersal limitations, and the mechanistic model accounts for the physiological limitations. While all species-environment relationships may change in the future with new climate conditions, a hybrid model perhaps accounts for variables to the best of our ability at present. For example, we could develop biophysical relationships between *G. orcuttii* and water temperature so that thresholds could be established at the upper and lower end. This perhaps would reduce the future distribution in the regions where the stream temperature is too hot. Biophysical relationships could be developed for different activities such as breeding, foraging, and egg/larval development.

Also in Chapter 3, it would be important to consider why a species is absent. In this research all absences were attributed to a lack of streamflow or temperature suitability when in fact, the species could be absent in streams with suitable streamflow and temperature conditions due to other circumstances such as dispersal barriers (dams), predation by invasive species, or disease. This may lead to erroneous results because we train our model to consider certain flow and temperature regimes as not suitable when in fact they are. Future work could begin to address this by *excluding* ‘absence’ data points that historically hosted a population that has since been extirpated due to anthropogenic impacts.

In Chapter 4, a spatial analysis would help explain the mechanisms that drove the trends we observed. For example, an issue with nest flooding might be represented by a lack of nesting in the lower elevation areas of the extent usually inhabited by breeding pairs, whereas an issue with scour of *S. foliosa* may be represented by a lack of nests in areas where the storm flows have the highest shear stress. A mechanistic model would also help to understand how the number of nesting pairs is related to water level, precipitation, and streamflow. There are likely mechanisms that are routed through marsh vegetation and direct bird mortality via predation and or flooding. A model that relates each of the physical parameters (streamflow, precipitation, and water level) to these different mechanisms would help managers decide on different restoration and conservation goals, such as investing in nesting habitat or upland habitat projections.

A major modeling challenge for all three chapters was addressing the inconsistencies of combining data sets, which was necessary due to the large regions and/or time periods that we used to develop the habitat suitability models. Combing data sets for use in a model is difficult because different sources can report different metrics, collect or model data differently, and make different assumptions during data compilation. For example, in Chapter 3 we needed the species observation data to be temporally and spatially consistent with the climate modeling in unaltered watersheds, or in the vicinity of a flow gage. This precluded the use of many species' observations. For example, survey data in the Ventura river watershed that occurred after 2014 was excluded from model training due to a temporal mismatch with the climate modeling output. Using presence and absence addressed the different amounts of effort that surveyors put toward counting the species present. However, sometimes, a survey targeted an organism, suggesting high search effort searching, whereas in other cases species were reported opportunistically, suggesting low search effort. Similarly, the distribution of species observation data sources was not even throughout the study area.

## *Conclusions*

Climate change will create additional stressors on wildlife and vegetation already responding to an increasingly fragmented and polluted landscape in a more connected world. Species at all trophic levels can respond to new conditions with either tolerance, adaptation and/or evolution, or stress, extirpation, and extinction. It is impossible to incorporate all the variables that impact species' distributions in a model, especially because we do not even understand all the variables and their interactions. It is even difficult to incorporate the few variables that we do know to be important because so often there are data limitations. I think the best things we can do for species distribution modeling is to continue to support monitoring programs for more robust species presence and absence, count, and abundance data sets and to continue to support experimental studies that create mechanistic models to explain the biological-environmental relationship. Large correlative analyses, like the models in this dissertation, which focus on major habitat drivers, are helpful for elucidating trends. Combining them with smaller scale mechanistic models that incorporate additional drivers of species occurrence can help with interpreting the results in individual watersheds.

Identifying species - environment relationships, combined with environmental projections, can empower managers to formulate monitoring and restoration initiatives at the local level for species projected to be vulnerable, despite the global drivers of the overlaying problem. I think that local management can have a massive impact for species resiliency, and studies like this one, with continued method improvement, will assist with problem identification and solution implementation for species struggling to adapt to a changing environment.

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