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Key Points:

- A positive correlation exists between the presence of treatment plants and threatened and endangered species in California watersheds
- One-third of watersheds, characterized by dense urbanization or agriculture, can receive most of their baseflow from effluent
- The fates of threatened and endangered species and effluent are interconnected in ways that are important for water policy

Supporting Information:

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

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The Intersection of Wastewater Treatment Plants and Threatened and Endangered Species in California, USA Watersheds

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Abstract A changing climate and often unregulated water extractions have exposed over 2 billion people to water stress worldwide. While water managers have explored a portfolio of options to reduce this stress, supply augmentation through reuse of treated municipal wastewater is becoming increasingly attractive. Wastewater treatment plants protect water quality and prevent sewage from contaminating waterways. Increasingly, this resource is utilized for numerous human (e.g., irrigation, drinking water, groundwater recharge) and conservation (e.g., stream and river recharge) needs in water stressed regions. To understand the role treated municipal wastewater plays in impacting conservation objectives we identified the intersection of wastewater treatment plant locations and occurrences of threatened and endangered (T&E) species in California and compared the permitted contribution of effluent to baseflow quantities of the receiving waterbody to assess the degree to which changes in effluent could affect instream waterbodies. We found a positive correlation between the presence of treatment plants and T&E species in California watersheds—a quarter of species have 100% of their range in watersheds with at least one treatment plant. This correlation is greatest for species associated with terraces and riparian habitat, followed by aquatic habitat and aquatic emergent vegetation. One-third of watersheds in our analysis can receive most of their cumulative watershed baseflow from effluent and are characterized by dense urbanization or agriculture. Our analysis demonstrates that the fates of T&E species and effluent are interconnected in ways important for water policy, suggesting that species conservation goals should be considered when making decisions about effluent reuse.

1. Introduction

A changing climate coupled with widespread and often unregulated human water extractions have exposed over 2 billion people to water stress worldwide in which the quantity and quality of water is insufficient to meet human and ecological demand (Gleick, 2000; Hamdhani et al., 2020; National Research Council, 2002; Olivieri et al., 2014; United Nations, 2021; Wang et al., 2021). While water managers have and continue to explore a portfolio of options to reduce this stress, supply augmentation through the reuse of treated municipal wastewater is becoming increasingly attractive (Tran et al., 2017). Indeed, the continued advancement of purification technology and overall freshwater scarcity in many urbanized regions has helped pave the way for treated municipal wastewater (hereafter referred to as “effluent”) to be utilized as a cost-effective augmentation of a region’s freshwater sources. In addition to helping meet freshwater demand for agriculture, landscape irrigation, and potable water generation (Hamdhani et al., 2020; Olivieri et al., 2014), effluent also has been used to recharge groundwater aquifers (Asano & Cotruvo, 2004; OCWD, 2023). Surplus effluent is discharged into oceans, streams, and watercourses, effectively supplementing flow in regions that experience anthropogenic flow withdrawal (Hamdhani et al., 2020).

The increasing reliance on effluent reuse in watershed management has been the focus of studies evaluating its effects on freshwater and ecosystem services. A recent review of literature on effluent-fed streams found that 85% of the 147 studies evaluated identified water quality as a major focus (Hamdhani et al., 2020). Studies have also explored consequences of effluent water quality on freshwater ecosystems and species (Brozinski et al., 2013; Herbert et al., 2015; Kinouchi et al., 2007; Martí et al., 2009; Sánchez-Morales et al., 2018; Vajda et al., 2011). For example, excessive eutrophication documented in effluent-fed streams (Martí et al., 2009) has been shown to restructure freshwater communities toward more tolerant or invasive taxa (Bellinger et al., 2006; Cook et al., 2018; Dunck et al., 2015).

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Despite the focus on the negative effects of effluent on water quality, recent research has documented its positive impacts as well. Effluent can create aquatic habitat in historically intermittent or perennial river systems that have had base flows diverted for human use. For instance, the Santa Cruz River in southern Arizona experiences large water withdrawals that have caused groundwater levels to drop and the river to flow ephemerally. Portions of the river wetted by effluent discharge have returned to a perennial flow regime; they are the only sections of the river that support dense riparian woodlands and high native biodiversity (Boyle & Fraleigh, 2003; Eppehimer et al., 2020). Effluent-fed rivers have supported rapid colonization of diverse dragonfly and damselfly species, suggesting that effluent can serve as an important input to habitats in urbanized landscapes (Bogan et al., 2020).

The many reuses of effluent can lead to unintended consequences from water management actions. In a notable case, government-mediated water conservation efforts during California's most recent drought from 2013 to 2017 led to reduced water intake to treatment plants (e.g., influent), leading to less available water for reuse (Tran et al., 2017), higher concentrations of total dissolved solids in discharged water, and overall less discharge released into streams (Schwabe et al., 2020). Treatment plant effluent also comprises greater than 50% of intermittent stream discharge during low-flow and drought conditions, magnifying both nutrient and salinity concentrations (Hur et al., 2007). Hence, many water management priorities are often in conflict (Mount et al., 2019), with agencies at the local, state, and federal levels adopting different objectives (Bhide et al., 2021).

To date, research into the consequences of effluent management has been mostly concentrated on water quality. However, with the growing use of effluent to restore habitat in hydrologically modified systems, we posit that there may exist large potential for emerging conflicts between aspects of effluent repurposing and threatened species management. Freshwater biodiversity is among the most imperiled across the planet (Almond et al., 2020; M. Jenkins, 2003; Reid et al., 2019); ecosystem health considerations are likely needed in most water management decision-making. Most studies on the ecological effects of effluent have been limited in spatial or taxonomic scope. A necessary step toward understanding the potential consequences of effluent management decisions on species conservation is to identify broader patterns of possible interdependence between the two.

Here, we studied the overlap between wastewater treatment plant locations and the occurrence of threatened and endangered species (hereafter “T&E species”) to present a holistic view of the intersection of effluent and species presence and the potential need for conservation considerations in effluent allocation decisions. By comparing the permitted contribution of effluent—an artificially created water source—to the baseflow quantities of the receiving waterbody, we assess the potential degree to which changes in effluent affect instream water bodies. To better understand the role treated municipal wastewater might play in conservation objectives we ask the following research questions:

1. what is the intersection of wastewater treatment plant locations and occurrences of threatened and endangered (T&E) species in California? and
2. what is the degree to which changes in effluent could affect instream waterbodies as assessed through comparison of the permitted contribution of effluent to baseflow quantities of the receiving waterbody?

The objectives of this analysis are not to diagnose effluent as beneficial or detrimental to a particular habitat or species within a watershed, but rather to highlight the extent to which effluent is widely present in areas with T&E species. Thus, we aim to understand whether the influence of effluent is likely to be widespread and therefore should be considered by water managers and conservation practitioners in decision-making processes.

2. Methods

2.1. Study System

This study was conducted at the watershed level within the state of California where freshwater biodiversity loss is pervasive due to high levels of species endemism, widespread land conversion, increasing natural disturbances, and extensive hydrologic modification concomitant with rapid human population growth, climate change, and related droughts in the region (Grantham et al., 2017; Moyle & Williams, 1990; Moyle et al., 2011). Wastewater treatment plants were born out of the need to protect water quality and prevent sewage from contaminating waterways. However, this resource has been utilized to service numerous human (i.e., irrigation, drinking water, groundwater recharge) and conservation needs (i.e., stream and river recharge) in areas that experience water stress. These needs often come into direct conflict with one another (Brooks et al., 2006; Luthy et al., 2015;

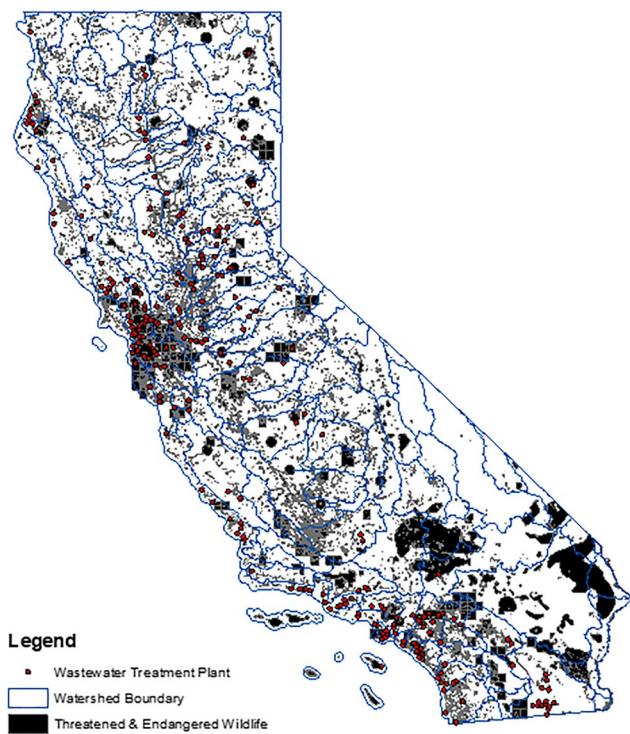


Figure 1. Spatial distribution of wastewater treatment plants, threatened and endangered (T&E) wildlife species polygons, and HUC-8 watersheds within California. While the full spatial distributions of T&E species occurrences are presented as in the California Natural Diversity Database, each polygon was reduced to its centroid for subsequent analyses. T&E wildlife, shown in the map as dark polygons, are distributed throughout California. While wastewater treatment plants (red dots) are prevalent throughout California, their highest clustering is located near metropolitan areas of the state.

tation (e.g., wetlands); riparian vegetation; terraces (e.g., alluvial fans, marine terraces); or uplands (meaning that the species is not associated with floodplains in any way). Terraces are formed on the longest time interval, as this habitat type is sustained by periodic flood events that occur on a longer climactic cycle. Thus, effluent effects on terrace habitats could be limited relative to larger impacts from flood control actions that attenuate the large flooding events that this habitat type relies on (Chock et al., 2020; US Fish and Wildlife Service, 1998). Indeed, terraces are the only floodplain habitat that would be expected to shrink with an increase in effluent flow. Terraces are a unique habitat type formed by larger scale disturbances (e.g., flooding) that restructure nutrients and sediment (Chock et al., 2020). This type of habitat can also overlap with low-flow channels in the absence of flow (i.e., rivers in arid environments that run dry in the summer and fall).

A total of 157 T&E species were documented within all of California's watersheds (Table 1). Fifty-six percent of these were identified as obligates to floodplain habitats (i.e., aquatic habitat, aquatic emergent vegetation, riparian vegetation, terraces), meaning that these species will almost always be found in their respective floodplain habitats. An additional 11% of these species are associated with floodplain habitats in a facultative capacity, meaning that they can be found in floodplain habitats, but also in upland habitats. Obligate freshwater species make up the largest proportion of T&E species, comprising 31% of the total (Table 1).

2.2. Threatened and Endangered Species Data

The threatened and endangered species that are the focus of this study are defined as animal taxa found within or off the coast of California that have been classified as endangered or threatened by the California Fish and Game Commission (state listed) or under the United States Endangered Species Act (federally listed). They

Poff et al., 1997) necessitating an evaluation of potential unforeseen consequences. Indeed, part of the impetus for a recent California law (SB 1157) was to provide funding to better understand the impact of indoor water-use efficiency standards on water systems, including influent and effluent quantity and quality and the environmental services effluent provides (California Water Code, 2022). In the Santa Ana River in southern California, for instance, treatment plant effluent has also substituted for natural flow and contributes significantly to sustaining one of the few remaining populations of the threatened Santa Ana sucker (*Catostomus santaanae*, J. A. Jenkins et al., 2009; Richmond et al., 2018). Documenting the degree of overlap between effluent dominance and species of concern is an important first step in mitigating potential conflicts.

The state of California contains 140 HUC-8 watersheds and 285 wastewater treatment plant facilities that discharge into waterways, of which 270 were included in the final analysis. These facilities are contained within 72 (51%) of California's watersheds (Figure 1). The majority of wastewater treatment plants are clustered in areas disturbed either by urbanization or agricultural production, such as the Los Angeles Basin and Inland Valleys of southern California, the San Francisco Bay Area in northern California, and the Central Valley region. The locations of wastewater treatment plants are correlated with urbanization ($\rho = 0.68, p = 2.2 \times 10^{-16}$), and to a lesser extent with agriculture ($\rho = 0.25, p = 0.003$) throughout California.

Our analyses focused on wildlife, or animal taxa (i.e., we did not include plants) listed under the federal or California Endangered Species Acts. The listed species are already legally designated as imperiled and, consequently, are likely to receive the greatest attention in water management decisions. For the purposes of this analysis, we focus on the floodplain habitats occupied by threatened and endangered taxa which are defined as all habitat types associated with a watercourse that rely on some frequency of flooding. Each species was associated with one of the following floodplain habitat types: aquatic habitat (meaning the species spends some portion of its life cycle submerged in water, e.g., fishes and amphibians); aquatic emergent vegetation

(e.g., wetlands); riparian vegetation; terraces (e.g., alluvial fans, marine terraces); or uplands (meaning

that the species is not associated with floodplains in any way). Terraces are formed on the longest time interval,

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effects on terrace habitats could be limited relative to larger impacts from flood control actions that attenuate the

large flooding events that this habitat type relies on (Chock et al., 2020; US Fish and Wildlife Service, 1998).

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and sediment (Chock et al., 2020). This type of habitat can also overlap with low-flow channels in the absence of

flow (i.e., rivers in arid environments that run dry in the summer and fall).

Table 1
Floodplain Use Attributes of California T&E Species

Floodplain habitat and frequency of use	Number of species	Percent of total
Aquatic		
Obligate—marine	6	3.8
Obligate—freshwater	48	30.6
Facultative	3	1.9
Aquatic vegetation		
Obligate	12	7.6
Facultative	1	0.6
Riparian vegetation		
Obligate	15	9.6
Facultative	3	1.9
Terraces (marine)		
Obligate	3	1.9
Facultative	3	1.9
Terraces (freshwater)		
Obligate	4	2.5
Facultative	7	4.5
<i>Floodplain subtotal</i>	105	66.9
Upland		
Obligate	44	28.0
Seasonal pools	8	5.1
<i>Upland Subtotal</i>	52	33.1
Grand Total^a	157	100

^aTotals may not add to 100% due to rounding.*Note.* Values in italics relate to number of species and percent subtotals for floodplains and uplands. Values in bold are grand totals of number of species.

are taxa which are in danger of extinction throughout all or a significant portion of their range. Wildlife species occurrence data was obtained from the California Natural Diversity Database (CNDDB), administered by the California Department of Fish and Wildlife (CDFW, 2019). This data set included all species' spatial occurrences that had been inventoried in the database through 5 January 2019. Wildlife species listed in the CNDDB were selected if, at the time of the data set download, they were cataloged by either the federal Endangered Species Act as "Endangered," "Threatened," "Candidate," "Proposed Threatened," or "Proposed Endangered" or by the California Endangered Species Act as "Endangered," "Threatened," "Candidate for Listing as Endangered," and "Candidate for Listing as Threatened" (CNDDB, 2019). Hereafter, all federal- and state-listed wildlife species described by the criteria above will be referred to as "T&E species" or just "species."

Each species was categorized by the floodplain habitat type they are most associated with, if applicable. The habitat associations for each species were determined by a review of available literature, including resource agency management plans and species reviews, as available, as well as other reputable natural history websites for more obscure species. Species were also classified as "obligate" if they require the habitat to survive or reproduce during some portion of their life history or "facultative" if they use but do not require that habitat.

The CNDDB functions as a data repository for rare species and has limitations to its utilization. Species absences are rarely noted in the database, so the occurrence data was used solely to document species presence and not species abundance. Given the disproportionate precision of spatial accuracy between species occurrences in the database, each species polygon was reduced to its centroid for consistent analysis. These limitations meant the species data was obtained and presented at a coarse resolution.

2.3. Watershed and Land Cover Data

All watershed analyses were conducted using the boundaries of the eight-digit Hydrologic Unit Codes (HUC 8), as defined by U.S. Geologic Survey

(USGS, 2019). The watershed data provided by the USGS is attributed to the California ecoregion (Region 18), an area not confined to any specific California political boundary (e.g., county or city designations). However, species and wastewater treatment plant data were spatially located within specific political boundaries, hence we further demarcated the watersheds according to these political boundaries in the analysis for consistency. This yielded 140 watersheds. Land cover data for the state of California was obtained from the 2014 Land IQ data set that delineates urbanization, agricultural, and natural land cover throughout the state (Kimmelman, 2017).

2.4. Wastewater Treatment Plant Data

Information on wastewater treatment plants was obtained from the California State Water Resources Control Board "Interactive Regulated Facilities Report" tool (State Water Resources Control Board, 2015). Using this tool, we analyzed all facilities that possessed a National Pollutant Discharge Elimination System (NPDES) permit. The NPDES is a federal program that regulates the discharge of wastewater to waters of the United States (such waters are legally defined as federally regulated waterways). Other wastewater treatment facilities regulated under other permitting structures were excluded because those treatment plants discharged to land-based resources and were not considered relevant to the research question. The list of wastewater treatment plants contained location data for most facilities. However, some facilities were missing location data, and these were manually added using information from the public record; two treatment plants were excluded from the analysis because locational data were unavailable. A total of 270 treatment plants were used for the analysis.

2.5. Flow Data

In order to estimate the proportion of discharge or flow potentially attributed to wastewater treatment plant outflow, associated permitted maximum discharge amounts for each treatment plant were obtained from individual NPDES permits. These data were then compared with water discharge data for the receiving streams using the “StreamNetworkTools” R package (Kopp, 2018). This R package streamlines the collection of covariates from the NHDPlus V2 data set (McKay et al., 2012) via the input of geographic coordinates. For this analysis, the geographic coordinates of all wastewater treatment plants were used to identify the nearest waterbody at a maximum distance of 1,500 m. Ten wastewater treatment plants were excluded from this portion of the analysis because they were further than 1,500 m from the receiving waterbody.

Flow covariates were collected for each identified waterbody. Covariates collected included cumulative mean annual runoff, minimum mean monthly discharge, maximum mean monthly discharge, coefficient of variation of mean monthly discharge, mean annual velocity, minimum mean monthly velocity, maximum mean monthly velocity, and coefficient of variation in mean monthly velocity. Flow covariates were available for a subset of the receiving waterbodies attributed to the treatment plants (181 out of 270 treatment plants); the ensuing analysis was performed on this subset only. Out of 72 total watersheds that contain treatment plants, 38 had flow covariate data for every treatment plant. A total of 29 watersheds had partial availability of flow covariate data for their treatment plants, and five watersheds had no records of flow covariate data. The remaining 68 watersheds do not contain treatment plants. All discharge data were $\log_{10} + 1$ transformed for data visualization purposes.

2.6. Spatial Analyses

The software ArcMap 10 (Esri, 2011) was used to organize and analyze the spatial data. Each watershed was attributed with the number of unique floodplain-associated species and wastewater treatment plants contained within its boundary.

Each species' range was quantified in relation to the presence of wastewater treatment plants within the state of California. For the purposes of this analysis, the species' range was defined by the watersheds in California that contained a positive occurrence of each individual species. For example, if least Bell's vireo (*Vireo bellii pusillus*) was documented as present in 44 of 140 total HUC-8 watersheds, its “range” was mapped as the area of these watersheds. This range was then overlain with the extent of wastewater treatment plants; if 33 of the 44 watersheds containing least Bell's vireo also contained a wastewater treatment plant, then 75% of the species' range overlaps with effluent-fed watersheds.

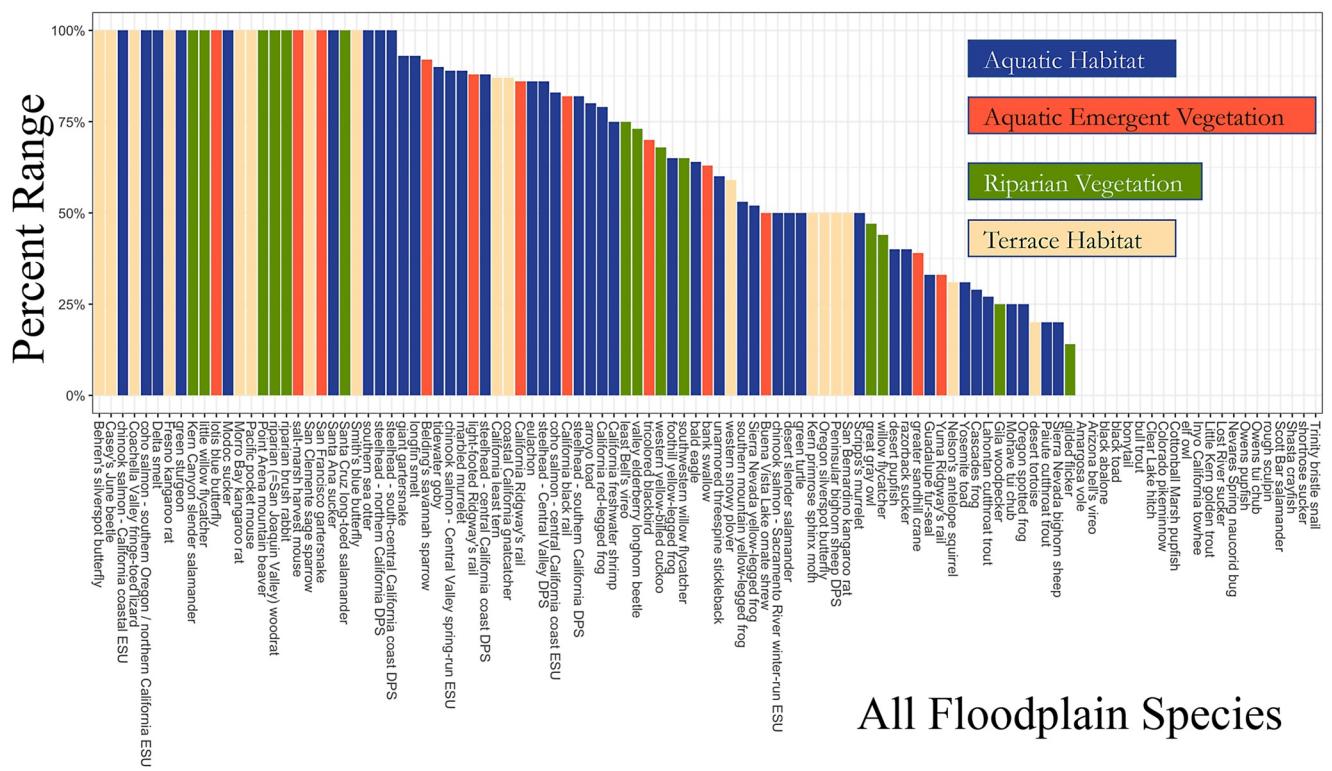
Species and wastewater treatment plant density were used in the analysis to adjust for the large variation in the sizes of the watersheds (although analyses with raw counts yielded similar patterns). For aquatic species, density was calculated using the area (acres) of NHD watercourse polygons as a coarse proxy for waterway area within each watershed. For other species, density was calculated using the total watershed area. The relationship between the density of wastewater treatment plants and density of floodplain-associated species within each watershed was evaluated using the non-parametric Spearman's rank correlation coefficient (ρ).

Land cover spatial data was overlain with the HUC-8 watershed data and the acreage of overlap was calculated using ArcMap 10. The acreage of “agriculture” and “urban” land covers was divided by the total acreage of each watershed to create an “urbanization distribution” and “agricultural distribution” per watershed.

3. Results

3.1. Spatial Overlap Between Wastewater Treatment Plants and Threatened and Endangered Species

Threatened and endangered floodplain-associated species were found in 138 of the 140 watersheds (99%) and in all 78 watersheds with wastewater treatment plants. There are many species that have high proportions of their ranges overlapping watersheds with treatment plant effluent. A total of 80% of floodplain-associated T&E species have some proportion of their range overlapping watersheds with wastewater treatment plants, with 25% (26 species) at 100% of their range; 38% (66 species) in the 50%–100% range; and 17% (18 species) in the 0%–50% range (Figure 2). Breaking this down by habitat type, 72% of aquatic-associated species, 92% of aquatic emergent vegetation species, 78% of riparian species, and 100% of terrace species have some proportion of their range overlapping watersheds with treatment plant effluent (Figure 3).



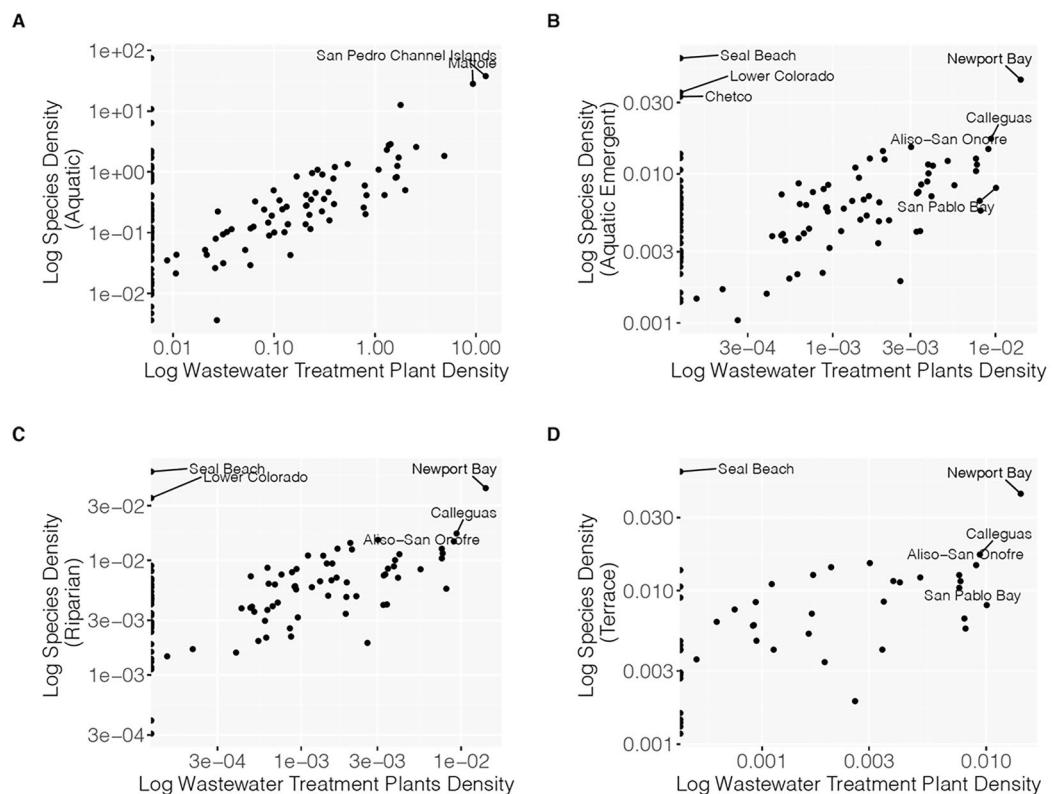


Figure 4. The relationship between the density of wastewater treatment plants and density of floodplain-associated T&E species per watershed. Each panel presents the relationship for species in a specific floodplain habitat type. Densities aggregated across habitat types are presented in Figure S1 in Supporting Information S1 while raw number per watershed are presented in Figure S2 in Supporting Information S1.

This correlation is observed most strongly with species associated with terraces ($\rho = 0.57, p = 2.5 \times 10^{-5}$) and riparian-associated habitat ($\rho = 0.51, p = 7.9 \times 10^{-8}$), followed by aquatic habitat ($\rho = 0.41, p = 1.2 \times 10^{-6}$) and aquatic emergent vegetation ($\rho = 0.41, p = 8.9 \times 10^{-6}$; Figure 4). Despite these correlations, there are many species occurrences in watersheds without wastewater treatment plants (Figure 4 and Figure S1 in Supporting Information S1). The correlation between the number of wastewater treatment plants and T&E species (i.e., not accounting for watershed area) was also significantly positive ($\rho = 0.64, p = 2.2 \times 10^{-16}$; Figure S2 in Supporting Information S1).

3.2. Discharge Analysis

When evaluating the permitted treatment plant outflow in relation to the receiving waterbody baseflow, we found that there are many watersheds that have the potential to receive the majority of their cumulative watershed baseflow from effluent. When comparing the maximum regulated discharge to the mean annual discharge of the receiving watershed, 23 out of 67 watersheds (34%, Figure 5a) and 83 out of 181 treatment plants (46%, Figure S3a in Supporting Information S1) documented higher potential outflow discharge than the receiving waterbody baseflow. When comparing to minimum monthly mean discharge, 46 watersheds (69%, Figure 5b) and 140 treatment plants (77%, Figure S3b in Supporting Information S1) documented higher permitted outflow discharge than the baseflow of its receiving waterbody. Finally, when comparing maximum monthly mean discharge, 12 watersheds (18%, Figure 5c) and 60 treatment plants (33%, Figure S3c in Supporting Information S1) documented higher permitted outflow discharge than the receiving waterbody baseflow.

4. Discussion

The aim of this paper is to analyze the degree to which wastewater treatment plant effluent and T&E wildlife species co-occur to understand the potential for future conflicts between effluent management and conservation.

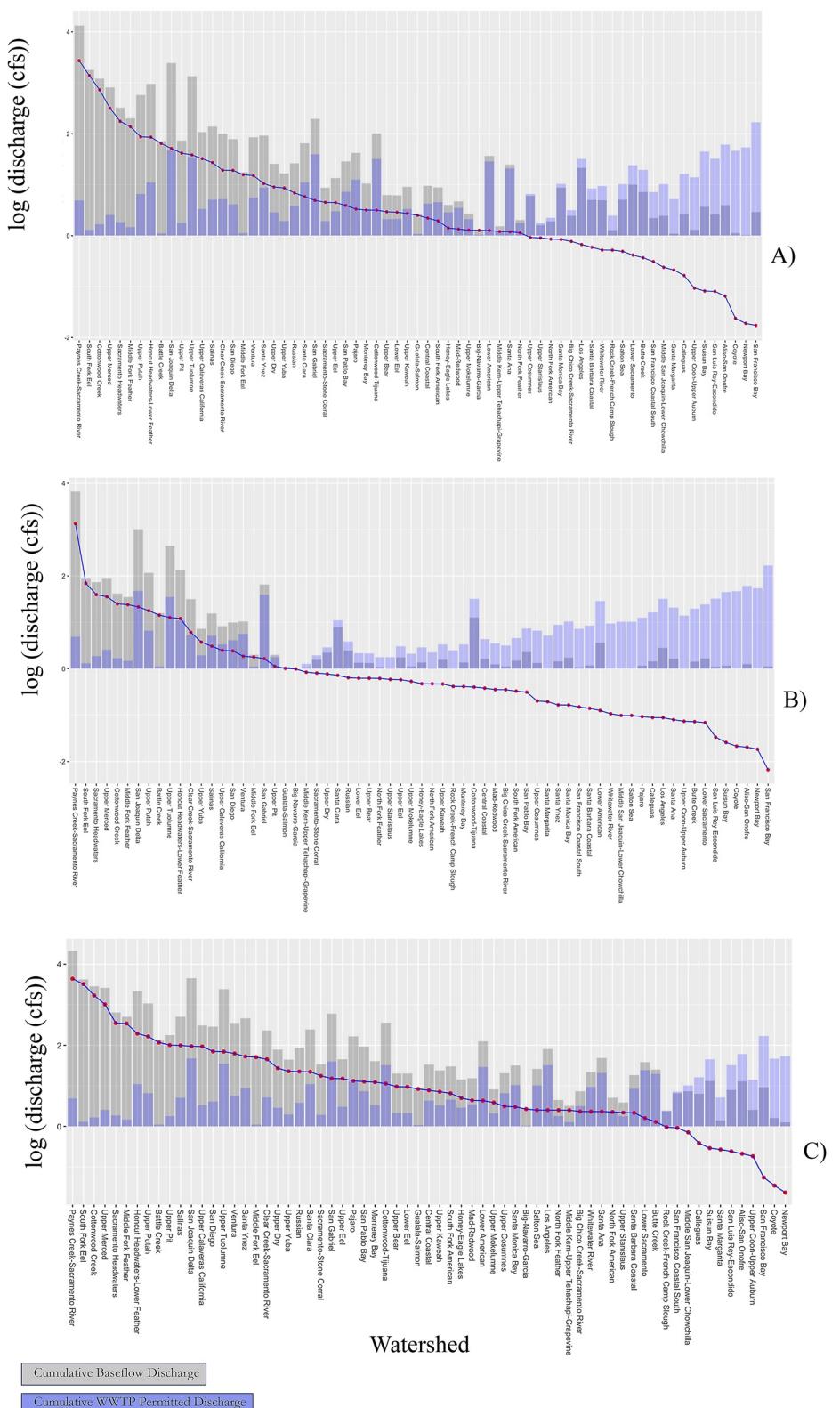


Figure 5.

We found that there is a positive correlation between the presence of treatment plants and T&E species in California watersheds, with a quarter of all species having 100% of their range in watersheds with at least one wastewater treatment plant. Together, these indicate a high degree of spatial overlap that warrants further research and management consideration. Additionally, we found that the permitted discharges for those treatment plants exceeded the observed natural baseflow in many cases. Thus, broad changes to effluent management have the potential to influence freshwater-associated T&E species in a large proportion of the state's watersheds.

Our study did not demonstrate a mechanism driving the correlation between the presence of treatment plants and T&E species, as each variable is likely responding to multiple similar drivers—land conversion, urbanization, and flood control, to name a few. As shown in Figure 1, the majority of wastewater treatment plants are in areas with disproportionate levels of hydrologic modification from either urbanization or agricultural production, including the Los Angeles Basin and Inland Valleys of southern California, the San Francisco Bay Area in northern California, and the Central Valley region. These areas are also likely to see the most complex interplay between water and species management objectives due to overlapping and conflicting water resource uses.

In one example of effluent management leading to unforeseen consequences, water conservation efforts were enacted by the California state legislature to curtail deleterious effects caused by drought (Schwabe et al., 2020). While these efforts did offset water shortages, they also resulted in a lower volume of water passing through wastewater treatment plants and discharging into rivers and streams. This caused extreme low flow events and high salinity concentrations within receiving waterbodies (Schwabe et al., 2020). Increases in salinity concentration reduce water quality and have harmful effects on wildlife (Patnode et al., 2015). Our analyses suggest that similar reductions in effluent discharge could lead to widespread degradation of habitat for species that have become accustomed to the presence of effluent as habitat.

4.1. Comparison of Natural Baseflow and Permitted Effluent Discharge

We found that many watersheds (34%) could potentially receive the majority of their cumulative watershed baseflow from effluent. These watersheds are located in areas with dense urbanization or agriculture that also host many wastewater treatment plants and T&E species (Figure 1 and Figure S4 in Supporting Information S1). We also found that 69% of studied watersheds are legally allowed to cumulatively receive more effluent than the baseflow discharge during minimum flow conditions (e.g., summer and fall). This suggests that in these cases waterbodies may not reach their natural low-flow points. Previous research has documented naturally ephemeral and intermittent streams that experience perennial flows as a result of treatment plant effluent (Brooks et al., 2006; Luthy et al., 2015), as well as effluent discharge increasing during low-flow conditions (White & Greer, 2006; Zimmerman et al., 2018). This is also consistent with studies across the United States that show that reliance on effluent has increased by up to 68% for municipal flows. Under low streamflow conditions increases ranged from 7% to 100%, illustrating the importance of wastewater in sustainable water supplies (Rice & Westerhoff, 2015; Rice et al., 2013). This raises the question of whether native species adapted to natural seasonal fluctuations are harmed by a dominance of stable effluent flows. For example, there is concern that stabilization of effluent flows in the Santa Ana River have promoted the increase in non-native piscivorous fishes at the expense of threatened native fishes (Huntsman et al., 2022). Significantly fewer (18%) watersheds in our study had cumulative permitted outflow that exceeded the maximum monthly mean discharges, indicating that at times of high-flow conditions (e.g., winter and spring), treatment plant effluent would likely not contribute as strongly to baseflow discharge.

Our comparison of treatment plant and natural flows was conducted at a relatively coarse scale because stream gage data were not available for the associated receiving waterbodies for all of the treatment plants. This necessitated an aggregation of flow data at the watershed level. However, this meant that some watersheds did not include effluent data for all the treatment plants within their boundary. In instances where effluent data for treatment plants was missing, the results may be an underrepresentation of the true contribution of effluent to baseflow.

Figure 5. Comparison of natural baseflow discharge and cumulative permitted wastewater treatment plant discharge in each watershed. The gray bars represent baseflow discharge and the underlying blue bars represent the permitted wastewater treatment plant discharge. Each bar represents one watershed within California. In areas where the gray bars are higher than the overlapping blue bar, wastewater treatment plant discharge is contributing less to the overall watershed discharge. In areas where the blue bars are higher than the overlapping gray bar, wastewater treatment plant discharge is contributing more flow than the natural baseflow. The red dots represent the difference in discharge between the baseflow and permitted amounts. (a) cumulative permitted watershed discharge compared with mean annual baseflow discharge; (b) cumulative permitted watershed discharge compared with minimum monthly mean baseflow discharge; and (c) cumulative permitted watershed discharge compared with maximum monthly mean baseflow discharge.

We were also unable to account for whether the stream gage that measured the receiving waterbody baseflow was upstream or downstream of the treatment plant outflow location. In events where the stream gage is located downstream of the treatment plant, the discharges from the treatment plant and receiving waterbody would have looked similar because the receiving waterbody gage would be capturing the treatment plant discharge. Finally, the baseflow discharge does not consider the multitude of other anthropogenic water withdrawals that could be occurring upstream of the stream gage location, particularly in urbanized landscapes.

Irrespective of the limitations described above, the conclusion that treatment plant effluent has the potential to shape species habitat within hydrologically modified landscapes across California does not change. An area of future study should include building upon natural flow modeling frameworks (e.g., Zimmerman et al., 2018) and quantifying the extent to which discharge from treatment plant effluent is replacing historical natural baseflows that have been removed through hydrologic modification. A useful analysis for water conservation policy would be an assessment of the quantity of water that has been removed for municipal purposes compared to a natural flow regime and in what ways effluent is replacing that removal.

It is also important to note that the flow analysis compared stream gage data (which was presented at the mean annual, minimum monthly mean, and maximum monthly mean time intervals) to the wastewater treatment plant discharge permitted by the state. The permitted values represent the maximum discharge permissible; however, it does not necessarily reflect the actual mean effluent discharges, nor does it reflect temporal variability of discharge at the day-to-day level within each treatment plant. Treatment plants discharge effluent at a fairly constant rate relative to a natural flow regime that includes seasonal and interannual fluctuation; however, treatment plant discharge still includes some variation. Generally, treatment plants produce outflow as a function of the inflow of wastewater they receive from their service region (i.e., how much municipal water is being sent down the drains). What is not recycled for other municipal needs is discharged into rivers and streams at a maximum discharge rate outlined in the treatment plant's permit from the state. The factors that determine this rate are based on the design capacity of the treatment plant, other municipal needs for the effluent, and the size and complexity of the service region. Human behavior also plays a role in discharge rates, with peak outflow occurring during daylight hours in response to the diurnal nature of most human activities (Butler & Graham, 1995; Enfinger & Stevens, 2006). While there is inherent variability in the discharge rate of a treatment plant relative to the maximum value listed on the permitting document, the variation is not comparable to what is seen in a flow regime intended to mimic natural conditions. An area of future study should include evaluating the daily discharge rates of a treatment plant in order to understand the true variability in discharge and compare it with both the receiving waterbody daily discharge and the historical natural flow regime. This would help fill the knowledge gap of how treatment plant discharge truly compares to a natural flow regime. It could ultimately lead to actionable suggestions that treatment plant operators could implement in order to mimic natural conditions and assist in species conservation.

4.2. Potential Interactions Between Effluent and Species Across Habitats

Freshwater biodiversity is imperiled globally (Reid et al., 2019). This extends to the state of California where we found that the majority (67%) of species protected under either the United States Endangered Species Act (16 U.S.C. §1531 et seq.) or the California Endangered Species Act (F.G.C § 2050–2089.25) are associated with floodplain habitats, which we defined as comprising instream aquatic habitat, aquatic emergent vegetation, riparian vegetation, or terraces. Additionally, we found that many of these species have high proportions of their range overlapping watersheds fed by treatment plant effluent; species in each habitat type generally showed the same high overlap, indicating all floodplain habitats have the potential to be influenced by treatment plant effluent. However, these habitat types and their associated species are likely to respond to effluent differently depending on spatial context and species traits.

Aquatic, in-stream species are expected to experience the most direct effects from effluent, particularly in regions where effluent comprises some of the only available aquatic habitat. For these species, effects of variation in effluent discharge would also be expected to occur on the shortest time interval, as this variation can instantaneously translate to variation in the availability of aquatic habitat. In an acute example in the Santa Ana River in southern California, periodic treatment plant shutdowns for routine maintenance ceased effluent inputs into the river, leading to rapid and near-complete flow reductions. The dramatic nature of these shutdowns, unbeknownst to conservation managers and treatment plant operators alike, lead to mortality of federally threatened Santa Ana

sucker (*Catostomus santaanae*) and had widespread effects on freshwater community composition (Saffarinia et al., 2022).

Riparian and aquatic emergent vegetation species would also experience effects from effluent, albeit at longer time intervals due to time lags in vegetation response to inundation or desiccation. Riparian and wetland habitat types can re-emerge as the direct result of an increased flow created by treatment plant effluent, especially in dry riverbeds where effluent causes a return to perennial flow (Stromberg et al., 2007; White & Greer, 2006). Riparian shrubland or woodland communities are present downstream of effluent outflows in several arid California sites, for example, within the Santa Ana River downstream of the Rapid Infiltration and Extraction Facility in Colton, CA, as well as within the Mojave River downstream of the Victor Valley Wastewater Reclamation Authority WTP in Victorville, CA. Similar to the analysis for aquatic-associated species, an increase in aquatic habitat from effluent could also drive an increase in riparian and wetland habitat types and support the species that rely on these habitat types in developed areas, given that treatment plants are most prevalent within urbanized and agriculturally driven landscapes.

Treatment plants, however, produce outflow at near constant rates, creating perennial waterbodies in systems that may have historically existed with an ephemeral or intermittent flow regime, a known phenomenon in arid environments (Brooks et al., 2006; Luthy et al., 2015). In this case, the presence of continuous treatment plant outflow could contribute to a decrease in the quality of habitat for terrace-associated species, especially when coupled with anthropogenic water withdrawal and flood control measures that limit the extent of flooding that these habitat types require (US Fish and Wildlife Service, 1998). Because of this, terraces are the most likely habitat types to exhibit correlations between T&E species and treatment plants, reflecting joint responses to urbanization rather than any causal links.

We acknowledge that this grouping of species solely represents those that have made it through the multitude of legal hurdles required for state and federal protection listings. There may be many other native species that are imperiled but remain understudied and have not yet received the attention or momentum necessary to begin the listing process. We also acknowledge that effluent may contain contaminants, in particular endocrine disruptors, antibiotics, and other pharmaceuticals, that escape treatment and result in concentrations that exceed safety thresholds (Ankley et al., 2007; Kamanmalek et al., 2022; Rice & Westerhoff, 2017). There is scant understanding of the prevalence, duration, and effects of these pollutants on at-risk species which create trade-offs on the quantity and quality of flow in effluent in streams.

Threats to freshwater species are widespread even if they do not result in T&E species listings in California (Moyle & Williams, 1990; Moyle et al., 2011) and also other Mediterranean regions (Arthington et al., 2016; Benson et al., 2021; Ellender et al., 2017). Additionally, effluent is a conservation issue in regions outside of California (Hamdhani et al., 2020; Segurado et al., 2016). Our analysis focused on legally protected species in California, USA watersheds due to their visibility within species conservation management and the malleability of their future trajectories; however, it is likely that the findings in this study can be extended to benefit other native floodplain species in the state of California and globally.

5. Conclusions

We have shown that there is substantial overlap between the presence of T&E species and the presence of wastewater treatment plants in California watersheds. We found a positive correlation between the presence of treatment plants and T&E taxa—a quarter of taxa have 100% of their range in watersheds with at least one treatment plant. This correlation is greatest for species associated with terraces and riparian habitat, followed by aquatic habitat and aquatic emergent vegetation. With this overlap there exists a large potential for conflicts among water management decisions shaping effluent use and species conservation. Our analysis demonstrates that the fates of these two resources—T&E species and effluent—are ultimately interconnected in ways that are important for water policy, suggesting that species conservation goals should be considered when making decisions about effluent allocations and reuse. The comparison of the permitted contribution of effluent to baseflow quantities of the receiving waterbody revealed that one-third of the watersheds in our analysis can receive most of their cumulative watershed baseflow from effluent and are characterized by dense urbanization or agriculture.

While our study does not demonstrate causality between the presence of wastewater treatment plants and T&E species, our analysis does demonstrate that the fates of these two resources are ultimately interconnected in ways

that are important for water policy. The co-occurrence patterns we have documented for California, USA, are likely true beyond our study area, as effluent fed streams are common throughout the globe (Brooks et al., 2006; Hamdhani et al., 2020). However, studies of effluent effects on wildlife remain overwhelmingly local in scope and broad scale studies such as ours are sorely needed (Hamdhani et al., 2020). We posit that knowledge gained from this and related future efforts will ultimately aid the development of decision-making tools that can be beneficial for both water and species conservation.

Data Availability Statement

Data from the California Natural Diversity Database were used in the creation of this manuscript. Threatened and endangered species data were extracted from the California Natural Diversity Database: species threat status from CNDDDB (2019) and species occurrences from CDFW (2019). The Watershed Boundary Data was used to demarcate sub-basins; this data was retrieved from USGS (2019). Land cover data for the state of California was obtained from the 2014 Land IQ data set that delineates urbanization and agricultural land cover throughout the state (Kimmelshue, 2017). Information on wastewater treatment plants was obtained from the California State Water Resources Control Board “Interactive Regulated Facilities Report” tool (State Water Resources Control Board (SWRCB), 2015). Water discharge data for the receiving streams of wastewater treatment plants was collected using the “StreamNetworkTools” R package (Kopp, 2018). This R package streamlines the collection of covariates from the NHDPlus V2 data set (McKay et al., 2012). The software ArcMap 10 (Esri, 2011) was used to organize and analyze the spatial data.

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References

Almond, R. E., Grooten, M., & Peterson, T. (2020). *Living Planet Report 2020-Bending the curve of biodiversity loss*. World Wildlife Fund.

Ankley, G. T., Brooks, B. W., Huggett, D. B., & Sumpter, A. J. P. (2007). Repeating history: Pharmaceuticals in the environment. <https://doi.org/10.1021/es072658j>

Arthington, A. H., Dulvy, N. K., Gladstone, W., & Winfield, I. J. (2016). Fish conservation in freshwater and marine realms: Status, threats and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 26(5), 838–857. <https://doi.org/10.1002/aqc.2712>

Asano, T., & Cotruvo, J. A. (2004). Groundwater recharge with reclaimed municipal wastewater: Health and regulatory considerations. *Water Research*, 38(8), 1941–1951. <https://doi.org/10.1016/j.watres.2004.01.023>

Bellinger, B. J., Cocquyt, C., & O'Reilly, C. M. (2006). Benthic diatoms as indicators of eutrophication in tropical streams. *Hydrobiologia*, 573(1), 75–87. <https://doi.org/10.1007/s10750-006-0262-5>

Benson, J. A., Stewart, B. A., Close, P. G., & Lymbery, A. J. (2021). Freshwater mussels in Mediterranean-climate regions: Species richness, conservation status, threats, and conservation actions needed. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(3), 708–728. <https://doi.org/10.1002/aqc.3511>

Bhade, S. V., Grant, S. B., Parker, E. A., Rippy, M. A., Godrej, A. N., Kaushal, S., et al. (2021). Addressing the contribution of indirect potable reuse to inland freshwater salinization. *Nature Sustainability*, 4(8), 699–707. <https://doi.org/10.1038/s41893-021-00713-7>

Bogan, M. T., Eppheimer, D., Hamdhani, H., & Hollien, K. (2020). If you build it, they will come: Rapid colonization by dragonflies in a new effluent-dependent river reach. *PeerJ*, 8, e9856. <https://doi.org/10.7717/peerj.9856>

Boyle, T. P., & Fraleigh, H. D., Jr. (2003). Natural and anthropogenic factors affecting the structure of the benthic macroinvertebrate community in an effluent-dominated reach of the Santa Cruz River, AZ. *Ecological Indicators*, 3(2), 93–117. [https://doi.org/10.1016/s1470-160x\(03\)00014-1](https://doi.org/10.1016/s1470-160x(03)00014-1)

Brooks, B. W., Riley, T. M., & Taylor, R. D. (2006). Water quality of effluent-dominated ecosystems: Ecotoxicological, hydrological, and management considerations. *Hydrobiologia*, 556(1), 365–379. <https://doi.org/10.1007/s10750-004-0189-7>

Brozinski, J. M., Lahti, M., Meierjohann, A., Oikari, A., & Kronberg, L. (2013). The anti-inflammatory drugs diclofenac, naproxen and ibuprofen are found in the bile of wild fish caught downstream of a wastewater treatment plant. *Environmental Science & Technology*, 47(1), 342–348. <https://doi.org/10.1021/es303013j>

Butler, D., & Graham, N. J. D. (1995). Modeling dry weather wastewater flow in sewer networks. *Journal of Environmental Engineering*, 121(2), 161–173. [https://doi.org/10.1061/\(asce\)0733-9372\(1995\)121:2\(161\)](https://doi.org/10.1061/(asce)0733-9372(1995)121:2(161))

California Natural Diversity Database (CNDDDB). (2019). State and federally listed endangered and threatened animals of California [Dataset]. California Department of Fish and Wildlife. Retrieved from <https://wildlife.ca.gov/Data/CNDDDB/Plants-and-Animals>

California Water Code. (2022). Senate Bill 1157. Chapter 679. Section 10609.4.

CDFW (California Department of Fish and Wildlife). (2019). Element occurrence query. California natural diversity database (CNDDDB) [Dataset]. RareFind, Version 5.2.14 (Commercial Subscription). Sacramento, California: CDFW, Biogeographic Data Branch. Retrieved from <https://apps.wildlife.ca.gov/myaccount/login?ReturnUrl=%2frafefind%2fview%2fRareFind.aspx>

Chock, R. Y., Hennessy, S. M., Wang, T. B., Gray, E., & Shier, D. M. (2020). A multi-model approach to guide habitat conservation and restoration for the endangered San Bernardino kangaroo rat. *Global Ecology and Conservation*, 21, e00881. <https://doi.org/10.1016/j.gecco.2019.e00881>

Cook, S. C., Housley, L., Back, J. A., & King, R. S. (2018). Freshwater eutrophication drives sharp reductions in temporal beta diversity. *Ecology*, 99(1), 47–56. <https://doi.org/10.1002/ecy.2069>

Dunck, B., Lima-Fernandes, E., Cássio, F., Cunha, A., Rodrigues, L., & Pascoal, C. (2015). Responses of primary production, leaf litter decomposition and associated communities to stream eutrophication. *Environmental Pollution*, 202, 32–40. <https://doi.org/10.1016/j.envpol.2015.03.014>

Ellender, B. R., Wasserman, R. J., Chakona, A., Skelton, P. H., & Weyl, O. L. (2017). A review of the biology and status of Cape Fold Ecoregion freshwater fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(4), 867–879. <https://doi.org/10.1002/aqc.2730>

Enfinger, K. L., & Stevens, P. L. (2006). Sewer sociology—the days of our (sewer) lives. In *WEFTEC 2006* (pp. 6962–6974). Water Environment Federation.

Eppehimer, D. E., Hamdhani, H., Hollien, K. D., & Bogan, M. T. (2020). Evaluating the potential of treated effluent as novel habitats for aquatic invertebrates in arid regions. *Hydrobiologia*, 847(16), 3381–3396. <https://doi.org/10.1007/s10750-020-04343-6>

Esri. (2011). ArcGIS desktop: Release 10 [Software]. Environmental Systems Research Institute. Retrieved from <https://desktop.arcgis.com/en/system-requirements/latest/arcgis-desktop-system-requirements.htm>

Gleick, P. H. (2000). The changing water paradigm: A look at twenty-first century water resources development: From water international. In *The sustainable urban development reader* (pp. 214–223). Routledge.

Grantham, T. E., Fesenmyer, K. A., Peek, R., Holmes, E., Quiñones, R. M., Bell, A., et al. (2017). Missing the boat on freshwater fish conservation in California. *Conservation Letters*, 10(1), 77–85. <https://doi.org/10.1111/conl.12249>

Hamdhani, H., Eppehimer, D. E., & Bogan, M. T. (2020). Release of treated effluent into streams: A global review of ecological impacts with a consideration of its potential use for environmental flows. *Freshwater Biology*, 65(9), 1657–1670. <https://doi.org/10.1111/fwb.13519>

Herbert, E. R., Boon, P., Burgin, A. J., Neubauer, S. C., Franklin, R. B., Ardón, M., et al. (2015). A global perspective on wetland salinization: Ecological consequences of a growing threat to freshwater wetlands. *Ecosphere*, 6(10), 1–43. <https://doi.org/10.1890/es14-00534.1>

Huntsman, B. M., Brown, L. R., Palenscar, K., Jones, C., Russell, K., Dyer, H., et al. (2022). *Joint-species analysis reveals potential displacement of native fishes by non-native fishes within the Santa Ana River, California*. Canadian Journal of Fisheries and Aquatic Sciences.

Hur, J., Schlautman, M. A., Karanfil, T., Smink, J., Song, H., Klaine, S. J., & Hayes, J. C. (2007). Influence of drought and municipal sewage effluents on the baseflow water chemistry of an upper Piedmont river. *Environmental Monitoring and Assessment*, 132(1), 171–187. <https://doi.org/10.1007/s10661-006-9513-1>

Jenkins, J. A., Goodbred, S. L., Sobiech, S. A., Olivier, H. M., Draugelis-Dale, R. O., & Alvarez, D. A. (2009). Effects of wastewater discharges on endocrine and reproductive function of western Mosquitofish (*Gambusia* spp.) and implications for the threatened Santa Ana sucker (*Catostomus santaanae*). *Jenkins, M. (2003). Prospects for biodiversity. Science*, 302(5648), 1175–1177. <https://doi.org/10.1126/science.1088666>

Kamanmalek, S., Brooks, B. W., & Rice-Boayue, J. (2022). Spatial hazards of antibiotic resistance in wastewater-impacted streams during low instream flow conditions. *AcS Es&T Water*, 2(3), 457–464. <https://doi.org/10.1021/acsestwater.1c00386>

Kimmelshue, J. (2017). Land use - 2014 - land IQ [ds2677] [Dataset]. Land IQ LLC. Retrieved from <https://map.dfg.ca.gov/metadata/ds2677.html>

Kinouchi, T., Yagi, H., & Miyamoto, M. (2007). Increase in stream temperature related to anthropogenic heat input from urban wastewater. *Journal of Hydrology*, 335(1–2), 78–88. <https://doi.org/10.1016/j.jhydrol.2006.11.002>

Kopp, D. (2018). StreamNetworkTools Version 1 [Software]. Github. Retrieved from <https://github.com/dkopp3/StreamNetworkTools>

Luthy, R. G., Sedlak, D. L., Plumlee, M. H., Austin, D., & Resh, V. H. (2015). Wastewater-effluent-dominated streams as ecosystem-management tools in a drier climate. *Frontiers in Ecology and the Environment*, 13(9), 477–485. <https://doi.org/10.1890/150038>

Martí, E., Riera, J. L., & Sabater, F. (2009). Effects of wastewater treatment plants on stream nutrient dynamics under water scarcity conditions. *Water scarcity in the mediterranean*, 173–195.

McKay, L., Bondelid, T., Dewald, T., Johnston, J., Moore, R., & Rea, A. (2012). NHDPlus Version 2: User guide [Dataset]. Retrieved from <https://www.epa.gov/waterdata/nhdplus-california-data-vector-processing-unit-18>

Mount, J., Gray, B., Bork, K., Cloern, J. E., Davis, F. W., Grantham, T., et al. (2019). *A path forward for California's freshwater ecosystems* (p. 32). Public Policy Institute of California.

Moyle, P. B., Katz, J. V., & Quiñones, R. M. (2011). Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation*, 144(10), 2414–2423. <https://doi.org/10.1016/j.biocon.2011.06.002>

Moyle, P. B., & Williams, J. E. (1990). Biodiversity loss in the temperate zone: Decline of the native fish fauna of California. *Conservation Biology*, 4(3), 275–284. <https://doi.org/10.1111/j.1523-1739.1990.tb00289.x>

National Research Council. (2002). *Privatization of water services in the United States: An assessment of issues and experience*. National Academies Press.

OCWD (Orange County Water District). (2023). GWRS (groundwater replenishment system). Retrieved from <https://www.ocwd.com/gwrs/>

Olivieri, A. W., Seto, E., Cooper, R. C., Cahn, M. D., Colford, J., Crook, J., et al. (2014). Risk-based review of California's water-recycling criteria for agricultural irrigation. *Journal of Environmental Engineering*, 140(6), 04014015. [https://doi.org/10.1061/\(asce\)ee.1943-7870.0000833](https://doi.org/10.1061/(asce)ee.1943-7870.0000833)

Patnode, K. A., Hittle, E., Anderson, R. M., Zimmerman, L., & Fulton, J. W. (2015). Effects of high salinity wastewater discharges on unionid mussels in the Allegheny River, Pennsylvania. *Journal of Fish and Wildlife Management*, 6(1), 55–70. <https://doi.org/10.3996/052013-jfwm-033>

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., et al. (1997). The natural flow regime. *BioScience*, 47(11), 769–784. <https://doi.org/10.2307/1313099>

Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T., et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, 94(3), 849–873. <https://doi.org/10.1111/brv.12480>

Rice, J., & Westerhoff, P. (2015). Spatial and temporal variation in de facto wastewater reuse in drinking water systems across the USA. *Environmental Science & Technology*, 49(2), 982–989. <https://doi.org/10.1021/es5048057>

Rice, J., & Westerhoff, P. (2017). High levels of endocrine pollutants in US streams during low flow due to insufficient wastewater dilution. *Nature Geoscience*, 10(8), 587–591. <https://doi.org/10.1038/ngeo2984>

Rice, J., Wutich, A., & Westerhoff, P. (2013). Assessment of de facto wastewater reuse across the US: Trends between 1980 and 2008. *Environmental Science & Technology*, 47(19), 11099–11105. <https://doi.org/10.1021/es402792s>

Richmond, J. Q., Backlin, A. R., Galst-Cavalcante, C., O'Brien, J. W., & Fisher, R. N. (2018). Loss of dendritic connectivity in southern California's urban riverscape facilitates decline of an endemic freshwater fish. *Molecular Ecology*, 27(2), 369–386. <https://doi.org/10.1111/mec.14445>

Saffarinia, P., Anderson, K. E., & Palenscar, K. T. (2022). Effects of urban spatial and temporal heterogeneity on benthic macroinvertebrate and diatom communities. *Fundamental and Applied Limnology*, 169(1), 57–73. <https://doi.org/10.1127/fal/2022/1481>

Sánchez-Morales, M., Sabater, F., & Muñoz, I. (2018). Effects of urban wastewater on hyporheic habitat and invertebrates in Mediterranean streams. *Science of the Total Environment*, 642, 937–945. <https://doi.org/10.1016/j.scitotenv.2018.06.132>

Schwabe, K., Nemati, M., Amin, R., Tran, Q., & Jassby, D. (2020). Unintended consequences of water conservation on the use of treated municipal wastewater. *Nature Sustainability*, 3(8), 628–635. <https://doi.org/10.1038/s41893-020-0529-2>

Segurado, P., Branco, P., Jauch, E., Neves, R., & Ferreira, M. T. (2016). Sensitivity of river fishes to climate change: The role of hydrological stressors on habitat range shifts. *Science of the Total Environment*, 562, 435–445. <https://doi.org/10.1016/j.scitotenv.2016.03.188>

State Water Resources Control Board (SWRCB). (2015). Interactive regulated facilities report [Dataset]. State of California. Retrieved from <https://ciwqs.waterboards.ca.gov/ciwqs/readOnly/CiwqsReportServlet?inCommand=reset&reportName=RegulatedFacility>

Stromberg, J. C., Beauchamp, V. B., Dixon, M. D., Lite, S. J., & Paradzick, C. (2007). Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. *Freshwater Biology*, 52(4), 651–679. <https://doi.org/10.1111/j.1365-2427.2006.01713.x>

Tran, Q. K., Jassby, D., & Schwabe, K. A. (2017). The implications of drought and water conservation on the reuse of municipal wastewater: Recognizing impacts and identifying mitigation possibilities. *Water Research*, 124, 472–481. <https://doi.org/10.1016/j.watres.2017.07.069>

United Nations. (2021). Summary progress update 2021: SDG 6 — water and sanitation for all United Nations. Retrieved from <https://www.unwater.org/publications/summary-progress-update-2021-sdg-6-water-and-sanitation-all>

US Fish and Wildlife Service. (1998). Endangered and threatened wildlife and plants; final rule to list the San Bernardino kangaroo rat as endangered. *Federal Register*, 63(185), 51005–51017.

USGS. (2019). USGS TNM hydrography (WBD). National geospatial program [Dataset]. Retrieved from <https://hydro.nationalmap.gov/arcgis/rest/services/wbd/MapServer>

Vajda, A. M., Barber, L. B., Gray, J. L., Lopez, E. M., Bolden, A. M., Schoenfuss, H. L., & Norris, D. O. (2011). Demasculinization of male fish by wastewater treatment plant effluent. *Aquatic Toxicology*, 103(3–4), 213–221. <https://doi.org/10.1016/j.aquatox.2011.02.007>

Wang, D., Hubacek, K., Shan, Y., Gerbens-Leenes, W., & Liu, J. (2021). A review of water stress and water footprint accounting. *Water*, 13(2), 201. <https://doi.org/10.3390/w13020201>

White, M. D., & Greer, K. A. (2006). The effects of watershed urbanization on the stream hydrology and riparian vegetation of Los Penasquitos Creek, California. *Landscape and Urban Planning*, 74(2), 125–138. <https://doi.org/10.1016/j.landurbplan.2004.11.015>

Zimmerman, J. K., Carlisle, D. M., May, J. T., Klausmeyer, K. R., Grantham, T. E., Brown, L. R., & Howard, J. K. (2018). Patterns and magnitude of flow alteration in California, USA. *Freshwater Biology*, 63(8), 859–873. <https://doi.org/10.1111/fwb.13058>