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Effects of urban spatial and temporal heterogeneity on benthic macroinvertebrate and diatom communities

Parsa Saffarinia^{1, 2, *}, Kurt E. Anderson^{1, 4}, Kai T. Palenscar^{3, 5}

With 6 figures and 1 table

Abstract: Water quality, distribution, and flow are often highly altered in rivers in urban watersheds, subjecting aquatic communities in the environment to novel spatial and temporal heterogeneity. An understanding of how novel spatial and temporal heterogeneity impacts aquatic communities is of paramount concern since these taxa are foundational to the urban food web. In this study, we documented the effects of flow perturbations on benthic macroinvertebrate and diatom communities relative to wastewater treatment plant outflows in a transect of an urbanized river in Southern California, USA. In particular, we analyzed trends in the richness and density of diatom and benthic macroinvertebrate communities in relation to novel flow heterogeneity introduced by wastewater treatment plants and urban storm runoff events. We found that diatom density decreased after a disturbance but quickly returned to its pre-disturbance levels, while the benthic macroinvertebrate community showed minimal shifts in composition and density after the disturbance, yet the sites had low richness of predominantly tolerant taxa. The locations of wastewater treatment plant outflows were found to exert a constant negative effect on density and richness in both communities. These results have implications for the conservation of endangered fish species in the urban Santa Ana River that depend on a thriving basal food web for survival.

Keywords: disturbance; effluent; benthic macroinvertebrates; diatoms; heterogeneity

1 Introduction

Freshwater ecology places spatial and temporal heterogeneity in a central role in structuring communities, viewing it as fundamental to describing patterns and managing freshwater diversity (Hutchinson 1953; Vannote et al. 1980; Cooper et al. 1997; Winemiller et al. 2010). The expansion of urban areas subjects freshwater communities to novel patterns of spatial and temporal heterogeneity (Paul & Meyer 2001). Urbanization results in heterogeneity such as altered hydrographs and simplified channel morphology, and can lead to novel biological communities (Stanford &

Ward 2001). Understanding how diversity responds to urban heterogeneity is important for also understanding community functioning since many urban dwelling communities subject to novel heterogeneity reflect fundamentally altered compositions (Walsh et al. 2005).

Urban rivers generally comprise a network of highly-controlled waterways that maximize efficiency and the predictability of flow distribution, especially in the southwestern US (Wohl 2018). The resulting flow regimes typically exhibit reduced natural seasonality, flow connectivity, and increased artificial flow signals, such as dam releases and flash floods caused

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by large areas of impervious surface (Kennedy et al. 2016; Ruhí 2018). For example, losses in flow connectivity compounded with urban discharge can lead to the removal of dispersal pathways (Blakely et al. 2006; Richmond et al. 2017), the alteration of substrate transport patterns (Nedeau et al. 2003; Blakely et al. 2006), and myriad changes in water quality (Pandey et al. 2018). Moreover, many urban water management activities, such as water retention, reuse, irrigation, hydropower, and flood control, can introduce spatially idiosyncratic alterations of physical structure, nutrient loadings, water temperature changes, and the source, timing, and rate of discharge. For example, hydropoeaking practices by dams result in unique patterns of discharge, while elevated stream temperatures have been directly related to wastewater treatment plant (WWTP) effluent discharge in proximal downstream environments (Kinouchi et al. 2007; Ruhí et al. 2018). Thus, patterns of spatial and temporal heterogeneity in habitat types and quality in urban rivers may depend on geographical context and human needs (Ripl 2003; Konrad & Booth 2005; Booth et al. 2016). However, although biotic and abiotic responses to flow variation by dams are well studied, responses to flow variation caused by urban flow events in effluent dominated systems are not (Desiante et al. 2022; Let et al. 2022).

Wastewater treatment plants are characteristic features of urban river networks, and they exert a strong influence on food webs in urban watersheds by altering the abiotic environment where they are located (Luo et al. 2014; Ziajahromi et al. 2016). Despite improved treatment capability, many WWTPs discharge treated sewage water with numerous contaminants directly into urban rivers (Carey & Migliaccio 2009; Bai et al. 2018). Because WWTPs emit large volumes of effluent, the river systems' natural capacity to dilute contaminants and nutrients can be overwhelmed (Lake 2003; Sánchez-Morales et al. 2018). In addition to an altered constituent profile, effluent temperature regimes are highly variable and dependent on the specific treatment practices of the WWTP. In particular, elevated temperatures have been found in winter and spring due to the prevalence of WWTP effluent (Kinouchi et al. 2007).

In addition to altering the physical environment, WWTPs have been shown to impact biodiversity patterns significantly in urban rivers. Altered habitat patches due to effluent flow facilitate the invasion and establishment of resilient generalist communities throughout the riverine food web, replacing taxa that require more pristine conditions (Roy et al. 2003;

Drury et al. 2013; Bourassa et al. 2017; Tornés et al. 2018). Moreover, WWTP effluent has been shown to decrease the abundance and diversity of benthic bacterial communities (Drury et al. 2013), decrease algal diversity (Tornés et al. 2018), increase benthic macroinvertebrate (BMI) density while decreasing diversity (Wright et al. 1995; Coimbra et al. 1996; Morrissey et al. 2012), and lower the richness and abundance of fish (Northington & Hershey 2006; Galib et al. 2018).

Despite their degraded conditions, many urban streams are home to threatened and endangered species (Morley & Karr 2002; Silver et al. 2018), and effluent flows from WWTPs can supplement low base flow in rivers, expanding available habitats for native species in certain circumstances (Nedeau et al. 2003). WWTP effluent output tends to elevate discharge year-round, with effluent flows comprising either a fraction or the entirety of the flow present, depending on the time of year (Goodrich et al. 2018). In some cases, effluent discharge represents the only source of running water for some species in flow-disconnected landscapes (Boyle & Fraleigh 2003). Thus, effluent has been used to restore habitats for species of concern, and urban river food webs and many conservation plans have been created for urban rivers that rely on effluent for habitat creation (Linke et al. 2010). Despite research on the effects of urbanization on the physical properties of rivers and the potential for WWTPs to positively and negatively impact biodiversity, no clear picture has emerged about how effluent influences freshwater communities (Hassett et al. 2018; Bogan et al. 2020; Eppehimer et al. 2020; Eppehimer et al. 2021).

Effluent-dominated freshwater systems, home to numerous species of concern and a dominant water source for human use, are particularly common in the arid southwest USA. In the Santa Ana River watershed—the largest watershed entirely within Southern California—there are over 20 species relying on a food web persisting in a valley dominated by river processes (ICF International 2014). The WWTPs' outflows into the Santa Ana River have unique discharge and water property characteristics that lead to notable temporal heterogeneity with respect to flow variability, and to spatial heterogeneity with respect to the novel physical stream habitats created by each WWTP and surrounding urban structures. Efforts are underway to document the habitat requirements of focal species of conservation concern, such as the Santa Ana sucker (*Catostomus santaanae*) and the Arroyo chub (*Gila orcuttii*), in order to preserve them under the multi-species Upper Santa Ana Habitat Conservation Plan (ICF

International 2014), but the distributions of the lower trophic levels that support the persistence of these threatened species are poorly understood (Brown et al. 2005). This is compounded by the fact that much of the temporal and spatial heterogeneity in the system is imposed by WWTP effluent dynamics, and studies are scarce that document the effects of novel WWTP-imposed flow and habitat heterogeneity on freshwater communities.

Here, we investigated the benthic community (diatoms and benthic macroinvertebrates) responses to temporal and spatial heterogeneity driven by WWTPs and associated urban structures in the Santa Ana River. Communities were sampled at multiple sites at increasing distances downstream of two WWTPs and their trajectories followed after WWTP flow drawdowns and an urban flood event. We specifically asked: (1) What was the magnitude of responses by urban stream communities to temporal flow perturbations from changes in WWTP discharge and urban runoff? (2) Were prior spatial patterns of density and richness reestablished by the benthic communities after flow disturbances? (3) Did the community responses depend on spatial heterogeneity in local environmental conditions? Answering these questions will assist in the management of benthic communities and the threatened freshwater species that interact with and rely on them in urban systems.

2 Methods

2.1 Study site

The Santa Ana River is embedded within the Santa Ana watershed in Southern California, with a majority of its headwaters originating in the San Bernardino Mountains. This region is subject to a Mediterranean climate with wet, cold winters and hot, dry summers. Historically, the Santa Ana watershed was a large branching river network with meandering courses, shifting ocean outlets, and significant flood events. However, after the 1950s, much of the network was dammed and otherwise managed with flood-control infrastructure, leading to permanent hydrologic isolation and resulting flow disconnection throughout the watershed (Richmond et al. 2017). Due to modern-day water diversions, much of the streambed is dry downstream of Seven Oaks Dam, only wetting during infrequent winter storm events. Further, natural flow has become short-lived but with greater intensity (flashy or high-peak flows). Seven Oaks Dam is located in

the upper portion of the Santa Ana River, in the San Bernardino Mountains, northeast of Redlands, California. Between Seven Oaks Dam and western Riverside County, the stream channel becomes re-wetted by WWTP effluent discharge.

The first major treatment plants that wet the Santa Ana River below Seven Oaks Dam are in Colton and Rialto, California (Fig. 1). The WWTP in Colton, the Rapid Infiltration and Extraction (RIX) facility, employs ultraviolet (UV) radiation and soil percolation to treat water to tertiary standards, while a second WWTP in the neighboring city of Rialto employs a traditional chlorination-dechlorination treatment method to treat water to tertiary standards. The Rialto WWTP releases water 1.2 km upstream of the RIX plant; the effluent flows over an unlined concrete channel before dropping into a riverbed dominated by a variable mix of cobble, pebbles, and sediment (Fig. 1). Rialto effluent joins the RIX facility's effluent adjacent to a “plunge pool” where the RIX WWTP discharges, and their combined discharge provides the majority of the flow in the Santa Ana River, especially during the drier parts of the year (Fig. 2). During the study period, RIX WWTP outflow averaged 45.6 cubic feet per second (cfs), while Rialto's outflow averaged 9.2 cfs at its discharging locations.

Historically, the RIX treatment plant introduced unique flow regimes into the Santa Ana River. Although flow is emitted at a standard discharge rate for most of the year, the RIX plant halts effluent discharge several times per year in order to access and maintain its UV lamps. These flow shutdowns have historically resulted in significant losses of discharge in the Santa Ana River, up to complete loss of surface water below site R3 (Fig. 1, Fig. 3), including during our study period. Despite being quite severe, these flow shutdowns can be brief (2–6 hours). They do not appear in daily discharge reports from the RIX WWTP (Fig. 2), as the plant increases its flows immediately following shutdowns to compensate, thereby reporting their typical daily average discharge values. As the Rialto discharge is much lower than that of RIX (9.2 cfs versus 45.6 cfs), it is normally not enough to offset high percolation rates in the riverbed. Thus, the discharge of Rialto water is not enough to provide a wetted stream when the RIX facility is shutdown. In the winter, flashy flows that result from precipitation runoff over impervious surfaces also contribute to the overall discharge present in the Upper Santa Ana River, and several of these events took place in November–December 2016, in the same month as a major RIX facility shutdown (Figs 2, 3).



Fig. 1. Benthic macroinvertebrate and diatom sampling locations relative to effluent outflows in the Upper Santa Ana River near Colton, California, USA. Sampling locations include RI-3 and SA1-5. Map data: Google Earth.

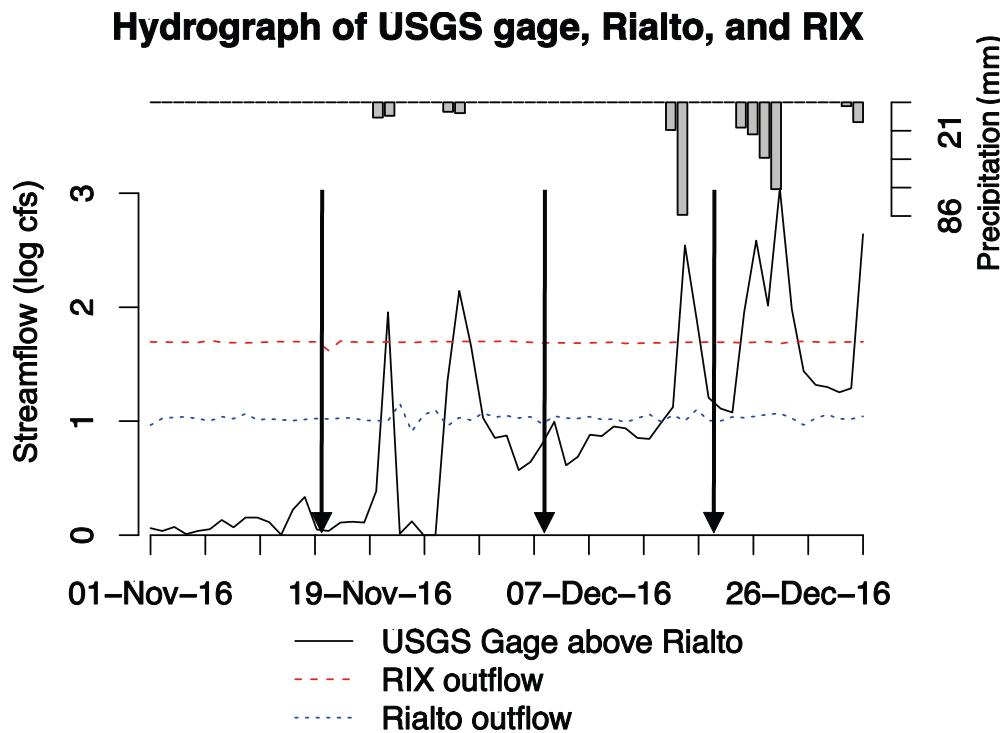


Fig. 2. Flow dynamics in the Upper Santa Ana River during sampling period spanning between November 1, 2016 to December 26, 2016. (1) USGS flow gage data gathered upstream of the Rialto WWTP outflow, serving as a proxy for background flow conditions driven by precipitation (black line, gage 11062810). Precipitation data were gathered from a nearby rain gage (data.countyofriverside.us). (2) Discharge rates from the RIX WWTP (red dashed line) and the Rialto WWTP (blue dotted line) at their outflows into the Santa Ana River (collected from monthly reports uploaded to waterboards.ca.gov). Black arrows indicate sampling events; the first black arrow also represents when a RIX flow shutdown occurred. Flow shutdowns from RIX are not seen in this figure because the plant compensated for them by increasing flows after shutdowns to reach its daily discharge average.



Fig. 3. Photo collage of flow dynamics and habitat heterogeneity in the Santa Ana River. **(A)** Flow being restored to a dry riverbed after a flow shutdown in 2016; **(B)** Santa Ana sucker found stranded on a dry riverbed; **(C)** Santa Ana sucker and arroyo chub facing severe habitat constriction to a draining pool during a summer flow shutdown; **(D)** downstream photo of Rialto WWTP effluent transitioning from the concrete transport channel to the riverbed during a mild storm event.

2.2 Field sampling and processing

To document the effects of urban-influenced flow regimes and spatial heterogeneity introduced by WWTPs on diatom and benthic macroinvertebrate (hereafter BMI) communities, we sampled along a transect that captured the influence of outflow from two WWTPs on three occasions in a single season. The selected reach of the stream exhibits high variation between sampling sites due to inputs from the WWTPs and

resulting variability in abiotic variables such as substrate, temperature, and canopy cover (Supplementary Fig. 1). We sampled at sites above and below the location of the RIX facility's outflow immediately before a flow shutdown event on November 16, 2016, and twice afterwards, on December 1 and 12, 2016. There were also several storm runoff events during the sampling period. As the Rialto plant still releases water during RIX flow-shutdown events, part of the river between

Rialto and the RIX facility remains wet, serving as a point of comparison with downstream sites. In total, we included eight sampling sites along the transect—three in the Rialto channel (R1-3), one at the RIX outflow (SA1), and four downstream of the RIX outflow (SA2-5, Fig. 1).

We measured habitat variables and diatom and BMI densities according to the Reachwide Benthos Multihabitat procedure defined in the standard operating procedures of the California Surface Water Ambient Monitoring Program (SWAMP; Ode et al. 2016). Dissolved oxygen (DO) and temperature were measured at sampling locations using a YSI Professional Plus. We collected BMIs using a 500- μm D-net and gently brushed all substrate in front of the D-net for approximately 30 seconds at 8 locations per site at intervals determined by standard SWAMP protocols. BMI abundance was converted to density by dividing abundances by surface area sampled (0.09 m^2 area sampled each time). Diatoms were collected in the field by choosing three fist-sized rocks from the same sampling reach from which the BMIs were collected, using SWAMP methods with advice from local experts. The rocks were then transported with a fine-mesh aquarium net to a tray in the field, where the rock was scraped with a plastic wire brush. All biofilm was brushed off the rock, and the rock was rinsed with clean water. Then, 1.5 ml of diatom solution was extracted from scrapings and immediately frozen on dry ice in the field.

Diatoms were cleared of organelles and other organic matter using a diluted bleaching method (Carr et al. 1986) and gently swirled by hand to break up any clumps of material. Afterward, the bleach was decanted using continuous inoculation with deionized water. Diatoms in cleaned samples were then identified to genus using the Flow-CAM particle imaging system due to the rapid processing capability of this system (Fluid Imaging Technologies, Inc.) following established methods with taxonomic keys (Camoying & Yñiguez 2016; Spaulding et al. 2022). Although Flow-CAM may not be as reliable for finer taxonomic resolutions compared to light microscopy, it has been shown to be more efficient at processing higher volumes and effective at identifying freshwater diatoms (Hrycik et al. 2019). The cleaned diatom solution was filtered through a 100- μm plastic mesh before being run through the Flow-CAM system. We determined that a 100- μm -deep flow cell (FC100) would yield the most precise results due to the average size distribution of diatoms in our samples checked with light microscopy. We assigned field density values for diatoms

by converting from diatoms captured per ml by Flow-CAM to the amount of surface area scrubbed per rock in the field, which allowed for a standardized measure of density and richness. All BMIs were sorted and identified to genus using dissecting microscopes, with the exception of chironomids, which were identified to family.

2.3 Adjacent fish surveys

During September 2016 and 2017, annual fish surveys were performed in the study area to determine the status of the Santa Ana sucker, the arroyo chub, and numerous invasive species. These surveys were conducted by our collaborative team of United States Geological Survey (USGS) researchers, United States Fish and Wildlife researchers and other agency staff, and citizen scientists. Methods included snorkeling, electrofishing, and seining, depending on the micro-habitat type being surveyed (Wulff et al. 2015). Physical habitat surveys were also conducted during this time, documenting canopy cover, substrate profile, reach width, reach depth, and flow velocity. Santa Ana sucker and other fish populations were estimated using the abundance value from one survey method (either seine, electrofishing, or snorkeling), depending on the field conditions at each site (Wulff et al. 2015). Daily temperature measurements were taken with remote sensors along the transect. These physical habitat survey data are included herein to describe long-term spatiotemporal variability in stream habitats along the Santa Ana River. Physical habitat data for each year from these surveys were used in this study, and data from fish surveys are available in the Supplementary Figs 2–9. Although the fish surveys were not conducted at a scale conducive to analysis, diatoms have been shown to be the primary food source of the Santa Ana sucker, and fish survey data is included for comparison (Greenfield et al. 1970).

2.4 Data analysis

To quantify patterns of spatial habitat heterogeneity along the Santa Ana River over a long timescale, we used data collected from annual surveys of the river from September 2016 collected as part of the Upper Santa Ana River Habitat Conservation Program, as well as DO and temperature measures taken during benthic sampling. We performed a principal component analysis (PCA) of scaled and centered environmental variables to visually determine which variables were most associated with different river locations. The factors ordinated and sorted by location included

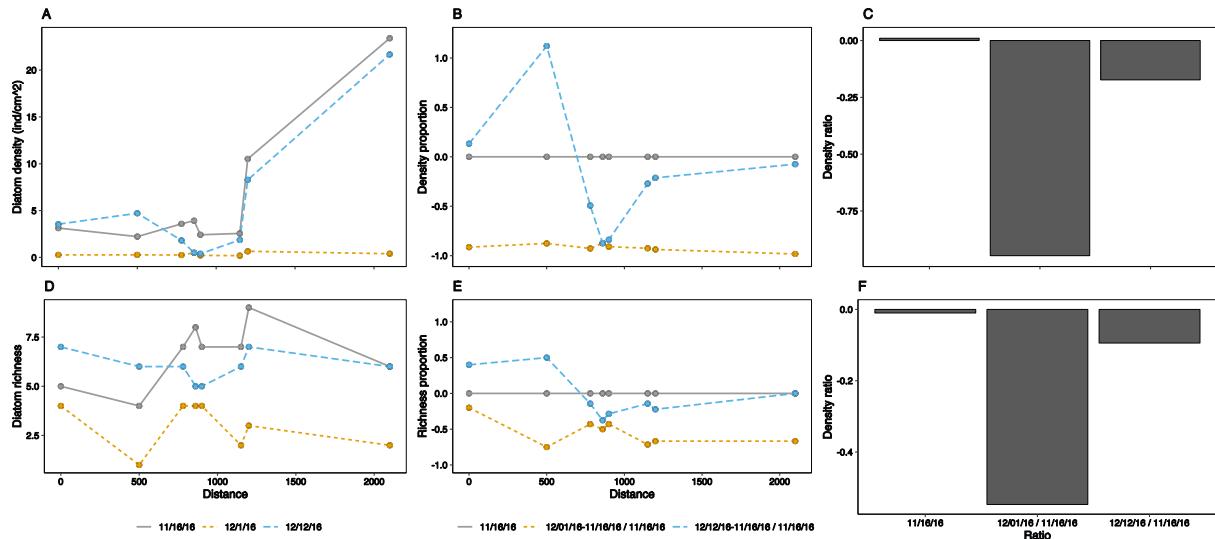


Fig. 4a. Diatom density (A) and richness (D) in the Santa Ana River during the study period. Diatom density and richness were plotted against the distance from the most upstream sampling site (R1). Points in the line graphs are the sampling locations shown in Fig. 1. Samples from November 16, 2016, were taken immediately before a flow shutdown by the RIX WWTP, while samples from December 1, 2016, and December 12, 2016, were taken approximately two and four weeks afterward, respectively. Proportions of diatom density and richness were calculated with respect to the communities sampled before the flow shutdown on November 16, 2016 (B and E). Proportions are presented for each site, as are averages across all sites sampled (C and F).

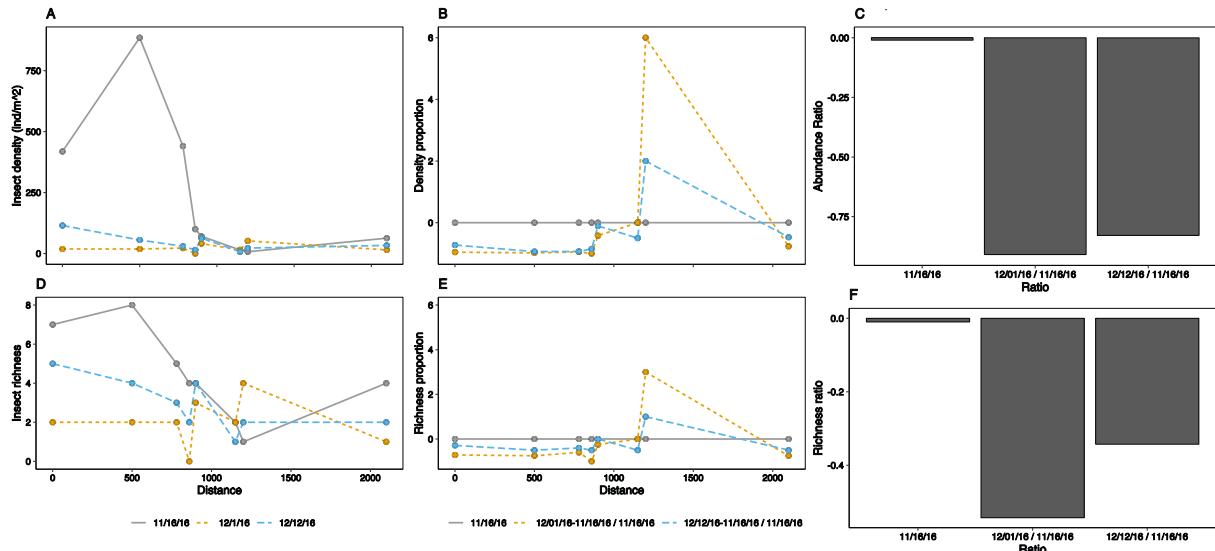


Fig. 4b. This figure depicts similar relationships to those mentioned in Figure 4a, except with BMI density and richness.

the mean values of channel depth, channel width, width:depth ratio, velocity, canopy cover, and substrate type (see Supplementary Figs 1–7). To better relate time-of-sampling to the hydrograph present in the selected section of the river, we plotted discharge from the treatment plants and from a nearby USGS gage (U.S. Geological Survey 2019) through time using the EcoHydRology package for R (ver. 3.5.2). The gage helped determine the number of storm flows contrib-

uting to overall discharge in the channel. These data were compared to data taken from a local precipitation gage (Riverside County Flood Control 2019).

The magnitude of response of diatom and BMI communities to urban flow disturbance (question 1) was assessed for each site by examining proportional changes through time before and after the RIX flow shutdown. To understand how benthic communities change relative to pre-perturbation levels across the

gradient of WWTP outflow, proportions were also calculated by averaging density and richness values through space (across all sampling sites, question 2). To determine the effects of the unique environmental conditions in each location we sampled (question 3), we examined the richness and density of diatoms and BMIs by distance from the most upstream site sampled (Rialto channel, where no flow shutdowns occurred). Because trends in BMI composition involved more taxa than diatoms, we conducted a non-metric multidimensional scaling with Bray-Curtis dissimilarity (NMDS) ordination for each sampling date.

We used generalized linear models to determine how unique sampling locations and date explained

variations in the density and richness of diatoms and BMIs. We determined site groupings for the location factor in statistical models by examining ordinations of physical data grouped by location, the results of which showed that sites in the Rialto channel share similar environmental conditions, suggesting a natural a priori grouping of all Rialto sites in the statistical model (R1-3, Supplementary Fig. 1). However, sites SA1, SA2, SA3, SA4, and SA5 exhibited more variable environmental conditions in the PCA. Therefore, we used a suite of statistical models and AIC with different groupings of SA sites to determine whether differences in environmental variables on different spatial scales translated into differences in density

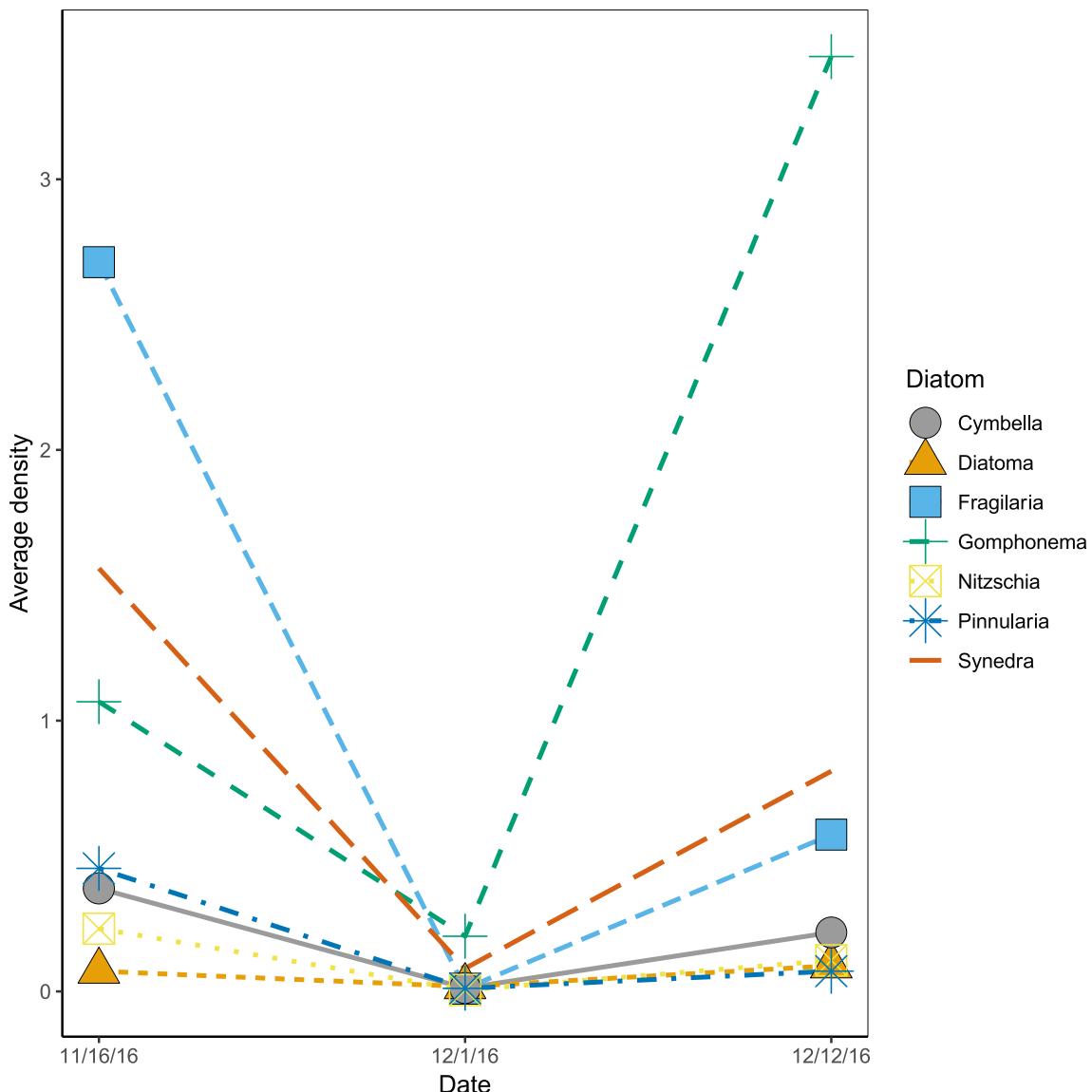


Fig. 5. The density of each diatom genus (ind/cm^2) was summed and across all sites and then averaged for each sampling date. November 16, 2016 (1), December 1, 2016 (2), and December 12, 2016 (3).

and richness. This allowed for understanding which habitat variables contributed most to explaining variation in the BMI community. Diatom density was log-standardized using the decostand function in the vegan package for R (Legendre & Gallagher 2001; Anderson et al. 2006). Model type and distribution were selected between negative binomial and Gaussian depending on Shapiro-Wilk tests on residuals and examining model fit for homogeneity of variances and normality. Statistical modeling was performed using MASS, fBasics, lme4, vegan, ggefortify, and ggplot2 packages for R.

3 Results

We found that the uppermost sites in the Rialto channel were consistently clustered around principal component axes structured by mean canopy cover and substrate profile, while sites downstream of the RIX outflow were structured by mean velocity, depth, and channel width (Supplementary Fig. 1). In general, sites R1, R2, and R3 were characterized by narrower wetted width, higher canopy cover, and larger cobble substrate (Supplementary Figs 3, 5, and 6), which contrasts with large amounts of sand being present at sites below RIX. The narrower Rialto channel, along with canopy may be one reason why more large substrate are exposed during scouring events in Rialto sites, which is not always apparent during spot measurements of substrate. The RIX outflow plunge pool (SA1) was notably faster-flowing and deeper than all other locations (Supplementary Figs 2 and 4). Channel width increased moving downstream of SA1; the river in this section is braided with a tendency to meander across the floodplain, so this is not always captured in measurements. Total discharge increases below RIX as base flow is composed of effluent from two WWTPs, while canopy decreases and substrate generally becomes smaller, especially in the absence of scouring floods. Temperature measurements taken near the Rialto and RIX outflows show that the Rialto channel experiences greater overall fluctuations in temperature following ambient fluctuations (between 20 °C and 30 °C), while RIX water is less variable (between 22 °C and 27.5 °C, Supplementary Fig. 10). This means that in the winter, RIX outflow is warmer than Rialto outflow, and in the summer, Rialto outflow is considerably warmer than RIX outflow (usually about a 2.5 °C difference in temperature; Supplementary Fig. 10).

The native arroyo chub and Santa Ana sucker increased in average abundance moving downstream of

the RIX and Rialto effluent outflows during September 2016 and 2017, while invasive yellow bullhead catfish were more abundant upstream in the Rialto outflows above RIX (see Supplementary Figs). Diatom density increased moving downstream of the Rialto-RIX transect prior to the RIX shutdown on November 16, 2016, except for slight decreases in the RIX outflow (Figure 4a). The statistical model in this study provided strong evidence for increases in diatom density moving downstream, with SA4 and SA5 having higher densities than SA1-3 (Table 1). Diatom richness was higher in sites downstream of the RIX outflow relative to upstream sites, although the statistical model provided only limited evidence for differences between upstream and downstream sites.

Both diatom density and richness changed dramatically between the first and second sampling (Fig. 4a, Table 1). Diatom density dropped to levels near zero at all sites two weeks after the RIX flow shutdown, while richness dropped by one-half or more, depending on the site. Non-effluent discharge increased between the second and third samples, and there were fewer high discharge events and no shutdowns (Fig. 2). In this period, diatoms re-established communities with densities and richness similar to pre-shutdown levels (Fig. 4a, Table 1). Both aggregate diatom density and richness as well as the spatial variation (location of sampling site) in these were very similar to patterns observed in the first sample period.

Despite changes in density and richness over the sampling period, the proportional composition of the diatom community did not change greatly. In the first sample, diatoms of the genera *Fragilaria*, *Synedra*, and *Gomphonema* had the highest average densities in the transect. Two weeks later, most diatoms had densities close to zero, suggesting similar susceptibilities among the diatom genera to the flow perturbations. Four weeks later, *Gomphonema* replaced *Fragilaria* as the most common diatom genus, exhibiting substantially higher densities compared to other diatoms, while other diatoms had similar densities (Fig. 5). In contrast with diatoms, BMI density and richness generally decreased moving downstream from Rialto on the first sampling date (Fig. 4b, Table 1). The primary insects found were in the orders of Ephemeroptera, Trichoptera, Diptera, Lepidoptera, and Odonata. Sites above the RIX plant tended to be dominated by *Helicopsyche* caddisflies, while *Baetis* mayflies and Libelulid dragonflies were mostly found far below RIX. BMI density and richness decreased in some locations after the shutdown and runoff perturbations. Sites upstream of RIX that were subjected

Table 1. GLMs used with abundance and richness as outcome variables. GLM models are used to explain variations in stream diatoms and BMIs through space and time. Several different spatial groupings of diatoms and BMIs were used to determine which spatial scale was most influential in explaining community responses. Spatial groupings included no spatial factors, SA1-4 and SA5, SA1-3 and SA4-5, SA1-2 and SA3-5, SA1 and SA2-5, above/below RIX (Rialto channel as one group, and every site below RIX as one group), and each site as its own group (SA1, SA2, SA3, SA4, and SA5). Sites in Rialto channel (R1, R2, and R3) were considered their own factor and are not reflected in the model output (they were the factor level among the spatial groupings chosen as the baseline). Models are ranked according to AICc values.

Model	Model predictors	df	ΔAICc	Weight
Diatom density	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	0.0	0.9910
	11/16/16, 12/01/16, 12/12/16, SA1, SA2, SA3, SA4, SA5	9	11.4	0.0034
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	11.9	0.0026
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA5	6	12.2	0.0023
	11/16/16, 12/01/16, 12/12/16	4	14.8	0.001
	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	17.7	0.001
	11/16/16, 12/01/16, 12/12/16, SA1, SA2-5	6	20.0	0.001
Diatom richness	11/16/16, 12/01/16, 12/12/16	4	0.0	0.719
	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	2.9	0.165
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA5	6	6.2	0.033
	11/16/16, 12/01/16, 12/12/16, SA1, SA2-5	6	6.5	0.028
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	6.5	0.027
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	6.5	0.027
	11/16/16, 12/01/16, 12/12/16, SA1, SA2, SA3, SA4, SA5	9	19.6	0.001
Insect density	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	0.0	0.4833
	11/16/16, 12/01/16, 12/12/16, SA1, SA2-5	6	2.0	0.1774
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	3.2	0.0990
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	3.5	0.0857
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA5	6	3.6	0.0806
	11/16/16, 12/01/16, 12/12/16	4	3.8	0.0723
	11/16/16, 12/01/16, 12/12/16, SA1, SA2, SA3, SA4, SA5	9	11.3	0.0017
Insect richness	11/16/16, 12/01/16, 12/12/16, above/below RIX	5	0.0	0.492
	11/16/16, 12/01/16, 12/12/16	4	2.6	0.133
	11/16/16, 12/01/16, 12/12/16, SA1-2, SA3-5	6	2.8	0.119
	11/16/16, 12/01/16, 12/12/16, SA1, SA2-5	6	3.3	0.092
	11/16/16, 12/01/16, 12/12/16, SA1-3, SA4-5	6	3.6	0.082
	11/16/16, 12/01/16, 12/12/16, SA1-4, SA5	6	3.6	0.081
	11/16/16, 12/01/16, 12/12/16, SA1, SA2, SA3, SA4, SA5	9	14.8	0.001

to runoff events but not to the flow shutdown showed the greatest decrease in both density and richness; changes downstream of RIX were generally lower in magnitude, with SA4 increased in density and richness. By December 12, 2016, BMI density and richness appeared to trend toward levels similar to those observed in the first sample. Increases in both density and richness were slightly greater in the Rialto channel, while changes at most sites downstream of RIX were not particularly significant. NMDS ordinations on the BMI community largely mirror visually the density and richness effects from the statistical modeling; shifts in composition in the Rialto channel were more pronounced than those in RIX, although they

both returned to similar composition levels following perturbation (Fig. 6).

4 Discussion

Urban watersheds are subject to novel patterns of spatiotemporal heterogeneity that affect the biological communities inhabiting them (Wohl 2018). Embedded within a Mediterranean climate, the Santa Ana River is subject to massive water extraction for human use. In turn, much of the upper watershed is reliant on WWTP effluent flows to prevent riverbed drying, although parts of the original riverbed remain dry. This

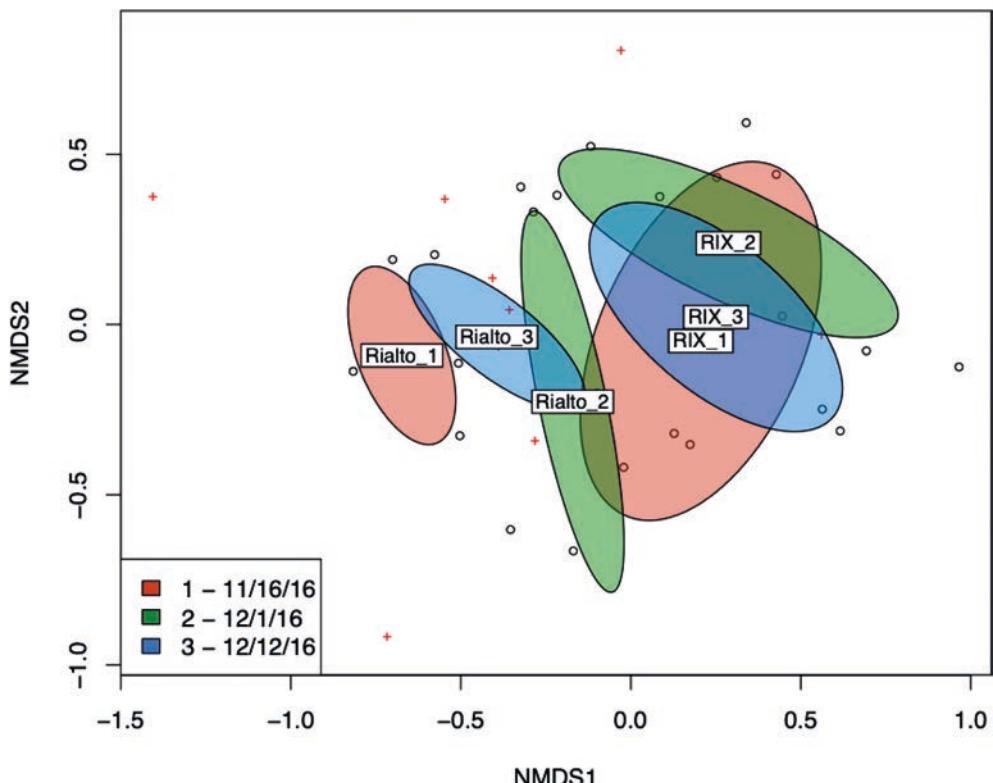


Fig. 6. NMDS ordination of BMI community composition during each sampling event, separated by location (“Rialto” means sites below Rialto channel but above RIX, and “RIX” means sites below the RIX WWTP). Numbers 1, 2, and 3, and colors red, green, and blue represent the timing of the sampling event. BMI data are shown grouped among sites. Ellipses are drawn around the centroids of each community.

unique flow distribution results in sections of the river being transformed into an intermittent flow regime wherein only large flood events in the winter re-wet dry reaches, while other sections remain perennial due to WWTP effluent. In the summer, flow shutdown events represent an isolated perturbation through time, whereas in the winter, flow shutdowns were found to be compounded with flood events composed of extensive urban runoff to impose a unique disturbance regime on the instream community. Addressing research questions (1) and (2), the magnitude of response of diatom and BMI communities to spatial and temporal variation was different. The sampled diatom community declined more notably after flow perturbation but also rebounded faster, though dominant taxa appeared to have shifted at the end of the study. On the other hand, the BMI community was most negatively impacted in the upstream Rialto channel compared to below the RIX WWTP following flow perturbations where the community did not achieve pre-perturbation levels. This could be attributed to the fact that Rialto channel biota had higher density, but were also strongly affected by flashy winter flows. Address-

ing research question 3, pre-existing spatial patterns in abundance and community composition reemerged following disturbances in accordance with the location of WWTPs within the watershed, even though some taxa were negatively affected by flow perturbations.

4.1 Community response to disturbance

The diatom community reacted strongly to observed flow perturbations, as a sharp decline in abundance and richness was observed immediately after the flow shutdown and November flood events, although populations partially increased to pre-disturbance abundances within the timescale of the study (Fig. 4a). The recolonizing taxa in later samples were similar to pre-disturbance ones except for the two most dominant genera. There could be multiple reasons for *Gomphonema* having replaced *Fragilaria* as the most dominant genus following flow perturbation. The interaction of flow disturbance timing with the stage of diatom community development is important. Factors such as season, flow rate before disturbance, and the presence of other algae taxa are significant in explaining the persistence of diatoms (Peterson & Stevenson

1992). Although priority effects such as timing of species arrival may have influenced the higher presence of *Gomphonema* at the end of the sampling period, a higher taxonomic resolution and a larger sampling timescale are needed to confirm this. Seasonal succession is likely to have contributed more notably, as the high frequency of flow disturbances, compounded by the shutdown and floods, may have rendered the environmental conditions too difficult for both taxa to persist. These taxa can form chains, stalks, and colonies that render them more vulnerable to perturbations and grazing (Passy 2007; Tornés et al. 2015; B-Béres et al. 2017). We posit that the dominant source of colonists from Rialto into RIX channel shifted seasonally, accounting for the difference in dominant taxa after the observed flow perturbations (Korhonen et al. 2013). Nonetheless, *Fragilaria* and *Gomphonema* are considered cosmopolitan taxa that occupy a wide range of ecological conditions and have been found to coexist in other polluted waters (Wojtal 2003).

BMI density responded weaker in the Santa Ana River channel compared to Rialto channel, possibly due to BMIs in the Santa Ana River being a species-poor, disturbance-tolerant group. Other studies have shown that BMI assemblages in pristine locations are sensitive to urbanization gradients and tend to degrade in composition, resulting in urbanized, degradation-tolerant communities forming quite rapidly, and the taxa in the Santa Ana River reflect this (Brown et al. 2005; Brown et al. 2009). Dragonflies of the genera *Libellula* and *Sympetrum* are relatively disturbance-tolerant, are well distributed in the region, and are capable of flying to other sources of water as adults during flow perturbations (Ferreras-Romero et al. 2009). Caddisfly filter-feeders in genus *Oecetis* are also tolerant to polluted waters, and these taxa reflect the general trend of disturbance tolerance across the sampled insect community (Hilsenhoff 1987).

Considering the life strategies of BMIs and diatoms within this study, the mechanisms that allow for the persistence of diatoms and BMIs may be different. While the BMI community appears to be a disturbance tolerant community, diatoms within the same genus can have vastly different levels of disturbance tolerance (Hill et al. 2001; Fore & Gafe 2002; Stevenson et al. 2008; Morin et al. 2015). The faster reproductive cycle of the diatoms may have enabled them to quickly recolonize previously dry areas via free-flowing upper areas of the watershed in the Rialto channel (Tornés et al. 2015).

Sequential flow perturbations may have proven especially detrimental to the persistence of BMI and

diatom communities in the Santa Ana River. The second (12/01/2016) sampling event measured community response after a flow shutdown and two runoff flood events. However, there was a third runoff flood event before the December 12, 2016, sampling date (Fig. 2). BMI and diatom communities did not appear to respond as significantly to the third runoff event. These results suggest that although BMI and diatom communities tend to be stress-adapted and able to withstand flood events in isolation, certain conditions may be more influential in determining losses in the benthic community. For example, a flood large enough to mobilize substrate could be more influential than one that does not, and a flow shutdown paired with a flood event may result in higher losses than one disturbance event in isolation.

4.2 Novel spatial and temporal heterogeneity

In watersheds subject to less flow impairment and a lower amount of total discharge composed of WWTP effluent, flow perturbations (e.g., droughts or floods) can structure communities differently than systems that have more flow impairment. Rivers with less flow impairment and higher connectance typically contain communities with higher taxonomic and functional diversity and higher food web stability (Cross et al. 2013), as a result, flow perturbations in these less degraded systems can lead to novel spatial heterogeneity with redistributions of preferred habitat, resulting in unique community assembly trajectories (Fisher et al. 1982; Stanley et al. 1994; Marks et al. 2000; Lake 2003; Power et al. 2008). In contrast, the perturbations imposed by WWTPs and urban caused high flow runoff as seen in the system covered by this study are twofold: they impose a constant, time-independent effect on the river network by continually releasing effluent at a constant temperature and flow rate, but they also impose a temporally-random effect of flow shutdowns and runoff that dries or floods parts of the riverbed. Thus, in the Santa Ana River, and potentially in other WWTP effluent-dominated watersheds, flow perturbations do not alter the BMI and diatom community for long. When flow returns after shutdowns, it is emitted at a constant rate that quickly re-asserts previous spatial patterns of available habitat and resulting communities. Floods caused by urban runoff result in the occasional movement of the channel in the river basin and can re-structure the riverine habitat, which can compound the effects of flow shutdowns. Thus, communities within the Santa Ana River are subject

to constant WWTP effluent and time-variable runoff floods, but the spatial patterns of diatom and BMI distributions are re-established within about four weeks.

Total abundance and richness are consistently lower near the WWTP plants, and their flow regimes not only affect BMI and diatom communities but also promote the prevalence of invasive species. The unique physical water properties of WWTP effluent impose novel spatial heterogeneity in the system and drive differences in communities between sites. Urban streams have been shown to exhibit extremely fluctuating and high thermal regimes as a result of impervious concrete-lined channels (Somers et al. 2013). Water flowing into the Rialto channel from the Rialto WWTP is extremely warm and tends to be strongly influenced by ambient temperatures due to the water running over a shallow, concrete-lined channel. As a result, it cannot support healthy native fish populations in the summer and autumn, effluent from the RIX WWTP has a constant temperature throughout the year, allowing the successful colonization and year-round establishment of a cosmopolitan tropical filamentous red alga thought to have been introduced from the aquarium trade, *Compsopogon caeruleus* (Necchi Junior et al. 1999). Additionally, invasive yellow bullhead catfish (*Ameiurus natalis*), largemouth bass (*Micropterus salmoides*), green sunfish (*Lepomis cyanellus*), and other non-native fish thrive in the warmer water and constant flow regime established from the WWTPs. In particular, yellow bullhead catfish have been observed living in Santa Ana sucker egg-laying habitats, and largemouth bass have been found with entire bodies of Santa Ana suckers inside their stomachs (Palenscar, pers. obs.). Aside from the temporal disturbance from flow shutdowns and floods, we believe that due to the consistent prevalence of *Compsopogon*, an elevated temperature profile, and invasive fish populations, both BMIs and diatoms have a difficult time establishing populations near the RIX WWTP outflow. Following drying events and flood flows throughout the year, consistent flow regimes of effluent appear to promote the persistence of a novel community, likely created with the establishment of the WWTPs.

In the present study, we identified novel flow regimes in an urbanized watershed as well as different aspects of the benthic riverine community that respond to this unique gradient of heterogeneity. Also, we observed that the effects of urban spatiotemporal heterogeneity were not uniform across the sampled communities. Future research is needed to determine whether the taxa are responding to different environmental

drivers, such as temperature, or are subject to species interactions, especially because it is unknown whether pre-disturbance communities in the Santa Ana River resemble assemblages present at other less-disturbed sites in the region that respond to well-documented habitat heterogeneity. The management of urban rivers in relation to the preservation of biodiversity should consider the different types of heterogeneity being introduced into the system. For instance, working with the U.S. Fish and Wildlife Service and local water districts has enabled the operators of the RIX WWTP to implement measures to reduce extreme desiccation events and resulting surface flow disconnection by using groundwater wells near the effluent outflow that activate and release water into the Santa Ana River when flow shutdowns occur. This action demonstrates the importance of research on urban rivers and its relevance to conservation outcomes, as studies such as this can provide a baseline for use in the assessment of restoration efforts and other conservation actions. Further research in urbanized watersheds across the globe will increase understanding of how novel spatiotemporal heterogeneity imposed on urban streams affects imperiled species as well as how to conserve urban streams in the face of continued human population expansion.

Data availability statement

Data are available upon reasonable request.

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Author contributions: PS and KEA developed and conceived the manuscript. PS and KTP conducted the field work, and PS identified the material. PS ran the statistical analyses. PS, KEA, and KTP analyzed and interpreted the results. PS led the writing, with contributions from KEA and KTP.

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