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# Macroinvertebrate community development and resilience to channel dredging following flow restoration using effluent in an urban desert river

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**Freshwater species face numerous threats across the globe, including urbanization. Within cities in regions with drier climates, dewatering and channelization of rivers commonly occur and reduce or eliminate freshwater biodiversity. The discharge of effluent (treated wastewater) has been used to restore flow in some of these rivers, but our knowledge is negligible about how ecological communities develop and change in these unique but increasingly common ecosystems. In this study, we quantified aquatic macroinvertebrate community development in the Santa Cruz River (Arizona, U.S.A.), where effluent-restored flow more than 100 years after the river dried up. We tracked community development over a 2-year period in reaches where flow had been restored and compared those findings with data from a reference reach. Our study period also encompassed a massive disturbance where effluent releases temporarily ceased and sediment was dredged from the channel, allowing us to quantify the impacts of urban channel maintenance activities on recovering communities. Macroinvertebrate colonization was rapid following the initial flow restoration and channel dredging, with density and species richness values reaching or exceeding those of the reference reach within a few months, but community composition remained quite distinct after 2 years. Flow duration and the number of dry days in the month prior to sampling were the most influential factors in macroinvertebrate metrics. Simply adding effluent to dewatered urban rivers has the potential to restore diverse aquatic fauna, but targeted reintroductions may be needed for sensitive or dispersal-limited taxa.**

**Key words: colonization, community assembly, flow restoration, invertebrates, management, treated effluent, urbanization, wastewater**

### Implications for Practice

- Diverse macroinvertebrate communities can develop quickly in formerly dewatered streams where flow has been restored with high-quality effluent (tertiary-treated wastewater). Biodiversity in restored reaches is likely to be higher when effluent baseflow is consistent throughout the year.
- Early colonists in effluent-restored reaches are often habitat generalists that persist in other urban waterbodies, so targeted translocations and reintroductions may be needed for more sensitive or dispersal-limited taxa. Creating additional flow restoration sites could provide "stepping stones" through dry urban stream networks and increase colonization rates for dispersal-limited taxa.
- Urban stream channel maintenance for flood control can destroy or radically alter aquatic habitat, but resident biota in some systems may be resilient to these changes.

## Introduction

The biota of rivers and streams faces numerous threats across the globe, with many freshwater species at risk of extinction (Dudgeon 2019). One of these threats is urbanization and water resource development associated with urban areas (Grimm et al. 2008). Urbanization can directly result in impaired water quality in, or downstream of, urban areas (Walsh et al. 2005). Additionally, stream channels often are structurally modified by urban development (Stein et al. 2013), causing riparian vegetation loss and homogenization of in-stream habitat, among other impacts (Smith et al. 2009). Further, the natural flow regimes of streams, upon which nearly all key ecological processes depend, are modified by urbanization, including both decreased baseflows due to water abstraction and increased peak flows due to urban run-off (Palmer & Ruhi 2019; Saffarinia et al. 2022).

In regions with drier climates, many streams and their supporting aquifers have been dewatered as cities increase in size (Gleeson et al. 2012; Webb et al. 2014). As those streams dry, their floodplains become desirable real estate, potentially leading to further channelization to facilitate development (Roberge 2002). This type of development frequently results in undersized channels that require infrastructure (e.g. paved banks and channel dredging) to maintain capacity (Webb et al. 2014). As a result, many urban streams are left dry and partly or wholly encased in concrete (Gumprecht 2001). Another byproduct of urbanization is treated effluent from wastewater treatment facilities, which historically had a negative impact on recipient streams (Brooks et al. 2006). However, improvements in treatment process over the last 25 years have greatly improved effluent quality (Hamdhani et al. 2020), especially tertiary-treated effluent that has been found to support endangered fish and amphibian species in several regions (Halaburka et al. 2013; Saffarinia et al. 2022; Sonoran Institute 2022). Despite these advancements in treatment processes, impairment of ecosystem function in recipient streams may still occur adjacent to effluent outfalls (González et al. 2023; Hamdhani et al. 2023).

For most aquatic species, though, any water is better than no water. In recent years, tertiary-treated effluent has been used to augment or restore flow in historically dewatered urban streams (Bischel et al. 2013; Luthy et al. 2015; Bogan et al. 2020). However, these flow restoration efforts are vulnerable to infrastructural issues (e.g. drying events during gaps in releases from treatment plants; Saffarinia et al. 2022) and political decisions about water resource use (e.g. choosing to use effluent for irrigation or direct potable reuse; Dow et al. 2019; Wolfand et al. 2022). Furthermore, channelized urban streams require periodic maintenance and sediment removal that can dramatically impact recovering ecosystems (Gumprecht 2001; Sonoran Institute 2022). Finally, because of the lack of coordination between urban planners and ecologists, there is often insufficient monitoring of ecosystem attributes and functioning in streams where flow has been restored using effluent (Bogan et al. 2020). As a result, our knowledge of aquatic diversity and how ecological communities colonize and change over time is negligible in these unique ecosystems.

These knowledge gaps must be bridged to improve the outcomes of restoration efforts (Palmer et al. 1997) and to understand community assembly in novel ecosystems (Gabriel et al. 2010). Understanding how communities initially develop and whether those processes are deterministic or stochastic has long been of interest to ecologists (Claeson et al. 2021). However, opportunities to study primary succession in streams are rare, and are often limited to volcanic or glacial landscapes (e.g. Milner et al. 2008). Urban stream restoration projects provide numerous, and at times replicated, opportunities to quantify community development in streams. Understanding community development is also important for restoration managers to know how founder effects of early colonizers might alter restoration outcomes (Barrett et al. 2021) and whether to translocate species into restored reaches (Clinton et al. 2022).

In this study, we quantified aquatic macroinvertebrate community development in the Santa Cruz River (Arizona, U.S.A.), where effluent was used to restore perennial flow more than 100 years after urban development led to the river drying up. Macroinvertebrates are critically important for the ecosystems services they provide (e.g. organic matter breakdown) and they serve as the primary food source for fish, riparian birds, bats, and other wildlife (Baxter et al. 2005). We tracked macroinvertebrate community development over a 2-year period in reaches where flow had been restored and compared those findings with data concurrently collected from a reference reach. Our study period also encompassed a massive disturbance, where the newly restored reach was dry for 6 weeks and two vertical meters of sediment were dredged from the channel, allowing us to quantify the impacts of channel maintenance activities on recovering communities. Our primary study questions were: (1) How quickly do macroinvertebrates return when flow is restored? (2) How does community composition differ between restored and reference reaches? And (3) how do short-term gaps in flows, channel dredging activities, and floods enhanced by urban run-off alter macroinvertebrate diversity and community development? The answers to these questions will help guide future flow restoration efforts and enhance aquatic biodiversity in urban streams, especially in arid and semiarid regions.

## Methods

### Study System

The Santa Cruz River encompasses a 22,000 $km^2$ basin in southern Arizona (U.S.A.) and northern Sonora (Mexico) that supported alternating sections of perennial and seasonal flow until the early twentieth century (Webb et al. 2014). However, groundwater pumping for agricultural use and the growing cities of Tucson and Nogales caused 99% of the river to dry by the 1940s; groundwater levels have since fallen to over 80 m below the riverbed in Tucson (Carlson et al. 2011). Since the 1970s, discharge of secondary-treated effluent into the dry riverbed has occurred near Tucson, restoring year-round surface flow (Fig. 1). However, water quality was poor for the first several decades, and supported limited aquatic life, but treatment plants were upgraded in 2013 and now produce high-quality tertiary-treated effluent that flows into the system (Sonoran Institute 2022).

In 2019, a third effluent-dependent portion of the river was created in downtown Tucson as part of the Santa Cruz River Heritage Project. The purpose of the project is to enhance aquifer recharge in the precise location where the river historically had naturally perennial flow (Tucson Water 2020). For this project, effluent is piped from the Agua Nueva treatment plant 10 km north of the outfall location (Fig. 1). Effluent releases at the Heritage Project began on 24 June 2019, but several flow reduction and cessation events occurred in the following months due to operational issues and infrastructure upgrades (Fig. S1). Additionally, in May 2020, effluent releases at the Heritage Project ceased for 6 weeks to allow for dredging to enhance channel flood capacity (Tucson Water 2020). After two vertical meters of sediment were removed from greater than 2 km of the channel (Fig. 2), effluent discharge resumed in late June 2020 and continued uninterrupted through the rest of the study period (Fig. S1).
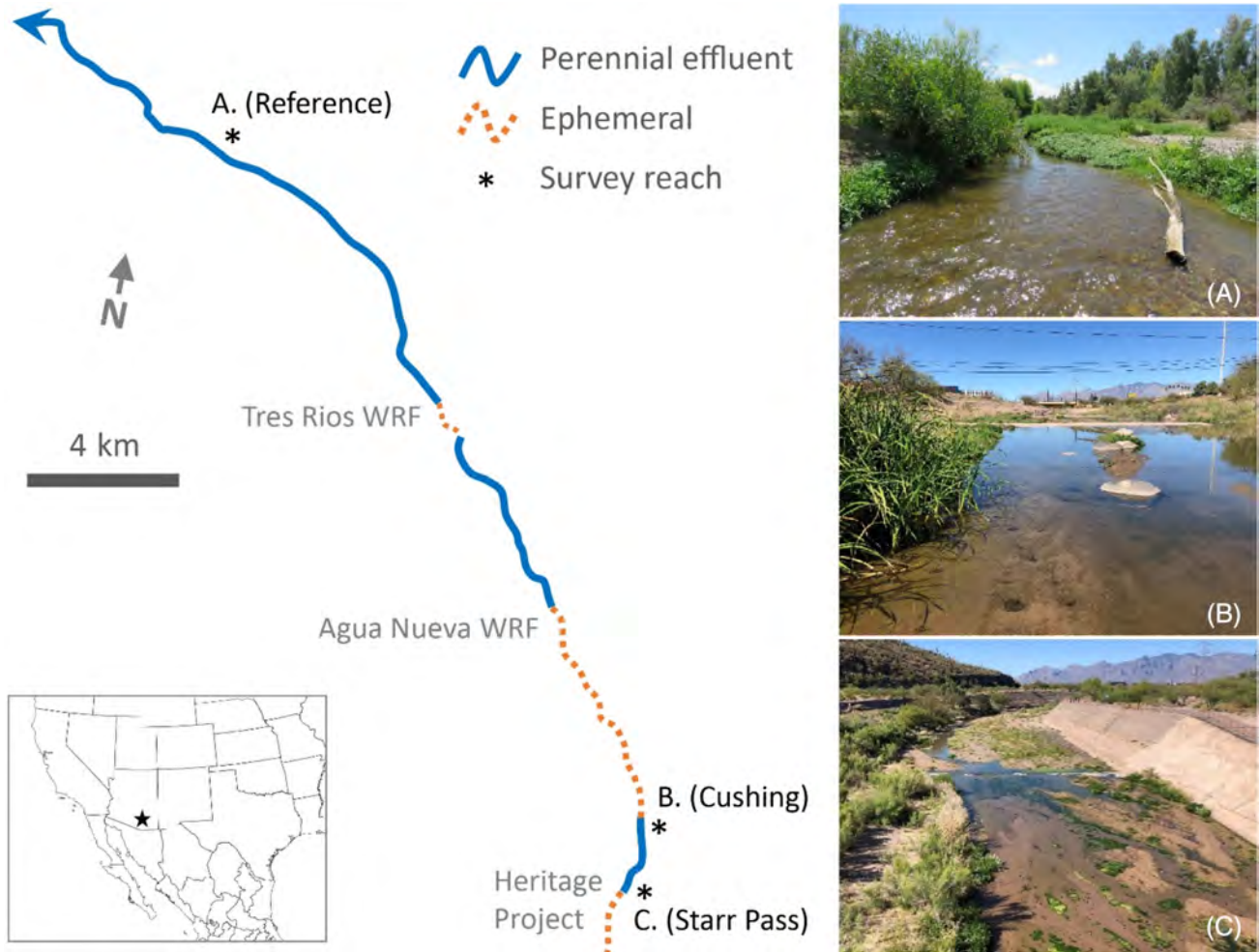
Figure 1. Map of the study reaches along the Santa Cruz River, Tucson, Arizona, including habitat photos of the three reaches (A: reference; B: Cushing; and C: Starr Pass). All perennial flow in the Santa Cruz River is dependent upon the release of effluent into the otherwise ephemeral riverbed. The Agua Nueva and Tres Rios Water Reclamation Facilities (WRF) have been releasing tertiary-treated effluent into the Santa Cruz River since 2013 and supporting long, flowing reaches. The Heritage Project began releasing effluent in June 2019 and supports a relatively short flowing reach of the river.

The Heritage Project is isolated hydrologically, being located 9 km upstream of the nearest effluent-dependent perennial reach (Fig. 1) and 65 km downstream of another effluent-dependent reach in the upper basin (Sonoran Institute 2022). The nearest naturally perennial stream is Sabino Canyon, a small, canyon-bound, headwater stream located 23 km away. The nearest low gradient naturally perennial rivers, structurally similar to the Santa Cruz, are the San Pedro and Gila Rivers, greater than 70 km to the east and northeast, respectively. As such, there are no naturally perennial river reaches in the watershed that could serve as a reference reach for the effluent-dependent reaches. However, numerous urban lentic water bodies, including city park ponds, recreational lakes, and golf course ponds, occur throughout the city of Tucson at distances from the Santa Cruz River ranging from 2 to 20 km.

Baseflow in all reaches of the lower Santa Cruz River is effluent-dependent, but rainfall occasionally causes run-off events. Multiple floods reaching magnitudes as high as 240 $m^3$/second may occur during the summer monsoon season (July–September), and winter precipitation (December–March) can produce small-magnitude floods as well (Eppehimer et al. 2020).

## Study Design

We measured basic water quality, hydrological, and substrate parameters and collected macroinvertebrate samples from three effluent-dependent reaches of the lower Santa Cruz River (Fig. 1) monthly from June 2019 to May 2021. First, we selected a long-established effluent-dependent portion of the river as a reference reach, as previous work had identified this reach as supporting the highest diversity of macroinvertebrates on the lower Santa Cruz River (Eppehimer et al. 2020). An ideal situation would be to have a naturally perennial reach serve as a reference or to have multiple independent effluent-dependent reference reaches to compare the newly flowing sites with, but neither are available in this watershed. However, we are confident in the

Figure 2. Photos of habitat changes through time at the Starr Pass study reach of the Santa Cruz River, Tucson, Arizona. In May 2020, the reach had been flowing with effluent discharge for 11 months. However, effluent discharge was shut off, and the channel was bulldozed for sediment removal in May and June 2020, before discharge resumed on 15 June 2020. There was abundant regrowth of riparian and wetland plants by May 2021, including *Lemna*, *Typha*, *Veronica*, and *Cyperus*. The Cushing study reach located 2 km downstream, experienced a similar trajectory.

ability of the reference reach to represent "best possible" biotic conditions given our previous monthly sampling at many locations along the river (Eppehimer et al. 2020).

Next, we established two study reaches in the Heritage Project, one just downstream of the effluent outfall (Starr Pass) and one 2 km downstream (Cushing), at the lower extent of the newly flowing stretch, where surface flow infiltrates completely into the ground (Bogan et al. 2020). Macroinvertebrate samples and habitat measurements were collected monthly across the 2-year study except in May and June 2020, when effluent releases ceased, the channel dried, and sediment removal occurred at the Heritage Project (Fig. 2).

At each reach in each month, we sampled macroinvertebrates along a designated 150 m reach following a reach-wide benthic sampling protocol (Eppehimer et al. 2020). Briefly, this approach produces a composite sample from 11 D-net kicks (0.09 m$^2$ surface area each, 500 μm-mesh net) collected every 15 m at alternating channel locations (left, right, and center) across the 150-m reach, for a total benthic area sampled of 1.02 m$^2$. This results in a composite sample that encompasses habitats (e.g. riffles and pools) in proportion to their occurrences across the reach. We supplemented these reach-wide benthic samples with "edge" samples, also collected using 500 μm D-nets. Edge samples were a composite of five sweeps (covering 0.33 m$^2$ each) through submerged vegetation, root masses, or mineral substrate along the banks (Bogan et al. 2015; Gill et al. 2024). All samples were preserved in 95% ethanol and enumerated and identified

individuals to the most practical taxonomic level, which was usually genus for insects and genus, family, or order for non-insects.

For statistical analyses, we calculated macroinvertebrate densities (number of individuals per square meter of stream bed) using the benthic samples. However, for species richness analyses, we combined macroinvertebrate taxa lists from benthic and edge samples to determine the total number of taxa detected for each month at each reach (Eppehimer et al. 2020). Additionally, for multivariate analyses, taxa present in edge but not benthic samples were added with an abundance of one to the benthic sample data matrix for that reach and month. This "plus one" method allows edge taxa to be considered in reach-scale community analyses but with relatively low weight (Gill et al. 2024).

To quantify habitat conditions, we measured the following water quality parameters immediately prior to each sampling event: dissolved oxygen (DO) (mg/L) (Apera Instruments AI480 DO850 probe), pH, temperature (°C), conductivity (μS/cm$^2$), oxidation–reduction potential (mV) (Apera Instruments SX823-B multiprobe), salinity (ppt) (Apera Instruments Salt20 m), water column chlorophyll-*a* (μg/L) (FluoroSense TD-700 fluorometer), alkalinity (CaCO$_3$ mg/L), and ammonia (NH$_3$ mg/L), nitrate (NO$_3$ mg/L), and phosphate (PO$_4$ mg/L) concentrations (YSI 9300 Photometer). To assess physical habitat conditions, we also made visual estimates of substrate size and composition (e.g. silt, sand, gravel, pebble, and cobble). To accomplish this, we estimated the relative abundances of substrate size classes within each "kick" of the benthic samples

to yield an overall relative abundance of substrate size classes for each benthic sample.

Finally, we calculated several flow metrics that were associated with each macroinvertebrate sample. These metrics included: (1) discharge at the time of sampling (*flow*), (2) total number of days the reach had been flowing since the previous drying event (*days flow*), (3) total number of days the reach had experienced drying in the previous month (*days dry*), (4) lowest magnitude flow event for the reach in the previous 30 days (*low flow*), and (5) highest magnitude flow event for the reach in the previous 30 days (*flood*). The *flow* factor was measured at the time of biological sampling using a standard channel cross-section and point velocity approach with a Marsh McBirney model 201D flow meter. The factor *days flow* and *days dry* were calculated using effluent release records from the City of Tucson and Pima County Regional Wastewater Reclamation Department. Finally, the factors of *low flow* and *flood* were estimated using data from three United States Geological Survey (USGS) stream flow gages (09482500, 09486500, and 09486520) adjacent to the three study reaches.

### Statistical Analyses

We tested for differences in measured water quality parameters among reaches using ANOVA. We plotted macroinvertebrate densities, taxon richness, and Ephemeroptera, Plecoptera, and Trichoptera (EPT) richness over time to visualize trends in the restored and reference reaches. We used multiple linear regression to test how flow metrics affected macroinvertebrate metrics. Sample size limited the number of predictor variables we were able to use in regression models, and because water quality parameters exhibited minor or no differences among reaches (see Section 3), we prioritized flow metrics in regression models. Prior to regression analyses, we assessed the collinearity of all flow metrics using Pearson correlation coefficients. We dropped *flow* and *low flow* from analyses, because they had correlation coefficients greater than 0.7 with other predictors and retained *days flow*, *days dry*, and *flood*. For each metric, we fit both a global model (including data from all three reaches) and models for the reference reach and the newly flowing reaches separately. For all models, we visually inspected autocorrelation function plots that depict correlations between model residuals and their lags, but substantial temporal autocorrelation was not detected. All univariate analyses were conducted in R (R Core Team 2022).

Differences in community composition of macroinvertebrates across reaches and time were visualized with nonmetric multidimensional scaling (NMS) in PC-ORD Version 6 (MJM Software, Gleneden Beach, OR, U.S.A.) using Bray–Curtis distance as the measure of community dissimilarity (McCune & Grace 2002). Prior to analyses, the densities of all taxa were square-root transformed to reduce the influence of highly abundant taxa, and taxa occurring in only a single sample were deleted to reduce noise in the ensuing ordination. We also calculated linear correlation values between taxon abundances and ordination axes, and between measured environmental variables and ordination axes. Next, we tested for differences in multivariate dispersion between restored and reference reaches using

analysis of multivariate homogeneity of group dispersions in the R package *vegan* using the functions *betadisper* and *permutest* with 9999 permutations (Oksanen et al. 2022). These functions compare beta diversity among groups by analyzing distributions of community dissimilarity values relative to group centroids (Anderson 2006; Anderson et al. 2006). Next, we tested for differences in community composition between restored and reference reaches using a multi-response permutation procedure (MRPP; Mielke & Berry 2001). When significant differences were found, we used indicator species analysis (ISA; Dufrêne & Legendre 1997) to determine which taxa were representative of each reach. MRPP and ISA analyses were conducted in PC-ORD Version 6.

## Results

### Univariate Analyses

Six of the 11 measured water quality parameters exhibited differences among the study reaches, but effect sizes were small (Table 1; Fig. S2). For example, mean values ranged from 8.5 to 10.9 mg/L for DO, from 8.0 to 8.6 for pH, and from 1170 to 1228 µS/cm for conductivity. Phosphate was the only measured water quality parameter with a relatively large effect size (restored reach: 2.6 mg/L; reference reach: 5.5 mg/L). Temperature, salinity, nitrate, ammonia, and chlorophyll-*a* concentrations did not differ among reaches (Table 1).

Across the entire study, 153 macroinvertebrate taxa were identified, including 56 true flies (Diptera), 30 beetles (Coleoptera), 22 dragonflies (Odonata), 19 non-insects, 13 true bugs (Hemiptera), 7 caddisflies (Trichoptera), 5 mayflies (Ephemeroptera), and 1 aquatic moth (Lepidoptera). Of these 153 taxa, 88 were identified from the reference reach, and 137 were found in the restored reaches (Cushing: 118 taxa; Starr Pass: 117 taxa).

Macroinvertebrate richness increased rapidly following flow restoration, reaching or exceeding levels observed in reference reach within 5 months (Fig. 3A). In the second year, when effluent releases were more stable (Fig. S1) after channel dredging (Fig. 2), richness values in the restored reaches were consistently higher than in the reference reach (Fig. 3A). The global model for richness was significant ($F_{[3,59]} = 9.925$, $p < 0.001$, adjusted $r^2 = 0.302$) and identified dry days as a strongly negative predictor ($\beta = -1.15$, $p < 0.001$) and days flowing as a moderately negative predictor ($\beta = -0.001$, $p = 0.031$). When considering the reference reach only, days flowing were identified as a negative predictor of richness ($\beta = -0.01$, $p = 0.018$), but the model was weak ($F_{[2,18]} = 3.427$, $p = 0.055$, adjusted $r^2 = 0.195$). In contrast, when only considering the restored reaches, dry days were a negative predictor of richness ($\beta = -0.64$, $p = 0.009$) and days flowing were a positive predictor ($\beta = 0.05$, $p < 0.001$) in the model ($F_{[3,38]} = 20.89$, $p < 0.001$, adjusted $r^2 = 0.593$).

In the restored reaches, EPT richness was low for the first year and was sensitive to short-term drying events (see Cushing November 2019 in Figs. 3B & S1). However, in the second year after flow stabilized, EPT richness levels occasionally reached those observed at the reference reach (Fig. 3B).

**Table 1.** Water quality parameters measured in the water column monthly at each of the three effluent-dependent study reaches of the Santa Cruz River. Values for each parameter include the mean ± 1 standard deviation of all monthly measurements across the study period, plus the results of ANOVA tests for each parameter.

| Parameter | Study reach | | | ANOVA | |
| --- | --- | --- | --- | --- | --- |
| | Starr Pass | Cushing | Reference | F | p Value |
| Dissolved oxygen (mg/L) | 8.8 ± 2.1 | 10.9 ± 3.5 | 8.5 ± 1.3 | 6.190 | 0.004 |
| Temperature (°C) | 24.7 ± 4.8 | 22.7 ± 9.0 | 22.1 ± 4.3 | 0.938 | 0.397 |
| pH | 8.0 ± 0.4 | 8.6 ± 0.4 | 8.0 ± 0.2 | 19.699 | <0.001 |
| Oxidation–reduction (mV) | −61.4 ± 21.7 | −99.1 ± 25.8 | −63.1 ± 13.5 | 21.575 | <0.001 |
| Conductivity (μS/cm) | 1215.1 ± 54.9 | 1228.1 ± 61.0 | 1170.1 ± 59.2 | 5.705 | 0.005 |
| Salinity (ppt) | 0.6 ± 0.0 | 0.6 ± 0.1 | 0.6 ± 0.1 | 2.017 | 0.153 |
| Alkalinity (CaCO$_3$ mg/L) | 197.2 ± 41.1 | 179.0 ± 32.4 | 142.8 ± 10.8 | 8.072 | 0.002 |
| Nitrate (mg/L) | 3.5 ± 1.9 | 3.0 ± 1.2 | 2.6 ± 1.5 | 0.761 | 0.477 |
| Ammonia (mg/L) | 0.1 ± 0.1 | 0.1 ± 0.1 | 0.2 ± 0.4 | 1.466 | 0.249 |
| Phosphate (mg/L) | 3.6 ± 1.3 | 2.6 ± 1.1 | 5.5 ± 1.0 | 15.529 | <0.001 |
| Chlorophyll-$a$ (μg/L) | 4.9 ± 2.8 | 6.4 ± 1.9 | 4.9 ± 1.0 | 1.009 | 0.381 |
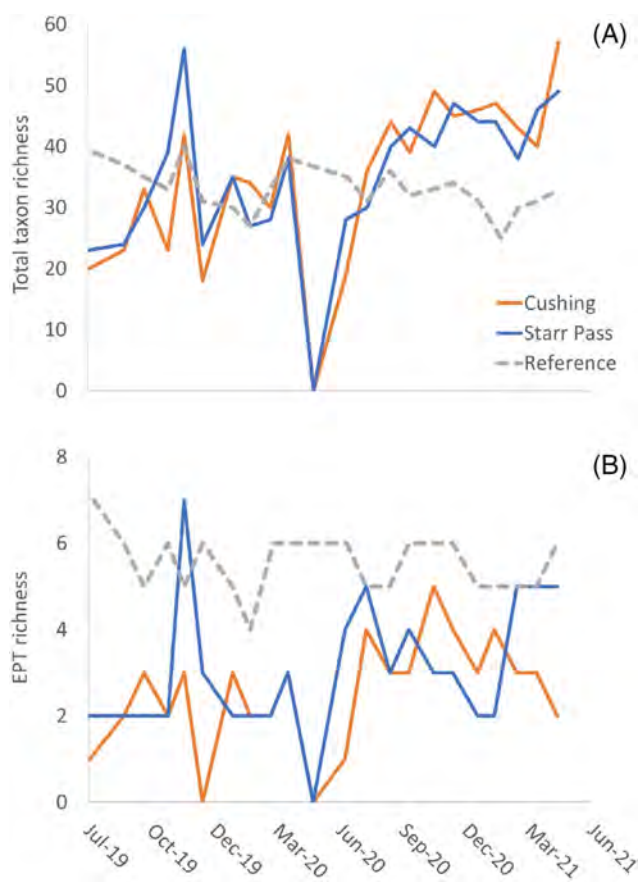


Figure 3. Total macroinvertebrate taxon richness (A) and richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa (B) across the 2-year study period at the three study reaches. At the Cushing and Starr Pass reaches, effluent discharge was shut off, and the channel was bulldozed for sediment removal in May and early June 2020.

Overall, we found a significant model for EPT richness ($F_{[3,59]} = 26.19$, $p < 0.001$, adjusted $r^2 = 0.549$), with days flowing as a positive predictor ($\beta = 0.00$, $p < 0.001$) and dry days as a negative predictor ($\beta = -0.07$, $p = 0.046$). However, no significant relationships were identified between flow factors and EPT richness when considering the reference ($p = 0.633$) or restored ($p = 0.086$) reaches separately. Finally, the highest flood magnitude in the previous 30 days was not a significant factor in explaining density, overall richness, or EPT richness in any of the models.

Macroinvertebrate densities increased rapidly in the restored reaches, and within 3 months densities reached or exceeded levels observed in the reference reach (Fig. 4). In the second year, following channel dredging, densities in the restored reaches exceeded those in the reference reach within 1 month (Fig. 4). Days flowing were negatively associated with density overall ($\beta = -2.26$, $p = 0.003$), but the global model was weak ($F_{[3,59]} = 6.049$, $p = 0.001$, adjusted $r^2 = 0.196$). Furthermore, no relationships were detected between density and any of the measured flow factors when considering the reference ($p = 0.241$) or restored ($p = 0.107$) reaches separately.

**Multivariate Analyses**

NMS resulted in a two-dimensional ordination (stress: 0.15; $p = 0.004$; final instability <0.00001; $r^2 = 0.85$; Fig. 5A). The number of dry days in the preceding month was positively correlated with NMS axis 1, while days flowing, flow volume, and minimum flow in the previous 30 days were all negatively correlated with NMS axis 2 (Table S1; Fig. 5B). No water quality or substrate composition factors were significantly associated with either NMS axis. Several dipteran taxa were positively correlated with NMS axis 1, while the moth *Petrophila* and the damselfly *Argia* were negatively correlated with NMS axis 1 (Table S2). Several snail taxa, ostracods, the mayfly *Fallceon*, the midge *Tanypus*, and one beetle and one damselfly taxon were positively correlated with NMS axis 2, while a broad array of caddisflies, damselflies, midges, and non-insect taxa were negatively correlated with NMS axis 2 (Table S2).

Macroinvertebrate samples from the reference reach exhibited lower multivariate dispersion than those from restored

reaches ($p < 0.001$). Reaches varied significantly in taxonomic composition ($A = 0.16$; $p < 0.0001$). However, the two restored reaches were not compositionally distinct from one another ($A = 0.01$, $p = 0.05$ [Bonferroni-corrected threshold = 0.017]), but the reference and restored reaches were distinct ($A = 0.18$, $p < 0.00001$). Indicator taxa for the reference reach included caddisflies, mayflies, damselflies, and midges (Table 2). In contrast, indicator taxa for the restored reaches were snails, ostracods,



Figure 4. Macroinvertebrate densities (individuals per square meter) on a log scale at the three sampling reaches across the 2-year study period. At the Cushing and Starr Pass reaches, effluent discharge was shut off and the channel was bulldozed for sediment removal in May and early June 2020.

beetles, true bugs, and the mayflies *Fallceon* and *Callibaetis* (Table 2).

Across the 2-year study, community composition in the reference reach remained fairly stable, whereas composition frequently changed dramatically from month-to-month in the restored reaches (Fig. 6). When flow first resumed, samples were located in the lower right portion of the NMS ordination plot but quickly moved up and left, reflecting higher abundances of damselflies (*Argia*), moths (*Petrophila*), water scavenger beetles (*Tropisterus*), and mayflies (*Fallceon*), and lower abundances of shore flies (Ephydridae) and the midges *Chironomus* and *Cricotopus* (Table S2). With consistent flows from month-to-month, taxonomic composition changed more slowly, but each time these reaches dried, composition shifted right on and down on the NMS plot (Fig. 6). Similar patterns were observed in both restored reaches, but the Cushing site experienced more frequent drying events and community changes.

## Discussion

### Rapid Recovery of Richness and Density in Restored Reaches

Macroinvertebrate species colonized quickly, with richness levels in the restored reaches matching or exceeding those in the reference reach within 5 months. Additionally, a total of over 120 taxa were found in each of the restored reaches within 2 years, which is much higher than has been observed in other studies. For example, only 35 taxa were detected in the 3 years following a stream restoration project in Canada (Gabriel et al. 2010), and less than 60 taxa have colonized new streams
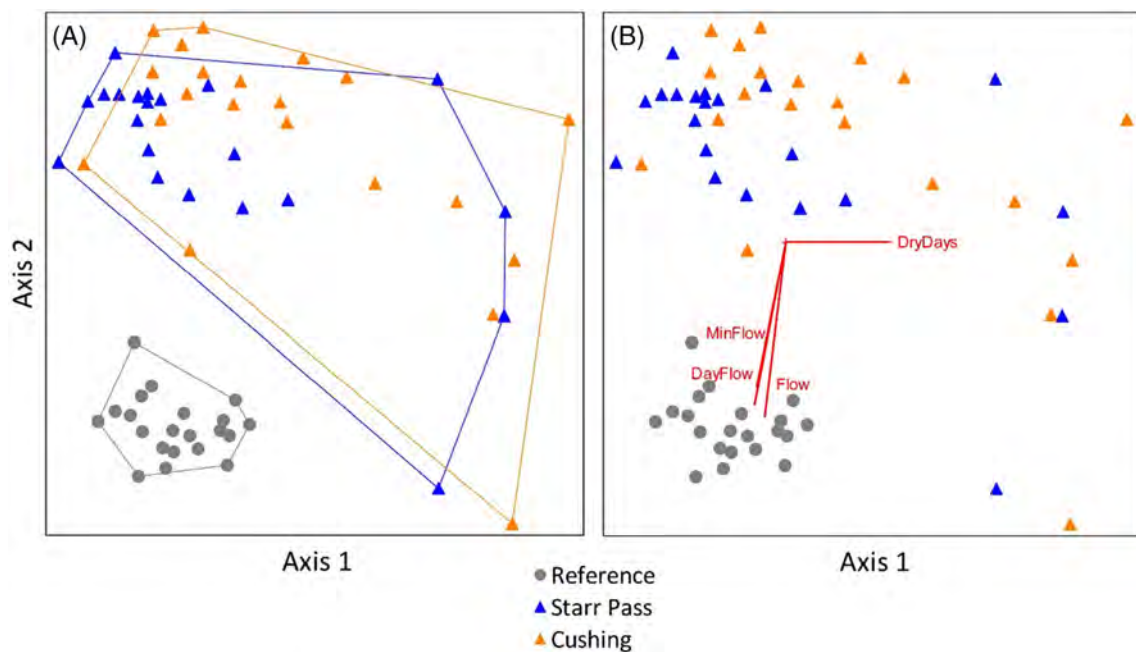


Figure 5. Nonmetric multidimensional scaling plots visualizing compositional differences in aquatic macroinvertebrate communities between the long-flowing effluent-dependent reference reach of the Santa Cruz River and two reaches in the newly flowing portion of the river upstream (Starr Pass and Cushing). The left plot is illustrated with convex hull polygons around samples from each of the three study reaches. The right plot includes significant correlations between measured environmental factors and ordination axis values (see Table S1 for codes).

**Table 2.** Macroinvertebrate indicator taxa for the reference reach versus the two newly flowing reaches (Starr Pass and Cushing) of the Santa Cruz River Heritage Project (IV = indicator value).

| Reaches | Taxon | IV | p |
|---|---|---|---|
| Reference | *Smicridea* | 99.3 | 0.0002 |
| | *Ferrissia* | 95.2 | 0.0002 |
| | *Polypedilum* | 90.3 | 0.0002 |
| | *Nectopsyche* | 89.5 | 0.0002 |
| | *Rheotanyarsus* | 84.4 | 0.0002 |
| | *Thiemanniella* cf. *xena* | 83.1 | 0.0002 |
| | Hirudinea | 81 | 0.0002 |
| | *Protoptila* | 79.1 | 0.0002 |
| | *Cladopelma* | 77.7 | 0.0002 |
| | *Hetaerina americana* | 76.2 | 0.0002 |
| | *Cryptochironomus* | 75.7 | 0.0002 |
| | *Hydroptila* | 61.8 | 0.0162 |
| | Oligochaeta (microdrile) | 60.2 | 0.010 |
| | *Cladotanytarsus* | 56.1 | 0.0002 |
| | *Camelobaetidius* | 53.3 | 0.0004 |
| | *Argia* | 50.6 | 0.061 |
| Newly flowing | *Physa* | 85.9 | 0.0002 |
| | Ostracoda | 81.7 | 0.0002 |
| | Ephydridae | 76.1 | 0.0002 |
| | *Apedilum* | 73.6 | 0.0004 |
| | *Fallceon* | 73.5 | 0.0002 |
| | *Tropisternus* | 71.4 | 0.0002 |
| | *Tanypus* | 71.2 | 0.0002 |
| | *Microvelia* | 69.8 | 0.0002 |
| | *Planorbella* | 68.5 | 0.0002 |
| | *Tanytarsus* | 66.6 | 0.017 |
| | *Callibaetis* | 62.8 | 0.0004 |
| | *Larsia* | 60.9 | 0.0106 |
| | *Dicrotendipes* | 59.7 | 0.013 |

in the volcanic blast zone of Mount St. Helens (U.S.A.) after 36 years (Claeson et al. 2021). The identities of early colonists in our study were also different from observations in previous studies. For example, aquatic snails took over 20 years to colonize new streams emerging from glacial cover in Alaska (Milner et al. 2008), but they were early colonists in our study. This rapid colonization by snails in the Santa Cruz River could be due to frequent visits by waterfowl, which have been shown to facilitate snail dispersal (Martin et al. 2020).

In many cases of stream restoration, macroinvertebrate richness does not increase, despite biodiversity being a major goal of restoration efforts (Clinton et al. 2022). So why did taxa arrive so quickly in our study? First, previous regional studies have documented a high propensity of species to disperse aerially (Bogan & Boersma 2012). Drying events are common in regional streams, meaning that species have to be mobile to persist (Bogan et al. 2015). Second, macroinvertebrate taxa adapted to intermittent streams, which are dominant in the study region, may inherently be more likely to persist and thrive in disturbed urban habitats (Smith et al. 2009). Finally, the warm summer air temperatures when flow was restored, as well as the region's generally warm climate, likely facilitate multiple generations of macroinvertebrates per year and more frequent aerial dispersal. Most previous studies of primary succession have occurred in

colder climates, where macroinvertebrates are univoltine and aerial colonization rates are significantly lower (Cushing & Gaines 1989).

Taxonomic richness increased with flow duration prior to sampling and decreased following drying events, as has been observed in previous studies (e.g. Boulton 2003; Datry et al. 2014; Gill et al. 2022). Although species in our region are quite tolerant of low water conditions (Boersma et al. 2014), most cannot survive complete drying (Eppehimer et al. 2020). In contrast, we did not find a relationship between taxonomic richness and flooding. Species in the region have adaptations to survive flooding events (e.g. Lytle & White 2007), and in general, macroinvertebrates recover quickly from floods (McMullen & Lytle 2012). However, the interactive effects of flow cessation and flooding have been shown to reduce richness in other effluent-dependent urban streams (Saffarinia et al. 2022). Finally, although flow cessation and channel dredging caused a major "reset" of our restored reaches after 1 year, trajectories of richness and density after dredging were almost identical to those after flow was first restored the prior year, suggesting repeatability of colonization patterns across years.

Macroinvertebrate densities in the restored reaches exceeded reference reach values even more quickly than richness—within 3 months—primarily due to rapid aerial colonization by true fly and mayfly taxa. In particular, several genera of non-biting midges (Chironomidae) were abundant soon after flow was restored, as observed in prior studies (Baho et al. 2021). Additionally, high numbers of the mayflies *Fallceon* and *Callibaetis* characterized early samples from the restored reaches; these taxa are often considered "weedy" and can colonize new habitats within a few weeks (Bogan & Boersma 2012).

## Lack of Community Convergence Between Restored and Reference Reaches

Community composition between restored and reference reaches remained distinct across our 2-year study. Time to convergence between restored and reference reaches varies widely among streams, and convergence may not always occur (Leps et al. 2016). For example, after only 2 years in the daylight stream in Norway, community composition in restored and reference reaches converged (Baho et al. 2021), but a similar study from New Zealand reported that communities were still distinct after 2 years (Neale & Moffett 2016). In Germany, convergence between reference and restored reaches did not occur for at least 9 years, and in some cases, it had not converged after more than 20 years (Winking et al. 2014). In a constructed river channel in England, composition only got more distinct from the reference reach through time, despite rapid colonization by numerous taxa (Robertson et al. 2014).

The lack of community convergence between restored and reference reaches in our study could be due to a combination of dispersal limitations, temporal scale, and founder effects. Dispersal limitations strongly influence community composition in the early years of restored streams (Patrick & Swan 2011). Community recovery can be rapid when colonization sources are nearby (<2 km), but may take decades in isolated reaches
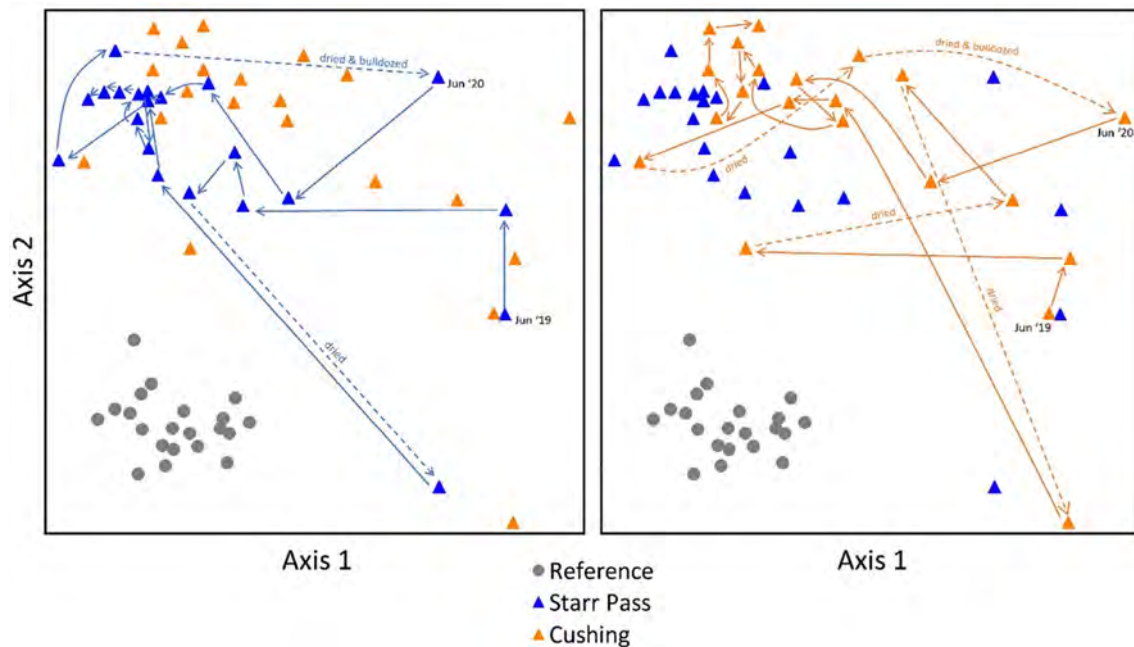
**Figure 6.** Nonmetric multidimensional scaling plots visualizing compositional differences in aquatic macroinvertebrate communities between the long-flowing effluent-dependent reference reach of the Santa Cruz River and two reaches in the newly flowing portion of the river upstream of the reference reach (Starr Pass and Cushing). Compositional changes across consecutive sampling months are illustrated via vectors for the Starr Pass (left) and Cushing (right) reaches; vectors are dashed when the reaches experienced drying between monthly macroinvertebrate sampling events. Between April 2020 and June 2020, the water was shut off and the stream channel bulldozed for sediment removal at the Starr Pass and Cushing sites.

(Parkyn & Smith 2011; Patrick et al. 2021); our restored reaches are greater than 10 km from other perennial effluent-dependent sections of the Santa Cruz River. With additional years of stable flow in our restored reaches, community composition may start to more closely resemble the reference reach. However, time can be a poor predictor of recovery in restored streams, especially with other confounding habitat issues in urban catchments (Leps et al. 2016).

Regardless of the isolation of restoration sites, species that are common across a region are more likely to colonize restored sites quickly (Tonkin et al. 2014). In our region, most of the indicator taxa for the restored reaches, including beetles, true bugs, and snails, are common inhabitants of both natural streams and natural and anthropogenic ponds (Bogan et al. 2013). As such, the long-established effluent-dependent portions of the river might not even be the primary source of colonists for the restored reaches. Instead, initial colonists may have arrived from city ponds, golf course water features, and other urban water bodies, many of which are less than 5 km from the restoration reaches. Although it is beyond the scope of this study, future studies should quantify the species pool of potential source populations in the urban environment around the river, not just those of other flowing portions of the river. Understanding how and why this specific community of beetles, true bugs, and snails is established in the restored reaches is also important when considering the potential for founder effects. Strong and rapid establishment of generalist taxa from urban ponds and parks might prevent riverine species from establishing later, when dispersal limitations are overcome (Barrett et al. 2021).

Although our reference reach historically supported the most diverse macroinvertebrate community along the Santa Cruz River (Eppehimer et al. 2020), it is also likely still in the process of recovery. This reach has received high-quality tertiary-treated effluent only for 8 years and is greater than 20 km from any naturally perennial streams that may serve as source populations (Bogan et al. 2020). In fact, only a few truly dispersal-limited riverine taxa inhabit the reference reach, including riffle beetles (*Microcylloepus*). As such, it is not surprising that those taxa have not yet colonized the restored reaches in the first 2 years, as they may have taken much longer to arrive to the reference reach in the first place. Given the spatial isolation of effluent-dependent perennial portions of the Santa Cruz River, translocation of some riverine taxa may be necessary in restored reaches (Clinton et al. 2022). Translocation immediately after flow restoration, especially, could be helpful given the potential founder effects of generalist taxa that quickly colonize restored reaches (Barrett et al. 2021). Additionally, if more flow restoration sites in intermediate locations along the Santa Cruz and its tributaries were established, these sites could provide movement "stepping stones" through the otherwise dry urban stream network and increase colonization rates for dispersal-limited taxa (Patrick et al. 2021).

Our results demonstrate that adding water to a previously dry channel can quickly lead to a diverse macroinvertebrate community in urban streams. Effluent is an important and underappreciated tool for creating new habitat for many riverine species in arid and semiarid regions (Halaburka et al. 2013; Hamdhani et al. 2023). Urban stream channel management activities,

including dredging, can cause dramatic but temporary setbacks to macroinvertebrate communities, especially when these activities are conducted during peak aerial dispersal season (e.g. early and mid-summer; Bogan & Boersma 2012). However, the reestablishment of sensitive or dispersal-limited taxa may take years or not happen at all without direct intervention. As such, municipal and natural resource managers should specify desired ecological outcomes before flow restoration efforts occur, so that these goals can guide decision-making processes about the level of intervention needed. Finally, close collaboration between managers and ecologists in the implementation and monitoring of flow restoration projects would allow for real-time feedback and adaptive management to maximize biodiversity outcomes in these complex urban ecosystems.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Effluent discharge (liters per minute) record for the outfall pipe of the Santa Cruz River Heritage Project across the 2-year study period in Tucson, Arizona.

**Figure S2.** Box-and-whiskers plots of selected water quality parameters across the study period (2019–2021) at the three study reaches of the Santa Cruz River.

**Table S1.** Pearson's correlation coefficients between environmental variables and nonmetric multidimensional scaling (NMS) ordination axes 1 and 2.

**Table S2.** Pearson's correlation coefficients between abundances of macroinvertebrate taxa and nonmetric multidimensional scaling (NMS) ordination axis values.