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Loss of dendritic connectivity in southern California's urban riverscape facilitates decline of an endemic freshwater fish

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Abstract

Life history adaptations and spatial configuration of metapopulation networks allow certain species to persist in extreme fluctuating environments, yet long-term stability within these systems relies on the maintenance of linkage habitat. Degradation of such linkages in urban riverscapes can disrupt this dynamic in aquatic species, leading to increased extinction debt in local populations experiencing environment-related demographic flux. We used microsatellites and mtDNA to examine the effects of collapsed network structure in the endemic Santa Ana sucker *Catostomus santaanae* of southern California, a threatened species affected by natural flood–drought cycles, "boom-and-bust" demography, hybridization and presumed artificial transplantation. Our results show a predominance of drift-mediated processes in shaping population structure and that reverse mechanisms for counterbalancing the genetic effects of these phenomena have dissipated with the collapse of dendritic connectivity. We use approximate Bayesian models to support two cases of artificial transplantation and provide evidence that one of the invaded systems better represents the historic processes that maintained genetic variation within watersheds than any remaining drainages where *C. santaanae* is considered native. We further show that a stable dry gap in the northern range is preventing genetic dilution of pure *C. santaanae* persisting upstream of a hybrid assemblage involving a non-native sucker and that local accumulation of genetic variation in the same drainage is influenced by position within the network. This work has important implications for declining species that have historically relied on dendritic metapopulation networks to maintain source–sink dynamics in phasic environments, but no longer possess this capacity in urban-converted landscapes.

KEYWORDS
bottleneck, conservation genetics, dendritic metapopulation, hybridization, sucker, urban riverscape

1 | INTRODUCTION

Repetitive population bottlenecks have the potential to purge genetic variation that is necessary for long-term species' survival (Frankham et al., 1999; Spielman, Brook, & Frankham, 2004), yet some species are naturally subject to this process because of the phasic environments in which they live (Jangjoo, Matter, Roland, & Keyghhbadi, 2016; Perkin, Shattuck, Gerken, & Bonner, 2013; Shama, Kubow, Jokela, & Robinson, 2011). These species can possess life history traits that enable rapid regeneration of individuals following crash cycles, combined with branching metapopulation networks that facilitate repatriation of lost individuals and genetic

variation into affected areas (Berthier, Charbonnel, Galan, Chaval, & Cosson, 2006; Busch, Waser, & DeWoody, 2007; Grant, Lowe, & Fagan, 2007; McEachern, Van Vuren, Floyd, May, & Eadie, 2011). The balance of such systems may be delicate, given that the environments responsible for serial bottlenecking can be so extreme that declines might exceed thresholds beyond which local recovery is not possible (Hollsinger, 2002), and/or changing landscapes produce gaps in the network that permanently alter source–sink dynamics (Fagan, 2002; Lowe, Likens, & Power, 2006). In many cases, the geometries of these networks (i.e., linear and unimodal vs. dendritic) may also be critical to maintaining and structuring genetic polymorphism, particularly if migration is asymmetric (Morrissey & de Kerckhove, 2009; Paz-Vinas & Blanchet, 2015; Thomaz, Christie, & Knowles, 2016).

Prior to urbanization, branching river networks traversing the Los Angeles Basin of southern California had meandering courses and shifting ocean outlets due to poor channel incision, with storm events occasionally inundating large portions of the coastal plain (Gumprecht, 2000; Orsi, 2004; Stein et al., 2007). Flooding had catastrophic consequences on a rapidly rising human population at the turn of the 19th century, resulting in the construction of an extensive flood control infrastructure that began in the late 1930s and was mostly completed by the late 1950s (although some occurred before and after that time frame as well). This led to the permanent hydrologic isolation of the regions' major watersheds and partitioning of suitable habitat within watersheds (Gumprecht, 2000; Orsi, 2004; Van Wormer, 1991; Figure 1). The consequences of this "riverscape conversion" on aquatic species are dramatic, eliminating opportunities for population admixture, reducing species' distributions and increasing susceptibility to extirpation from catastrophic events (Fagan, Unmack, Burgess, & Minckley, 2002). The extent to which these factors have impacted the spatial genetic diversity of native freshwater fish in southern California remains largely unexplored (but see Abadıa-Cardoso et al., 2016; Benjamin, May, O'Brien, & Finger, 2016; Clemento, Anderson, Boughton, Girman, & Garza, 2009; Richmond et al., 2014), despite the need for such information in developing species' recovery plans in this biodiversity and endangerment hot spot (Dobson, Rodriguez, Roberts, & Wilcove, 1997; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000).

The endemic Santa Ana sucker *Catostomus santaanae* is one of a few native fish species surviving in coastal southern California and is considered threatened by U.S. Fish and Wildlife Service (USFWS 2000) and endangered by the International Union for Conservation

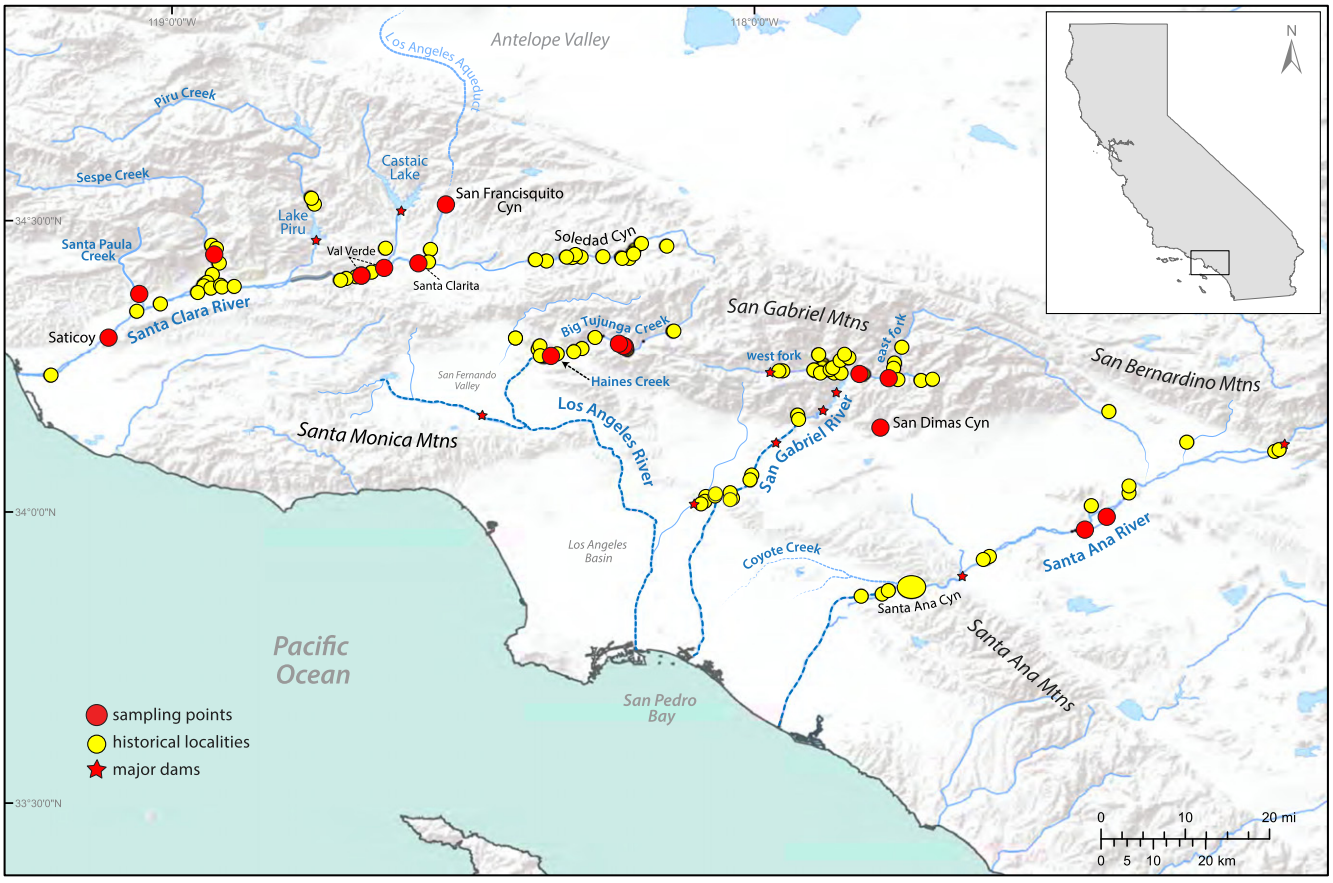


FIGURE 1 Distribution and sampling locations for *C. santaanae*. Yellow dots indicate historic records in the California Natural Diversity Database (CNDDB); red dots indicate sampling locations for this study; red stars show the locations of flood control dams. Dark blue hatching identifies channelized reaches of the major drainages in the lower flood plain. Dark grey line in the Santa Clara River (between Val Verde and the mouth of Piru Creek) approximates the location of the Piru Dry Gap [Colour figure can be viewed at wileyonlinelibrary.com]

of Nature (ICUN: NatureServe, 2014). It exists in the three watersheds that drain into the Los Angeles Basin and a fourth that drains into the Ventura coastal plain (Figure 1). Loss of an estimated 70%–80% of the historical range (Moyle, 2002; O'Brien, Hansen, & Stephens, 2011; Thompson, Baskin, Swift, Haglund, & Nagel, 2010) has disrupted fractal-like connectivity between low-order reaches in the mountains surrounding the greater Los Angeles area and high-order reaches in alluvial basins to the west–southwest. Some populations survive in stream sections that are dependent on the effluent from wastewater treatment facilities, and a host of non-native plant (e.g., *Arundo donax* and *Compsopogon coeruleus*) and animal species (e.g., largemouth bass *Micropterus salmoides*, red shiner *Cyprinella lutrensis* and green sunfish *Lepomis cyanellus*) pose threats to survival (Jenkins et al., 2009; Moyle, 2002; Swift, Haglund, Ruiz, & Fisher, 1993; USFWS, 2017). A non-native sucker has also been introduced to the northern part of the range (Bell, 1978; Hubbs, Hubbs, & Johnson, 1943; Miller, 1973) and adds to many examples where human disturbance has led to hybridization between sucker species that would not normally interbreed (Bangs, 2016; McDonald, Parchman, Bower, Hubert, & Rahel, 2008).

The perennial streams inhabited by *C. santaanae* are also subject to severe, episodic floods, combined with extended periods of low flow caused by drought (Moyle, 2002; O'Brien et al., 2011; Swift et al., 1993). Populations show "boom-and-bust" cycles that coincide with these events (Greenfield, Ross, & Deckert, 1970), which are correlated with the El Niño Southern Oscillation climate phenomenon (Cayan, Redmond, & Riddle, 1999; Dettinger, Cayan, Diaz, & Meko, 1998; Redmond & Koch, 1991). To counteract "bust" cycles, *C. santaanae* has a short generation time (i.e., rapid maturity), high fecundity and a long spawning period, enabling them to rapidly rebound by producing large numbers of young over a longer amount of time (Greenfield et al., 1970; Moyle, 2002). However, the fitness advantages conferred by these traits may have been fully realized only within the context of functional dendritic metapopulations, given that dendritic networks exhibit unique properties with respect to the maintenance and structuring of genetic variation compared to simple linear or lattice-like configurations (Morrissey & de Kerckhove, 2009; Paz-Vinas & Blanchet, 2015; Thomaz et al., 2016).

There are also open-ended questions regarding the introduced status of *C. santaanae* in one of California's largest coastal watersheds, the Santa Clara River, and in a now-isolated tributary of the San Gabriel River, San Dimas Canyon (Figure 1). The Santa Clara River introduction is presumed to have occurred sometime prior to 1924 (Hubbs Archives, Scripps Institute of Oceanography, May 2012; copied by C. Swift), whereas the San Dimas Canyon population was discovered only recently in 2008 (Morrissey, 2009). Genetic data have never been used to verify the native or non-native status of these populations and only the latter is protected under the listed entity (USFWS 2017), a concern given how little-preferred habitat remains in the Los Angeles Basin. Previous population genetic studies on *C. santaanae* have been limited to allozymes and mtDNA haplotype frequency data (Buth & Crabtree, 1982; Buth, Sim, & Swift, 2008; Chabot et al., 2009; Crabtree & Buth, 1981), with more recent phylogenetic analyses including one or a few samples of *C. santaanae* to estimate species-level relationships within the catostomids (e.g., Bangs, 2016; Chen & Mayden, 2012; Doosey, Bart, Saitoh, & Miya, 2010; Unmack et al., 2014).

In this study, we used microsatellites and mtDNA sequence data to describe the genetic outcomes of disintegrated metapopulation structure in *C. santaanae*, where life history adaptations, ephemeral river capture across watersheds and dendritic connectivity were probable factors that enabled this species to persist in an extreme fluctuating environment. We also tested for genetic effects of boom-and-bust demography associated with flood–drought cycling (and more recently, "fire-flood" cycling), measured hybridization with a distantly related, non-native sucker in the northern part of the species' range and identified the sources of presumed, artificially introduced populations of *C. santaanae*, to better understand the processes that gave rise to the historic distribution and current spatial genetic variation. The collapse of metapopulation structure in urban riverscapes is a pressing issue for *C. santaanae* and other declining fish species that have historically relied on dendritic networks as a means for local genetic rescue in phasic environments (Grant et al., 2007; Morrissey & de Kerckhove, 2009) and where global climate change is predicted to make those environments even more extreme in the future (Dettinger, 2011; Seager et al., 2007; Westerling, Hidalgo, Cayon, & Swetnam, 2006).

2 | MATERIALS AND METHODS

2.1 | Field sampling

We sampled *C. santaanae* from all drainages where the species is still known to occur using seine or dip nets (Figure 1). Specimens and tissue samples (fin clips stored in 95% ethanol) were collected with authorization from the U.S. Fish and Wildlife Service—Section 10(a)(1)(A) Recovery Permit TA-045994 and the California Department of Fish and Wildlife—Scientific Collecting Permits 90, 838, and 5429. Permit restrictions prevented us from collecting whole fish except where the species is not protected (i.e., Santa Clara River) and during a mass mortality event in the Los Angeles River in the late summer of 2011.

We provide brief descriptions for sampling locations in the Supplemental Materials, and georeferenced sampling points are available from the ScienceBase digital repository (see "Data Accessibility" section). We sampled *C. santaanae* from all drainages forming the species range, although at the time of field sampling, sucker were at low abundance and populations tended to be concentrated in small stream sections. The only site where *C. santaanae* still occurs but we were unable to obtain specimens was Soledad Canyon in the upper Santa Clara River (Figure 1), where local landowners precluded river access. We sampled more individuals and locations in the Santa Clara River because it is the only drainage where sucker were not limited to localized reaches at the time of field collection, and because of a large dry, stable gap that separates the upper and lower parts of the watershed (Figure 1). Surface flow across the gap,

informally referred to as the Piru Gap, is limited to exceptional storm flows (Beller et al., 2011; Mann, 1959; Stillwater Sciences 2011).

We also obtained tissues from 13 individuals of the Owens sucker *C. fumeiventris* from Mammoth Creek (Mono County, CA) to evaluate hybridization and introgression with *C. santaanae* in the Santa Clara River. *Catostomus fumeiventris* was introduced to the upper Santa Clara River via conveyance from the Owens River through the Los Angeles Aqueduct (Bell, 1978; Hubbs et al., 1943; Miller, 1973), with hybridization historically limited to downstream sections of the river (Buth & Crabtree, 1982; Swift et al., 1993). At the time of this work, the geographic limits of hybrids and/or pure *C. fumeiventris* and levels of introgression were unknown.

2.2 | DNA extraction and marker development

We extracted DNA from muscle tissue or fin clips using a Qiagen® DNeasy Blood & Tissue Kit and collected microsatellite allele frequency data and mtDNA haplotype sequences. We identified microsatellites from libraries developed for *C. santaanae* following the protocol of Hamilton, Pincus, Di Fiore, and Fleischer (1999). Because Catostomid fish are tetraploids (Uyeno & Smith, 1972), we also screened a subset of loci from Tranah, Agresti, and May (2001) known to amplify bi-allelic polymerase chain reaction (PCR) products in other sucker species. PCR products from the final pool of 17 polymorphic loci (Table S1) were analysed on an ABI 3730xl DNA Analyzer at Bio Applied Technologies Joint (San Diego, CA; PCR reagents and cycling conditions followed the Qiagen Multiplex PCR Kit® protocol). We scored the raw data in Gene-Marker v1.90 (SoftGenetics) and screened for null alleles and scoring errors using Microchecker (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004).

We sequenced a subset of individuals from each location (N_{total} = 63) for the mitochondrial NADH dehydrogenase subunit 2 gene (ND2), five flanking tRNAs, the 5′ end of cytochrome oxidase I (1483 nt). Primer sequences and PCR cycling conditions are provided in the Supplemental File. We performed Sanger DNA sequencing using Big Dye v3.1 chemistry on an ABI3730XL DNA analyzer at Genewiz (La Jolla, CA). Sequence data were edited using Sequencher v5.1 (Gene Codes Corporation, Ann Arbor MI) and manually aligned by eye.

2.3 | Genetic diversity

For microsatellites, we tested for linkage disequilibrium (LD) by population using Genepop On The Web (Raymond & Rousset, 1995; Rousset, 2008). We used HPRare (Kalinowski, 2005) to estimate allelic richness A_r (no. of alleles corrected for variance in sample size) and GenoDive 2.0b22 (Meirmans & Van Tienderen, 2004) to estimate observed heterozygosity H_o, expected frequency of heterozygotes H_s and the inbreeding coefficient G_{is} at each sampling location. We also tested for differences in A_r, H_o and H_s across watersheds using a nonparametric permutation test in FStat v2.9.3.2 (1000 replicates; Goudet, 1995).

To infer bottlenecks, we used the two-phased mutation model to simulate the distribution of expected heterozygosity under mutation–drift equilibrium and a Wilcoxon's signed rank test in Bottleneck (Cornuet & Luikart, 1996) to test whether samples exhibited a significant number of loci with heterozygosity excess. Bottlenecked populations are predicted to show heterozygosity excess given that the number of alleles declines more quickly than heterozygosity in populations with large, recent reduction in N_e (Nei, Maruyama, & Chakraborty, 1975). Because the expected distribution of heterozygosity can vary with respect to the underlying mutation model (Peery et al., 2012), we explored a nested series of analyses where we set the variance in the mean size of multistep repeats δ_g to either 30 or 15 and adjusted the proportion of strict one-step mutations p_g to .00, .05, .10, .20 and .30 among successive runs to assess sensitivity of the results.

For mtDNA, we identified unique haplotypes, average number of nucleotide differences *k* and number of segregating and phylogenetically informative sites. We also tested whether any samples of *C. santaanae* from the Santa Clara River (based on assignment coefficients *q* of their genotypes) had haplotypes belonging to *C. fumeiventris*, and whether those haplotypes were dispersed on both sides of Piru Gap.

2.4 | Population structure and relatedness

We used Structure v2.3 (Pritchard, Stephens, & Donnelly, 2000) to characterize population structure and measure allelic admixture across sampling areas. We estimated assignment coefficients *q* for a range of cluster *K* values (2–6) using an admixture model with uncorrelated allele frequencies. For each *K*, we performed 25 runs of 250,000 steps and discarded the first 100,000 samples as burn-in. We summarized the assignment matrices for the 10 best-scoring runs at each *K* using the GREEDY algorithm in CLUMPP v1.1 (Jakobsson & Rosenberg, 2007) and visualized the alignments as assignment plots using Distruct (Rosenberg, 2004). We used ΔK statistic (Evanno, Regnaut, & Goudet, 2005) and inflection of the ln(Pr(X|*K*) curve (Pritchard et al., 2000) to approximate the number of clusters in the data set, but considered results across a range of *K* because useful information about demographic and historical processes is often gained by doing so (Rosenberg et al., 2005; Meirmans, 2015).

We performed a second set of Structure analyses using the Santa Clara River samples only and included *C. fumeiventris* (*n* = 12) collected from Mammoth Creek (Mono County CA) to identify stream reaches where hybrids or pure *C. fumeiventris* might still exist. In this case, we assumed correlated allele frequencies and assigned individuals at *K* = 2–4 (*K* ≥ 5 showed no further structure), summarizing the data across runs as described above. Individuals were assigned to one of three genotypic classes based on their assignment coefficients *q*: pure *C. santaanae* (>0.875), pure *C. fumeiventris* (<0.125) or hybrids (0.125–0.875). We also calculated the maximum-likelihood estimate of Buerkle's (2005) hybrid index *h* for samples collected west of the Piru Gap based on two data set configurations, both treating *C. fumeiventris* as a reference species and either the San Francisquito Canyon or Val Verde-Santa Clarita samples as the

alternative (i.e., *C. santaanae*). We considered the two upper Santa Clara River sites separately because cluster assignments and pairwise F_{st} values (Weir & Cockerham, 1984) indicated some differences between them (see "*Population* Structure" in Results). *F* statistics corresponded to those defined by Weir and Cockerham (1984), and we tested for significance by permuting the genotypes 999 times in GENODIVE.

To test for phylogeographic structure in *C. santaanae*, we conducted a model-partitioned phylogenetic analysis using haplotype sequences generated from this study and published ND2 data for the desert sucker *C. clarkii* (outgroup) in MRBAYES v3.2 (Ronquist et al., 2012). We also constructed a TCS network (Clement, Snell, Walke, Posada, & Crandall, 2002) with a 95% connection limit to better visualize the haplotype differences. To assess the phylogenetic distance and timing of divergence between *C. santaanae* and *C. fumeiventris*, we performed additional analyses in BEAST v2.4.6 (Bouckaert et al., 2014) using published ND2 data for other sucker species and a subset of *C. santaanae* and *C. fumeiventris* from this study. We used two fossil calibrations from Unmack et al. (2014) to date the tree, with the goal of assessing whether the divergence time between these two hybridizing species was on the order of tens of thousands, hundreds of thousands or many millions of years. Further details on these analyses are presented in the Supplemental File.

2.5 | Testing for anthropogenic introductions

To further test for and estimate the timing of artificial introductions, we used approximate Bayesian methods in *DIYABC* v.2.1.0 (Cornuet et al., 2014) to simulate data sets according to different scenarios representing alternative sources for the San Dimas Canyon and Santa Clara River populations. Scenarios producing simulated data sets that were most similar to the observed data were considered the best explanation for population history. We treated all scenarios with equal prior probability and specified uniform priors for all parameters that defined each scenario, including the timing of splitting events *t*, effective population size N_e and duration of bottlenecks *db*. Because *DIYABC* defines time in numbers of generations, we used a generation time of 2 years for *C. santaanae* to infer time in years (Greenfield et al., 1970; Moyle, 2002).

We performed four sets of *DIYABC* analyses to address population origins for San Dimas Canyon and the Santa Clara River. In the first set, we compared two models that differed in the sequence of branching events for the San Gabriel River, Santa Ana River and San Dimas Canyon, and a third positing that the San Dimas Canyon population arose from an admixture event between the San Gabriel and Santa Ana River (Figure 2a). We enforced a bottleneck in the San Dimas population for time *db* (uniform prior *U*[2−50]) following an introduction event at time *t* (*U*[2−50]), with the condition that $db \leq t$. The bottleneck N_e was set between *U*[5−50] and the contemporary N_e was set at *U*[10−250], with the latter based on a census size estimate at the time of sampling (~40–45 fish; Morrissey, 2009).

In the second set, we constructed four additional scenarios for San Dimas Canyon that were modifications of the best-ranked scenario identified in the first set of analyses (Figure 2b). Each scenario differed in the nature (abrupt vs. gradual) and timing of the bottleneck as follows: (i) bottleneck due to a recent founder event at time *t* (*U*[2−5] generations in the past); (ii) a recent but slightly older bottleneck *U*[20−50]; (iii) an historical bottleneck *U*[75−200]; (iv) recent gradual decline in population size (Figure 2b). The "recent founder event" scenario assumed a bottleneck N_e between *U*[2−15], as might have been the case if a small number of fish were artificially moved to San Dimas Canyon, whereas the remaining scenarios were set between *U*[5−50]. To model a gradual population decline, we enforced a decrease in N_e from *U*[100−600] to *U*[10−250] during the past *U*[10−500] generations, with the constraint that contemporary $N_e <$ historical N_e.

In the third set of analyses, we randomly selected 30 genotypes from each watershed and tested three scenarios that differed in the divergence history of populations occupying those drainages (Figure 2c). Specifically, we altered the placement of the Santa Clara River group with respect to the other drainages to pinpoint the most probable genetic source of that group, ensuring that only genotypes of pure *C. santaanae* were included. Each scenario restricted the San Gabriel and Santa Ana River groups to be on sister branches given the consistent, close relationship between them in all analyses. We also constrained the ancestral N_e's to be greater than or equal to descendant N_e's given that population sizes have been declining since the mid-20th century (USFWS 2017). Prior distributions for model parameters were as follows: *U*[10–5,000] for N_e for Santa Clara and Los Angeles Rivers, *U*[10–10,000] for N_e for San Gabriel and Santa Ana Rivers; *U*[10–10,000] for *t*1–*t*3, with constraints $t2 \geq t1$ and $t3 > t2$.

Using the top-ranked scenario from the preceding analysis as a baseline representation of colonization history, we then tested three variants of that same scenario (i.e., same divergence history), each differing in the timing of the split between the Santa Clara River group and its nearest relative (Figure 2d). The first modelled a bottleneck (i.e., founder event) in the Santa Clara River lasting *U*[2–10] generations after the split from the sister group *U*[40–60] generations in the past (the prevailing theory on the timing of the introduction); the second modelled the same split *U*[100–600] generations in the past with a gradual decline in N_e since the split; and a third increased the age of the split to *U*[1,000–10,000] generations, again with a gradual decline in N_e. We specified the same uniform priors for N_e as above.

All *DIYABC* analyses involved the same procedures: (i) estimate summary statistics (i.e., genetic diversity and differentiation indices) based on the observed data; (ii) simulate 1×10^6 data sets for each scenario; (iii) calculate the same summary statistics on the simulated data and identify the scenario producing data sets that are closest to the observed data (Beaumont, Zhang, & Balding, 2002; Cornuet et al., 2008). We measured the probability of each scenario by calculating the proportion of each scenario in the pool of simulated data sets that was closest to the observed data (i.e., the "direct" approach; Miller et al., 2005; Pascual et al., 2007) and by performing a weighted logistic regression of each scenario probability to

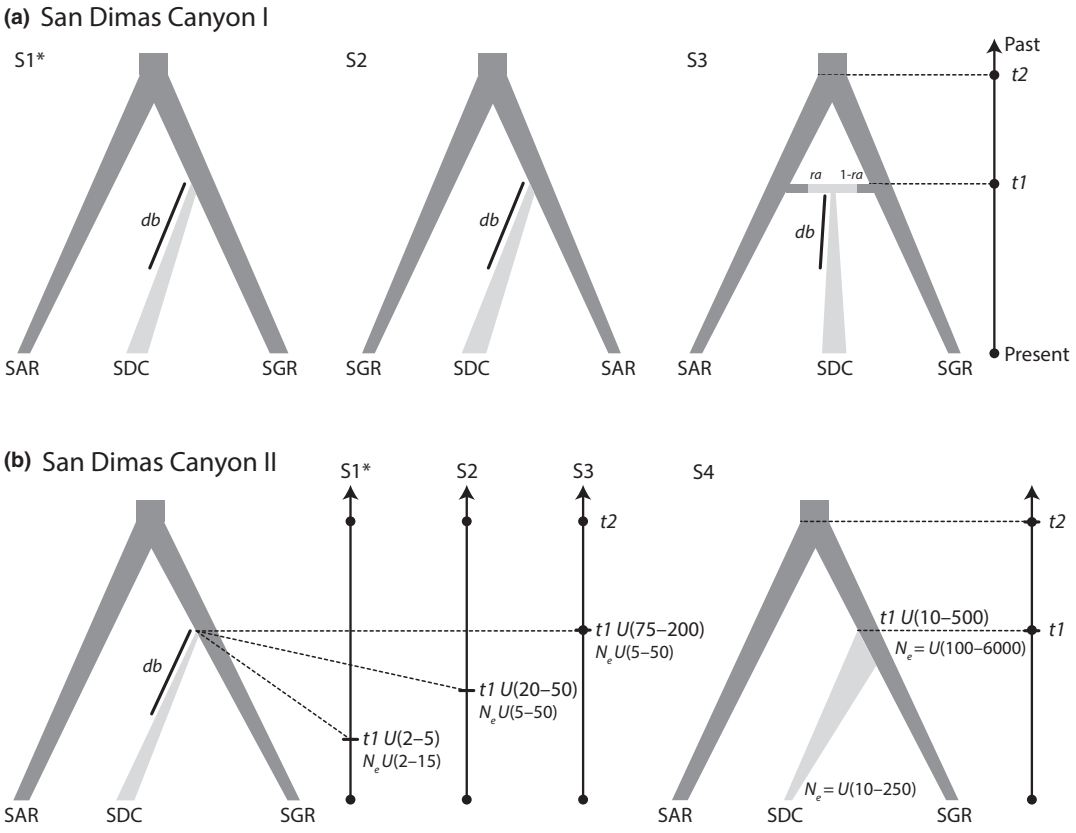

(a) San Dimas Canyon I
S1*
S2
S3
Past
t2
t1
ra
1-ra
db
Present
SAR
SDC
SGR
(b) San Dimas Canyon II
S1*
S2
S3
S4
t2
t1 U(75–200)
Ne U(5–50)
t1 U(20–50)
Ne U(5–50)
t1 U(2–5)
Ne U(2–15)
t1 U(10–500)
Ne = U(100–6000)
Ne = U(10–250)
(c) Ancestry of the Santa Clara River
S1
S2
S3
Past
t3
t2
t1 ≤ t2
Present
SCR
LAR
SGR
SAR
(d) Santa Clara River colonization timing
S1
S2
S3
Past
t3
t2 U (40–50)
t2 U (100–600)
t2
U (1x10³-x10⁵)
t1 ≤ t2
Present

FIGURE 2 Historical scenarios (S) used to model source populations for San Dimas Canyon [SDC] and to test for the timing and source of establishment in the Santa Clara River [SCR]. Time *t*, in numbers of generations, is shown from the present (tree tips) to the past; grey branches tapered towards the tip denote decreasing effective population size N_e; *db* indicates duration of a bottleneck; *U* specifies a uniform prior distribution. In (a), the three scenarios modelled different probable sources for SDC; in (b), S1–3 differ in the timing (recent vs. historical) and severity of a population bottleneck in SDC, whereas S4 modelled a gradual population decline; (c) scenarios differ in the placement of the SCR branch to infer its most probable ancestral source; (d) scenario with the highest posterior probability in "c" is used as a baseline for distinguishing among scenarios that differed in the timing of colonization for the SCR. Los Angeles River (LAR); San Gabriel River (SGR); Santa Ana River (SAR)

compare the deviations between simulated and observed summary statistics (Beaumont, 2008; Fagundes et al., 2007). Based on these summary statistics, we generated principle components plots of the prior and posterior predictive distributions to ensure that simulated data were plausible representations of the real data (Cornuet, Ravigné, & Estoup, 2010). We provide descriptions of the different summary statistics and mutation models used for these analyses in the Supplemental file.

To assess confidence in scenario rankings, we calculated a type I error rate by simulating 500 data sets based on parameter prior distributions for the top-ranked scenario, then measuring the proportion of times that scenario had a closer fit to the observed data (i.e., higher posterior probability) compared to the 2nd-ranked scenario. This represented the probability of rejecting the top-ranked scenario even though it is the "true" scenario (i.e., the scenario upon which the data were simulated), or type I error. We measured the type II error rate using a similar approach, but instead, we simulated the 500 data sets based on the 2nd-ranked scenario. This represented the probability of favouring of the top-ranked scenario when it is not the "true" scenario, or type II error.

3 | RESULTS

3.1 | Genetic diversity

Table 1 provides microsatellite diversity measures for all sampling locations. Some loci deviated from Hardy–Weinberg proportions by site but none showed consistent deviation across sites (Table S2). Only two populations showed significant LD for one pair of loci (Cs290 and Dlu416); removal of Dlu416 had no qualitative effects on estimates of diversity, divergence or assignments, so we included both markers in our analyses. Grouping the data by watershed showed significant differences in A_r (p = .003), H_o (p = .001) and H_S (p = .002), with San Gabriel and Santa Ana River populations displaying considerably higher genetic diversity than those in the Los Angeles or Santa Clara Rivers (Table S3).

We recovered 12 mtDNA haplotypes from 63 *C. santaanae* representing all drainages (19 phylogenetically informative sites), differing on average by 3.65 nucleotides. Santa Ana River fish had the highest haplotype diversity, followed by the San Gabriel, Los Angeles and Santa Clara Rivers (Table S4). Only four haplotypes were shared among some of drainages and none was shared across all. Three of eight *C. santaanae* from the lower Santa Clara River had haplotypes of *C. fumeiventris* (based on comparison with *C. fumeiventris* from the Owens River), but none of these haplotypes were recovered from the upstream side of the Piru Gap. The single haplotype of *C. santaanae* found in the Santa Clara River had a frequency of 0.73 in the total sample and was absent only from Los Angeles River.

3.2 | Population structure, divergence and relatedness

The ΔK statistic (Table S5) and mean ln(Pr(X|*K*) scores (Figure S1) identified 4–6 clusters as a "best-fit" to the data (Figure 3); however, other important patterns emerged at lower *K*, namely that Santa Clara River samples were consistently distinguished from all Los Angeles Basin samples at $K \geq 2$, followed by exclusive grouping of Los Angeles River samples at $K \geq 3$. Additional structure emerged in the Santa Clara River at $K \geq 4$, with separate clusters on opposite sides of the Piru Gap. Admixture proportions of San Gabriel River samples showed a slight influence from the Los Angeles River at $K \geq 3$, but were clearly more admixed with the Santa Ana River over the full range of *K*. San Dimas Canyon samples were distinguishable at $K \geq 5$, associating with San Gabriel River populations at $K = 5$ but appearing more exclusive at $K = 6$ (an artefact of population demography, see "*Nonequilibrium processes drive divergence*" in the Discussion).

Assignments using only *C. santaanae* from the Santa Clara River and *C. fumeiventris* from Mammoth Creek again showed structure corresponding to opposite sides of the Piru Gap and that genetic input from *C. fumeiventris* is limited to areas downstream of this reach (Figure 3). Assignment proportions revealed a predominance of alleles belonging to *C. santaanae* below the Piru Gap and essentially no trace of alleles belonging to *C. fumeiventris* above the gap. Only 2/22 downstream samples assigned to pure *C. fumeiventris* at (K = 3–4: q_3 = 0.983/0.988; q_4 = 0.976/0.981), whereas 16 and 15 fish ($K = 3$ & 4, respectively) assigned to pure *C. santaanae* ($q \geq 0.875$). Four to five individuals were classified as hybrids, with q ranging from 0.378 to 0.684. Only 6/16 loci amplified in *C. fumeiventris*, presumably because of mutations in the primer-annealing sites that were based on sequence data from *C. santaanae*.

We found similar trends in the maximum-likelihood estimates for the hybrid index h (range h = 0–1.0; values near 1.0 indicated greater similarity to *C. santaanae* and those near zero were more similar to *C. fumeiventris*) regardless of the reference population for *C. santaanae* (Spearman's $\sigma = 0.85$, $p < .01$); however, median h values were marginally different between the two (one-tailed t test, $t = -1.79$, p = .04) such that a greater proportion of the genotypes from lower Santa Clara River were more closely allied with *C. fumeiventris* when the *C. santaanae* reference was from higher in the watershed (San Francisquito Canyon) vs. lower in the watershed

TABLE 1 Genetic diversity for sampling locations

Location	N	L_p	A	A_r	A_{pr}	H_O	H_s	G_{is}
Lower Santa Clara River	22	15	4.50	4.03	8	0.44	0.53	0.17
San Francisquito Canyon (SCR)	24	14	3.40	3.15	0	0.48	0.47	−0.03
Val Verde-Santa Clarita (SCR)	41	16	4.53	3.71	5	0.41	0.48	0.16
Big Tujunga Canyon (LAR)	47	16	5.20	4.06	4	0.50	0.52	0.04
Haines Creek (LAR)	24	16	3.80	3.58	0	0.46	0.52	0.11
San Gabriel River	28	16	7.73	6.63	10	0.63	0.62	−0.03
San Dimas Canyon (SGR)	16	15	3.80	3.80	0	0.71	0.59	−0.20
Santa Ana River	40	16	7.62	6.35	9	0.61	0.65	0.06
C. fumeiventris (OWR)	13	6	5.17	4.60	11	0.43	0.47	0.09

Three letter acronyms indicate the main drainages to which tributary samples belong (SCR, Santa Clara River; LAR, Los Angeles River; SGR, San Gabriel River; OWR, Owens River); mainstem samples are designated as such. Indices are as follows: N = sample size; L_p = no. of polymorphic loci; A = no. of observed alleles; A_r = allelic richness, adjusted for sample size; A_{pr} = no. of private alleles; H_o = observed frequency of heterozygotes within populations; H_s = expected frequency of heterozygotes within sampling locations (i.e., gene diversity, Nei, 1987; includes a correction for sampling bias); G_{is} is the ratio of the observed to expected heterozygosity and ranges from −1 to 1 (analogous to the inbreeding coefficient F_{is}).

(Val Verde-Santa Clarita; Table S6). Consistent with this pattern, pairwise F_{ST} estimates show that *C. santaanae* sampled successively further west towards the river mouth were increasingly more similar to *C. fumeiventris* (mean F_{ST} range = 0.08–0.61; Table S7). When using the Val Verde-Santa Clarita reference set, 82% (or 18/22) of the samples in the lower Santa Clara River had median h values >0.50, 73% (16/22) were >0.80, and 59% (13/22) were >0.90. In contrast, no samples had h values <0.10. Although the 95% confidence intervals were broad based on only six loci, these patterns again show that most of the genetic variation in the Santa Clara River is representative of *C. santaanae*.

Pairwise F_{ST} estimates across all drainages indicate significant population divergence in nearly all cases, except for Los Angeles River tributaries (i.e., Big Tujunga Canyon and Haines Creek; Table S8). San Gabriel and Santa Ana River populations showed little difference from each other, and only slightly more than the two Los Angeles River samples (F_{st} = 0.033 vs. 0.019, respectively). The San Dimas population was nearly equally divergent from the San Gabriel and Santa Ana River populations, but slightly less so from the former (F_{st} = 0.054 vs. 0.060, respectively). Estimates for population pairs on opposite sides of the Piru Gap in the Santa Clara River (range F_{st} = 0.206–0.236) were higher than those among all pairs in the Los Angeles Basin drainages (range F_{st} = 0.019–0.194; Table S8).

For ND2 sequences, 92 sites were phylogenetically informative (including *C. clarkii*), but network- and tree-based analyses were unable to detect any phylogeographic structure in *C. santaanae* haplotypes (Figure S2, Supplemental File). Species-level analyses showed that *C. santaanae* and *C. fumeiventris* are nested in separate clades within the Catostomini, with the former belonging to the monophyletic *Pantosteus* group (the "mountain suckers") and the latter belonging to a second clade that includes all remaining *Catostomus* (but placement of the longnose sucker *Catostomus catostomus* was unresolved; Figure S3, Supplemental File). Although uncertainty around the age estimate is high, these results indicate that *C. santaanae* and *C. fumeiventris* diverged from a common ancestor approximately ~22.1 million years ago (95% highest posterior density = 14.2–32.0; Figure S4, Supplemental File).

3.3 | Historical demography

With the exception of Val Verde-Santa Clarita, Big Tujunga Canyon and the San Gabriel River, we detected significant bottlenecks in all samples (although even Big Tujunga Canyon and the San Gabriel River showed marginally significant signals with larger variance δ_g and low proportions of single step mutations p_g; Table 2). This result was robust to the full range of parameter values for the different mutation models. Val Verde-Santa Clarita was the only population for which we did not detect heterozygosity excess under any model.

In the first set of *DIYABC* analyses, comparison of scenarios representing alternative sources for the San Dimas Canyon population favoured the San Gabriel River as the most likely source (Scenario 1; Figure 4a). Model comparison in the second set of analyses showed strong support for a recent, severe bottleneck (i.e., founder event as few as 2–5 generations in the past) in San Dimas Canyon over other scenarios that modelled older bottlenecks or a gradual decline in N_e (Figure 4b). Type I errors were 0.15 and 0.08 for the direct and logistic regression approaches, respectively, whereas type II errors were 0.08 and 0.013, indicating high confidence in the recent bottleneck scenario. The posterior predictive distribution further confirmed that simulated data were an appropriate fit to the observed data (results not shown). These findings support the hypothesis that this population was artificially seeded, as interchange with the San Gabriel River was not possible during the time frame specified by the model with the highest posterior probability.

In the third set of analyses modelling different colonization histories for the Santa Clara River, we found support for scenario 2, which had paired splitting events between the San Gabriel and Santa Ana Rivers ($t1$) and the Santa Clara and Los Angeles Rivers ($t2$), with $t2$ inferred to be slightly older than $t1$ ($t1$, 0.025 and 0.975 quantiles = [31.7, 379.0]; $t2$, $Q_{0.025,\ 0.975}$ = [56.4, 790.0]; Figure 2c). Only

FIGURE 3 (a) Estimated assignment coefficients for all sampled individuals of *C. santaanae* for K = 2−6. (b) Stream network topology and estimated assignments for the Santa Clara River only, including *C. fumeiventris* sampled from Mammoth Creek, Mono County, CA [Colour figure can be viewed at wileyonlinelibrary.com]

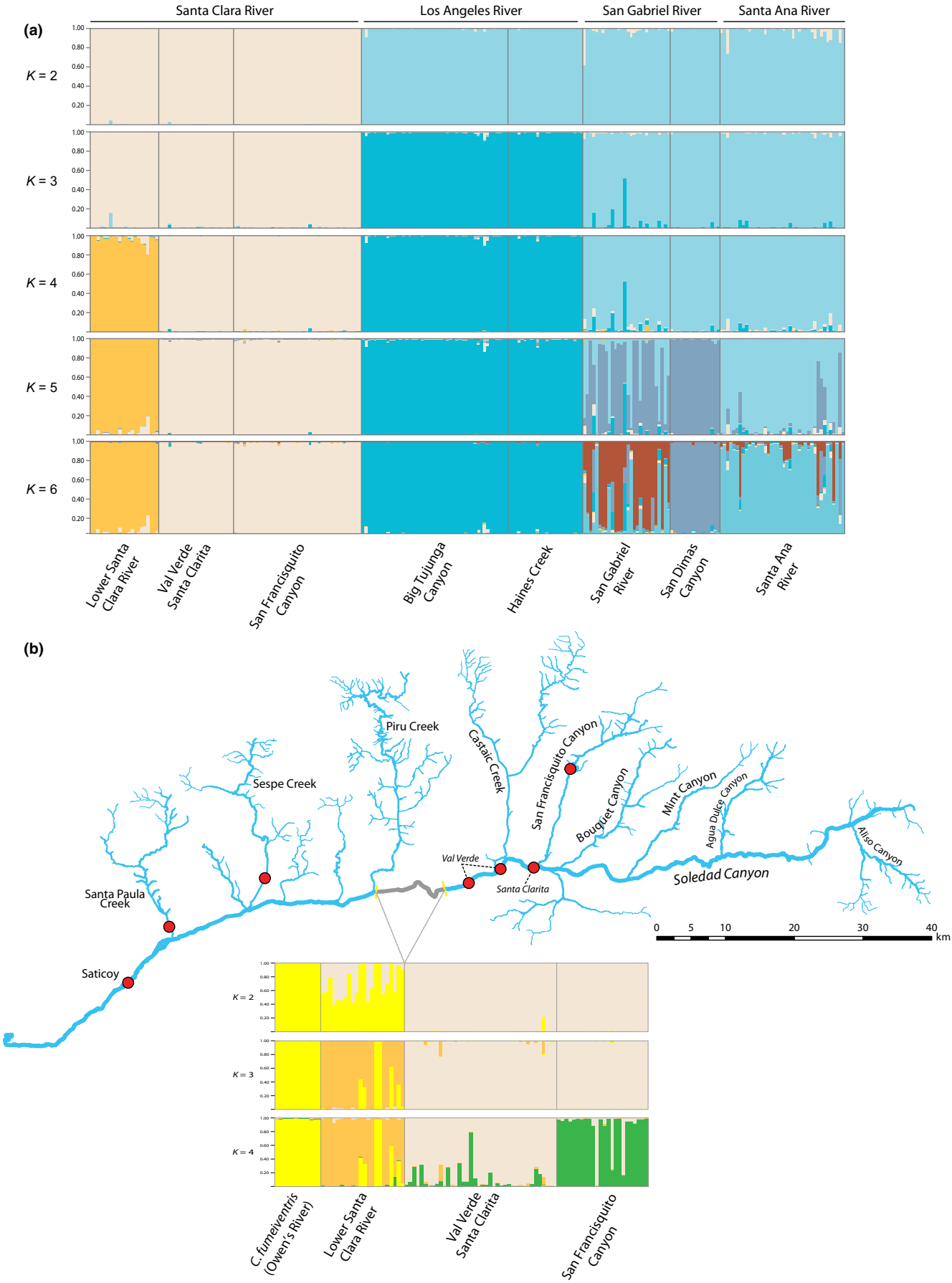

(a)
Santa Clara River
Los Angeles River
San Gabriel River
Santa Ana River
K = 2
K = 3
K = 4
K = 5
K = 6
Lower Santa Clara River
Val Verde Santa Clarita
San Francisquito Canyon
Big Tujunga Canyon
Haines Creek
San Gabriel River
San Dimas Canyon
Santa Ana River
(b)
Piru Creek
Castaic Creek
San Francisquito Canyon
Bouquet Canyon
Mint Canyon
Agua Dulce Canyon
Aliso Canyon
Sespe Creek
Val Verde
Santa Clarita
Soledad Canyon
Santa Paula Creek
Saticoy
0 5 10 20 30 40
km
K = 2
K = 3
K = 4
C. fumeiventris (Owen's River)
Lower Santa Clara River
Val Verde Santa Clarita
San Francisquito Canyon

TABLE 2 Results of heterozygosity excess tests by sampling location

Site	H_{def}	H_{exe}	l_{mono}	0.00	0.05	0.10	0.20	0.30	0.40
LSCR	3	11	1	**0.002/0.008**	**0.003/0.010**	**0.007/0.010**	**0.010/0.010**	**0.010/0.010**	**0.014/0.021**
SNF	2	11	2	**0.002/0.003**	**0.002/0.003**	**0.002/0.002**	**0.002/0.003**	**0.003/0.003**	**0.003/0.003**
VVSC	7	8	0	0.165/0.227	0.180/0.244	0.165/0.227	0.244/0.262	0.262/0.262	0.262/0.262
BTC	4	11	0	**0.042**/0.076	**0.042**/0.084	0.054/0.076	0.060/0.084	0.094/0.115	0.115/0.244
HCK	2	13	0	**0.000/0.001**	**0.001/0.001**	**0.001/0.001**	**0.001/0.001**	**0.001/0.001**	**0.002/0.006**
SGR	5	10	0	**0.037**/0.060	**0.042**/0.054	0.054/0.084	0.054/0.094	0.076/0.110	0.115/0.180
SDC	1	13	1	**0.000/0.000**	**0.000/0.000**	**0.000/0.000**	**0.000/0.000**	**0.000/0.000**	**0.000/0.000**
SAR	2	13	0	**0.004/0.009**	**0.005/0.013**	**0.006/0.013**	**0.013/0.015**	**0.015/0.018**	**0.018/0.028**

We report the number of loci showing heterozygosity deficiency H_{def}, heterozygosity excess H_{exe} and the number of monomorphic loci l_{mono}. Remaining columns represent the proportions of strict one-step mutations p_g assumed for different mutation models—numbers are the *p*-values for Wilcoxon tests (one tail for H_{exe}; bold values indicate significant results) for models that differed in the variance in the mean size of multistep repeats δ_g (30 vs. 15, denoted as a backslash). Site codes: LSCR, lower Santa Clara River; SNF, San Francisquito Canyon (upper Santa Clara River); VVSC, Val Verde-Santa Clarita (upper Santa Clara River); BTC, Big Tujunga Canyon (Los Angeles River); HCK, Haines Creek (Los Angeles River); SGR, San Gabriel River; SDC, San Dimas Canyon; SAR, Santa Ana River.

the logistic regression method could distinguish among the three scenarios with high confidence, with scenario 2 having a posterior probability of 0.8206 [$Q_{0.025,\ 0.975}$ = 0.8089, 8322] (Figure 4c). Type I error rates were 0.31 and 0.27 for direct and logistic approaches, respectively, and type II error rates were 0.31 and 0.22, indicating moderate confidence in favour of scenario 2 as the best-fit to the real data.

Using scenario 2 from the preceding analysis as a baseline for the ancestry of Santa Clara River samples, we found support for a splitting event from the Los Angeles River ~40–50 generations prior to sampling followed by a short-term, severe bottleneck (Figure 2d). Again, only the logistic regression method could distinguish between the two top-ranked models (Figure 4d). Type I and II error rates for these analyses were 0.47 and 0.18 (direct/logistic regression) and 0.42 and 0.19, showing even greater disparity between the two methods in assessing confidence for the best-fit scenario. Nonetheless, the relatively low error rate inferred using the regression approach combined with a posterior probability of 0.7780 [$Q_{0.025,\ 0.975}$ = 0.7591–0.7968] for scenario 1 lends support to the prevailing hypothesis that *C. santaanae* was imported into the Santa Clara River as recently as 80–100 years ago.

4 | DISCUSSION

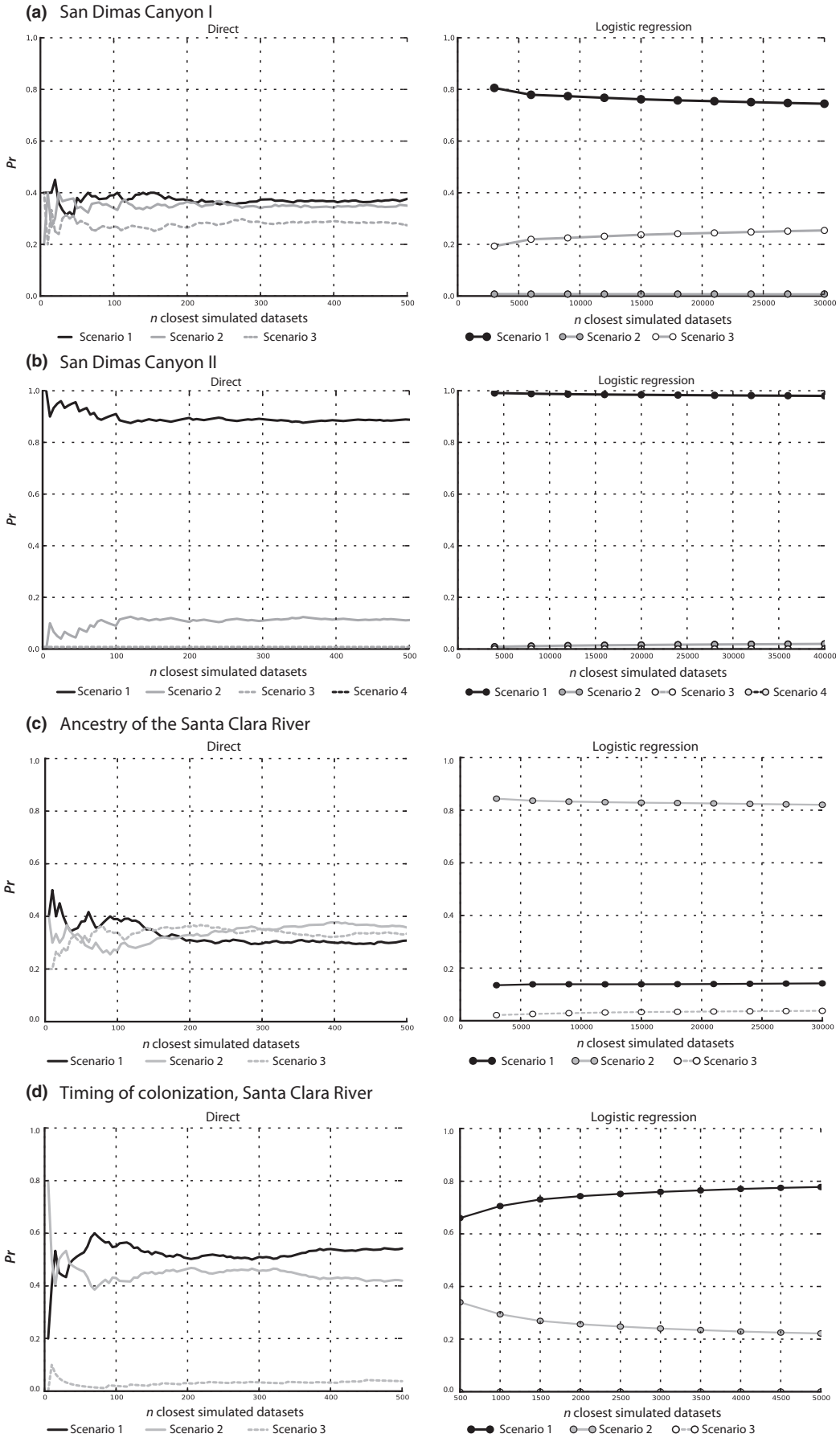
To date, most research investigating the dynamics of dendritic population networks has involved theoretical and simulation studies, with only a few empirical studies beginning to shed light on their predictions. Of the few empirical studies involving genetics, two happen to include different sucker species occupying intact dendritic systems within minimal anthropogenic influence, providing good null references for those systems under natural conditions (Pilger, Gido, Propst, Whitney, & Turner, 2017; Salisbury, McCracken, Keefe, Perry, & Ruzzante, 2016). This study approaches the subject from the opposite extreme—a highly imperilled species, *C. santaanae*, struggling to survive in small, remnant patches of a former dendritic network within a major metropolitan area.

4.1 | Nonequilibrium processes drive divergence

The association between flood–drought cycles, boom-bust demography and a variety of current landscape factors led us to hypothesize that at least some local bottlenecks would be detectable in a range-wide sample of *C. santaanae*. Our results not only support this hypothesis, but also demonstrate that bottlenecking is more the norm for contemporary populations of *C. santaanae* than the exception (Table 2). The widespread nature of the phenomenon is cause for concern given the degree to which regional and within-drainage network connectivity is disintegrated, eliminating the capacity for migrant exchange to counterbalance the nonequilibrium effects of cyclical bottlenecks (Fagan et al., 2002; Jangjoo et al., 2016; Salisbury et al., 2016; Shama et al., 2011).

Although "natural" environmental fluctuation continues to promote local fluctuation in N_e, drift-related effects of founder events provide another example of how rapid allele loss has accelerated population divergence in this system. Although we find support for a recent introduction, the San Dimas Canyon population already displays some clustering exclusivity (K = 5–6; Figure 3), and F_{st} values indicate less similarity to its San Gabriel River source than the source does to Santa Ana River populations (Table S8). Spatial structure in this part of the range therefore appears to be modulated by two drift-related factors – a founder event in San Dimas Canyon has caused rapid divergence after translocation from the upper San Gabriel River, while at the same time, greater retention of shared

FIGURE 4 Results for the direct and logistic regression approaches to estimating the posterior probability of the different scenarios for each set of *DIYABC* analyses (a–d). The *x*-axis represents the number of simulated data sets closest to the observed data, and the *y*-axis denotes the median posterior probability for a given scenario


(a) San Dimas Canyon I
Direct
Logistic regression
Pr
n closest simulated datasets
Scenario 1
Scenario 2
Scenario 3
(b) San Dimas Canyon II
Direct
Logistic regression
Pr
n closest simulated datasets
Scenario 1
Scenario 2
Scenario 3
Scenario 4
(c) Ancestry of the Santa Clara River
Direct
Logistic regression
Pr
n closest simulated datasets
Scenario 1
Scenario 2
Scenario 3
(d) Timing of colonization, Santa Clara River
Direct
Logistic regression
Pr
n closest simulated datasets
Scenario 1
Scenario 2
Scenario 3

alleles, higher diversity at more polymorphic loci and large N_e (results not shown) in the San Gabriel and Santa Ana River have acted to preserve signals of historic gene exchange.

The widespread nature of remaining bottleneck examples points to interfacing contemporary and historical factors as drivers of population decline in *C. santaanae*, including prolonged droughts punctuated by major floods (Dettinger, 2011, 2013), changes in stream morphology and connectivity over the past century (Thompson et al., 2010; USFWS 2017), and in recent decades, increased incidence of catastrophic fires and associated debris flows (Moody, Shakesby, Robichaud, Cannon, & Martion, 2013; Steel, Safford, & Viers, 2015; Syphard et al., 2007; Westerling et al., 2006). Wholesale species decline may be progressing through a ratcheting effect (Birkeland, 2004), as reduced capacity to offset the genetic effects of bottleneck cycles is further compromised by the increasing severity of the environmental factors that create them, many of which are predicted to worsen with climate change (Dettinger, 2011; Seager et al., 2007; Westerling et al., 2006). This self-reinforcing process could be adding to an already considerable extinction debt in *C. santaanae*, as reciprocal mechanisms once present in the historic network (e.g., migrant exchange enabled by stream capture and within-drainage connectivity) are no longer sufficient to promote local recovery (Fagan et al., 2002).

At least one reciprocal mechanism for counterbalancing nonequilibrium processes is seemingly intact for Santa Clara River populations, where stream architecture and position within the drainage acts to concentrate genetic variation in certain parts of the network. For example, the only samples showing no signal of recent bottlenecking were from the Santa Clarita-Val Verde reach, a coalescence point for the entire upper Santa Clara River watershed (Figure 3). This node has numerous braids and side channels that slow flow and provide refugia, and lack of consistent surface water across the Piru Gap impedes downstream dispersal beyond this reach. These physical features may promote migration–drift equilibrium and contribute to the local accumulation of genetic variation, a finding consistent with the predictions of dendritic systems in simulation studies (Grant et al., 2007; Morrissey & de Kerckhove, 2009; Thomaz et al., 2016). Co-occurring threespine stickleback *Gasterosteus aculeatus* show the same pattern of elevated diversity in this reach compared to upstream areas (Richmond et al., 2014), providing further evidence that network location influences spatial genetic variation in this drainage. Namely, the most downstream populations do not have the highest genetic diversity, as is generally expected based on flow directionality.

4.2 | Two-tiered disintegration of network structure in *C. santaanae*

Our results also reveal genetic structuring in *C. santaanae* at multiple spatial scales, occurring in both the "trunks" of the regional network (i.e., channelized parts of the Los Angeles Basin) and towards the interior branches (upper main stem or tributary reaches within watersheds). This is a common artefact of dendritic networks, where connectivity patterns and asymmetric dispersal rates have predictable consequences for the distribution of genetic variation at hierarchical levels (Hughes, Schmidt, & Finn, 2009; Morrissey & de Kerckhove, 2009; Thomaz et al., 2016).

At the highest level, among-watershed isolation has led to considerable divergence for Santa Clara and Los Angeles River populations, which were distinctive at the lowest clustering partitions (K = 2–3; Figure 3). In contrast, San Gabriel and Santa Ana River populations were highly admixed and distinguishable only at higher partitions (K = 5–6; Figure 3), consistent with these drainages being the last to undergo channelization in the lower floodplain. Historically, Santa Ana River floodwaters flowed westward out of Santa Ana Canyon and into the San Gabriel River via Coyote Creek, one of the San Gabriel's main tributaries (Fehrenbach, 2000; Figure 1). Gene flow via this route could have occurred as recently as the late 1930s following floods that transformed nearly all of northern Orange County into a large lake (Orsi, 2004). Persistence of larger N_e over time and/or less severe cyclical bottlenecking may have further influenced the preservation of shared ancestral polymorphism between these drainages (Weckworth et al., 2013). Stream capture between the lower San Gabriel and Los Angeles Rivers is also known to have occurred throughout the early 19th century (Gumprecht, 2000; Stein et al., 2007); however, admixture proportions of contemporary samples leave very little indication of past population interchange ($K \geq 3$; Figure 3).

The exclusivity of Los Angeles River populations is accentuated by their position in distal stream branches and longer-term isolation above channelized reaches, where genetic differences are predicted to be higher due to increased distance in the stream network (Hughes et al., 2009; Hutchinson & Templeton, 1999; Thomaz et al., 2016). In the pre-urban riverscape, gene exchange between watersheds would have been concentrated in the Los Angeles Basin (Grant, 2011; Hughes et al., 2009), precisely where the river courses are now channelized (Figure 1). Thus, flood control barriers are not only preventing new sources of genetic diversity from entering separate watersheds, but ensuring that the most differentiated allele pools within *C. santaanae* and presumably other native fish species remain isolated (e.g., *G. orcutti*; Benjamin et al., 2016). A similar process has been shown for Sonoran Desert fishes, where human habitat alteration has restricted opportunities for population admixture during periods of high flow, which in turn has permanently disrupted source–sink dynamics (Fagan et al., 2002).

We also found evidence of longitudinal structuring within drainages (Figure 3; see also Table S7), although most of the information again comes from the Santa Clara River due to population dispersion and a strong effect of the Piru Gap on partitioning genetic variation. A consensus exists that the gap has never been closed by perennial water because of the deep bedrock and increased channel width in this reach, where surface water abruptly sinks and spreads (Beller et al., 2011; Mann, 1959; Stillwater Sciences 2011); however, saturation during major floods occasionally promotes dispersal across the barrier. Similar genetic divisions have been documented in sympatric *G. aculeatus* (Richmond et al., 2014) and in the spring snail *Pyrgulopsis castaicensis* (Hershler & Liu, 2010), highlighting the gap's role as an ecotone in influencing spatiotemporal dynamics in this watershed

(see Erös & Grant, 2015). Because the Santa Clara River is the only drainage now occupied by *C. santaanae* with preserved flow regimes over most of its course, we suspect that the longitudinal patterning in this system is generally representative of historic, within-drainage conditions for *C. santaanae*.

4.3 | Does location within the stream network constrain the effects of hybridization?

Catostomids are notorious for hybridization despite deep divergence between the species involved (Bangs, 2016; McDonald et al., 2008; Smith, Stewart, & Carpenter, 2013; Unmack et al., 2014), and those studied here are no exception (Figure S3). Even though hybrids and non-native *C. fumeiventris* are restricted to stream reaches west of the Piru Gap, the predominant genotypes and mtDNA haplotypes belong to *C. santaanae*. These findings parallel those of previous allozyme and morphological studies (Buth & Crabtree, 1982; Buth et al., 2008; Miller, 1968; Swift et al., 1993). While specifics about the introduction of *C. fumeiventris* are lacking, it is known that they entered the Santa Clara River via the Los Angeles Aqueduct, which now connects through San Francisquito Canyon (Figure 1). Thus, a conundrum has always existed as to why hybrids and/or *C. fumeiventris* have never been detected upstream of the Piru Gap, particularly because of the gap's ability to retain fish in the upper watershed.

One explanation is the St. Francis Dam break of 1928, where 47 + billion litres of water exited the dam via San Francisquito Canyon in approximately 70 minutes (Begnudelli & Sanders, 2007). This event had permanent scouring effects on drainage hydrology (Stillwater Sciences 2011) and may have purged most aquatic vertebrates from San Francisquito Canyon down through the Piru Gap (Figure 1). Below the gap, fish were more likely to remain in the system as the water spread over the floodplain and into lower tributaries. Sucker persisting upstream of San Francisquito Canyon (e.g., Soledad Canyon) would have been left to recolonize extirpated areas. At least one other aquatic species, the California red-legged frog *Rana draytonii*, shows evidence of a founder event in San Francisquito Canyon that coincides with the timing of the St. Francis Dam break (Richmond, Barr, Backlin, Vandergast, & Fisher, 2013), suggesting that this event was a key influence on the historical demography of some of the Santa Clara River watershed's most imperilled taxa.

The repeated finding that hybrids and pure *C. fumeiventris* are restricted to the lower watershed suggests that the probability of non-native genetic variation ever diffusing into the upper watershed is low. This emphasizes the Piru Gap's dual role in governing temporal gene mixing in the downstream direction while preventing upstream spread of non-native alleles. The continued predominance of alleles belonging to *C. santaanae* and limited hybrid backcrossing (see also Buth & Crabtree, 1982; Buth et al., 2008) also suggests that natural selection and or postzygotic genetic incompatibilities may be further constraining the extent of hybridization and introgression. This limited introgressive influence of *C. fumeiventris* is not surprising given its ancient divergence from a common ancestor with *C. santaanae*, but more work is needed to precisely measure introgression given that relatively few of the same markers amplified for both species. This is especially true if Santa Clara River populations are ever needed to safeguard the species from extinction, which seems increasingly more likely if functional habitat cannot be restored in the Los Angeles Basin.

4.4 | Origins, timing and validity of suspected introductions

Populations established through artificial transplantation may be of less conservation concern than those forming the natural distribution, unless they were intentionally established as a resource subsidy for management. In the two putative cases of artificial transplantation of *C. santaanae*, only the San Dimas Canyon population fits the genetic profile of a recent introduction with strong support. This inference is further supported by the absence of any historical records for *C. santaanae* in the canyon and low suitability of the habitat where the fish were discovered.

In contrast, the non-native status of Santa Clara River populations is more equivocal. On the one hand, cluster assignments revealed no admixture that identifies a definitive source among the Los Angeles Basin drainages, and where Santa Clara River populations form a distinctive unit that is no less differentiated from native populations in the Los Angeles Basin than those populations are to each other (with the exception of the San Gabriel/Santa Ana River populations). Exclusive clustering of Santa Clara River populations also makes biogeographic sense under a natural dispersal scenario because it is the only drainage occupied by *C. santaanae* that does not flow into the Los Angeles Basin, where ephemeral river capture would have created opportunities for gene flow to homogenize variation across watersheds.

On the other hand, a nested set of historical demographic simulations offered support for a scenario in which the Santa Clara and Los Angeles River assemblages diverged ~80–100 years ago following a short-term bottleneck, consistent with the prevailing theory that the former was artificially imported. However, confidence measures based on type I and type II error rates showed some but not overwhelming confidence in favour of the preferred scenarios (Figure 4c,d; although Cornuet et al. (2008) notes that clear-cut differences in model fit are required for the direct method to generate low error rates in differentiating alternative scenarios).

An important caveat of these analyses is that continuous, temporal fluctuation in N_e, underscored by consistent population declines since the mid-20th century (USFWS 2017), are difficult parameters to model and estimate with precision. A second caveat is that random allele sorting in the absence of gene flow has led to a high probability that the alleles within drainages occupied by *C. santaanae* are identical by decent, diminishing phylogenetic signal and reducing imprints of genetic isolation by distance (Hutchinson & Templeton, 1999; Slatkin 1993). Other sucker species show evidence of this same process, where low N_e shapes population structure irrespective of landscape features (Pilger et al., 2017; Salisbury et al., 2016). It probably also explains the high exclusivity among populations of *G. orcutti* that co-

occur with *C. santaanae* (Benjamin et al., 2016), suggesting that collapse of the same river network is simultaneously raising the extinction debt of southern California's few remaining endemic fish species.

4.5 | The fate of species with conflicting historical vs. contemporary evolutionary ecologies

Efforts to expand and restore habitat in parts of the range of *C. santaanae*, as well as re-introduce fish from captive-bred colonies, are currently underway for the Santa Ana River. It is possible that restoration of spatially repeating but indirectly (or ephemerally) linked branches could introduce spatial heterogeneity in gene diversity that mimics historical network processes. If branches can be repatriated using appropriate numbers of fish with local genetic backgrounds, prescribed gene flow using a limited number of immigrants from nonlocal sources could then be used to facilitate introgression without overriding any locally adaptive variation (Mills & Allendorf, 1996; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015). Ideally, small dosages of new, nonlocal alleles could supply additional genetic variation for selection to act upon while lowering the frequency of deleterious alleles (Tallmon, Luikart, & Waples, 2004; Whiteley et al., 2015), and better mimic gene flow during a time when the different river courses naturally meandered in the Los Angeles Basin. Because the immigrants could be sourced from other *C. santaanae* populations, the likelihood of outbreeding depression is expected to be very low given that gene exchange has occurred within the past 500 years (Frankham et al., 2011) and recipient and donor environments could be easily matched between watersheds.

For *C. santaanae* and other co-occurring native fishes in southern California, recovery planning could benefit from theoretical work characterizing the relationship between network configuration and population interactions, evolutionary dynamics, extirpation risk and response to flood–drought cycles in the preconverted landscape. Information about how these species have responded to the disintegration of such networks (this study) combined with data on how they likely functioned in historically configured conditions could help frame recovery goals in a manner consistent the species' evolutionary ecologies and in turn could improve the outcomes for success.

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DATA ACCESSIBILITY

The data sets are publicly available through the ScienceBase digital repository supported by the U.S. Geological survey (https://doi.org/10.5066/f7z31xmz). GenBank Accession numbers for mtDNA sequences are MF918422 – MF918481. Specimens are accessioned at the Los Angeles County Museum of Natural History (LACMNH 58475-58481), and DNA samples are in archival frozen storage at the U. S. Geological Survey's San Diego Field Station.

AUTHOR CONTRIBUTIONS

JQR designed the study, conducted field sampling, collected and analyzed the data, and wrote the paper. ARB managed permits, conducted field sampling, and contributed to the text. CG-C provided logistical support with USFWS, conducted field sampling, and commented on the manuscript. JWO provided logistical support with CADFW, conducted field sampling, and commented on the manuscript. RNF helped procure funding and contributed to the text.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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