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Recent declines in genetic diversity with limited dispersal among coastal cactus wren populations in San Diego County, California

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Abstract

Habitat loss and fragmentation can lead to smaller and more isolated populations and reduce genetic diversity and evolutionary potential. Conservation programs can benefit from including monitoring of genetic factors in fragmented populations to help inform restoration and management. We assessed genetic diversity and structure among four major populations of the Cactus Wren (*Campylorhynchus brunneicapillus*) in San Diego County in 2011–2012 and again in 2017–2019, using 22 microsatellite loci. We found a significant decline in heterozygosity in one population (San Pasqual) and a decline in allelic richness and effective population size in another (Sweetwater). Genetic diversity in the remaining two populations was not significantly different over time. Local diversity declined despite evidence of dispersal among some populations. Approximately 12% of genetically determined family groups (parents, offspring, siblings) included one or more members sampled in different territories with distances ranging from 0.2 to 10 km. All but one inferred dispersal events occurred within the same genetic population. Population structure remained relatively stable, although genetic differentiation tended to increase in the later sampling period. Simulations suggest that at currently estimated effective sizes, populations of Cactus Wrens will continue to lose genetic diversity for many generations, even if gene flow among them is enhanced. However, the rate of loss of heterozygosity could be reduced with increased gene flow. Habitat restoration may help bolster local population sizes and allelic richness over the long term, whereas translocation efforts from source populations outside of San Diego may be needed to restore genetic diversity in the short term.

KEYWORDS

allelic richness, *Campylorhynchus brunneicapillus*, forward-time simulations, genetic monitoring, heterozygosity, microsatellite loci

1 | INTRODUCTION

Habitat loss and fragmentation are some of the main drivers of decline in population and loss of biodiversity globally (Foley et al., 2005; Gonçalves-Souza et al., 2020; Haddad & Baum, 1999). Efforts to protect remaining small populations of threatened species often rely on consistent monitoring efforts to address basic information needs—where individuals are found (distribution); how many are present (abundance); are they able to survive and reproduce (population dynamics and vital rates); what factors or threats promote or, conversely, impede population growth and persistence (habitat and threat associations); and the effects of management actions on these factors (Stem et al., 2005; Yoccoz et al., 2001). Although monitoring programs often apply field research techniques to gather appropriate data and detect trends over time (Elzinga et al., 2009), repeated genetic sampling also can provide important information to support monitoring metrics and objectives (Noss, 1990; Schwartz et al., 2007; Vandergast, 2017). Genetic monitoring tracks changes in the amount and distribution of genetic diversity across populations over time, specifically to quantify gene flow, breeding population size and genetic diversity, and evaluate the effects of ongoing management against baseline standards.

Genetic diversity provides the raw material for selection and diversification and is tied to population size and connectivity, and, thus, to persistence and adaptive potential (Hoffmann et al., 2017; Kardos et al., 2021). Genetic diversity will decline in populations subject to reductions in size and increased isolation through genetic drift, increased inbreeding, and reduced gene flow (Schlaepfer et al., 2018; Wright, 1931). These genetic changes can occur rapidly in low vagility species with small populations and can contribute to extinction risks (Bozzuto et al., 2019; Gilpin & Soulé, 1986; Saccheri et al., 1998; Spielman et al., 2004). Genetic sampling can help identify populations with low or declining genetic diversity for management and enhancement. Collecting genetic data at a single time point can create a "snapshot" of population genetic structure and diversity, which can act as a baseline for comparing future surveys against. Neutral genetic markers with high rates of mutation and diversity provide an efficient means of estimating important parameters including gene flow, breeding population size, allelic richness, and heterozygosity, and can detect changes over several generations, particularly in rapidly changing environments (Hoban et al., 2014; Vandergast et al., 2016, 2019). These parameters are important for evaluating the health and connectedness of populations in managed landscapes.

The southern California coastal populations of the nonmigratory songbird, the Cactus Wren (*Campylorhynchus brunneicapillus*), exemplify the issues facing habitat specialists in small, fragmented populations. The Cactus Wren range extends from central Mexico into the American southwest. Although not cactus-obligate range-wide (Hamilton et al., 2011), in southern California, individuals nest exclusively in prickly pear (*Opuntia* sp.) and cholla (*Cylindropuntia* sp.) cacti. These cacti are most common in coastal sage scrub, and Cactus Wren populations have declined in recent decades with the loss of this habitat (Unitt, 2008), leaving the few remaining populations fragmented and numbering in the low 10s of individuals (Lynn et al., 2022; Lynn & Kus, 2021). Dispersal is also limited relative to other songbirds, with dispersing fledglings observed to move an average 0.66–1.59 km, and maximum 5–10 km (Atwood et al., 1998; Preston & Kamada, 2012). Wildfire and drought further threaten remaining populations (Bontrager et al., 1995; Preston & Kamada, 2012), particularly because cactus patches damaged or destroyed by fire or drought can take years or decades to recover to sizes needed for nesting habitat. Cactus Wren nest productivity has also been linked to precipitation, with low productivity during drought periods (Kamada, 2008; Preston & Kamada, 2009).

Given these characteristics and threats, the Cactus Wren is recognized as a focal species in efforts to conserve remaining coastal sage scrub habitat in southern California (Pollak, 2001; Unitt, 2008), and listed and managed in several regional multispecies conservation plans, including the Management and Monitoring Strategic Plan of San Diego County (MSP; SDMMP & TNC, 2017). As part of monitoring efforts, Cactus Wren populations from Ventura County south through San Diego County were sampled and genetically characterized using microsatellite loci starting in 2011 (Barr et al., 2015). This initial study found that genetic differentiation among remaining populations increased with increasing habitat fragmentation and distance between remaining habitat fragments, suggesting habitat availability limited connectivity. Within populations, allelic richness was positively associated with the amount of suitable habitat, and genetic bottlenecks were documented in areas that had experienced more frequent wildfires. These results indicated that habitat fragmentation and disturbance reduced genetic connectivity and diversity of Cactus Wren populations in coastal southern California. These trends may continue, particularly as climate change is anticipated to lead to warmer temperatures, more frequent and intense drought, and increased wildfire risk throughout the region (Berg & Hall, 2015; Cayan et al., 2010; Kam & Sheffield, 2016; Swain, 2015). Incorporating genetic results into active management and monitoring plans, the San Diego MSP called for habitat restoration within and among existing aggregations of

Cactus Wrens to enhance populations, annual surveys, detailed demographic studies, and repeated genetic sampling to establish trends in genetic diversity and connectivity throughout the San Diego Management and Monitoring Strategic Plan Area (MSPA; SDMMP & TNC, 2017).

Here, we examined trends in genetic diversity and differentiation over time in coastal Cactus Wren aggregations on conserved lands within the San Diego MSPA. Our goals were to estimate genetic differentiation, diversity, and effective population size, and to test for changes in these metrics over ~2–3 generations. We hypothesized that documented declines in abundance and loss of habitat would result in declines in genetic diversity and increase genetic differentiation among populations. In addition to population genetic metrics, we comprehensively sampled family groups from field-monitored nests and developed a genetic pedigree to better understand recent movement among sites. Finally, we used forward-time simulations to generally investigate whether increasing gene flow through translocation could improve retention of genetic diversity in this system of populations over time. Results can be used to inform ongoing management strategies of the San Diego MSP aimed at improving habitat and protecting remaining populations.

2 | METHODS

2.1 | Study sites and genetic sample collection

In initial genetic surveys in San Diego County, aggregations of birds sampled on lands within the MSPA were found to comprise four geographic-genetic populations: San Pasqual, Lake Jennings, Sweetwater, and Otay (Barr et al., 2015; Figure 1). Ongoing monitoring of these populations was initiated soon thereafter, including additional genetic monitoring reported here and nest productivity and dispersal monitoring in three of the four populations (Lake Jennings, Sweetwater and Otay, Lynn et al., 2022; Lynn & Kus, 2021). In each population we collected blood or pin feathers from adults and fledglings using mist nets and song playbacks to attract birds to nets, as well as from nestlings in accessible nests between 2011–2012 (hereafter 2011 sample period) and between 2017–2019 (hereafter 2017 sample period). Sample collection activities were authorized under California Department of Fish and Wildlife Scientific Collection permit S-190290006-20062-001 to BEK. All samples were stored in lysis buffer and frozen at −80°C prior to extraction.

Feather and tissue samples from both sample periods were extracted and genotyped at the same time using the same extraction and amplification protocols. We isolated DNA from feathers and blood samples using the Gentra Puregene Tissue Kit (Qiagen) according to manufacturer's instructions with some modifications. Briefly, pin feathers (cut into quarters or eighths) or blood in storage buffer were incubated at 56°C overnight on a rotator in 250 µl Cell Lysis Buffer, 2 µl Proteinase K (20 mg/ml) and 10 µl dithiothreitol (1 M). We added 125 µl protein precipitation solution, vortexed and incubated the samples at −20°C for 30 min and centrifuged at 4°C and 21,000×*g* for 20 min. We transferred the supernatant containing the DNA to a clean 1.7 ml tube, to which we added 3X volume of 100% ethanol and 1 µl GlycoBlue (Thermo Fisher Scientific). To facilitate DNA precipitation, samples were rotated for 10 min at room temperature and then stored overnight at −20°C. Samples were centrifuged at 21,000×*g* for 15 min at 4°C, discarding the supernatant, and the pellet washed in 750 µl of 70% ethanol. Lastly, we rehydrated the DNA pellet in 25–100 µl of 1X TE and quantified using a Qubit fluorometer (Thermo Fisher Scientific).

2.2 | Genotyping

We amplified 22 polymorphic loci described in Barr et al. (2015) in two multiplexed polymerase chain reactions (PCR; Table S1). Loci were amplified using the Type-it Microsatellite PCR kit (Qiagen) in reactions consisting of 5 µl Master Mix, 1 µl Primer Mix, 2 µl water, and 2 µl genomic DNA per reaction. Thermocycler conditions were 95°C for a 5-min hot-start activation, followed by 28 cycles of: 30-s 95°C denaturation, 3-min 56°C annealing, and 30-s 72°C extension, with a final 30-min extension at 68°C. PCR product (1.5 µl) was then added to 10 µl HiDi (Thermo Fisher) and 0.5 µl Liz (Thermo Fisher) and sent to Eton Biosciences (San Diego, CA) for genotyping. Roughly 10% of samples were amplified and genotyped twice to ensure consistency. Genotypes were scored using Genemarker v.3.0.1 (SoftGenetics) and processed in R v.3.5 (R Core Team) with the package MsatAllele v.1.05 (Alberto, 2009).

2.3 | Genetic data and population analysis

Data were checked for duplicates using the strataG package v.2.4.905 (Archer, 2014) in R and for null alleles in MICRO-CHECKER (Van Oosterhout et al., 2004). The field sampling schemes differed between 2011 and 2017 sample periods, with only one nestling sampled per nest along with some mistnetted adults in 2011 and full

sampling of all nestlings in nests and some adults in territories in 2017. Therefore, to make specific comparisons of genetic structure and diversity metrics between 2011 and 2017 (detailed in the section below), we reduced the 2017 dataset to include one randomly selected individual per family group. We also analyzed the full 2017 dataset including all members of family groups to investigate dispersal of close relatives. We used COLONY v2.0.6.6 (Wang, 2014) to identify first order relatives (full-sibling groups) in the 2011 and the full 2017 sample sets

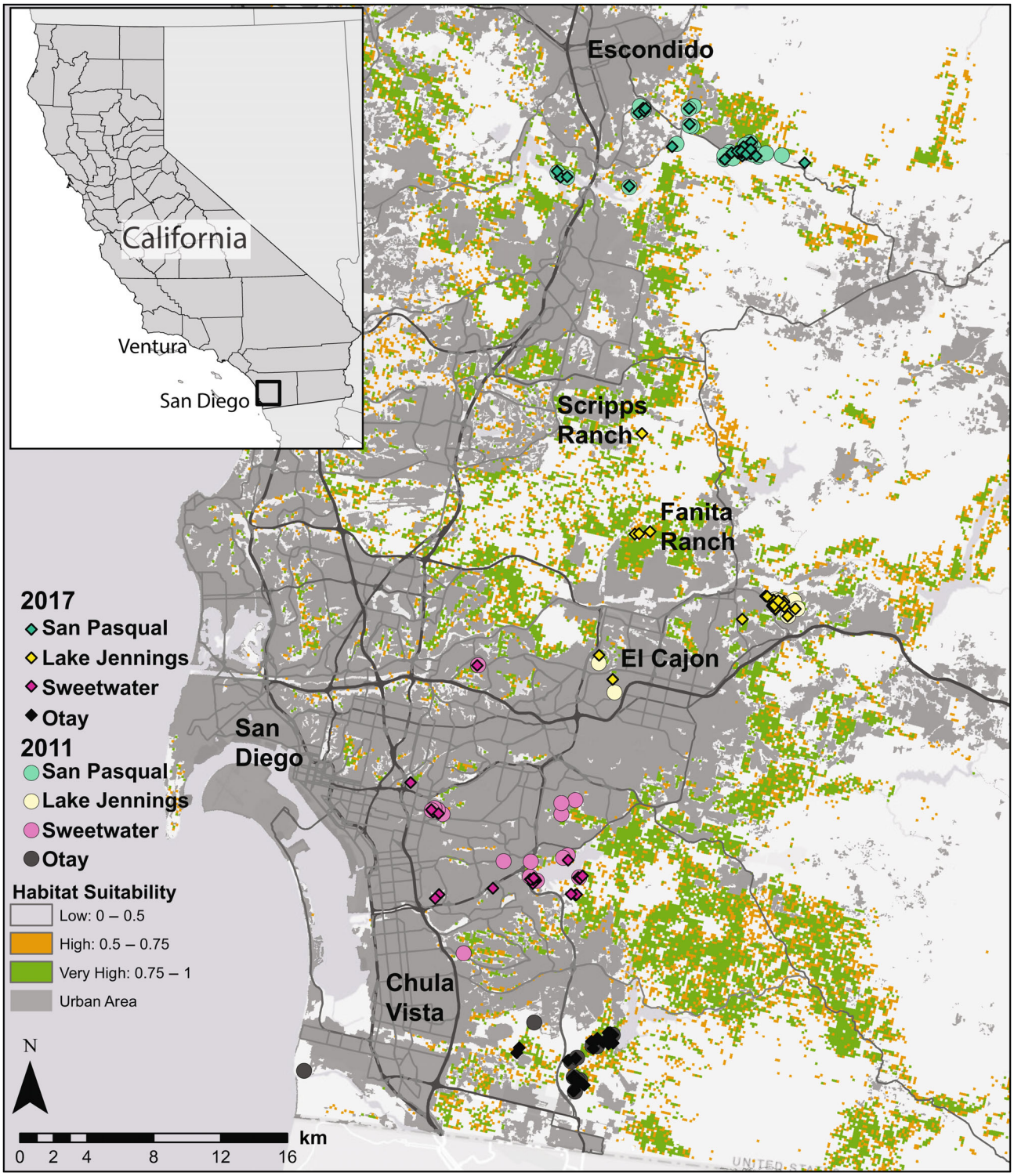

FIGURE 1 Map of study area in San Diego County with individual Cactus Wren sampling locations colored by genetic population. The habitat suitability map layer and habitat categories were derived from the species distribution model described in Preston et al. (2020)

respectively. All individuals were input as offspring assuming polygamy and inbreeding and runs were repeated six times to check for consistency. When full-sibling groups had a probability of ≥0.9 across at least four of six runs, all but one individual from each group were removed from the final population genetic datasets. In the full 2017 dataset, we noted when full sibling groups included individuals sampled in different territories. These were considered inferred recent dispersal events and Euclidean distances among territories were calculated in ArcGIS 10.4.1 (ESRI).

Linkage disequilibrium (LD) was evaluated in GENEPOP (Raymond & Rousset, 1995; Rousset, 2008) and genetic diversity statistics including expected and observed heterozygosity (H_e and H_o respectively), Hardy Weinberg equilibrium (HWE), and genetic differentiation (F_{ST}) were calculated in the strataG package in R (Archer, 2014). Individual inbreeding coefficients (F_i) were calculated in SPAGeDi 1.5 (Hardy & Vekemans, 2002), with significance (F_i<>0) assessed with 10,000 randomizations of gene copies among individuals. Values close to zero are expected under random mating, while substantial positive values can indicate inbreeding or undetected null alleles. Negative values indicate an excess of heterozygosity. Allelic richness (A_r) was corrected by sample size in HP-RARE using a rarefaction curve (Kalinowski, 2005), and effective population size (N_e) was calculated in NeEstimator v2.1 (Do et al., 2014) using the LD method and a minimum allele frequency of 0.05. Within each population, we tested for significant differences in H_e, H_o, and A_r between the 2011 and the 2017 datasets using paired *t*-tests across loci in R. Pairwise F_{ST} among populations and individual-based genetic distances $\hat{a}$ (Rousset, 2000) were calculated between pairs of individuals within the 2011 and 2017 datasets respectively, and regressed against pairwise geographic distances in SPAGeDi 1.5 (Hardy & Vekemans, 2002). Results were graphed to visualize whether population or individual genetic distances had increased between the two sampling periods and significance of slopes were assessed with 10,000 permutations of the genetic matrix.

The number of genetic clusters and individual assignments were examined within each dataset (2011 and 2017) separately using Bayesian clustering in STRUCTURE v.2.3.4 (Pritchard et al., 2000) and discriminant analysis of principal components (DAPC) in adegenet v.2.1.3 (Jombart et al., 2010). In STRUCTURE we performed 500,000 Markov chain Monte Carlo (MCMC) iterations and a 500,000 burn-in for $k = 1$–6 putative populations with 10 replications per population (k), all run both with and without the location prior (LOCPRIOR). Results were evaluated using STRUCTURE Harvester (Earl, 2012) by inspecting both mean LnP(D|K) and delta k (Evanno et al., 2005). Graphic representations of runs were compiled using CLUMPAK (Kopelman et al., 2015) and STRUCTURE PLOT (Ramasamy et al., 2014). For DAPC we examined discrimination among a priori populations. We retained the number of principal components with the lowest root mean square error in the cross-validation examination. All analyses were executed in R.

TABLE 1 Number of individuals sampled (N), diversity indices (H_e, H_o, A_r), individual inbreeding coefficients (F_i) and associated *p*-values (p) are provided by population and sampling period

Year and pop	N	H_e	H_o	A_r (22 genes)	F_i	p
2011						
San Pasqual	34	0.68	0.68	4.86	−0.008	NS
Lake Jennings	11	0.62	0.61	4.5	0.019	NS
Sweetwater	19	0.64	0.64	5.17	−0.001	NS
Otay	12	0.69	0.72	4.96	−0.040	NS
Global	76	0.70	0.67	4.87	0.051	0.000
2017						
San Pasqual	26	0.66	0.63	4.74	0.050	0.057
Lake Jennings	25 (20[a])	0.62 (0.61[a])	0.63 (0.62[a])	4.56 (4.31[a])	−0.016 (−0.016[a])	NS
Sweetwater	26	0.63	0.62	4.68	0.018	NS
Otay	36	0.67	0.69	4.84	−0.032	NS
Global	113	0.70	0.65	4.75	0.079	0.000

Note: Significance was assessed with 10,000 randomizations of alleles among individuals. NS = *p*-value >.1.
[a]Fanita Ranch and Scripps Ranch ($N = 5$) individuals removed.

2.4 | Simulations

To evaluate the impacts of different gene flow and genetic rescue alternatives on the global genetic diversity of the San Diego County Cactus Wren populations, we conducted simulations in EASYPOP v.2.0.1 (Balloux, 2001), which simulates neutral genetic variation using a forward time, individual-based model. We ran three baseline simulation scenarios, each for 100 generations: (1) a single population with a $N_e = 200$—representing the "best case" single panmictic population in San Diego County with similar total size to that found across the county; (2) There are four small subpopulations each with $N_e = 50$, with "worst case" zero gene flow, and (3) There are four small ($N_e = 50$) populations with one migrant per generation in a one-dimensional stepping stone fashion (representing the pattern of occasional gene flow among neighboring sites, observed with banded birds and in previous genetic results). To these we added three assisted island model gene flow scenarios to the observed stepping-stone gene flow starting at generation 50: (1) There is one additional migrant per generation among populations; (2) 10% migration per generation among populations, and (3) A 20% migration per generation among populations. All gene flow scenarios assumed equal proportions of migrants between populations. In all simulations, sex ratios were equal, and breeding was set to monogamous with 10% extra-pair mating (Brouwer & Griffith, 2019) and identical male and female migration rates. We simulated 50 genetic markers with free recombination, a mutation rate of 0.0001, a stepwise mutation model, and a maximum of 50 allelic states. Initial variability was set as maximal, with randomly assigned alleles. In each simulation, population genetic data were sampled every generation for 100 generations, and we performed 10 replicate runs of each scenario. The global average allelic richness, observed heterozygosity, and population differentiation (F_{ST}) were plotted by generation to compare values over time. To simulate adding migrants from a larger cluster (e.g., the larger central Orange County cluster; Barr et al., 2015) into the genetic rescue scenarios, we repeated all simulations with a fifth population of $N_e = 200$ added.

3 | RESULTS

3.1 | Data quality

In total, we genotyped 83 individuals collected between 2011–2012, and 446 individuals sampled between 2017–2019 in the same geographic areas (Figure 1). After removing full-siblings, the final 2011 dataset included 76 individuals (ranging from 11 to 34 per population), and the 2017 dataset included 113 (ranging from 25 to 36). While sample sizes are small, these are reflective of small population sizes at these locations (Lynn et al., 2022), and likely represent a large fraction of the total population in each site. After Bonferroni correction, no loci were in LD across all populations, nor were any significantly different from HWE. There was no evidence of null alleles. The 2011 dataset had no missing data and the 2017 dataset had <1% missing data. The sampled areas overlapped geographically in 2011 and 2017 with a few geographic outliers (Figure 1). In 2011, there was one

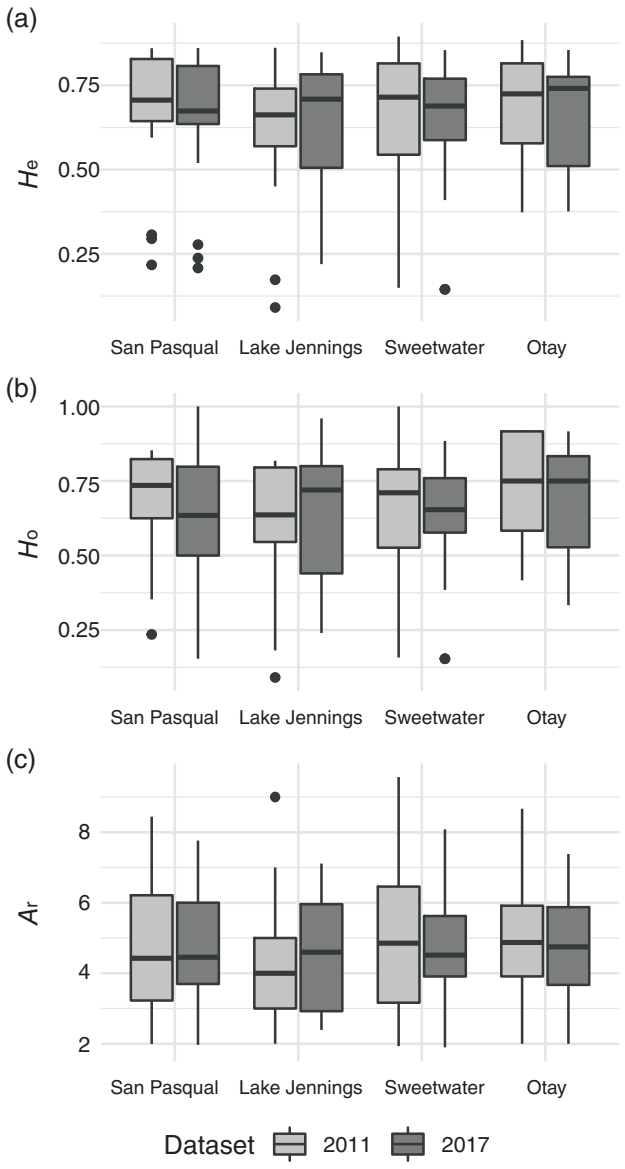

FIGURE 2 Diversity indices estimated for each population in 2011 and 2017. (a) Expected heterozygosity; (b) observed heterozygosity; and (c) allelic richness. Box plots show the median estimate at the center line, 75% range in the box, and 95% range in the whiskers across 22 sampled loci

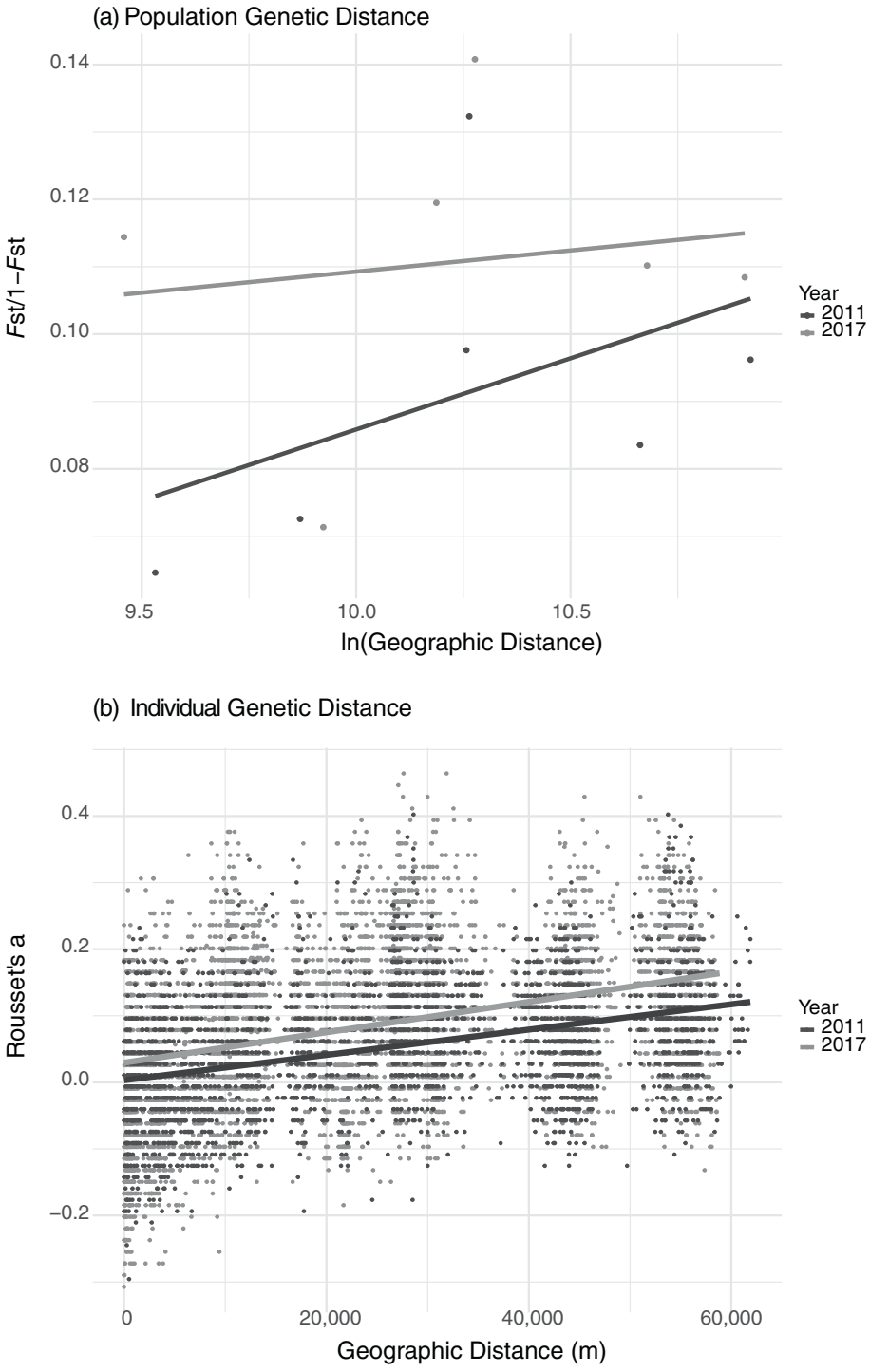

FIGURE 3 Pairwise isolation by distance plots. (a) Pairwise linearized F_{ST} among genetic clusters. All pairwise F_{ST} values in 2011 and 2017 were significantly different from zero. Slopes were not significantly different from zero in either dataset or from each other. Average pairwise F_{ST} trended upwards over time, but not significantly so. (b) Individual genetic distance (Rousset's $\hat{a}$) by geographic distance for the 2011 (gray) and 2017 (black) sample periods. Point clouds overlapped, showing stable genetic structure across sampling periods

bird sampled near the Tijuana Estuary that clustered with the Otay population (based on STRUCTURE results); this site was no longer occupied in 2017. In 2017 there was one bird sampled in Scripps Ranch and four birds sampled in Fanita Ranch that clustered with the Lake Jennings population. These sites were added in the later sampling period, after birds were detected there. These were retained in all analyses, and 2017 diversity statistics were calculated both with and without the Fanita and Scripps Ranch individuals.

3.2 | Genetic diversity

Genetic diversity indices were either stable or decreased over time, and genetic differentiation tended to increase (Table 1, Figures 2 and 3). Observed and expected heterozygosity were significantly lower in San Pasqual in 2017 than in 2011 (H_o: 8% decline; $t = 1.86$, df $= 21$, $p = .04$; H_e: 2% decline; $t = 1.70$, df $= 21$, $p = .05$; Figure S1A,B). In addition, the inbreeding coefficient was significantly positive in San Pasqual in 2017 (Table 1).

Allelic richness, rarified to 22 gene copies, declined on average by 9.4% in Sweetwater, and was significantly lower in 2017 than in 2011 at this site ($t = 1.68$, df = 21, $p = .05$; Figure S1C). Diversity metrics did not differ significantly among sampling periods in Lake Jennings or Otay (Table 1). Effective population size (N_e) was significantly lower in 2017 in Sweetwater (non-overlapping confidence intervals), and trended lower in Otay and San Pasqual. It was slightly higher in Lake Jennings in 2017 than in 2011 (Table 2). In all populations and sampling periods, effective population sizes were less than 100 individuals. Global genetic differentiation (F_{ST}) across all populations was significantly different from zero in both time periods (2011 $F_{ST} = 0.08$, $p < .001$; 2017 $F_{ST} = 0.1$, $p < .001$) but did not increase significantly over time. Pairwise F_{ST} among populations and individual genetic distances (Rousset's $\hat{a}$) showed similar upward trends (Figure 3a,b).

TABLE 2 Effective population size estimates for the four Cactus Wren populations on conserved lands in San Diego County. 95% confidence intervals are included in parentheses

	Effective population size	
Population	**2011**	**2017**
San Pasqual	88.3 (59.5–158.1)	50.6 (35.1–84.4)
Lake Jennings	12.4 (7.8–21.9)	18.4 (14.8–23.5)
		16[a] (12–20.8)
Sweetwater	43.4 (29.7–75)	18.3 (14.9–22.8)
Otay	41.6 (21.6–202)	25.7 (21.7–30.9)

[a]Fanita Ranch and Scripps Ranch ($N = 5$) individuals removed.

3.3 | Population structure

Individual-based clustering analyses did not detect any major differences in population structure over time.

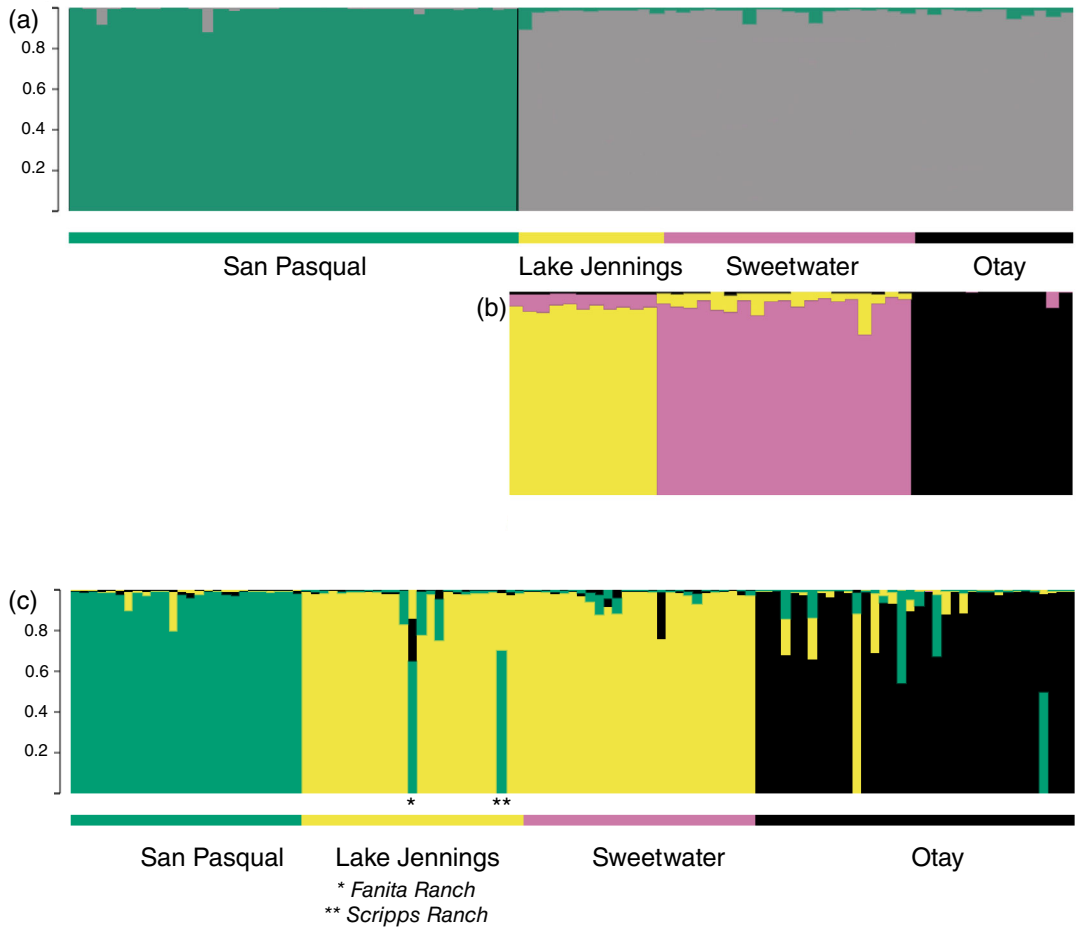

FIGURE 4 STRUCTURE without locprior results for (a) 2011 full dataset with $K = 2$, San Pasqual and San Diego. (b) Hierarchical results showing $K = 3$ subclusters within San Diego (Lake Jennings, Sweetwater, Otay). (c) Results for 2017 supported $K = 3$ clusters: San Pasqual, Lake Jennings plus Sweetwater and Otay. Individuals with mixed San Pasqual ancestry in the Lake Jennings cluster were sampled at Fanita Ranch (*) and Scripps Ranch (**), and one individual in Otay had more affiliation with the Lake Jennings/Sweetwater cluster

STRUCTURE results were nearly identical in analysis with or without LOCPRIOR, so we present only the results without LOCPRIOR. Two clusters ($K = 2$) were supported in the 2011 dataset (Figure S2), separating San Pasqual from the other three sites (Figure 4a). However, with a hierarchical approach, the three remaining populations were separated from one another (Figure 4b; Figure S3). In 2017, $K = 3$ was the best supported model, separating Otay and San Pasqual, while Lake Jennings and Sweetwater formed a single cluster (Figure 4c; Figure S4). In 2017 there were two individuals with mixed San Pasqual ancestry in the Lake Jennings cluster; one was sampled at Fanita Ranch and the other at Scripps Ranch. These two sites are geographically intermediate between Lake Jennings proper and San Pasqual. One individual sampled in Otay was genetically assigned to the Lake Jennings/Sweetwater cluster. These mixed-ancestry individuals indicate recent gene flow between populations. The DAPC analysis discriminated all four populations in both time periods (Figure S5).

3.4 | Inferred dispersal in 2017–2019

Of 123 recovered full family groups in the 2017 full dataset, only 16 family groups included individuals sampled in different territories (Table 3). The mean Euclidean geographic distance among these was 3 km. The longest inferred dispersal (10 km) was the only one detected between two populations (Sweetwater and Otay). The second longest inferred dispersal was within the Lake Jennings population between Lake Jennings proper and Fanita Ranch (9 km).

3.5 | Population simulations

In simulations, roughly 80% of the allelic richness in the system was lost after 100 generations and was still declining (Figure 5a). Loss was most rapid early on, with over half of the variation lost after 20 generations. There was no discernable difference in overall loss of allelic richness in any gene flow scenario. This suggests that regardless of gene flow, a stable population of 200 breeding individuals in San Diego County is not large enough to reduce the overall loss of genetic diversity by random genetic drift. However, heterozygosity (H_o) and population differentiation (F_{ST}) (Figure 5b,c) were improved with translocation scenarios, becoming more similar to a panmictic population after about 25 generations (depending on the percent of gene flow added). There was little difference between 10% and 20% gene flow and panmixia after about 25 generations in either metric. Generally, adding in a fifth larger population slowed the rate of loss of allelic richness and heterozygosity (flatter slopes). In five-population scenarios, the different translocation scenarios improved heterozygosity and population differentiation similarly to the four-population scenario.

TABLE 3 Genetically inferred dispersal events during the 2017–2019 sample period among territories (given as field codes), populations and Euclidean distances between territories

Territory 1	Territory 2	Territory 3	Population	Distance (km)
OWL	VUL		Otay	4.0
FOO	RAN		Sweetwater	1.2
PIO	TOL		Sweetwater	2.0
CON	RES		Otay	0.3
POW	JUI		Lake Jennings	0.3
RAV3	RAV4	RAN	Sweetwater	2.6
564c	568c	573c	Lake Jennings	1.3
312c	CA01c		Sweetwater	5.3
POW	Fa01c		Lake Jennings - Fanita Ranch	9.3
CHE	184c		San Pasqual	1.0
202c	BV01		San Pasqual	6.0
283c	580c		Sweetwater	0.7
RIC	RAV		Sweetwater	0.2
194c_01	219c	CHE2	San Pasqual	4.4
196c	207c		San Pasqual	0.4
PIO	HAR		Sweetwater – Otay	10.0

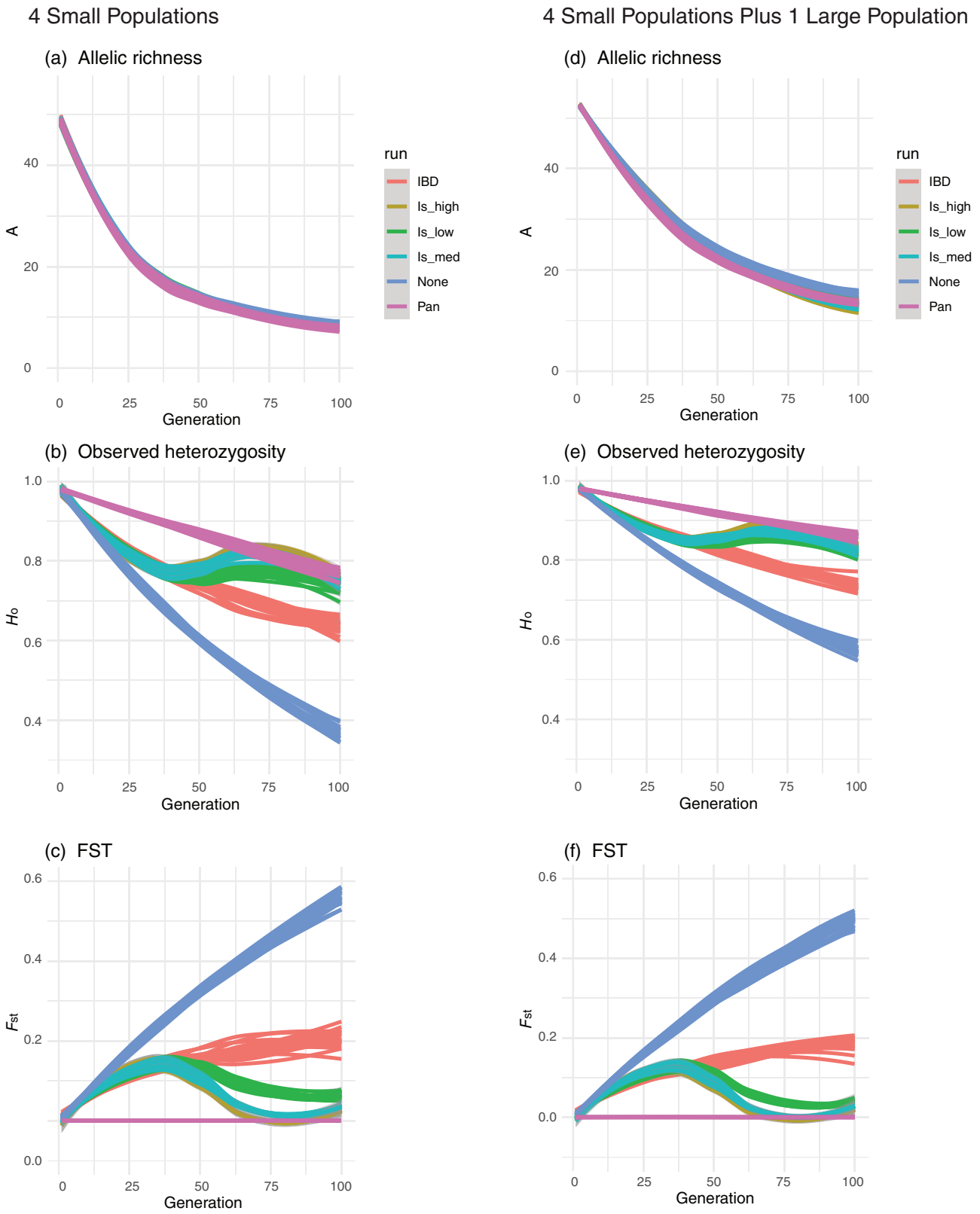

FIGURE 5 Gene flow simulation results for four small populations ($N_e = 50$; left column) and four small populations plus a larger population ($N_e = 50$ or 200; right column). All simulations were run for 100 generations with 20 replicate runs of each gene flow scenario. Summary metrics include: (a) global average allelic richness, (b) global average observed heterozygosity, and (c) population differentiation F_{ST}. Gene flow scenarios include: None—no gene flow for 100 generations (blue); Pan—a panmictic population for 100 generations (pink); IBD—1% isolation by distance gene flow for 100 generations (red; current condition); Is_low—added island migration of 1% starting at generation 50 (green); Is_med—added island migration of 10% starting at generation 50 (turquoise); Is_high—added island migration of 20% starting at generation 50 (gold)

4 | DISCUSSION

Further evaluation of the genetic structure of San Diego County Cactus Wren populations 6–8 years (~2–3 generations) after initial surveys revealed a mix of stable or declining trends in diversity and effective population size, and stable to increasing genetic differentiation. These trends suggest that genetic drift is outpacing dispersal and gene flow among these small aggregations. Although Lake Jennings appears to be an exception to this trend, slight increases in diversity there are likely due to the inclusion of newly sampled territories in Scripps and Fanita Ranch, ~12 km northwest of Lake Jennings proper. Mixed assignment of individuals from these two sites and the population in San Pasqual is encouraging, as it suggests past connectivity or colonization. This could be facilitated by one or more unknown and unsampled aggregations between these two sites or the occasional long-distance dispersal between them. We also inferred one dispersal event between Lake Jennings proper and Fanita Ranch from the pedigree analysis, indicating recent connectivity between these two sites. The occasional longer distance dispersals inferred in our genetic data were very similar to those documented with resightings of individually color banded birds over the same time period. There were six dispersal events observed with banded bird resightings; five between Otay and Sweetwater, and one between Lake Jennings and San Pasqual (Lynn et al., 2022). In nearly all cases, detected dispersals appear to be between neighboring populations or aggregations, suggesting a stepping-stone pattern of connectivity.

Nest monitoring identified annual precipitation as a significant driver of productivity and population growth (Lynn et al., 2022), and thus may affect dispersal as well as cause rapid changes in population size that reduce genetic diversity. When the initial genetic samples were collected in 2011, San Diego County was experiencing a prolonged drought. By 2014, an extreme drought year, the Otay Cactus Wren population had dropped to a quarter of its size in the early 1990s, and exhibited near total reproductive failure (TNC & SDMMP, 2015). Since 2015, precipitation has been at or above average in 4 of 6 years, and Cactus Wren populations at Lake Jennings, Sweetwater and Otay collectively have doubled in size (Lynn et al., 2022; Lynn & Kus, 2021).

Despite evidence of movement and gene flow and documented increase in abundance in monitored populations, significant declines in genetic diversity metrics were detected in two populations (San Pasqual and Sweetwater), and similar trends in a third (Otay). This suggests that San Diego County may not support enough individuals to retain existing genetic diversity. Nest monitoring and the genetic pedigree analysis detected ~125 unique family groups across all populations in San Diego County. Effective population size (N_e) estimates were also low across the County. N_e was significantly below 100 in San Pasqual and significantly below 50 in Lake Jennings, Sweetwater and Otay. Small populations ($N_e \leq 50$–100) are more likely to experience inbreeding depression and loss of adaptive genetic diversity (Frankham, 2005; Frankham et al., 2014; Shaffer, 1981). These factors can reduce individual fitness and compromise the capacity to adapt to changing environmental conditions (Reed et al., 2002; Reed & Frankham, 2003).

Our simulations suggested different potential outcomes of assisted gene flow on two different measures of genetic diversity: allelic richness and heterozygosity. Allelic richness estimates the total number of gene variants in a population and reflects the long-term evolutionary potential of a population. Allelic richness can be lost very quickly due to drift and can take thousands of generations to regain through the process of gene mutation (Cornuet & Luikart, 1996). Heterozygosity reflects the genomic diversity within individuals and has been linked to individual fitness in birds and other animals (Foerster et al., 2003; Mitrus et al., 2020; Seddon et al., 2004; Vandewoestijne et al., 2008). Heterozygosity is lost in small populations where inbreeding is high, and can lead to decreased fitness and increasing extinction risks (Fagan & Holmes, 2006). Under all gene flow scenarios, total allelic richness across the whole metapopulation system continued to decline at the current breeding population size of 50–200 (if panmictic) individuals. Although total allelic richness across the metapopulation system would still decline with or without gene flow, gene flow could help retain a higher proportion of the richness within each sub-population. Our simulations suggest that assisted gene flow among all populations could slow the loss of heterozygosity and reduce genetic differentiation across the entire San Diego region by more closely matching the trajectory of a single panmictic population rather than four populations linked by low stepping-stone gene flow. Consequently, assisted migration among San Diego sites could positively impact fitness in comparison to no or low stepping-stone gene flow. Outcomes may improve further if individuals from larger or more diverse populations outside of the region are added into the assisted gene flow network. As an extension of this work, population viability modeling that includes genetic factors could be conducted to better model the interactions between demographic and genetic factors and predict population trends under various restoration scenarios (e.g., Benson et al., 2019). Spatially explicit population modeling has been applied to evaluate conservation strategies for Cactus Wrens in the San

Pasqual Valley. In the short term, these models favored habitat enhancement around existing populations over creating stepping-stones between existing populations to mitigate wildfire risks (Conlisk et al., 2014). However, the models did not include genetic factors, which could favor stepping-stones to enhance movement and gene flow.

Whether inbreeding depression is detectable deserves further study in this system, and investigations of diversity-fitness associations are ongoing. Significant relationships among genetic diversity, parental relatedness, and reproductive success have been found in other bird species (Harrison et al., 2011; Mitrus et al., 2020; Seddon et al., 2004), although associations between heterozygosity and fitness can vary in strength depending on environmental conditions (Ferrer et al., 2016; Harrison et al., 2011), and may be difficult to detect (Coltman & Slate, 2003). While many studies have focused on nest productivity as a measure of fitness, genetic diversity may affect offspring fitness in later life stages as well. For example, in populations of Blue Tits (*Cyanistes caeruleus*), high parental relatedness negatively affected offspring immune response (Arct et al., 2019).

Management to slow the loss of genetic diversity and isolation in this system could include a two-pronged approach that combines translocation (e.g., reinforcement or augmentation, Novak et al., 2021) and habitat restoration. Reinforcement translocation of individuals or eggs could be considered to assist gene flow over the short term. This could help to boost local heterozygosity relatively quickly to avoid or reduce inbreeding depression (Weeks et al., 2011). Our simulations suggested that even the addition of a single successful migrant per generation would be helpful in retaining more genetic diversity and that 10%–20% gene flow rates would be close to the maximum retention potential. Hedrick (1995) showed that augmentation into recipient populations should not exceed rates of 20% gene flow from the sources to avoid losing uniquely adapted alleles in the recipient population. While past translocation experiments with adult Cactus Wrens have been successful (Kamada & Preston, 2013), perhaps a more efficient and less disruptive technique is to swap eggs (Westemeier et al., 1991). Given that populations of Cactus Wrens are very small (numbering in the 10s of individuals) and unlikely to grow much larger in the short term without substantial habitat restoration, reinforcement translocations may need to occur at some regular frequency. Cactus Wrens reach maturity within 1 year and can live up to 7 years; however, only a small proportion (<11%) live to breed more than three seasons (Hamilton et al., 2011). Regular translocations could target rates of up to 10%–20% over 3-year periods that likely approximate a generation. Donor populations outside of San Diego County may provide unique genetic variation and admixture potential beyond what is available locally. For example, the genetic population with the highest allelic richness noted in Barr et al. (2015) extended through the Santa Ana foothills from El Modena through southern Marine Corps Base Camp Pendleton. This population could provide a more diverse, and geographically close, source population for translocation. Understanding the feasibility of regular reinforcement translocations, and estimating survival and breeding rates of translocated individuals, are topics worthy of further investigation in this system. Reinforcement translocation has been successful in restoring genetic diversity in other birds including the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*; Bouzat et al., 2009) and Gunnison Sage-Grouse (*Centrocercus minimus*; Zimmerman et al., 2019).

Our results also underscore that sustaining larger local populations would be beneficial for retaining and re-building genetic diversity over the long term. Cactus planting and habitat restoration to control annual herbaceous vegetation and thinning shrubs in cactus patches has likely improved habitat suitability and promoted recent cactus wren population growth in San Diego County (Bennett & Dodero, 2011; Dodero, 2015; Goddard, 2019; Lynn et al., 2022). Continuing habitat restoration efforts around existing populations could support more territories in the long term. This two-pronged approach of restoring connectivity and habitat could help maximize the retention of genetic diversity in remaining Cactus Wren populations in San Diego County.

The reductions in genetic diversity observed in the Cactus Wren in San Diego County are predictable in fragmented populations, and reflected in global trends (Leigh et al., 2019; Willoughby et al., 2015). Genetic monitoring, therefore, is useful to integrate into conservation and restoration efforts, not only to establish population trends, but also to evaluate the success of translocations and other management strategies that are becoming increasingly important to slow population declines and the global loss of biodiversity.

AUTHOR CONTRIBUTIONS

Amy G. Vandergast and Barbara E. Kus conceived, designed, and obtained funding for the study; Barbara E. Kus led field work and sample collection; Julia G. Smith and Anna Mitelberg conducted laboratory data collection; Julia G. Smith and Amy G. Vandergast analyzed the data; Amy G. Vandergast wrote the paper with significant contributions from all authors.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Genotype and location data are available as a U.S. Geological Survey Data Release: https://doi.org/10.5066/P92A0B0P (Vandergast et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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