BIODIVERSITY RESEARCH

Drifting to oblivion? Rapid genetic differentiation in an endangered lizard following habitat fragmentation and drought

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ABSTRACT

Aim The frequency and severity of habitat alterations and disturbance are predicted to increase in upcoming decades, and understanding how disturbance affects population integrity is paramount for adaptive management. Although rarely is population genetic sampling conducted at multiple time points, pre- and post-disturbance comparisons may provide one of the clearest methods to measure these impacts. We examined how genetic properties of the federally threatened Coachella Valley fringe-toed lizard (*Uma inornata*) responded to severe drought and habitat fragmentation across its range.

Location Coachella Valley, California, USA.

Methods We used 11 microsatellites to examine population genetic structure and diversity in 1996 and 2008, before and after a historic drought. We used Bayesian assignment methods and F-statistics to estimate genetic structure. We compared allelic richness across years to measure loss of genetic diversity and employed approximate Bayesian computing methods and heterozygote excess tests to explore the recent demographic history of populations. Finally, we compared effective population size across years and to abundance estimates to determine whether diversity remained low despite post-drought recovery.

Results Genetic structure increased between sampling periods, likely as a result of population declines during the historic drought of the late 1990s–early 2000s, and habitat loss and fragmentation that precluded post-drought genetic rescue. Simulations supported recent demographic declines in 3 of 4 main preserves, and in one preserve, we detected significant loss of allelic richness. Effective population sizes were generally low across the range, with estimates ≤100 in most sites.

Main conclusions Fragmentation and drought appear to have acted synergistically to induce genetic change over a short time frame. Progressive deterioration of connectivity, low N_e and measurable loss of genetic diversity suggest that conservation efforts have not maintained the genetic integrity of this species. Genetic sampling over time can help evaluate population trends to guide management.

Keywords
conservation, disturbance, gene flow, genetic diversity.

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INTRODUCTION

Rates and severity of habitat loss and disturbance have increased over the past century and are predicted to accelerate in upcoming decades (Turner, 2010). Furthermore, anthropogenic habitat alterations such as fragmentation are often coupled with changing natural disturbance regimes (Darling & Côté, 2008). Key areas of emerging research, therefore, are determining the degree to which organisms are resilient to the combined impacts of habitat alterations and

disturbances (Darling & Côté, 2008) and optimally managing natural systems in the light of environmental change (Millar *et al.*, 2007).

Severe disturbances (e.g. fire, drought, hurricanes, harvest) can impact population structure within individual species (Peakall & Lindenmayer, 2006; Evanno *et al.*, 2009; Oklander *et al.*, 2010; Apodaca *et al.*, 2013; Pinsky & Palumbi, 2014) and elicit rapid changes in community composition (Turner & Romme, 1994). Within metapopulations, resiliency to periodic and local disturbance may be imparted by movement and recolonization among local populations (reviewed in Hanski, 1991; Hanski *et al.*, 1994). However, habitat loss and fragmentation can disrupt movement and recolonization among patches, reducing resiliency to other disturbances and increasing local and global extinction risks, and community instability (*e.g.* extinction debts, Gilpin & Soulé, 1986; Tilman *et al.*, 1994; Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009).

Genetic monitoring over time may provide early detection of changes to connectivity that may impact long-term metapopulation persistence and inform conservation efforts. In addition, changes to genetic diversity are important for rare species management, because loss of genetic diversity and accumulation of deleterious mutations can contribute to extinction risks in small, fragmented populations (Shaffer, 1981; Frankham, 2005). These factors may reduce fitness and compromise the capacity of species to adapt to changing environmental conditions (Reed *et al.*, 2002; Reed & Frankham, 2003; Markert *et al.*, 2010). In fact, several empirical studies report higher extinction rates of low variability populations than high variability populations even when abiotic factors and census numbers are similar (Newman & Pilson, 1997; Saccheri *et al.*, 1998; Higgins & Lynch, 2001; Driscoll, 2004). Thus, monitoring genetic diversity may provide greater insight into the status of threatened populations than just tracking numerical abundance.

Here, we examined the extent to which coupled habitat alteration and disturbance (habitat fragmentation and drought) may have altered population genetic structure and diversity in a rare species, the Coachella Valley fringe-toed lizard (*Uma inornata*). *Uma inornata* is a federally threatened and state endangered lizard endemic to the Coachella Valley, California, USA (Fig. 1), where it is restricted to aeolian sand habitats (Turner *et al.*, 1984). *Uma inornata* historically
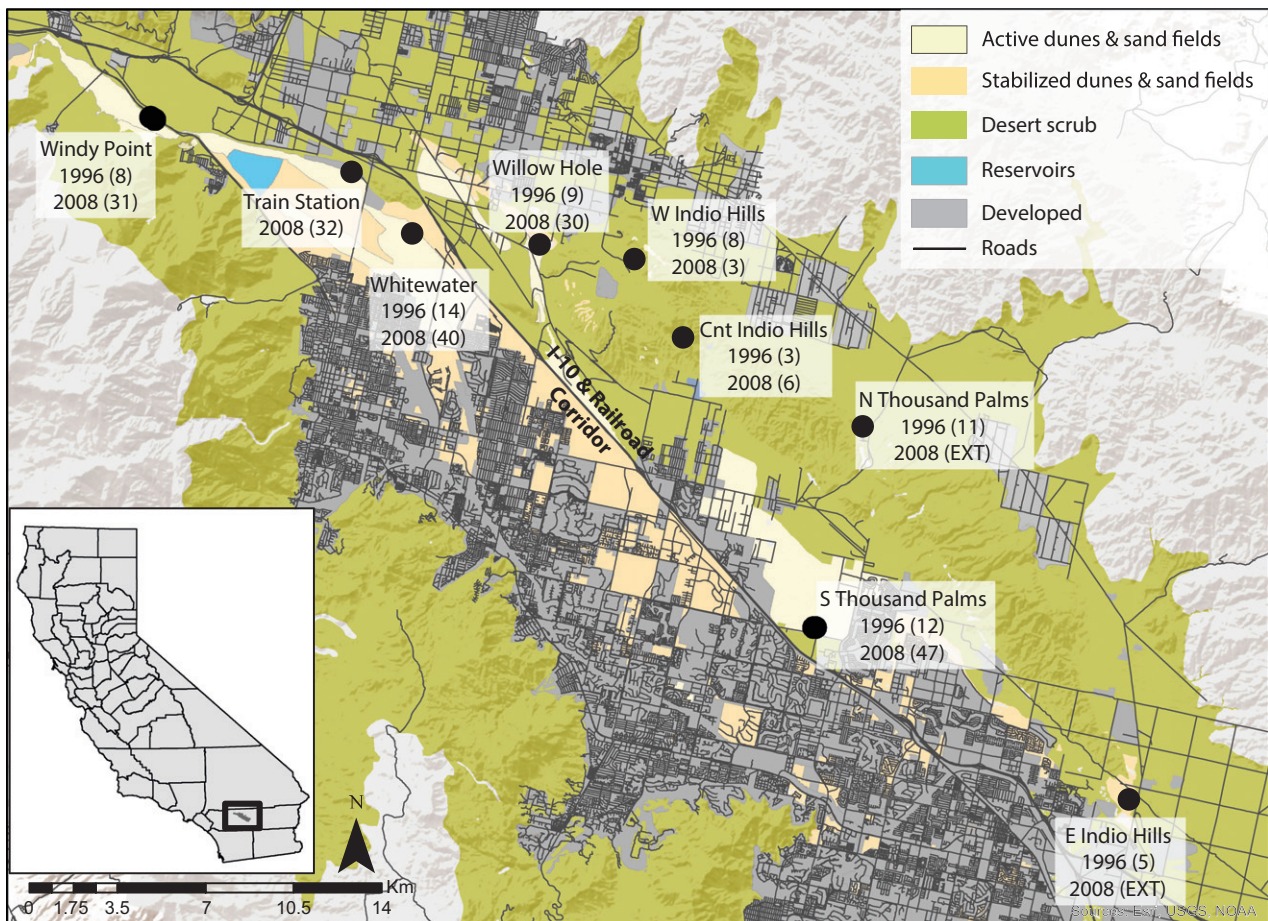

Figure 1 Map of the study region in the Coachella Valley, Riverside County, CA, USA. 1996 and 2008 collection sites (black dots) and number of individuals sampled. *Uma inornata* habitat is comprised of active sand dunes (cream) surrounded by stabilized dunes (peach) and desert scrub (green). Urban and developed areas are shown in grey.

existed as a large, interconnected metapopulation with local changes in population size, reproductive rates and extinctions linked to periodic droughts, flood and scouring events (Barrows, 2006; Hedtke *et al.*, 2007). Previous genetic studies recovered genetic panmixia reflective of historically high gene flow and natural extinction and recolonization dynamics (Hedtke *et al.*, 2007). However, the amount and connectivity of habitat for this species has declined precipitously as a result of urban development and the interruption of sand deposition and movement. Fragmentation in the Coachella Valley began in the 1950s with the construction of Interstate 10, the railroad alignment and tamarisk (*Tamarix aphylla*) windbreak across the valley. Collectively, this barrier impacts sand movement and lizard density (Turner *et al.*, 1984) and likely reduces or precludes movement among local populations. More recent urbanization and warming trends have led to further loss of sand habitat and fragmentation (Griffiths *et al.*, 2002; Katra *et al.*, 2009). Remaining habitat is estimated at 5–16% of the historical distribution (Fig. 2a; Barrows *et al.*, 2008). In addition, the Coachella Valley experienced several years of extreme drought between the late 1990s and early 2000s (Fig. 2b) during which declines in lizard densities and reproductive rates and extirpations of several populations of *U. inornata* were documented (Barrows & Allen, 2007).

We compared genetic structure among *U. inornata* populations before and after this extreme drought using microsatellite markers. We hypothesized that reduced movement and gene flow among populations due to habitat fragmentation would increase population genetic structure and that in the absence of gene flow, drought-induced mortality would reduce genetic diversity and effective population sizes within local populations. We analysed population genetic structure using assignment methods and F-statistics and estimated allelic richness and relatedness within populations at the two sample periods. We employed approximate Bayesian computing methods and bottleneck tests to explore the recent demographic history of populations. Finally, we compared past and present effective population size estimates in relation to abundance estimates and discuss whether further management actions may be needed to retain genetic diversity in this species.

METHODS

Species and sample information

The range of *U. inornata* extends roughly 40 km east-west across the Coachella Valley but is now fragmented into five populations on the valley floor and smaller populations in the Indio Hills (Fig. 1). All extant populations occur on protected dunes. To quantify genetic changes over time, we compared samples collected in 1996, prior to the drought, to those collected in 2008, post-drought, and when lizard abundances had recovered. We obtained blood samples previously collected in 1996 (Fig. 1; Table 1; Hedtke *et al.*, 2007) and collected tissue samples (tail tips or toe clips) in 2008 at seven sites (Fig. 1; Table 1), which included six sites sampled in 1996 and one site not previously sampled. No lizards were found in 2008 at North Thousand Palms Preserve and East

(a)
Depiction of dune habitat loss and fragmentation in the Coachella Valley since 1950

(b)
Annual and 4-year average precipitation recorded at South Thousand Palms Preserve
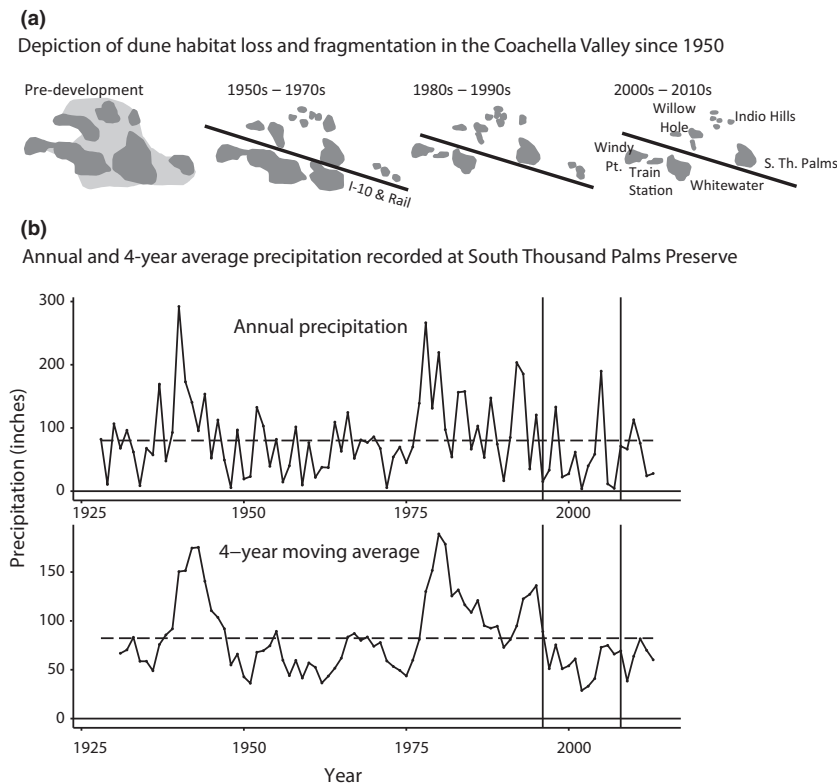

Figure 2 Disturbances in the Coachella Valley. (a) Depiction of habitat loss and fragmentation over time in the Coachella Valley from the 1950s to 2010, light grey shading depicts probable historical connectivity. (b) Yearly average rainfall and 4-year running average rainfall for the South Thousand Palms Preserve in the Coachella Valley, CA. The lowest yearly rainfalls on record were recorded in 2002 and 2007, and the two lowest 4-year averages occurred in 2002 and 2003. Vertical lines indicate the genetic sampling periods in 1996 and 2008, and the dashed lines indicate the mean values for annual precipitation and the 4-year moving average. Rainfall data were taken from the Western Region Climate Center (http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca4259) and by CWB.

Table 1 Number of individuals sampled, number of alleles, adjusted allelic richness, observed and expected heterozygosity, inbreeding coefficient and relatedness coefficients and *P*-values across populations in 1996 and 2008. Indices are reported for sites with sample sizes of 5 or more. Major preserves sampled in both 1996 and 2008 are bolded. In 2008, both North Thousand Palms Preserve and East Indio Hills were unoccupied.

Sampling year	Sampling location (West to East)	*N*	A	Ar*	Ho	He	*F*	*R*	*R P*-value
1996	**Windy Point**	**8**	**3.455**	**2.88**	**0.562**	**0.512**	**−0.084**	**0.124**	**0.02**
	Whitewater	**14**	**5.000**	**3.17**	**0.584**	**0.561**	**−0.029**	**0.066**	**0.019**
	Willow Hole	**9**	**4.182**	**3.28**	**0.610**	**0.585**	**−0.036**	**−0.036**	**NS**
	West Indio Hills†	8	4.000	3.05	0.523	0.509	0.034	0.161	0.003
	Central Indio Hills‡	3	2.636	–	–	–	–	–	–
	North Thousand Palms Preserve§	11	4.091	3.18	0.617	0.592	−0.028	−0.016	NS
	South Thousand Palms Preserve§	**12**	**4.727**	**3.32**	**0.621**	**0.598**	**−0.019**	**−0.027**	**NS**
	East Indio Hills	5	3.182	3.03	0.350	0.531	0.287	0.075	NS
2008	**Windy Point**	**31**	**4.636**	**2.84**	**0.539**	**0.500**	**−0.057**	**0.224**	**0.001**
	Train Station	32	4.909	2.98	0.605	0.539	−0.117	0.166	0.001
	Whitewater	**40**	**5.636**	**3.21**	**0.631**	**0.612**	**−0.019**	**0.026**	**NS**
	Willow Hole	**30**	**5.455**	**3.30**	**0.643**	**0.608**	**−0.029**	**0.001**	**NS**
	West Indio Hills	3	2.364	–	–	–	–	–	–
	Central Indio Hills	6	3.273	2.86	0.606	0.511	−0.177	0.204	0.016
	South Thousand Palms Preserve	**47**	**6.091**	**3.36**	**0.695**	**0.625**	**−0.078**	**−0.009**	**NS**

*Ar rarefied to 8 gene copies (*N* = 4).

†Site denoted as Sleeping Man Dunes in Hedtke *et al.* (2007).

‡Site denoted as A-1 Aggregate in Hedtke *et al.* (2007).

§Sites denoted as north and south Coachella Valley Preserve in Hedtke *et al.* (2007).

Indio Hills, consistent with annual surveys indicating they were extirpated (Barrows & Allen, 2007). Because 2008 sampling occurred over several days at most sites, we marked lizards to prevent resampling. Demographic (snout-to-vent length, sex, relative age) and locality data were taken for each lizard, and tissues were stored in 95% ethanol.

Genetic data collection

We extracted genomic DNA from samples using DNeasy blood and tissue kits (Qiagen, Valencia, CA, USA) following standard protocols. We isolated microsatellite loci from genomic DNA following standard cDNA library preparation and cloning protocols (Hamilton *et al.*, 1999) and shotgun sequencing on a 454Jr-automated DNA sequencer (Roche). We evaluated 80 loci that contained flanking regions for which primers could be designed.

We tested all novel loci and three previously developed loci (Hedtke *et al.*, 2007) for polymorphism on a subset of samples. We scored raw data in GENE-MARKER v1.90 (SoftGenetics) and used MICROCHECKER (Van Oosterhout *et al.*, 2004) to screen for null alleles. We tested for linkage disequilibrium (LD) and deviations from Hardy–Weinberg expectations (HWE) across loci and populations in GENEPOP. We used COLONY (Jones & Wang, 2010) to detect full sibships, the presence of which may confound clustering algorithms (Anderson & Dunham, 2008; Rodriguez-Ramilo & Wang, 2012). COLONY analyses assumed an inbreeding model and a polygamous mating system, and all individuals were coded as offspring. All subsequent analyses were run with and without full sibs.

Comparing pre- and post-drought genetic structure

Theoretical expectations of population structure under different gene flow regimes allow a framework for inferring process from observed genetic patterns. Under a classical metapopulation model with high genetic connectivity, we expect to see low genetic differentiation among local populations, as drift is counteracted by gene flow, and low overall genetic diversity reflective of extinction and recolonization (Slatkin, 1985; Wade & McCauley, 1988; Harrison & Hastings, 1996). However, a reduction in gene flow should lead to an increase in population genetic structure (Slatkin, 1987; Harrison & Hastings, 1996). Because drift acts more rapidly in small vs. large populations, drought-induced population declines should strengthen the signal of genetic differentiation, and we should see evidence of declines in genetic diversity in local populations, such as a loss of allelic richness, and declining effective population size over time (Lacy, 1987; Slatkin, 1987).

We used Bayesian clustering analyses and global and pairwise estimates of genetic differentiation to compare genetic structure between 1996 and 2008. We inferred genetic clusters in 1996 and 2008 with STRUCTURE version 2.3.2 (Pritchard *et al.*, 2000), using an admixture model with correlated frequencies and LOCPRIOR (incorporating location information). *K* was inferred by comparing the results from the mean $\ln P(D|K)$ score against K_{MAX} (i.e. where the $\ln P(D|K)$ curve plateaus) and the ΔK criterion (Evanno *et al.*, 2005). We estimated the probability of $K = 1–7$ using 500,000 Markov chain Monte Carlo (MCMC) iterations following a 500,000 iteration burn-in,

with 10 replicate runs to verify consistency across chains. Because the number of individuals sampled can affect the number of inferred clusters (Rosenberg *et al.*, 2005; Fogelqvist *et al.*, 2010), we also investigated the sensitivity of our results to sample size differences between 1996 and 2008. For 10 replicates, we randomly selected individuals at each site from the 2008 dataset until sample sizes were equal to those in 1996. We used the same sample parameters as before for $K = 1–7$ and assumed the highest value of ΔK corresponded to the optimal number of clusters.

We assessed population differentiation with F_{ST}. Global and pairwise Weir & Cockerham's (1984) θ were calculated in FSTAT v. 2.9.3 (Goudet, 1995, 2001). To compare between years, we restricted analyses to four main preserves sampled with at least eight individuals at both time periods (Windy Point, Whitewater, Willow Hole and South Thousand Palms Preserve). We calculated θ among preserves for both time periods, with 95% confidence intervals estimated with 10,000 bootstraps over loci. θ is an unbiased estimator of F_{ST} that should not depend on sample size (Weir & Cockerham, 1984), although variance will be greater for smaller sample sizes. We examined the sensitivity of θ estimates to sample size following a subsampling procedure. For each site in 2008, we randomly selected the same number of individuals that were sampled in 1996 and calculated global and pairwise θ values among the four preserves. We repeated this 1000 times and examined the distributions of θ and associated *P*-values (1000 permutations). Analyses were performed in R 3.1.2 (R Core Development Team, 2011), using the STRATAG package (Archer, 2014).

Patterns of genetic differentiation by geographic distance can also provide insight into the extent to which populations are connected by gene flow, or influenced by drift (Slatkin, 1993; Hutchinson & Templeton, 1999). We tested for isolation by distance in both 1996 and 2008 using Mantel tests, with significance assessed with 10,000 randomizations of the genetic distance matrix in IBDWS (Jensen *et al.*, 2005). We included all locations with ≥ 6 individuals sampled.

Genetic diversity

Number of alleles, allelic richness, observed and expected heterozygosity and relatedness were calculated in FSTAT v. 2.9.3 (Goudet, 1995, 2001). To examine genetic diversity loss over time, we compared allelic richness (adjusted for sample size differences using rarefaction) between years using the comparisons among groups option in FSTAT, with randomization tests conducted with 15,000 permutations. We examined site-specific differences in adjusted allelic richness between years using paired t-tests replicated over loci. We examined allelic richness because it is more sensitive to population size reductions than other diversity measures (Nei *et al.*, 1975; Leberg, 2002).

Bottlenecks and N_e

Significant declines in population size should leave a detectable genetic signature. We used approximate Bayesian computation (ABC) to determine if recent reductions in N_e were consistent with the observed data. We used the software DIYABC v2.0.4 (Cornuet *et al.*, 2014) to model three different demographic scenarios and compared these to observed data in the four main preserves. *Uma inornata* typically reach adult size and breed within one-to-four years depending on rainfall, with the highest averages occurring during extended drought (MF & CWB, unpubl. data). Therefore, we assumed an average generation time of two years to bound bottleneck time estimates. We modelled three scenarios: (1) a recent reduction in N_e timed with the recent drought [1–5 generations ago], (2) a historical reduction in N_e timed with habitat loss and fragmentation from 1950 to 1990 [9–29 generations ago] and (3) constant N_e (Fig. 3a). DIYABC does not allow for gene flow in demographic models, so we investigated each preserve separately; however, high historical gene flow was likely among all four modelled preserves, which were genetically panmictic in 1996 (see results). We examined the impact of including the entire metapopulation sample in 1996 vs. the smaller preserve specific samples in preliminary runs and found better discrimination among scenarios in which the entire metapopulation was used. In final analyses, we represented the 1996 metapopulation with all samples in each analysis. Other priors and conditions are given in Table S1. We evaluated the fit of scenarios to the observed data by estimating posterior probabilities and 95% CIs from 10 subsets of the 4×10^6 simulated data and used the 'logistic' option to rank the posterior probabilities from each scenario. Distances between the scenarios were based on normalized Euclidean distances between summary statistics (mean number of alleles, mean gene diversity, mean allele size variance, mean M index and shared allele distance) estimated from the observed and simulated datasets. For scenarios with the highest posterior probabilities, we assessed the goodness of fit between the summary statistics of the observed dataset and the corresponding posterior predictive distribution using PCA. The model is considered an appropriate fit if the observed data are nested within the prior and posterior distributions. Finally, we measured confidence in the best-fit scenario for each site by estimating the type I and type II error rates.

We tested for recent bottlenecks using the heterozygote excess method in BOTTLENECK 1.2.02 (Piry *et al.*, 1996) with significance assessed with 10,000 replicates and a Wilcoxon signed-rank test (Cornuet & Luikart, 1996). Because the sensitivity of this method depends upon the mutational model under which the null range of alleles are simulated (Peery *et al.*, 2012), we examined the infinite alleles model (IAM), step-wise mutation model (SMM), and the hybrid two-phase model (TPM) employing a range of variances in multistate mutational sizes (4, 16) and per cent of loci adhering to
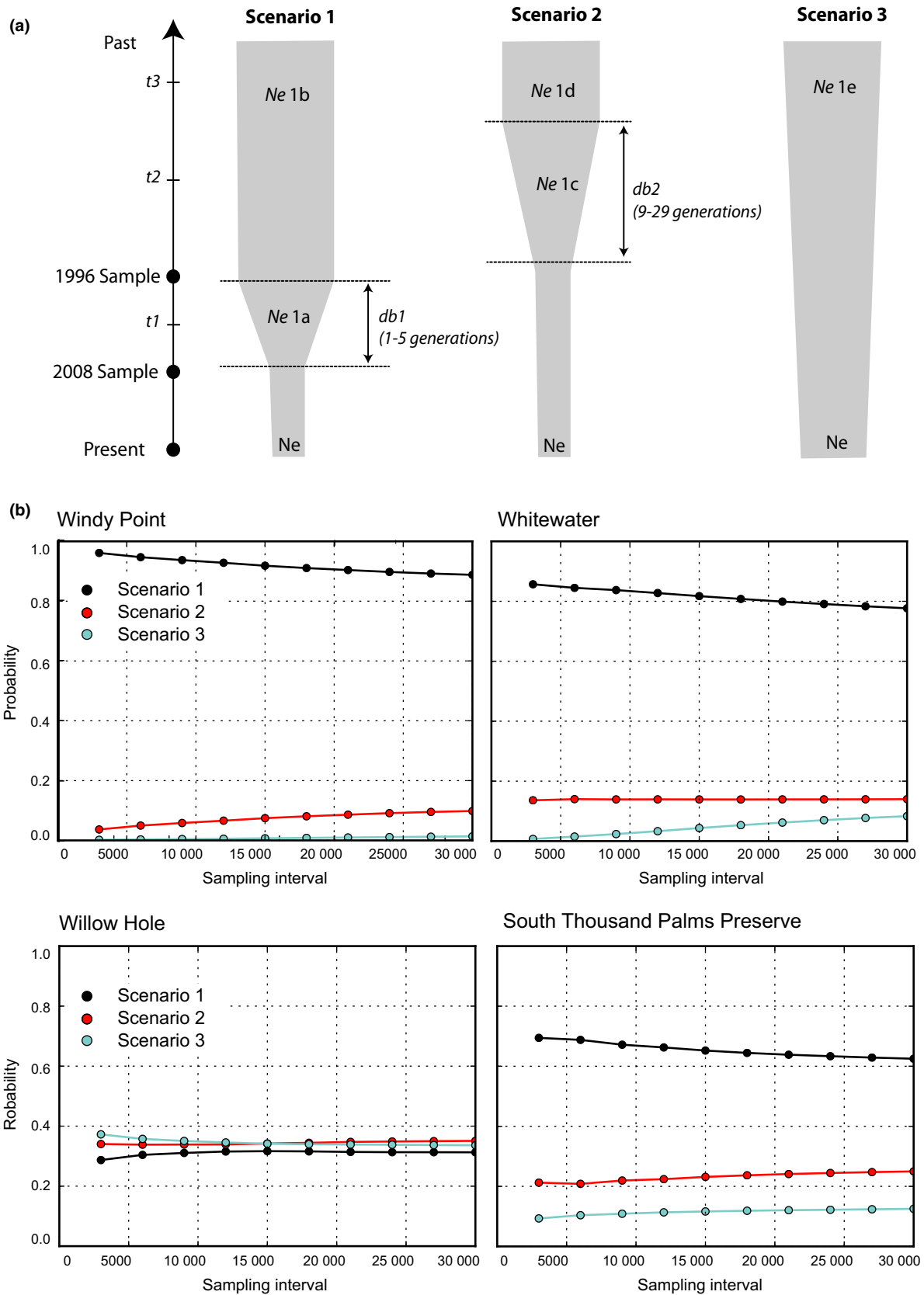
Figure 3 DIYABC modelling scenarios (a) and results (b) for the four main preserves sampled in both 1996 and 2008. The three modelled scenarios were ranked using the logistic regression approach Beaumont *et al.*, 2002), which sampled the 4×10^6 simulated datasets across 10 intervals and computed probability values for each scenario.

SMM (20, 40, 60 and 80%). These bounds were chosen based on reported empirical ranges for vertebrates (Peery *et al.*, 2012).

We estimated effective population sizes for the total 1996 sample and 2008 main preserves using two estimators. First, we used approximate Bayesian computation in ONeSAMP (Tallmon *et al.*, 2008), in which the observed estimates of eight population genetic summary statistics are compared to values obtained from simulated Wright–Fisher populations of known N_e. We specified lower and upper priors on N_e of 20 and 5000 and performed replicates to verify consistency. We also estimated N_e using the temporal method (utilizing both 1996 and 2008 data) in NeEstimator V2 (Do *et al.*, 2014; Plan II sampling scheme, sampled at 0 and 6 generations). Temporal N_e estimates are based on variances in change in allele frequencies over time. In simulations, ONe-SAMP outperformed temporal methods at estimating N_e in closed populations, but temporal methods performed better at estimating N_e in systems with gene flow. (Gilbert & Whit-lock, 2015). Finally, we compared 2008 estimates of N_e to abundance estimates based on tracking and mark–recapture surveys in 2008 (methods in Appendix S1). Because clustering results and geographic proximity suggested Windy Point and Train Station formed a single genetic cluster in 2008, we also estimated a combined N_e for these sites.

RESULTS

We identified 13 variable loci that amplified consistently (see Table S2). We genotyped 274 individuals (70 from 1996 and 204 from 2008) at all 13 loci. Two loci (TETZJ and TRI498) deviated significantly from HWE in most populations and were removed from subsequent analysis. All LD tests were non-significant after Bonferroni correction in both 1996 and 2008. We detected several full sibling relationships within the 2008 dataset (Windy Point, $n = 4$; Train Station, $n = 3$; Whitewater, $n = 7$; and Willow Hole, $n = 1$). None were detected between sites in 2008, nor in the 1996 dataset. We removed one individual from each sibship pair prior to running final analyses and the results are reported using this reduced 2008 dataset ($n = 189$).

Changes in genetic structure over time

Genetic structure among collection sites increased from 1996 to 2008. Bayesian clustering analyses of 1996 samples suggested that all collection sites comprised a single cluster (Figs 4a and S1). However, in 2008, three genetic clusters were detected (Figs 4b and S1). Individuals from western sites were assigned to two different clusters. The first comprised Windy Point, Train Station and West Indio, and Whitewater was assigned to the second. The eastern sites, Central Indio Hills and South Thousand Palms Preserve, were assigned to a third cluster, although these individuals shared ~30% of their overall membership probabilities with more western sites. Individuals at Willow Hole, the most

centrally located site, showed admixture of all three genetic clusters (Fig. 4b). 2008 clustering results did not appear to be sensitive to reduced sample size. In the 10 reduced sample size replicates, the optimal K varied between three and four clusters (Table S3). Average individual membership to each of the clusters at $K = 3$ was similar to those recovered from the full dataset, but $K = 4$ resulted in a non-informative grouping (a highly admixed fourth cluster) suggesting that the data were overfit at $K = 4$.

The main preserves were not significantly differentiated in 1996, both globally ($\theta = 0.012$, 95% CIs -0.007–0.032), and among population pairs (Table 2). However, in 2008, we detected significant genetic differentiation globally ($\theta = 0.041$; 95% CIs $0.027 - 0.054$) and among all population pairs (Table 2). 2008 global θ was robust to reduced sample size. In 1000 subsamples, global θ ranged from 0.016 to 0.07 with associated P-values ranging from 0.001 to 0.017. Pairwise estimates of θ varied more widely in sensitivity to reduced sample size. In particular, in all comparisons including Willow Hole, the upper 95%tile of θ included estimates near or below zero, with mean P-values >0.05 (Table S4). However, taken in total, these analyses suggest that the measured increases in population genetic structure cannot be solely attributable to larger sample sizes.

While we did not find isolation by distance in either sample period, θ among population pairs in 2008 averaged 2.25 times that in 1996 (Fig. 5). Significant pairwise genetic differentiation and a lack of isolation by distance can indicate a system dominated by genetic drift rather than gene flow (Slatkin, 1993; Hutchinson & Templeton, 1999).

Population declines

ABC analyses provided insight into the timing of population declines across the valley. Model comparisons suggested that Windy Point, Whitewater and South Thousand Palms Preserve have most likely experienced a reduction in effective population size (N_e) that occurred during the recent drought (scenario 1; Fig. 3b; Table S5). Posterior probability comparisons for the three historical scenarios consistently showed that scenario 1 had the highest statistical support and that scenario 3 (constant size) had the lowest statistical support. However, we could not differentiate among the three scenarios at Willow Hole (Fig. 3b). For Windy Point, Whitewater and South Thousand Palms Preserve, posterior model checking confirmed the fit of our model parameters for scenario 1 and the observed data (Fig. S2). The estimated type I and type II error rates for scenario 1 ranged from 0.14 to 0.22 and from 0.12 to 0.21, respectively, indicating moderately high confidence in scenario 1 as the best fit among the different models tested. Although large, the CIs around N_e in the preferred scenario overlapped with those calculated with other methods (see results below), and modes were similar in magnitude to the point estimates obtained with these methods (Table S5).

We found limited additional support for genetic bottlenecks with significant heterozygote excess in 2008 Whitewater
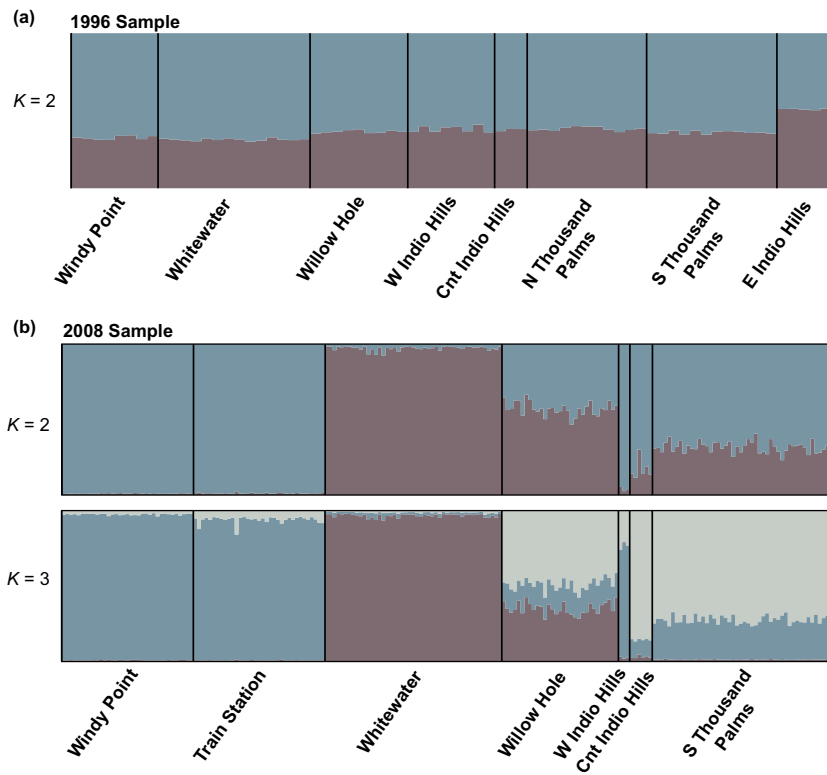
Figure 4 STRUCTURE results for 1996 (a) and 2008 (b) samples. For each sample period, the number of clusters was inferred on the basis of the posterior probability distribution of the data given a range of K (1–7; S4). In 1996, one genetic cluster was most highly supported, or, as pictured, complete admixture of two genetic clusters across individuals and sites. In 2008, up to three genetic clusters were supported; higher K values resulted in non-informative grouping of allelic information.

Table 2 Pairwise estimates of population differentiation (θ; Weir & Cockerham, 1984) between main preserves in 2008 (above diagonal, bolded) and in 1996 (below diagonal). Train Station was not sampled in 1996. All 2008 samples were significantly differentiated from one another with P values <0.001 (Bonferroni corrected P-value = 0.005 for α = 0.05). None of the 1996 samples were significantly differentiated after Bonferroni correction.

Preserve	Windy Point	Train Station	Whitewater	Willow Hole	South Thousand Palms
Windy Point	–	**0.027**	**0.078**	**0.051**	**0.046**
Train Station	NS	–	**0.069**	**0.051**	**0.051**
Whitewater	−0.007	NS	–	**0.014**	**0.039**
Willow Hole	0.011	NS	0.013	–	**0.018**
South Thousand Palms	0.019	NS	0.023	0.002	–

NS, Not sampled.

and 1996 North Thousand Palms under both the IAM, and a small range of TPM (Table S6). The most consistent bottleneck signature was detected at North Thousand Palms, which was no longer occupied in 2008.

Genetic diversity and N_e

Despite recovering signatures of increased genetic differentiation, and recent declines in N_e, similar levels of adjusted allelic richness were measured in total across the 4 main preserves in 1996 (3.836) and 2008 (3.844; P = 0.532 from 1500 permutations). When each preserve was examined individually, only Whitewater showed a significant decline in allelic richness between sampling periods (mean of paired differences = −0.3759, t-statistic = −1.855 w/10 df,

$P \leq 0.0466$; Table S7). Average relatedness among individuals within sites varied over the two sampling periods and was significantly greater than expected by chance in sites southwest of the Railroad and I-10 corridor, and in the smaller, isolated sites within the Indio Hills (Table 1).

The genetic effective population size (N_e) estimate for the total population in 1996 was 141, whereas in 2008, the main preserves ranged from 31 (Whitewater) to 143 (Willow Hole). Although N_e point estimates differed between estimators and were generally higher using the temporal method, the confidence intervals obtained with both estimators overlapped within all preserves except Willow Hole (Table 3). At three of the five sites (Train Station, Whitewater and Willow Hole), 95% upper CIs for 2008 ONᴇSAMP estimates were <100 and less than the lower CI for the total population in

1996. Abundances extrapolated from density estimates in 2008 were also lowest at Train Station and Willow Hole and of similar magnitude to N_e estimates. At the three remaining sites (Windy Point, Whitewater and South Thousand Palms), abundances were at least an order of magnitude higher than N_e estimates. In 2008, Windy Point and South Thousand Palms Preserve retained relatively high N_e, with upper confidence intervals exceeding 100 for both estimators (Table 3).

DISCUSSION

Emerging genetic structure

Our study indicates that changes in the distribution of genetic diversity in *U. inornata* are underway across the Coachella Valley. We hypothesized that habitat fragmentation and drought could act to increase among-site genetic structure and reduce within-site diversity. Our results provide strong support for the first hypothesis and moderate support for the second. The differences in cluster assignment and increased global and pairwise estimates of genetic differentiation suggest gene flow among populations has been
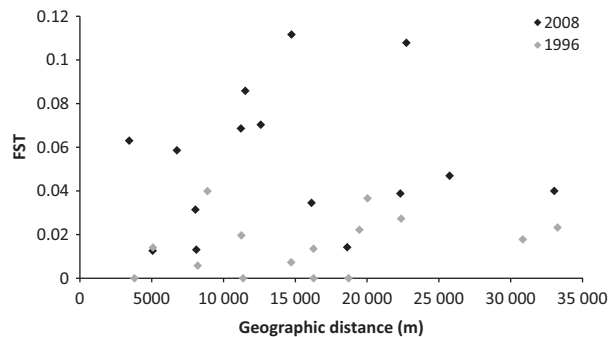

Figure 5 Genetic differentiation (θ) among pairs of populations plotted by geographic distance among populations. Pairwise genetic differentiation increased from 1996 to 2008, without isolation by distance.

disrupted. The formation of significant population genetic structure over such a short time frame (5–10 generations) is striking. This observed rapid accumulation in allele frequency differences among sites was likely a result of increased genetic drift following reductions in population size associated with the drought coupled with a reduction in movement and gene flow among sites caused by fragmentation.

Prior to habitat fragmentation, high recolonization and gene flow rates among active dunes likely imparted resiliency to local extinction and genetic drift caused by previous rainfall fluctuations and local disturbances, resulting in a panmictic metapopulation (Hedtke *et al.*, 2007). Despite the fact that significant loss and fragmentation of habitat began roughly 50 years before initial genetic sampling, *U. inornata* populations were genetically homogenous in 1996. This is not surprising, as large local population sizes can buffer the effects of drift (Wright, 1978), leading to significant lag times in detectability of genetic differentiation in fragmented populations (Richmond *et al.*, 2009). However, monitoring indicated that *U. inornata* population sizes and reproductive rates decreased dramatically during the 1999–2004 drought, and extirpations of several small populations were also documented (Barrows & Allen, 2007). These findings, plus evidence of genetic bottlenecks timed with the drought in some local populations, lend support to our hypothesis that genetic structure emerged via rapid genetic drift during the drought. Although census population sizes increased leading up to the 2008 sampling in response to several subsequent years of above-average rainfall (Fig. 2b), genetic structure remained, suggesting that habitat fragmentation may currently prevent genetic rescue and recolonization of extirpated sites. Furthermore, emerging genetic structure is spatially concordant with patterns of development and loss of sand habitat. Populations to the west of the Interstate 10/railroad alignment, for example, are generally more genetically distinct and have higher intrapopulation relatedness than to the east of this break. Thus, it appears that neither fragmentation nor drought alone induced rapid emergence of genetic structure in *U. inornata*, but in combination, led to a measurable effect.

Table 3 Effective population size point estimates and 95% confidence intervals estimated from the total 1996 sample, and 2008 major preserves using ONeSAMP and from 1996 to 2008 samples using the temporal method of Jorde & Ryman (2007). Average mark–recapture and track-based density estimates made in 2008 are shown (See Appendix S1 Tables S1, S4 and 5). Numbers after slashes indicate densities in lower quality habitat. Abundance per site was calculated as density × estimated ha occupied.

Year/ Sample sites	ONeSAMP N_e	Temporal N_e	2008 Adult density (No. ha^{-1})	2008 Density from tracks (No. ha^{-1})	2008 Adult abundance per site (MR - track survey)
1996 Total	140.9 (98.5–399.7)				
2008 Windy Point/ Train Station	213.0 (128.8–983.9)	—	—	—	—
2008 Windy Point	91.7 (52.3–141.8)	84.7 (50.3–128.0)	7.93	21	975–2583
2008 Train Station	44.4 (37.0–71.3)	—	7.69	6	36–46
2008 Whitewater	31.3 (27.7–39.7)	47.1 (25.8–272.1)	—	6	948
2008 Willow Hole	32.5 (28.6–45.1)	142.5 (88.8–208.7)	8.93	17	63–122
2008 South Thousand Palms	79.0 (55.8–166.9)	101.5 (59.9–331.4)	20.44	27/2	3332–5249

Other studies have also demonstrated that among-site divergence can increase following disturbance on ecological time-scales. For example, Evanno *et al.* (2009) showed that F_{ST} values among populations of freshwater snails increased over a two-year period following severe drought that reduced population sizes. Similarly, genetic differentiation increased between 1944 and 1997 in brown trout likely as a result of population reduction due to drought (Ostergaard *et al.*, 2003), and habitat fragmentation coupled with wildfire led to a rapid decay in genetic diversity of a population of endangered possums (Mitrovski *et al.*, 2008). Empirical data on disturbance impacts to genetic structure are rare, however, because of the scarcity of before and after sampling (Banks *et al.*, 2013). Our work and these recent studies suggest that disturbance has the potential to alter genetic structure among populations over short time periods, and points to the usefulness of sampling over time (genetic monitoring) to detect changes that may be important from a conservation perspective.

Genetic diversity

Despite recovering increased genetic structure and signatures of population declines in some preserves, we detected a significant decline in allelic richness only at Whitewater. However, an eventual loss of genetic diversity may be anticipated at all sites if connectivity is severed. There are several possible explanations for lack of detection. First, we may simply lack power to detect change. Sample sizes were lower in 1996 than in 2008, ranging from eight to 14 individuals vs. 31 to 47. Although we used rarefaction to account for this difference, these sample sizes may be too small to accurately estimate richness. When rarefied to ≤8, loss of allelic richness at Whitewater is no longer statistically supported (*e.g.* Table 1). A small number of loci may also limit detectability (Hoban *et al.*, 2014). Second, theoretical, simulation and empirical studies have shown that population subdivision will affect genetic differentiation more rapidly than diversity (Latter, 1973; Varvio *et al.*, 1986; Keyghobadi *et al.*, 2005). Third, rapid demographic recovery through increased reproductive output following droughts may act to reduce loss of genetic variation. Observed lizard densities range from <1 per ha during droughts to >100 per ha during wet periods; Fisher & Muth, unpubl. data; Barrows, 2006. If the maintenance of genetic diversity that we measured at three of the four main preserves is reflective of genomic diversity, this may bode well for *U. inornata* recovery, because it suggests that restoration and management actions can be implemented while diversity is still relatively high.

N_e and conservation implications

Long-term maintenance of genetic diversity is a listed recovery criterion for *U. inornata* (U.S.F.W.S., 1984). The observed loss of genetic connectivity over a 12-year period, loss of genetic diversity in one site and low effective population sizes for most sites suggest that this goal is not being met. Therefore, it may be appropriate to enact further management actions to ameliorate changes. Recent literature reviews have suggested $N_e > 100$ is needed to avoid the effects of inbreeding depression and fitness loss, and $N_e > 1000$ to maintain adaptive potential to environmental change (Willi *et al.*, 2006; Frankham *et al.*, 2011; Weeks *et al.*, 2011). In all populations, our empirical estimates of N_e fall below this upper threshold of $N_e > 1000$, and in three of the five main preserves (Train Station Whitewater and Willow Hole), the ONeSAMP upper 95% CIs fall below the lower threshold of $N_e > 100$. However, genetic estimates of N_e can be biased when model assumptions are violated. For instance, sampling populations with overlapping generations can lead to downwardly biased effective sizes (Waples & England, 2011; Ryman *et al.*, 2014; Waples *et al.*, 2014), although Waples *et al.* (2014) suggested that this bias may be negligible in species with a generation length ≤3 years and when mixed cohorts are sampled. Both factors likely apply to our study. Actions to increase N_e in the major preserves could include habitat restoration at existing sites, and/or restoration of genetic connectivity among sites. Connectivity could be increased through habitat restoration of movement corridors, re-establishment at unoccupied sites to provide stepping stones, or translocation among existing local populations.

One possible concern with restoring connectivity among subdivided populations is disruption of local adaptation (Kawecki & Ebert, 2004). This may be relevant in the Coachella Valley where an east-west climate gradient has been shown to impact occupancy across the valley (Barrows & Allen, 2007). Local adaptation will be important to investigate in *U. inornata*. However, extinction risks and inbreeding depression may outweigh risks of outbreeding depression when population subdivision is a recent phenomenon (Templeton *et al.*, 1990; Frankham *et al.*, 2011), and low levels of gene flow (<20% of recipient population size) should not swamp adaptive alleles (Hedrick, 1995; Lopez *et al.*, 2009). Rates of translocation of one (breeding) migrant per generation may be enough to counter inbreeding depression (Mills & Allendorf, 1996; Weeks *et al.*, 2011), but greater rates (up to 20%) may be necessary when populations fluctuate in size (Vucetich & Waite, 2000).

CONCLUSIONS

We documented a rapid increase in population genetic structure and more limited evidence of a decline in genetic diversity likely due to habitat fragmentation and severe drought in a previously panmictic species. Emergence of genetic structure joins occupancy, density, habitat and hydrological evidence supporting that *U. inornata* has undergone a state change from a well-connected metapopulation to a collection of more isolated units. Long-term conservation of the species may benefit from management actions aimed at restoring connectivity. More broadly, our study highlights that distur-

bance can alter genetic structure relatively quickly and that periodic genetic monitoring can provide the pre- and post-disturbance samples needed to quantify this change. Resulting information can then be used to assess the status of rare species. Genetic monitoring will likely be necessary for modern day adaptive management in an age when habitat fragmentation is widespread and disturbance regimes are changing at unprecedented rates as a result of climate change.

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DATA ACCESSIBILITY

Genotypic and sample data are available in tabular format from the Dryad Digital Repository: (http://dx.doi.org/10.5061/dryad.30t5b).

SUPPORTING INFORMATION

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

Appendix S1 Abundance estimates methods and results.

Table S1 DIYABC parameters and priors.

BIOSKETCH

Amy G. Vandergast is a USGS research geneticist, stationed in San Diego. She applies genetic analyses to support conservation and management of rare species and landscapes. Author contributions: A.G.V., D.A.W., T.J.G. and A.R.T. conceptualized the study. A.R.T., M.F., T.J.G. and D.A.W. collected samples. A.R.T., M.F., C.W.B. provided density estimates. D.A.W. performed laboratory work. A.G.V., D.A.W. and A.R.T. conducted genetic analyses. A.G.V., D.A.W. and A.R.T. wrote the manuscript with contributions from M.F., C.W.B. and T.J.G.

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