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TITLE: Factors affecting intra-island genetic connectivity and diversity of an abundant and widespread island endemic, the San Clemente Island night lizard.

Stephen E. Rice[1] (SER) and Rulon W. Clark[1] (RWC)

1. San Diego State University, Dept of Biology, 5500 Campanile Drive, San Diego, California, 92182

KEYWORDS: landscape genetics, Xantusia, Channel Islands, microsatellites, isolation by resistance

CORRESPONDING AUTHOR:

Stephen E. Rice, San Diego State University, Department of Biology, 5500 Campanile Drive, San Diego, California, 92182-4614. Fax: (619) 594-5676. Email: srice001@ucr.edu

RUNNING TITLE: Landscape genetics of *Xantusia riversiana*

ABSTRACT

Habitat fragmentation and loss are fundamental conservation concerns. Because protected areas are often "habitat islands" isolated by human development, studies of physical islands which document genetic patterns associated with natural versus anthropogenic fragmentation may provide insight into the management of anthropogenic habitat islands. The San Clemente Island night lizard, *Xantusia riversiana reticulata*, is a highly abundant endemic to two California Channel Islands (San Clemente and Santa Barbara Islands), each with a history of anthropogenic

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disturbance, and was recently delisted from the Endangered Species Act. We genotyped 917 individuals at 23 microsatellite loci to estimate genetic divergence between collection sites and identify natural and anthropogenic landscape features correlated with genetic divergence for *X. r. reticulata* throughout its range. Genepool delineation resulted in each well-sampled collection site acting as a distinct population, pairwise Fst values were small but significant, and STRUCTURE detected 2 populations on San Clemente Island and 4 populations on Santa Barbara Island. Active sand dunes on San Clemente Island acted as a barrier whereas cholla phase maritime desert scrub, secondary roadways, and canyons > 500ft in length acted as resistant surfaces. Resistant surfaces on Santa Barbara Island were woolly seablite, crystalline iceplant, barren ground, and herbaceous vegetation. Conductance models included California boxthorn and prickly pear cactus on both islands with additional minor features unique to each island. We recommend the application of conductance and resistance models within "habitat islands" to better inform management for species persistence when the intervening habitat between reserves cannot be improved.

INTRODUCTION

The ecological impacts of anthropogenic activity are a focal concern of conservation biology (Fordham *et al.* 2013; Regan *et al.* 2010). Species are vulnerable to the effects of human-mediated habitat changes (e.g. habitat fragmentation and loss) which can act synergistically with altered fire regimes and climate change to increase population and species-level extinction risks (Keith *et al.* 2008; Regan *et al.* 2010; Swab *et al.* 2012). A common conservation paradigm presents isolated habitat patches as hospitable islands surrounded by an inhospitable matrix, similar to oceanic islands, although species' responses to the matrix can vary even among closely related syntopic species (e.g. Hokit *et al.* 1999; Ricketts 2001; Prugh *et al.* 2008). Additionally,

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isolated fragments within the same region may be managed independently by different agencies bereft of the ability to modify the intervening matrix. Studies which provide a generalizable approach to identify common mitigation strategies with site-specific landscape influences may prove invaluable in the management of fragmented and isolated habitat patches. These small isolated patches may function similarly to small oceanic islands with histories of anthropogenic disturbance.

The California Channel Islands are small oceanic islands off of the coast of Southern California which may yield insight into the effects of habitat fragmentation and alteration given the constraints of inhabitable area, isolation from potential source populations, and long-term natural fragmentation and recent anthropogenic modifications of the native habitat on each island. Oceanic islands are often considered natural laboratories in which evolutionary processes can be studied in closed systems, under more well-defined spatial and temporal scales. Additionally, due to their limited sizes and isolated nature, island ecosystems may be highly susceptible to ecological disturbances (e.g. Biber 2002; Gillespie *et al.* 2008; Harradine *et al.* 2015). By quantifying the contemporary genetic patterns of island endemics, researchers can provide a baseline for monitoring efforts (sensu Schwartz *et al.* 2007; reviewed in Stetz *et al.* 2011), a framework for investigating the potential effects of management actions or habitat modifications, and the tools to infer potential effects of environmental change in the near-future (e.g. Row *et al.* 2014). Furthermore, research on islands can also inform conservation and management science by providing comparisons with fragmented mainland ecosystems, which often operate as “habitat islands” due to changes in community composition, connectivity, and decreased population sizes (e.g. Hokit *et al.* 1999; Driscoll 2004; Wang *et al.* 2009). For organisms distributed both on the mainland and islands, studies of island systems may identify patterns related to metapopulation

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connectivity (e.g. Harradine *et al.* 2015) or may further identify management actions on the mainland to improve species persistence and the maintenance of genetic diversity in small patches. Additionally, studies on islands with a history of anthropogenic modifications, such as the introduction of grazing animals or invasive species, may identify vital resources for protection and allow for the investigation of broader questions regarding species persistence, interdependent relationships among native species, and ecosystem "economics" (e.g. Leigh *et al.* 2009).

Reptiles are an excellent group for studies of fragmentation due to their intermediate dispersal distances, relatively high population densities, tightly coupled habitat associations, plasticity of responses even across closely related species, thermal physiology, and vulnerability to habitat modifications (e.g. Hokit *et al.* 1999; Jordan & Snell 2008; Wang *et al.* 2009; Tseng *et al.* 2015). Projections indicate 11-49% of endemic reptiles will face extinction in the coming decades (Thomas *et al.* 2004; Urban *et al.* 2014) and a study by Sinervo *et al.* (2010) estimated a global loss of 30% of all lizard species by 2080 due to thermal physiology alone. Therefore even for highly abundant species within a confined area, dispersal limitations paired with habitat sensitivity could lead to a range of evolutionary trajectories along a continuum of extinction to fine-scale speciation (e.g. Gillespie *et al.* 2008; Tseng *et al.* 2015).

The island night lizard, *Xantusia riversiana* (Cope 1883), is an endemic to 3 California Channel Islands: Santa Barbara Island, San Clemente Island, and San Nicolas Island (Fig. 1). *Xantusia riversiana* was delisted from its threatened status under the Endangered Species Act in May 2014 by the United States Fish and Wildlife Service (USFWS 2014); delisting requires the monitoring of populations and prime habitat on each island over the next decade. Two subspecies have been recognized on the basis of morphological differences (Smith 1946): the San Nicolas Island night lizard (*X. r. riversiana*) and the San Clemente Island night lizard (*X. r. reticulata*),

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which occurs on San Clemente and Santa Barbara Islands. The current island night lizard population is estimated at 21.35 million individuals with 99.85% (21.3 million) occupying San Clemente Island and the remainder of the population split between Santa Barbara Island (0.08%, 17,600) and San Nicolas Island (0.07%, 15,300) (USFWS 2014).

Each island is characterized by a Mediterranean climate with differences in island size, total precipitation, and average temperatures. Island sizes are markedly different with San Clemente Island being the largest (15,054 ha), followed by San Nicolas Island (5,698 ha) and Santa Barbara Island (259 ha) (USFWS 2014). Each island has a history of habitat degradation and disturbance from anthropogenic activities, such as the introduction of grazing animals and non-native vegetation. Plant assemblages on the islands are similar with California boxthorn (*Lycium californicum*), prickly pear cactus (*Opuntia littoralis*), and rocky areas supporting the greatest lizard abundances (Fellers & Drost 1991; Mautz 1993). Prime habitat dominated by California boxthorn or prickly pear cactus support densities in excess of 1,400 individuals/ha on San Clemente Island and in excess of 3,200 individual/ha on Santa Barbara Island (Fellers & Drost 1991; Mautz 1993). On San Clemente Island, lizards are found in all habitats except for deep canyons, sand dunes, and canyon woodland (Mautz 1993). On Santa Barbara Island, lizards are found primarily in prime habitat to the exclusion of grasslands (Fellers & Drost 1991).

Even though the island night lizard is locally abundant, several life history traits make this long-lived species potentially vulnerable to habitat change and fragmentation: slow growth, late maturity, vivaparity, and very low dispersal distances (Fellers & Drost 1991; Mautz 1993). We utilized microsatellites with clustered sampling at collection sites across each island to investigate population substructure and contemporary landscape correlates of genetic differentiation of the San Clemente Island night lizard throughout its range. Due to the large estimated population size

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and relatively small area of each island, we expected to find little-to-no genetic differentiation between collection sites within each island and a single population on each island. We anticipated that any detected genetic divergence between collection sites on each island would be best described by a pattern of isolation by distance due to limited movement distances, averaging 3 m (Mautz 1993), and isolation by resistance when analyzing landscape features. We tested isolation by resistance models of landscape conductance, which modeled landscape features as facilitating movement expressed as decreased effective distance between collection sites relative to patches best described as geographic distance. We also modeled landscape resistance with landscape features as resistant surfaces which increased the effective cost between collection sites. Conductance and resistance models focused initially on relevant habitat identified by ecological studies (Fellers & Drost 1991; Mautz 1993) followed by statistical optimization of conductant and resistant surfaces from existing GIS data for each island. To support post-deslistment monitoring, we also estimated population genetic parameters for each collection site to develop baselines for future comparisons.

MATERIALS AND METHODS

Field Sites and Sample Collection

Sample collection was conducted on San Clemente Island from February through November of 2013 and Santa Barbara Island from May through September 2015. Collection sites on San Clemente Island (Fig. 2 and Fig. S1, Supporting information) were selected to provide systematic coverage of the island from the airport terminal to the southern end of the island as well as contrasts at different scales near features of interest, such as roadways, sand dunes, and areas of habitat transition. Collection sites on Santa Barbara Island (Fig. 3 and Fig. S2, Supporting information) were chosen to represent systematic sampling across the maximum

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distance of the island and to investigate areas of habitat transitions. Hence, sites were not randomly chosen and were selected based on distance from previous sites, suitable habitat to support field collections, and investigation of features of interest.

Island night lizards were captured by turning cover items and setting live traps in prime habitat along well-worn trails. When multiple lizards were encountered, we made attempts to capture and sample all lizards. Target sample size for each collection site was a minimum of 30 individuals (Hale *et al.* 2012). Captured lizards were processed following the United States Geological Survey herpetofaunal monitoring protocols (Fisher *et al.* 2008), sex was determined by probing lizards ≥ 60 mm snout-vent length (Fellers & Drost 1991) and GPS coordinates were recorded with hand-held units with an estimated accuracy of 5 m. Tissue samples consisted of toes that were clipped at the distal knuckle, which also served as a unique 4-digit identification, and a 10 mm segment from the tail tip. Tissues were preserved in 95% ethanol and stored at -20°C.

Sampling and Genotyping

We collected tissue samples from 605 island night lizards from 18 collection sites on San Clemente Island and 312 island night lizards from 7 collection sites and 3 smaller opportunistic areas on Santa Barbara Island. We extracted DNA from preserved tissues with a standard salt digestion (Appendix S1) and genotyped individuals at 23 polymorphic microsatellite loci (Rice *et al*. 2016) arranged into 8 reactions (Appendix S1 and Table S1, Supporting information). We scored alleles twice with GENEMAPPER vers 4.0 (Applied Biosystems) for consistency; loci missing data or with inconsistent allele calls were reamplified and rescored to generate a consensus genotype. We performed a second round of genotyping beginning with DNA

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extraction for 35 individuals on San Clemente Island and 16 individuals on Santa Barbara Island to assess error rates associated with allele calls (Pompanon *et al.* 2005).

Quality Control

We removed individuals from analyses if amplification was successful at less than 16 loci. We then constructed a relatives removed data set for each island by identifying inferred first-order relatives (full-sibling, parent-offspring) through a consensus approach. Pairwise relationships were inferred for samples within each collection site and were considered first order relatives when at least 2 of 3 methods inferred the relationship. The methods we chose for inference were COLONY vers 2.0.5.9 (Jones & Wang 2010) under three high-precision medium-length full-likelihood runs, CERVUS vers 3.07 (Kalinowsi *et al.* 2007) under parent pairs with known sexes, and COANCESTRY vers 1.0.1.5 (Wang 2011) with the DyadML estimator and a threshold determined by simulating 2000 known relationships from empirical data. Individuals were removed from the dataset to retain the largest sample size.

The relatives removed data set was used to evaluate the suitability of loci for analyses following the recommendations of Selkoe and Toonen (2006) for each island. We used collection sites as populations in all quality control procedures. We examined loci for linkage disequilibrium (LD) and conformance to Hardy-Weinberg and random mating proportions (HWE) in GENEPOP vers 4.5 (Rousset 2008) with p-values corrected for multiple comparisons through sequential Bonferroni testing (Holm 1979). The presence of null alleles was assessed with MICROCHECKER vers 2.2.3 (Van Oosterhout *et al.* 2004). We examined the putative neutrality of loci with the program LOSITAN (Beaumont & Nichols 1996; Antao *et al.* 2008) under the infinite alleles model with neutral Fst estimation. Loci were removed if they failed to amplify in fewer than 75% of individuals, were identified as under selection by LOSITAN, contained null

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alleles in a majority of sampled sites, or when identified as in linkage disequilibrium with another locus. The data for all further analyses consisted of the relatives removed data set. We utilized the package diveRsity (Keenan *et al.* 2013) in the R statistical environment (R Core Team 2016) and GENEPOP to generate summary statistics for each collection site and each island based on the overall loci retained for each respective data set (Table S2, Supporting information).

Population Structure

We utilized the approach of Waples and Gaggiotti (2006) to delineate genepools on each island. We conducted an exact test for genetic differentiation for all pairs of collection sites in GENEPOP. We combined probabilities with Fisher's method (Fisher 1932) using 0.0001 as the lower bound for individual test probabilities; combined probabilities were corrected using sequential Bonferroni testing. Collection sites were aggregated if no significant difference was found and the procedure was repeated until all pairwise comparisons were significant.

We estimated the degree and significance of genetic differentiation among collection sites with ≥ 20 individuals by calculating pairwise Fst estimated by Weir and Cockerham's Θ (1984) with 95% bias corrected confidence intervals generated by 1000 bootstraps over individuals in the R package diveRsity. We defined differentiation as significant when the confidence interval did not overlap 0.

We used the program STRUCTURE vers 2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003) to estimate the number of populations on each island using data from all collection sites. STRUCTURE was run with a K of 1 to 18 for San Clemente Island and K of 1 to 10 for Santa Barbara Island. Analyses for both island consisted of 20 runs with a 500,000 burn-in period and 1,000,000 MCMC iterations under the admixture model with uncorrelated and correlated allele frequency models (Pritchard *et al.* 2010). We used the Evanno *et al.* (2005) method as

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implemented in STRUCTURE HARVESTER (Earl & vonHoldt 2012) to estimate the number of populations. We generated the ancestry matrix for individuals and for each collection site with the greedy algorithm in the program CLUMPP vers 1.1.2 (Jakobsson & Rosenberg 2007); barplots were generated with the program DISTRUCT vers 1.1 (Rosenberg 2004) for the best supported value of K for each island.

Additionally, we utilized the multivariate technique Discriminant Analysis of Principal Components (DAPC, Jombart *et al.* 2010) as implemented in the R package adegenet (Jombart 2008) to assess the number of genetic clusters useful for statistically classifying the data. We used sequential k-means clustering as implemented with the *find.clusters* function and retained all principal components. The number of clusters chosen for each island corresponded to the lowest value(s) for the Bayesian Information Criteria. The results of k-means clustering were used as group assignments for DAPC analyses, in which we retained 150 principal components for analyses and all eigenvalues.

Isolation by Distance and Isolation by Resistance Analyses

We examined landscape features correlated with pairwise genetic distance between collection sites on each island using an isolation by resistance framework to model conductance and resistance (IBR, McRae 2006). The accepted null model in explanations including landscape-level correlates is a pattern of isolation by distance (IBD, Wright 1943) which is the observation of spatial autocorrelation within the genetic data, i.e. individuals/populations that are closer in geographic space are less differentiated (reviewed in Meirmans 2012). The IBR framework models pairwise connectivity with circuit theory; connectivity is modeled as current among nodes (collection points) or regions across all possible paths. Circuit theory can be applied in a spatially-explicit manner through a raster map which expresses the relative cost of movement

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across a raster cell as a resistance or conductance cost relative to 1. In resistance modeling, the greater the cost the more movement across that cell is penalized and effective distance is increased; in conductance models the greater the number the easier movement becomes and effective distance is reduced. Models use a reference value of 1, which denotes neither conductance nor resistance within a raster cell and approximates log-transformed geographic distance (Lee-Yaw *et al.* 2009).

To assess the degree and significance of IBD on each island we employed non-parametric rank-based multiple regression on distance matrices (MRDM, Lichstein 2007) using the function *MRM* in the R package ecodist (Goslee & Urban 2007) with 10,000 permutations, pairwise Fst as the response variable, and pairwise Euclidean distance as the predictor. As an extension of the Mantel test framework, results of MRDM are comparable to Mantel results with a single predictor matrix. We employed CIRCUITSCAPE version 4.0.5 (McRae & Beier 2007) for IBR analyses in which we modeled conductance and resistance of landscape elements separately on each island. Only those collection sites with at least 20 individuals in the relatives removed data set were included in IBD and IBR analyses.

The methods used to construct habitat resistance rasters and evaluate model fit were consistent between islands; however, the resolution of the data and the thematic content of GIS layers differed due to coarseness of GIS data. Input rasters were made within QGIS vers 2.12.3 (QGIS Development Team, 2016). Resistance values for each investigated feature ranged from conductance values of 100, 50, and 2 (equivalent to resistance values of 0.01, 0.02, and 0.5 respectively) to resistance values of 2, 50, and 100 (Table S5 and Table S6, Supporting information). Collection sites were represented as focal regions of the minimum-spanning convex hulls generated from capture coordinates.

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We utilized non-parametric MRDM with 10,000 permutations to assess categorical features for each island in models ranging from single features to full models of all statistically supported features. Feature inclusion proceeded in a stepwise fashion. Single features entered the model-building framework (Appendix S2) if their inclusion was significant and the coefficient of determination (R^2) was greater than the null model. The null model consisted of all features with a resistance value of 1. Resistance-distance matrices for single factor models were used to estimate the regression effect of higher-order models with MRDM (Appendix S3). We constructed the top 10% of estimated models for each GIS layer and additive models across GIS layers for each island. In additive models, raster cells had either a cumulative value based on the presence of all features in the cell, values for each distinct feature class, or 1 when no focal feature was present.

Final selection of resistance and conductance models was performed separately through a consensus approach which considered the ranked-order of best models across MRDM, corrected AIC, and marginal R^2_β. We used the *lmer* function in the R package lme4 (Bates *et al.* 2015) to construct maximum-likelihood population effects (MLPE) models (Clarke *et al.* 2002) fit with residual maximum likelihood (REML) estimation with collection site as a random factor. We used the *KRmodcomp* function in the R package pbkrtest (Halekoh & Højsgaard 2014) to calculate the marginal $R^2_\beta$of Edwards *et al.* (2008) from the MLPE models (Appendix S3). Corrected AIC was calculated with the R package MuMIn (Bartoń 2016) for MLPE models fit without REML estimation, as variables contributing the fixed effects differed between models (reviewed in Van Strien *et al.* 2012).

San Clemente Island

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Resistance-based analyses of San Clemente Island focused on three layers: vegetation classification (RECON, Inc 2012), roadway classification (Naval Facilities and Engineering Command South West (NAVFACSW), date unknown), and canyon classification (NAVFACSW, date unknown). We estimated the coarseness of resolution of the GIS data to be 1 ha, therefore all rasters were produced with 100 m cell sizes.

The vegetation layer was parsed into 11 classes based on least-cost transect analyses groupings (Fig. S1, Supporting information). Due to a strong signal of genetic differentiation we investigated different null models for IBR analyses (see results), and chose the null model best supported by MRDM analyses which modeled active sand dunes as an absolute barrier. The habitat area of active sand dunes was included as an absolute barrier in all maps, including those of roadways and canyons. There are two types of roads on San Clemente Island: paved roads, which serve as primary traffic conduits along the spine of the island and within more populated areas, and secondary roads, which are unpaved access roads (Fig. S1, Supporting information). We applied a 5 m buffer to all road types to eliminate breaks in the linear features when rasterized. Canyons were divided into three length classes of small (0-499 ft), medium (500-999 ft), and large (≥ 1000 ft).

Santa Barbara Island

Resistance-based analyses of Santa Barbara Island focused on three layers: vegetation classification (National Park Service (NPS), 2010) (Fig. S2, Supporting information), western seagull (*Larus occidentalis*) nesting sites which can cover large areas of the island, and home range of a resident population of barn owls (*Tyto alba)*, a potential predator. There are no roads on Santa Barbara Island. Vegetation was classified into 14 groups based on dominant vegetation alliances; due to observations of woolly seablite (*Suaeda taxifolia*) provisional shrubland alliance

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transitioning seasonally into crystalline iceplant (*Mesembryanthemum crystallinum*) dominated habitat (pers. comm., Rodriguez 2016) we grouped these vegetation alliances into a single class. The presence of western seagull nesting colonies was included in resistance analyses by digitizing seabird nesting locations from 2015 (NPS 2015); classifications were presence/absence with presence assigned the full range of resistance values and absences given a value of 1 (data not shown). The presence of barn owls was digitized from Figure 1 of Thomsen *et al.* (2014) and classified as presence/absence as with the western gull resistance analysis (data not shown). Resolution on vegetation data was listed as 1 ft (NPS 2010), however our capture coordinates had an error of up to 5 m, consequently raster maps were generated with a cell size of 5 m for all layers.

RESULTS

Quality Control and Summary Statistics

Three loci were removed from the San Clemente Island data set and 2 loci from the Santa Barbara data set, resulting in 20 loci for San Clemente Island and 21 loci for Santa Barbara Island (Table S1, Supporting information). No loci were discarded due to LD or non-robust amplification. Three different loci on each island differed significantly from HWE; however, these loci were not removed on this finding alone. A single locus (Xari22) was removed due to null alleles in 12 of 18 collection sites on San Clemente Island; no loci were removed from the Santa Barbara Island data set due to null alleles. The program LOSITAN identified 2 loci (Xari33, Xari44) as under selection for San Clemente Island and 2 loci (Xari18, Xari30) as under selection for Santa Barbara Island. These loci were removed from further analyses.

The error rates associated with our genotyping for San Clemente Island were 0.062% per allele and 0.272% per allele for Santa Barbara Island; overall rates of non-robust amplification

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were 7.14% for San Clemente Island and 3.80% for Santa Barbara Island. We removed 18 individuals from the San Clemente Island data set due to missing data; no individuals were removed from the Santa Barbara Island data set for this reason. The consensus approach revealed 75 first-order relationships among 114 individuals on San Clemente Island, 53 of these were removed. On Santa Barbara Island, 65 first-order relationships among 97 individuals were identified; 41 of these individuals were removed from the data set. These removals resulted in sample sizes for all further analyses of 534 individuals from San Clemente Island and 271 from Santa Barbara Island.

Sample sizes for San Clemente Island collection sites ranged from 12-70 individuals. Rarefied allelic richness based on all collection sites ranged from 5.46 to 9.31; excluding the only collection site with fewer than 20 individuals allelic richness ranged from 6.28 to 11.0. Observed heterozygosity ranged from 0.62 to 0.88 whereas expected heterozygosity ranged from 0.69 to 0.87. Collection site 8, which is a coastal site bordered by ocean and active sand dunes on all but one side, had the lowest allelic richness, observed heterozygosity, and expected heterozygosity. Only collection site 8 had significant departure from HWE after applying sequential Bonferroni corrections.

Sample sizes for Santa Barbara Island collection sites ranged from 21-60 individuals whereas the three opportunistic collection areas ranged from 8-12 individuals. Rarified allelic richness based on all 10 collection sites ranged from 5.62 to 6.65. When the three opportunistic areas were removed, allelic richness ranged from 7.17 to 8.65. Observed heterozygosity ranged from a low of 0.76 to a high of 0.85 for focal sites and up to 0.89 for opportunistic areas. Expected heterozygosity ranged similarly from 0.78 to 0.83. No significant departures from HWE were detected after applying sequential Bonferroni correction.

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Population Structure

Contingency table analysis of allele frequency heterogeneity resulted in the identification of all collection sites on San Clemente Island as distinct genepools, with combined p-values ranging from functionally 0 to 1.02 x 10^{-5}. Two collection sites on Santa Barbara Island were aggregated (LC and GC) whereas all other comparisons were distinct genepools with p-values ranging from functionally 0 to 1.71 x 10^{-7}. Aggregated summary statistics for LC and GC are presented in Table S2 (Supporting information); however, due to the limited sample size of LC, LC and GC were not aggregated in further analyses.

Pairwise Fst values between collection sites revealed subtle but significant structure on San Clemente Island (Table S3, Supporting information) with values ranging from 0.0022 to 0.1278. The largest values for Fst involved collection site 8. The best supported number of genetic clusters detected by STRUCTURE for San Clemente Island was 2 (Fig. 2 and Fig. S3a, Supporting information) based on the Evanno *et al.* (2005) method for both correlated and uncorrelated allele frequencies. Sequential k-means clustering supported values of K ranging from 2 to 4 (Fig. S3b, Supporting information).

On Santa Barbara Island pairwise Fst also showed subtle but significant structure (Table S4, Supporting information) with values ranging from 0.0199 to 0.0590. STRUCTURE analyses with correlated and uncorrelated allele frequencies converged on solutions of K=4 and K=7; both models were detected using the Evanno *et al.* (2005) method but the magnitude of peaks differed between allele frequency model. We chose the solution of K=4 (Fig. 3 and Fig. S4a, Supporting information) as the K=7 solution displayed clusters with minimal contributions. Sequential K-means clustering most strongly supported K=2 (Fig. S4b, Supporting information).

Isolation by Distance

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We detected significant IBD on both San Clemente Island and Santa Barbara Island at the inter-collection site level. On San Clemente Island, analyses of the 17 collections sites resulted in no detection of IBD (p=0.145, R^2=0.0249; Fig. S5, Supporting information); we attribute this to the non-linear and non-monotonic relationship between Fst and Euclidean distance resulting from the strong signal of genetic differentiation associated with the inclusion of collection site 8. Removal of this site resulted in a significant finding of IBD among the remaining 16 collection sites (p=0.001, R^2=0.2060). Santa Barbara Island also displayed significant patterns of IBD when evaluated with the 7 primary collection sites (p=0.0174, R^2=0.4258, Fig. S6, Supporting information).

Isolation by Resistance

San Clemente Island

As with IBD analyses, IBR analyses were sensitive to the inclusion of collection site 8. Therefore, we constructed 4 variations of null model to estimate whether the effect associated with collection site 8 could be best attributed to the collection site or active sand dunes acting as a barrier. The four null models and MRDM results were: standard with all habitat types and 17 collection sites (p=0.0149, R^2=0.0681), standard with collection site 8 removed (p=0.0020, R^2=0.1121), active sand dunes as a complete barrier with 17 collection sites (p=0.0005, R^2=0.2602, Fig. S5, Supporting information), and active sand dunes as a complete barrier with collection site 8 removed (p=0.0096, R^2=0.0848). Thus, we chose to model active sand dunes as a complete barrier in all models.

Models of conductance (Table 1, Fig. 4) that included California boxthorn and prickly pear cactus had the strongest support. Four models were equivalent in significance (p=0.0001) with only minor differences in R^2 which ranged from 0.6433 to 0.6602. The model with the

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greatest R^2 contained California boxthorn and prickly pear cactus as highly conductive with a value of 100 and small canyons as low conductance with a value of 2 (R^2=0.6602). Ranking models by corrected AIC (AICc) led to equivalence between two models that differed only by the inclusion of grasslands as low conductance; the model with the lowest AICc (-957.56) and highest R_β^2 value (0.7257) contained both grasslands and small canyons as low conductance (Fig. S7, Supporting information).

Models of landscape resistance (Table 1, Fig. 4) with cholla phase maritime desert scrub, canyons, and secondary roads were best supported across methods. Corrected AIC could not differentiate between the best models as all contained the same features (AICc: -972.94 to -974.47); the primary difference among models was the resistance value assigned to large canyons and the inclusion of small canyons as low resistance value of 2. In the top performing models cholla, medium-sized canyons, and secondary roadways were moderately resistant with a value of 50, large canyons were moderate to high resistance with values of 50 and 100 (Fig. S8, Supporting information). The model best supported by MRDM (p=0.0001, R^2=0.5125) and R_β^2 statistic (R_β^2 = 0.8606) was a model with cholla, medium-sized canyons, and secondary roads as moderately resistant, and large canyons as highly resistant. The greatest R^2 for all resistance models was 0.5175 with the primary difference between this model and the previous model being the inclusion of small canyons as low resistance.

Santa Barbara Island

The null model on Santa Barbara Island was also significant (p=0.0214, $R^{2=}$0.4804). Evaluating models of conductance (Table 2, Fig. 5), models with California boxthorn and prickly pear cactus had the best support across methods. The R^2 for conductance models ranged from

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0.8596 to 0.8877, the lowest of which had only California boxthorn as moderately conductive with a value of 50 and prickly pear cactus as highly conductive with a value of 100 (p=0.0003). The model with the greatest R^2 had both California boxthorn and prickly pear cactus as highly conductive with the addition of giant coreopsis (*Leptosyne gigantean*) habitat as lowly conductive (p=0.0008, Fig. 5 and Fig. S10, Supporting information). Eight models had AICc values within 2 units of the model with lowest AICc value (AICc range -151.976 to -153.318). Applying the R_β^2 statistic to this subset of 8 models resulted in the top model (R_β^2=0.8718) being congruent with the model best supported by MRDM. Statistical methods did not show congruence among model rankings after the best supported model.

Models of landscape resistance which included woolly seablite and crystalline iceplant as medium resistant values of 50 were the highest supported models (Table 2). Seven models had equivalent coefficients of determination (R^2=0.8582) and highly significant p-values ranged from 0.0003 to 0.0007. These models included seablite and iceplant as medium resistance and ranged across permutations of 3 and 4 habitat type inclusions: barren ground as medium or high resistance, needle goldfields (*Lasthenia gracilis*) as high resistance, and common fiddleneck (*Amsinckia intermedia*) as medium resistance. Corrected AIC parsed these models into two groups; the best supported group had AICc values of -149.043 to -150.066. These models differed only in the resistance assigned to barren ground (medium or high) and whether needle goldfields were included as a resistant surface. The model with the greatest R_β^2 statistic within those supported by AICc included needle goldfields as highly resistant and barren ground as medium resistance. The models with the greatest R_β^2 values overall contained seablite and iceplant as low-resistance habitat with barren ground as medium (R_β^2=0.8867) and high

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resistances (R^2_β=0.8853); these models also fell within the range of AICc values for the best models but their R^2 values were much lower, 0.6919 and 0.6879 respectively. We chose the model in which combined seablite and iceplant with barren ground and common fiddleneck were medium resistance (Fig. 5 and Fig. S11, Supporting information) as the addition of stronger resistances and landscape elements failed to significantly improve the model (Table 2).

DISCUSSION

We conducted a detailed genetic assessment of the San Clemente Island night lizard on San Clemente and Santa Barbara Islands to inform conservation and management approaches. We utilized island-wide sampling designs with 23 microsatellite loci to estimate baseline parameters for each collection site and identify population substructure. We used a landscape genetics approach to estimate connectivity between collection sites and identify landscape factors that may influence spatial genetic patterns on each island. We found that San Clemente Island night lizards are admixed on each island displaying shallow, but significant, population structure. Each island is characterized by a pattern of IBD with additional patterns of connectivity through prime habitat of California boxthorn and prickly pear cactus. We also found habitat resistance patterns distinctive to each island, and identified active sand dunes as a unique barrier to gene flow on San Clemente Island.

Population Substructure

San Clemente Island was characterized by 2 genetic clusters associated with the northern and southern ends with varying levels of admixture across the island. The clustering solution inferred by STRUCTURE could result from the clustered sampling of a ubiquitously distributed organism characterized by a neighbor-mating life history with limited dispersal (Schwartz &

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McKelvey 2009). However the congruence between genepool delineation, multivariate approaches, and pairwise Fst corroborate the inferences made by STRUCTURE.

Surprisingly, Santa Barbara Island displayed a greater degree of population structure than San Clemente Island, despite its much smaller size. The clustering solution inferred by STRUCTURE sorted the island samples into a western population on Webster Point, a northern population along Cliff Canyon and Arch point, a mid-island cluster, and a south-eastern cluster. The western and northern clusters displayed little admixture whereas the mid-island and south-eastern clusters were more admixed but still showed large contributions from different clusters. Sequential k-means clustering supported a similar pattern with the western and northern collection sites clustering separately from all others. Similarly, genepool delineation and pairwise Fst corroborated the STRUCTURE findings, revealing significant differentiation even for those sites <400 m apart.

The overall pattern on each island is characterized by subtle but significant population structure between collection sites. The average dispersal distance noted by Mautz (1993) of 3 m and the maximum observed value in the literature of 29 m (Mautz *et al.* 1992) suggest that limited dispersal even at small spatial scales may explain a portion of the observed population structure. It is notable that the global Fst estimates generated by diveRsity for each island are remarkably similar (0.0341 and 0.0346), despite large differences in island size and sampling scale. This suggests that regardless of island history or size, a subtle pattern of genetic differentiation should be expected, most likely due to the patterns of IBD noted in the results.

Isolation by Resistance - Conductance

California boxthorn and prickly pear cactus support the greatest abundances of island night lizards and are prime habitat types indicated for continued monitoring under the USFWS

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post-delistment plan on each island. Our analyses also identified these habitats as highly conductive on each island, corroborating the ecological data. Surprisingly, grasslands were also identified as a conductive element on San Clemente Island even though ecological data suggested grasslands are poor habitat (Fellers & Drost 1991). This may be attributable to the presence of cover items, such as rocks, within the San Clemente Island grasslands. As thermoconformers (Regal 1968; Fellers & Drost 1991) cover items are important landscape features for thermal regulation, and any habitat with suitable cover may be conductive. For example, island night lizards on San Nicolas Island can be found in beach habitat with little vegetation, so long as cover rocks are present (Fellers *et al.* 1998). The best supported conductance model for Santa Barbara Island contained only one additional habitat type, giant coreopsis, as weakly conductive. The distribution of this habitat type on Santa Barbara Island is such that it is generally contiguous with patches of California boxthorn and prickly pear cactus so it is difficult to analyze the importance of this habitat type on its own.

Isolation by Sand Dunes

Active sand dunes along the north coast of San Clemente Island were the only habitat we identified as a barrier correlated with island night lizard genetic structure. This habitat was best modeled as an absolute barrier to dispersal due to the level of genetic differentiation between collection site 8 and all others. This finding is supported by the ecological literature (Mautz 1993), which reports lizards as absent from dunes. It is likely that this finding could hold true on San Nicolas Island as well; however the effect of sand dunes on this island has yet to be assessed. There are no sand dunes present on Santa Barbara Island.

Isolation by Resistance – San Clemente Island

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Models of habitat resistance were not congruent between the two islands, with no features identified as resistant on both islands. This finding probably reflects differences in topography, the extent of certain vegetation types, and anthropogenic development. On San Clemente Island we identified cholla phase maritime desert scrub, secondary roadways, and medium and large canyons as resistant features. The association of canyons with increased genetic differentiation between collection sites is supported by ecological studies by Mautz (1993). This is possibly due to the difficulty in crossing canyons, and lack of resources for establishment and recruitment because of restricted vegetative growth.

The establishment of the Naval base in the early 19th century and subsequent infrastructure and training activities also appear to have an effect, as secondary roadways impede connectivity. It is of note that the primary roadway was not identified as a resistant surface, even though it is paved and has more traffic. However, this primary road is one relatively short road running down the middle of the island, whereas the network of secondary roads is extensive and bisects multiple collection sites. Predation pressure from feral domestic cats may also differ between primary and secondary roadways. Removal efforts targeting feral cats, a known predator of the island night lizard (Mautz *et al.* 1992), are conducted more frequently along the primary road (pers. comm., Booker 2015).

The habitat type most strongly associated with genetic differentiation was cholla phase maritime desert scrub, a vegetation community that is distributed extensively on San Clemente Island but not on Santa Barbara Island. Coastal cholla may act as a resistant surface as the spines readily pierce flesh and could injure or debilitate fleeing or dispersing individuals. Indeed, we have witnessed island night lizards becoming stuck on cholla propagules when fleeing and were unable to free themselves. The large cholla phase maritime desert scrub patch separating the

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collection sites at the southern end of the island is of particular interest as it could easily limit the dispersal of individuals across the landscape. The increased disturbance to the southern portion of the island through active bombardment may further propagate cholla, thus increasing its density and distribution within the bombardment areas.

Santa Barbara Island - Resistance

Resistance model selection across statistical methods was not congruent for Santa Barbara Island. Two habitat types were consistent among all models: woolly seablite grouped with crystalline iceplant and barren ground. Two additional habitat types, needle goldfields and common fiddleneck, were included as resistant surfaces in several models but were not congruent across statistical methods. Due to the spatial and temporal transitions between seablite and iceplant habitat types (pers. comm., Rodriguez 2016), we could not determine the independent contributions of each habitat type to genetic differentiation. Crystalline iceplant can modify soil through the deposition of retained salt deposits, rendering areas unsuitable for other vegetation (Vivrette & Muller 1977). This may limit the cover for foraging, thermoregulation, or dispersal due to the barren areas which result from plant death (Fellers & Drost 1991). The identification of barren ground on Santa Barbara Island as medium to high resistance is unsurprising and attributable to the lack of cover and soil fissures used by island night lizards. Fellers and Drost (1991) found that ground fissures were important refugia for island night lizards, even in prime habitat, therefore barren ground without fissures and little other cover options are likely difficult for lizards to move through or occupy.

The absence of grassland habitats from the final resistance models is notable. Fellers and Drost (1991) found that lizards were largely absent from grasslands during their study, requiring an equivalent number of trap days to sample lizards as habitat dominated by seablite and iceplant.

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The identification of common fiddleneck within the best supported model and subsequent identification of needle goldfields within similarly supported models are not congruent with the dietary analyses nor ecological study of Fellers and Drost (1991). These habitat types were identified through statistical optimization and could represent biases in this process. However, these habitats may be associated with resistance due to their proximity to seablite and iceplant as well as being herbaceous cover types offering little shelter or resources to island night lizards. Of note, the NP collection site occurred primarily within a habitat dominated by needle goldfields with only a few small California boxthorn shrubs present; however a large number of rocks were present, thus supplementing the cover available to island night lizards. It is likely that when herbaceous cover is dense enough to cause fissures in the soil (Fellers & Drost 1991) which can be used for refugia or supplemented by cover items within the habitat, the resistant nature of the habitat may be minimized and may result from the close association with other strongly resistant habitat

Management Implications

The island night lizard is an abundant island endemic with a restricted range which was delisted from the Endangered Species Act in 2014 contingent on monitoring over a 10-year period (USFWS 2014). Among the requirements are monitoring prime habitat of prickly pear cactus and California boxthorn on each island as well as evaluating recruitment and estimated population sizes of island night lizards on each island. The abundance of this species and recent delistment suggest that active management is no longer required, but actions should be identified to better support the monitoring framework. Our genetic analyses indicate that some management actions can be taken in common across the two islands, whereas other approaches should apply only within an island. Common management actions should focus on habitat protection and

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restoration supporting California boxthorn and prickly pear cactus to improve connectivity and localized abundances.

Management action focused on mitigating the impact of resistant surfaces on island night lizard populations would be unique not only to each island, but also to differing sections of San Clemente Island. On Santa Barbara Island, we recommend removing crystalline iceplant and restoring native vegetation to improve the quality of the habitat matrix. On San Clemente Island, natural population fragmentation results from canyons and active sand dunes, but mitigation efforts could be applied to secondary roadways by limiting the fragmentation of prime habitat and adding cover items or corridors to provide a more permeable surface. Finally, the further propagation of cholla phase maritime desert scrub could be minimized through more targeted training activities to avoid spreading propagules or active management to minimize its presence within bombardment areas.

Based on this study, there are generalizations that can be made about the inference of connectivity patterns within non-insular habitat that may be fragmented by anthropogenic modifications (e.g. Sunnucks 2011). We found that even highly abundant lizards on relatively small oceanic islands display genetic patterns consistent with contemporary anthropogenic activity in addition to genetic patterns correlated with natural fragmentation. Thus, management activities can be identified which can be applied to islands managed by separate entities without the ability to improve the intervening matrix (i.e. the ocean) between islands . This management scenario is similar to protected areas on the mainland of Southern California where continued population growth, infrastructure, and invasive species continue to degrade native habitat through increased edge effects, decreased habitat area, and increased competition for resources.

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For example, the mainland California Floristic Province is under increasing synergistic threats from climate change, urbanization, and altered fire regimes (e.g. Syphard *et al.* 2007; Regan *et al.* 2012). Management strategies to maintain population persistence will likely need to incorporate information on conductance and resistance for habitat patches that increasingly act in isolation. As many management actions are spatially explicit it is increasingly important to characterize genetic patterns using spatially explicit methods (Schaffer *et al.* 2015). An exemplar region which could benefit from such an approach is the peninsular region of Southern California, Point Loma. Point Loma includes residential neighborhoods, Naval installations, and Cabrillo National Monument; management of this area varies by location as there are multiple agencies and is further complicated by land use practices. This region is expected to experience increased extinction risks of plant and animal species (e.g. Lawson 2011) and genetic studies of lizards (Luckau 2015) and small mammal community (Lion 2016) reveal consistent patterns of significant genetic differentiation and decreased genetic diversity. Application of these modeling frameworks within each of the management units within Point Loma can support overall management for herpetofaunal species persistence within the region by identifying and mitigating the unique resistant features within each managed area that occur through different land-use practices while simultaneously increasing conductive landscape features within and between management areas.

We encourage the comparison of fine-scale patterns within and between regional management units, as analyses focused on identifying conductive habitat features may lead to common mitigation strategies within and between protected areas. Resistance-based analyses may identify unique features acting at relatively fine scales within management units that could be actively managed to better sustain local demes or populations. A combined approach of

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minimizing resistant features while maximizing conductive features can be applied to increase probabilities of species persistence by increasing the prime habitat area and improving the matrix quality (e.g. Fahrig 2001).

TABLES

Table 1: San Clemente Island competing conductance and resistance models. The best-supported conductance and resistance models for each layer are shown with the associated p-value (p) and coefficient of determination from non-parametric rank-based regressions (R^2) from the resulting MRDM analysis. The corrected AIC value (AICc) and R_β^2 value are also presented (see text for methods).

	p	R^2	AICc	R_β^2
Null	0.0005	0.2602	-912.35	0.2825
Conductance Models				
Null + California boxthorn (100c) + Prickly pear cactus (100c)	0.0001	0.6554	-951.04	0.5630
Null + California boxthorn (100c) + Prickly pear cactus (100c) + Grassland (2c)	0.0001	0.6433	-952.10	0.6769
Null + California boxthorn (100c) + Prickly pear cactus (100c) + Canyons < 500 ft (2c)	0.0001	0.6602	-955.75	0.6116
Null + California boxthorn (100c) + Prickly pear cactus (100c) + Grassland (2c) + Canyons < 500 ft (2c)	0.0001	0.6461	-957.56	0.7257
Resistance Models				
Null + Cholla (50r) + Secondary Roads (50r) + Canyons 500-1000 ft (50r) + Canyons > 1000 ft (50r)	0.0002	0.5039	-974.47	0.8607
Null + Cholla (50r) + Secondary Roads (50r) + Canyons 500-1000 ft (50r) + Canyons > 1000 ft (100r)	0.0001	0.5125	-974.39	0.8606
Null + Cholla (50r) + Secondary Roads (50r) + Canyons 500-1000 ft (50r) + Canyons > 1000 ft (50r) + + Canyons < 500 ft (2r)	0.0002	0.5137	-973.19	0.8445
Null + Cholla (50r) + Secondary Roads (50r) + Canyons 500-1000 ft (50r) + Canyons > 1000 ft (100r) + + Canyons < 500 ft (2r)	0.0004	0.5175	-972.94	0.8427

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Table 2: Santa Barbara Island competing conductance and resistance models. The best-supported conductance and resistance models for each layer are shown with the associated p-value (p) and coefficient of determination for non-parametric rank-based regressions (R^2) from the resulting MRDM analysis. The corrected AIC value (AICc) and R^2_β value are also presented (see text for methods).

	p	R^2	AICc	R^2_β
Null	0.0212	0.4804	-140.12	0.6911
Conductance Models				
Null + California Boxthorn(100c)+ Prickly pear cactus (50c) + Common fiddleneck (2c)	0.0013	0.8611	-151.98	0.8614
Null + California Boxthorn(100c)+ Prickly pear cactus (50c) + Goldfields (2c)	0.0003	0.8801	-151.98	0.8624
Null + California Boxthorn(100c)+ Prickly pear cactus (2c)	0.0002	0.8653	-152.12	0.8667
Null + California Boxthorn(50c)+ Prickly pear cactus (2c)	0.0012	0.8617	-152.36	0.8683
Null + California Boxthorn(100c)+ Prickly pear cactus (50c) + Giant Coreopsis (2c)	0.0005	0.8677	-153.13	0.8716
Null + California Boxthorn(100c)+ Prickly pear cactus (100c)+ Giant Coreopsis (2c)	0.0008	0.8877	-153.19	0.8718
Null + California Boxthorn(100c)+ Prickly pear cactus (50c) + Oatgrass (2c)	0.0006	0.8693	-153.23	0.8709
Null + California Boxthorn(100c)+ Prickly pear cactus (100c) + Oatgrass (2c)	0.0010	0.8693	-153.32	0.8713
Resistance Models				
Null + Seablite with iceplant (50r) + Barren ground (100r) + Common fiddleneck (50r)	0.0003	0.8582	-149.69	0.8076
Null + Seablite with iceplant (50r) + Barren ground (50r) + Common fiddleneck (50r)	0.0005	0.8582	-149.39	0.7490
Null + Seablite with iceplant (50r) + Barren ground (100r) + Common fiddleneck (50r) + Goldfields (100r)	0.0004	0.8582	-149.04	0.8371
Null + Seablite with iceplant (50r) + Barren ground (50r) + Common fiddleneck (50r) + Goldfields (100r)	0.0005	0.8582	-150.07	0.8704
Null + Seablite with iceplant (2r) + Barren ground (50r)	0.0027	0.6919	-150.221	0.8867

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FIGURES

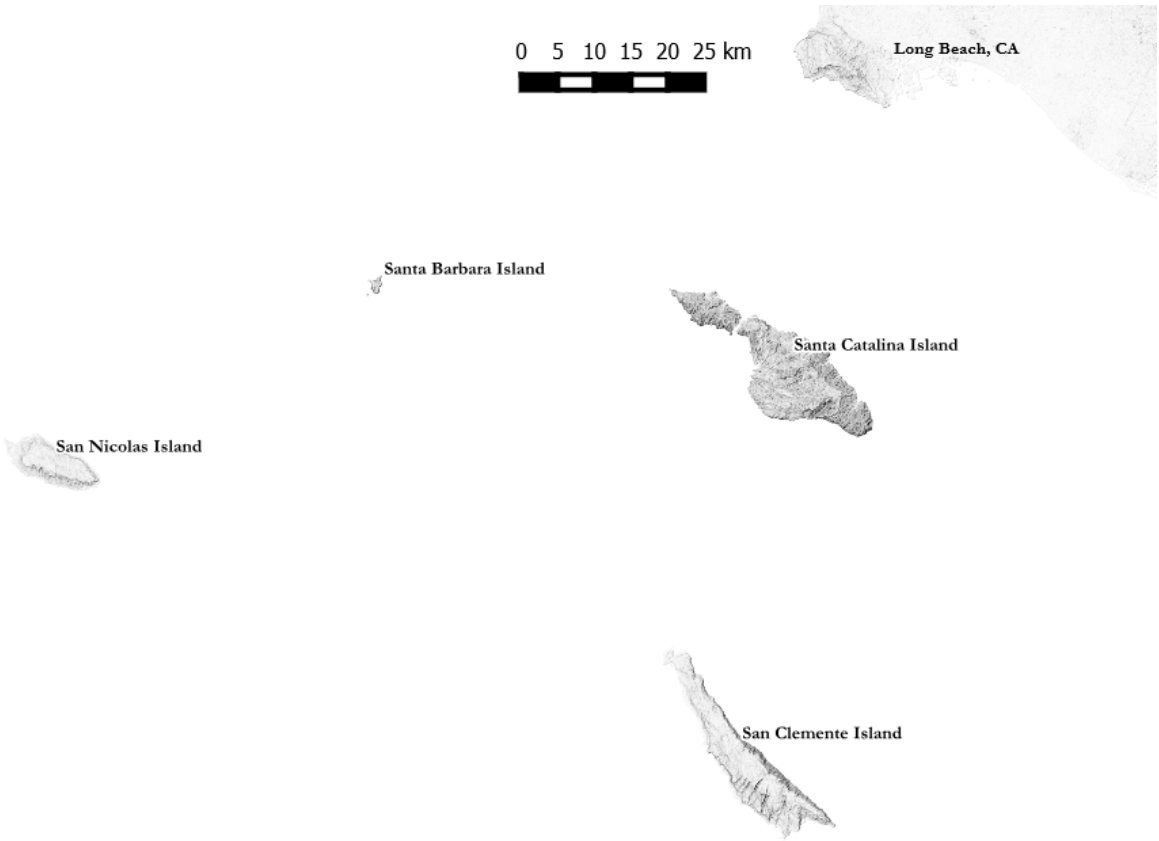

Fig. 1: Location of Channel Islands inhabited by the island night lizard. The island night lizard is endemic to 3 Channel Island: San Clemente Island, Santa Barbara Island, and San Nicolas Island.

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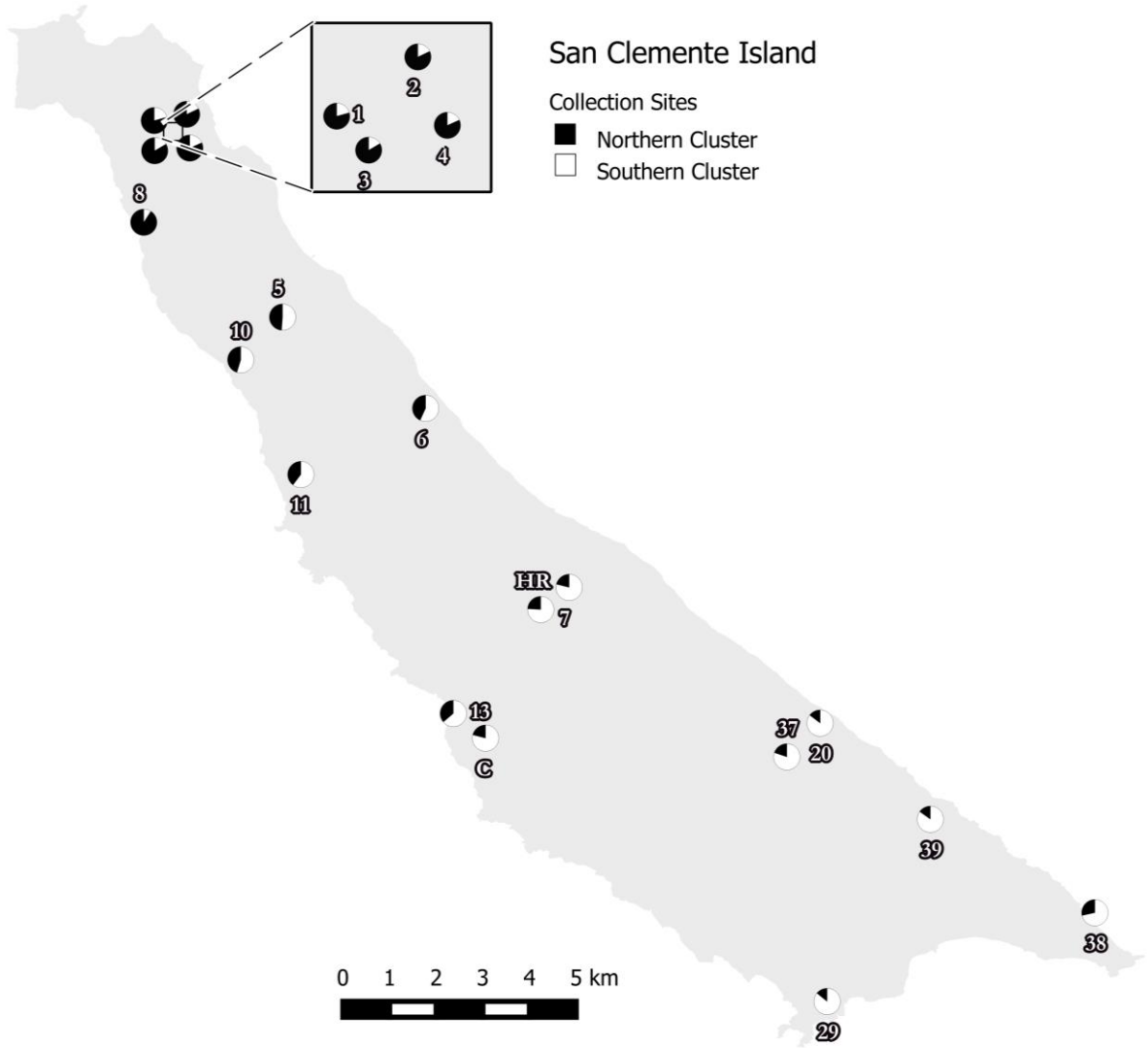

Fig. 2: San Clemente Island Collection sites with Coancestry Proportions. All collection sites on San Clemente Island are shown. Pie charts represent the site-level coancestry proportions for the STRUCTURE solution K=2 as calculated from the CLUMPP outputs. STRUCTURE barplot is shown in Fig. S3a, Supporting information.

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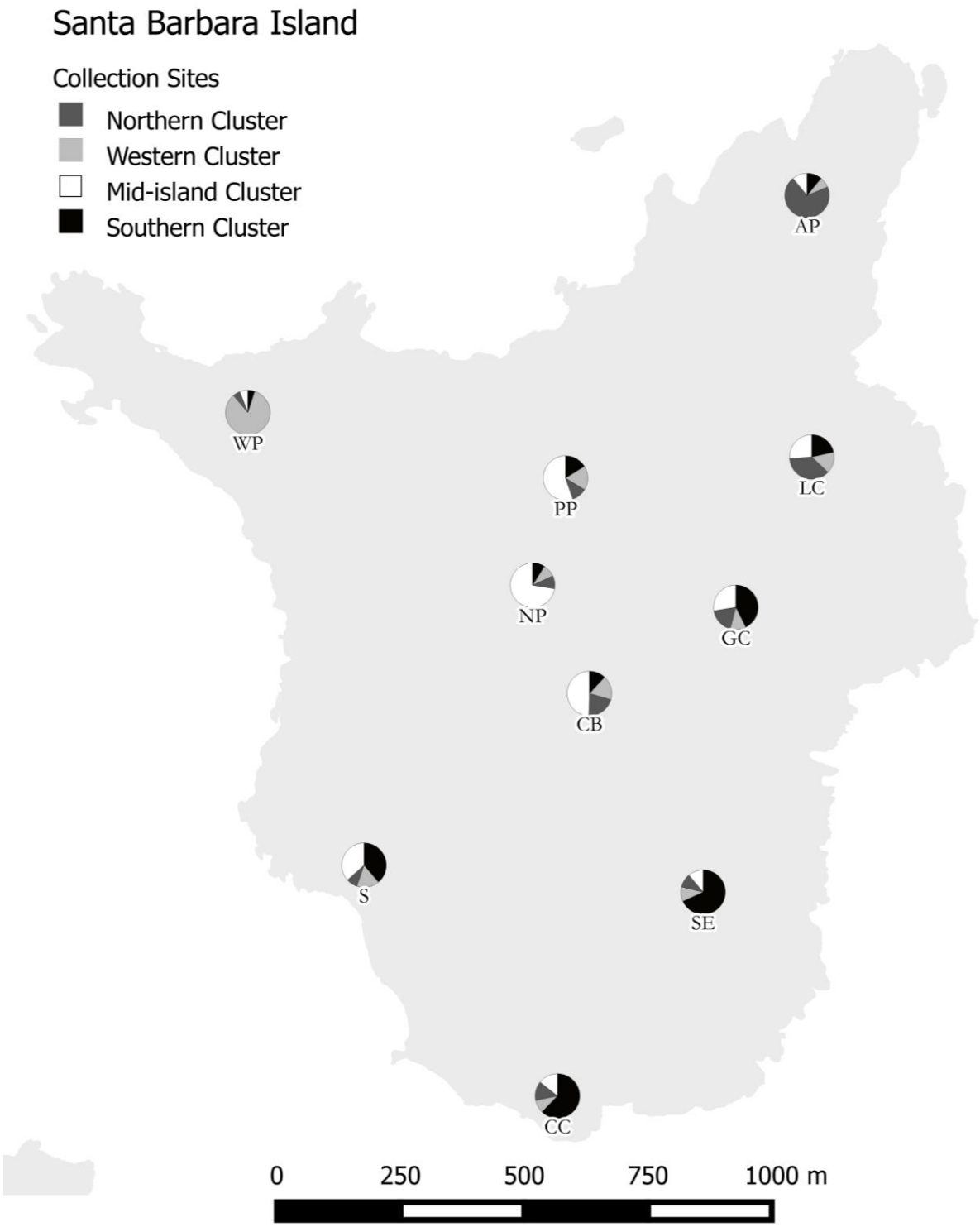

Fig. 3: Santa Barbara Island Collection sites with Coancestry Proportions. All collection sites on San Clemente Island are shown. Pie charts represent the site-level coancestry proportions for the STRUCTURE solution K=4 as calculated from the CLUMPP outputs. STRUCTURE barplot is shown in Fig. S4a, Supporting information.

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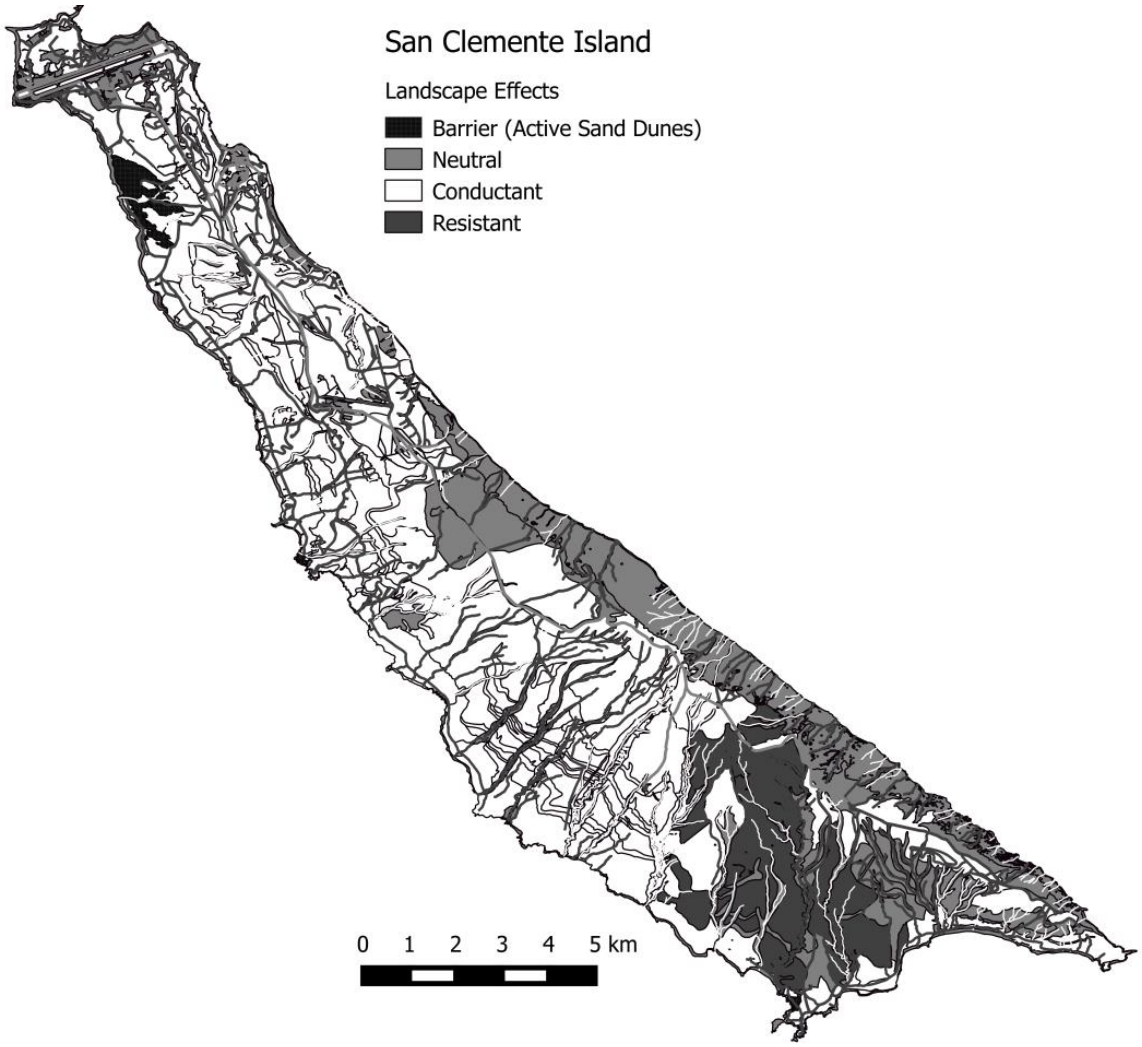

Fig. 4: San Clemente Island Landscape Effects. The landscape-level features identified by analyses (see results) incorporated as a composite image. See Fig. 2 for location of collection sites. Active sand dunes were identified as a barrier (black). Landscape features which were neither conductant nor resistant were given values of 1 and considered neutral (gray). Conductant features (California boxthorn, prickly pear cactus, grasslands, and canyons < 500ft in length) are shown in white. Resistant habitat (cholla phase maritime desert scrub secondary roadways, canyons > 500ft in length) are shown in dark gray. See Supplement Figs. 1, 7, and 8 for specific landscape features and models.

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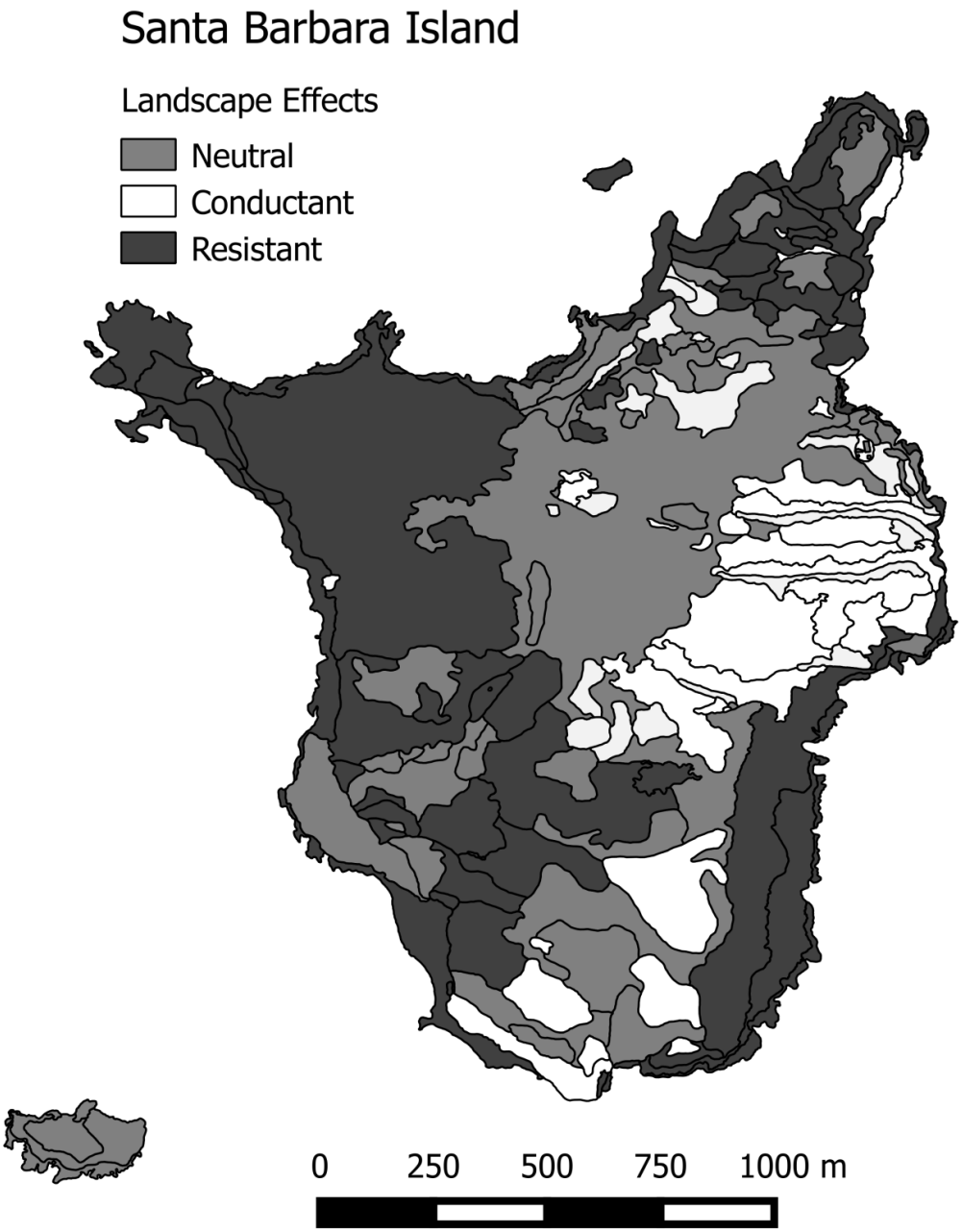

Fig. 5: Santa Barbara Island Landscape Effects. The landscape-level features identified by analyses (see results) incorporated as a composite image. See Fig. 3 for location of collection sites. Landscape features which were neither conductant nor resistant were given values of 1 and considered neutral (gray). Conductant features (California boxthorn, prickly pear cactus, and giant coreopsis) are shown in white. Resistant habitat (woolly seablite with crystalline iceplant,

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barren ground, and common fiddleneck) are shown in dark gray. See Supplement Figs. 2, 10, and 11 for specific landscape features and models.

ACKNOWLEDGEMENTS

Support for this research came from United States Department of Defense (Award Number W9126G-12-2-0060) and the Southern California Research and Learning Center (Award Number S18309). We would like to thank the National Park Service for access to Santa Barbara Island and providing landscape-level GIS layers, San Clemente Naval Base for access to San Clemente Island and providing landscape-level GIS layers, and our field assistants. In addition we would like to thank Drs. A. Bohonak (SDSU), H. Regan (UCR), K. Anderson (UCR), and J. Gatesy (UCR) for comments receive during manuscript preparation.

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DATA ACCESSABILITY

Genotyping and relevant field data provided by SER upon request and will be stored online via Google Drive maintained by RWC. Data will additionally be published as a supplemental appendix to SER's dissertation and will include raw genotypes for each individual with GPS coordinates, sex, and collection site. SER's dissertation is to be published by San Diego State University/University of California Riverside in 2017.

AUTHOR CONTRIBUTIONS

SER and RWC designed sampling procedures and conducted field work. SER conducted laboratory and statistical analyses. SER and RWC wrote the manuscript. SER and RWC secured funding for the study.