1 TITLE: Factors affecting genetic connectivity and diversity of the island night lizard.

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14 RUNNING TITLE: Landscape genetics of the San Clemente Island night lizard.

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18 **Abstract**

19 Habitat loss and fragmentation is one of the most severe threats to global
20 biodiversity. Because human development often fragments natural areas into habitat
21 “islands”, studies which characterize the genetic structure of species isolated on oceanic
22 islands may provide insight into the management of anthropogenic habitat islands. The
23 San Clemente Island night lizard, *Xantusia riversiana reticulata*, is endemic to two
24 California Channel Islands, each with a history of anthropogenic disturbance. We
25 genotyped 917 individuals from San Clemente Island and Santa Barbara Island at 23
26 microsatellite loci to quantify population structure and identify natural and anthropogenic
27 landscape features affecting intra-island connectivity. We found significant, but shallow,
28 population structure on each island with sites < 400 m apart identified as distinct
29 genepools. Landscape genetic analyses identified conductive habitat as California
30 boxthorn and prickly pear cactus on both islands. Landscape features which decreased
31 connectivity were unique to each island and included natural and human-mediated
32 features. These results can inform management plans on each island by identifying
33 habitat targets for mitigation and restoration efforts designed to improve connectivity.
34 Our results highlight the need for considering fine-scale features correlated with
35 contemporary and historical patterns of fragmentation, especially in small and isolated
36 habitats on the mainland that may be analogous to oceanic islands.

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38 **KEYWORDS:** Landscape genetics, Channel Islands, Fragmentation, Conservation

39

40 **Introduction**

41 Habitat fragmentation is a leading cause of global biodiversity loss.

42 Fragmentation can decrease metapopulation connectivity, increase genetic divergence,

43 and increase extinction risk (e.g. Frankham 2005; Sumner 2005; Vandergast et al. 2016).

44 Fragmented and isolated habitat patches often form “habitat islands”, patches of suitable

45 habitat embedded within an inhospitable matrix, such as a nature preserve surrounded by

46 human housing developments (e.g. Hokit et al. 1999; Driscoll 2004; Wang et al. 2009).

47 When this occurs, the ecological effects of fragmentation can be further exacerbated by

48 management practices, as isolated fragments may be managed independently by different

49 agencies, which may result in variable outcomes in terms of conservation goals, even

50 when different fragments share common species and habitats. Thus, one goal of modern

51 conservation is to identify generalizable approaches which can be readily implemented

52 across administrative boundaries to improve the management of fragmented and isolated

53 habitat patches. This approach requires examining genetic connectivity and diversity both

54 within and between fragments, in order to distinguish features shared in common among

55 fragments that can impede or enhance connectivity, as well as features that may be

56 specific to each fragment. Although these types of comparisons are often made in the

57 context of actual oceanic islands, they are less commonly applied to habitat islands. Here,

58 we conduct a management case study of a species distributed across two oceanic islands

59 managed by different agencies. We believe this and other case studies can serve as

60 valuable exemplars for conservation approaches that could also be applied to species

61 distributed across habitat islands.

62 The California Channel Islands are small oceanic islands off Southern
63 California's coast which share the Mediterranean climate of the mainland and have
64 experienced habitat degradation and fragmentation due to anthropogenic activities (e.g.
65 Fellers and Drost 1991; Fellers et al. 1998; Sturgeon 2000). Different islands are
66 managed by different government agencies, although they share several species of
67 conservation concern in common. Thus characterizing the contemporary genetic patterns
68 of Channel Island endemics will also provide critical data for monitoring and
69 management directed toward island endemics (Schwartz et al. 2007; reviewed in Stetz et
70 al. 2011) and serve as a case study for habitat islands.

71 Reptiles are an excellent group for studies of fragmentation due to their
72 intermediate dispersal distances, relatively high population densities, plasticity of
73 responses, thermal physiology, and potential vulnerability to habitat modifications (e.g.
74 Hokit et al. 1999; Jordan and Snell 2008; Wang et al. 2009; Tseng et al. 2015). One of the
75 few reptiles endemic to the Channel Islands is the island night lizard, *Xantusia riversiana*
76 (Cope 1883). This species was delisted from the Endangered Species Act in 2014,
77 contingent on continued monitoring (United States Fish and Wildlife Service (USFWS)
78 2014). Two subspecies are recognized (Smith 1946), *X. r. reticulata*, the San Clemente
79 Island night lizard, endemic to San Clemente Island and Santa Barbara Island (Figure 1)
80 and *X. r. riversiana* endemic to San Nicolas Island. These subspecies differ in both life
81 history traits and habitat use (Fellers and Drost 1991; Fellers et al. 1998). On San
82 Clemente Island lizards are found primarily in habitats dominated by California boxthorn
83 (*Lycium californicum*) and prickly pear cactus (*Opuntia littoralis*), and avoid deep

84 canyons, sand dunes, and canyon woodland (Mautz 1993). On Santa Barbara Island,
85 lizards are found primarily in habitats dominated by California boxthorn and prickly pear
86 cactus, and tend to avoid grasslands (Fellers and Drost 1991). In prime habitat *X. r.*
87 *reticulata* may reach densities in excess of 3,200 individuals/ha (Fellers and Drost 1991;
88 Mautz 1993).

89 Although the island night lizard can reach very high population densities in prime
90 habitat, this long-lived species may be vulnerable to habitat fragmentation and
91 disturbance due to a combination of life history traits and very low dispersal distances
92 (Fellers and Drost 1991; Mautz 1993). As part of an ongoing post-delisting monitoring
93 effort, we characterized the genetic structure and connectivity of *X. r. riversiana* across
94 its entire geographic range, sampling sites spread across both San Clemente and Santa
95 Barbara Islands. We also characterized habitat, anthropogenic structures, and other
96 geographic features that may serve as potential barriers to population connectivity. Based
97 on large population sizes and near-continuous distribution of viable habitat, we
98 hypothesized that population genetic structure would be minimal on each island but
99 influenced by roads and other anthropogenic barriers, as well as non-preferred habitat
100 types. We also hypothesized that detected patterns of genetic differentiation would be
101 primarily correlated with Euclidean distance, due to limited dispersal (Fellers and Drost
102 1991; Mautz 1993).

103 **Materials and Methods**

104 *Sample Collection and Genotyping*

105 We collected samples on San Clemente Island (Figure 2) from February through
106 November of 2013 and Santa Barbara Island (Figure 3) from May through September
107 2015. Island night lizards were captured by turning cover items and setting live traps
108 along well-worn trails. When multiple lizards were encountered, we made attempts to
109 capture and sample all lizards. Target sample size for each collection site was a minimum
110 of 30 individuals (Hale et al. 2012). Samples were also collected opportunistically from
111 encountered individuals. Captured lizards were processed following the United States
112 Geological Survey herpetofaunal monitoring protocols (Fisher et al. 2008) and GPS
113 coordinates were recorded with an estimated accuracy of 5 m. Tissue samples consisted
114 of toes that were clipped at the distal knuckle, which also served as a unique 4-digit
115 identification, and a 10 mm segment from the tail tip. Tissues were preserved in 95%
116 ethanol and stored at -20°C.

117 We extracted DNA with a standard salt digestion and genotyped individuals at 23
118 polymorphic microsatellite loci arranged into 8 reactions (Rice et al. 2016; Rice 2017
119 Appendix A, B). We scored alleles twice with GENEMAPPER for consistency; loci missing
120 data or with inconsistent allele calls were reamplified and rescored to generate a
121 consensus genotype. We assessed per-allele error rates (Pompanon et al. 2005) by
122 extracting and genotyping 35 individuals on San Clemente Island and 16 individuals on
123 Santa Barbara Island a second time.

124 *Quality Control and Summary Statistics*

125 We removed individuals from analyses if amplification was successful at fewer
126 than 16 loci. We removed first-order relatives (full siblings, parent-offspring) from data

127 sets for each island to prevent biases in detected population structure. We inferred
 128 pairwise relationships for samples within each collection site when at least 2 of 3
 129 methods were concordant. The methods we chose for inference were COLONY (Jones and
 130 Wang 2010), CERVUS (Kalinowski et al. 2007), and the DyadML estimator as calculated in
 131 COANCESTRY (Wang 2011). Individuals were removed from each data set to retain the
 132 largest sample size. Final data sets with relatives removed were used in all further
 133 analyses.

134 We evaluated the quality of each locus for each island at the level of collection
 135 sites following Selkoe and Toonen (2006). Loci were removed if amplification occurred
 136 in fewer than 75% of individuals, when in linkage disequilibrium (LD) with another
 137 locus, when null alleles occurred in a majority of sampled sites, or when the assumption
 138 of neutrality was violated. We examined loci for LD and conformance to Hardy-
 139 Weinberg and random mating proportions (HWE) in GENEPOP (Rousset 2008) with p-
 140 values corrected for multiple comparisons through sequential Bonferroni testing (Holm
 141 1979). We assessed the presence of null alleles with MICROCHECKER (Van Oosterhout et
 142 al. 2004). We examined the putative neutrality of loci with LOSITAN (Beaumont and
 143 Nichols 1996; Antao et al. 2008) under the infinite alleles model and neutral F_{st}
 144 estimation. We used the package DIVERSITY (Keenan et al. 2013) in the R statistical
 145 environment and GENEPOP to generate summary statistics for each collection site and
 146 each island (Table 1).

147 *Population Structure*

148 We delineated genepools on each island following Waples and Gaggiotti (2006).
149 We conducted an exact test for genetic differentiation for all pairs of collection sites in
150 GENEPOP. We combined probabilities with Fisher's method (Fisher 1932) with 0.0001 as
151 the lower bound for individual test probabilities; combined probabilities were corrected
152 using sequential Bonferroni testing. Collection sites were grouped if no significant
153 difference was found and the procedure was repeated until all pairwise comparisons were
154 significant.

155 We estimated genetic differentiation between collection sites with ≥ 20
156 individuals with Weir and Cockerham's (1984) estimate of F_{st} with 95% bias corrected
157 confidence intervals generated by 1,000 bootstraps over individuals in DIVERSITY. We
158 defined differentiation as significant when the confidence interval did not overlap 0.

159 We used the program STRUCTURE (Pritchard et al. 2000; Falush et al. 2003) to
160 estimate the number of populations on each island (K) using data from all collection sites.
161 We used values of K from 1 to 18 for San Clemente Island and 1 to 10 for Santa Barbara
162 Island. Analyses for both island consisted of 20 runs with a 500,000 burn-in period and
163 1,000,000 MCMC iterations under the admixture model with uncorrelated and correlated
164 allele frequency models (Pritchard et al. 2010). We used the Evanno et al. (2005) method
165 as implemented in STRUCTURE HARVESTER (Earl and vonHoldt 2012) to estimate the
166 number of populations. We generated ancestry matrices with the greedy algorithm in the
167 program CLUMPP (Jakobsson and Rosenberg 2007) to produce barplots with the program
168 DISTRUCT (Rosenberg 2004) for the best supported value of K for each island.

169 *Isolation by Distance*

170 We examined patterns of isolation by distance (IBD, Wright 1943) at the level of
171 collection sites for each island. We used non-parametric rank-based multiple regression
172 on distance matrices (MRDM, Lichstein 2007) using the function *MRM* in the R package
173 ECODIST (Goslee and Urban 2007). As an extension of the Mantel test framework, results
174 of MRDM are comparable to Mantel results with a single predictor matrix. Analyses
175 were ran with 10,000 permutations, pairwise *Fst* as the response variable, and pairwise
176 Euclidean distance as the predictor.

177 *Landscape Features Affecting Connectivity*

178 We used the isolation by resistance framework (IBR, McRae 2006) as
179 implemented in the program CIRCUITSCAPE (McRae and Beier 2007) to model
180 conductance and resistance of landscape features on each island. Resistance and
181 conductance were modeled separately to clearly delineate landscape features with
182 positive and negative correlations with pairwise genetic distances. Raster cell values for
183 each feature ranged from 2 (low), 50 (moderate), and 100 (high). These values were
184 chosen to identify candidate landscape features and attribute a coarse value to each for
185 modelling purposes only and were not chosen to represent the true and unknown values
186 of landscape features. Collection sites were represented as focal regions composed of the
187 minimum-spanning convex hulls generated from capture coordinates.

188 We used non-parametric MRDM with 10,000 permutations to assess the
189 categorical features for each island. Models ranged from single features to full models of
190 all statistically supported features. Single features entered the model-building framework
191 if their inclusion was significant and the coefficient of determination (R^2) was greater

192 than the null model. The null model consisted of bounded Euclidean distance wherein all
193 terrestrial raster cells had a value of 1. In full models, raster cells had either the sum of
194 resistance values for all features within the cell or 1 when no focal feature was present.

195 We used a consensus approach for model selection which considered the ranked-
196 order of best models across MRDM, corrected Akaike information criterion (AICc), and
197 marginal R^2_β (Edwards et al. 2008; Van Strien et al. 2012). We used the *lmer* function in
198 the R package LME4 (Bates et al. 2015) to construct maximum-likelihood population
199 effects (MLPE) models (Clarke et al. 2002) fit with residual maximum likelihood
200 (REML) estimation with collection site as a random factor. We used the *KRmodcomp*
201 function in the R package PBKRTEST (Halekoh and Højsgaard 2014) to calculate the
202 marginal R^2_β from the MLPE models. We calculated AICc with the R package MUMIN
203 (Bartoń 2016) for MLPE models fit without REML estimation, as variables which
204 contributed the fixed effects differed between models (reviewed in Van Strien et al.
205 2012).

206 Analyses of San Clemente Island focused on three categorical GIS layers:
207 vegetation type (RECON, Inc 2012), roadways type (Naval Facilities and Engineering
208 Command South West (NAVFACSW), date unknown), and canyon length
209 (NAVFACSW, date unknown). Vegetation was parsed into 11 classes based on least-cost
210 transect analysis groupings. Roadways were divided into two classifications: paved roads,
211 which served as primary traffic conduits along the spine of the island and within more
212 populated areas, and secondary roads, which were generally unpaved access roads.
213 Canyons were divided into three length classes of small (0-499 ft), medium (500-999 ft),

214 and large ($\geq 1,000$ ft). We applied a 5 m buffer to roadways and canyons to eliminate
 215 breaks in the linear features when rasterized and produced maps with a 100 m resolution
 216 Analyses of Santa Barbara Island focused on three layers: vegetation type
 217 (National Park Service (NPS), 2010), presence of western seagull (*Larus occidentalis*)
 218 nesting colonies, and presence of a potential predator, barn owls (*Tyto alba*). There are no
 219 roads on Santa Barbara Island. Vegetation was classified into 14 groups based on
 220 dominant vegetation alliances; due to observations of woolly seablite (*Suaeda taxifolia*)
 221 dominated habitat transitioning seasonally into crystalline iceplant (*Mesembryanthemum*
 222 *crystallinum*) dominated habitat (pers. comm., Rodriguez 2016) we grouped these
 223 alliances into a single class. Western seagull nesting colony presence was included by
 224 digitizing seabird nesting locations from 2015 (NPS 2015). Potential barn owl presence
 225 was included by extracting and digitizing home ranges from Figure 1 of Thomsen et al.
 226 (2014). Resolution on vegetation data was listed as 1 ft (NPS 2010); however raster maps
 227 were generated with a cell size of 5 m for all layers due to the uncertainty in GPS
 228 coordinates.

229 **Results**

230 *Quality Control*

231 We sampled 605 island night lizards from 18 collection sites on San Clemente
 232 Island and 312 island night lizards from 7 collection sites and 3 smaller opportunistic
 233 areas on Santa Barbara Island. We removed 18 individuals from the San Clemente Island
 234 data set due to missing data; no individuals were removed from the Santa Barbara Island
 235 data set for this reason. We identified 75 first-order relationships among 114 individuals

236 on San Clemente Island and 65 first-order relationships among 97 individuals on Santa
237 Barbara Island. We removed 53 individuals from the San Clemente Island data set and 41
238 individuals from the Santa Barbara Island data set due to these relationships. These
239 removals resulted in sample sizes of 534 individuals from San Clemente Island and 271
240 from Santa Barbara Island.

241 Final data sets consisted of 20 loci for San Clemente Island and 21 loci for Santa
242 Barbara Island. A single locus was removed due to null alleles in 12 of 18 collection sites
243 on San Clemente Island; no loci were removed from the Santa Barbara Island data set due
244 to null alleles. The program LOSITAN identified 2 loci as under selection for San
245 Clemente Island and 2 different loci as under selection for Santa Barbara Island. These
246 loci were removed from further analyses within each respective data set. The per-allele
247 error rates associated with genotyping were 0.062% for San Clemente Island and 0.272%
248 for Santa Barbara Island. Rates of non-robust amplification were 7.14% for San Clemente
249 Island and 3.80% for Santa Barbara Island.

250 *Summary Statistics*

251 Sample sizes for San Clemente Island collection sites ranged from 12-70
252 individuals. Rarefied allelic richness for collection sites with ≥ 20 samples ranged from
253 6.28 to 11.0. Observed heterozygosity ranged from 0.62 to 0.88 whereas expected
254 heterozygosity ranged from 0.69 to 0.87. Collection site 8, which is a coastal site
255 bordered by ocean and active sand dunes on all but one side was the only site which
256 deviated from HWE and also had the lowest allelic richness, observed heterozygosity,
257 and expected heterozygosity (Table 1).

258 Sample sizes for Santa Barbara Island collection sites ranged from 21-60
259 individuals and 8-12 individuals for three opportunistic collection areas. Rarified allelic
260 richness for the 7 main collection sites ranged from 7.17 to 8.65. Observed
261 heterozygosity ranged from 0.76 to 0.89. Expected heterozygosity ranged similarly from
262 0.78 to 0.83. No significant departures from HWE were detected (Table 1).

263 *Population Structure*

264 All collection sites on San Clemente Island were identified as distinct genepools
265 with combined p-values from functionally 0 to 1.02×10^{-5} . Pairwise Fst values between
266 collection sites revealed subtle but significant structure on San Clemente Island (Table
267 S1, supplemental) with values ranging from 0.0022 to 0.1278. The largest values for Fst
268 involved collection site 8. The best supported clustering solution found by STRUCTURE
269 for San Clemente Island was K=2 (Figure 2).

270 All collection sites on Santa Barbara Island, except two, were distinct genepools
271 with p-values ranging from functionally 0 to 1.71×10^{-7} . Summary statistics for the
272 grouped sites (LC and GC) are presented independently and together in Table 1. Since
273 LC was an opportunistic site with few samples, LC and GC were not aggregated for
274 further analyses. On Santa Barbara Island pairwise Fst also showed subtle but significant
275 structure (Table S2, supplemental) with values ranging from 0.0199 to 0.0590.
276 STRUCTURE analyses with correlated and uncorrelated allele frequencies converged on
277 solutions of K=4 and K=7. We chose the solution of K=4 (Figure 3) as the K=7 solution
278 displayed clusters with minimal contributions.

279 *Factors Positively Affecting Connectivity*

280 On San Clemente Island, conductance models (Table 2) that included California
281 boxthorn (boxthorn) and prickly pear cactus (prickly pear) had the strongest support
282 across methods. Four models were equivalent in significance ($p=0.0001$, R^2 range:
283 0.6433-0.6602). Ranking these models by AICc led to equivalence between two models
284 that differed only by the inclusion of grasslands as low conductance; the model with the
285 lowest AICc (-957.56) and highest R^2_{β} value (0.7257) contained both grasslands and
286 small canyons as low conductance (Figure 4).

287 On Santa Barbara Island, conductance models (Table 3) which included boxthorn
288 and prickly pear were also the best supported across methods. Eight models had AICc
289 values within 2 units of the best model (AICc range -151.976 to -153.318). The R^2 for
290 conductance models ranged from 0.8596 to 0.8877. The model with the greatest R^2 and
291 R^2_{β} (0.8718) had both boxthorn and prickly pear with high conductance and giant
292 coreopsis (*Leptosyne gigantea*) as low conductance ($p=0.0008$; Figure 5). Statistical
293 methods did not show congruence among model rankings after the best supported model.

294 *Factors Negatively Affecting Connectivity*

295 We detected significant patterns of IBD between collection sites with ≥ 20
296 samples on both San Clemente Island ($p=0.001$, $R^2=0.2060$; Figure S3, supplemental)
297 and Santa Barbara Island ($p=0.0174$, $R^2=0.4258$, Figure S4, supplemental). On San
298 Clemente Island, initial analyses resulted in no detection of IBD ($p=0.145$,
299 $R^2=0.0249$). We attributed this to the non-linear and non-monotonic relationship between
300 F_{st} and Euclidean distance resulting from the strong signal of genetic differentiation

301 between collection site 8 and all other sites. Removal of this site as an outlier resulted in a
302 significant finding of IBD among the remaining collection sites.

303 IBR analyses of San Clemente Island were also sensitive to the inclusion of
304 collection site 8. We evaluated 4 models to determine if the observed patterns could be
305 attributed to collection site 8 as an outlier or active sand dunes acting as a barrier. The
306 best supported model placed active sand dunes as a complete barrier ($p=0.0005$,
307 $R^2=0.2602$, Figure S3, supplemental), followed by a distance-only model with collection
308 site 8 removed ($p=0.0020$, $R^2=0.1121$), collection site 8 removed and active sand dunes
309 as a complete barrier ($p=0.0096$, $R^2=0.0848$), and a bounded Euclidean distance (IBR
310 null) model with all collection sites ($p=0.0149$, $R^2=0.0681$, Figure S3, supplemental).

311 On San Clemente Island, resistance models (Table 2) with cholla phase maritime
312 desert scrub (cholla), canyons > 500 ft, and secondary roads were best supported across
313 methods. The best models contained the same features, preventing model selection by
314 AICc (AICc: -972.94 to -974.47). In the top performing models cholla, medium canyons,
315 and secondary roadways were moderate resistance whereas large canyons were moderate
316 to high resistance. The model best supported by MRDM ($p=0.0001$, $R^2=0.5125$) and R^2_{β}
317 (0.8606) contained cholla, medium canyons, and secondary roads with moderate
318 resistance and large canyons with high resistance (Figure 4).

319 The IBR null model on Santa Barbara Island was significant ($p=0.0214$,
320 $R^2=0.4804$; Figure S4, supplemental). Resistance models which included woolly seablite
321 (seablite) and crystalline iceplant (iceplant) as moderately resistant were the best
322 supported models (Table 3). Seven models had equivalent R^2 (0.8582) and highly

323 significant p-values ($p < 0.001$). Four of these models had AICc values of -149.043 to -
 324 150.066 and differed only in the resistance value assigned to barren ground and the
 325 inclusion of needle goldfields (*Lasthenia gracilis*). The model with the greatest R^2_{β} and
 326 within the AICc range contained seablite and iceplant as low resistance with barren
 327 ground as moderate ($R^2_{\beta}=0.8867$); however, this model had a lower R^2 value (0.6919).
 328 We chose the model in which combined seablite and iceplant with barren ground and
 329 common fiddleneck had moderate resistance (Figure 5) as increased resistance and
 330 additional habitat types failed to greatly improve the model (Table 3).

331 Discussion

332 We used a single marker set to conduct a detailed genetic assessment of *X.*
 333 *riversiana* on San Clemente Island and Santa Barbara Island to inform conservation and
 334 management approaches across these independently managed islands. We used island-
 335 wide sampling with 23 microsatellite loci to estimate baseline parameters for each
 336 collection site, quantify population structure, and identify landscape factors correlated
 337 with genetic distance on each island. We found island night lizards were admixed on each
 338 island with shallow, but significant, population structure. Each island also shared
 339 common patterns of isolation by distance, with California boxthorn and prickly pear
 340 cactus identified as the most conductive habitat. Active sand dunes were identified as a
 341 barrier to gene flow on San Clemente Island but are absent on Santa Barbara Island.
 342 Unlike conductive habitat, habitat resistance patterns were unique to each island and
 343 included both natural and anthropogenic features.

344 Population Structure

STRUCTURE identified 2 populations on San Clemente Island associated with the northern and southern ends and with strong admixture across the island (Figure 2). Surprisingly, STRUCTURE identified 4 populations on Santa Barbara Island despite its much smaller size. These populations were strongly associated with the western collection site (WP), northern collection site (AP), mid-island collection sites, and the south-eastern collection sites (Figure 3). The western and northern populations on Santa Barbara Island displayed relatively little admixture whereas other populations were admixed.

It is notable that the global F_{st} estimates for San Clemente Island and Santa Barbara Island were remarkably similar (0.0341 and 0.0346 respectively) despite large differences in island size and sampling scale. Our detection of population genetic structure on each island could result from the clustered sampling of a ubiquitously distributed organism characterized by limited dispersal (Schwartz and McKelvey 2009). However, congruence between methods corroborates the finding that multiple genepools exist across each island even at distances less than 400 m.

Factors Positively Affecting Connectivity

California boxthorn and prickly pear cactus support the greatest abundances of island night lizards and are prime habitat types subject to continued monitoring (USFWS 2014). Our analyses identified prime habitat as highly conducive on both islands, which is supported by ecological data (Fellers and Drost 1991; Mautz 1993). Surprisingly, grasslands were identified as conducive on San Clemente Island even though previous research indicated that grasslands are poor habitat (Fellers and Drost 1991). Grasslands

367 and small canyons on San Clemente Island may be conducive due to the presence of
368 foraging resources and cover items. Cover items are important landscape features for
369 thermoregulation (Regal 1968; Fellers and Drost 1991) and any habitat with suitable
370 cover and resources may be conducive. For example, island night lizards on San Nicolas
371 Island can be found in beach habitat with little vegetation, so long as cover rocks are
372 present (Fellers et al. 1998). The Santa Barbara Island conductance model also included
373 giant coreopsis as weakly conducive. The distribution of this habitat type on Santa
374 Barbara Island is generally contiguous with prime habitat and difficult to analyze
375 independently.

376 *Factors Negatively Affecting Connectivity*

377 No habitat features were identified as resistant on both San Clemente Island and
378 Santa Barbara Island. This finding probably reflects differences in topography, the extent
379 of certain vegetation types, and history of anthropogenic development. Each island is thus
380 characterized by unique factors which correlate with increased effective distances
381 between collection sites and may constrain dispersal and connectivity. Active sand dunes
382 on San Clemente Island were the only habitat we identified as an absolute barrier to
383 dispersal, which is supported by Mautz (1993). There are no sand dunes present on Santa
384 Barbara Island. It is likely that active sand dunes on San Nicolas Island act as barriers as
385 well, although this hypothesis has yet to be assessed.

386 On San Clemente Island, cholla cactus may act as a resistant surface as the spines
387 readily pierce flesh and could injure or debilitate fleeing or dispersing individuals
388 (personal obs.). The southern bombardment area of San Clemente Island is of particular

389 interest as increased disturbance may further propagate cholla increasing its density and
 390 distribution. If further fragmentation of populations within the southern portion of San
 391 Clemente Island becomes a management concern, we recommend controlling or
 392 minimizing the propagation of cholla through habitat restoration or more targeted training
 393 activities. Cholla habitat occurs in sparse and small patches on Santa Barbara Island
 394 likely resulting in the lack of congruent detection across islands.

395 On Santa Barbara Island, multiple habitat types were identified as resistant:
 396 common fiddleneck, needle goldfields, barren ground, and seablite grouped with iceplant.
 397 The identification of common fiddleneck and needle goldfields within similarly
 398 supported resistance models are not consistent with the ecological study of Fellers and
 399 Drost (1991) and could represent biases in the statistical optimization process. Notably,
 400 grassland habitats were absent from the final resistance model despite Fellers and Drost
 401 (1991) finding that grasslands required equivalent capture efforts to seablite and iceplant
 402 habitats. It is likely that when cover is dense enough to cause refugial fissures in the soil
 403 or supplemented by cover items, resistance may be minimized. Iceplant may render areas
 404 unsuitable for other vegetation (Vivrette and Muller 1977) and may, as with barren
 405 ground, limit the cover necessary for foraging, thermoregulation, and dispersal (Fellers
 406 and Drost 1991). However, we could not determine the independent contributions of
 407 seablite and iceplant habitats due to the spatial and temporal transitions between them
 408 (pers. comm., Rodriguez 2016). Thus, on Santa Barbara Island, we recommend habitat
 409 remediation efforts which prioritize iceplant removal and revegetation with prime habitat.

410 Canyons >500 ft in length and secondary roadways were also detected as resistant
411 on San Clemente Island. The association of canyons with increased genetic
412 differentiation between collection sites is supported by ecological research, and may be
413 due to both difficulty in crossing canyons and a lack of resources within them (Mautz
414 1993). Secondary roadways form extensive networks which fragment prime habitat of
415 boxthorn and prickly pear with barren ground, particularly along the western escarpment
416 of the island. Notably, the primary roadway was not identified as a resistant surface, even
417 though it is paved and has more traffic. However, this primary road is a relatively short
418 road running down the middle of the island and is unlikely to significantly influence
419 connectivity patterns. Thus, any efforts to mitigate fragmentation should be applied to
420 secondary roadways.

421 *Management Implications*

422 Management of species that persist on oceanic islands needs to examine the
423 conductance and resistance of habitat within islands and compare between them to derive
424 generalizable actions. As many management actions are spatially explicit, it is important
425 to characterize genetic patterns using spatially explicit methods (Shaffer et al. 2015). The
426 workflow used in our study can be generalized to examine connectivity patterns within
427 mainland ecosystems that are fragmented into habitat islands to inform management
428 actions within and between independently managed habitat fragments.

429 An exemplar region which could benefit from this approach is the peninsular
430 region of Southern California, which is separated into several administrative units tasked
431 with management and monitoring activities. This region may experience increased

432 extinction risks of plant and animal species (e.g. Lawson 2011) and genetic studies of
 433 terrestrial vertebrates have revealed patterns of significant genetic differentiation and
 434 decreased genetic diversity (Luckau 2015; Lion 2016). The modeling frameworks we
 435 present can be applied to support management efforts of peninsular species through the
 436 identification of fine-scale resistant features, for targeted mitigation efforts within each
 437 management area, while also identifying key landscape features within and between
 438 management areas which support connectivity. This combined approach may better
 439 identify management strategies aimed at sustaining local populations, such as increasing
 440 the area of prime habitat and improving the quality of the intervening matrix (e.g. Fahrig
 441 2001).

442 The contemporary genetic patterns we identify for *X. riversiana* can inform
 443 management and monitoring practices on each independently managed island. Common
 444 management strategies across islands include restoring invasive vegetation to prime
 445 habitat to support intra-island connectivity and increase population sizes. Improving
 446 intra-island connectivity and population size may also increase species resilience to
 447 potential threats of climate change or other catastrophic events by increasing genetic
 448 diversity and decreasing the effects of demographic stochasticity. We encourage the
 449 comparison of fine-scale patterns within and between regional management units to
 450 identify common strategies and unique factors to inform mitigation efforts.

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

Figure 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 (barplot).

Figure 3. Santa Barbara Island collection sites with coancestry proportions. All collection sites on Santa Barbara Island are shown. Pie charts represent the site-level coancestry proportions for the STRUCTURE solution K=4 (barplot).

Figure 4. San Clemente Island landscape effects. The landscape-level features correlated with genetic distance incorporated as a composite image. Active sand dunes were identified as a barrier (black). Landscape features in gray were neutral with respect to connectivity. Conductant features (California boxthorn, prickly pear cactus, grasslands, and canyons < 500ft in length) are shown in white. Resistant features (cholla phase maritime desert scrub secondary roadways, canyons > 500ft in length) are shown in dark gray.

Figure 5. Santa Barbara Island landscape effects. The landscape-level features correlated with genetic distance incorporated as a composite image. Landscape features in gray were neutral with respect to connectivity. Conductant features (California boxthorn, prickly pear cactus, and giant coreopsis) are shown in white. Resistant habitat (woolly seablite with crystalline iceplant, barren ground, and common fiddleneck) are shown in dark gray.

Table 1. Summary statistics for each island and collection site. Collection sites are listed under their respective islands with the total samples for that location (N) and those in the reduced data set (Nrr). Summary statistics were: rarefied allelic richness for all collection sites (Ar), rarefied allelic richness for only those sites with ≥ 20 individuals in the reduced data set (Ar (≥ 20)), expected heterozygosity (He), observed heterozygosity (Ho), HWE probabilities (HWE) with probabilities < 0.0001 set to 0.0001 at the locus level. Island-level comparisons were generated from the reduced data sets, analyzed at the 18 shared loci. The inbreeding coefficient (Fis) was calculated by allele identity within GENEPOP overall and for each site. NA denotes analysis not applicable.

Site	N	Nrr	Ar	Ar (≥ 20)	He	Ho	HWE	Fis
San Clemente Island	609	534	21.47	NA	0.89	0.84	< 0.0001	0.0459
1	33	31	8.98	10.35	0.86	0.87	0.8981	0.0137
2	39	33	8.78	10.08	0.86	0.86	0.2835	0.0148
3	86	71	9.31	11.0	0.86	0.87	0.1168	0.0027
4	30	25	8.53	9.77	0.86	0.87	0.6173	0.0019
5	28	24	8.59	9.92	0.86	0.88	0.3311	0.0018
6	31	29	8.24	9.50	0.84	0.86	0.4165	0.0044
HR	36	28	8.07	9.25	0.84	0.86	0.3063	-0.0008
7	32	30	8.21	9.49	0.84	0.83	0.2200	0.0317
8	27	20	5.46	6.28	0.69	0.62	0.0005	0.1157
10	30	30	9.20	10.80	0.86	0.87	0.1464	-0.0022
11	31	28	8.55	9.94	0.85	0.82	0.0089	0.0508
13	29	28	9.07	10.69	0.87	0.88	0.1188	0.0089
C	13	12	7.34	NA	0.82	0.86	0.4647	-0.0056
20	36	34	8.27	9.57	0.84	0.85	0.0838	0.0023
29	29	27	8.17	9.28	0.85	0.86	0.0488	0.0062
37	34	27	8.26	9.63	0.84	0.83	0.3470	0.0319
38	30	28	9.21	10.83	0.87	0.86	0.9637	0.0275
39	31	29	8.31	9.65	0.84	0.85	0.2572	0.0097
Santa Barbara Island	312	271	13.82	NA	0.86	0.82	< 0.0001	0.0473
AP	28	21	5.85	7.20	0.80	0.80	0.2612	0.0292
CB	8	8	5.62	NA	0.79	0.83	0.8888	-0.0051
CC	31	24	6.44	8.18	0.83	0.83	0.3197	0.0086
GC	39	38	6.65	8.65	0.83	0.84	0.6265	0.0134
LC	9	8	5.97	NA	0.81	0.89	0.9830	-0.0208
NP	69	60	6.49	8.42	0.82	0.82	0.0227	0.0134
PP	37	33	6.28	7.87	0.82	0.81	0.1433	0.0251
S	13	12	5.92	NA	0.79	0.77	0.1239	0.0581
SE	35	31	6.56	8.36	0.83	0.85	0.6892	0.0026
WP	43	36	5.67	7.17	0.78	0.76	0.1836	0.0453
Aggregate LC+GC	48	46	6.77	8.88	0.84	0.84	0.3103	0.0089

Table 2. San Clemente Island competing conductance and resistance models. The best-supported conductance and resistance models 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^2_{β} value are also presented and were used in model selection. Model components are listed with the value assigned to each factor in parentheses.

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

Table 3. Santa Barbara Island competing conductance and resistance models. The best-supported conductance and resistance models 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^2_{β} value are also presented and were used in model selection. Model components are listed with the value assigned to each factor in parentheses.

	P	R^2	AICc	R^2_{β}
Null	0.0212	0.4804	-140.12	0.6911
Conductance Models				
Null + California Boxthorn(100)+ Prickly pear cactus (50) + Common fiddleneck (2)	0.0013	0.8611	-151.98	0.8614
Null + California Boxthorn(100)+ Prickly pear cactus (50) + Needle goldfields (2)	0.0003	0.8801	-151.98	0.8624
Null + California Boxthorn(100)+ Prickly pear cactus (2)	0.0002	0.8653	-152.12	0.8667
Null + California Boxthorn(50)+ Prickly pear cactus (2)	0.0012	0.8617	-152.36	0.8683
Null + California Boxthorn(100)+ Prickly pear cactus (50) + Giant Coreopsis (2)	0.0005	0.8677	-153.13	0.8716
Null + California Boxthorn(100)+ Prickly pear cactus (100)+ Giant Coreopsis (2)	0.0008	0.8877	-153.19	0.8718
Null + California Boxthorn(100)+ Prickly pear cactus (50) + Oatgrass (2)	0.0006	0.8693	-153.23	0.8709
Null + California Boxthorn(100)+ Prickly pear cactus (100) + Oatgrass (2)	0.0010	0.8693	-153.32	0.8713
Resistance Models				
Null + Seablite with iceplant (50) + Barren ground (100) + Common fiddleneck (50)	0.0003	0.8582	-149.69	0.8076
Null + Seablite with iceplant (50) + Barren ground (50) + Common fiddleneck (50)	0.0005	0.8582	-149.39	0.7490
Null + Seablite with iceplant (50) + Barren ground (100) + Common fiddleneck (50) + Needle goldfields (100)	0.0004	0.8582	-149.04	0.8371
Null + Seablite with iceplant (50) + Barren ground (50) + Common fiddleneck (50) + Needle goldfields (100)	0.0005	0.8582	-150.07	0.8704
Null + Seablite with iceplant (2) + Barren ground (50)	0.0027	0.6919	-150.22	0.8867