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RESEARCH ARTICLE

Conservation genetics of three flightless beetle species in southern California

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Abstract Regional scale conservation decisions can be aided by information on the distribution of intraspecific diversity, especially the extent to which patterns are common to multiple species. We compare patterns of intraspecific mitochondrial cytochrome oxidase I (COI) variation among three flightless beetles (Coleoptera: Tenebrionidae: *Nyctoporis carinata* LeConte; Staphylinidae: *Sepedophilus castaneus* (Horn); Carabidae: *Calathus ruficollis* Dejean) in the southern part of the California Floristic Province biodiversity hotspot. All species exhibit moderate to high levels of total variation, ranging from 2% to 10% (maximum uncorrected distance). Most populations of all species exhibit unique haplotypes, but few populations' haplotypes constitute exclusive clades. Many adjacent pairs of populations show indications of some, though limited, genetic connectedness, due either to gene flow or ancestral polymorphism. However, in most cases this diminishes sharply over greater distances. By both statistical and phylogenetic measures, Sierra Nevadan populations are highly distinct from those in the coast and transverse ranges. Among the latter, the eastern transverse ranges are generally most unique and isolated, with diversity in the western parts of these ranges showing fewer barriers. Otherwise, few measures agree on areas of highest conservation value, and overall patterns tend to be species-specific.

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Introduction

One of the principal goals of biodiversity conservation is to preserve the evolutionary potential of biological entities (Forest et al. 2007), be they species or populations. This forward-looking approach is paradoxically best served by a backward-looking perspective. That is, a species' past is one of the best predictors of its future. Population genetic, phylogeographic, and phylogenetic methodologies peer progressively further back in time to reconstruct the patterns and processes that have led to the distribution of genetic diversity presently observed in species, and yield insights into the factors that have influenced this distribution. Studies on the conservation genetics of individual species can provide important information applicable to that species' long term preservation. However, extending such studies to multiple codistributed species can provide information applicable to the conservation of entire biodiversity landscapes. In this paper we compare intraspecific patterns of genetic diversity among three codistributed, flightless beetle (Coleoptera) species in the southern part of the California Floristic Province (CFP).

While the CFP as a whole is recognized as an internationally significant biodiversity hotspot (Myers et al. 2000), the California Transverse Ranges have stood out as an area of particular biogeographic interest. The Transverse Ranges represent a major, anomalous topographic feature in the southern part of the CFP. This series of ranges (Fig. 1) stretches from the Pacific coast to the eastern edge of the CFP, where it meets the southwestern U.S. deserts, isolating the southern cismontane (seaward) one-third of the region

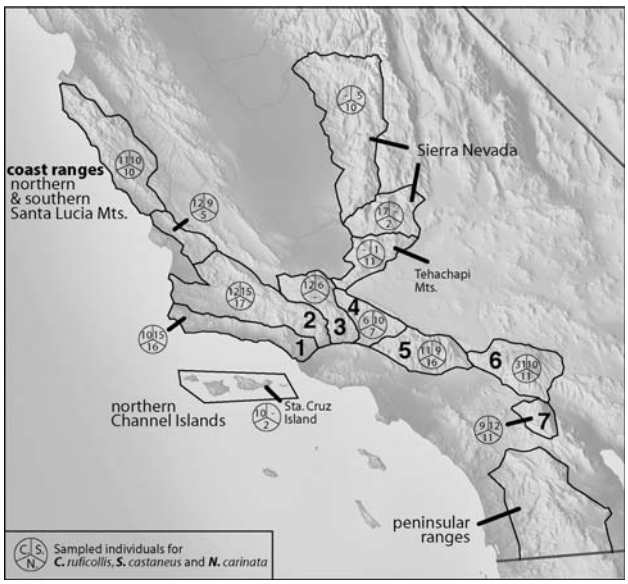

Fig. 1 Map of southern California showing Transverse ranges and other areas of endemism as recognized in this paper. The Transverse ranges proper are numbered as follows: 1: Santa Ynez Mts., 2: NW Transverse Ranges, 3: Central Transverse Ranges, 4: Sierra Pelona, 5: San Gabriel Mts., 6: San Bernardino Mts., 7: San Jacinto Mts. Sampled individuals of all three species are indicated in the circles for each area. See Appendix 1 for exact collection localities

from the north. This series of ranges has become 'Transverse' through rotational movements associated with the Pacific-North American plate boundaries, and contrast in this respect from typically north–south trending ranges of the American West (Harden 2004). Most of this area is considered to reside within the 'Southwestern' subregion of the CFP (following Hickman 1993), which is distinguished on topographic, floristic, and climatic grounds. Three other major subregions, however, the Central Western (mainly Coast Ranges), Great Central Valley, and Sierra Nevada, abut this region along its northern edge. Major genetic disjunctions have been observed to correspond, at least loosely, with this boundary (Calsbeek et al. 2003; Rissler et al. 2006), and recent work has focused on understanding more precisely how it has influenced dispersal patterns in different organisms (Chatzimanolis and Caterino 2007b).

Understanding the genetic landscape in southern California is particularly urgent, as southern California is one of the most densely populated and rapidly developing areas in the world. The CFP's designation as a hotspot reflects not only its high levels of diversity and endemism, but the intensity of these anthropogenic threats as well. Southern California is home to more endangered species than nearly any other part of the United States (Dobson et al. 1997). The threats to these and other species take many forms. Urbanization of wildlands in the area has proceeded steadily, with no end in sight (Rundel and King 2001; Syphard et al. 2005). Development has been accompanied by invasive species, pollution, and increased frequency of fire, all of which have had detrimental effects on native biodiversity (Fisher et al. 2002; Seabloom et al. 2006; Schwartz et al. 2006; Syphard et al. 2006). Beyond these direct effects, remaining habitat has been fragmented, which both exacerbates some of the above problems (Suarez et al. 1998; Bolger et al. 2000), and through demographic and population genetic effects, imposes challenges of its own (Wilcox and Murphy 1985). Losses of genetic diversity through fragmentation have already occurred in southern California arthropods (Vandergast et al. 2007). Furthermore, these effects may be manifested at surprisingly low levels of urbanization (Riley et al. 2005). It has also been demonstrated that habitat fragments sufficient to host some of the region's endangered vertebrates do not necessarily protect insects associated with these habitats (Rubinoff 2001).

On a more positive note, the obvious threats to the unique biodiversity of southern California has motivated a strong and active conservation community. Local, state, federal, and private agencies have come together in ecosystem level planning, most notably through the Natural Community Conservation Planning (NCCP) effort, coordinated by the California Department of Fish and Game (CDFG 2007). The NCCP process aims to incorporate all relevant science in its planning, including information on population genetics of species concerned. The NCCP's flagship plan, the San Diego Multiple Species Conservation Program, aimed at preserving coastal sage scrub communities, has garnered national attention, paving the way for additional science-based conservation in densely populated southern California.

The incorporation of invertebrates into such integrative planning has been hampered by a dearth of even basic natural history information, let alone detailed data on population genetic relationships. Arthropods, mainly insects, represent an overwhelming fraction of the region's biodiversity, yet population genetic and phylogeographic relationships have been investigated for only a small number. Most studies that have been done have demonstrated significant genetic divergence over short geographic distances (Landry et al 1999; Seagraves and Pellmyr 2001; Bond 2004; Chatzimanolis and Caterino 2007b), corresponding, in some, to species level divergence (Law and Crespi 2002). In some cases this has been attributed, at least in part, to contemporary environmental factors (Vandergast et al. 2007). Unfortunately, due largely to real distributional differences among these taxa, sampling in previous studies has been varied enough in location and intensity to preclude straightforward synthesis from a regional perspective.

Our goal in this paper is to analyze three species of co-occurring beetles in southern California's Transverse Ranges from a conservation genetic perspective. In particular we are interested how isolated populations in the major components of these ranges are from one another. This includes analysis of gross distribution of genetic diversity, to discover areas that

might harbor unusually high or relictual diversity, as well as analysis of connectedness among regions, to determine how recently populations have been in genetic contact, or indeed, how important ongoing contact through migration may be to maintaining genetic diversity patterns. By examining multiple species together, we can determine the extent to which these patterns are idiosyncratic or shared, offering hope for developing additional multiple species conservation strategies. And by examining these patterns in a phylogenetic context, we can shed light on the historical factors responsible for current patterns, and future prospects for maintaining them.

Materials and methods

Sampling

This study uses beetles to examine the questions above. Beetles represent the largest single fraction of global biodiversity, and are represented by nearly 8000 described species in California (Caterino 2006). We analyze data from three species: *Calathus ruficollis* Dejean (Carabidae), *Sepedophilus castaneus* (Horn) (Staphylinidae), and *Nyctoporis carinata* (LeConte) (Tenebrionidae). All three of these species are flightless, and their relative immobility should promote geographically-limited patterns of genetic diversity. Detailed phylogeographic analyses of *C. ruficollis* and *S. castaneus* have previously been published (Chatzimanolis and Caterino 2007a, b, respectively), but data for *N. carinata* are newly presented here. In addition we have added 7 individuals of *C. ruficollis* from the San Gabriel Mts., two of which share a haplotype not previously reported. Data for sampling sites and GenBank Acc. #s (EU037099-EU037184, EU037191) are given in Appendices 1 and 2. Some regrouping of populations in *C. ruficollis* and *S. castaneus* has been done for statistical analyses to match sampling for *N. carinata* so some specific results may differ slightly from those previously presented. Each species is represented by multiple individuals (at least 10 where possible) from each of 10 areas, though not all species were found in all areas (Fig. 1). These areas represent variably discrete subunits of the Transverse Ranges, including, from west to east, the Santa Ynez Mts., Sierra Pelona, San Gabriel Mts., San Bernardino Mts., and San Jacinto Mts. While the eastern-most of these are separated by distinct valleys, corresponding in most cases to major faults, the western ranges merge with each other and with more northern ranges with little in the way of obvious (modern) barriers. These divisions follow major drainages and low passes, and offer contiguous and roughly similar-sized areas for comparison. Two additional areas, the northern and southern Santa Lucia Mountains are not considered to belong among the Transverse Ranges, but they often show phylogeographic relationships to Transverse Range regions (Chatzimanolis and Caterino 2007b), and provide additional context for comparison. In the cases of *C. ruficollis* and *S. castaneus*, the sampled localities represent a fairly small portion of their total ranges, which extend in both cases from near the U.S.-Mexico border north along the coast into Oregon and Washington. Our samples of *N. carinata* do represent most of its supposed range, and include samples of a questionably distinct congener, *N. vandykei* Blaisdell, in the southwestern Sierra Nevada.

These analyses are all based on sequences of the mitochondrial cytochrome oxidase I gene, which has been widely used in intraspecific studies of insect diversity (Caterino et al. 2000). Specimens were collected into 100% ethanol or directly frozen and stored at −70°C. DNA voucher specimens are deposited at the Santa Barbara Museum of Natural History and their corresponding data are available through the California Beetle Project database at http://www.sbcollections.org/cbp/cbpdatabase1.aspx. Total genomic DNA was extracted using the DNeasy Tissue kit (Qiagen, Valencia, CA). An approximately 826bp fragment of the COI gene was amplified using the primers C1-J-2183 ('Jerry': CAACATTTATTTTGATTTTTTGG) and TL2-N-3014 ('Pat': TCCAATGCACTAATCTGCCATATTA). PCRs included an initial denaturation of 5 min at 94°C, 35 cycles of: 45 s at 94°C, 30 s at 45°C and 1 min at 72°C; followed by a 2 min final extension at 72°C. PCR products were purified using the QIAquick PCR Purification kit (Qiagen, Valencia, CA) and sequencing was performed by Macrogen, Inc. (Seoul, Korea). All fragments were sequenced in both directions.

Genetic diversity

We quantified genetic diversity in each population by several measures. To assess raw diversity within each population we calculated nucleotide diversity (equivalent to average uncorrected, or 'p', distance among individuals within each population). This captures some phylogenetic depth albeit in a phenetic manner. To measure uniqueness of each population we calculated fraction of unique haplotypes within each area and examined monophyly of each population's haplotypes. Distinctness of the haplotype complement for each population is measured by the average uncorrected pairwise distance to all other populations.

Connectedness of populations

To assess the relative isolation of populations of each species we examined interpopulation connectedness by several means. First, Arlequin (ver. 3.1; Excoffier et al. 2005) was used to calculate interpopulation F_{ST} values (10,000 permutations; TrN93 + Γ model (Tamura and Nei 1993)). These provide an indication of the extent and strength of subdivision among all pairs of populations based on haplotype frequencies. To test for isolation-by-distance relationships we used

the Isolation-by-distance web service (IBDWS; Jensen et al. 2005), performing a Mantel test on untransformed F_{ST} values for all species against straight-line geographic distance. Geographic distance was measured between sampling points using tools available in the BerkeleyMapper, with specimen point data from the California Beetle Project database. To test for correlation in specific pairwise population parameters (F_{ST}) among species we used permutation tests, as implemented in the program Permute! (v3.4α9; Casgrain 2001), with 1000 permutations. For the newly generated *N. carinata* data, we performed AMOVA (Analysis of Molecular Variance; Excoffier et al., 1992) to test the potential significance of alternate subgroupings of populations according to significant results from the other species, principally those from *S. castaneus* (Chatzimanolis and Caterino 2007b). We also conducted AMOVA on *C. ruficollis* data following slightly different population groupings from Chatzimanolis and Caterino (2007a). Altogether the breaks tested included successively more southern divisions adding areas to the northern group as follows: southern and SW Sierra Nevada vs. everything south (Fig. 2a); adding northern and southern Santa Lucias to northern group (Fig. 2b); NW Transverse Ranges (Fig. 2c); Santa Ynez Mts. (Fig. 2d); Central Transverse Ranges (Fig. 2e); Sierra Pelona (Fig. 2f); San Gabriels (Fig. 2g); San Bernardinos (Fig. 2h). The Channel Islands samples for *N. carinata* and *C. ruficollis* were excluded, since *S. castaneus* data were not available from this area. AMOVA comparisons were based on Tamura and Nei distances with 10,000 permutations.

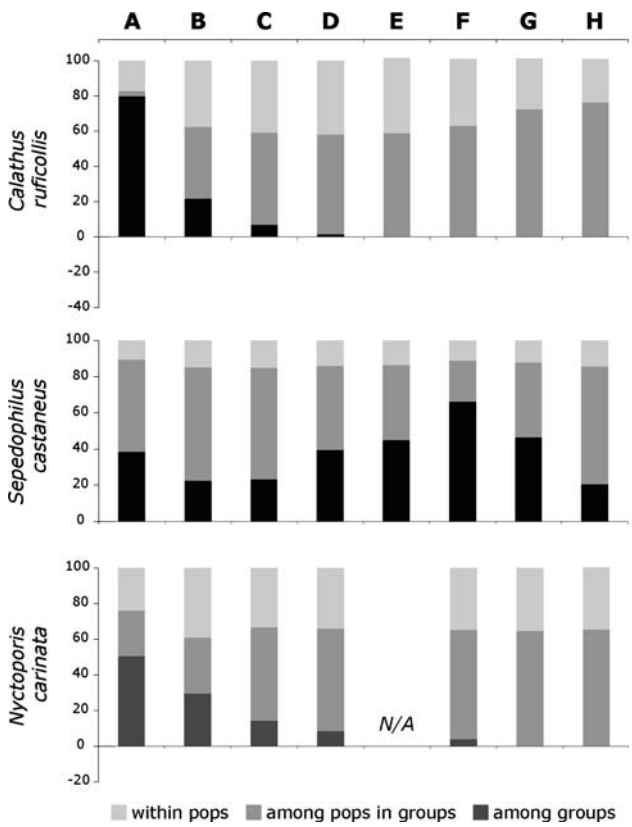

Fig. 2 Comparative AMOVA results, showing percentage of within group, among population within group, and among group variation across 8 tested two-group splits. Negative values calculated for comparisons E–H for *C. ruficollis* and G–H for *N. carinata* have been zeroed, as negative values are generally seen as statistical artifacts associated with lack of among group variation. The two-group splits A–H tested correspond to selected north–south groupings involving the Transverse Ranges as described in the text

Demographics

We investigated demographic trends of population expansion or contraction as an indication of population robustness. Fu's Fs (Fu 1997) and Tajima's D (Tajima 1989) were examined in Arlequin for departures from an equilibrium population. We also calculated the exponential growth parameter 'g' using Metropolis–Hastings sampling of the genealogy implemented in the program Fluctuate (Kuhner et al. 1998). We used the F81 (Felsenstein 1981) model with empirical (uneven) base frequencies and a ti/tv ratio as estimated by ModelTest (see below), and a Watterson initial estimate of Θ, running 10 short chains of 20,000 steps and 2 long chains of 2,000,000 steps, sampling every 20 or 200 steps, respectively. Fluctuate was also used to estimate the population parameter Θ, which, assuming a roughly constant mutation rate among species and lineages, provides a measure of effective population size.

Historical patterns

To assess shared history in a broader sense, we conducted phylogenetic analyses of non-redundant haplotypes of all three species (58 for *C. ruficollis*, 45 for *S. castaneus*, and 91 for *N. carinata*). Phylogenetic trees were estimated using Bayesian methods. The maximum likelihood model for the COI gene was estimated using ModelTestServer version 1.0 (running ModelTest version 3.8) (Posada 2006) using the corrected Akaike Information Criterion (AICc). Bayesian analysis was performed in MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) using three runs with 4×10^6 generations, each having four Markov chains, heating equal to 0.2 and sampling every 100th generation. For *N. carinata*, sequences of *Nyctoporis aequicollis* and *Coelus ciliatus* (Tenebrionidae; GenBank Acc.#s, EU037190 and EU032421, respectively) were included as outgroups. Additional details for analyses of *C. ruficollis* and *S. castaneus* have been presented previously (Chatzimanolis and Caterino 2007a, b)

Assessing conservation value

Assessing conservation value from population genetic data can take a couple of broad perspectives. Systematists have

generally sought phylogenetically distinct, unusually divergent, or unusually diverse species subsegments for prioritization as some sort of evolutionarily significant units (e.g. Moritz 1994) and this has been extended in a comparative context to identify generally significant areas (Calsbeek et al. 2003; Moritz and Faith 1998; Rissler et al. 2006). It is also increasingly possible to discern contemporary demographic patterns as well as recent disruptions of these patterns (Frankham 1995; Vandergast et al. 2007). We primarily take the first approach, focusing on intraspecific diversity and its phylogeographical distribution. We first calculated averages of raw diversity measures directly. However, these numbers are biased in most cases by the absolute value of the more divergent species. We also assigned a rank to each value across populations within each species, with 1 indicating the highest conservation value (indicating greatest diversity or greatest isolation), finally averaging these ranks across species by population.

Results

Overall diversity

All three species examined here exhibit moderate to high levels of overall intraspecific diversity (Table 1), especially considering the relatively restricted portion of their respective ranges represented. Both *C. ruficollis* and *S. castaneus* exhibit nearly half as many haplotypes as individuals, while in *N. carinata* almost every sampled individual has a unique haplotype. Beyond simply having numerous haplotypes, these haplotypes represent considerable phylogenetic depth. In *C. ruficollis*, showing the shallowest total divergence, pairwise distances range to 2%, while in *N. carinata* they exceed 10%. This diversity is variably partitioned among populations, but almost all populations of all species possess unique haplotypes. There was little consistency among species as to which populations exhibited the extremes of haplotype diversity as measured by simple number of haplotypes. Based on average ranks Santa Cruz Island populations rank highest, but this is based on only *C. ruficollis* and *N. carinata*. The second ranking southwestern Sierra Nevada populations are similarly represented by only two species. The most diverse area overall with all species represented is the Santa Ynez Mountains, which exhibit largely (*C. ruficollis*) or entirely (*N. carinata*) unique haplotypes. However, this is the least unique of *S. castaneus* populations, exhibiting no unique haplotypes there.

Nucleotide divergence among haplotypes within populations offers a better indication of their total phylogenetic diversity. These results are similar to simple proportions of unique haplotypes, but are more sensitive to the presence of multiple lineages in populations. The greatest average within population divergence is seen in the southwestern Sierra Nevada. These mountains represent the southernmost extent of the Sierra Nevada, which in general have exhibited disproportionate divergence in all beetles examined (Chatzimanolis and Caterino 2007a, b). While interesting and indicative of a major phylogeographic break, this region lies outside of the Transverse Ranges, and serves here primarily to put the Transverse Ranges into perspective. This is also true to a lesser extent of the Santa Lucias, in the central coast ranges, and we limit our discussions below mainly to parts of the Transverse Ranges. Here the top-ranking within population diversity is seen in the Sierra Pelona, with all species showing moderately high diversity in this region. This region does not, however, contain the highest diversity of any of them individually, and these species maxima are scattered, including the northwestern Transverse Ranges, the Santa Ynez Mountains, and the central Transverse Ranges, for *S. castaneus*, *N. carinata*, and *C. ruficollis*, respectively.

Considering the divergence among populations, most show considerable distinctness. The average distances among populations of *N. carinata* are highest overall and individually by population in all cases, with no population averaging closer than 6% to all others. In *S. castaneus*, most populations are more than 3% divergent. Divergences among populations of *C. ruficollis* are in line with expectations for a more or less panmictic species, with nearly all exhibiting <1% average divergence. Among Transverse Range areas, the among population divergences averaged across species are largely similar among areas. Each species shows some slight outliers: in both *S. castaneus* and *N. carinata*, the San Bernardino and San Jacinto populations are slightly more divergent. In *C. ruficollis* the Central Transverse Ranges appear most distinctive, although this is due mainly to the presence of a divergent Sierra Nevada haplotype in this population. But in general, within species, the populations exhibit surprisingly constant levels of divergence among one another.

Connectedness

Our primary measure of population connectedness was pairwise F_{ST} values (Table 1; Appendix 3). For each population we measured this as the number of significant F_{ST} values to all other populations. In *S. castaneus* and *N. carinata*, all or nearly all interpopulation comparisons were significant, with, in the latter, only Sierran, Coast Range and, surprisingly, Santa Cruz Island populations showing insignificant separation (this last likely due to low sample size). In *C. ruficollis*, the most isolated population is that of the Central Transverse Ranges, and this agrees with phylogenetic results which support this as a distinct clade (Chatzimanolis and Caterino 2007a). San Jacinto and San Gabriel populations also appear isolated from most others. The best connected populations appear to be the northwestern Transverse Ranges and Sierra Pelona, both insignificantly isolated from the majority of other populations.

Both *S. castaneus* and *N. carinata* show strongly significant isolation-by-distance (Table 2) over their ranges.

Table 1 Genetic diversity statistics by area

POPULATIONS	Northern Santa Lucias	Southern Santa Lucias	NW Transverse Ranges	Santa Ynez Mts.	Central Transverse Ranges	SW Sierra Nevada	Southern Sierra Nevada	Sierra Pelona	San Gabriels	San Bernardinos	San Jacintos	Northern Channel Islands	
Sample size													**Total**
C. ruficollis	11	12	15	7	12	-	17	6	11	31	9	10	**141**
S. castaneus	10	9	15	15	6	5	-	10	9	10	11	-	**100**
N. carinata	10	5	18	15	-	10	2	7	16	11	11	2	**107**
No. haplotypes													**Total**
C. ruficollis	4	12	10	6	6	-	6	4	7	11	6	8	**58**
S. castaneus	6	7	7	1	3	4	-	4	5	5	6	-	**45**
N. carinata	4	3	16	15	-	9	1	7	14	7	8	2	**91**
fraction unique haplotypes													
C. ruficollis	0.75	0.83	0.40	0.83	0.67	-	0.33	0.25	0.00	0.27	0.67	0.63	
S. castaneus	0.50	0.71	0.57	0.00	0.67	0.75	-	0.50	0.60	0.80	0.50	-	
N. carinata	0.75	0.33	0.94	1.00	-	0.89	1.00	1.00	0.86	0.57	0.63	1.00	
Avg. 'p' distance to neighboring populations													
C. ruficollis	0.006	0.007	0.007	0.007	0.008	-	0.026	0.007	0.007	0.007	0.007	0.008	
S. castaneus	0.032	0.032	0.028	0.027	0.028	0.044	-	0.027	0.033	0.032	0.033	-	
N. carinata	0.061	0.059	0.059	0.059	-	0.088	0.084	0.081	0.056	0.057	0.061	0.060	
Avg. 'p' distance within population													
C. ruficollis	0.002	0.006	0.005	0.005	0.005	-	0.002	0.005	0.004	0.005	0.004	0.006	
S. castaneus	0.010	0.007	0.011	0.000	0.001	0.003	-	0.008	0.001	0.005	0.002	-	
N. carinata	0.005	0.022	0.021	0.039	-	0.044	0.000	0.023	0.020	0.021	0.021	0.002	
No. significant pairwise Fst to all other pops													
C. ruficollis	7	5	3	6	10	-	10	3	7	5	8	6	
S. castaneus	9	9	9	9	9	9	-	9	9	9	9	-	
N. carinata	11	10	11	11	-	11	10	11	11	11	11	9	
Fu's Fs - bold are significant													
C. ruficollis	0.683	**-8.834**	-2.852	-1.751	0.499	-	-0.286	0.821	-1.524	-1.237	-1.162	-1.248	
S. castaneus	1.653	-0.875	2.649	0.000	0.117	-0.567	-	3.742	**-1.995**	1.215	**-2.295**	-	
N. carinata	2.672	5.241	-2.976	-2.818	-	0.902	0.000	-0.551	-2.117	2.874	1.571	0.693	
Tajima's D - bold are significant													
C. ruficollis	-0.785	-1.101	0.096	-0.934	**-2.043**	-	-0.913	-0.338	-0.678	-0.708	-0.860	-0.039	
S. castaneus	1.462	**-1.685**	0.894	0.000	-0.447	-0.668	-	1.655	-0.689	-0.549	-0.404	-	
N. carinata	**-1.850**	1.869	0.138	0.680	-	0.600	0	0.560	-0.400	-0.762	0.046	0.000	
Θ_{ML}													
C. ruficollis	0.003	0.419	0.020	0.104	0.006	-	0.006	0.012	0.009	0.010	0.008	0.024	
S. castaneus	0.005	0.009	0.005	0.001	0.404	0.027	-	0.003	0.138	0.005	0.005	-	
N. carinata	0.004	0.006	0.006	0.132	-	0.040	-	0.066	0.103	0.118	0.014	-	
Population expansion or contraction													
C. ruficollis		+ (1853.49)	+ (864.91)	+ (1790.41)								+ (687.15)	
S. castaneus					- (-0.99)	+ (1705.03)			+ (9060.68)				
N. carinata			+ (117.60)	+ (76.76)				+ (148.54)	- (-2.77)	- (-2.48)			

Fu's Fs, and Tajima's D statistics were calculated in Arlequin. Θ_{ML} was estimated using FLUCTUATE, as was possible expansion or contraction of populations ('+' or '−', respectively, shown with ML estimate of exponential growth parameter only if significant). For Fu's Fs and Tajima's D values all calculable values are shown, with significant values bolded. Where multiple species for a given measure agree in supporting a particular area as the most genetically valuable, values for that area are boxed

This indicates that what gene flow may occur is strongly attenuated with distance. A permutation test examining the correlation of F_{ST} values across specified populations of the three species finds no significant pairwise correlations (Table 3), indicating that geographic patterns of isolation are largely distinct among species.

Two-group AMOVA analyses for *N. carinata* populations agreed with *C. ruficollis* in a strong separation of Sierran (and Tehachapi – not present in *C. ruficollis* samples) populations from Coast and Transverse Range populations (Fig. 2a). This was somewhat consistent in *S. castaneus*, where maximum among-group variation was found when separating northern (including Sierran) and southern groups between the Sierra Pelona and San Gabriel mountains (Fig. 2e), splitting the Transverse Ranges between major genetic groups (for further discussion of this break see Chatzimanolis and Caterino 2007b).

Historical patterns

Phylogenetic analyses (Fig. 3) underscore many of the preceding results. Populations of all species in the Sierra Nevada are highly distinct from populations in the Transverse Ranges and coast ranges. This represents the fundamental split within *N. carinata* and *C. ruficollis*. In *S. castaneus*, there are several roughly regional clades, but relationships among them are poorly supported. A well supported eastern Transverse Range clade in *S. castaneus* has some correspondence with *N. carinata*, in which a San Jacinto Mts. clade is sister to all other Transverse Range populations. But in *N. carinata* the San Bernardino and San Gabriel Mts. are not closely related to most San Jacinto haplotypes (with one exception, an apparent San Jacinto to San Bernardino migrant). Otherwise, populations in the more western portions of the Transverse Ranges

exhibit little phylogenetic coherence. This is most obvious in *C. ruficollis*, in which many haplotypes are distributed throughout the region. However, even in the much more strongly structured species, there is extensive phylogenetic intermingling among areas, despite the generally significant F_{ST} values among them. In *S. castaneus*, western Transverse Range individuals appear in a basically coast range clade, while a coast range individual appears in an otherwise western and central Transverse Range clade. In *N. carinata*, haplotype relationships show even less geographic structure, with few populations appearing monophyletic.

Demographics

There was little consistency among measures supporting any significant trends in population expansion or contraction. If anything there are indications that several populations may have undergone recent expansion. In *C. ruficollis* Chatzimanolis and Caterino (2007a) attributed apparent expansion in several populations to somewhat anthropophilic tendencies in this species. However, no such habits are obvious in the other species. In almost every area some species shows signs of population expansion, with the southern Santa Lucias, the (adjacent) northwestern Transverse Ranges, Santa Ynez Mts., and San Gabriels indicating expansion by some measure for two of the three species. Fluctuate provided the greatest number of significant results, though not supporting expansion scenarios deemed significant by Fu's Fs or Tajima's D in all cases (noteably that indicated for *S. castaneus* for the southern Santa Lucias), perhaps indicating that the departures from neutrality these latter statistics indicate derive from other factors. From a conservation perspective, population contraction is of particular interest, and Fluctuate indicated significant contraction for the central Transverse Range population of *S. castaneus*, and the San Gabriel and San Bernardino populations of *N. carinata*, but for no area for more than a single species. At this point we cannot determine the recency of any of these changes in population size, and would not suggest that any necessarily represent response to anthropogenic factors.

Discussion

Examining population genetic patterns across multiple co-distributed species would ideally reveal consistent patterns of diversity and isolation, pointing toward clear assessments of relative conservation significance of different areas. The purpose of this analysis was not specifically to establish conservation priorities in these three beetle species, but rather to assess the extent to which their distributions of genetic diversity identified similar regions of genetic interest. At a general level, these three flightless beetle species all exhibited remarkable intraspecific diversity, even just within what, for two of them, is a small portion of their total range. While in *Calathus ruficollis* this diversity shows little geographic structure, indicating considerable recent gene flow, in both *Sepedophilus castaneus* and *Nyctoporis carinata*, mitochondrial diversity shows much more geographic structure, and even where populations contain representatives of multiple haplotype clades, there is little evidence of recent contact (in that the putative migrant haplotypes are not represented in 'source' areas). The clearest conservation message that can be built on these observations is that the Transverse Ranges are by no means a genetically homogenous block, and all of its subregions exhibit unique genetic variants, some of which are highly divergent.

On a less satisfying note, patterns of the distribution of diversity among species shows little consistency. The most consistent finding separates Sierra Nevadan populations from most (*S. castaneus*) or all others. Sampled populations in the Coast ranges, the northern and southern Santa Lucia Mts. are less distinctive, but still exhibit relatively high divergence, diversity, and some degree of phylogenetic unity for two of our three species, the northern portions, especially. Among areas within the Transverse ranges, every measure we examined identified a different area as most significant. And for no measure did all the species rank the chosen area unanimously high. For example the most divergent area as assessed by averaging pairwise distances to other populations is the San Jacinto Mts. (Table 1). However, this is not the most divergent area for any of them, individually. For *C. ruficollis* it is the central Transverse Ranges, for *N. carinata* the San Bernardinos, and for *S. castaneus*, the San Gabriels. In fact, every area we recognize in the Transverse Ranges is ranked as most or second-most significant by one or another measure. This might be taken to underscore our previous point, that all areas here protect significant genetic diversity, and none are expendable or interchangeable. This does imply a rather high management burden, but better prioritization with data from additional species remains a possibility.

Table 2 Isolation by distance (IBD) using untransformed F_{ST} and geographic distance

	Z	R^2	P
Calathus ruficollis	2387.44	0.0157	0.638
Sepedophilus castaneus	4888.45	0.270	<0.001*
Nyctoporis carinata	7458.47	0.142	0.015*

Asterisks indicate significant IBD

Table 3 Pairwise F_{ST} correlation tests using Permute! and deleting all localities not shared by all

	Calathus ruficollis	*Sepedophilus castaneus*
Calathus ruficollis		
Sepedophilus castaneus	0.405	
Nyctoporis carinata	0.052	0.310

P-values shown only

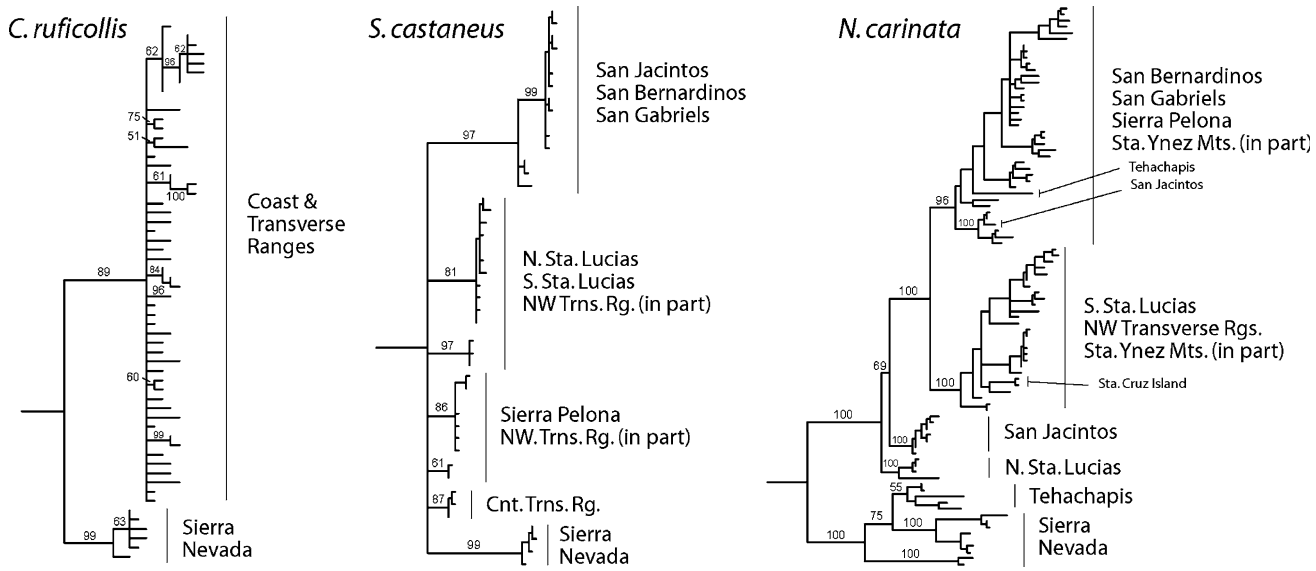

Fig. 3 Bayesian phylogenetic trees, with areas indicated for geographically coherent terminal clades, and posterior probabilities >50% on branches. For details of trees for *C. ruficollis* and *S. castaneus* see Chatzimanolis and Caterino (2007a, b, respectively)

Connectedness of populations may be an important determinant of long-term viability of species. The occasional influx of individuals and novel genetic variants can buffer a population from inbreeding, stochastic effects and localized selection events (Newman and Tallmon 2001). So whatever insights into migration routes among subregions in the Transverse ranges can be gleaned from population level data are valuable. Significant migration may occur over a broad time scale, ranging from the very recent, as indicated by shared haplotypes, to the historic, as seen in disjunct distributions within haplotype clades. Our main indicator of recent migration is interpopulation F_{ST}. By this measure only *C. ruficollis* shows any indication of significant dispersal, with nearly all adjacent populations showing insignificant F_{ST} values. Significant subdivision is only apparent between more distant sites. Given the strong geographic fidelity of the other two species, it is conceivable that some apparent *C. ruficollis* migration is very recent, i.e., anthropogenic (Chatzimanolis and Caterino 2007a).

Taking a longer view, all species do show signs of historical population connections. Several populations in both *S. castaneus* and *N. carinata* comprise haplotypes from multiple clades. In particular the populations in the southern coast ranges (Santa Lucias) and western and northwestern Transverse ranges contain mixtures of haplotypes, suggesting occasional movement between them. On the other hand, although covering a large area, these regions are not separated by very clear topographic or environmental boundaries, and these 'populations' may well all be connected, with distance being the main isolating factor. In a few other cases, more distinct signatures of unique migrations may be seen. In particular the appearance of individuals of the San Bernardino clade of *N. carinata* in the Tehachapi Mts. and in the San Jacintos clearly indicates dispersal. These areas otherwise host highly distinct lineages. While the importance of these unique events to long-term viability is impossible to assess, we should consider these dispersal corridors, across the Antelope Valley in the first case, and San Gorgonio Pass in the second, as potentially significant. The latter in particular, now traversed by a major highway, Interstate 10, is probably no longer viable for a flightless insect.

The clearest message we can distill out of our results is that relatively small areas in southern California can host distinctive and isolated genetic diversity. Two of the three species examined here support this strongly, and many of other organisms studied in detail in the region have as well. Though we hoped our data might provide a clear ranking of areas in terms of their conservation value, this has not been possible, because even in our limited sampling the species disagree on which these would be. While this seems unfortunate in that it does not help set regional conservation priorities, it may (if such a pattern continues to hold) free land managers to focus on regions experiencing the most pressing threats.

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Appendices

Appendix 1 Sampling localities by region, with haplotypes represented in each

Population	N	Locality	Coordinates	Haplotypes
Calathus ruficollis				
San Gabriel Mts.	1	CA: Los Angeles Co., Angeles NF, San Dimas Exp. Forest	34.1962° N, 117.7653° W	C59
	6	CA: Los Angeles Co., Angeles NF, San Dimas Exp. Forest	34.2012° N, 117.7736° W	C59(1), C2(1), C5(2), C6(1), C34(1)
Coelus ciliatus				
	1	CA: Santa Barbara Co., UC Coal Oil Point Reserve	34.4126° N, 119.8781° W	CC1
Nyctoporis carinata				
Northern Santa Lucias	10	CA: Monterey Co., Arroyo Seco County Park	36.2341° N ,121.4886° W	N88(1), N89(7), N90(1), N91(1)
Total	10			
Southern Santa Lucias	5	CA: San Luis Obispo Co., LPNF, Cuesta Ridge	35.3731° N, 120.6859° W	N13(2), N14(2), N15(1)
Total	5			
Northwest Transverse Ranges	1	CA: Ventura Co., LPNF, north slope Pine Mt.	34.6585° N, 119.3800° W	N1
	1	CA: Santa Barbara Co., LPNF, Sunset Valley	34.7538° N, 119.9429° W	N3
	1	CA: Santa Barbara Co., LPNF, Big Pine Mt.	34.7021° N, 119.6547° W	N4
	2	CA: Santa Barbara Co., LPNF, Big Pine Mt.	34.7032° N, 119.6526° W	N36, N38
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.6796° N, 120.0387° W	N9
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.6825° N, 120.0445° W	N9
	2	CA: Santa Barbara Co., UC Sedgwick Reserve	34.6842° N, 120.0459° W	N11, N12
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.6889° N, 120.0428° W	N49
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7127° N, 120.0396° W	N35
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7132° N, 120.0395° W	N41
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7164° N, 120.0396° W	N23
	2	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7197° N, 120.0366° W	N31, N39
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7261° N, 120.0483° W	N43
	1	CA: Santa Barbara Co., UC Sedgwick Reserve	34.7269° N, 120.0474° W	N9
	1	CA: Santa Barbara Co., LPNF, Rancho Alegre	34.5410° N, 119.9110° W	N24
Total	18			
Santa Ynez Mts.	3	CA: Ventura Co., Ventura	34.293° N, 119.204° W	N28, N29, N30
	1	CA: Ventura Co., Upper Ojai Valley	34.4504° N, 119.1207° W	N42
	1	CA: Santa Barbara Co., Santa Barbara	34.47° N, 119.73° W	N44
	5	CA: Ventura Co., LPNF,Murrietta Tr.	34.5009° N, 119.3899° W	N50, N51, N52, N53, N54
	3	CA: Santa Barbara Co., Arroyo Hondo Preserve	34.4855° N, 120.1423° W	N64, N65, N66
	2	CA: Santa Barbara Co., Arroyo Hondo Preserve	34.4855° N, 120.1417° W	N7, N8
Total	15			

Appendix 1 continued

Population	N	Locality	Coordinates	Haplotypes
Southwestern Sierra Nevada	6	CA: Tulare Co., Sequoia NF, UC Whitaker Forest	36.7025° N, 118.9322° W	N72, N73, N74, N75, N76, N77
	1	CA: Tulare Co., Sequoia NF, Whitaker Forest Rd.	36.6783° N, 118.9661° W	N72
	2	CA: Fresno Co., Sequoia NF, SE of Hume Lk.	36.7718° N, 118.8854° W	N78, N79
	1	CA: Tulare Co., Sequoia NF, F.S. 14S75	36.6720° N, 118.9798° W	N80
Total	10			
Southern Sierra Nevada	2	CA: Kern Co., Sequoia NF, Kern Cyn.	35.4753° N, 118.7284° W	N2
Total	2			
Tehachapi Mts.	5	CA: Kern Co., Oak Ck. Cyn.	35.0506° N, 118.3567° W	N61, N62, N63
	2	CA: Kern Co., Oak Ck. Cyn.	35.0487° N, 118.3605° W	N61, N62
	3	CA: Kern Co., Tehachapi Mt. Rd.	35.0673° N, 118.4820° W	N81, N82
	1	CA: Kern Co., Woodford-Tehachapi Rd.	35.1807° N, 118.5150° W	N82
Total	11			
Sierra Pelona	7	CA: Los Angeles Co., Angeles NF, Grass Mt.	34.6408° N, 118.4148° W	N10, N18, N26, N37, N46, N47, N48
Total	7			
San Gabriel Mts.	2	CA: Los Angeles Co., Angeles NF, Angeles Crest Hwy.	34.2717° N, 118.0608° W	N25, N27
	3	CA: Los Angeles Co., Angeles NF, Hwy N3	34.2964° N, 118.1625° W	N25, N67, N68
	2	CA: Los Angeles Co., Angeles NF, Hwy N3	34.2910° N, 118.1695° W	N71, N85
	7	CA: Los Angeles Co., Placerita Cyn. Co. Pk.	34.3764° N, 118.4403° W	N55, N56(2), N57, N58, N59, N60
	2	CA: Los Angeles Co., Angeles NF, San Dimas Exp. Forest	34.2012° N, 117.7736° W	N86, N87
Total	16			
San Bernardino Mts.	1	CA: San Bernardino Co., SBNF, Deer Ck.	34.1741° N, 116.9844° W	N40
	1	CA: San Bernardino Co., SBNF, City Ck.	34.1864° N, 117.1836° W	N45
	2	CA: San Bernardino Co., SBNF, W. of Barton Flats	34.1678° N, 116.9143° W	N5, N6
	4	CA: San Bernardino Co., SBNF, Santa Ana R.	34.1819° N, 116.8884° W	N6, N70(3)
	2	CA: San Bernardino Co., SBNF, Camp Cedar Falls	34.1646° N, 116.9366° W	N69
	1	CA: San Bernardino Co., SBNF, Hwy 173	34.2955° N, 117.2134° W	N84
Total	11			
San Jacinto Mts.	8	CA: Riverside Co., UC James Reserve	33.8092° N, 116.7650° W	N16, N17(2), N19, N20, N21(2), N22
	1	CA: Riverside Co., UC James Reserve	33.8081° N, 116.7784° W	N83
	1	CA: Riverside Co., SBNF, F.S. 4S01	33.8448° N, 116.7322° W	N19
	1	CA: Riverside Co., SBNF, Marion Mt.	33.7949° N, 116.7214° W	N32
Total	11			
Santa Cruz Isl.	2	CA: Santa Barbara Co., Santa Cruz Isl.	34.0191° N, 119.6878° W	N33, N34
Total	2			

Two new localities for *Calathus ruficollis* supplement data in Chatzimanolis and Caterino (2007a); their haplotype codes are consistent with that paper's

Appendix 2 Haplotypes and GenBank accession numbers

Haplotype	GenBank#
C59	EU037191
CC1	EU032421
N1	EU037099
N2	EU037100
N3	EU037101
N4	EU037102
N5	EU037103
N6	EU037104
N7	EU037105
N8	EU037106
N9	EU037107
N10	EU037108
N11	EU037109
N12	EU037110
N13	EU037111
N14	EU037112
N15	EU037113
N16	EU037114
N17	EU037115
N18	EU037116
N19	EU037117
N20	EU037118
N21	EU037119
N22	EU037120
N23	EU037121
N24	EU037122
N25	EU037123
N26	EU037124
N27	EU037125
N28	EU037126
N29	EU037127
N30	EU037128
N31	EU037129
N32	EU037130
N33	EU037131
N34	EU037132
N35	EU037133
N36	EU037134
N37	EU037135
N38	EU037136
N39	EU037137
N40	EU037138
N41	EU037139
N42	EU037140
N43	EU037141
N44	EU037142
N45	EU037143
N46	EU037144
N47	EU037145
N48	EU037146
N49	EU037147
N50	EU037148
N51	EU037149
N52	EU037150
N53	EU037151
N54	EU037152
N55	EU037153
N56	EU037154
N57	EU037155
N58	EU037156
N59	EU037157
N60	EU037158
N61	EU037159
N62	EU037160
N63	EU037161
N64	EU037162
N65	EU037163
N66	EU037164
N67	EU037165
N68	EU037166
N69	EU037167
N70	EU037168
N71	EU037169
N72	EU037170
N73	EU037171
N74	EU037172
N75	EU037173
N76	EU037174
N77	EU037175
N78	EU037176
N79	EU037177
N80	EU037178
N81	EU037179
N82	EU037180
N83	EU037181
N84	EU037182
N85	EU037183
N86	EU037184
N87	EU037185
N88	EU037186
N89	EU037187
N90	EU037188
N91	EU037189

Some apparently missing haplotype numbers represent populatons not included in the present study. 'C' haplotype refers to *Calathus ruficollis*; 'CC' to *Coelus ciliatus*; and 'N' haplotypes to *Nyctoporis carinata*

Appendix 3 Pairwise population F_{ST} values

Population 1	Population 2	*Calathus ruficollis*	*Sepedophilus castaneus*	*Nyctoporis carinata*
Northern Santa Lucias	Southern Santa Lucias	0.04341	0.27617	0.80131
Northern Santa Lucias	NW Transverse Ranges	0.05496	0.47585	0.72661
Northern Santa Lucias	Santa Ynez Mts.	0.10952	0.82072	0.56031
Northern Santa Lucias	Central Transverse Ranges	0.37848	0.71334	N/A
Northern Santa Lucias	SW Sierra Nevada	N/A	0.79523	0.74035
Northern Santa Lucias	Southern Sierra Nevada	0.88772	N/A	0.94209
Northern Santa Lucias	Sierra Pelona	0.08289	0.62622	0.74486
Northern Santa Lucias	San Gabriel Mts.	0.16531	0.86919	0.71606
Northern Santa Lucias	San Bernardino Mts.	0.08065	0.82626	0.74385
Northern Santa Lucias	San Jacinto Mts.	0.33377	0.87255	0.62651
Northern Santa Lucias	Northern Channel Islands	0.15051	N/A	0.90927
Southern Santa Lucias	NW Transverse Ranges	−0.01717	0.47091	0.28371
Southern Santa Lucias	Santa Ynez Mts.	0.06615	0.87608	0.24741
Southern Santa Lucias	Central Transverse Ranges	0.27826	0.80456	N/A
Southern Santa Lucias	SW Sierra Nevada	N/A	0.85445	0.63084
Southern Santa Lucias	Southern Sierra Nevada	0.83817	N/A	0.81763
Southern Santa Lucias	Sierra Pelona	0.0422	0.69735	0.54467
Southern Santa Lucias	San Gabriel Mts.	0.11293	0.91227	0.60026
Southern Santa Lucias	San Bernardino Mts.	0.04178	0.86838	0.60431
Southern Santa Lucias	San Jacinto Mts.	0.09618	0.91291	0.61172
Southern Santa Lucias	Northern Channel Islands	−0.01218	N/A	0.45827
NW Transverse Ranges	Santa Ynez Mts.	0.07604	0.19898	0.31802
NW Transverse Ranges	CentTrRg	0.30633	0.56615	N/A
NW Transverse Ranges	SW Sierra Nevada	N/A	0.77352	0.69071
NW Transverse Ranges	Southern Sierra Nevada	0.84102	N/A	0.79638
NW Transverse Ranges	Sierra Pelona	0.05109	0.31352	0.57749
NW Transverse Ranges	San Gabriel Mts.	0.12852	0.83387	0.61444
NW Transverse Ranges	San Bernardino Mts.	0.03372	0.79556	0.62067
NW Transverse Ranges	San Jacinto Mts.	0.06314	0.83807	0.62934
NW Transverse Ranges	Northern Channel Islands	−0.02988	N/A	0.39768
Santa Ynez Mts.	Central Transverse Ranges	0.26393	0.97241	N/A
Santa Ynez Mts.	SW Sierra Nevada	N/A	0.98175	0.58455
Santa Ynez Mts.	Southern Sierra Nevada	0.86862	N/A	0.64746
Santa Ynez Mts.	Sierra Pelona	−0.01593	0.64086	0.18638
Santa Ynez Mts.	San Gabriel Mts.	0.02762	0.987	0.24658
Santa Ynez Mts.	San Bernardino Mts.	0.02648	0.94756	0.38019
Santa Ynez Mts.	San Jacinto Mts.	0.19441	0.98117	0.42312
Santa Ynez Mts.	Northern Channel Islands	0.10922	N/A	0.26024
Central Transverse Ranges	SW Sierra Nevada	N/A	0.94766	N/A
Central Transverse Ranges	Sierra Pelona	0.26437	0.4823	N/A
Central Transverse Ranges	San Gabriel Mts.	0.26906	0.96035	N/A

Appendix 3 continued

Population 1	Population 2	*Calathus ruficollis*	*Sepedophilus castaneus*	*Nyctoporis carinata*
Central Transverse Ranges	San Bernardino Mts.	0.25475	0.89192	N/A
Central Transverse Ranges	San Jacinto Mts.	0.37957	0.95317	N/A
SW Sierra Nevada	Sierra Pelona	N/A	0.8448	0.62958
SW Sierra Nevada	San Gabriel Mts.	N/A	0.96097	0.69651
SW Sierra Nevada	San Bernardino Mts.	N/A	0.90811	0.67677
SW Sierra Nevada	San Jacinto Mts.	N/A	0.9569	0.66628
Southern Sierra Nevada	Sierra Pelona	0.86514	N/A	0.79145
Southern Sierra Nevada	San Gabriel Mts.	0.87058	N/A	0.80827
Southern Sierra Nevada	San Bernardino Mts.	0.83861	N/A	0.81771
Southern Sierra Nevada	San Jacinto Mts.	0.87089	N/A	0.79413
Southern Sierra Nevada	Northern Channel Islands	0.84273	N/A	0.98684
Sierra Pelona	San Gabriel Mts.	−0.00093	0.88004	0.22731
Sierra Pelona	San Bernardino Mts.	−0.02925	0.82911	0.45567
Sierra Pelona	San Jacinto Mts.	0.25116	0.8814	0.55146
Sierra Pelona	Northern Channel Islands	0.10929	N/A	0.61843
San Gabriel Mts.	San Bernardino Mts.	0.00488	0.25626	0.4737
San Gabriel Mts.	San Jacinto Mts.	0.29773	0.11882	0.56232
San Gabriel Mts.	Northern Channel Islands	0.19083	N/A	0.63415
San Bernardino Mts.	San Jacinto Mts.	0.16385	0.15064	0.55698
San Bernardino Mts.	Northern Channel Islands	0.08474	N/A	0.63636

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