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Narrow water barriers prevent multiple colonizations and limit gene flow among California Channel Island wild buckwheats (*Eriogonum*: Polygonaceae)

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The relative roles of chance colonization and subsequent gene flow in the development of insular endemic biotas have been extensively studied in remote oceanic archipelagos, but are less well characterized on nearshore island systems. The current study investigated patterns of colonization and divergence between and within two wild buckwheat species (Polygonaceae), *Eriogonum arborescens* and *E. giganteum*, endemic to the California Channel Islands to determine whether geographical isolation is driving diversification. Using plastid and nuclear sequence data and microsatellite allele frequencies, we determined that gene flow in these *Eriogonum* spp. is restricted by isolation. The data suggest that successful colonization of and gene flow among the islands are infrequent. Colonization appears to have followed a stepping-stone model that is consistent with a north-to-south pattern across the islands. This colonization pattern coupled with relatively little post-colonization inter-island gene flow, particularly among southern islands, has generated a pattern of more divergent lineages on the isolated southern islands. These results run counter to the general expectation that all islands close to a continental source should receive a high level of gene flow. Finally, management recommendations focused on protecting the lineages from loss of private alleles and the erosion of the remaining genetic diversity are offered. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **181**, 246–268

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INTRODUCTION

Islands by their nature have reduced areas, depauperate biotic communitites and limited immigration compared to continental systems. As simplified model systems, they are natural laboratories for investigations of allopatric divergence and speciation (Simberloff, 1974). Individual islands and archipelagos of varying ages, sizes and isolation have been compared to continental areas and each other to understand the spatial and temporal scales at which different evolutionary processes are most important (Whittaker, Triantis & Ladle, 2008). For example, the biotas of isolated oceanic islands appear to be largely shaped by rare long-distance dispersal events and ecological release, whereas nearshore continental islands are expected to have biotas primarily drawn from the adjacent mainland and shaped by loss of species as newly isolated biotas experience higher extinction rates (Simberloff, 1974). Similarly, the spatial and temporal arrangement of islands in an archipelago may have important evolutionary consequences. The general dynamic theory of Whittaker *et al.* (2008) predicts lineages established on older islands will be the source of colonists to young emergent islands (the progression rule; Funk & Wagner, 1995) in hotspot archipelagos. In less isolated archipelagos, large, nearshore islands may be dispersal targets and intermediate stepping-stones for colonization of more distant islands (e.g. Madiera and Canaries; Fernández-Palacios *et al.*, 2011). These stepping-stones may also allow rapid accumulation of genetic diversity in island lineages through multiple colonizations of closely related (i.e. 'surfing syngameon'; Caujapé-Castells, 2011) or more distantly related (i.e. hybrid swarm; Seehausen, 2004) individuals during the early establishment phase.

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Although recent studies have greatly advanced our understanding of the complex biogeography of some island systems, including the Hawaiian (Keeley & Funk, 2011) and Macronesian (Fernández-Palacios *et al.*, 2011) archipelagos, other systems remain poorly understood. Knowledge is especially limited about nearshore oceanic islands. There are few oceanic island systems separated from a mainland source of colonists by < 100 km. Less isolated island systems are generally continental shelf islands that have been isolated only since the submergence of Pleistocene land bridges and that, consequently, have biotas influenced more by vicariance than by colonization histories (e.g. Ryukyu and Zhoushan archipelagos; Zhai *et al.*, 2012; Lee *et al.*, 2013).

The California Channel Islands are generally closer to a large landmass than other well-studied island chains because all the islands lie in the California Bight on the continental margin of western North America (Fig. 1). These islands were long thought to harbour a primarily relictual biota of limited evolutionary importance (Oberbauer, 2002; but see Lyon, 1886). Early biogeographers concluded that there was little influence of island isolation on diversity and that size, coupled with habitat diversity or precipitation regime, was more important than isolation in determining island biotas (Diamond, 1969; Power, 1976; Rentz & Weissman, 1981; but see Savage, 1967). However, there is evidence that the water barrier, though modest (*c.* 20–100 km), has been an effective filter for many organisms. In particular, the islands nearest the mainland have much larger native biotas and proportionally smaller percentages of endemism than more isolated islands (Moody, 2000; Oberbauer, 2002; Schoenherr, Feldmeth & Emerson, 2003). Additionally, molecular genetic methods have revealed substantial divergence of insular populations (e.g. Delaney & Wayne, 2005; Floyd *et al.*, 2011; McGlaughlin *et al.*, 2015a,b). The evidence of isolation-mediated diversification, the distribution of the endemic taxa and the range of geographical isolation in the system combine to provide an excellent natural laboratory to investigate the influence of isolation on gene flow and taxonomic divergence on nearshore islands.

Colonization of the California Channel Islands has been relatively recent, geologically speaking, because the modern islands formed by relatively slow uplift during the late Tertiary and Quaternary. Using late Quaternary uplift rates (Muhs *et al.*, 2012; Muhs, Groves & Schumann, 2014) and the highest elevations of the modern islands, the highest parts of San Clemente Island could have emerged as long ago as ~3.0 Ma, whereas San Nicolas Island might have only emerged as recently as ~1.2 Ma. With low late Quaternary uplift rates on the northern Channel Islands (Pinter *et al.*, 1998), the highest parts of Santa Cruz Island and Santa Rosa Island might have emerged considerably prior to ~3.0 Ma. Furthermore, the geography of the islands changed during glacial–interglacial cycles of the Quaternary, with low-elevation portions being submerged during interglacial highstands of sea and later emergent during glacial lowstands of sea (Muhs *et al.*, 2004). Relative isolation in the archipelago was dramatically reduced as recently as the last glacial period (~27 to ~15 ka), when sea level was low, shorelines were greatly expanded and at least nine additional islands were emergent (Kinlan, Graham & Erlandson, 2005; Muhs *et al.*, 2009). At that time, the modern northern islands formed a single large island, Santarosae (Orr, 1968), separated from the mainland only by a narrow (*c.* 4 km) deep-water channel, whereas the southern islands remained isolated by broad deep-water basins (Johnson, 1983; Kinlan *et al.*, 2005; Fisher *et al.*, 2009).

Given the young age of the current islands, insular endemic taxa are likely to reflect only shallow phylogenetic divergence. The northern islands, in particular, which have recently and repeatedly been united are less likely to harbour divergent taxa and genetically depauperate lineages than the southern islands. Additionally, Santarosae, the largest and closest target for mainland colonizers during the Pleistocene, may have functioned as a stepping-stone to further colonization throughout the archipelago, as has been suggested in other island systems (Oiki *et al.*, 2001; Fernández-Palacios *et al.*, 2011; Keeley & Funk, 2011; Yamada & Maki, 2012). If stepping-stone colonization has occurred, northern island endemics should have an early-branching placement in phylogenetic trees, potentially with descendant southern taxa nested within northern lineages. This would be particularly likely among wind-dispersed taxa, as the dominant north-westerly air currents affecting the islands flow through the northern to the southern islands (Dong, Idica & McWilliams, 2009; Riley & McGlaughlin, 2016).

The expected pattern of greater taxonomic diversity on the northern California Channel Islands has been observed in many groups (e.g. Rentz & Weissman, 1981; Rust, 1985; Oberbauer, 2002; Powell, 2005; Riley & McGlaughlin, 2016), although some have suggested the depauperate southern biotas are caused by increased aridity rather than increased isolation (Rentz & Weissman, 1981; but see Moody, 2000). The expected patterns of north-to-south colonization routes and of greater genetic divergences among southern island taxa have been less well resolved and only recently addressed with methods capable of recovering the subtle genetic signal of recent, shallow divergence. Among the flora, several

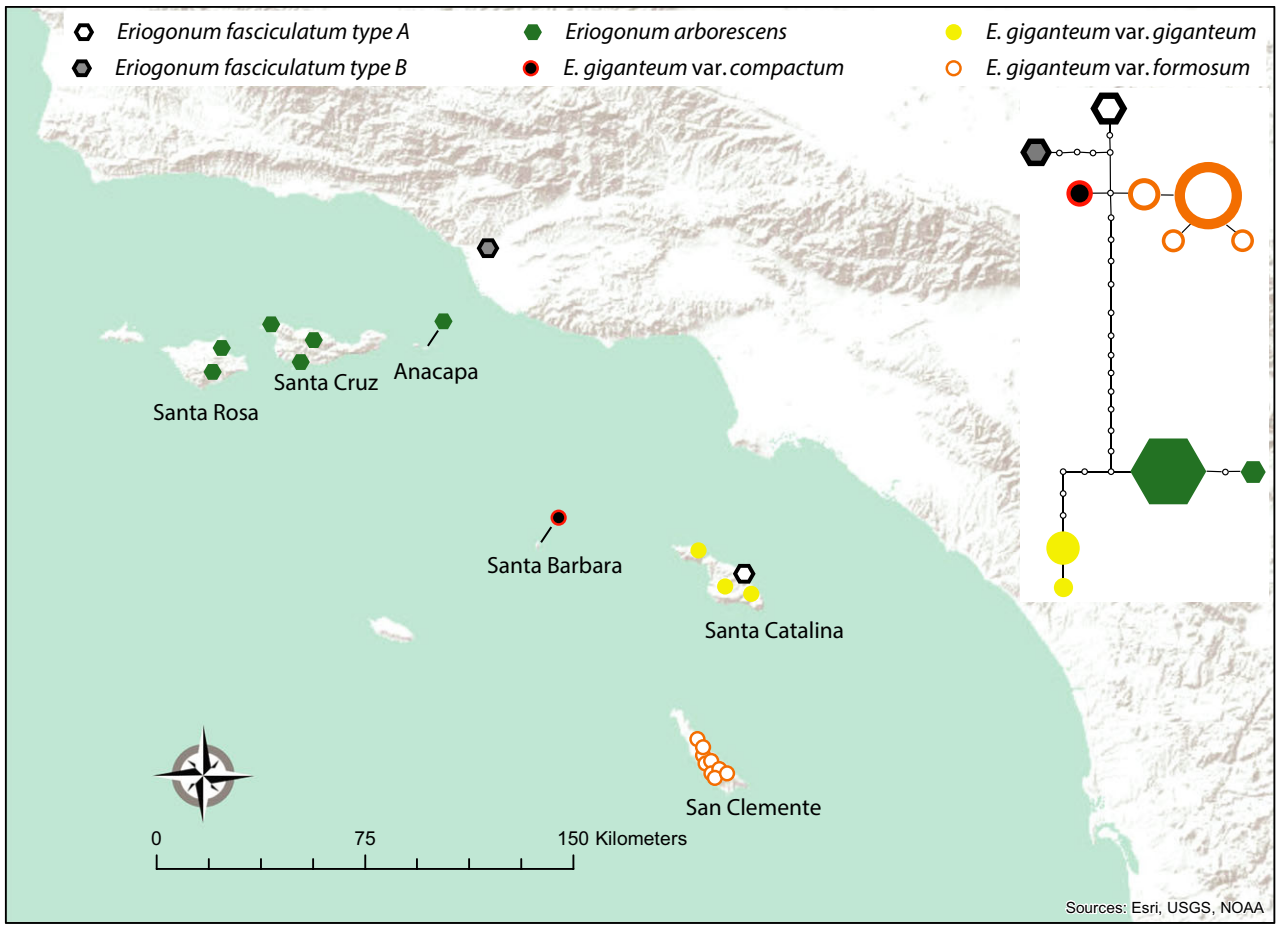

Figure 1. Plastid haplotype network (symbol size proportional to the number of copies recovered; inferred changes indicated by small black circle) and approximate locations of the California Channel Islands and sampled *Eriogonum* populations: *Eriogonum arborescens* (solid hexagons: Anacapa, Santa Cruz and Santa Rosa Islands), *E. giganteum* var. *giganteum* (solid circles: Santa Catalina Island), *E. giganteum* var. *compactum* (filled circle: Santa Barbara Island), *E. giganteum* var. *formosum* (open circles: San Clemente Island) and *E. fasciculatum* (open and filled hexagons, Santa Catalina Island and mainland California).

lineages have diversified throughout the islands and may provide insight into the influence of island geography on patterns of colonization and gene flow (Wallace, 1985; Baldwin, 2007). Although several lineages are currently under investigation [e.g. *Acmispon* Raf. (Fabaceae), McGlaughlin *et al.*, 2015b; and *Malacothrix* Greene (Asteraceae)], no archipelago-wide plant phylogeographies have been published.

The current study investigates the role of geographical isolation in shaping colonization and diversification patterns between *Eriogonum arborescens* Greene and *Eriogonum giganteum* S.Watson (Polygonaceae). We used DNA sequencing and microsatellite allele frequency data from locations throughout the islands to determine (1) the path of colonization of the islands, (2) the role of physical isolation in limiting contemporary gene flow and (3) appropriate conservation measures given the levels of genetic isolation and divergence in the archipelago.

MATERIAL AND METHODS

Study organisms

The genus *Eriogonum* Michx. is largely confined to western North America (Reveal, 2005) and is exceptionally diverse in California (118 species), where most (69) species are found in, and many (44) are endemic to, the California Floristic Province (Stebbins & Major, 1965; Costea & Reveal, 2013). Sediment cores indicate that *Eriogonum* spp., which are common in mainland coastal communities, have been present on the northern islands since the shift from closed pine forests to more open scrub communities

c. 12 000 years ago (Anderson, Starratt & Jass, 2010). *Eriogonum arborescens* and *E. giganteum* are California Channel Island endemics noted for island gigantism (Thorne, 1969), seen in both woodiness and overall size (30–350 cm; Costea & Reveal, 2013) when compared to mainland relatives. Together, the species are found throughout the archipelago; *E. arborescens* occurs on three of the four northern islands and *E. giganteum* occurs on three of the four southern islands (Fig. 1). Within the latter species, three single-island endemic varieties are recognized based on distribution, overall size and inflorescence, flower and fruit size (Costea & Reveal, 2013). Because the single-island endemic taxa have restricted ranges, the California Native Plant Society (CNPS) classifies *E. giganteum* var. *giganteum* as uncommon and vulnerable and *E. giganteum* var. *formosum* Brandegee as fairly endangered and vulnerable (CNPS, 2014). *Eriogonum giganteum* var. *compactum* Dunkle is a state-listed rare (California Natural Diversity Database, 2015) and CNPS (2014) rare and imperiled taxon.

The outgroup, *Eriogonum fasciculatum* Benth., a widespread subshrub common in California coastal scrub communities, was selected based on Kempton's (2012) molecular systematic treatment of Eriogonoideae, indicating that *E. fasciculatum* is closely related to *E. arborescens* and observations that *E. fasciculatum* readily hybridizes with *E. arborescens* and *E. giganteum* (Reveal, 2005). Although no large-scale systematic treatments have included *E. giganteum*, *E. giganteum* has been inferred to be sister to *E. arborescens* based on morphology (Watson, 1885; Raven, 1967). *Eriogonum giganteum* and *E. arborescens* also readily hybridize (Philbrick, 1980).

Little is known about the reproductive ecology of the study taxa. Mating systems vary widely in *Ergionum*, ranging from genetic self-incompatiblity to habitual selfing (Moldenke, 1976). Although pollination studies have not been published for these taxa, *Eriogonum* in general and *E. fasciculatum* in particular appear to attract a wide variety of beneficial insects (Junak *et al.*, 1995; Junak & Wilken, 1998; Morandin *et al.*, 2011; James *et al.*, 2014). The study taxa all have large floral displays with open bisexual flowers and pollen available to generalist pollinators (Montalvo, 2004; M. E. McGlaughlin, pers. observ.). A distantly related California Channel Island *Eriogonum*, *E. grande* Greene var. *rubescens* Munz, with a similar floral display is known to be self-compatible, but requires pollinator visitation for maximal seed set (McEachern, Wilken & Chess, 1997). The importance of vegetative reproduction in the study taxa is also unknown. *Eriogonum fasciculatum* does produce adventitious roots (Little, 1981), but no note was made of vegetative reproduction in a study of establishment in *E. arborescens* (Yelenik & Levine, 2010a). Based on the available data and extensive field observations it seems likely that all the study taxa are self-compatible and that any vegetative reproduction is limited.

Few studies have systematically examined the dispersal ecology of these *Eriogonum* taxa. All have small (1.8–3.5 mm), glabrous fruits (Costea & Reveal, 2013). Although Montalvo (2004) noted that in *E. fasciculatum* the calyx may be persistent and aid in wind or water dispersal, Keeley (1991) considered *E. fasciculatum* to be auto-dispersed, Junak & Wilken (1998) considered *E. giganteum* var. *formosum* to be gravity- and wind-dispersed, and DeSimone & Zedler (2001) noted that *E. fasciculatum* had no apparent adaptations to wind dispersal except small seed size. Studies of recruitment in *E. fasciculatum* found no evidence of seed dispersal beyond 5 m (DeSimone & Zedler, 2001). In contrast, Yelenik & Levine (2010a) found evidence of limited seed dispersal in *E. arborescens* beyond 5 m; although they found some seeds at low densities (2.8 ± 1.3 seeds m^{-2}) in grasslands, up to 20 m from possible parents, they recorded higher densities (569 ± 123 seeds m^{-2}) adjacent to adult plants. These data suggest that long-distance dispersal, either from the mainland to the islands or between islands, is likely to be rare.

Sample collection and preparation

Leaf tissue (*c*. 1 g) was collected from all study taxa on every island of occurrence (one to ten locations per island, see Supporting Information, Appendix S1; Fig. 1). Tissue was collected from every individual detected at populations with < 30 plants and from 30–32 individuals from populations with 30 or more plants. Leaf tissue was also collected from ten individuals of a mainland population of the widespread close relative *E. fasciculatum* (Kempton, 2012). An additional, introduced population of *E. fasciculatum* from Santa Catalina was sampled and included in the nrITS and plastid DNA sequencing to investigate the possibility of recent introgression. Genomic DNA was extracted from frozen tissue ground under liquid nitrogen using a modified CTAB protocol (Doyle & Doyle, 1987) followed by an ethanol precipitation. Extracts were dissolved in TE buffer and diluted to *c*. 50 ng μL^{-1} in water prior to amplification.

Sequence amplification and data collection

We targeted the nuclear *LFY* and *nrITS* regions, which were employed in previous studies on *Eriogonum* systematics (Sanchez & Kron, 2008; Kempton, 2012) and the most variable plastid regions

determined by a preliminary screening of primers for 12 of the highly variable regions reported in Shaw *et al.* (2005, 2007). Plastid sequence and nrITS data were collected from one to two individuals per location (see Supporting Information, Appendix S1). Sequences for ITS1, ITS2 and the intervening 5.8S region were amplified using the universal primers ITS.leu (Baum, Yoon & Oldham, 2005) and ITS4 (White, 1990). Sequences for the plastid regions were amplified using the primers given in Shaw *et al.* (2005) for *rpoB–trnC* and Shaw *et al.* (2007) for *atpI–atpH* and *ndhA*. Sequence data were collected from the second intron of the nuclear gene *LFY* of one to five individuals per population, except the introduced *E. fasciculatum* population on Santa Catalina that was not included in the *LFY* study. Among the mainland *E. fasciculatum* accessions, *LFY* sequences were generated using the LFYsx1-1 and LFYtxr primers from Frohlich & Meyerowitz (1997). Among *E. arborescens* and *E. giganteum* accessions, *LFY* sequences were generated using *Eriogonum*-specific primers (LFYerF: TCTCTCCCATCTTTACGAGC and LFYerR: GTACCTGAACACCTGGTTTG) developed from the degenerate primers LFY.F2 and LFY.R1 of Howarth & Baum (2005). All *LFY* amplicons were cloned (Promega PGEM-easy vector cloning kit, following the manufacturer's instructions in 1/4 reactions) and one clone per individual was sequenced. Amplification conditions and sequencing protocols followed Riley (2012). Nuclear sequence data, *LFY* and ITS, are biparentally inherited tracking both pollen and seed movement, whereas plastid regions are maternally inherited, providing evidence of seed dispersal.

Sequence alignment

Sequences were initially aligned with Muscle (Edgar, 2004) in Geneious v.5.4 (Biomatters). Ambiguous initial alignments (< 90% identical sites and pairwise similarity < 95%) were refined with Guidance (Penn *et al.*, 2010a, b) using the Muscle alignment tool and 100 bootstrap repetitions. All sequences and positions aligned with $P > 0.95$ were retained. The presence of recombinant or paralogous sequences in each alignment was assessed with a phi-test in SplitsTree v.4.1 (Huson, 1998; Bruen, Philippe & Bryant, 2006; Huson & Bryant, 2006) and Bellerophon (Huber, Faulkner & Hugenholtz, 2004). Strongly divergent sequences were removed to generate conservative alignments of only presumed orthologous sequences prior to analysis.

Sequence diversity and population structure

Sequence diversity and pairwise genetic distances of aligned regions were calculated with DnaSP v.5.2 (Librado & Rozas, 2009) with gaps treated as missing data. AMOVAs and pairwise F_{st} values were calculated in Arlequin v.3.5 (Excoffier, Laval & Schneider, 2005). The partitions considered for AMOVAs were sampled population, island and named taxon. Maximum-likelihood (ML) estimates of migration between islands were calculated from the *LFY* and plastid alignments in Migrate-N (Beerli, 2009) using the model of sequence evolution, empirical base frequencies and the default transition–transversion ratios, with ten short chains (500 generations), one long chain (5000 generations) and a burn-in of 10 000.

Phylogenetic reconstruction and haplotype network

Neutrality tests were conducted with Tajima's *D* (Tajima, 1989) calculated in Arlequin. The most appropriate model for nucleotide evolution was determined from Akaike's information criterion and Bayesian information criterion scores of competing models computed in JModelTest (Guindon & Gascuel, 2003; Posada, 2008) on the CIPRES teragrid (Miller *et al.*, 2009). Phylogenetic recontructions were estimated for ingroup and in- plus outgroup alignments in ML and Bayesian frameworks. ML estimates were performed with 100 bootstrap replicates in GARLI v.1.0 (Zwickl, 2006) implemented on the CIPRES teragrid. Majority rule consensus trees were generated from GARLI bootstrap replicates in Geneious. Bayesian estimates were conducted in MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) implemented on GreenButton (http://www.greenbutton.net) for outgroup-rooted estimation and in BEAST v.1.6.2 (Drummond & Rambaut, 2007) for unrooted estimation. All runs employed the substitution models and parameters selected by JModel Test as priors. Adequate mixing and stationarity was assessed after a 25% burn-in using MrBayes or Tracer v.1.5 (Rambaut & Drummond, 2007). Maximum clade credibility or majority rule consensus trees were calculated with a posterior probability limit of 50% after a burn-in of 25% using Geneious or TreeAnnotator v.1.6 (Rambaut & Drummond, 2010). Phylogenetic trees from alignments with duplicate sequences removed were estimated in MrBayes and GARLI v.2.0 with the conditions above to ensure that the low levels of variability within taxa were not biasing the results. A haplotype network was estimated from the plastid DNA alignment in TCS (Clement, Posada & Crandall, 2000) with single base pair gaps removed and larger gaps (6, 9 or 72 bp) coded as single changes and considered as fifth states.

Biogeographical reconstruction

Colonization history was inferred in BayArea (Landis *et al.*, 2013) implemented in RASP (Yu *et al.*, 2015) from the most likely *LFY* gene tree estimated in GARLI. Samples from the northern islands were coded with a distribution of Santarosae, with a location of 34.06033°N, 119.63588°W. Samples from the southern islands were coded with a distribution of the island of occurrence: Santa Barabara, 33.46920°N, 119.03950°W; Santa Catalina, 33.37897°N, 118.40307°W; and San Clemente, 32.89862°N, 118.47624°W. Ten independent runs were performed with a chain length of 5 000 000, sampling every 1000 and a burn-in of 50 000. Other options were left at the recommended default settings. Results from the independent runs were combined in RASP to infer the most likely biogeographical history.

Microsatellite amplification and data collection

One small ($N = 21$) population (Pyramid Canyon on San Clemente Island; see Supporting Information, Appendix S1) was excluded from the microsatellite study, because of the increased risk of repeadedly sampling the same individual in the event of any clonal reproduction. Data were collected from all sampled individuals from the remaining populations. Five microsatellite loci (EGIC_82, ERAR_85, EGIC_96, ERGI_99 and EGIC_110) amplified consistently across all sampled taxa following the protocols of Riley, McGlaughlin & Helenurm (2011). Amplification products were diluted with water and electrophoresed with the LIZ-500 (Applied Biosystems) size standard on an Applied Biosystems 3500 Genetic Analyser, following the manufacturer's instructions. Fragments were sized with GeneMarker software (Softgenetics).

Microsatellite diversity and population structure

The presence of null alleles and size scoring errors were assessed for all loci in all populations with Micro-Checker (Van Oosterhout *et al.*, 2004). Neutrality of microsatellite loci was assessed with both Bayescan (Foll & Gaggiotti, 2008) and Lositan (Antao *et al.*, 2008). The latter was implemented with the neutral mean F_{st} option to reduce the chance of false positives, as recommended by Lotterhos & Whitlock (2014).

Population-level parameters, including the proportion of polymorphic loci, expected heterozygosities (H_E) under Hardy–Weinberg equilibrium (HWE) and taxon-level inbreeding coefficients (F_{IS}) were calculated with GenAlEx 6.5 (Peakall & Smouse, 2012). Inbreeding coefficients for each population were calculated with Genepop 4.2 (Raymond & Rousset, 1995; Rousset, 2008) based on allele identity. Deviations from HWE expectations and the presence of linkage disequilibrium (LD) between loci were also assessed with Genepop. Deviations from HWE expectations were considered significant at $P < 0.01$ because the test statistics used to test for HWE have been shown to underestimate the error rate both for multiallelic data and for small sample sizes (Lauretto *et al.*, 2009).

Principal component analysis (PCoA), analysis of molecular variance (AMOVA), pairwise F_{ST} values and effective number of migrants (N_M) based on F_{ST} were calculated in GenAlEx. The partitions considered for AMOVAs were sampled population, island and named taxon. An individual-centred network was calculated in EdeNetwork v.2.16 (Kivelä, Arnaud-Haond & Saramäki, 2011) using individual genotypes as nodes and the distance measure based on allele sharing as links. Networks were calculated with the default parameters of collapsed clones and automatic thresholding to identify strongly clustered genotypes and visualize patterns of connectivity. Neighbour-joining trees based on Nei's genetic distance were constructed in PopTree2 (Takezaki, Nei & Tamura, 2010), with 10 000 bootstrap replicates.

Bayesian estimates of recent migration between all populations were calculated from microsatellite data in BAYESASS 1.3 (Wilson & Rannala, 2003) with 3 000 000 iterations, a sampling frequency of 2000, a burn-in of 999 999 and all delta values set to 15. The overall levels of historical migration were estimated from microsatellite data using Slatkin's (1985) private allele method with GENEPOP.

Bayesian estimation of population membership ($K = 1$–20) was implemented in Structure 2.3.4 (Pritchard, Stephens & Donnelly, 2000; Falush, Stephens & Pritchard, 2003; Hubisz *et al.*, 2009) using flat priors under models of admixture and uncorrelated allele frequencies. Twenty independent runs of 100 000 steps, after a burn-in of 25 000 steps, were performed for each K with and without recessive alleles, to account for the possibility of null alleles. In the latter runs, recessive alleles were designated for all loci, but amplification failures (one of 580 amplifications for EGIC_96 and three of 580 amplifications for ERGI_99) were coded as missing data. The number of clusters was determined by examining the rate of change of K following the method of Evanno, Regnaut & Goudet (2005) as calculated by Stucture Harvester (Earl, 2012). Because selfing can inflate estimates of admixture and K, InStruct (Gao, Williamson & Bustamante, 2007), which jointly infers K clusters and cluster-specific selfing rates, was implemented for Structure-inferred groupings

in which the average probability of membership in a single cluster was $P < 0.95$.

RESULTS

Sequence alignment

Final datasets contained 44–75 individuals and *c*. 650 (nrITS), 1050 (*LFY*) and 2400 (plastid DNA) aligned base pairs (Table 1). Initial nrITS and plastid DNA Muscle alignments were unambiguous (pairwise identities of 95–99%) and had no phylogenetic signal of recombination (phi-test $P > 0.81$, data not shown). The initial Muscle alignment for *LFY* had a pairwise identity of 85.1% and was refined with Guidance. After refinement and removal of 29 positions with *P*-values < 0.95, the alignment had no signal of recombination (phi-test, $P = 0.9987$).

Sequence diversity and population structure

The plastid DNA alignment showed low diversity ($\pi = 0.00460$; Table 1). Eleven plastid haplotypes with 30 segregating sites were recovered, but most islands harboured only a single haplotype. The nrITS alignment was more diverse ($\pi = 0.01396$; Table 1) than the plastid alignment. Twenty-three nrITS haplotypes (two to ten haplotypes per island) with a total of 39 segregating sites were recovered. The *LFY* alignment was the most variable ($\pi = 0.03680$). Fifty haplotypes (four to 24 haplotypes per island) with a total of 148 segregating sites were recovered.

Because plastid sequence diversity was low, pairwise F_{ST} values calculated from these data were either one or zero (data not shown). For nuclear data, negative F_{ST} values were treated as $F_{ST} = 0$. Pairwise F_{ST} values calculated from the nrITS data ranged from 0.00 to 1.00, with a mean of 0.702 (see Supporting Information, Appendix S2). F_{ST} values were generally large between (mean $F_{ST} = 0.820$) and small within (mean $F_{ST} = 0.247$) named taxa. Pairwise F_{ST} values calculated from the *LFY* alignment ranged from 0.000 to 0.983, with a mean of 0.687 (Table 2). The pattern of differentiation was similar to that of the nrITS alignment, with low divergences within (mean $F_{ST} = 0.106$) and high divergences between (mean $F_{ST} = 0.857$) named taxa. Taxonomic identity or location by island, which parallels *E. giganteum* taxonomy, explained most of the variation in the sequence-based AMOVAs (Table 3).

Among the southern islands, little signal of either pollen or seed inter-island migration was detected. Among the northern islands the number of migrants per generation calculated from pairwise F_{ST} values from the *LFY* data were larger than $N_m = 1$ for all inter-island combinations (see Supporting Information, Appendix S3). From the same data, Migrate-N estimates of long-term average migration (*M*,

Table 1. DNA diversity for the sequenced *LFY* and *nrITS* regions and the concatenated sequences for three plastid regions

	LFY (1040 bp)			nrITS (641 bp)			Plastid (2387 bp)		
	N	*H*	π	*N*	*H*	π	*N*	*H*	π
Overall	75	50	0.03680	74	23	0.01396	46	11	0.00397
By species									
E. arborescens	26	17	0.00319	24	8	0.00214	13	2	0.00024
E. giganteum	47	41	0.01820	43	10	0.00755	26	7	0.00291
E. fasciculatum	2	2	0.00410	4	3	0.00260	5	2	0.00101
By species and island									
E. arborescens									
Anacapa (ANA)	5	5	0.00407	3	2	0.00104	2	1	0.00000
Santa Cruz (SCR)	12	9	0.00258	12	6	0.00234	6	1	0.00000
Santa Rosa (SRI)	9	6	0.00318	9	4	0.00217	5	1	0.00000
E. giganteum									
Santa Barbara (SBI)	5	4	0.00283	5	2	0.00094	2	1	0.00000
Santa Catalina (SCA)	15	13	0.00558	13	4	0.00164	5	2	0.00017
San Clemente (SCL)	27	24	0.00573	25	4	0.00260	19	4	0.00032
E. fasciculatum									
Santa Catalina (SCA)	–	–	–	3	2	0.00104	3	1	0.00000
Mainland (MNL)	2	2	0.00410	4	3	0.00260	2	1	0.00000

The aligned length for all sequences without gaps is given in parentheses. Number of individuals sequenced (*N*), number of haplotypes recovered (*H*) and nucleotide diversity (π).

Table 2. Pairwise F_{ST} values based on microsatellite allele frequencies (above diagonal) and *LFY* sequence divergence (below diagonal)

	MNL	SRI		SCR			ANI	SBI	SCA			SCL							
	SP	LC	CH	WP	HK	777	AN	C	CC	PS	RM	BSC	CHC	LT	TD	WC	MR	BOX	BR	HC
SRI LC	0.958		0.218	0.081	0.082	0.061	0.211	0.533	0.653	0.655	0.633	0.702	0.716	0.611	0.691	0.717	0.664	0.576	0.603	0.623
SRI CH	0.974	0.000		0.172	0.197	0.195	0.195	0.606	0.700	0.707	0.687	0.723	0.734	0.620	0.682	0.738	0.676	0.582	0.618	0.616
SCR WP	0.978	0.033	0.000		0.029	0.026	0.100	0.537	0.662	0.660	0.640	0.724	0.740	0.634	0.717	0.743	0.689	0.598	0.626	0.649
SCR HK	0.959	0.019	0.000	0.000.		0.006	0.065	0.547	0.669	0.666	0.647	0.737	0.748	0.646	0.733	0.755	0.704	0.623	0.641	0.667
SCR 777	0.970	0.000	0.000	0.000	0.000		0.071	0.547	0.669	0.667	0.648	0.735	0.747	0.645	0.730	0.749	0.697	0.618	0.636	0.665
ANI AN	0.958	0.158	0.071	0.000	0.031	0.064		0.600	0.708	0.704	0.688	0.777	0.792	0.691	0.773	0.798	0.748	0.675	0.687	0.713
SBI C	0.974	0.951	0.972	0.977	0.954	0.967	0.953		0.663	0.662	0.536	0.758	0.768	0.652	0.748	0.771	0.702	0.633	0.602	0.665
SCA CC	0.967	0.935	0.958	0.964	0.938	0.952	0.937	0.899		0.084	0.312	0.786	0.804	0.661	0.789	0.805	0.762	0.678	0.705	0.688
SCA PS	0.975	0.949	0.971	0.977	0.952	0.966	0.950	0.931	0.533		0.274	0.791	0.817	0.680	0.802	0.818	0.775	0.689	0.720	0.706
SCA RM	0.961	0.926	0.949	0.954	0.929	0.943	0.928	0.888	0.386	0.000		0.789	0.812	0.683	0.797	0.813	0.769	0.691	0.711	0.707
SCL BSC	0.979	0.953	0.977	0.983	0.955	0.971	0.954	0.928	0.832	0.903	0.818		0.475	0.475	0.443	0.536	0.480	0.519	0.538	0.542
SCL CHC	0.964	0.928	0.952	0.958	0.931	0.946	0.930	0.864	0.723	0.806	0.727	0.167		0.486	0.453	0.545	0.502	0.539	0.548	0.508
SCL LT	0.969	0.937	0.961	0.967	0.940	0.955	0.939	0.890	0.776	0.848	0.771	0.000	0.125		0.452	0.423	0.356	0.374	0.333	0.260
SCL TD	0.970	0.939	0.962	0.968	0.942	0.956	0.940	0.897	0.796	0.861	0.789	0.429	0.364	0.333		0.506	0.428	0.336	0.502	0.417
SCL WC	0.974	0.945	0.969	0.975	0.948	0.963	0.946	0.909	0.803	0.875	0.794	0.000	0.143	0.000	0.375		0.155	0.554	0.452	0.554
SCL MR	0.969	0.936	0.960	0.966	0.939	0.954	0.937	0.883	0.750	0.833	0.750	0.000	0.000	0.000	0.333	0.000		0.444	0.221	0.410
SCL BOX	0.979	0.953	0.977	0.983	0.955	0.971	0.954	0.928	0.832	0.903	0.818	0.000	0.167	0.000	0.429	0.000	0.000		0.427	0.213
SCL BR	0.976	0.947	0.972	0.979	0.950	0.966	0.949	0.913	0.795	0.877	0.787	0.000	0.000	0.000	0.400	0.000	0.000	0.000		0.331
SCL HC	0.974	0.944	0.969	0.975	0.947	0.963	0.945	0.905	0.788	0.867	0.781	0.000	0.000	0.000	0.375	0.000	0.000	0.000	0.000	

Shaded cells indicate intra-island comparisons. Island abbreviations as in Table 1. Sample populations are arranged from west to east and north to south (see Supporting Information, Appendix S1). Sample codes: SP, Santa Paula; LB, Lobo Canyon; CH, Cherry Canyon; WP, West Point, HK, Hooker Canyon; 777, Peak 777; AN, Anacapa East; C, Cat Canyon; CC, Cherry Cove; PS, Pump Station; RM, Renton Mine Road; BSC, Boy Scout Camp; CHC, Chamish Canyon; LT, Lemon Tank; TD, Twin Dams; WC, Waynuk Canyon; MR, Middle Ranch; BOX, Box Canyon; BR, Bryce Canyon; HC, Horse Canyon.

Table 3. AMOVAs based on: A, *LFY* sequences; B, nrITS sequences; and C, plastid sequences, considering either taxon (left) or island (right) as structuring populations

Source of variation	d.f.	SS	% Var.	Source of variation	d.f.	SS	% Var.
A							
Among taxa	3	5503.29	97.61	Among islands	5	5508.05	97.27
Among populations	16	55.45	0.27	Among populations	14	50.70	0.36
Within populations	52	125.30	2.12	Within populations	52	125.30	2.36
Total	71	5684.04		Total	71	5684.04	
B							
Among taxa	3	180.74	83.39	Among islands	5	182.06	81.53
Among populations	16	14.83	1.61	Among populations	14	13.51	2.09
Within populations	47	32.55	15.01	Within populations	47	32.55	16.38
Total	66	228.12		Total	66	228.12	
C							
Among taxa	3	840.56	99.53	Among islands	5	840.56	99.40
Among populations	16	5.00	0.47	Among populations	14	5.00	0.60
Within populations	21	0.00	0.00	Within populations	21	0.00	0.00
Total	40	845.56		Total	40	845.56	

migration/mutation rate) were zero, with the exceptions of Santa Catalina to Santa Barbara ($M = 79$), Santa Barbara to Anacapa ($M = 22$), Anacapa to Santa Cruz ($M = 937$) and Santa Cruz to Santa Rosa ($M = 3941$). From the plastid data, Migrate-N estimates were also zero with the exceptions of Santa Cruz to Santa Catalina ($M = 801$) and Anacapa ($M = 3937$) and Santa Rosa ($M = 45\,039$) to Santa Cruz. A signal of both pollen (*LFY*) and seed (*LFY* plus plastid) long-term average migration was found only from Anacapa to Santa Cruz. These migration estimates support the strong connection between the northern islands.

Phylogenetic reconstruction and haplotype network

All Tajima's *D* tests for neutrality were non-significant, indicating that the loci are not under selection (data not shown). Models selected by jModelTest were F81 + G for the plastid data, HKY+I+G for the nrITS data and HKY for the *LFY* data.

Phylogenetic trees estimated from the full alignments (see Supporting Information, Appendix S4) were consistent with those estimated from the alignments with duplicate sequences removed (Fig. 2). There was no evidence of recent introgression, as indicated by shared haplotypes, from the introduced Santa Catalina *E. fasciculatum* populations in phylogenetic trees estimated from the nrITS or plastid DNA. The ML and Bayesian phylogenetic methods estimated similar topologies in the *E. arborescens*–*E. giganteum* lineage. In the plastid analysis, without an outgroup (data not shown) or with *E. fasciculatum* as an outgroup (Fig. 2A), all varieties are supported as monophyletic, but *E. giganteum* is not a monophyletic species: *E. arborescens* is sister to *E. giganteum* var. *giganteum* and joins *E. giganteum* var. *compactum* and *E. giganteum* var. *formosum* in a basal polytomy. The nrITS tree is fairly unresolved. Each variety is recovered as a clade, but the branching order cannot confidently be inferred (Fig. 2B). The *LFY* phylogenetic trees, however, are more resolved and support *E. arborescens* and *E. giganteum* as sister taxa (Fig. 2C). Additionally, as in the plastid estimates, single-island monophyly of the *E. giganteum* varieties is supported. Single-island *E. arborescens* clades are not recovered with any method or dataset.

The plastid haplotype analysis recovered six haplotype clusters: separate clusters for the mainland and introduced Santa Catalina populations of *E. fasciculatum* and one cluster for each of the named island taxa (Fig. 1). The *E. giganteum* var. *formosum* and *E. giganteum* var. *compactum* haplotypes are separated by two inferred changes and are closely allied with both *E. fasciculatum* haplotypes. The *E. giganteum* var. *giganteum* and *E. arborescens* clusters are more similar to one another (six inferred changes between common haplotypes) than to the *E. fasciculatum* or other *E. giganteum* haplotypes (ten shared inferred changes, including a 72-bp indel).

Biogeographical reconstruction

No specific colonization history was strongly supported, although the combined runs inferred an initial colonization of Santarosae with low support ($P = 0.1439$), subsequent colonization of the southern islands from the north (Santarosae) to the south

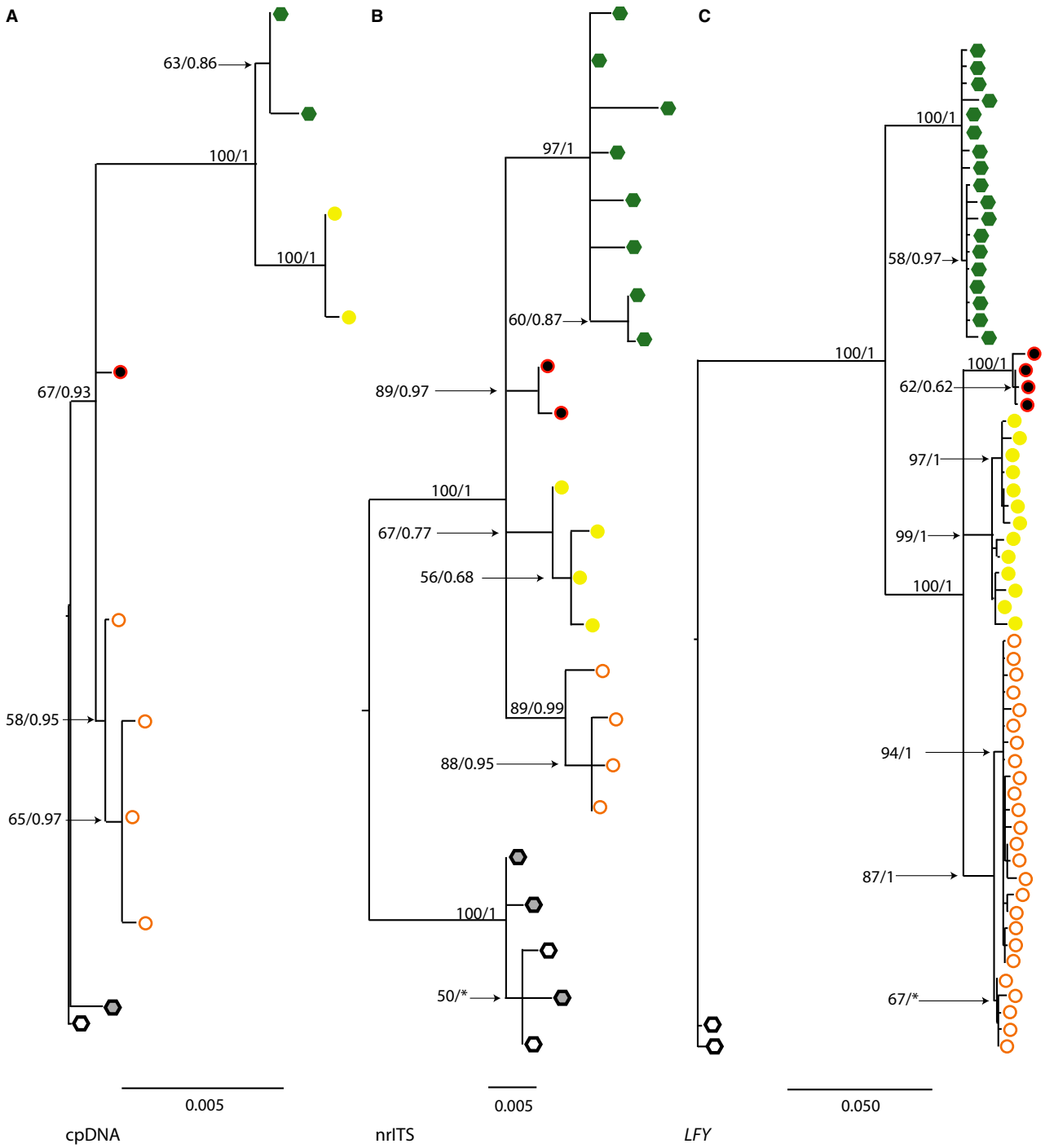

Figure 2. *Eriogonum arborescens* and *E. giganteum* consensus trees estimated from: A, plastid DNA with *E. fasciculatum* as an outgroup; B, nrITS; and C, *LFY* data, with duplicate sequences removed. Garli ML bootstrap support values above and MrBayes posterior probabilities below selected branches are shown. Taxon symbols as in Fig. 1. *Posterior probability < 0.50.

(Santa Catalina plus San Clemente; $P = 0.0627$) and an additional inter-island dispersal event in the south (Santa Catalina plus San Clemente to Santa Barbara; $P = 0.2192$). Although each inferred dispersal event had a low probability, the relative probabilities of the biogeographical ranges at cladogenesis are consistent with the dispersal history recovered with other analyses (see Supporting

Information, Appendix S5). For example, the relative probability of an island-only, rather than mainland or mainland-plus-island range of the ancestor at the basal split was only 5.78% (Table 4; see Supporting Information, Appendix S5). Other ancestral distributions were less strongly supported. Santarosae, at 21.80%, was inferred to be the single most probable range of the ancestor of the *E. arborescens* and *E. giganteum* split, but some southern island ranges had relative probabilities > 5%. Similarly, Santa Catalina is most frequently included in the ranges of the ancestor to *E. giganteum* var. *giganteum* plus the ancestor of *E. giganteum* var. *compactum* and the ancestor of each variety, but the combined relative probabilities for ranges including Santa Catalina are < 70% in both cases (Table 4; see Supporting Information, Appendix S5).

Table 4. Inferred ancestral range of nodes with > 10% estimated mixed ancestry (the range with the highest relative probability at cladogenesis is indicated in bold type)

	Mainland					Northern Islands				Southern Islands						
						Santarosae				South	SBI		SCA			
Split	Only	SRS	SBI	SCA	SCL	Only	SBI	SCA	SCL	ALL	Only	SCA	SCL	Only	SCL	SCL Only	Varied Other
A	**66.03**	8.26	6.04	7.16	6.73	0.74	0.10	0.06	0.11	0.01	0.22	0.07	0.05	0.22	0.05	0.20	3.95
B	4.77	6.84	1.28	2.02	1.71	**21.8**	6.88	10.55	8.14	0.46	4.15	1.68	1.16	7.24	2.35	5.70	13.24
C	0.26	0.02	0.19	0.76	0.40	0.77	0.41	1.48	0.96	6.13	6.42	11.91	6.05	21.56	**26.49**	13.35	2.85
D	0.30	0.02	0.18	0.43	0.52	0.63	0.43	0.83	1.12	6.59	7.94	9.44	10.65	15.26	**23.73**	19.69	2.22

Major splits are between A, sampled *E. fasciculatum* and the island taxa; B, *E. arborescens* and *E. giganteum*; C, *E. giganteum* var. *giganteum* and the other *E. giganteum* varieties; and D, *E. giganteum* var. *compactum* and *E. giganteum* var. *formosum*. Single-region ranges are indicated by 'Only'. Ranges that span more than one region are indicated by the second island or 'All' for all the southern islands. Areas not recovered at > 5% at any node are combined as 'Other'. Region abbreviations: MNL, mainland California; SRS, Santarosae (Anacapa, Santa Cruz and Santa Rosa considered as a single region); SBI, Santa Barbara; SCA, Santa Catalina; SCL, San Clemente.

Microsatellite amplification

All five microsatellite loci amplified among all populations. Most loci had only four or five alleles across all populations and only one or two alleles per population. Microchecker identified the majority of the microsatellite loci as failing to meet HWE expectations and therefore as potentially harbouring null alleles, in at least one population (proportion of populations failing to meet HWE expectations ranged from 0.05 to 0.47 per locus; mean = 0.20). Loci that were not consistently identified as failing to meet HWE expectations were generally fixed in several populations (proportion of populations fixed for a single allele ranged from 0 to 0.63 per locus; mean = 0.30). Estimates of null allele frequencies ranged from 0.03 to 0.31. Only one highly variable locus, ERGI_99, which was identified as having potential null alleles in nearly half the populations, was inferred to have null alleles in populations that were both variable and otherwise apparently at HWE. Both Lositan and Bayescan identified ERGI_99 as an outlier F_{ST} (Lositan, $P = 1 \times 10^{-6}$; Bayescan $P = 0.26$). Because the calculated alpha in Bayescan was −0.005, indicating balancing selection, which would lead to more conservative estimates of divergence among populations, but not affect individual-centred analyses, (Beaumont, 2005; Garcia-Verdugo *et al.*, 2015) Locus ERGI_99 was retained in downstream analyses.

Microsatellite diversity and population structure

Microsatellite diversity was generally low (Table 5). Within populations, the number of alleles per locus ranged from 1.6 to 5.2 (mean = 2.8), but the number of effective alleles per locus ranged only from 1.1 to 3.5 (mean = 1.8) and expected heterozygosities were

Table 5. Microsatellite diversity within *E. arborescens* and *E. giganteum* populations

Island and location	N	A	A_E	P	H_o	H_E	F_{IS}
Santa Rosa							
LC*	32.0	4.0	2.8	0.60	0.24	0.33	0.29
CH	29.0	3.2	1.8	0.60	0.24	0.28	0.14
Santa Cruz							
WP*	31.0	3.6	2.5	0.80	0.17	0.30	0.46
HC*	31.0	5.2	3.1	0.80	0.18	0.28	0.38
777*	31.8	4.8	3.5	0.60	0.23	0.29	0.19
Anacapa							
AN*	31.4	3.6	2.4	0.40	0.14	0.20	0.34
Santa Barbara							
C	29.0	3.2	1.8	0.80	0.23	0.27	0.15
Santa Catalina							
CC*	31.0	2.2	1.5	0.80	0.22	0.25	0.14
PS	32.0	2.2	1.7	0.40	0.22	0.23	0.08
RM*	28.0	2.6	1.8	0.80	0.19	0.27	0.30
San Clemente							
BSC*	30.0	2.2	1.2	0.80	0.03	0.12	0.78
CHC†	32.0	1.6	1.2	0.40	0.13	0.10	-0.19
LT*	32.0	2.4	1.5	0.80	0.12	0.28	0.58
TD	32.0	1.8	1.2	0.40	0.13	0.13	0.07
WC*	29.0	1.8	1.1	0.60	0.05	0.09	0.49
MR	30.0	2.2	1.3	0.60	0.16	0.17	0.10
BOX	27.0	2.4	1.5	0.60	0.20	0.24	0.19
BR	29.0	2.6	1.6	0.60	0.22	0.26	0.15
HC*	32.0	2.6	1.5	0.80	0.14	0.24	0.43
Taxon means							
E. arborescens	31.0	4.1	2.7	0.64	0.20	0.28	0.30
E. giganteum							
var. *compactum*	29.0	3.2	1.8	1.00	0.23	0.27	0.15
var. *giganteum*	29.8	3.1	1.6	0.74	0.21	0.24	0.11
var. *formosum*	30.3	2.2	1.3	0.62	0.13	0.18	0.31

*Sampling population failing to meet HWE expectations (multi-locus exact test $P < 0.01$).
†Sampling population for which data were insufficient to calculate the probability of being at HWE.
N, number of individuals successfully amplified; A, alleles per locus; A_E, effective alleles per locus; P, percentage polymorphic loci; H_o, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient. Sample populations are arranged from west to east and north to south (see Supporting Information, Appendix S1). Sample codes as in Table 2.

all below 0.35 (Table 5). Every population was fixed for a single allele for at least one locus and all but one population either failed to meet HWE expectations (multi-locus exact test $P < 0.01$) or was fixed for a single allele in at least one-third of the amplified loci (Table 5). Populations were relatively differentiated, with most harbouring at least one unique allele. Inbreeding coefficients varied broadly from $F_{IS} = -0.19$ to 0.78 (mean = 0.27), with the highest values in *E. giganteum* var. *giganteum* populations.

Each *E. giganteum* variety and *E. arborescens* were recovered as segregate clusters in both individual-centred (see Supporting Information, Appendix S6; first two axes = 56.99%) and population-centred (see Supporting Information, Appendix S6; first two axes = 80.38%) PCoAs. Similarly, taxonomic identity explained the majority of variation in microsatellite AMOVAs, although more variation was found within and among populations in the microsatellite data (Table 6) than in the sequence data (Table 3). Location by island, which parallels taxonomy among the southern populations, explained nearly as much of the microsatellite variation.

Although population-centred analyses should be interpreted cautiously, genetic differentiation was inferred to be higher among southern populations than among northern populations. The mean pairwise F_{ST} was 0.58 (0.01–0.82), but was higher among southern (mean = 0.58) than northern (mean = 0.11) populations (Table 2). Among the

Table 6. AMOVAs based on microsatellite allele frequency data, considering either taxon (left) or island (right) as structuring populations

Source of variation	d.f.	SS	VC	% Var.	Source of variation	d.f.	SS	%. Var.
Among taxa	3	909.5	1.15	57.99	Among islands	5	925.53	54.23
Among populations	15	237.94	0.25	12.61	Among populations	13	221.91	15.55
Within populations	1141	664.62	0.58	29.41	Within populations	1141	664.62	30.22
Total	1159	1812.06	1.98		Total	1159	1812.06	

southern island populations, the mean intra-island $F_{ST} = 0.42$ and the mean inter-island $F_{ST} = 0.73$. Among the northern island populations, the mean intra-island $F_{ST} = 0.07$, whereas the mean inter-island $F_{ST} = 0.13$. The mean number of effective migrants (N_M) based on pairwise populations F_{ST} values was $N_M = 5.49$ (0.89–39.95) among *E. arborescens* populations and $N_M = 0.27$ (0.06–2.73) among *E. giganteum* populations (see Supporting Information, Appendix S3). Similarly estimates based on Slatkin's (1985) private allele method were much higher in *E. arborescens* (4.69) than in *E. giganteum* (0.303). Such indirect estimates of N_M are imprecise (Whitlock & McCauley, 1999), but the agreement of estimates derived from such different underlying theoretical models suggest that there is much greater connectivity among *E. arborescens* populations than among *E. giganteum* populations.

Neighbour-joining phenograms with bootstrap resampling based on Nei's genetic distances were well resolved, with *E. giganteum* var. *formosum* inferred as sister to *E. giganteum* var. *giganteum* plus *E. giganteum* var. *compactum* and the *E. giganteum* clade sister to *E. arborescens* (Fig. 3). All named taxa were recovered as monophyletic. Monophyletic island lineages were strongly supported on all the southern islands, but none of the northern islands. Similarly, the EdenNetwork network connecting individual geneotypes based on allele sharing (automatic threshold = 0.5) revealed no inter-taxonomic sharing and inter-island sharing only among populations of *E. arborescens* on the northern islands (Fig. 3).

The results of Structure with and without recessive alleles were consistent in the assignment of individuals and optimal number of clusters, indicting that the analyses were not influenced by the presence of null alleles. Structure identified three primary segregate clusters, with little admixture (average estimate of single population membership = 0.981; Fig. 3). The recovered clusters correspond closely to three of the four clusters identified by PCoA (see Supporting Information, Appendix S6) and the three major groups in the neighbour-joining phenogram (Fig. 3). All *E. arborescens* and *E. giganteum* var. *formosum* were inferred to belong to separate, single clusters. The third recovered cluster consisted of all *E. giganteum* var. *giganteum* and *E. giganteum* var. *compactum* individuals.

Data congruence

The sequence data indicate that, despite the nearshore location of the islands, the California Channel Islands harbour an endemic *Eriogonum* lineage genetically distinct from the sampled mainland population of *E. fasciculatum*. Within the lineage, *E. arborescens* and *E. giganteum* var. *formosum* are separate clades (sequence data) or form distinct evolutionary clusters (microsatellite data) in all analyses, whereas *E. giganteum* var. *compactum* and *E. giganteum* var. *gignateum* are separate monophyletic lineages based on sequence data, but are less distinct based on microsatellite data (e.g. Structure analysis). Additionally, the relationships among the varieties of *E. giganteum* are unresolved in the nrITS tree and are paraphyletic in the plastid tree (Fig. 2). Thus, the three endemic *E. giganteum* varieties are monophyletic at the island level and endemic *E. arborescens* is monophyletic at the northern regional level. Additionally, if the *LFY* gene tree is an accurate estimate of the nuclear genome, *E. giganteum* is monophyletic and *E. giganteum* and *E. arborescens* are supported as sister taxa, as suggested by previous researchers (Watson, 1885; Raven, 1967). Subsequent inferences about colonization and gene flow will be made accepting the traditional taxonomic divisions, which are supported by morphological data (Costea & Reveal, 2013) and the molecular data presented here.

DISCUSSION

Colonization

Although multiple early colonization events cannot be ruled out, the monophyly inferred from moderately diverse markers, with different modes of inheritance and rates of evolution, suggests that dispersal and establishment in *Eriogonum* is neither frequent nor random. However, it also appears that the entire archipelago is generally within the dispersal range of

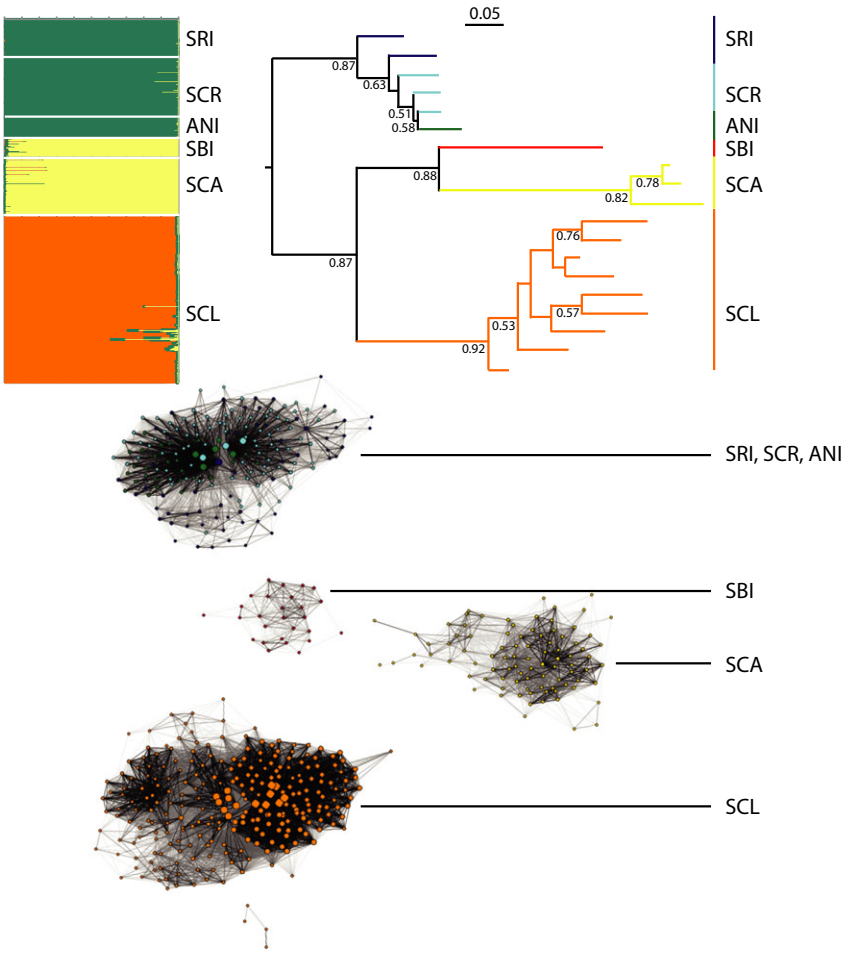

Figure 3. Results of analyses of genetic differentiation based on microsatellite allele frequencies. Top left, STRUCTURE results indicating $K = 3$. Top right, neighbour-joining tree based on Nei's genetic distance; bootstrap values > 50% are reported below branches. Bottom, EdeNetwork with automatic thresholding (0.5) based on allele sharing. Island abbreviations as in Table 1.

these taxa. The *E. arborescens–E. giganteum* lineage is represented on all the larger islands and two of the four smaller islands. As the probability that successful colonists would go extinct is higher on small islands (Johnson, 2003), the current absence of the lineage on two small islands is not evidence that those islands are beyond the dispersal range of the lineage. In fact, recent studies on Santa Barbara Island, which harbours *E. giganteum* var. *compactum*, indicate that the colonization rate by plants is high (0.85 new species per year), but establishment is low (no robust establishment of a California native in 30 years; Drost & Junak, 2009).

The *LFY* data support a single colonization of the islands. BAYAREA consistently inferred a single colonization from the mainland to the islands, albeit with low support. The data are also consistent with initial colonization of a close island (i.e. one of the northern islands or Santa Catalina Island) and subsequent dispersal throughout the archipelago. Because *E. giganteum* is not a nested subset of *E. arborescens* in the *LFY* gene tree and the BAYAREA analyses lack resolution in ancestral range reconstruction at the split between *E. arborescens* and *E. giganteum*, our data do not provide strong support for an initial northern island colonization. Although the data do not rule out initial colonization of Santa Catalina, plant diversity on all the islands appears to be best explained by dispersal primarily from the north-west to the south-east due to dominant wind direction (Riley & McGlaughlin, 2016), which these results generally support. The second nuclear sequencing partition, nrITS, offers no additional insight into colonization patterns (Fig. 2B). Although the monophyly of *E. arborescens–E. giganteum* with respect to the sampled populations of *E. fasciculatum* is supported, there is no resolution of branching order or relationships among taxa within the island lineage.

Similarly, although the three *E. giganteum* varieties are individually resolved, the dataset is uninformative with respect to branching order and does not strongly support any inferences about colonization routes.

The evolutionary relationships inferred from the plastid DNA do not echo those inferred from the nuclear DNA (Fig. 2A). Phylogenetic analyses of regions of the plastid genome suggest that *E. arborescens* and *E. giganteum* var. *giganteum* are sister taxa. The *E. arborescens*–*E. giganteum* var. *giganteum* clade is unresolved relative to the *E. giganteum* var. *compactum* and *E. giganteum* var. *formosum* clades. In contrast, the nuclear data suggest that *E. giganteum* is monophyletic and sister to *E. arborescens*. Additionally, the plastid data contradict the nuclear data with respect to the tempo or timing of evolution. Divergences are shallow among *E. giganteum* varieties in the nuclear partitions, but are deep among *E. giganteum* var. *giganteum* and the other *E. giganteum* varieties in the plastid partition.

Although it is possible that the *LFY* gene tree is not tracking the species history and is uninformative with respect to colonization history, this is unlikely for a combination of reasons. The coalescence of individual *LFY* copies within each taxon, long branches between recognized species and concordance of the molecular, morphological and traditional taxonomic data suggest that the *LFY* gene tree reflects the species tree. In that case, the discordant plastid gene tree is most likely the result of coalescent processes or of divergent evolutionary histories. The latter would be expected in the event of recent plastid capture from outside the island lineage (e.g. through *E. arborescens* and into *E. giganteum* var. *giganteum* or vice versa). This type of plastid capture has been inferred in other island plant groups (e.g. Mort *et al.*, 2002; McGlaughlin & Friar, 2011; Wallace *et al.*, 2011). The possible plastid introgression could be interpreted as corroboration of the general pattern seen in the nuclear data as the least isolated islands (northern islands and Santa Catalina Island) share a unique plastid type, although spread throughout the southern archipelago has been incomplete.

A pattern of north-to-south colonization, consistent with the branching patterns recovered from both the sequence and the microsatellite data, would be expected as the result of two complementary large-scale processes. First, the central northern island, Santa Cruz Island, is the highest and most topographically diverse in the archipelago and may have acted as a refugium for insular lineages during periods of partial or complete inundation of the lower islands (Muhs *et al.*, 2004). Periodic waves of extinction on lower-lying islands followed by re-colonization from the north would generate a phylogenetic signal of older, more diverse lineages on the northern islands and descendant lineages on the southern islands. This would be expected to leave a genetic signal in disparate taxa of many alleles on southern islands dating to a colonization pulse following the last sea-level highstand (e.g. *c*. 100 000 years ago; Muhs *et al.*, 2004). The only taxa for which phylogenetic dates have been estimated have diverged much more recently (e.g. lizards, Mahoney, Parks & Fellers, 2003; foxes, Rick *et al.*, 2009; skunks, Floyd *et al.*, 2011) and, thus, do not provide an adequate test of this pattern. Our sequence data do not allow estimation of reliable divergence dates, but there is no evidence of more diverse lineages on the northern islands (Table 1), although an early split between *E. arborescens* and *E. giganteum* is inferred in every tree (Fig. 2). In the microsatellite data, which are expected to reflect more recent microevolutionary processes (Wang, 2010), the northern island populations generally have more alleles per locus and higher expected heterozygosoties (Table 5).

Second, the narrow water barrier and the large combined size of the northern islands make them the more likely site of colonizations. Frequent colonization of the northern islands combined with biotic or abiotic factors that favour southward expansion would also be expected to generate patterns of more diverse lineages on the northern islands and descendant lineages on the southern islands. In this case, however, the timing of divergences would be expected to be more varied, rather than correlated with sea-level changes. North-to-south patterns have been suggested among some invertebrate taxa (e.g. Weissman & Rentz, 1976; Rust, 1985; Ramirez & Beckwitt, 1995; Chatzimanolis, Norris & Caterino, 2010), but have not received widespread attention. Vertebrate phylogeographies do not support a general north-to-south colonization route, perhaps because of reliance on different dispersal mechanisms (i.e. rafting on the outwash from periodic floods or human-mediated dispersal; Schoenherr *et al.*, 2003; Rick *et al.*, 2009; Floyd *et al.*, 2011). Small invertebrates, however, and passively dispersed plants, including *Eriogonum*, might be expected to depend on the prevailing northwesterly air currents for colonization. Indeed, archipelago-wide analyses of the relationship between plant diversity and distances to the mainland indicate that north-to-south colonization best explains the diversity of the flora (Riley & McGlaughlin, 2016).

Inter-island gene flow

The data are consistent with observations that *E. giganteum* var. *formosum* is the most morphologically distinct of the *E. giganteum* varieties (Costea &

Reveal, 2013). *Eriogonum giganteum* var. *formosum* is the only variety recovered as a segregate genetic cluster in PCoA (see Supporting Information, Appendix S6), EDENETWORK thresholded networks (Fig. 3) and Bayesian population assignment (Fig. 3). Whereas the phylogenetic reconstructions (Fig. 2) lack resolution among the *E. giganteum* varieties, the data are not inconsistent with the most distant island, San Clemente, harbouring the most divergent taxon. The data are thus consistent with the central prediction of Johnson, Adler & Cherry (2000) that, if isolation is the primary force determining gene flow, the most divergent lineages should be found on the most distant large island.

The data provide little support for Johnson's (2003) expansion of the island biogeographical theory of MacArthur & Wilson (1967) that predicts that small islands should be characterized by less divergent lineages than larger islands. Whereas *E. arborescens* on Anacapa Island (2.9 km^2) is undifferentiated from *E. arborescens* on other islands, the lack of divergence is probably due to the close proximity to and recent connection with the large northern islands; *E. arborescens* from Santa Cruz (294 km^2) and Santa Rosa (217 km^2) is similarly undifferentiated (e.g. Fig. 3). In contrast, the *E. giganteum* variety from the smallest island, *E. giganteum* var. *compactum* from Santa Barbara Island (2.6 km^2), is somewhat less divergent than *E. giganteum* var. *formosum* from San Clemente Island (145 km^2). Accessions of the former form a clade within the nuclear gene trees, but are part of a polytomy among all *E. giganteum* varieties (*LFY*; Fig. 2) or island accessions (nrITS; Fig. 2) and are part of a basal polytomy within the plastid gene tree (Fig. 2). Similarly, *E. giganteum* var. *compactum* is not recovered as a segregate cluster in STRUCTURE analysis (Fig. 3), although it is recovered by PCoA (see Supporting Information, Appendix S6) and by minimum spanning and threshold networks (Fig. 3).

The data also support the prediction, based on the findings of Stuessy *et al.* (2006), that taxa on low and relatively homogeneous islands should be characterized by low divergence within islands, but high divergence among islands. This prediction is especially strongly supported if the islands that were joined as Santarosae during the last glacial maximum are considered as a single island. The sharp break between intra- and inter-island divergences is seen most clearly in the EDENETWORK threshold network (Fig. 3), but is also supported by the intra-island monophyly recovered in individual gene trees (Fig. 2) and the high F_{ST} values among islands for both microsatellite and *LFY* data (Table 2). Additionally, both sequence-based and microsatellite-based AMOVAs support the inference that much of the molecular variation occurs among, rather than within, islands (Tables 3, 6).

The geological history of the islands combined with the clear genetic divergences among *E. giganteum* varieties suggest that the southern islands have never experienced high connectivity. The northern islands, which have been physically separated only since the end of the Pleistocene, have a much stronger genetic signal of inter-island connectivity, as evidenced by much lower levels of intra-specific differentiation (Fig. 3), lower inter-island F_{ST} values (Table 2) and higher estimates of inter-island gene flow (see Appendices S2, S3). Although contemporary gene flow may be responsible for the observed pattern, the low island-wide N_E values, high F_{IS} values and slightly higher inter- than intra-island divergences that were inferred suggest that even populations on separate northern islands may be undergoing genetic drift independently.

Intra-island gene flow

Although the population-centred microsatellite-based analyses should be interpreted cautiously, the generally high intra-island microsatellite-based F_{ST} values (mean = 0.338; Table 2) suggest that the sampled populations are genetically distinct. Within the northern islands, however, the intra-island microsatellite-based F_{ST} values are generally low (mean = 0.070) and, throughout the archipelago, sequence-based intra-island F_{ST} values are low (e.g. *LFY* mean = 0.047). Furthermore, the individual-based microsatellite analyses, STRUCTURE, PCoA and EDENETWORK, failed to detect strongly differentiated intra-island population structure (Fig. 3; see Supporting Information, Appendix S6). The loss of large numbers of individuals, coupled with self-compatibility (McEachern *et al.*, 1997) and dependence on passive dispersal, would quickly result in the high population subdivision, high proportion of fixed alleles and low levels of genetic diversity observed in the data.

Comparison with other island systems

Investigations into colonization patterns on well-studied nearshore island systems, such as the Canaries, frequently find evidence for multiple successful colonizations (e.g. Carine *et al.*, 2004; Díaz-Pérez *et al.*, 2008; Desamor *et al.*, 2012; Gruenstaeudl, Santos-Guerra & Jansen, 2013). Additionally, researchers regularly report indications of inter-island gene flow within archipelagos (e.g. Rumeu *et al.*, 2011; Zhai *et al.*, 2012; Lee *et al.*, 2013; Chiang *et al.*, 2014). Some systems, like the Izu islands which range from *c.* 20 to 200 km from the larger islands of Japan,

even show evidence of ongoing gene flow with the mainland (e.g. Kato *et al.*, 2011; Yamada & Maki, 2012). Although multiple, independent colonizations of such nearshore archipelagos might be expected, not all Izu endemic plants exhibit this pattern. Studies of *Campanula microdonta* Koidz. (Campanulaceae; Oiki *et al.*, 2001) and *Weigela coraeensis* Thunb. (Caprifoliaceae; Yamada & Maki, 2012) indicate that these Izu endemics probably colonized the islands only once and moved through the chain in a stepping-stone fashion. Similarly, we find little evidence in our data for repeated colonizations of the California Channel Islands and evidence for modern gene flow only among the *E. arborescens* found on the islands previously joined as Santarosae. Finally, although the nearest islands are only *c*. 20 (Anacapa Island) or 30 km (Santa Catalina Island) from the mainland and *E. arborescens* and *E. giganteum* readily hybridize with mainland *E. fasciculatum*, we found no evidence of contemporary gene flow from the mainland.

The striking genetic divergence among California Channel Island *Eriogonum* populations suggests that the narrow water barriers effectively limit dispersal. This is especially likely because both species have dry, gravity-dispersed fruits. Dry fruits have been found to be commonly associated with low levels of inter-island colonization and high levels of inter-island genetic divergence (García-Verdugo *et al.*, 2014). Additionally, early colonists may have competitively excluded later dispersers (i.e. niche pre-emption; Silvertown, 2004; Silvertown, Francisco-Ortega & Carine, 2005). Niche pre-emption would explain the observation of Drost & Junak (2009) that dispersal to Santa Barbara Island was high, but establishment was low. The niche pre-emption hypothesis may be supported by the observation that two distinct plastid lineages are found among *E. giganteum*, but that the spread of each has been incomplete. Even if the first arriving plastid excluded the other, gene flow via pollen could serve to homogenize the nuclear genomes of all *E. giganteum* varieties. Without greater sampling of both island populations, to confirm that there is only a single plastid lineage on each island and potential mainland ancestral plastid lineages it is not possible to determine that niche pre-emption has occurred.

Conclusions and recommendations

Overall, our results suggest that these California Channel Island *Eriogonum* taxa represent a monophyletic lineage. Within the lineage, the *E. arborescens* of the northern islands are not strongly differentiated from one another, but are distinct from *E. fasciculatum*. In contrast, the *E. giganteum* varieties of the southern islands are strongly differentiated from *E. arborescens* and from one another. Finally, the relatively high intra-island genetic diversity within *E. giganteum* suggests that this lineage may have largely recovered from initial founder effects. Diversity within each variety rivals the diversity found within the more broadly distributed *E. arborescens*, as expected for anagenetically derived taxa during the later stages of divergence.

Although these *Eriogonum* taxa persist on all the California Channel Islands from which they were originally described, their long-term population viability may be compromised by low genetic diversity, low effective population sizes (N_E) and low census sizes. Even the most diverse populations have low neutral genetic diversity compared to other island endemics. The average $H_E = 0.249$ we found for *Eriogonum* is low compared to averages for other perennial California Channel Island species such as *Acmispon argophyllus* (A.Gray) Brouillet and *A. dendroidius* (Greene) Brouillet (Fabaceae; $H_E = 0.32$ and $H_E = 0.42$, respectively, McGlaughlin *et al.*, 2015a, b), *Crossosoma californicum* Nutt. (Crossosomataceae; $H_E = 0.38$, Wallace & Helenurm, 2009) and *Galium catalinense* A.Gray subsp. *acrispum* Dempster (Rubiaceae; $H_E = 0.55$, Riley, McGlaughlin & Helenurm, 2010). The microsatellite data lacked sufficient variation for robust N_E estimation, but the relatively high proportion (*c*. 27%) of duplicate multilocus microsatellite genotypes suggests that effective population sizes are lower than the number of observed stems. The inferred low effective populations combined with actual census sizes below the *c*. 2500–16 000 determined by Traill, Bradshaw & Brook (2007) to be sufficient to ensure 95% probability of persistence over 40 generations suggest that these *Eriogonum* taxa may not have the genetic or demographic capacity for long-term persistence on the Channel Islands without direct management.

At the largest scale, management goals should be to build and maintain large census sizes on each island to maintain lineage-wide diversity and limit the erosion of variability due to genetic drift. Within islands, the data as a whole are somewhat ambiguous regarding the need to manage each population separately. The southern islands, in particular, seem to support strongly subdivided populations. However, because PCoA, Structure and EdeNetwork failed to recover segregate intra-island populations, it seems likely that the subdivided genetic structure inferred by intra-island F_{ST} values reflects recent genetic drift associated with population declines rather than more gradual processes leading to differentiation. If these *Eriogonum* taxa were previously more broadly and continuously distributed on each island, restoring historical processes of gene flow and

dispersal would require supporting the numerical growth and spatial expansion of each population. Management goals should focus on limiting the loss of private alleles and, perhaps, of re-establishing intra-island migration. Although gene flow via seeds, which are presumed to be gravity-dispersed, may remain low, population connectivity via pollen flow might be re-established with larger census sizes, because *Eriogonum* taxa attract a variety of vagile pollinators (Junak *et al.*, 1995).

Substantially increasing the census size of individual populations and facilitating re-establishment of additional populations may be a realistic management goal. Channel Island *Eriogonum* taxa appear to be effective early colonizers of disturbed areas (Allen *et al.*, 2000; Corry *et al.*, 2009) and have been increasing in census size since herbivore removal (Corry, 2006; Corry *et al.*, 2009; Yelenik & Levine, 2010b). However, population growth appears to be limited by survival at the seedling establishment phase (Yelenik & Levine, 2010a). In *Eriogonum*, as in many California Channel Island natives, establishment is severely restricted by allelopathy from invasive fennel [*Foeniculum vulgare* Mill. (Apiaceae)] (Erskine Ogden & Rejmánek, 2005). Thus, fennel eradication efforts, which benefit the entire native flora, should be continued (Colvin & Gliessman, 2002; Erskine Ogden & Rejmánek, 2005; Flory & Clay, 2009). Seedling establishment is also limited by competition from non-native grasses and by water availability (Yelenik & Levine, 2010a). Because seedling establishment increases by almost an order of magnitude in wet years, water augmentation in drier years should be considered (L. C. Stratton, unpubl. data, but see Padgett, Kee & Allen, 2000). Beyond enhancing the long-term viability of *Eriogonum* populations, such activities have the potential to facilitate recovery of other native plants. *Eriogonum* taxa change the nitrogen profile of the soil, seem to limit the growth of non-native grasses and may act as effective nurse plants for natives (Corry *et al.*, 2009; Yelenik & Levine, 2010b, 2011). Thus, increasing the range and census size of *Eriogonum* on the Channel Islands may enhance conditions for other components of the native flora.

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REFERENCES

Allen EB, Eliason SA, Marquez VJ, Schultz GP, Storms NK, Stylinski CD, Zink TA, Allen MF. 2000. What are the limits to restoration of coastal sage scrub in Southern California? In: Keeley JE, Baer-Keeley M, Fotheringham X, eds. *2nd Interface between ecology and land development in California*. USGS Report 00-62, 253–262.

Anderson RS, Starratt S, Jass RMB. 2010. Fire and vegetation history on Santa Rosa Island Channel Islands and longterm environmental change in southern California. *Journal of Quaternary Science* **25:** 782–797.

Antao T, Lopes A, Lopes RJ, Beja-Pereira A, Luikart G. 2008. LOSITAN: a workbench to detect molecular adaptation based on a F_{ST}-outlier method. *BMC Bioinformatics* **9:** 323.

Baldwin B. 2007. Adaptive radiation of shrubby tarweeds *Deinandra* in the California Islands parallels diversification of the Hawaiian silversword alliance Compositae–Madiinea. *American Journal of Botany* **94:** 237–248.

Baum DA, Yoon H-S, Oldham RL. 2005. Molecular evolution of the transcription factor *LEAFY* in Brassicaceae. *Molecular Phylogenetics and Evolution* **37:** 1–14.

Beaumont MA. 2005. Adaptation and speciation: what can F_{ST} tell us? *Trends in Ecology & Evolution* **20:** 435–440.

Beerli P. 2009. How to use MIGRATE or why are Markov chain Monte Carlo programs difficult to use. *Population Genetics for Animal Conservation* **17:**42–79.

Bruen TC, Philippe H, Bryant D. 2006. A simple and robust statistical test for detecting the presence of recombination. *Genetics* **172:** 2665–2681.

California Natural Diversity Database. 2015. State and federally listed endangered, threatened and rare plants of **California.** https://www.dfg.ca.gov/biogeodata/cnddb/pdfs/TEPlants.pdf (accessed August 2015).

Carine MA, Russell SJ, Santos-Guerra A, Francisco-Ortega J. 2004. Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple

colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany* **91:** 1070–1085.

Caujapé-Castells J. 2011. Jesters, red queens, boomerangs and surfers: a molecular outlook on the diversity of the Canarian endemic flora. In: Bramwell D, Caujapé-Castells J, eds. *The biology of island floras*. Cambridge: Cambridge University Press, 284–324.

Chatzimanolis S, Norris LA, Caterino MS. 2010. Multi-island endemicity: phylogeography and conservation of *Coelus pacificus* Coleoptera: Tenebrionidae darkling beetles on the California Channel Islands. *Annals of the Entomological Society of America* **103:** 785–795.

Chiang TY, Chen SH, Kato H, Hwang CC, Moore SJ, Hsu TW, Hung KH. 2014. Temperate origin and diversification via southward colonization in *Fatsia* (Araliaceae), an insular endemic genus of the West Pacific Rim. *Tree Genetics & Genomes* **10:** 1317–1330.

Clement M, Posada D, Crandall KA. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9:** 1657–1660.

CNPS. 2014. California Native Plant Society inventory of rare plants. Available at: http://www.rareplants.cnps.org (accessed August 2014).

Colvin WIC, Gliessman SR. 2002. Fennel *Foeniculum vulgare* management and native species enhancement on Santa Cruz Island California. In: Brown DR, Mitchell KL, Chaney HW, eds. *Proceedings of the Fifth California Islands Symposium*. Santa Barbara: Santa Barbara Museum of Natural History, 184–188.

Corry PM. 2006. Vegetation dynamics following grazing cessation on the Channel Islands California. Unpublished D. Phil. Thesis, University of North Carolina Chapel Hill.

Corry PM, McEachern AK, Damiani CC, Garcelon DK. 2009. Patterns in post-grazing vegetation changes among species and environments San Miguel and Santa Barbara Islands. In: Damiani CC, Garcelon DK, eds. *Proceedings of the Seventh California Islands Symposium*. Arcata, CA: Institute for Wildlife Studies, 182–183.

Costea M, Reveal JL. 2013. Eriogonum. In: Jepson Flora Project, eds. *Jepson eFlora*. Available at: http://ucjeps.berkeley.edu/cgi-bin/get_IJM.pl?tid=24695 (accessed 15 November 2014).

Delaney KS, Wayne RK. 2005. Adaptive units for conservation: population distinction and historic extinctions in the island scrub-jay. *Conservation Biology* **19:** 523–533.

Desamor A, Laenen B, Gonzalez-Mancebo JM, Jaén Molina R, Bystriakova N, Martinez-Klimova E, Carine MA, Vanderpoorten A. 2012. Inverted patterns of genetic diversity in continental and island populations of the heather *Erica scoparia s.l*. *Journal of Biogeography* **39:** 574–584.

DeSimone AS, Zedler PH. 2001. Do shrub colonizers of southern Californian grassland fit generalities for other woody colonizers? *Ecological Applications* **11:** 1101–1111.

Diamond JM. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences* **64:** 57–63.

Díaz-Pérez A, Sequeira M, Santos-Guerra A, Catalán P. 2008. Multiple colonizations, *in situ* speciation, and volcanism-associated stepping-stone dispersals shaped the phylogeography of the Macaronesian red fescues (*Festuca* L., Gramineae). *Systematic Biology* **57:** 732–749.

Dong C, Idica EY, McWilliams JC. 2009. Circulation and multiple-scale variability in the Southern California Bight. *Progress in Oceanography* **82:** 168–190.

Doyle JJ, Doyle JL. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin, Botanical Society of America* **19:** 11–15.

Drost CA, Junak SA. 2009. Colonizers waifs and stowaways: arrival of new plant species on Santa Barbara Island over a 30-year period. In: Damiani CC, Garcelon DK, eds. *Proceedings of the Seventh California Islands Symposium*. Arcata, CA: Institute for Wildlife Studies, 215–228.

Drummond A, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Earl DA. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetic Resources* **4:** 359–361.

Edgar RC. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32:** 1792–1797.

Erskine Ogden J, Rejmánek M. 2005. Recovery of native plant communities after the control of a dominant invasive plant species *Foeniculum vulgare*: implications for management. *Biological Conservation* **12:** 427–439.

Evanno G, Regnaut S, Goudet J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* **14:** 2611–2620.

Excoffier L, Laval G, Schneider S. 2005. Arlequin version 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* **1:** 47.

Falush D, Stephens M, Pritchard JK. 2003. Inference of population structure: extensions to linked loci and correlated allele frequencies. *Genetics* **164:** 1567–1587.

Fernández-Palacios JM, de Nascimento L, Otto R, Delgado JD, García-del-Rey E, Arévalo JR, Whittaker RJ. 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography* **38:** 226–246.

Fisher MA, Langenheim VE, Nicholson C, Ryan HF, Sliter RW. 2009. Recent developments in understanding the tectonic evolution of the southern California offshore area: implications for earthquake-hazard analysis. *Geological Society of America Special Papers* **454:** 229–250.

Flory SL, Clay K. 2009. Invasive plant removal method determines native plant community responses. *Journal of Applied Ecology* **46:** 434–442.

Floyd CH, Van Vuren DH, Crooks KR, Jones KL, Garcelon DK, Belfiore NM, May B. 2011. Genetic differentiation of island spotted skunks *Spilogale gracilis amphiala*. *Journal of Mammalogy* **92:** 148–158.

Foll M, Gaggiotti O. 2008. A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* **180:** 977–993.

Frohlich MW, Meyerowitz EM. 1997. The search for flower homeotic gene homologs in basal angiosperms and Gnetales: a potential new source of data on the evolutionary origin of flowers. *International Journal of Plant Sciences* **15:** S131–S142.

Funk VA, Wagner WL. 1995. Biogeographic patterns in the Hawaiian Islands. In Wagner VA, Funk WL, eds. *Hawaiian biogeography: evolution on a hot spot archipelago*. Washington, DC: Smithsonian Institution Press. 379–419.

Gao H, Williamson S, Bustamante CD. 2007. A Markov chain Monte Carlo approach for joint inference of population structure and inbreeding rates from multilocus genotype data. *Genetics* **176:** 1635–1651.

García-Verdugo C, Baldwin BG, Fay MF, Caujape-Castells J. 2014. Life history traits and patterns of diversification in oceanic archipelagos: a meta-analysis. *Botanical Journal of the Linnean Society* **174:** 334–348.

García-Verdugo C, Sajeva M, La Mantia T, Harrouni C, Msanda F, Caujapé-Castells J. 2015. Do island plant populations really have lower genetic variation than mainland populations? Effects of selection and distribution range on genetic diversity estimates. *Molecular Ecology* **24:** 726–741.

Gruenstaeudl M, Santos-Guerra A, Jansen RK. 2013. Phylogenetic analyses of *Tolpis* Adans. (Asteraceae) reveal patterns of adaptive radiation, multiple colonization and interspecific hybridization. *Cladistics* **29:** 416–434.

Guindon S, Gascuel O. 2003. A simple fast and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **525:** 696–704.

Howarth DG, Baum DA. 2005. Genealogical evidence of homoploid hybrid speciation in an adaptive radiation of *Scaevola* (Goodeniaceae) in the Hawaiian islands. *Evolution* **59:** 948–961.

Huber T, Faulkner G, Hugenholtz P. 2004. Bellerophon: a program to detect chimeric sequences in multiple sequence alignments. *Bioinformatics* **20:** 2317–2319.

Hubisz MJ, Falush D, Stephens M, Pritchard JK. 2009. Inferring weak population structure with the assistance of sample group information. *Molecular Ecology Resources* **9:** 1322–1332.

Huelsenbeck JP, Ronquist F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17:** 754–755.

Huson DH. 1998. SplitsTree: analyzing and visualizing evolutionary data. *Bioinformatics* **14:** 68–73.

Huson DH, Bryant D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* **23:** 254–267.

James DG, Seymour L, Lauby G, Buckley K. 2014. Beneficial insects attracted to native flowering buckwheats (*Eriogonum* Michx) in central Washington. *Environmental Entomology* **43:** 942–948.

Johnson DL. 1983. The California continental borderland: landbridges, watergaps and biotic dispersals. In: Masters PM, Flemming NC, eds. *Quaternary coastlines and marine archaeology: towards the prehistory of land bridges and continental shelves*. New York: Academic Press, 481–527.

Johnson K, Adler F, Cherry J. 2000. Genetic and phylogenetic consequences of island biogeography. *Evolution; International Journal of Organic Evolution* **54:** 387–396.

Johnson KP. 2003. Island biogeography and evolution: genetic divergence and speciation of island taxa. *Comments on Theoretical Biology* **8:** 339–356.

Junak S, Halvorson WL, Schwemm CA, Keeney T. 1995. *Sensitive plants of San Nicolas Island California phase 1. Technical report No. 51*. Tucson, AZ: United States Geological Survey, Cooperative Park Studies Unit.

Junak S, Wilken DH. 1998. *Sensitive plant status survey, Naval Auxiliary Landing Field, San Clemente Island, California*. Final Report. Santa Barbara, CA: Santa Barbara Botanic Garden.

Kato S, Iwata H, Tsumura Y, Mukai Y. 2011. Genetic structure of island populations of *Prunus lannesiana* var. *speciosa* revealed by chloroplast DNA, AFLP and nuclear SSR loci analyses. *Journal of Plant Research* **12:** 11–23.

Keeley JE. 1991. Seed germination and life history syndromes in the California chaparral. *The Botanical Review* **57:**81–116.

Keeley SC, Funk VA. 2011. Origin and evolution of Hawaiian endemics: new patterns revealed by molecular phylogenetic studies. In: Bramwell D, Caujapé-Castells J, eds. *The biology of island floras*. Cambridge: Cambridge University Press, 57–88.

Kempton EA. 2012. Systematics of Eriogonoideae *ss* Polygonaceae. *Systematic Botany* **37:** 723–737.

Kinlan BP, Graham MH, Erlandson JM. 2005. Late-Quaternary changes in the size and shape of the California Channel Islands: implications for marine subsidies to terrestrial communities. In: Garcelon DK, Schwemm CA, eds. *Proceedings of the Sixth California Island Symposium*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 119–130.

Kivelä M, Arnaud-Haond S, Saramäki J. 2011. EDENetworks: ecological and evolutionary networks. Computer program and documentation distributed by the authors. Available at: http://becs.aalto.fi/edenetworks

Landis MJ, Matzke NJ, Moore BR, Huelsenbeck JP. 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* **62:** 789–804.

Lauretto MS, Nakano F, Faria SR Jr, Pereira CAB, Stern JM. 2009. A straightforward multiallelic significance test for the Hardy-Weinberg equilibrium law. *Genetics and Molecular Biology* **32:** 619–625.

Lee JH, Lee DH, Choi IS, Choi BH. 2013. Phylogeography and genetic diversity of East Asian *Neolitsea sericea* (Lauraceae) based on variations in chloroplast DNA sequences. *Journal of Plant Research* **12:** 193–202.

Librado P, Rozas J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* **25:** 1451–1452.

Little RJ. 1981. Adventitious rooting in coastal sage scrub dominants. *Madroño* **28:** 96–97.

Lotterhos KE, Whitlock MC. 2014. Evaluation of demographic history and neutral parameterization on the performance of FST outlier tests. *Molecular Ecology* **23:** 2178–2192.

Lyon WS. 1886. The flora of our southwestern archipelago II. *Botanical Gazette* **11:** 330–336.

MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Mahoney MJ, Parks DSM, Fellers GM. 2003. *Uta stansburiana* and *Elgaria multicarinata* on the California Channel Islands: natural dispersal or artificial introduction? *Journal of Herpetology* **37:** 586–591.

McEachern K, Wilken D, Chess KA. 1997. *Inventory and monitoring of California Islands candidate plant taxa*. US Geological Survey Open-File Report 00-73.

McGlaughlin ME, Friar EA. 2011. Evolutionary diversification and geographical isolation in *Dubautia laxa* (Asteraceae), a widespread member of the Hawaiian silversword alliance. *Annals of Botany* **107:** 357–370.

McGlaughlin ME, Riley L, Brandsrud M, Arcibal E, Helenurm MK, Helenurm K. 2015a. How much is enough? Minimum sampling intensity required to capture extant genetic diversity in *ex situ* seed collections: examples from the endangered plant *Sibara filifolia* (Brassicaceae). *Conservation Genetics* **16:** 253–266.

McGlaughlin ME, Wallace LE, Wheeler GL, Bresowar GE, Riley L, Britten NR, Helenurm K. 2015b. Do the island biogeography predictions of MacArthur and Wilson hold when examining genetic diversity on the near mainland California Channel Islands? Examples from endemic *Acmispon* (Fabaceae). *Botanical Journal of the Linnean Society* **174:** 289–304.

Miller MA, Holder MT, Vos R, Midford PE, Liebowitz T, Chan L, Warnow T. 2009. The CIPRES portals. CIPRES. Available at: http://www.phylo.org/sub_sections/portal

Moldenke AR. 1976. California pollination ecology and vegetation types. *Phytologia* **34:** 304–361.

Montalvo AM. 2004. *Eriogonum fasciculatum*. In Francis JK, ed. *Wildland shrubs of the United States and its Territories: thamnic descriptions. volume 1*. Gen. Tech. Rep. IITF-GTR-26. San Juan, PR; and Fort Collins, CO: U.S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, and U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 314–318.

Moody A. 2000. Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California. *Journal of Biogeography* **27:** 711–723.

Morandin L, Long R, Pease C, Kremen C. 2011. Hedgerows enhance beneficial insects on farms in California's Central Valley. *California Agriculture* **65:** 197–201.

Mort ME, Soltis DE, Soltis PS, Francisco-Ortega J, Santos-Guerra A. 2002. Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from nuclear and chloroplast sequence data. *Systematic Botany* **27:** 271–288.

Muhs DR, Groves LT, Schumann RR. 2014. Interpreting the paleozoogeography and sea level history of thermally anomalous marine terrace faunas: a case study from the last interglacial complex of San Clemente Island, California. *Monographs of the Western North American Naturalist* **7:** 82–108.

Muhs DR, Simmons KR, Schumann RR, Groves LT, Mitrovica JX, Laurel D. 2012. Sea-level history during the Last Interglacial complex on San Nicolas Island, California: implications for glacial isostatic adjustment processes, paleozoogeography and tectonics. *Quaternary Science Reviews* **37:** 1–25.

Muhs DR, Skipp SG, Schumann RR, Johnson DL, McGeehin JP, Beann J, Damiani CC. 2009. The origin and paleoclimatic significance of carbonate sand dunes deposited on the California Channel Islands during the last glacial period. In: Damiani CC, Garcelon DK, eds. *Proceedings of the Seventh California Islands Symposium*. Arcata, CA: Institute for Wildlife Studies, 3–14.

Muhs DR, Wehmiller JF, Simmons KR, York LL. 2004. Quaternary sea level history of the United States. *Developments in Quaternary Science* **1:** 147–183.

Oberbauer T. 2002. Analysis of vascular plant diversity on the Pacific coast islands of Alta and Baja California. In: Browne DRK, Mitchell L, Chaney HW, eds. *Proceedings of the Fifth California Islands Symposium*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 201–211.

Oiki S, Kawahara T, Inoue K, Ohara M, Maki M. 2001. Random amplified polymorphic DNA (RAPD) variation among populations of the insular endemic plant *Campanula microdonta* (Campanulaceae). *Annals of Botany* **87:** 661–667.

Orr PC. 1968. *Prehistory of Santa Rosa Island*. Santa Barbara, CA: Santa Barbara Museum of Natural History.

Padgett PE, Kee SN, Allen EB. 2000. The effects of irrigation on revegetation of semi-arid coastal sage scrub in southern California. *Environmental Management* **26:** 427–435.

Peakall R, Smouse PE. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. *Bioinformatics* **28:** 2537–2539.

Penn O, Privman E, Ashkenazy H, Landan G, Graur D, Pupko T. 2010a. GUIDANCE: a web server for assessing alignment confidence scores. *Nucleic Acids Research* **38:** W23–W28.

Penn O, Privman E, Landan G, Graur D, Pupko T. 2010b. An alignment confidence score capturing robustness to guide tree uncertainty. *Molecular Biology and Evolution* **27:** 1759–1767.

Philbrick RN. 1980. Distribution and evolution of endemic plants of the California islands. In: Power DM, ed. *The California Islands: proceedings of a multidisciplinary symposium*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 173–188.

Pinter N, Lueddecke SB, Keller EA, Simmons KR. 1998. Late Quaternary slip on the Santa Cruz Island fault, California. *Geological Society of America Bulletin* **110:** 711–722.

Posada D. 2008. JModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25:** 1253–1256.

Powell JA. 2005. Assessment of inventory effort for Lepidoptera (Insecta) and the status of endemic species on Santa Barbara Island California. In: Garcelon DK, Schwemm CA, eds. *Proceedings of the Sixth California Island Symposium*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 351–371.

Power DM. 1976. Avifauna richness on the California Channel Islands. *Condor* **78:** 394–398.

Pritchard JK, Stephens M, Donnelly P. 2000. Inference of population structure using multilocus genotype data. *Genetics* **15:** 945–959.

Rambaut A, Drummond AJ. 2007. Computer program and documentation distributed by the author. Available at: http://beast.bio.ed.ac.uk/Tracer

Rambaut A, Drummond AJ. 2010. Computer program and documentation distributed by the author. Available at: http://beast.bio.ed.ac.uk/TreeAnnotator

Ramirez MG, Beckwitt RD. 1995. Phylogeny and historical biogeography of the spider genus *Lutica* (Araneae, Zodariidae). *Journal of Arachnology* **23:** 177–193.

Raven PH. 1967. The floristics of the California Islands. In: Philbrick RN, ed. *Proceedings of the Symposium on the Biology of the California Islands*. Santa Barbara, CA: Santa Barbara Botanic Garden, 57–67.

Raymond M, Rousset F. 1995. GENEPOP version 1.2: population genetics software for exact tests and ecumenicism. *Journal of Heredity* **86:** 248–249.

Rentz DC, Weissman DB. 1981. Faunal affinities, systematics and bionomics of the Orthoptera of the California Channel Islands. *University of California Publications in Entomology* **94:** 1–241.

Reveal JL. 2005. Polygonaceae Jussieu subfam. Eriogonoideae Arnott. Wild buckwheat subfamily. In Flora of North America Editorial Committee, ed. *Flora of North America 7*. New York: Oxford University Press, 218–478.

Rick TC, Erlandson JM, Vellanoweth RL, Braje TJ, Collins PW, Guthrie DA, Stafford TW Jr. 2009. Origins and antiquity of the island fox *Urocyon littoralis* on California's Channel Islands. *Quaternary Research* **7:** 93–98.

Riley L. 2012. Comparative phylogeography of California Channel Island endemic *Eriogonum* Polygonaceae. Unpublished D. Phil. Thesis, University of South Dakota.

Riley L, McGlaughlin ME. 2016. Endemism in native floras of California's Channel Islands correlated with seasonal patterns of aeolian processes. *Botany-Botanique* **94:** 65–72.

Riley L, McGlaughlin ME, Helenurm K. 2010. Genetic diversity following demographic recovery in the insular endemic plant *Galium catalinense* subspecies *acrispum*. *Conservation Genetics* **11:** 2015–2025.

Riley L, McGlaughlin ME, Helenurm K. 2011. Microsatellite primers for the narrowly endemic shrub *Eriogonum giganteum* Polygonaceae. *American Journal of Botany* **98:** e352–e355.

Rousset F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources* **8:** 103–106.

Rumeu B, Caujapé-Castells J, Blanco-Pastor JL, Jaén-Molina R, Nogales M, Elias RB, Vargas P. 2011. The colonization history of *Juniperus brevifolia* (Cupressaceae) in the Azores Islands. *PLoS ONE* **6:** e27697.

Rust R. 1985. A biogeographic comparison of the bees sphecid wasps and mealybugs of the California Channel Islands Hymenoptera Homoptera. In Miller D, Menke A, eds. *Entomology of the California Channel Islands*. Santa Barbara, CA: Santa Barbara Museum of Natural History, 29–59.

Sanchez A, Kron KA. 2008. Phylogenetics of Polygonaceae with an emphasis on the evolution of Eriogonoideae. *Systematic Botany* **33:** 87–96.

Savage JM. 1967. Evolution of the insular herpetofaunas. In Philbrick RN, ed. *Proceedings of the Symposium on the Biology of the California Islands*. Santa Barbara, CA: Santa Barbara Botanic Garden, 219–227.

Schoenherr AA, Feldmeth CR, Emerson MJ. 2003. *Natural history of the islands of California*. Oakland, CA: University of California Press.

Shaw J, Lickey EB, Beck JT, Farmer SB, Liu W, Miller J, Siripun KC, Winder CT, Schilling EE, Small RL. 2005. The tortoise and the hare II: relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *American Journal of Botany* **92:** 142–166.

Seehausen O. 2004. Hybridization and adaptive radiation. *Trends in Ecology & Evolution* **19:**198–207.

Shaw J, Lickey EB, Schilling EE, Small RL. 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. *American Journal of Botany* **94:** 275–288.

Silvertown J. 2004. The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology* **92:** 168–173.

Silvertown J, Francisco-Ortega J, Carine M. 2005. The monophyly of island radiations: an evaluation of niche preemption and some alternative explanations. *Journal of Ecology* **93:** 653–657.

Simberloff DS. 1974. Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics* **15:** 61–182.

Slatkin M. 1985. Rare alleles as indicators of gene flow. *Evolution* **39:** 53–65.

Stebbins GL, Major J. 1965. Endemism and speciation in the California flora. *Ecological Monographs* **35:** 2–35.

Stuessy TF, Jakubowsky G, Gomez RS, Pfosser M, Schluter PM, Fer T, Sun B-Y, Kato H. 2006. Anagenetic evolution in island plants. *Journal of Biogeography* **33:** 1259–1265.

Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123:** 585–595.

Takezaki N, Nei M, Tamura K. 2010. POPTREE2: software for constructing population trees from allele frequency data and computing other population statistics with Windows interface. *Molecular Biology and Evolution* **27:** 747–752.

Thorne RF. 1969. The California islands. *Annals of the Missouri Botanical Garden* **56:** 391–408.

Traill LW, Bradshaw CJA, Brook BW. 2007. Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biological Conservation* **13:** 159–166.

Van Oosterhout C, Hutchinson W, Wills DPM, Shipley P. 2004. Micro-checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4:** 535–538.

Wallace G. 1985. *Vascular plants of the Channel Islands of southern California and Guadalupe island Baja California, Mexico*. Los Angeles: Natural History Museum of Los Angeles County.

Wallace LE, Culley TM, Weller SG, Sakai AK, Kuenzi A, Roy T, Wagner WL, Nepokroeff M. 2011. Asymmetrical gene flow in a hybrid zone of Hawaiian *Schiedea* (Caryophyllaceae) species with contrasting mating systems. *PLoS ONE* **6:** e24845.

Wallace LE, Helenurm K. 2009. Has herbivory negatively impacted genetic variability in the flora of the California Channel Islands? Insights from *Crossosoma californicum* (Crossosomataceae). *International Journal of Plant Sciences* **17:** 311–322.

Wang IJ. 2010. Recognizing the temporal distinctions between landscape genetics and phylogeography. *Molecular Ecology* **19:** 2605–2608.

Watson S. 1885. Contributions to American botany. *Proceedings of the American Academy of Arts and Sciences* **20:** 324–378.

Weissman DB, Rentz DC. 1976. Zoogeography of the grasshoppers and their relatives Orthoptera on the California Channel Islands. *Journal of Biogeography* **32:** 105–114.

White EE. 1990. Chloroplast DNA in *Pinus monticola*. *Theoretical and Applied Genetics* **79:** 119–124.

Whittaker RJ, Triantis KA, Ladle RJ. 2008. A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35:**977–994.

Whitlock MC, McCauley DE. 1999. Indirect measures of gene flow and migration: FST≠ 1/(4Nm+ 1). *Heredity* **82:** 117–125.

Wilson GA, Rannala B. 2003. Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* **16:** 1177–1191.

Yamada T, Maki M. 2012. Impact of geographical isolation on genetic differentiation in insular and mainland populations of *Weigela coraeensis* (Caprifoliaceae) on Honshu and the Izu Islands. *Journal of Biogeography* **39:** 901–917.

Yelenik SG, Levine JM. 2010a. Processes limiting native shrub recovery in exotic grasslands after non-native herbivore removal. *Restoration Ecology* **18:** 418–425.

Yelenik SG, Levine JM. 2010b. Native shrub reestablishment in exotic annual grasslands: do ecosystem processes recover? *Ecological Applications* **203:** 716–727.

Yelenik SG, Levine JM. 2011. The role of plant–soil feedbacks in driving native-species recovery. *Ecology* **92:** 66–74.

Yu Y, Harris AJ, Blair C, He X. 2015. RASP (reconstruct ancestral state in phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution* **87:** 46–49.

Zhai SN, Comes HP, Nakamura K, Yan H-F, Qiu Y-X. 2012. Late Pleistocene lineage divergence among populations of *Neolitsea sericea* (Lauraceae) across a deep sea-barrier in the Ryukyu Islands. *Journal of Biogeography* **39:** 1347–1360.

Zwickl DJ. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Unpublished D. Phil. Thesis, University of Texas at Austin.

SUPPORTING INFORMATION

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

Appendix S1. *Eriogonum* sample locations and GenBank accession numbers.
Appendix S2. Pairwise F_{ST} values and estimates of migration (N_M) calculated from nrITS data.
Appendix S3. Pairwise estimates of migration (N_M) based on F_{ST} values calculated from *LFY* and microsatellite data.
Appendix S4. *Eriogonum arborescens* and *E. giganteum* consensus trees estimated from all accessions of (a) plastid, (b) nrITS and (c) *LFY*.
Appendix S5. Relative probabilities of biogeographical range at cladogeneis and inter-region dispersal events inferred in BayArea.
Appendix S6. Plots of axes 1 and 2 of individual-centred PCoA and population-centred PCoA based on Nei's genetic distance.