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Generation and Maintenance of Diversity in an Island: A History of Fragmentation, Secondary Contact and Admixture

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ABSTRACT

Aim: To gain detailed insights into how vertebrate intraspecific diversity can be generated and maintained within volcanic islands, using genomic data.

Location: The Canary Islands of Tenerife and La Palma.

Time Period: Tissue samples were obtained in 2003. Genomic analyses were performed in 2023–25.

Taxon: The endemic gecko, *Tarentola delalandii*.

Methods: Genotyping-by-sequencing of DNA from 109 *Tarentola delalandii* from the islands of Tenerife (31 sites) and La Palma. SNPs and sequence tags were analysed to identify genomic groups from ancestry coefficients. Bayesian multicoalescent and other phylogenetic approaches allowed determination of relationships among individuals and groups, times of divergence and secondary contact. Levels of admixture were evaluated using hybrid indices, multicoalescent approaches and ancestry coefficients.

Results: Six genomic clusters were detected within Tenerife (plus one from La Palma). Within-island population divergence events beginning some 1.3–2.7 Ma ago explain diversification. Divergence time estimates were more recent than previous mtDNA-based estimates but aligned closely with estimates for other Tenerife species. Population fragmentation on the east coast appears to have been mediated by the Güimar valley mega-landslide some 0.8 Ma ago. Despite strong spatial associations, divergence of lineages to the NW (Teno) and NE (Anaga) of the Teide stratovolcano post-dated the appearance of respective Miocene and Pliocene shield volcanoes. Instead, these long-term geologically stable regions likely provided refugia during eruptions on the central shield. Multiple secondary contact of divergent populations likely occurred in the late Pleistocene. Limited introgression across contact zones has potentially maintained ancient genomic structuring. La Palma was colonized 0.3–0.8 Ma ago from a Tenerife north coast lineage.

Main Conclusions: We outline how present-day spatial genomic structuring might be created and maintained within a small island. Mega-landslides and volcanic eruptions initially fragmented populations during the Pleistocene while limited introgression following secondary contact has maintained stable associations of lineages with geographical areas.

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1 | Introduction

A substantial body of research over the last 40 years has examined population divergence within oceanic islands. Islands can offer relatively small discrete areas, often with well-characterised, independent geological histories that are ideal for examining intraspecific analyses of spatial genetic variation and the historical events that have shaped it. Historical population fragmentation driven by volcanic activity appears to have been a significant driver of present-day within-island spatial structuring (e.g., Carson and Kaneshiro 1976; Beheregaray et al. 2003; Bloor et al. 2008; Goodman et al. 2012; Moya et al. 2004; Vandergast et al. 2004) although strongly divergent selection between habitats without interruptions to gene flow has also been supported by some studies (e.g., Brown, Jin, et al. 2023; Brown, Sun, et al. 2023; de Leon et al. 2010; Recuerda et al. 2023). The historical-fragmentation-by-volcanism theory has been most strongly supported by findings of geographical distributions of parapatric mtDNA lineages and sequence divergence times that coincide with specific geological events (Gübitz et al. 2005; Opatova and Arnedo 2014; Suárez et al. 2014; Noguerales et al. 2024). Where speciation is incomplete, divergent lineages meet at secondary contact zones (O'Connell et al. 2021; Brown et al. 2025). Among vertebrates, some of the best examples have been found in lizards endemic to the Canary Islands (e.g., Thorpe and Malhotra 1996; Gübitz et al. 2000, 2005; Brown et al. 2006; Suárez et al. 2014).

The majority of within-island studies to date have used mtDNA and/or morphology (exceptions include Suárez et al. 2014; Brown et al. 2016; O'Connell et al. 2021) which, while informative, have limitations. For example, mtDNA spatial patterns can be influenced by differences in male–female dispersal between lineages (due to maternal inheritance), while lack of mtDNA recombination does not allow detection of admixed individuals. Another potential limitation of older mtDNA studies has been the use of sequence divergence as a proxy of lineage/species divergence time. This approach does not account for ancestral polymorphism and may have led to dating errors and hence incorrect biogeographical inferences. In contrast, dating methods that incorporate stochasticity in the coalescent across large numbers of loci are theoretically superior.

Key biogeographic questions remain regarding the processes that generate and maintain within-island diversification on oceanic islands. In particular, it is unclear whether large-scale geomorphological events (such as debris avalanches) or more frequent volcanic eruptive processes are the primary drivers of long-term population fragmentation; how permeable the resultant barriers to gene flow are over evolutionary timescales; and whether secondary contact occurs relatively soon after fragmentation, indicating long-term stability of within-island patterns, or relatively recently due to (for example) anthropogenic changes.

The present study aimed to examine within-island genomic variation in the Canary Island gecko, *Tarentola delalandii*. It is found on Tenerife (2034 km^2) and La Palma (708 km^2), the latter being ~85 km to the NW of Tenerife at their closest points. Three deep parapatric mtDNA lineages have previously been described corresponding to: (i) NE Tenerife, including the entire Anaga region, most of the north coast and the island of La Palma, (ii) NW Tenerife including the Teno region (this lineage occupies the smallest geographical area), (iii) most of southern Tenerife including the Adeje region (Figure 1; Gübitz et al. 2000). Gübitz et al. (2000) analysis indicated that La Palma had been colonised from the north coast of Tenerife. This colonisation must have been recent: La Palma started to emerge above sea-level about 1.7 Ma ago and so is much younger than Tenerife, which first emerged 11.6 Ma ago (Guillou et al. 2001, 2004;). The most basal split among the three *T. delalandii* mtDNA groups was estimated to have considerably predated this, occurring within Tenerife around 9–10 Ma ago, while the subsequent split between south Tenerife and Teno lineages was broadly dated at 7.6 Ma ago (Gübitz et al. 2000). The prevailing geological hypothesis at the time was that Tenerife was formed by the union of up to three independent ancient islands: Teno, Anaga and Adeje (Ancochea et al. 1990). Hence, early mtDNA results naturally led to the conclusion that divergence followed dispersal/colonisation between precursor islands. However, the geological consensus has subsequently shifted to a model in which Tenerife originated as a single, extensive central volcanic shield during the Miocene, approximately 11.9–8.9 Ma, with smaller shield volcanoes—Teno (6.4–5.1 Ma) in the northwest and Anaga (4.9–3.9 Ma) in the northeast—subsequently developing on the periphery of this central structure (Figure 1; Guillou et al. 2004). This new geological interpretation appears to invalidate the hypothesis of dispersal between ancient islands, which had been proposed as a cause of divergence within Tenerife for several fauna and flora groups (see Brown et al. 2017).

Other geological events may have shaped intraspecific evolution. One such event was the massive debris avalanche in the Güímar valley on the east coast of Tenerife: the timing (0.8 Ma ago) and location of this mega-landslide coincide with mtDNA structuring in the lizard *Gallotia galloti* (Brown et al. 2006). A

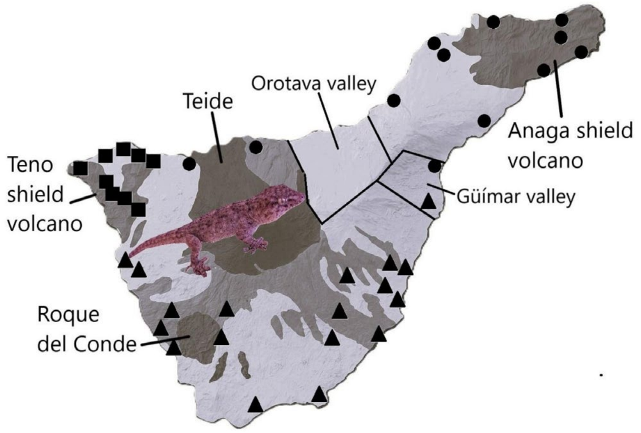

FIGURE 1 | A summary of (i) previous mtDNA findings for *T. delalandii* and (ii) geological events/features previously considered relevant to the intraspecific evolution of this and other Tenerife species. The three mtDNA lineages detected at different sample sites by Gübitz et al. (2000) are distinguished as circles, squares, and triangles. The Miocene central shield volcano was formed first and then overlain during recent periods of erosion and eruptions (such as the Teide region). Lighter shading indicates the general extent of this shield. Roque del Conde is the only remaining exposed area of the shield. The Pliocene Anaga (NE) and Miocene Teno (NW) shield volcanos that formed on the periphery of the central shield are shown, as are the locations of major flank collapses in the Güímar and La Orotava valleys.

comparable landslide in the Orotava Valley on the north coast, dated to approximately 0.5 Ma, may have also influenced among-island patterns by mediating colonisation of La Palma by the weevil *Laparocerus tessellatus* (Hunt et al. 2014; García-Olivares et al. 2017). Noguerales et al. (2024) have recently argued that mega-landslides have played a primary role in determining genomic variation in *L. tessellatus* within Tenerife.

Here, large numbers of genomic loci from *T. delalandii* were analysed in order to advance previous mtDNA inferences about its biogeographical history within Tenerife (and also its relationship with populations on the island of La Palma). Genome-wide SNPs were used to identify within-island genetic groups, assign individuals to these groups and estimate levels of admixture among them. Complementary Bayesian coalescent analyses of genome-wide sequence data yielded robust estimates of historical relationships among island lineages and their divergence times.

2 | Materials and Methods

2.1 | Sample Sites

Tenerife *T. delalandii* tail tips were available from previous fieldwork supervised by the lead author and authorised by the Cabildo Insular de Tenerife, Servicio Administrativo del Medio Ambiente (permit EIC-177/2003–2). Samples were obtained in 2003 and were stored in 100% ethanol at 4°C–7°C. The locations of the sample sites are provided in Figure 2 with latitudes and longitudes in Table S1. Three ethanol-preserved tail samples from the island of La Palma were provided by the University of Bangor (obtained between 1996 and 1999; exact capture location(s) unknown). A total of 109 tail tips were selected for genotyping-by-sequencing (GBS), amounting to 106 individuals from 31 sites on Tenerife and three individuals from La Palma.

2.2 | Genotyping-By-Sequencing

DNA extractions and Genotyping-By-Sequencing (GBS) were performed on all 109 specimens by Novogene in 2023 using the two-enzyme protocol outlined here. Genomic libraries were constructed by first digesting the DNA with the restriction enzyme MseI, followed by a second digestion with NlaIII. Digested DNA was PCR amplified, and the resultant fragments were pooled and size-selected using electrophoresis before purification. Illumina sequencing was used for paired-end 150 bp sequencing of the DNA fragments.

Adapters and barcodes were removed from the sequence reads. Paired reads were removed when fewer than 90% of bases could be read and/or when more than 50% of the single-end sequencing read contained low-quality bases.

2.3 | Alignment of Sequencing Reads and SNP Calling

Reads were aligned to a genome of the related *Tarentola boettgeri* from the neighbouring island of Gran Canaria (Brown et al. 2025) using *ipyrad* (ver. 0.9.93) (Eaton and Overcast 2020). Default values were specified in the *ipyrad* parameters file with the following exceptions (with respective rationales following in parentheses): the maximum cluster depth (maxdepth) within samples was set to 300 (avoid loss of high-coverage loci that appeared valid in preliminary runs); the minimum length of reads after adapter trim (filter_min_trim_len) was set to 130 (retain only long reads after adapter trimming to improve clustering reliability/alignment quality); the maximum number of unknown bases in the consensus (max_Ns_consens) was 0.01 (very low tolerance for ambiguous bases to greatly reduce inclusion of any low-quality consensus sequences); the maximum number (proportion) of SNPs per locus (max_SNPs_locus) was 0.25 (exclude any unusually variable loci, which could represent misassemblies, paralogs or alignment artefacts); the maximum number of indels per locus (max_Indels_locus) was 5 and the maximum heterozygous sites per locus (max_shared_Hs_locus) was 0.25 (to filter loci with excessive heterozygosity that may indicate paralogous sequences). Three bases were trimmed from the start of R1 and R2 reads to remove potential low-quality and library-derived sequence prior to clustering. A population assignment file was used to: (i) assign specimens to one of three groups (using Gübitz et al. 2000 and preliminary analyses of SNP divergence) and (ii) specify a minimum number of successfully sequenced individuals within each group for a locus to be retained, namely, 65 of 86 individuals from the south and extreme west; 4 out of 6 individuals from the south coast of north-eastern Tenerife; 13 of 17 individuals from La Palma and the north coast.

Genomic data were output in two formats: (i) SNPs—the full set of SNPs called by ipyrad was filtered using VCFtools v. 0.1.15 (Danecek et al. 2011) with the following options: min-meanDP = 5; max-meanDP = 300; max-missing = 0.85; mac =1; min-alleles = 2; max-alleles = 2 and then subsampled using the script subsetSNPs.py (https://github.com/ksil91/Scripts/blob/master/subsetSNPs.py) to obtained a thinned set of SNPs, consisting of one SNP per tag, (ii) sequence tags—a subsample of 1100 sequence tags from the set retained by ipyrad were extracted for selected single ancestry individuals.

2.4 | Genetic Clusters and Admixture

The R package LEA v2.0 (Frichot and François 2015; R v4.2, R Core Team 2022) was used to help infer the number of ancestral genetic clusters (K) and individual admixture proportions (i.e., ancestry coefficients). The number of ancestral clusters was evaluated with the sNMF algorithm by examining the cross-entropy criterion for K = 1–15 (20 replicates per K) using the thinned SNP dataset. The corresponding matrix of ancestry coefficients and their standard errors were extracted after identification of the best-supported value of K.

2.5 | Hybrid Zones on the East Coast of Tenerife

Higher sampling density on the east coast allowed investigation of introgression between distinct genetic clusters. Introgression was estimated using the R package INTROGRESS ver. 1.2.3 (Gompert and Buerkle 2010) which contains functions that estimate individual-based clines in genotypic frequency along a region of genomic admixture (i.e., hybrid zone) using multinomial

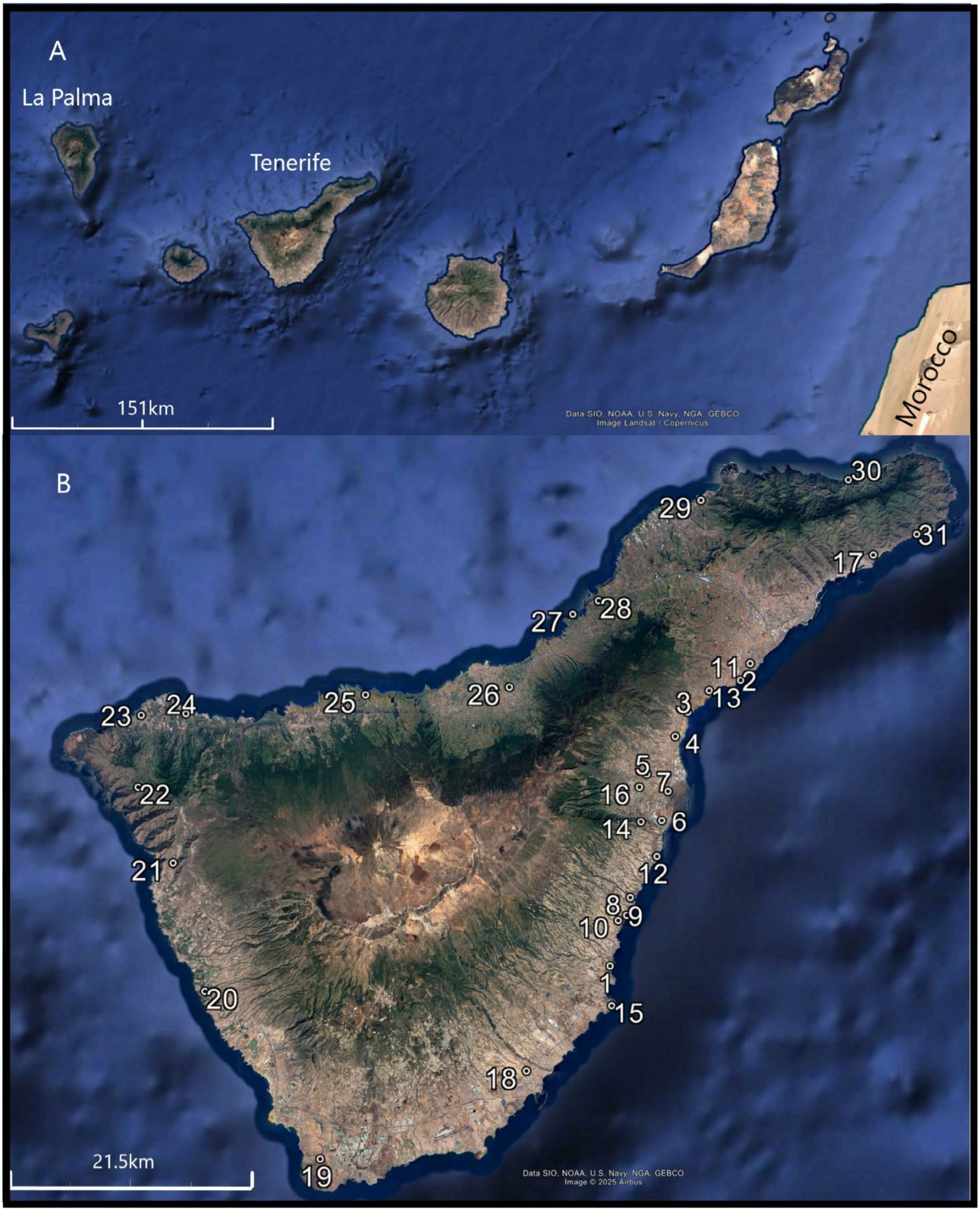

FIGURE 2 | The locations of La Palma and Tenerife within the Canary Islands (2A) and the locations of the 31 sample localities within Tenerife (2B). Details of sample sites' longitudes/latitudes and sample sizes are available in the supporting materials.

regression. It estimates hybrid indices for each individual, which are conceptually analogous to and therefore comparable with, the ancestry coefficients provided by LEA. The thinned SNP dataset was used for all analyses.

The most northerly east coast (NEC) transect extended 14.3 km from site 11 in the north to site 16 just south of the Güímar valley and also included sites 2, 3, 4, 5, 7,13 (46 individuals analysed). Individuals from the northern (site 11;

$n = 11$) and southern (site 16; $n = 3$) extremes had high single ancestry coefficients in the LEA analysis and were selected as the two distinct parental types. Hybrid indices (with upper and lower 95% confidence limits) were obtained for all individuals using the est.h function and the significance of deviations from neutrality, per-locus, tested using the INTROGRESS genomic.clines function.

The more southerly east coast (SEC) transect overlaps with the southern end of the transect described above. It extended 19.3 km from site 7 on the southern edge of the Güímar valley, southwards to site 15 and also included sites 1, 6, 8, 9, 12, 14, 16 (29 individuals analysed). The two parental types were defined as follows: (i) six individuals from sites 7 and 16 in the north and (ii) six individuals from site 15 in the south, based on high ancestry coefficients. Hybrid indices and significance testing were performed using the same methods described for the NEC transect.

Admixture, introgression probabilities and timing of secondary contact were also examined for specific individuals from the NEC and SEC transects using the program BPP v.4.7 (Yang 2015) in A00 mode (MSci model C in Flouri et al. 2020). The evolutionary model in BPP is appropriate for sequences, not SNPs, so whole sequences were extracted from the GBS data (as described under 'Genotyping-by-Sequencing'). Individuals with ancestry coefficients ≥ 95%, as determined by the LEA analysis, were selected from sites with single ancestry coefficients at the upper and lower ends of the transect as well as individuals from intermediate sites with intermediate ancestry coefficients. For the NEC transect, individuals from the northern extreme were selected from sites 11 ($n = 7$; northern group), 13 ($n = 9$; intermediate group) and sites 5 and 16 ($n = 3$; southern group) (Figure S1). For the SEC transect, northern group individuals were from sites 5 and 16 ($n = 3$), the intermediate group was from site 14 ($n = 3$) and the southern group was from sites 1 and 9 ($n = 3$) (Figure S1). In both sets of analyses the tree was fixed as a bifurcating topology with two tips representing the two single ancestry sample sites (representing northern and southern groups) with a third tip for an intermediate group created by hybridization after secondary contact (see Figure S1). The Jukes Cantor model of DNA substitution was specified and population size parameters (all θs) were integrated out to improve convergence. The prior on the divergence time of the root (τ_R) was specified from the inverse gamma distribution: InvG(4, 0.01). The prior on the introgression probability was specified from the beta distribution: $\beta(1,1)$ to provide a constant probability density function across the interval [0,1]. The first 25,000 steps of the MCMC chains were disregarded as burn-in. The remaining 1.5 million steps were sampled at 10 step intervals and log-likelihoods examined to ensure convergence. Three replicate analyses, starting from different values, were used to check convergence on the same posterior.

2.6 | Phylogenomic Inference

Estimation of the phylogenomic history was achieved using 35 selected individuals, all with single ancestry coefficients ≥ 95% in the LEA analysis (at least two individuals were selected from each genomic cluster). The evolutionary histories of these individuals/groups were inferred using several alternative methods, described below.

First, the full set of SNPs was concatenated and relationships among individuals were inferred using the maximum likelihood (ML) approach implemented in RAXML-NG v.1.2.1 (Kozlov et al. 2019). The GTGTR4 unphased diploid genotypes model with Lewis ascertainment bias correction was specified. Analyses were performed on 1000 bootstrap replicates of the data and a consensus tree calculated using the same program.

Second, a species tree was inferred, also from the full set of SNPs, using SVDquartets (Chifman and Kubatko 2014) within PAUP (ver. 4.0a) (Swofford 2003). A priori defined "species" corresponded to LEA genomic clusters. The QFM tree assembly algorithm was used, with all possible quartets evaluated. Support for branches was assessed from 1000 bootstrap replicates.

Finally, BPP v.4.7 in A01 mode was used to infer species trees using the DNA sequences from the 1100 subsampled sequenced tags (Yang 2015). To improve computational efficiency, loci with > 99 site patterns in the compressed alignment after BPP phasing were removed from the 1100 subsampled sequence tags, leaving 1041 loci for analysis. (Explanation: the haplotype phasing function in BPP enumerates and then averages over all possible heterozygote resolutions of the diploid sequence leading to high computational demands where there are large numbers of heterozygous sites). The Jukes Cantor model of sequence evolution was used. Population size parameters were integrated out. Following preliminary runs, the priors on the divergence time of the root and the population size were specified from inverse gamma distributions, i.e., tauprior = InvG($\alpha = 4$, $\beta = 0.01$) and thetaprior = InvG($\alpha = 1.2$, $\beta = 0.001$). The MCMC chains were run for 2×10^6 iterations, sampled every 20 iterations (with a burn-in period of 10,000 iterations). Three replicate analyses were performed, each from a different starting point.

2.7 | Divergence Time Estimation

The favoured species tree topology from the BPP A01 analysis was specified as the fixed tree input for a BPP A00 analysis (Yang 2015) to estimate species divergence times using sequences from the same 1041 loci, under a strict clock. The priors/run settings previously described for the A01 analysis were used. It was theoretically possible to use a diffuse 0.0–1.7 Ma node age prior to calibrate the rate of sequence divergence, using the emergence time of La Palma. However, this would lead to very broad posterior node age estimates of limited evolutionary significance. Instead, and similar to the approach proposed by Angelis and Dos Reis (2015), we calibrated the rate using a value of 4.812×10^{-4} subs/site/Ma and associated standard deviation of 8.490×10^{-5} estimated from equivalent GBS data for the congeneric, *Tarentola boettgeri* from the neighbouring islands of Gran Canaria and El Hierro (Brown et al. 2025). Although this rate originated from (less diffuse) geological calibrations on nodes, practical advantages of using a rate, rather than the La Palma node age calibration were: (i) it allowed evaluation of whether posterior estimates were consistent with well-established geological information, i.e., estimated divergence time of the La Palma should predate the appearance of La Palma, (ii) it allows estimation of the actual timing of colonisation of La Palma. Posterior divergence times (from the MCMC chain) were converted to years by dividing by values sampled from a Normal distribution specified from the *T. boettgerii* rates.

3 | Results

3.1 | GBS Reads and Alignment With Reference Genome

The ipyrad pipeline initially called 370,200 SNPs, although this was reduced to 163,068 SNPs (corresponding to a mean of 12 SNPs per sequence tag) after further filtering with VCFtools. Sampling of one SNP per tag from the latter provided a thinned dataset containing 13,500 SNPs.

3.2 | Identification of Genetic Clusters and Estimation of Ancestry Coefficents

The lowest mean cross-entropy values from LEA replicates corresponded to K = 5 and K = 6 genetic clusters (Figure S2). Nonetheless, this appeared to significantly underestimate the structure in the data. K = 7 clusters was preferred because, unlike lower values of K, specimens from the island of La Palma were then assigned to a distinct cluster which was strongly supported by previous mtDNA analyses: (Gübitz et al. 2000). Geographic distributions of ancestry coefficients are shown graphically in Figure 3. Geographical structuring of these coefficients is clear and can be broadly summarised as: (i) a Teno cluster from the NW (sites 21–24), (ii) a south Anaga cluster found only at sites 17 and 31 in the NE, (iii) a north coast cluster found right across this region apart from Teno in the NW, (iv) a widely-distributed southern cluster, found across the entire southern half of the island, (v) a Güímar valley cluster mainly occupying the area within this geological feature, (vi) a north of Güímar valley cluster (sites 2, 11, 13), (vii) the island of La Palma. It is notable that the north coast cluster, the southern Anaga cluster and—as expected—the La Palma

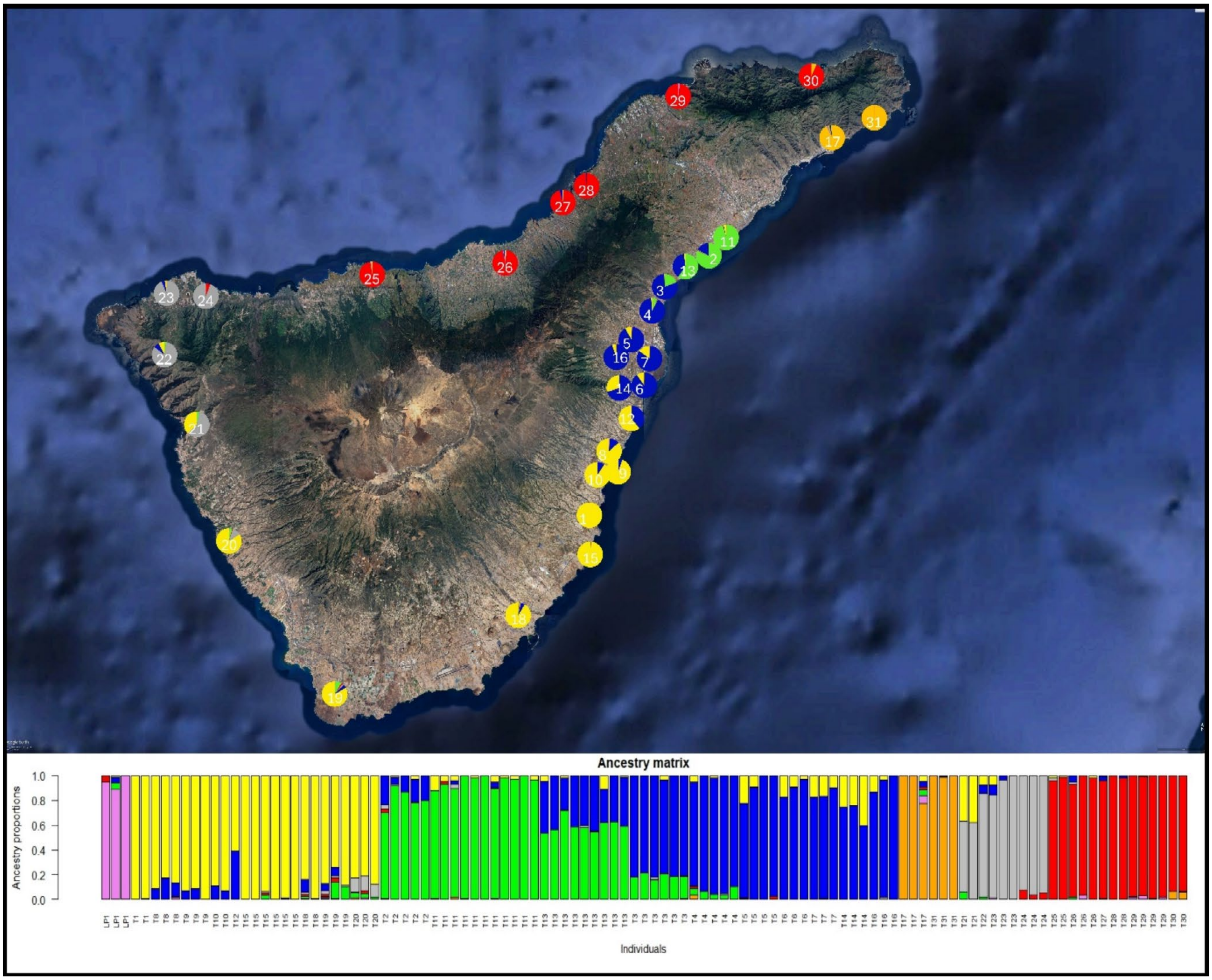

FIGURE 3 | Results of admixture analysis using LEA. Pie charts on the Tenerife satellite image are labelled with site numbers (Tenerife sites are prefixed with T and La Palma specimens with LP as in Table S1) and provide the average ancestry proportions of individuals at each site. The lower graph displays the ancestry proportions of each individual.

cluster show predominantly single ancestry coefficients for their respective groups. In other areas there appeared to be greater levels of admixture at sites where lineages meet.

3.3 | Hybrid Zones on the East Coast of Tenerife

For the INTROGRESS analyses, the SEC transect showed a gradual cline in hybrid indices from north to south (Figure 4A). The genomic.clines per-locus test of whether introgression across the genomic cline significantly deviated from the genome-wide expectation (the neutral model), revealed $p \leq 0.050$ for 851 of the 13,500 SNPs. In contrast, LEA ancestry coefficients showed a much sharper transition zone along the same transect, with only 4/29 individuals from the centre of the transect found to have significant mixed ancestry (Figure 4A). The 95% confidence intervals for the LEA ancestry coefficients (obtained by applying the critical value of the standard normal distribution to the standard errors output by the program) were also generally narrower than the 95% confidence intervals obtained for hybrid indices. Finally, the BPP analyses of the SEC transect revealed that the intermediate individuals from site 14 received more alleles from the north (Güímar valley), as opposed to the south end of the transect: corresponding posterior mean introgression probability, $\varphi = 0.651$, with a 95% highest posterior density (HPD) of 0.499–0.897. The posterior mean for timing of introgression was 0.000023 (0.000004–0.000049) (measured in expected number of mutations per site). Using the 95% HPD for evolutionary (GBS) rate in *T. boettgerii* (Brown et al. 2025), the posterior mean is equivalent to 34 Ka–64 Ka ago.

The NEC transect also showed a very gradual cline in hybrid indices with values close to 0 and 1 only being found at the ends of the transect (Figure 4B). The per-locus test of deviation from the expectation of neutral introgression across the transect revealed $p \leq 0.050$ in 309 of the 13,500 SNPs. Similar to the SEC transect, the cline in ancestry coefficients was much steeper than for hybrid indices with significantly mixed ancestry coefficients only being found at sites 3 and 13 (15 individuals) in the centre of the transect. BPP analyses of individuals on the SEC transect revealed that the intermediate individuals from site 13 received fewer alleles from the north (Güímar), relative to the south end of the transect: corresponding posterior mean introgression probability, $\varphi = 0.289$, with a 95% highest posterior density (HPD) of 0.242–0.339. The posterior mean for timing of introgression was 0.000059 mutations/site (0.000019–0.000092). Using the same calculation described for the SEC transect, this posterior mean is equivalent to 88–165 Ka ago.

3.4 | Phylogenomics and Divergence Time Estimation

The unrooted tree derived from the RAXML-NG v.1.2.1 analysis of all concatenated SNPs data revealed closest (100% bootstrap support) relationships between La Palma and the north coast individuals (Figure 5). Specimens from southern Anaga sites 31 and 17 were grouped together, as were Teno specimens from sites 23 and 24. Individuals from the S and the E coast (sites 11–18) were also grouped together (Figure 5).

The SVDquartets species tree analysis provided parallel findings. One of the two main lineages contained three groups and grouped La Palma most closely with the north coast lineage and also the south Anaga region. The other main lineage indicated early divergence of Teno populations, followed by divergence of populations just north of the Güímar valley from populations from the Güímar valley itself and southern populations (Figure 5). Bootstrap support was 100% for all internal branches.

The BPP A01 analysis (Yang 2015) inferred the same species tree to that provided by SVDquartets (Figure 6). Posterior probabilities were 1.0 for all internal branches. The subsequent BPP A00 analysis showed recent divergence between the North coast and La Palma groups (Figure 6). The 95% HPD was 0.32–0.70 Ma, which significantly post-dated the emergence of La Palma 1.7 Ma ago. The oldest split within *T. delalandii* (between the North Coast/La Palma/Anaga) lineage and the lineage consisting of populations from Teno, together with the West, South and most of the East coasts, had a 95% HPD of 1.30–2.68 Ma.

4 | Discussion

4.1 | Island Biogeography

This study supports previous proposals (Brown et al. 2006; García-Olivares et al. 2017) that ancient mega-landslides on volcanic islands have led to diversification within volcanic islands. Nonetheless, we also suggest that more frequently occurring within-island volcanic eruptions have also played a significant role. Together, these events appear to have triggered multiple within-island fragmentation episodes and generated substantial spatial genetic structure. Subsequent within-island range expansions appear to have created secondary contact zones across which gene flow is limited. Limited gene flow is indicative of considerable genomic divergence at initial contact which would originate if fragments were isolated for long periods. We show that these contact zones are unlikely to be recent, indicating long-term stability and therefore explaining how signatures of ancient fragmentation might be maintained within small islands. We also find spatial and temporal evidence consistent with the colonisation of a neighbouring island following a mega-landslide, similar to that proposed for invertebrates (García-Olivares et al. 2017).

4.2 | Historical Biogeography of *Tarentola delalandii*

Historical population fragmentation and secondary contact started within Tenerife around 2 Ma ago. The spatial associations that were detected between genomic clusters and areas with differing geological histories support the role of volcanic events on fragmentation. Secondary contact of the lineages, with limited introgression, seems to have started during the late Pleistocene, at least on the east coast. Colonisation of La Palma by a north coast Tenerife lineage occurred around 0.5 Ma ago, broadly coinciding with the timing of the La Orotava north coast mega-landslide.

An early mtDNA study revealed a similar within-Tenerife spatial pattern to that described here and similarly inferred colonisation of La Palma from the north coast (Gübitz et al. 2000). General

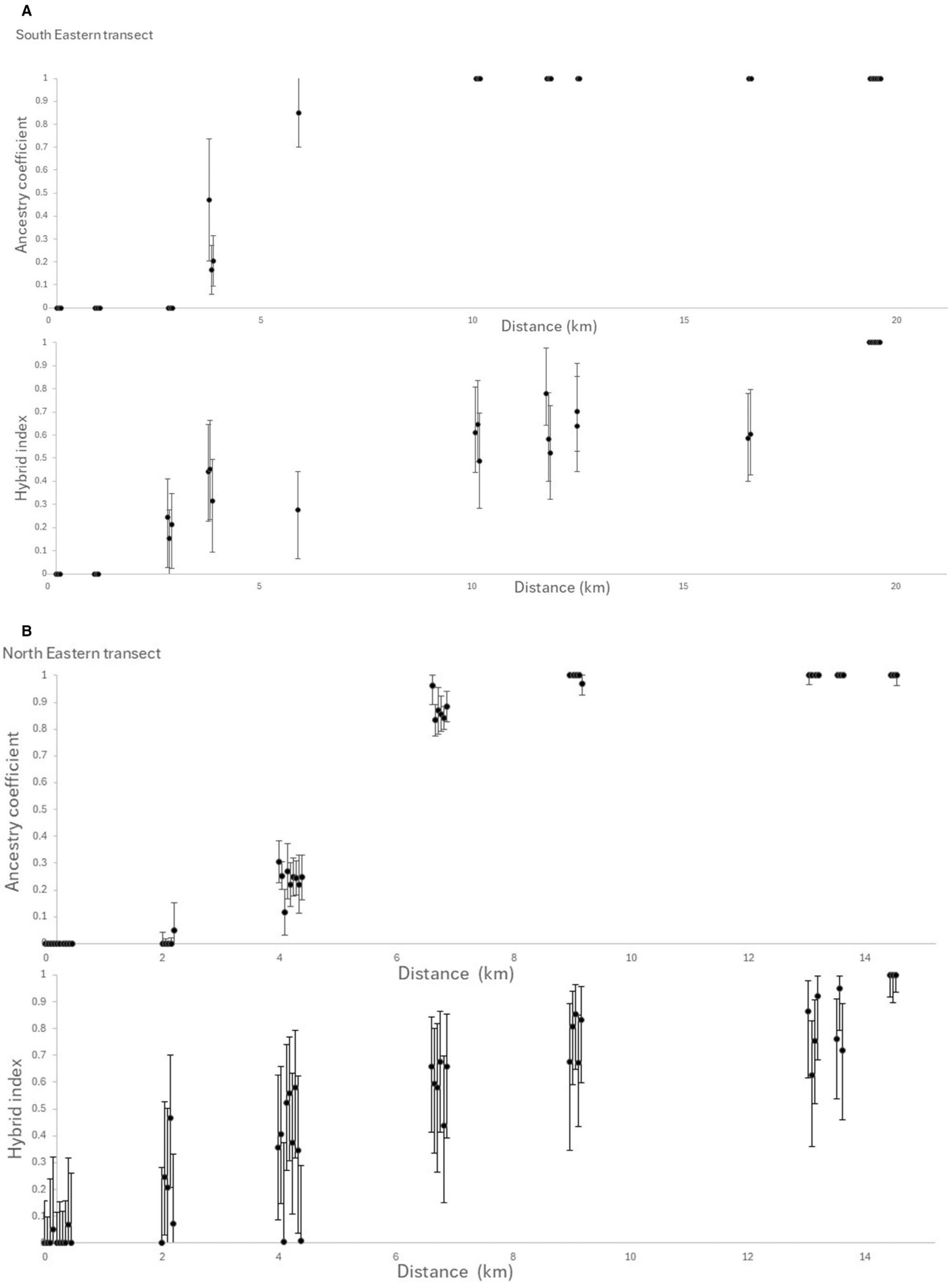

FIGURE 4 | Legend on next page.

FIGURE 4 | Estimates of admixture/introgression along two transects on the East coast using two different approaches. A. Ancestry coefficients and hybrid indices along the most southern transect (SEC), with the former showing a sharper transition than the latter. B. Ancestry coefficients and hybrid indices along the most northern east coast transect (NEC), with the former again showing a much sharper transition than the latter. Error bars are 95% confidence intervals in both cases. Jitter has been added to distance values to separate individual points.

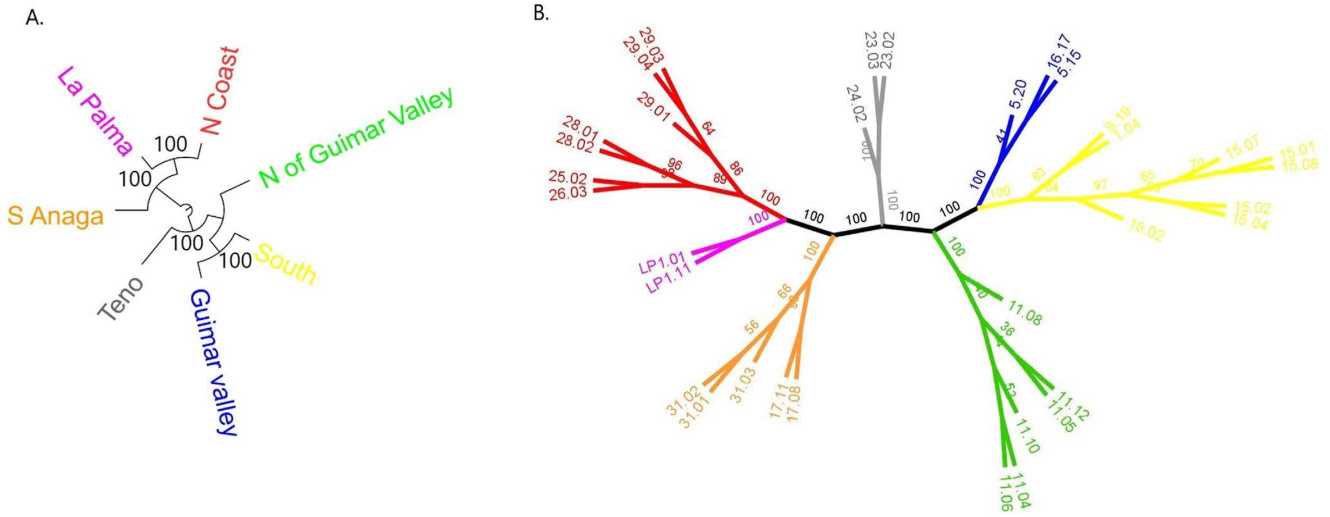

FIGURE 5 | Relationships among identified genomic clusters and individuals using SNPs from selected non-admixed individuals (colours correspond to those shown for the different clusters in Figure 3). A. Midpoint-rooted multispecies coalescent radial tree from SVDquartets analysis. B. Unrooted network from RAXML analysis of concatenated SNPs across individuals. Bootstrap values are shown on the internal edges/branches.

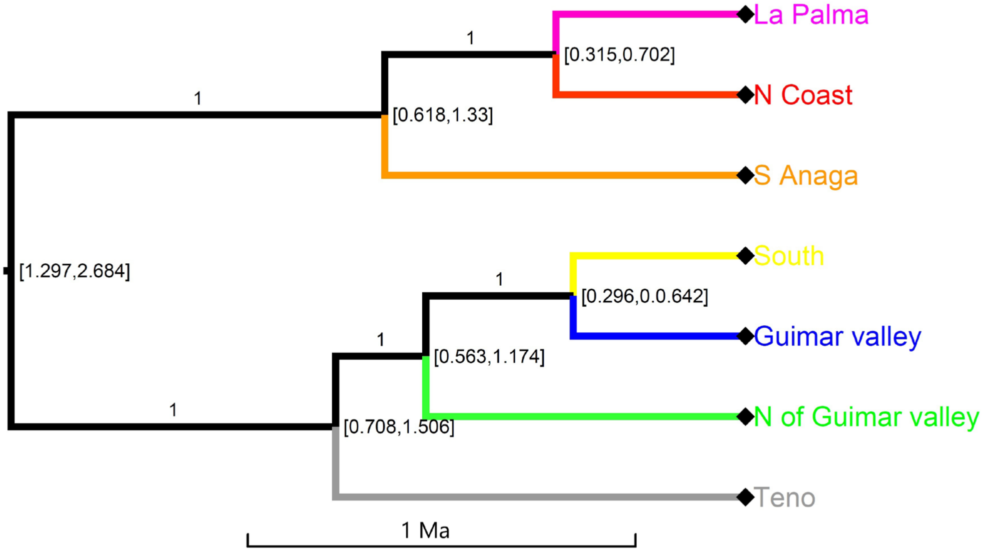

FIGURE 6 | The multicoalescent species tree topology inferred from 1041 genomic sequences using BPP in A01 mode and the divergence times subsequently estimated by BPP in A00 mode (colours of external branches/tip labels correspond to those in Figure 3). Posterior probabilities are shown above branches; posterior divergence times in Ma (95% HPDs) are shown at each node.

concordance between the distinct molecular markers strengthens support for the historical scenario presented here. Where the studies differ is that Gübitz et al. (2000) detected only 3 mtDNA groups within Tenerife *T. delalandii*: (i) Anaga and the north coast (and La Palma), (ii) Teno and (iii) all of central southern Tenerife. Here, we detected six phylogeographic groups, with the additional three groups all being associated with the east coast of the island, probably due to the greater resolution of 13.5K genomic SNPs versus ~370bp of cytochrome b mtDNA sequence.

Timings of divergence differ considerably between mtDNA and nuclear sequences: Gübitz et al. (2000) inferred the earliest divergence time as ~7.5Ma while our divergence times are much younger, starting 1.9Ma ago. Methodological reasons for this difference are discussed below. After this initial split, the earliest divergence within one of the daughter sub lineages led to a Teno NW lineage some 0.7–1.5Ma ago. A NE lineage, found in Anaga, similarly originates from the most basal node within the other sub lineage, 0.6–1.3Ma ago. It is often not possible to assign regions to ancestral nodes with any certainty (see Brown and Pestano 1998). Nonetheless, this pattern is consistent with the hypothesis that all Tenerife (and La Palma) lineages were derived from either Anaga or Teno lineages.

The finding of an ancient Teno lineage is a common pattern on Tenerife: it has been reported in the skink *Chalcides viridanus* (Brown et al. 2000, 2017), several insects (Emerson et al. 1999, 2000; Hochkirch and Görzig 2009; Moya et al. 2004; Rees et al. 2001; Salomone et al. 2002) and also plants (Puppo et al. 2014; Rincón-Barrado et al. 2024). Lineages confined to Anaga have similarly been detected by these and other studies (e.g., the lizard *Gallotia galloti*: Brown et al. 2016). Estimated divergence times of the Teno and Anaga lineages generally postdate the emergence of these volcanic shields (5.16.4–6.4 Ma and 3.9–4.9 Ma ago, respectively) by a significant amount. It is possible that Anaga-Teno populations became mutually isolated when intermediate populations on the central shield were extinguished by volcanic activity or landslides (Brown et al. 2017). The central volcano underwent a period of explosive activity from 1.8 Ma until around 169 Ka in four main cycles with associated collapse events (Carracedo et al. 2007) which fits this explanation. Our findings coincide closely with the mtDNA phylogeography of the endemic skink *Chalcides viridanus* (Brown et al. 2017), which shows similar divergence times between ancient Teno and Anaga lineages.

MtDNA analyses of the Tenerife lizard *G. galloti* revealed a divergence time and lineage distribution that showed a very close fit to the Güímar valley debris avalanche some 0.83 Ma ago (Brown et al. 2006). Here, we find an almost identical posterior mean split time (0.81 Ma) across the Güímar valley, indicating a major impact on lineage diversification within the island. Our analyses of ancestry/introgression revealed genomic clines extending from ~9 km north of the northern limit of the valley to its southern edge, placing it slightly north of the mtDNA lineage transition in *G. galloti* (Brown et al. 2006). Interestingly, a subsequent split was found across the southern rim of the same valley, around 0.44 Ma ago. The Güímar landslide appears to have been followed by partial refilling from subsequent volcanism. It might be possible to explain the slightly more complex pattern revealed by our genomic data if more detailed knowledge of this mega-landslide becomes available.

Timings of divergence and locations of secondary contact do not always coincide with known mega-landslides, indicating the effects of other events. Divergence of north coast and southern Anaga lineages ~0.9 Ma ago is one example. The Taganana mega-landslide shows a spatial correspondence, but occurred ~4.5 Ma ago and so significantly predated even the earliest within-island divergence (Troll and Carracedo 2016). In another example, the position of the Roques de Garcia landslide and the position of the earlier Teno landslide (Masson et al. 2002) coincide well with the contact zone between the Teno and the north coast lineages. However, these correspond to sublineages within the two main lineages which split long before the Roques de Garcia landslide. Furthermore there appears to be no history of mega-landslides that explain divergence of the Teno and adjacent sister group comprising the three western/southern/east coast sublineages. Lava flows from Holocene eruptions would have isolated Teno populations, surrounding them and likely isolating them in a way that closely matches the area currently occupied by the Teno lineage (Troll and Carracedo 2016). However, these eruptions greatly postdate the estimated divergence time which illustrates the difficulties of associating volcanic events with population fragmentation.

4.3 | Comparison With Previous mtDNA Divergence Times

Likely explanations for differences in divergence times between the mtDNA study of Gübitz et al. (2000) and the current study are: (i) incorrect rates of molecular evolution when converting molecular divergence to time, (ii) use of multispecies coalescent methods here, (iii) the impact of introgressive hybridization (within Tenerife) on nuclear DNA divergence (unlike non-recombining mtDNA).

MtDNA rates were less well-characterised prior to Gübitz et al. (2000), who applied a rate that assumed La Palma was colonised soon after emergence, which now appears unlikely. This is consistent with overestimation of mtDNA lineage divergence times and supports explanation (i). Consistent with explanation (ii), estimates from rate-calibrated multispecies coalescent analyses tend to be younger than estimates from sequence divergence (Tiley et al. 2020). Finally, introgressive hybridization could reduce within-island nuclear divergence, unlike mtDNA. However, if historic gene flow had reduced genomic divergence within Tenerife then a different overall tree topology might be expected, particularly within the La Palma/north coast/Anaga group, e.g., a relatively long La Palma branch would be predicted, due to lack of introgression, but this is not found. In sum, differences in divergence times between the current genomic and previous mtDNA studies are likely explained by improvements in rate calibrations and use of multispecies coalescent methods.

4.4 | Estimation of Admixture

Estimation of admixture/introgression of alleles between lineages help advance knowledge of within-island patterns. Both LEA and INTROGRESS analyses point to restrictions in gene flow across areas of the areas of secondary contact although the former indicated much steeper transitions in ancestry coefficients across the east coast hybrid zone transects (see below). Together with the multispecies coalescent analyses, the findings provide empirical evidence for a scenario in which the long-term stability of the within-island spatial patterns has been maintained by limited introgression following ancient secondary contact.

With respect to differences between the two methods, the likelihood-based regression method in INTROGRESS provides proportions of individual ancestry (hybrid index) derived from two defined parental individuals' hybrid indices, while the sparse Non-negative Matrix Factorization method in LEA is more similar to that implemented within the programs Structure (Pritchard et al. 2000) and Admixture (Alexander et al. 2009). There are some quite significant differences between the two approaches which may explain different results. First, INTROGRESS requires definition of parental genotypes for each lineage. If selected parental individuals showed greater introgression than that assumed, then hybrid indices will be underestimated for other individuals. Second, the sparse algorithm in LEA favours individual ancestry coefficients close to zero for as many clusters as possible (rather than evenly distributed ancestry coefficients across clusters). This could lead to inference of less admixture per individual and a steeper estimated hybrid zone. For instance, sNMF is less likely to assign ancestry coefficients of 0.5 to F1 hybrids, whereas INTROGRESS should correctly return a hybrid index of 0.5 (if parental genotypes are accurately defined). Further research into statistical estimation of admixture/introgression will help to establish guidelines on the appropriateness of different methods.

5 | Conclusions

Using genome-wide SNPs and a broad suite of statistical analyses, we uncover new insights into how diversity has not only been generated but also persisted within volcanic oceanic islands. Remarkably high levels of diversification can arise and persist at microgeographic scales and appear to have been first initiated by major geomorphological events, such as mega-landslides and volcanic eruptions and then maintained by reduced gene flow across secondary contact zones.

Author Contributions

Richard P. Brown designed the study. Richard P. Brown supervised and performed field sampling. Yuanting Jin commissioned genomic sequencing from the samples. Richard P. Brown analysed and interpreted the data. Richard P. Brown wrote the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data for this manuscript have been uploaded to Dryad, with DOI: 10.5061/dryad.n5tb2rc9k.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Sample sites of specimens used in the study. Specimen labels refer to the island (T [Tenerife] or LP [La Palma]), the site and the number of the individual at that site, e.g., T1.04 is specimen 4 from Tenerife sample site 1 (see Figure 1). **Figure S1:** Secondary contact model tested using the program BPP (A): Lineages A and B diverge at time τR and evolve into populations A and B. The two lineages come into contact to form the hybrid, I, at time τI. Probabilities of introgression into I at time τI are given as φA→I and φB→I. The hybrid, I, evolves into the admixed population sampled in our analysis. θs are used to denote population size parameters throughout. The two contact zones studied using this model were NEC (B) and SEC (C). Site numbers are provided along with letters in parentheses to indicate the component of the model they correspond to, e.g., 9 (B) in image C indicates site 9, which corresponds to lineage B in figure A. **Figure S2:** Cross entropies (means and 95% confidence intervals) from the LEA sNMF analysis of ancestry coefficients, for different numbers of genomic clusters (K) within the *Tarentola delalandii* SNP data.