Molecular Ecology (2008) **17**, 854–866 doi: 10.1111/j.1365-294X.2007.03575.x

Recent volcanism and mitochondrial DNA structuring in the lizard *Gallotia atlantica* from the island of Lanzarote

P. BLOOR,* S. J. KEMP† and R. P. BROWN*
**School of Biological & Earth Sciences, Liverpool John Moores University, Liverpool L3 3AF, UK,*
†School of Biological Sciences, Liverpool University, Liverpool L69 7ZD, UK

Abstract

The phylogeography of the lacertid lizard *Gallotia atlantica* from the small volcanic island of Lanzarote (Canary Islands) was analysed based on 1075 bp of mitochondrial DNA (mtDNA) sequence (partial cytochrome *b* and *ND2*) for 157 individuals from 27 sites (including three sites from neighbouring islets). Levels of sequence divergence were generally low, with the most distant haplotypes separated by only 14 mutational steps. MtDNA divergence appears to coincide with formation of the middle Pleistocene lowland that united formerly separate ancient islands to form the current island of Lanzarote, allowing rejection of a two-island model of phylogeographical structure. There was evidence of large-scale population expansion after island unification, consistent with the colonization of new areas. A nested clade phylogeographical analysis (NCPA) revealed significant phylogeographical structuring. Two-step and higher-level clades each had disjunct distributions, being found to the east and west of a common area with a north–south orientation that extends between coasts in the centre-east of the island (El Jable). Other clades were almost entirely restricted to the El Jable region alone. Bayesian Markov chain Monte Carlo analyses were used to separate ongoing gene flow from historical associations. These supported the NCPA by indicating recent (75 000–150 000 years ago) east–west vicariance across the El Jable region. Lava flows covered El Jable and other parts of the central lowland at this time and likely led to population extinctions and temporary dispersal barriers, although present-day evidence suggests some populations would have survived in small refugia. Expansion of the latter appears to explain the presence of a clade located between the eastern and western components of the disjunct clades. Direct relationships between mtDNA lineages and morphology were not found, although one of two morphological forms on the island has a disjunct distribution that is broadly concordant with east–west components of the phylogeographical pattern. This work demonstrates how recent volcanic activity can cause population fragmentation and thus shape genetic diversity on microgeographical scales.

Keywords: Canary Islands, incomplete lineage sorting, morphology, phylogeography, vicariance, volcanism

Received 27 May 2007; revision received 4 September 2007; accepted 4 September 2007

Introduction

Volcanic islands are dynamic environments. They have undergone changes in size and shape during their formation. Surfaces have been buried and reburied by new lava flows, destroying habitats and creating new ones. Such events modify the genetic structure and content of populations through repeated local extinctions, fragmentation, and range changes. The fact that populations on volcanic islands may frequently be subject to such effects means that they offer ideal models for testing evolutionary processes underlying genetic variation in relation to changing geographical area at the population level, particularly in the presence of detailed data on the chronology of geological events. A number of examples have been analysed in sufficient detail to provide insights into the processes underlying their evolution. For example, the union of formerly separate ancient islands

Correspondence: Paul Bloor, Fax: +(44) 151 2312159; E-mail: pbloor@gmail.com

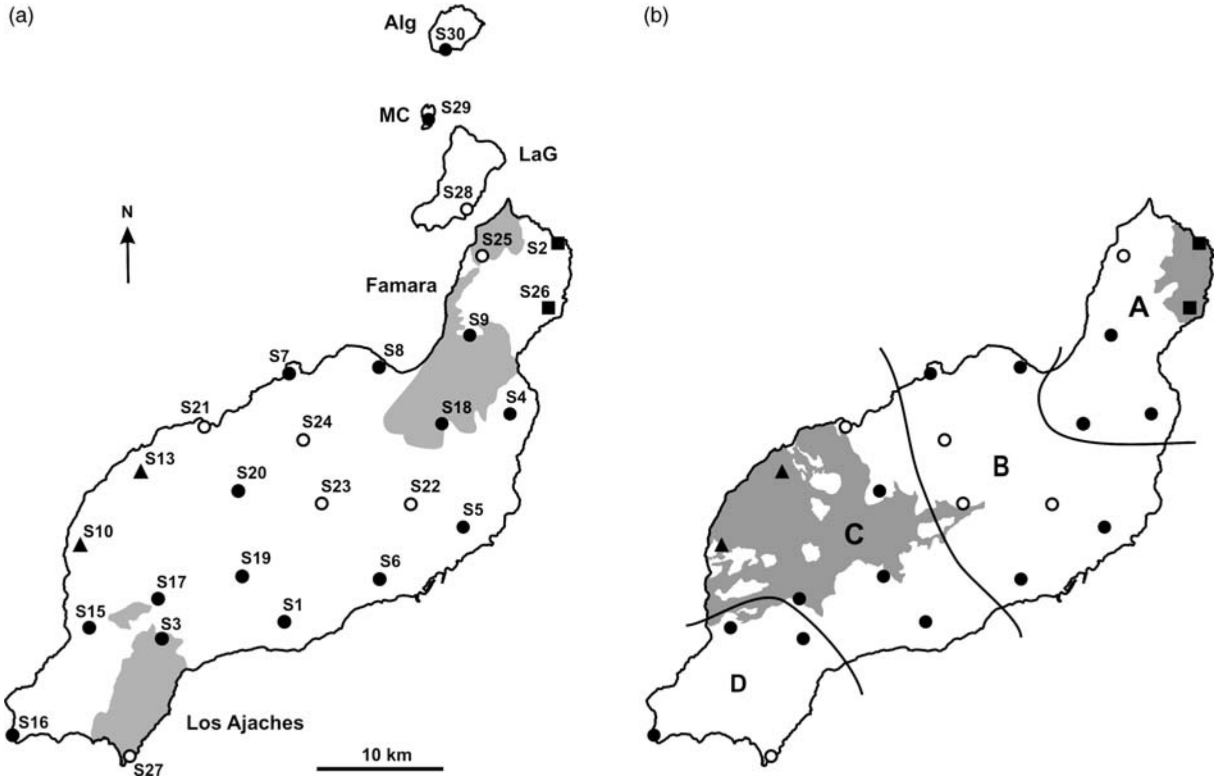

Fig. 1 (a) Sample sites on Lanzarote and northern islets (Alegranza, Alg; Montaña Clara, MC; La Graciosa, LaG). Shaded areas represent ancient deposits on Lanzarote in areas of Famara (northeast) and Los Ajaches (southwest). Sites are marked as circles, except for Malpaís de la Corona sites, which are identified by squares, and Timanfaya sites, which are identified by triangles; filled site symbols identify the 18 sites used in the previous morphological analyses (Bloor & Brown 2005). (b) Shaded areas represent main areas of *malpaís* habitat in the centre–west (Timanfaya lava field) and northeast (Malpaís de la Corona lava field) with letters identifying geographical regions referred to in the text: north (A), centre–east (El Jable) (B), centre–west (C), and south (D).

(by volcanic activity) containing differentiated populations may explain the presence of several mitochondrial DNA (mtDNA) lineages in some species (e.g. Thorpe *et al*. 1996; Gübitz *et al*. 2000), while vicariance (with local extinction) associated with lava flows may explain similar patterns in others (e.g. Carson *et al*. 1990; Pestano & Brown 1999; Malhotra & Thorpe 2000; Beheregaray *et al*. 2003; Vandergast *et al*. 2004; Gübitz *et al*. 2005). This study investigates a species in which both of these processes have potentially had an impact on within-island geographical variation.

The volcanic islands of the Canary Islands lie off the northwest coast of Africa. The two large islands of Gran Canaria and Tenerife have provided some of the clearest examples of the association between island evolution and intraspecific/intrageneric patterns of within-island diversity in several different groups (e.g. Brown *et al*. 2000, 2006; Juan *et al*. 2000; Contreras-Diaz *et al*. 2003; Moya *et al*. 2004; Emerson *et al*. 2006). Situated in the east of the archipelago are the oldest islands of Lanzarote and Fuerteventura (15–20 million years; Coello *et al*. 1992). They have received relatively little attention possibly because of lower altitudes and the consequent narrower range of habitats that prevail. Although most of the current island of Lanzarote is relatively young (middle Pleistocene), there are two areas of ancient volcanic deposits that represent separate precursor islands that had formed by about 8.7–10.2 million years ago (mya) (Coello *et al*. 1992): Los Ajaches in the southwest and Famara in the northeast (Fig. 1a). Volcanic activity joined these ancient (Miocene-Pliocene) islands approximately 0.8 mya by an extensive volcanic lowland to form a single island (Carracedo & Rodríguez-Badiola 1993). Recurrent volcanic activity over the central lowland continued until quite recently (i.e. 130 000–75 000 years ago), with the area entering a quiescent phase during or just after the last interglacial (Zazo *et al*. 1997, 2002; Dunai & Wijbrans 2000; Meco 2003). Some of the most recent basaltic lava flows on the island have left large areas of *malpaís* (or volcanic badlands) habitat in the centre–west (Timanfaya lava field) and north–east (Malpaís de la Corona lava field) of the island (Fig. 1b) (Carracedo *et al*. 1992, 2003). The existence of both *malpaís* and arid habitat creates considerable ecological variation across the island.

The complexity of the geological history of Lanzarote produces several competing (but nonmutually exclusive) hypotheses to explain phylogeographical structuring and genetic diversity for species on this island. First, the 'two-island' hypothesis assumes both precursor islands (Los Ajaches and Famara) contained differentiated populations (as a result of transmarine colonization prior to island union) that met once the ancient islands were joined by the volcanic lowland. Colonization of the newly formed central lowland and dispersal between the formerly isolated areas would have followed. This hypothesis predicts substantial divergence and phylogeographical structure in some species on Lanzarote. The same scenario could explain the presence of two or more distinct within-island lineages in each of the lizards *Gallotia galloti*, *Chalcides viridanus*, and *Tarentola delalandii* on Tenerife (Thorpe *et al*. 1996; Brown *et al*. 2000; Gübitz *et al*. 2000). Second, postcolonization expansion of a population from a single precursor island (the 'single-island' hypothesis) predicts little or no divergence, or phylogeographical structure. Third, more recent volcanic activity has likely led to local extinction and the creation of temporary dispersal barriers (i.e. lava flows) associated with the dispersal of local populations across the newly formed central lowland (the 'mid-Pleistocene vicariance' hypothesis), modifying the basic pattern of postcolonization dispersal. This hypothesis leads to the prediction of shallow divergence and weak phylogeographical structure in some species on Lanzarote.

The lacertid lizard, *Gallotia atlantica*, is endemic to the Eastern Canary islands and represents a model species to assess hypotheses of phylogeographical structuring and genetic diversity on Lanzarote. This is, in part, because it is distributed throughout the island, which allows very complete sampling of all geological areas, but more importantly because it appears to have colonized one or more of the two ancient islands prior to their union (González *et al*. 1996). Moreover, Lanzarote populations are divergent and reciprocally monophyletic with respect to Fuerteventura populations (González *et al*. 1996), so potentially confounding multiple colonization events do not appear to contribute to within-island diversity. The first aim of this paper was to test the *a priori* predictions of phylogeographical structuring and genetic diversity based on the geological history of Lanzarote for the lizard *G. atlantica*.

In addition, *G. atlantica* exhibits within-island variation in morphology (Bloor & Brown 2005). Two morphological forms have been related to the different habitat types within the island: a '*malpaís*' form from areas of *malpaís* habitat, and a non*malpaís* form from habitats elsewhere (López-Jurado & Mateo 1992). Subspecies have been assigned that broadly reflect these differences (Castroviejo *et al*. 1985; López-Jurado *et al*. 1995): *G. a. laurae* to populations on the Malpaís de la Corona lava field, with *G. a. atlantica* to populations across the rest of the island. A more detailed analysis supported the dichotomous pattern of within-island differentiation, but the association with *malpaís* areas was not as clear as previously thought (Bloor & Brown 2005), with the putative *malpaís* form having a disjunct distribution, being found on the Malpaís de la Corona lava field and small habitat 'islands' in the southern extension of the Timanfaya lava field. However, not all populations studied from the Timanfaya lava field exhibited the *malpais* form, nor are the habitat islands themselves covered by recent lava flows (although populations within them are intimately associated with areas of *malpaís* around the edge of the habitat islands), running counter to the habitat association hypothesis.

This morphological variation could be explained by historical relationships between populations (rather than being a result of current processes). Under this hypothesis, correspondence between phylogeography (i.e. distribution of distinct mtDNA lineages) and morphological variation would be predicted. Similar patterns have been found in lizards on other islands (e.g. Pestano & Brown 1999), although morphological variation is discordant with phylogeography in others (e.g. Gübitz *et al*. 2005). Alternatively, morphological variation may be the result of adaptation (e.g. Malhotra & Thorpe 1991), phenotypic plasticity (e.g. Losos *et al*. 2000), or both, in relation to the habitat types on the island. This would be supported by the finding of little mtDNA structuring, and/or otherwise incompatible morphological-mtDNA patterns. The second aim of this work was to assess the causes of morphological variation in *G. atlantica*.

These aims are addressed by comprehensive island-wide sampling, and subsequent phylogeographical and coalescent-based analyses based on sequence data from rapidly evolving regions of mtDNA. In this way, our results can provide insights into the processes underlying genetic and morphological variation on volcanic islands.

Materials and methods

Sampling and molecular data

Gallotia atlantica were sampled in August/September 1999 and October 2002 from 24 sites representing all ecological and geological regions of Lanzarote (Fig. 1a; sample details available on request). The sites included 18 of those used in the previous analysis of morphological variation (Bloor & Brown 2005) with the addition of sites S21–S25 and S27 to allow accurate description of lineage distributions across the island.

Whole genomic DNA was extracted from tail samples (stored in 95% ethanol) using standard phenol-chloroform extraction and ethanol precipitation protocols (Hillis *et al*. 1996). We designed the primers CytbGat.L (5′-CCACCGTCATCACCAACCT-3′) and CytbGat.H (5′-TACTGGCTGTCCTCCGATTC-3′) to amplify a 563-base pair (bp) fragment of the cytochrome *b* gene, and ND2Egr.L (5′-CACCCACGTGC-

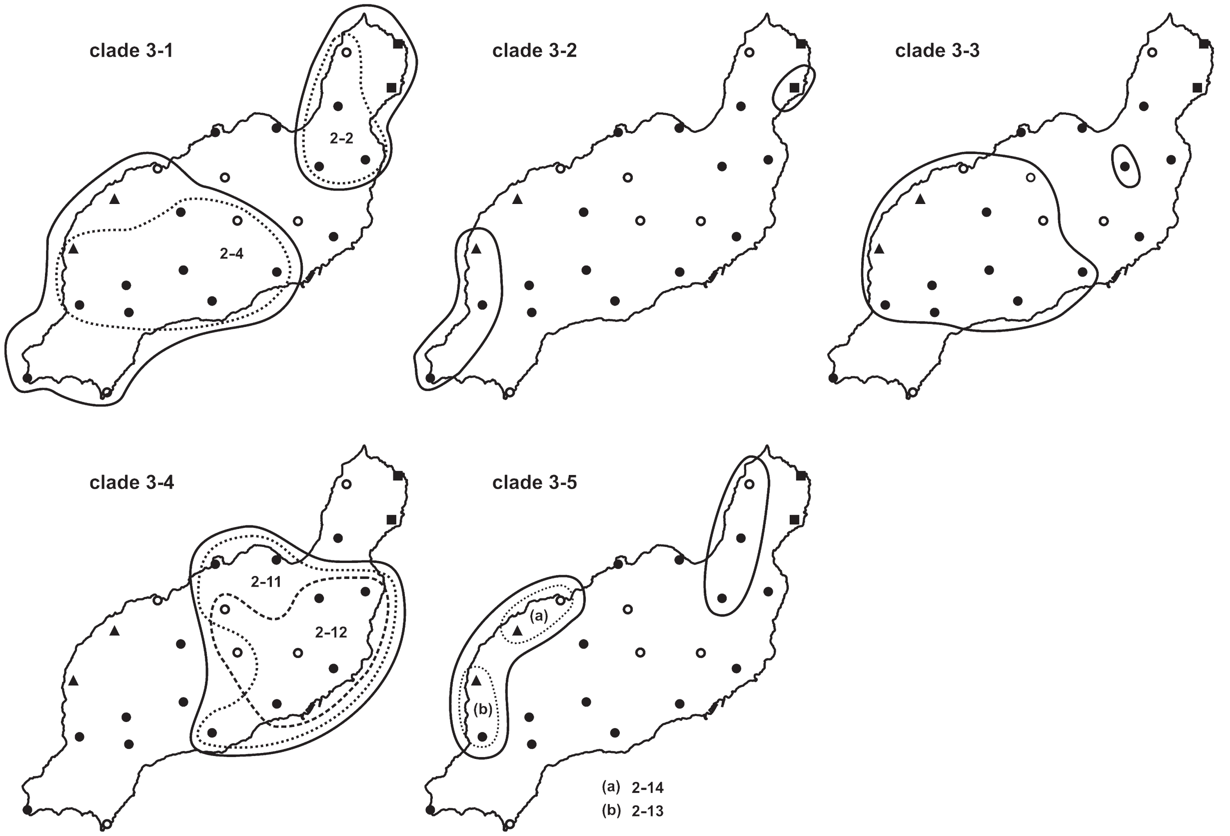

Fig. 2 The geographical distribution of main clades from cladogram on Lanzarote. The geographical distribution of three-step clades (thick lines) and two-step clades (dashed lines) from the cladogram (Fig. 2) are overlaid on the map.

CACTGAAG-3′) and ND2Egr.H (5′-AATGAGCGGGGG-TAGACCTC-3′) to amplify a 591-bp fragment of the NADH dehydrogenase subunit II (*ND2*) gene. The cytochrome *b* primers were designed from *G. atlantica* sequence (accession no. AY762378; this study), and the *ND2* primers designed from published *Eremias grammica* sequence (accession no. U71331; Macey *et al*. 1997). Polymerase chain reactions (PCR) were carried out in 30-μL reaction volumes containing 1× ABgene PCR Master Mix (2.0 mM $MgCl_2$, 0.2 mM of each dNTP, and 0.75 U *Taq* Polymerase) and 0.4 μM of each primer. Cycling conditions were 1 min at 94 °C followed by 35 cycles of 30 s at 94 °C, 30 s at 55 °C, and 30 s at 72 °C. The light strand was sequenced for six individuals from each site except for S27 for which a single individual was sequenced. Where haplotypes were represented by a single sequence in the sample, both strands were sequenced. In addition to 139 Lanzarote *G. atlantica* individuals, 18 individuals were sequenced from the same *G. atlantica* clade (González *et al*. 1996) from three islets to the north of Lanzarote (La Graciosa, Montaña Clara, and Alegranza: one site per islet, six individuals per site) and two individuals from the reciprocally monophyletic *G. atlantica* clade (González *et al*. 1996) on the island of Fuerteventura (two sites: Tesjuate and Triquivijate, one individual per site). Sequences were aligned using the program CLUSTAL W (Thompson *et al*. 1994) and fragments combined. The neutrality of mutations in the mtDNA fragments used here was tested using the McDonald–Kreitman test (McDonald & Kreitman 1991) using *G. atlantica* sequence from Fuerteventura as an 'outgroup' (program DNASP version 4.10; Rozas *et al*. 2003).

Analyses

Phylogenetic relationships among haplotypes were estimated using a network based on the 95% probability under parsimony criterion (program TCS version 1.21; Clement *et al*. 2000). In resolving ambiguous connections, we followed the usual criteria described in Crandall & Templeton (1993) and Posada & Crandall (2001). Clades were nested using standard nesting rules (Templeton *et al*. 1987; Crandall 1996), and a nested clade phylogeographical analysis computed (NCPA; Templeton *et al*. 1995) using the program GEODIS version 2.5 (Posada *et al*. 2000). This procedure revealed several clades each with east–west disjunct distributions (these will be referred to hereafter as the 'disjunct clades') separated by a clade located between them in the centre–east of the island (Fig. 2). The common area that separates the east–west components will hereafter be referred to as 'El Jable': it broadly corresponds with a region of sand deposits and sparse vegetation known locally by this name. There is no formal interpretative framework for making biological inferences from such a pattern in NCPA, so the east–west components of the disjunct clades were separated for the analysis. The present geographical analysis focused on processes underlying geographical associations within Lanzarote and so samples from the islets to the north of Lanzarote were not included. Analyses were organized into two sets (A and B), with the relative frequency of haplotypes at each site maintained for the separate analyses: (A) eastern components of disjunct clades and the centre–eastern clade (hereafter referred to as the El Jable clade) and (B) western components of disjunct clades and the El Jable clade. Although computing NCPA in this way could lead to lower statistical power (because of reduced sample sizes) it should minimize inference errors. Latitudes and longitudes of sites were obtained from large-scale maps. Inferences were based on statistically significant distances within clades and geographical distribution of clades (www.darwin.uvigo.es/download/geodisKey_11Nov05.pdf).

Divergence times between Lanzarote and Fuerteventura lineages were estimated (based on cytochrome *b* fragments only) with the aid of data on island age and emergence to provide a calibration point for the estimation of mutation rate per year per sequence (μ) for the combined sequence. The cytochrome *b* fragments were aligned with sequences from the islands of La Palma (*G. galloti* — three individuals; S. Carranza, unpublished), El Hierro and La Gomera (*G. caesaris* — three individuals from each island; S. Carranza, unpublished), *G. simonyi* (GenBank) AF101217, *G. stehlini* (three individuals; P. Bloor, unpublished), and *Psammodromus algirus* (GenBank) AF101217 (outgroup). This resulted in 343 bp of homologous sequence. The obtained tree was in agreement with the widely accepted tree topology for *Gallotia* (e.g. González *et al*. 1996). Posterior distributions of rates and node dates for this topology were generated using a Bayesian Markov chain Monte Carlo approach as implemented by the program MULTIDIVTIME (Thorne *et al*. 1998) using the approach described by Rutschmann (2004) (see also Thorne & Kishino 2002; Yang & Yoder 2003). Node constraints followed those in Brown *et al*. (2006). They were based on the emergence of El Hierro approximately 1.12 mya (Guillou *et al*. 1996) (*G. caesaris* appears to have colonized El Hierro very soon after its appearance; see Brown *et al*. 2006) and an upper limit to the colonization of La Palma constrained by its subaerial appearance 1.77 mya (Guillou *et al*. 2001 and references therein). The final run was based on 2×10^6 generations, sampled at 100 generation intervals, and with the first 1×10^5 cycles discarded as 'burn-in'.

A Bayesian Markov chain Monte Carlo method was used to distinguish between ongoing gene flow and historical association (after recent vicariance) as possible causes of the closely related east–west components of the disjunct clades: west ($n = 67$) and east ($n = 28$) (program IM, Hey & Nielsen 2004). Individuals with haplotypes corresponding to the El Jable clade (3–4) were regarded as representing admixture so were excluded from the analysis. To examine the effects of unequal sample sizes, runs were also made with a subsample of individuals from the western component. Runs using both full and reduced datasets produced similar results, so results from full analyses are presented here. Starting values for the prior distributions were empirically obtained by running IM with large parameter intervals and the Hasegawa-Kishino-Yano mutation model (Hasegawa *et al*. 1985) to ensure that posterior distributions fell completely within the prior distributions. Three final runs (model parameter values: $m_1 = 3$, $m_2 = 1.5$, $q_1 = 120$, $q_2 = 45$, $q_A = 5$, $t = 3$) were made using different starting points (random number seeds) and a single chain (5×10^7 steps, sampling interval 10 000) with the first 1 000 000 samples discarded as 'burn-in'. Assessment of autocorrelation parameter values over the course of each independent run showed that the Markov chain simulations converged on the true stationary distribution. The peaks of the resulting marginal posterior distributions were taken as estimates of the parameters (Nielsen & Wakeley 2001).

Finally, changes in population size (as expected from the colonization of the newly formed central lowland and dispersal between the formerly isolated areas) were estimated from the mismatch distribution using a generalized least-square approach (program ARLEQUIN version 3.11; Excoffier *et al*. 2005). This allowed estimation of the time since expansion, $\tau = 2ut$, where t is the time in generations and u is the mutation rate of the sequence. This distribution is typically multimodal for sequences sampled from populations at demographic equilibrium, but typically unimodal for populations having passed through a recent demographic expansion (Slatkin & Hudson 1991; Rogers & Harpending 1992) or through a range expansion with high levels of migration between adjoining populations (Ray *et al*. 2003). Using the same procedures and program, bootstrap support values for the fit of the estimated model and confidence intervals for associated parameter estimates were determined using 5000 replicates. The parameter τ was scaled to mutation rate per year by dividing the estimate by 2u (where u is the mutation rate of the entire fragment per generation) and multiplied by the length of a generation. Mismatch distributions were computed separately on samples from east and west components of the disjunct clades, on clades (as defined by NCPA) when there were statistically significant geographical associations within clades, and on the island-wide sample. To correct for homoplasy (convergent site changes or reverse mutations), the number of mutational steps along the resolved parsimony network (NCPA) between any two haplotypes was used.

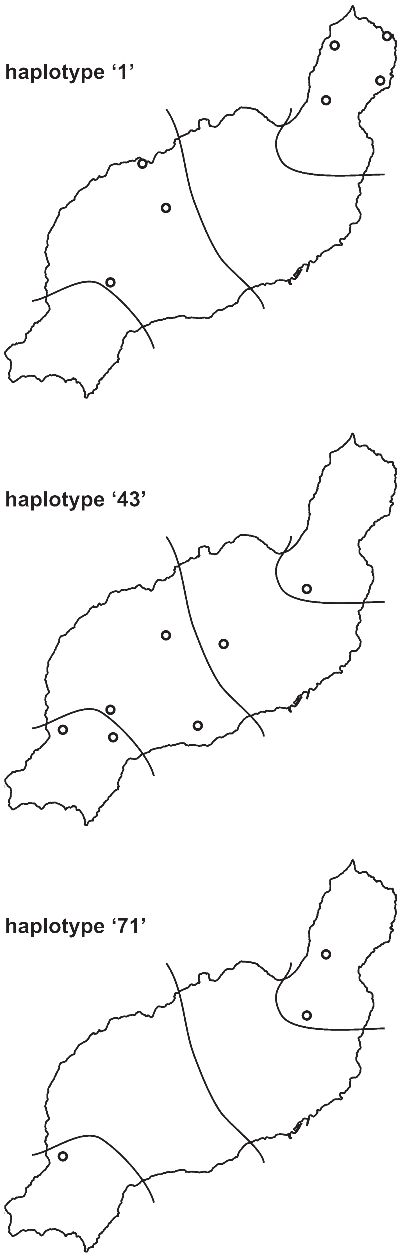

Fig. 3 The geographical distributions of haplotypes detected on either side of El Jable region.

Results

Molecular variation

A total of 1075 bp of homologous sequence was obtained for all individuals (GenBank accessions: AY762379-AY762456 and AY762457-AY762534). Eighty-seven variable sites were detected in the Lanzarote *G. atlantica* clade, with synonymous substitutions at all but 19 of these (Table S1). Seventy different haplotypes were detected among the 139 Lanzarote samples (Table S2), of which only 12 haplotypes were detected at more than one site: only haplotypes '1', '43', and '71' were detected in samples on either side of El Jable (Fig. 3). Haplotypes were connected into a single network (Fig. 4) under the 95% probability of parsimony criterion (14 steps allowed). 'Outgroup' haplotypes could not be connected under the limits of parsimony. Five three-step clades were detected (Fig. 4) (islet haplotypes were nested well within the Lanzarote haplotypes). The most divergent clades were 3–4 and 3–5 (mean and maximum uncorrected sequence divergences 0.75% and 1.40%, respectively). Clades 3–1 and 3–3 were the least divergent clades (mean and maximum uncorrected sequence divergences 0.31% and 0.74%, respectively). Mean and maximum uncorrected sequence divergences averaged over all clades were 0.56% and 1.04%, respectively. There was no evidence of selection in the sequence under study (McDonald–Kreitman test; Fisher's exact test, $P = 0.81$).

There is clear geographical structuring in *G. atlantica* within Lanzarote. Four of the main clades (3–1, 3–2, 3–3, and 3–5) are mostly or completely overlapping with east–west disjunct components, separated by a common area (El Jable) in the centre–east of the island (although the western limit of clade 3–3 is represented by a single specimen at site S18) (Fig. 2). Clade 3–4 (El Jable clade) is a centre–eastern clade. It is mostly or completely nonoverlapping with the east–west components of the disjunct clades, but some sites have representatives from both: site S1 is typically centre–western but with El Jable haplotypes (two specimens), while S18 is typically northern but with El Jable haplotypes (two specimens). The El Jable clade shows some north–south structuring with mostly overlapping subclades (clades 2–12 and 2–11). The disjunct clade 3–1 has further east–west structuring, with geographically separated subclades on both sides of the El Jable region: clade 2–4 in the south and centre–west, and clade 2–2 in the north. Together, these analyses point to a recent east–west separation of populations with close historical relationships on either side of the centre–east of the island. The long-term stability of this pattern suggests restrictions on contemporary dispersal.

A NCPA revealed statistically significant associations between haplotypes and geography in five clades representing two separate analyses (A and B; Table 1). Geographical associations in the western component (geographical regions south and centre–west) of the disjunct clades were compatible with restricted gene flow with isolation by distance (clade 3–1) and allopatric fragmentation (clade 3–5): the fragmentation event was identified between the southerly coastal clade (2–13) and northerly coastal clade (2–14) that are separated by lava flows from historical Timanfaya eruptions. In the centre–east, geographical associations supported restricted gene flow with isolation by distance (clade 3–4). The pattern of clade distributions at the 'cladogram' level

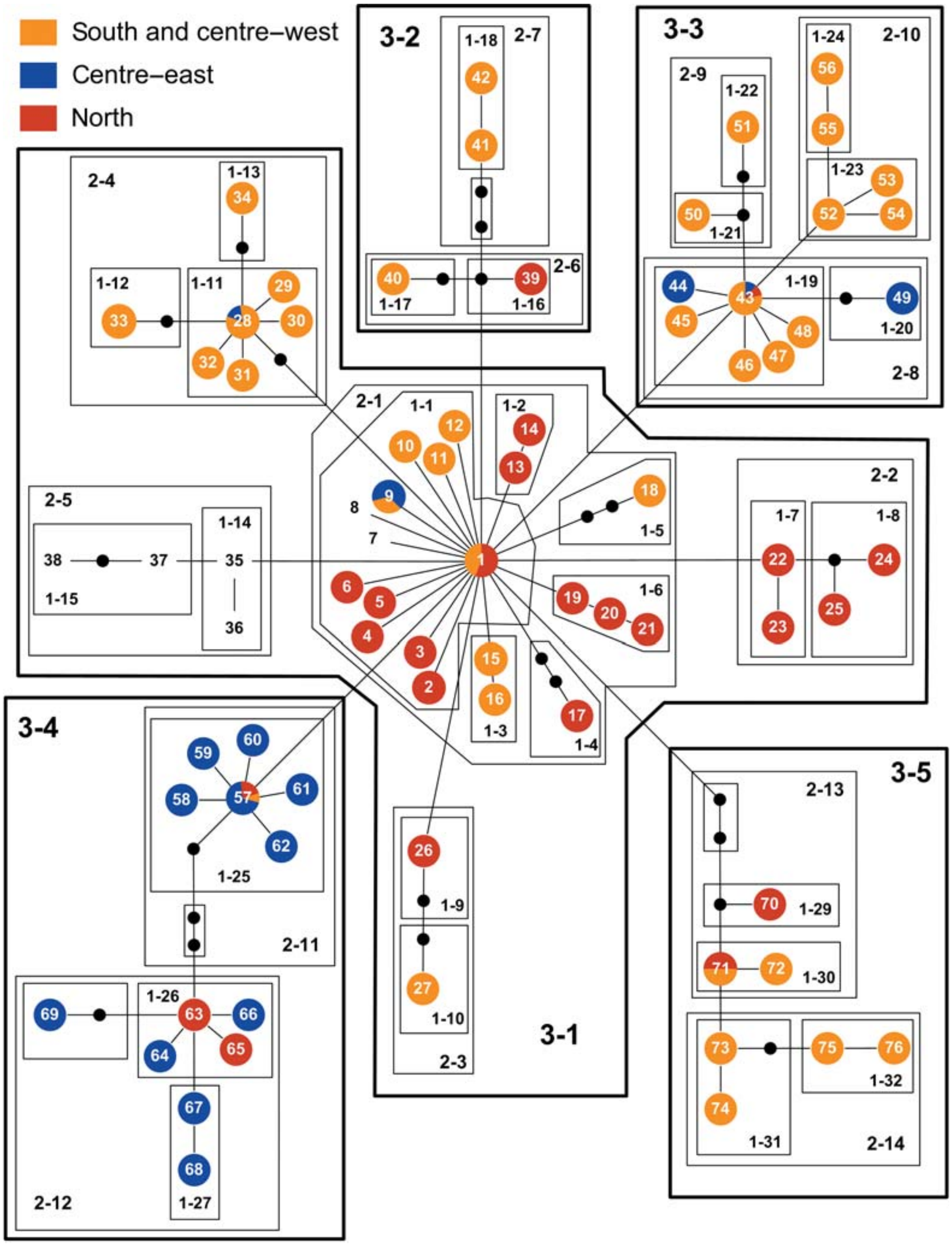

Fig. 4 Haplotype network and nested clades for the mtDNA haplotypes of *Gallotia atlantica*. Haplotypes are numbered 1–76; small filled circles indicate 'missing' or extinct haplotypes. A number identifying the nesting level, followed by a number specific to the clade, designates clades. Haplotypes are coloured according to the respective geographical regions of the three main clade distributions representing the separate eastern and western components of the disjunct clades, and the El Jable clade (see Fig. 1b); see text for details.

(analyses A and B) was compatible with past fragmentation followed by range expansion (rather than long-distance colonization possibly linked with subsequent fragmentation). No statistically significant geographical associations were detected in the eastern component of the disjunct clades.

The Bayesian time estimate for the *G. atlantica* Lanzarote/Fuerteventura node was 1.88 mya (95% confidence interval: 1.28, 3.27), which is in keeping with estimates published by other studies (e.g. Maca-Meyer *et al*. 2003; Arnold *et al*. 2007). We were concerned about the reliability of the estimate of mutation rate per year per sequence based on this point

Table 1 Inferences obtained from the nested clade phylogeographical analysis for the separate analyses when there were statistically significant ($P < 0.05$) geographical associations: eastern components of disjunct clades and El Jable clade (A) and western components of disjunct clades and El Jable clade (B); see text for details

Analysis	Clade	Inference chain	Outcome
(A)	3–1	1-2-3-4 No	Restricted gene flow with isolation by distance
	3–4	1-2-3-4 No	Restricted gene flow with isolation by distance
	3–5	1–19 No	Allopatric fragmentation
	‘Total’ cladogram	1-2-11-12-13 Yes	Past fragmentation followed by range expansion
(B)	3–4	as for analysis (A)	
	‘Total’ cladogram	1-2-11-12-13 Yes	Past fragmentation followed by range expansion

estimate. Therefore, independent rate estimates for the combined sequence were used in other analyses, using plausible lower and upper limits of 1.3% and 2.6% per million years for mtDNA sequence divergence, respectively, based on published rates for lizards (Macey *et al*. 1998, 1999; Carranza *et al*. 2004; Carranza & Arnold 2006).

The results of the IM analysis are summarized in Fig. 5. Bayesian estimates of migration rates (scaled for mutation rate) revealed strong peaks at zero for both migration rate parameters (from east to west and west to east), indicating strong restrictions on gene flow between the eastern and western components of the disjunct clades. The sharp peak in the marginal posterior probability distribution of the divergence time parameter strongly indicates a recent east–west vicariance of populations over the El Jable region. When converted to a scale of years for the given range of mutation rates, the location of the peak ($t = 1.05$) corresponds to 75 107–150 214 years (49 821, 111 536; 99 643, 223 071: 90% highest posterior density intervals for upper and lower mutation rates, respectively). The position of the peaks of the marginal posterior densities for both population size parameters suggest that present-day populations of the east–west disjunct clades have substantially larger effective populations than the ancestral population (congruent with changes in population size estimated by other methods, see later).

Mismatch distribution estimates based on Lanzarote haplotypes provide clear evidence of population growth both in the east–west components of the disjunct clade group and the island-wide sample (Fig. 6; not all mismatch distributions are shown due to the redundancy of patterns at lower clade levels). The broad similarity between the mismatch distributions for samples on either side of the El Jable region supports the idea that they belong to the same period of expansion. Although the bimodal distribution of El Jable clade (3–4) does not differ significantly from the model, the subsequent estimate of τ is likely an overestimate. Given the range of mutation rates (and form of the mismatch distribution), τ for the island-wide sample suggests expansion of a historically unsundered precursor population about 86 000–172 000 years ago.

Morphology

Individual populations are classified into one of two discrete morphological categories, referred to as *‘malpaís’ (*four sites corresponding to recent lava fields) or ‘widespread’ (populations from the rest of the island: only a small number of which are associated with recent lava fields) (Bloor & Brown 2005). Haplotypes associated with the morphological categories are distributed throughout the haplotype network (not shown). Moreover, several haplotypes were shared between morphotypes. These included the ancestral haplotype ‘1’ that was detected in seven individuals from sites on Lanzarote for which morphology had previously been recorded: three from sites assigned to the *malpaís* form (sites S2 and S26, Malpaís de la Corona lava field), and four from sites assigned to the widespread form (sites S17, S20, and S9). No haplotypes detected in more than one individual were confined to sites assigned to the *malpaís* form. This indicates a lack of association between the two morphological variants and distinct evolutionary (mtDNA) lineages.

Discussion

The phylogeographical structure in Lanzarote *G. atlantica* does not appear to be explained by predifferentiated lineages from the ancient precursor islands of Los Ajaches and Famara (the absence of separate Los Ajaches and Famara lineages either reflecting colonization failure or subsequent extinction). Not only are the ancient islands extremely old relative to the extent of divergence, but also Lanzarote lineage coalescence (i.e. average divergence from haplotype ‘1’) occurs at or after the time of island union. Moreover, Lanzarote has been exhaustively sampled, so deep lineages would be revealed by the phylogeographical analysis if they were present. Consequently, the ‘two-island’ hypothesis can be rejected in favour of the ‘single-island’ hypothesis, as it appears that *G. atlantica* lineages diverged *in situ* on Lanzarote soon after the precursor population dispersed across the newly formed central lowland joining the ancient precursor islands (see later).

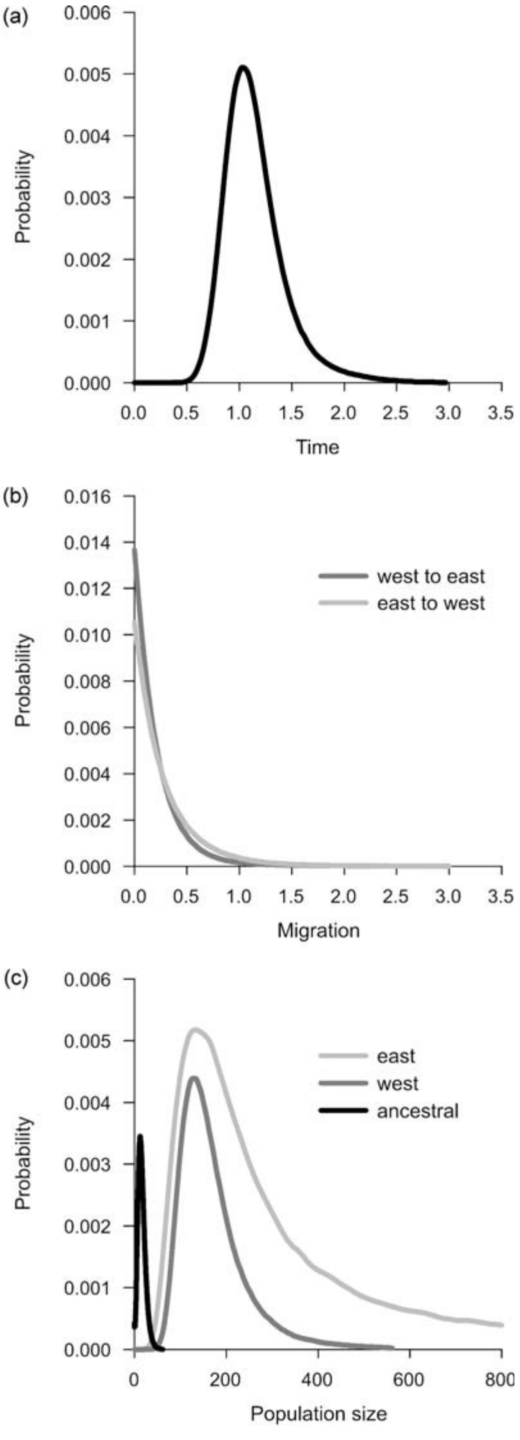

Fig. 5 Marginal posterior probability distributions for model parameters (IM) estimates (scaled by mutation rate) of time of population splitting (a), migration rate (b), and population size (c).

More detailed consideration of the results suggests that the phylogeographical structure in Lanzarote *G. atlantica* is the result of a three-stage process: (i) a single Pleistocene postcolonization expansion that occurred after the two ancient precursor islands were united by a volcanic lowland. The substantial population growth detected in the mismatch distribution for the island-wide sample is consistent with the postcolonization range expansion of a historically unsundered precursor population from one of the ancient islands into areas of the volcanic lowland about 180 000 years ago. This scenario of postcolonization expansion following the union of formerly separate islands is similar to that proposed for other species. For example, distinct lineages of both the gecko *Tarentola delalandii* (Gübitz *et al*. 2000) and the skink *Chalcides viridanus* (Brown *et al*. 2000) show evidence of population expansions after the precursor islands of Teno, Anaga, and Roque del Conde were joined to form Tenerife. (ii) Subsequent east–west vicariance across the centre–east (El Jable) of the island. Several lines of evidence support the recent (mid-Pleistocene) vicariance hypothesis. Allopatric fragmentation at the cladogram level leading to the east–west disjunct clade distributions was detected by the NCPA and supported by the IM analysis. Lavas from the last interglacial covered large areas of the centre–east of the island (Zazo *et al*. 1997, 2002; Meco 2003). Detailed information on the extent of this volcanic activity is not available but the boundaries between the El Jable clade (3–4) and the east–west components of the disjunct clades do appear to coincide quite well with the known distributions of these lava flows. We propose that this volcanic cycle caused extinctions over the immediate area, with some local populations isolated in small refugia, separating eastern and western subpopulations on either side of an inhospitable volcanic barrier and initiating their independent evolution. This is not biologically unrealistic because it is exactly what is currently observed in the Timanfaya lava field in the centre–west of the island (Bloor & Brown 2005). In addition, the divergence estimate (IM) for east–west components (75 000–150 000 years ago) fits particularly well with the ages of these lava flows, providing further support for this hypothesis. (iii) Postvicariance dispersal of surviving populations and re-establishment of a continuous distribution. Past fragmentation followed by range expansion at the 'cladogram' level (analyses A and B) was detected by the NCPA. Small isolated refugia populations from the centre–east could have subsequently expanded to form the current El Jable clades, located between the east–west components of the disjunct clades.

Although the NCPA did not provide statistical support for fragmentation within clade (3–4) from El Jable, the larger than average number of steps connecting El Jable two-step clades, together with evidence of recent expansion by other methods (mismatch distributions; Fig. 6e, f), does point to fragmentation; rather than restricted gene flow with isolation by distance, as inferred from the NCPA. The analysis presented here is a microgeographical application of NCPA and anything other than an extreme restriction on movement of individuals of formerly isolated populations

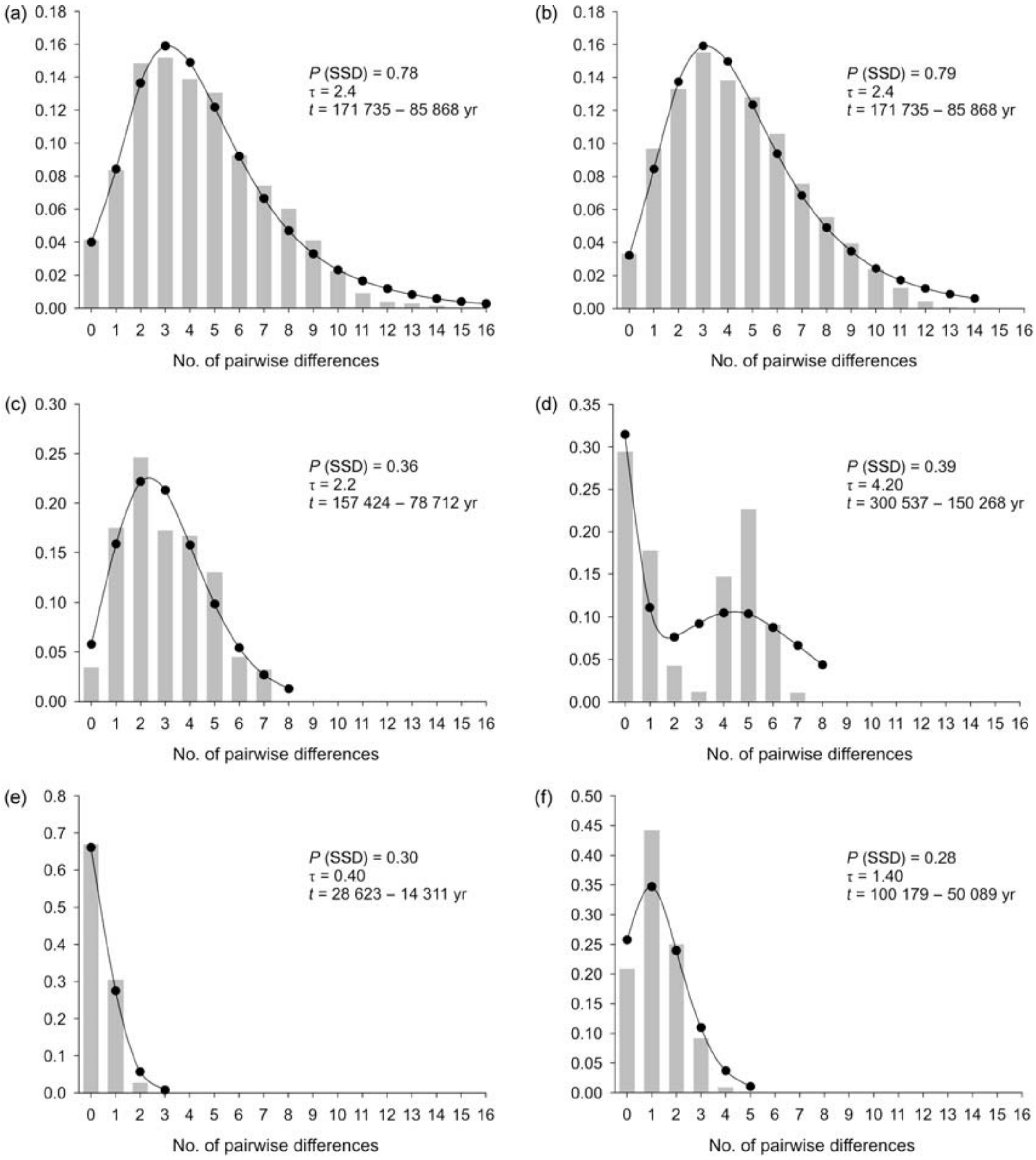

Fig. 6 Model of expansion fitted to data. The grey bars show the observed distributions of pairwise nucleotide differences. The solid lines and circles show the expected distribution: island-wide sample (a), western component of disjunct clades (b), eastern component of disjunct clades (c), El Jable clade (d), El Jable subclade 2–11 (e), El Jable subclade 2–12 (f); see text for details. Model (SSD) *P*-value and estimates of *t* scaled to mutation rate per generation and years (*t*) for the given lower and upper limits for mtDNA sequence divergence rates (see results) are given.

will lead to considerable overlap between clades within such a small area, making the inference key less able to discriminate isolation-by-distance from allopatric fragmentation. Analysis using more rapidly evolving markers combined with more detailed sampling is required to resolve the processes underlying the clade distributions in this area.

While the distinct east–west phylogeographical structure may be explained by recent within-island volcanism, there are several possible explanations for the negligible degree of admixture between the east–west components of the disjunct clades and the El Jable clade (3–4). It is possible that an important component of the pattern of clade admixture revealed here is attributable to sex-biased dispersal with female philopatry. This is an appealing explanation because it could also explain the maintenance of strong phylogeographical structure over small distances in the absence of any readily obvious present-day physical barriers to lizard dispersal. The possible effects of sex-biased dispersal on phylogeographical structure have been put forward to explain similar patterns in the gecko *Tarentola boettgeri* on the island of Gran Canaria (Gübitz *et al*. 2005), while discordant patterns of mtDNA and nuclear variation (indicative of sex-biased dispersal) in the lacertid *G. galloti* on the island of Tenerife (Thorpe & Richard 2001) and the anole *Anolis oculatus* on the island of Dominica (Stenson *et al*. 2002) are also suggestive of this. However, habitat preference would also seem plausible given that the boundaries broadly coincide with the transition from *jable* habitat (areas of sand deposits and sparse vegetation) to adjacent habitat. Alternatively, it could result from differential selection against individuals with mtDNA from the east–west components and El Jable nuclear genomes (or vice versa) because of the disruption of co-evolved interactions between them (Rand *et al*. 2004; Ellison & Burton 2006). Similar explanations have been given for negligible admixture between distinct mtDNA clades in the skink *C. sexlineatus* on Gran Canaria (Pestano & Brown 1999) and the gecko *T. delalandii* on Tenerife (Gübitz *et al*. 2000). However, lack of information from nuclear markers means that it is currently difficult to distinguish between these alternatives. In a future study, we aim to examine critically the hypothesis of sex-biased dispersal through estimation of nuclear gene flow, using microsatellite markers.

The analysis of mtDNA variation allows evaluation of the basis of the two main morphological forms within Lanzarote. The *malpaís* morphology is found in the centre–west of the island (from the southern extension of the Timanfaya lava field) and the northeast (Malpaís de la Corona lava field) (Fig. 1b), and therefore separated by the El Jable region. The hypothesis that morphological variation could reflect historical relationships between populations (rather than being a result of current processes) predicts correspondence between phylogeography (i.e. distribution of distinct mtDNA lineages) and morphological variation. Although the lack of general association between morphology and mtDNA lineages (i.e. there was not a close concordance on a site-by-site basis) allows rejection of the 'historical' hypothesis, the fact that both systems exhibit similar disjunct distributions over an intermediate area that incorporates the El Jable region is intriguing. If we assume that the coincidence of these patterns is merely a chance effect, then ecotypic differentiation (e.g. Thorpe & Malhotra 1996; Malhotra & Thorpe 2000) or phenotypic plasticity (e.g. Losos *et al*. 2001; Shine & Elphick 2001) would be inferred. However, the situation is likely to be quite complex: like the mtDNA markers, the *malpaís* morphology could have a historical (genetic) basis related to east–west vicariance over the El Jable region, but no longer shows a close concordance with the mtDNA distribution due to differences in subsequent processes, such as rates of gene flow, which could differ substantially between nuclear and mtDNA markers (e.g. García-París *et al*. 2003).

This detailed analysis demonstrates how recurrent within-island volcanism may explain phylogeographical structuring over small geographical areas within a terrestrial species with relatively low vagility. It also provides new insights into the genesis of phylogenetically deeper, clearer patterns (i.e. distinct clades with strong clade localization) found on other islands. Subsequent divergence, together with lineage extinctions, could lead to a reduced number of differentiated lineages within *G. atlantica* on Lanzarote, which would mirror the patterns found in lizards from Tenerife and Gran Canaria.

Acknowledgements

We thank the Consejería de Medio Ambiente (Cabildo Insular, Lanzarote) and the staff of the Parque Nacional de Timanfaya (particularly A. Centellas Bodas) for granting fieldwork permits and transportation, Salvador Carranza for the *Gallotia galloti*/*Gallotia caesaris* sequences, Juan Manuel Acosta for the Fuerteventura *Gallotia atlantica* samples, and José Pestano for contributions to one of the trips to Lanzarote. We would also like to thank two anonymous referees for useful suggestions on an earlier version of the manuscript and Ursula Bloor for useful discussions on the statistical analyses. Liverpool John Moores University provided funding for this research through a studentship to PB.

References

Arnold EN, Arribas O, Carranza S (2007) Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa*, **1430**, 1–86.

Beheregaray LB, Ciofi C, Geist D, Gibbs JP, Caccone A, Powell JR (2003) Genes record a prehistoric volcano eruption in the Galapagos. *Science*, **302**, 75–75.

Bloor P, Brown RP (2005) Morphological variation in *Gallotia atlantica* from the volcanic island of Lanzarote: subspecies designations and recent lava flows. *Biological Journal of the Linnean Society*, **85**, 395–406.

Brown RP, Campos-Delgado R, Pestano A (2000) Mitochondrial DNA evolution and population history of the Tenerife skink *Chalcides viridanus*. *Molecular Ecology*, **9**, 1061–1067.

Brown RP, Hoskisson PA, Welton JH, Báez M (2006) Geological history and within-island diversity: a debris avalanche and the Tenerife lizard *Gallotia galloti*. *Molecular Ecology*, **15**, 3631–3640.

Carracedo JC, Rodríguez-Badiola E, Soler V (1992) The 1730–1736 eruption of Lanzarote, Canary Islands — a long, high-magnitude basaltic fissure eruption. *Journal of Volcanology and Geothermal Research*, **53**, 239–250.

Carracedo JC, Rodríguez-Badiola E (1993) Evolución geológica y magmática de la isla de Lanzarote (Islas Canarias). *Revista de la Academia Canaria de la Ciencia*, **4**, 25–58.

Carracedo JC, Singer B, Jicha B *et al*. (2003) La erupción y el tubo volcánico del volcán Corona (Lanzarote, Islas Canarias). *Estudios Geológicos*, **59**, 277–302.

Carranza S, Arnold EN (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **38**, 531–545.

Carranza S, Arnold EN, Amat F (2004) DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? *Systematics and Biodiversity*, **2**, 57–77.

Carson HL, Lockwood JP, Craddock EM (1990) Extinction and recolonization of local populations on a growing shield volcano. *Proceedings of the National Academy of Sciences of the United States of America*, **87**, 7055–7057.

Castroviejo J, Mateo JA, Collado E (1985) Sobre la sistemática de *Gallotia atlantica* (Peters y Doria, 1882). *Doñana Acta Vertebrata (Publicación ocasional)*, 1–85.

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1659.

Coello J, Cantagrel JM, Hernan F *et al.* (1992) Evolution of the eastern volcanic ridge of the Canary Islands based on new K-Ar data. *Journal of Volcanology and Geothermal Research*, **53**, 251–274.

Contreras-Diaz HG, Moya O, Oromi P, Juan C (2003) Phylogeography of the endangered darkling beetle species of *Pimelia* endemic to Gran Canaria (Canary Islands). *Molecular Ecology*, **12**, 2131–2143.

Crandall KA (1996) Multiple interspecies transmissions of human and simian T-cell leukemia/lymphoma virus type I sequences. *Molecular Biology and Evolution*, **13**, 115–131.

Crandall KA, Templeton AR (1993) Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Genetics*, **134**, 959–969.

Dunai TJ, Wijbrans JR (2000) Long-term cosmogenic ^{3}He production rates (152 ka-1.35 Ma) from ^{40}Ar/^{39}Ar dated basalt flows at 29 degrees N latitude. *Earth and Planetary Science Letters*, **176**, 147–156.

Ellison CK, Burton RS (2006) Disruption of mitochondrial function in interpopulation hybrids of *Tigriopus californicus*. *Evolution*, **60**, 1382–1391.

Emerson BC, Forgie S, Goodacre S, Oromi P (2006) Testing phylogeographic predictions on an active volcanic island: *Brachyderes rugatus* (Coleoptera: Curculionidae) on La Palma (Canary Islands). *Molecular Ecology*, **15**, 449–458.

Excoffier L, Laval G, Schneider S (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online*, **1**, 47–50.

García-París M, Alcobendas M, Buclkey D, Wake DB (2003) Dispersal of viviparity across contact zones in Iberian populations of fire salamanders (Salamandra) inferred from discordance of genetic and morphological traits. *Evolution*, **57**, 129–143.

González P, Pinto F, Nogales M, Jiménez-Asensio J, Hernández M, Cabrera VM (1996) Phylogenetic relationships of the Canary Islands endemic lizard genus *Gallotia* (Sauria: Lacertidae), inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, **6**, 63–71.

Gübitz T, Thorpe RS, Malhotra A (2000) Phylogeography and natural selection in the Tenerife gecko *Tarentola delalandii*: testing historical and adaptive hypotheses. *Molecular Ecology*, **9**, 1213–1221.

Gübitz T, Thorpe RS, Malhotra A (2005) The dynamics of genetic and morphological variation on volcanic islands. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 751–757.

Guillou H, Carracedo JC, Duncan RA (2001) K-Ar, ^{40}Ar-^{39}Ar ages and magnetostratigraphy of Brunhes and Matuyama lava sequences from La Palma Island. *Journal of Volcanology and Geothermal Research*, **106**, 175–194.

Guillou H, Carracedo JC, Torrado FP, Rodríguez-Badiola E (1996) K-Ar ages and magnetic stratigraphy of a hotspot-induced, fast grown oceanic island: El Hierro, Canary Islands. *Journal of Volcanology and Geothermal Research*, **73**, 141–155.

Hasegawa M, Kishino H, Yano TA (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, **22**, 160–174.

Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D-persimilis*. *Genetics*, **167**, 747–760.

Hillis DM, Moritz C, Mable BK (1996) *Molecular Systematics*, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Juan C, Emerson BC, Oromi P, Hewitt GM (2000) Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology and Evolution*, **15**, 104–109.

López-Jurado LF, Mateo JA (1992) Two models of evolution in Canarian lizards based on the use of spatial resources. *Biological Journal of the Linnean Society*, **46**, 25–37.

López-Jurado LF, Mateo JA, Geniez P (1995) Los fenotipos y subespecies de *Gallotia atlantica*. *Boletín de la Asociación Herpetológica Española*, **6**, 2–6.

Losos JB, Creer DA, Glossip D *et al.* (2000) Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution*, **54**, 301–305.

Losos JB, Schoener TW, Warheit KI, Creer D (2001) Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards. *Genetica*, 112–113, 399–415.

Maca-Meyer N, Carranza S, Rando JC, Arnold EN, Cabrera VM (2003) Status and relationships of the extinct giant Canary Island lizard Gallotia goliath (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. *Biological Journal of the Linnean Society*, **80**, 659–670.

Macey JR, Larson A, Ananjeva NB, Papenfuss TJ (1997) Replication slippage may cause parallel evolution in the secondary structures of mitochondrial transfer RNAs. *Molecular Biology and Evolution*, **14**, 30–39.

Macey JR, Schulte JA, Ananjeva NB *et al.* (1998) Phylogenetic relationships among agamid lizards of the *Laudakia caucasia* species group: testing hypotheses of biogeographic fragmentation and an area cladogram for the Iranian Plateau. *Molecular Phylogenetics and Evolution*, **10**, 118–131.

Macey JR, Wang YZ, Ananjeva NB, Larson A, Papenfuss TJ (1999) Vicariant patterns of fragmentation among gekkonid lizards of the genus *Teratoscincus* produced by the Indian collision: a molecular phylogenetic perspective and an area cladogram for Central Asia. *Molecular Phylogenetics and Evolution*, **12**, 320–332.

Malhotra A, Thorpe RS (1991) Experimental detection of rapid evolutionary response in natural lizard populations. *Nature*, **353**, 347–348.

Malhotra A, Thorpe RS (2000) The dynamics of natural selection and vicariance in the Dominican anole: Patterns of within-island molecular and morphological divergence. *Evolution*, **54**, 245–258.

McDonald JH, Kreitman M (1991) Adaptive protein evolution at the Adh locus in *Drosophila*. *Nature*, **351**, 652–654.

Meco J (2003) *Paleoclimatología de Lanzarote y La Graciosa (yacimientos paleontológicos)* Cabildo de Lanzarote-Universidad de Las Palmas de Gran Canaria.

Moya O, Contreras-Diaz HG, Oromi P, Juan C (2004) Genetic structure, phylogeography and demography of two ground-beetle species endemic to the Tenerife laurel forest (Canary Islands). *Molecular Ecology*, **13**, 3153–3167.

Nielsen R, Wakeley J (2001) Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics*, **158**, 885–896.

Pestano J, Brown RP (1999) Geographical structuring of mitochondrial DNA in *Chalcides sexlineatus* within the island of Gran Canaria. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **266**, 805–812.

Posada D, Crandall KA (2001) Intraspecific gene genealogies: trees grafting into networks. *Trends in Ecology and Evolution*, **16**, 37–45.

Posada D, Crandall KA, Templeton AR (2000) GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. *Molecular Ecology*, **9**, 487–488.

Rand DM, Haney RA, Fry AJ (2004) Cytonuclear coevolution: the genomics of cooperation. *Trends in Ecology and Evolution*, **19**, 645–653.

Ray N, Currat M, Excoffier L (2003) Intra-deme molecular diversity in spatially expanding populations. *Molecular Biology and Evolution*, **20**, 76–86.

Rogers AR, Harpending H (1992) Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution*, **9**, 552–569.

Rozas J, Sanchez-DelBarrio JC, Messeguer X, Rozas R (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, **19**, 2496–2497.

Rutschmann F (2004) *Bayesian Molecular Dating Using PAML/Multidivtime. A Step-by-Step Manual*. University of Zurich, Zurich, Switzerland.

Shine R, Elphick MJ (2001) The effect of short-term weather fluctuations on temperatures inside lizard nests, and on the phenotypic traits of hatchling lizards. *Biological Journal of the Linnean Society*, **72**, 555–565.

Slatkin M, Hudson RR (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. *Genetics*, **129**, 555–562.

Stenson AG, Malhotra A, Thorpe RS (2002) Population differentiation and nuclear gene flow in the Dominican anole (*Anolis oculatus*). *Molecular Ecology*, **11**, 1679–1688.

Templeton AR, Boerwinkle E, Sing CF (1987) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping. I. Basic theory and an analysis of alcohol dehydrogenase activity in *Drosophila*. *Genetics*, **117**, 343–351.

Templeton AR, Routman E, Phillips CA (1995) Separating population structure from population history: a cladistic analysis of the geographical distribution of mitochondrial DNA haplotypes in the Tiger salamander, *Ambystoma tigrinum*. *Genetics*, **140**, 767–782.

Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W — Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, **22**, 4673–4680.

Thorne JL, Kishino H (2002) Divergence time and evolutionary rate estimation with multilocus data. *Systematic Biology*, **51**, 689–702.

Thorne JL, Kishino H, Painter IS (1998) Estimating the rate of evolution of the rate of molecular evolution. *Molecular Biology and Evolution*, **15**, 1647–1657.

Thorpe RS, Black H, Malhotra A (1996) Matrix correspondence tests on the DNA phylogeny of the Tenerife lacertid elucidate both historical causes and morphological adaptation. *Systematic Biology*, **45**, 335–343.

Thorpe RS, Malhotra A (1996) Molecular and morphological evolution within small islands. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences*, **351**, 815–822.

Thorpe RS, Richard M (2001) Evidence that ultraviolet markings are associated with patterns of molecular gene flow. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 3929–3934.

Vandergast AG, Gillespie RG, Roderick GK (2004) Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth and the potential for accelerated evolution. *Molecular Ecology*, **13**, 1729–1743.

Yang ZH, Yoder AD (2003) Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Systematic Biology*, **52**, 705–716.

Zazo C, Goy JL, Hillaire-Marcel C *et al*. (2002) Raised marine sequences of Lanzarote and Fuerteventura revisited — A reappraisal of relative sea-level changes and vertical movements in the eastern Canary Islands during the Quaternary. *Quaternary Science Reviewss*, **21**, 2019–2046.

Zazo C, Hillaire-Marcel C, Goy JL, Ghaleb B, Hoyos M (1997) Cambios del nivel del mar-clima en los últimos 250Ka (Canarias Orientales). *Boletín Geológico y Minero*, **108**, 159–169.

P. Bloor is a PhD student at Liverpool John Moores University with an interest in processes underlying population differentiation and microgeographical patterns of evolution, as well as the current factors that maintain these geographical patterns. R.P. Brown (PhD supervisor) is a reader in Animal Evolution at Liverpool John Moores University with interests in patterns and processes of intraspecific evolution, mainly using vertebrates from South-western Europe and North Africa. S.J. Kemp heads the Animal Genetics Laboratory (Liverpool University) and has interests in the application of molecular genetic techniques, particularly microsatellites, to a variety of evolutionary problems.

Supplementary material

The following supplementary material is available for this article:

Table S1 Variable sites for 76 mtDNA haplotypes based on 1075 bp of cytochrome *b* and *DN2* sequence from 157 individuals of *G. atlantica*.

Table S1 Number of *Gallotia atlantica* haplotypes detected among sites and regions on Lanzarote.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/
10.1111/j.1365-294X.2007.03575.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.