ORIGINAL ARTICLE

Evidence for mega-landslides as drivers of island colonization

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ABSTRACT

Aim How non-dispersive taxa colonize islands is generalized as being by wind, or rafting, with the implicit assumption that such events involve one (wind) or a few (rafting) individuals. However, because of the evolutionary time-scale for colonization events, the fit of individual species to a conceptual model of wind or rafting is difficult to assess. Here, we describe an alternative testable geological model for inter-island colonization that can result in larger effective founding population sizes than traditionally accepted colonization mechanisms. We then test for the fit of genetic data to this model using weevils from the *Laparocerus tessellatus* species complex.

Location Canary Islands.

Methods Using a combination of geological data for the Canary Islands, and mtDNA data from a weevil radiation within the Canary Islands, we test three species-level predictions for mega-landslides as drivers of oceanic rafting between islands and subsequent speciation: (1) colonization should involve multiple female lineages, (2) founding lineages should have a common geographical origin, consistent with a mega-landslide event, and (3) colonization direction should be consistent with ocean currents.

Results Both individual-level and population-level analyses support a mega-landslide event as the driver of colonization from the island of Tenerife to La Palma. At least four female lineages colonized La Palma from Tenerife, with the geographical range of ancestral sequences to these four lineages describing the limits of the La Orotava mega-landslide in Tenerife.

Main conclusions In the context of island biogeographical theory, mega-landslides may be an important driver of colonization, and subsequent lineage diversification. They provide a framework for hypothesis testing using genetic data from species, or closely related species, with ranges that encompass landslides and potential areas of colonization.

Keywords
biogeography, Canary Islands, equilibrium theory, invertebrate, landslide, long-distance dispersal, phylogeography, rafting

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INTRODUCTION

Our understanding of speciation within oceanic archipelagos has advanced considerably in recent decades (Warren *et al.*, 2015), in large part as a consequence of continued efforts to analyse phylogenetic data from a diversity of taxa with geographical, ecological and geological data. In contrast, there has been little investigation of the mechanisms promoting dispersal among islands within an archipelago, a process that underpins island biogeographical theory (MacArthur & Wilson, 1963, 1967). Dispersal from one island to another must be either airborne or waterborne. For invertebrate taxa, which typically comprise the dominant component of species richness on oceanic islands, airborne colonization may involve secondary transport by birds, or wind. Secondary transport by birds is likely important for ectoparasitic

invertebrate taxa, or non-ectoparasitic taxa transported through ingestion (e.g. Wada *et al.*, 2011). However, transport by ingestion is unlikely to account for more than a very small proportion of invertebrate species, and likely limited to those that feed within seeds (Gillespie *et al.*, 2012). Wind-borne colonization should be important for flighted invertebrates, but less consequential for flightless invertebrates. Unless windborne colonization involves a gravid female, a female with stored sperm, or a parthenogenetic individual, colonization would not be followed by establishment, as it is unlikely that wind-transported individuals would arrive within the geographical proximity of each other required for subsequent mating. Even allowing for the colonization of a multiply mated female, successful establishment of a wind-borne colonist could be challenging due to low genetic variation and inbreeding, although this is not always the case (e.g. see Edelaar *et al.*, 2015). In contrast to windborne dispersal, colonization by oceanic rafting may result in multiple individuals arriving, but is expected to involve a limited number of individuals of coastal or riverine affinity (Gillespie *et al.*, 2012). Thus, the conceptual model of colonization by wind or rafting is expected to result in extreme founder events, something seen as a potential driver of insular speciation (Carson & Kaneshiro, 1976; Templeton, 1980, 2008). It is also expected to be mostly relevant for flighted species, or flightless species with coastal distributions, or with freshwater connections to the coast. Colonization by non-coastal flightless species is harder to explain.

In their consideration of long-distance dispersal (i.e. from continents to archipelagos), Gillespie *et al.* (2012) point out that the ability of organisms to disperse by oceanic drift, or rafting on flotsam, is a function of the interaction of four variables: (1) ocean dynamics, (2) survival *en route*, (3) geomorphology and (4) proximity to the ocean, given that rafts are initiated from areas proximate to oceans. With regard to ocean dynamics, although they may vary through geological time, they are idiosyncratic in nature and island or archipelago specific. However, the remaining three points suggest oceanic drift or rafting may be very consequential at the inter-island scale. Regarding point (2), the comparatively short distances between islands must greatly increase survival probability, compared to the long distances that typically characterize continental source areas and isolated oceanic archipelagos. With regard to points (3) and (4), oceanic island geomorphology provides for periodic, expected and large-scale deposition of biota into the ocean, spanning large altitudinal ranges, through mega-landslide events. This has the potential to promote the synchronous rafting of individuals sampled across broad geographical areas, something that could result in much larger effective founding population sizes than traditionally accepted colonization mechanisms.

Biotic consequences of volcanic flank collapse

When volcanic edifices reach high elevations from the ocean floor, they are prone to suffer flank collapses for several reasons, principally gravitational instability, volcanic or tectonic seismicity, and dyke injections (McGuire, 2003). Areas in excess of hundreds of square kilometres can be affected, with flank collapse triggering substantial downslope movement of terrain, movements that can occur in only a few minutes at calculated velocities exceeding 100 km/h (Siebert, 1984). These mega-landslide events can generate ocean floor deposits of hundreds of square kilometres, measuring hundreds of kilometres in length, involving volumes in the order of thousands of cubic kilometres (Canals *et al.*, 2000). Such mega-landslides are not infrequent events, as revealed by terrestrial geological studies, sonar, three-dimensional bathymetry, offshore seismic analysis and even historical records (e.g. Ward & Day, 2003). There is both inland and sea floor evidence for numerous mega-landslides in the Hawaiian Islands (e.g. Moore *et al.*, 1994), Canary Islands (e.g. Carracedo *et al.*, 2009), Réunion (e.g. Oehler *et al.*, 2004), French Polynesian Islands (e.g. Clément *et al.*, 2002), Tristan da Cunha Island (e.g. Holcomb & Searle, 1991), Cape Verde Islands (e.g. Masson *et al.*, 2008) and the Lesser Antilles Islands (e.g. Samper *et al.*, 2008), among others. The most detailed long-term data on flank collapses within an archipelago comes from a 17 Myr (million years) record for the Canary Islands. Hunt *et al.* (2014) reveal that the mean recurrence of landslides across the Canary Islands over the last 17 Myr is 135 kyr (thousand years), with the last 7 Myr characterized by a similar mean recurrence of 135 kyr.

Within the Canary Islands the biggest recorded mega-landslides occurred on the island of Tenerife, with 11 documented events that affected vast areas of the island, in some cases from more than 2000 macsl (metres above current sea level) to the coast, resulting in the transfer of enormous debris deposits to the seafloor (Fig. 1, Table S1.1 in Appendix S1, Supporting Information). While many landslides have been overwritten by subsequent lava deposits, the Orotava and Güímar valleys present clear evidence, with flat floors flanked by steep scarps defining most of their perimeter (Masson *et al.*, 2002). The within island evolutionary significance of such landslides is well understood, as they have produced important habitat discontinuities implicated in divergent evolution between populations on opposing flanks (e.g. Brown *et al.*, 2006; Macías-Hernández *et al.*, 2013; Mairal *et al.*, 2015), the biogeographical relevance of which has also been recognized (Whittaker *et al.*, 2008). What is less understood is the fate of the vast biomass that was deposited into the ocean.

The landslide of La Orotava was initiated at sea level, followed by the rapid downslope movement of higher altitude terrains up to several hundred metres deep. During the subaerial phase of this process, maximum terrain destruction occurs at depth, with limited transformation of the surface, meaning that surface organic material likely remains relatively intact prior to entering the ocean. An obvious consequence of this dynamic would be the flotation of organic matter, derived from more than 100 km^2 of diverse habitat, from the coastline to altitudes exceeding 2000 macsl (Fig. 2).
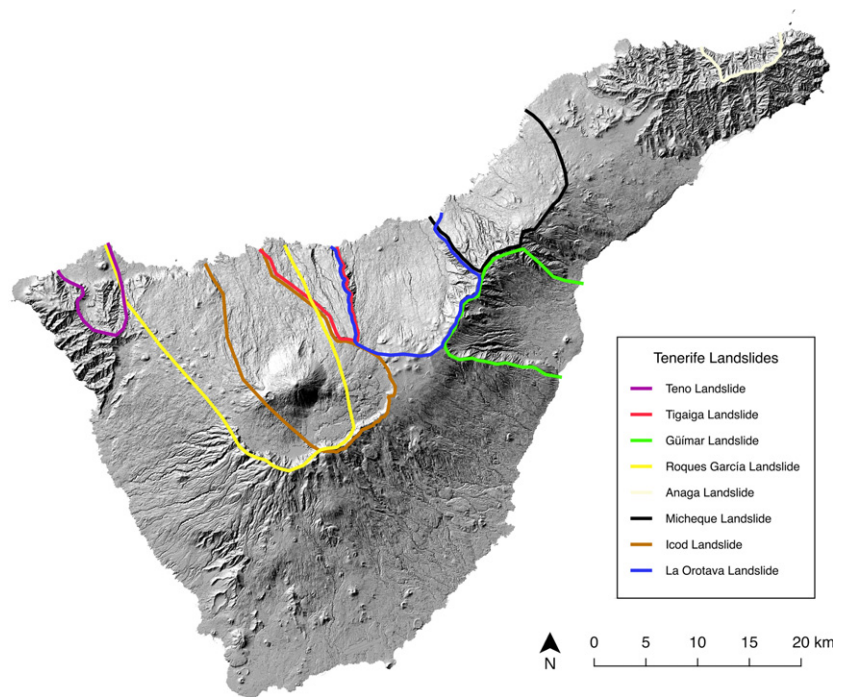
Figure 1 Mega-landslides on the island of Tenerife. Seven of the 11 documented landslides are sufficiently unaffected by subsequent volcanic activity to be able to identify their geographical limits. Landslides are colour coded according to the inset. See Table S1.1 in Appendix S1 for more details, including estimated ages.

Oceanic rafting on this scale, with favourable ocean currents, could potentially favour the synchronous transport of many individuals to neighbouring islands, providing a suitable scenario for testable predictions.

Predictions for colonization from a mega-landslide

Three testable predictions can be made for the colonization of an invertebrate species originating from a mega-landslide. The first is that colonization should have involved multiple female lineages. The second is that founding lineages should share a common geographical origin that is spatially consistent with a mega-landslide event. The third is that colonization direction should be consistent with ocean currents. Here, we evaluate evidence for these predictions using mtDNA sequence data for a complex of flightless beetle species on the Canary Islands. Among the more than 128 species within the weevil genus *Laparocerus* in the Canary Islands, the *L. tessellatus* complex comprises 11 taxonomically described species, each being a single island endemic. A recent molecular genetic analysis of the complex (Faria *et al.*, 2016) that sampled nine species (two new species were subsequently described by Machado, 2016) revealed complex relationships among individual-level patterns of nuclear and mtDNA sequence relatedness, and taxonomy (see Faria *et al.*, 2016 for details). Of relevance to the above-mentioned predictions, it was revealed that the single species from the island of La Palma was founded by individuals of related species from the islands of Tenerife and Gran Canaria (Faria *et al.*, 2016). In the case of Tenerife, two founding mtDNA haplotypes to La Palma were inferred from sequences sampled from several localities above the

steep scarps defining the perimeter of the Orotava valley. This provides a minimum estimate of two colonizing female lineages, and is suggestive of a possible role for the La Orotava mega-landslide. We evaluate this hypothesis by sampling the *L. tessellatus* complex to specifically test the prediction of multiple founding female lineages to La Palma from the region of the Orotava valley. We use DNA sequence data from the mitochondrial genome, as its characteristic female inheritance and absence of recombination allows for robust inferences of the minimum number of founding female lineages through the reconstruction of coalescent ancestry.

MATERIALS AND METHODS

Sampling and laboratory procedures

We increased previous geographical sampling for the *L. tessellatus* complex (Faria *et al.*, 2016) by visiting collecting localities for species of the *L. tessellatus* complex within the collection of AM, and several other new localities. From two to five individuals were sequenced from each locality on the island of Gran Canaria. As our focus is on the mtDNA relatedness between La Palma and Tenerife, we took an iterative approach to sequencing. Two individuals from each sampling locality were sequenced in the first instance for the mtDNA COII gene region for joint analysis with published data (Faria *et al.*, 2016). Localities in Tenerife yielding mtDNA sequences closely related to La Palma were then sequenced for a further three individuals (unless limited by sample numbers). Similarly, all localities in La Palma with mtDNA sequences closely related to sequences from Tenerife were
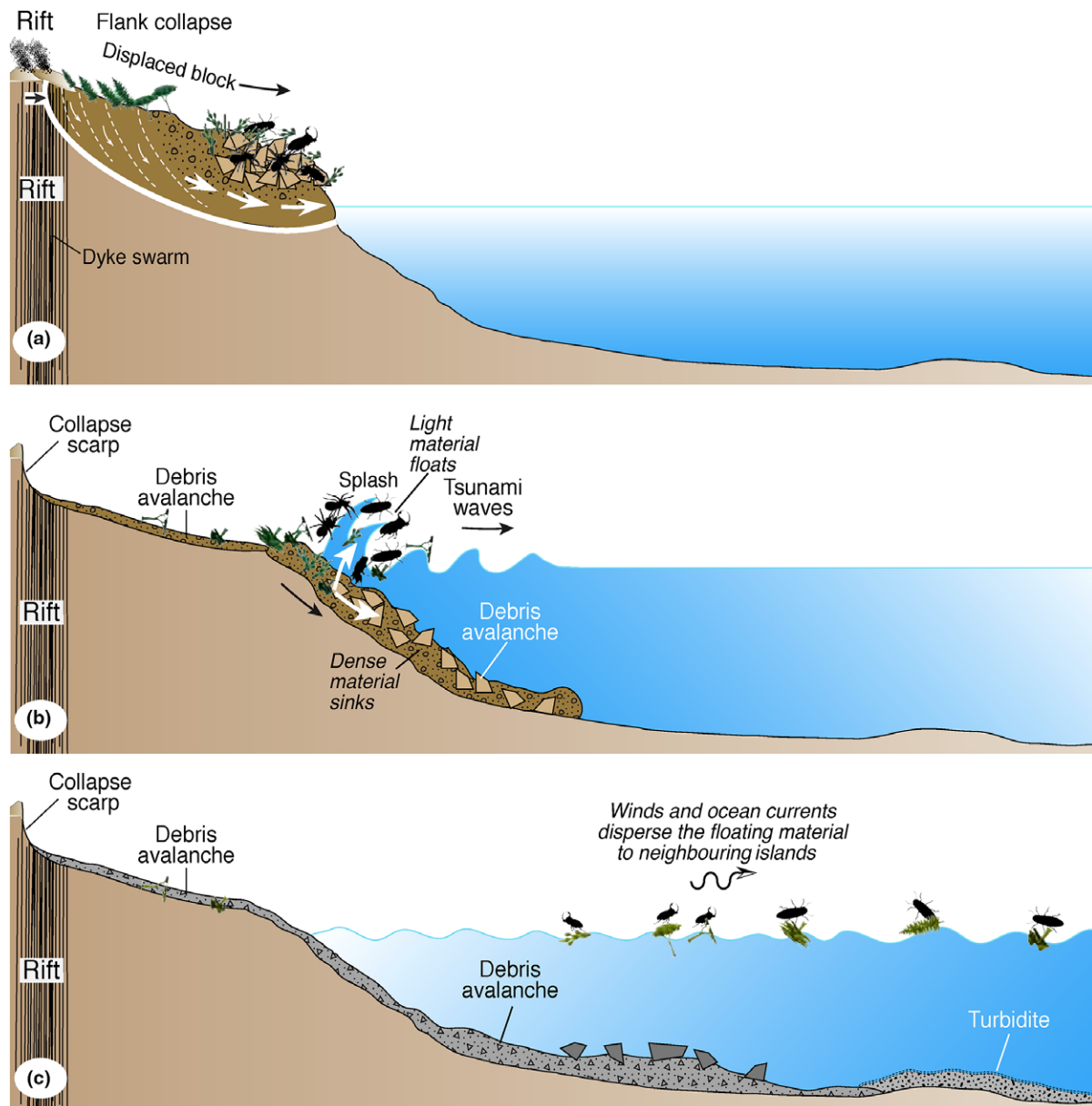
Figure 2 Biotic consequences of a volcanic flank collapse. (a) Flank collapse is initiated near sea level, causing the downslope movement of a block of terrain. The surface of the affected terrain suffers limited transformation, with maximum transformation occurring along the sliding plane. (b) A consequence of the dynamic described in A is that much of the organic surface layer may enter in the ocean practically intact, with a high proportion remaining on the surface due to its high floatability. (c) The ocean surface will contain a vast amount of organic debris derived from the surface of the landslide, including living animals and plant material. This flotsam, together with favourable winds and marine currents, would favour the dispersal of animals and plant species between islands.

sequenced for a further three individuals. Total genomic DNA was extracted from the two hind legs using a Chelex extraction protocol (Casquet *et al.*, 2012). The mitochondrial COII gene was amplified using previously described conditions (Faria *et al.*, 2016) and sequenced using the Sanger DNA sequencing service of Macrogen (www.macrogen.com). Sequences were edited with GENEIOUS R8 8.0.3 (http://geneious.com, Kearse *et al.*, 2012), aligned using MEGA 6.06 (Tamura *et al.*, 2013), and unique haplotypes were collapsed using FABox 1.41 (Villesen, 2007).

Haplotype network and Bayesian phylogenetic tree construction

Statistical parsimony was used to infer a haplotype network using POPART (Leigh & Bryant, 2015). Predictions from coalescent theory, related to the frequency and geographical distribution of haplotypes, are often applied to resolve reticulations within haplotype networks (Posada & Crandall, 2001). However, the strong geographical structuring of mtDNA variation within the *L. tessellatus* complex (Faria

et al., 2016) precludes the use of probability-based predictions derived from coalescent theory to solve reticulations (Posada & Crandall, 2001). We therefore used an alternative probability-based approach where, for each reticulation, we evaluated alternative solutions under an appropriate model of DNA sequence evolution. This was achieved by constructing a Bayesian tree from the sequence data with MrBayes 3.2.5 (Ronquist et al., 2012) under a general time reversible model of sequence evolution with a gamma correction (GTR + G) without modelling invariant sites (I), as in Faria et al. (2016). Four analyses were each run for 100 million generations using four Markov chain Monte Carlo (MCMC) chains, starting from a random tree, and sampling trees every 1000 generations. For both the network and Bayesian analyses a sequence from the closely related species L. vicinus was used as an outgroup. Stationarity and convergence of the chains were determined by graphical inspection of the values of the log-likelihoods of the four MCMC analyses; confirmation that the average standard deviation of split frequencies was below 0.01 at the completion of the analysis; and verification that effective sample size (ESS) values were above 200 using the log files in Tracer 1.6 (Rambaut, 2016). A burn-in of 25% was removed from each run, and the remaining trees were used to construct a majority-rule consensus tree.

Minimum estimation of founding female lineages

We used a rooted haplotype network of geographically referenced mtDNA sequences, to infer the dispersal history of maternal lineages (e.g. Emerson et al., 2006). The rooted mtDNA haplotype network was used to estimate the minimum number of mtDNA haplotypes that are, or have been, shared between islands, with the direction of dispersal inferred from the order of geographical state change from the root of the network (Fig. 3). This provides a minimum estimate of the number of female lineages that have dispersed between islands. One or more geographical states (islands) can be assigned to each sampled haplotype, and on the basis of these known states, one can infer the geographical states of missing (extinct or unsampled) haplotypes within the network. We inferred haplotype sharing (female dispersal) either (1) directly, when a sampled haplotype had two geographical states (Fig. 3a), or (2) indirectly, when the geographical state changed between an ancestral and descendent haplotype (Fig. 3b-f).

Analyses of population structure

We defined three geographical regions based upon the relatedness of mtDNA haplotypes between La Palma and Tenerife. The first region consists of all sites on La Palma sampled for mtDNA lineages derived from Tenerife. The second region is a polygon describing the minimum geographical range of mtDNA haplotypes and their descendants from Tenerife that are ancestral to La Palma haplotypes. To construct the polygon we applied an iterative approach, using the minimum convex polygon method (Mohr, 1947). In a first iteration a polygon describing the geographical range of this group of haplotypes was constructed. Subsequent iterations removed haplotypes from populations at the periphery of the polygon if they were also present within interior population, until no more haplotypes could be removed. The third region comprises the remaining sampling sites on Tenerife that fall outside the polygon.

To test whether the distribution of mtDNA genetic diversity reveals a phylogeographical pattern within the L. tessellatus complex distributed across the three regions, genetic differentiation among populations was estimated using both F_{ST} (genetic distance among haplotypes is unweighted) and N_{ST} (genetic distance among haplotypes is weighted). When mutation rate exceeds dispersal rate, haplotypes within regions will be more closely related than haplotypes compared among regions (Pons & Petit, 1996). Under these conditions, N_{ST} will exceed F_{ST}, indicating a greater role of mutation and the phylogeographical structuring of genetic variation over evolutionary time-scales, compared to the structuring of genetic variation by gene flow and genetic drift over ecological time-scales. To test whether N_{ST} was significantly higher than F_{ST}, a randomization procedure permuting haplotype assignation in the matrix of genetic distances among haplotypes was performed and repeated 10,000 times in SPaGeDi 1.4b (Hardy & Vekemans, 2002).

RESULTS

Haplotype network and Bayesian phylogenetic tree

Forty-seven sites were sampled in Tenerife, 32 in La Palma and 21 in Gran Canaria (Fig. 4, Table S2.2 in Appendix S2). A total of 255 new individuals were sequenced, yielding 394 DNA sequences together with previously published sequences (Faria et al., 2016). DNA sequences were collapsed to 195 unique haplotypes, characterized by 164 polymorphic sites across 633 bp, 127 of which were parsimony informative. A single haplotype network was obtained from the statistical parsimony analysis, with a total of 44 reticulations, of which all but two were solved with the Bayesian phylogenetic reconstruction (Fig. S2.1 in Appendix S2). The resolved network (Fig. 5) thus presents comparable geographical clusters of sequences, branching relationships among them, and root location, as those obtained in the Bayesian phylogenetic analysis (Fig. S2.1 in Appendix S2).

Number and origin of founding female lineages from Tenerife to La Palma

The rooted haplotype network reveals that the mtDNA variation in the L. tessellatus complex across the four islands has involved the establishment of at least 11 female lineages by inter-island colonization (Fig. 5). Our sampling reveals a total of six colonizing haplotypes to the island of La Palma, doubling a previous estimate (Faria et al., 2016), of which
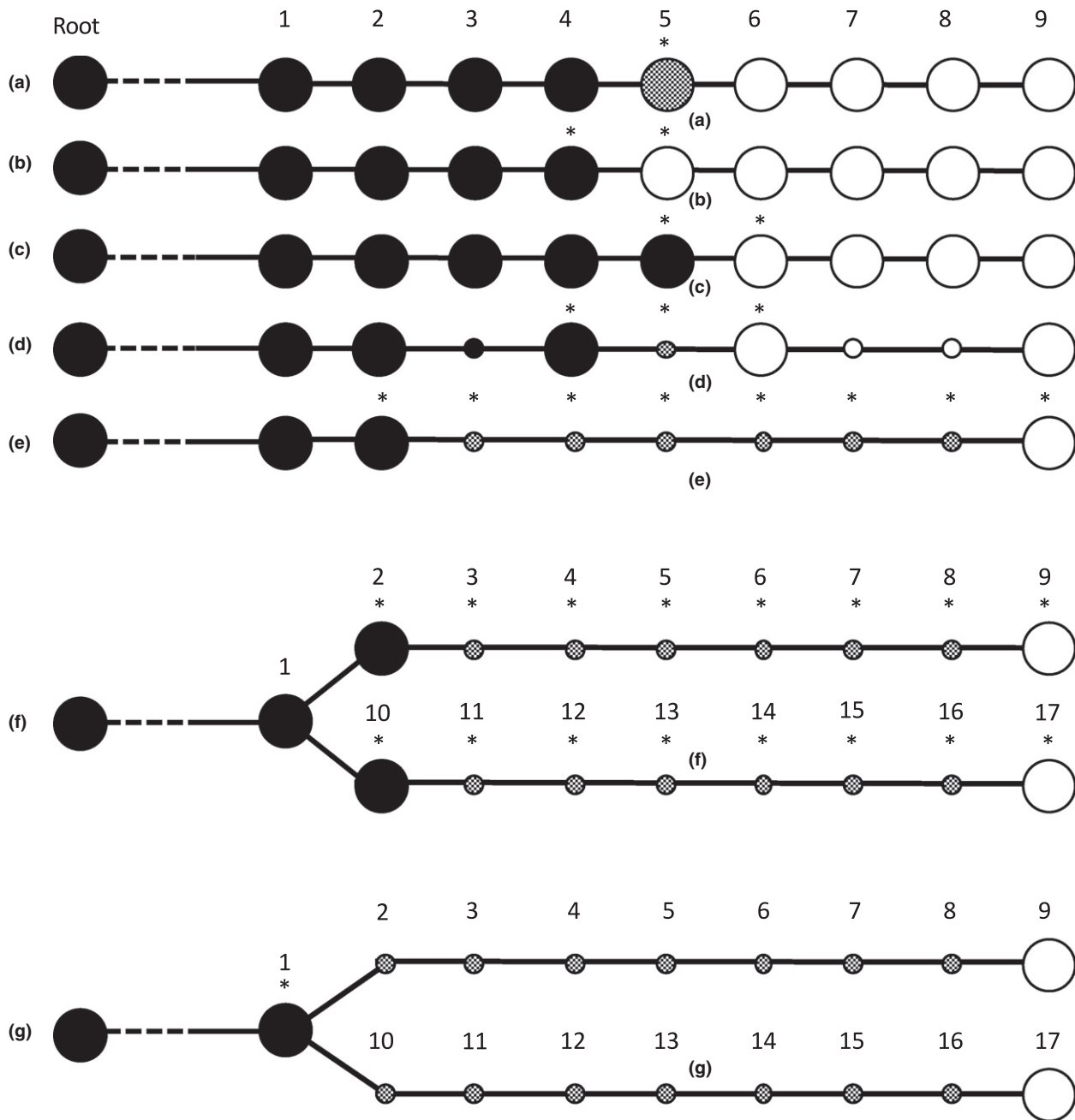
Figure 3 Inferring sets of potential colonist (geographically shared) haplotypes, and the minimum number of colonizing haplotypes. Haplotypes from an ancestral island (X) are represented as black filled circles. Haplotypes from a colonized island (Y) are represented as white filled circles. Haplotypes found on both X and Y are shown in hatching. Large circles represent sampled haplotypes. Small circles represent missing (extinct or unsampled) haplotypes, whose *potential* geographical states are inferred based on the known geographical states of immediately ancestral and descendent sampled haplotypes. For each of the scenarios A-G, asterisks indicate the set of haplotypes from which a minimum of one haplotype is inferred to have colonized from X to Y. (a) represents no haplotype extinction and sampling of all haplotypes, while B-E represent the same scenario but with some extinct or unsampled haplotypes, and F-G represent alternative scenarios with coalescence. (a) 5 is identified as the colonizing haplotype as it is shared across both islands. (b) Either 4 or 5 is the colonizing haplotype: 4 colonized Y and is unsampled or extinct on Y, or 5 colonized Y and is unsampled or extinct on X. (c) Either 5 or 6 is the colonizing haplotype: 5 colonized Y and is unsampled or extinct on Y, or 6 colonized Y and is unsampled or extinct on X. (d) Either 4, 5 or 6 is the colonizing haplotype: 4 colonized Y and is unsampled or extinct on Y, or 5 colonized Y and is unsampled or extinct on both islands, or 6 colonized Y and is unsampled or extinct on X. (e) Any of haplotypes 2–9 may have colonized from X to Y: 2 colonized Y and is unsampled or extinct on B, or one of haplotypes 3-8 colonized Y and is unsampled or extinct on both islands, or 9 colonized Y and is unsampled or extinct on X. (f) At least two colonizing haplotypes are inferred, due to the sampling of haplotypes 2 and 10 on X, with a minimum of one shared haplotype between haplotypes 2–9, and the other between 10–17. (g) Similar to F, but unsampled or extinct haplotypes 2 and 10 result in a minimum inference of 1 colonizing haplotype.

two are derived from Gran Canaria, with the remaining four derived from Tenerife. Twenty mtDNA haplotypes from Tenerife were identified either as ancestral to La Palma (2), or derived from ancestral haplotypes (18) by no more than four mutations (Fig. 5) and were sampled from 18 of the 47 sampling sites. For ease of understanding we refer to these as TF-LP haplotypes. The mean divergence between the 18 derived TF-LP haplotypes and the most closely related sampled or unsampled ancestral haplotype was one mutation. A polygon describing the minimum geographical range of the 20 TF-LP haplotypes was arrived at after four iterations, and included a total of 18 sampling sites, 14 of which contain TF-LP haplotypes, which broadly describes the Orotava valley (Fig. 4). All but 2 of the 18 sites are above the steep escarpments or within the Orotava valley, with the remaining two sites on the geographically proximate southern slope of the Güímar valley. The 18 sampling sites within the polygon were sampled for a total of 80 individuals, of which 49 presented a TF-LP haplotype, with the remaining 31 presenting one of the 18 other haplotypes sampled within this region. The remaining 29 Tenerife sampling sites outside the polygon were sampled for a total of 89 individuals and 39 haplotypes.

The global N_{ST} of 0.34 is significantly higher ($P < 0.001$) than the global F_{ST} of 0.03 ($P < 0.001$), indicating the dominant role of geographical isolation and mutation over gene flow and genetic drift for the structuring of genetic variation across the three regions. All pairwise F_{ST} and N_{ST} comparisons are significantly different from zero and N_{ST} were consistently significantly higher than F_{ST} ($P < 0.001$; Table 1). The two regions of Tenerife are the least differentiated from each other. La Palma is similarly differentiated from the Orotava valley and all other Tenerife sampling sites for F_{ST} (0.04 for both), but less differentiated from the polygon representing the Orotava valley for N_{ST} (0.38 from the Orotava valley and 0.45 from the rest of Tenerife). Thus, mtDNA variation in La Palma is less differentiated from mtDNA variation in the Orotava valley than it is from the rest of Tenerife, supporting the hypothesis that the Orotava valley is the source area for individuals that colonized La Palma.

DISCUSSION

In support of predictions one and two, we find that multiple founding individuals to La Palma share a common geographical origin consistent with the mega-landslide event of the Orotava valley. Marine currents between Tenerife and La Palma provide support for prediction three. The Canary Current is estimated to have been relatively unchanged over the past 22 Myr, passing southward along the northwest African coast, until reaching the Canary Islands, the geomorphology of which forces it to pass among the islands.
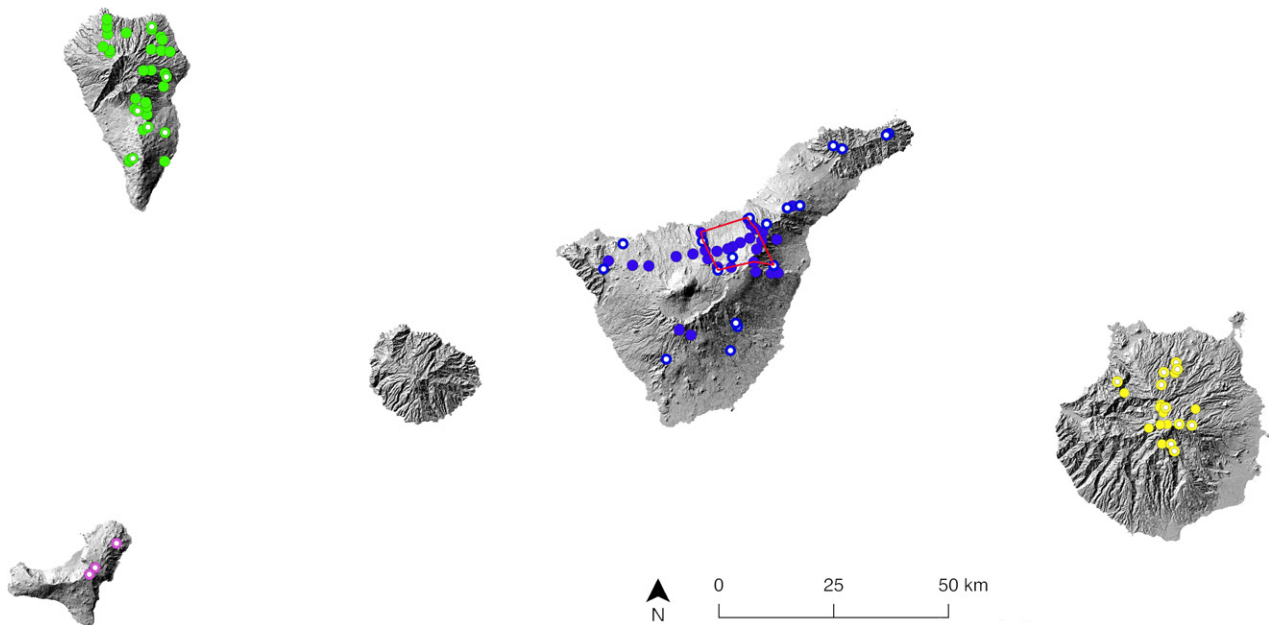

Figure 4 Map of sampling sites for the *Laparocerus tessellatus* complex. The 11 taxonomically defined species within the complex are all single-island endemics. Gran Canaria (5 species): *L. microphthalmus* Lindberg, 1950, *L. obsitus* Wollaston, 1864; *L. osorio* Machado, 2012; *L. tirajana* Machado, 2012; and *L.* sp. aff. *tirajana*. Tenerife (4 species) *L. tessellatus* Brullé, 1839; *L. freyi* Uyttenboogaart, 1940; *L. punctiger* Machado, 2016; and *L. canescens* Machado, 2016; La Palma (1 species): *L. auarita* Machado, 2016;. El Hierro (1 species): *L. bimbache* Machado, 2011. Sampling sites are colour coded to be consistent with island colour coding in Figs 5 & S2.1. Geographical coordinates of sampling sites, and the taxonomic species assignment of samples from each location are provided in Table S2.2 in Appendix S2. Also shown is a polygon describing the minimum geographical range of mtDNA haplotypes and their descendants from Tenerife that are ancestral to La Palma haplotypes (see text). Sampling sites from Faria *et al.* (2016) are indicated with a white dot inside the coloured circle.
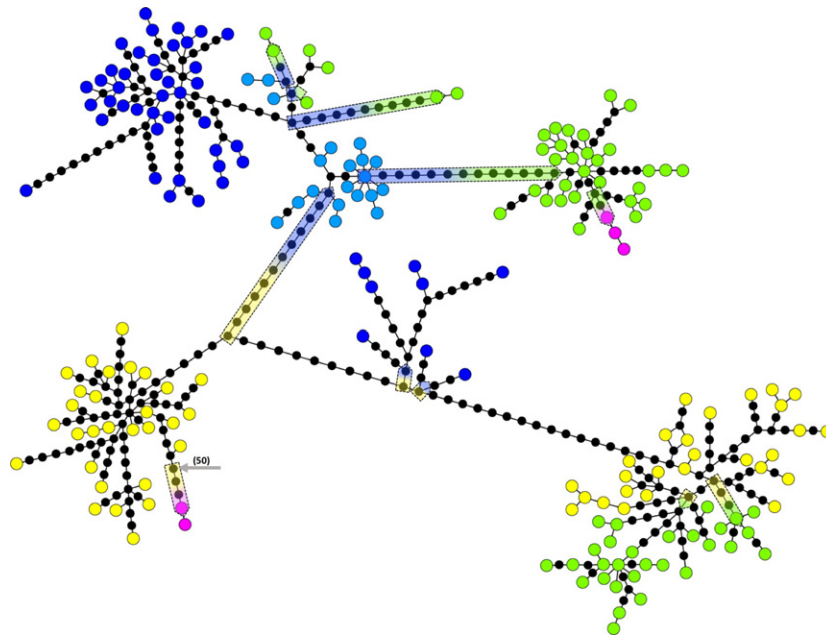
Figure 5 Haplotype network. A resolved haplotype network representing the relationships among 195 mtDNA haplotypes obtained from 633 bp of mtDNA sequence data for the COII gene for 396 individuals of the *Laparocerus tessellatus* complex. Haplotypes are colour coded with respect to island: yellow – Gran Canaria, blue – Tenerife, green – La Palma, pink – El Hierro. Haplotypes from Tenerife that are ancestral to La Palma, or closely related to haplotypes that are ancestral to La Palma (referred to as TF-LP haplotypes in the text), are shown in light blue. Extinct or unsampled haplotypes are shown as small black filled circles. The grey arrow indicates the most recent common ancestral haplotype of the complex, determined by rooting with the closely related species *L. vicinus* Lindberg, 1953. The number in brackets is the inferred number of mutations from *L. vicinus*. Coloured, pointed rectangles represent sets of potential ancestral haplotypes, from which at least one haplotype colonized a new island, with colonization direction indicated by a colour gradient and pointed end to the rectangle (see Fig. 3).

Table 1 Pairwise F_{ST} (below) and N_{ST} (above) values calculated using mtDNA COII sequence data for the *Laparocerus tessellatus* complex sampled from the Orotava Valley, Tenerife (excluding the Orotava valley) and La Palma. *P*-values indicate the probability that F_{ST} is significantly different from zero after 10,000 permutations of specimens among the three regions. *P*-values for N_{ST} indicate the probability that N_{ST} is significantly different from F_{ST} after 10,000 permutations of the matrix of genetic distances among haplotypes.

	Orotava valley	Tenerife	La Palma
Orotava valley	–	0.130***	0.377***
Tenerife	0.022***	–	0.452***
La Palma	0.042***	0.041***	–

***$P < 0.001$.

Of particular relevance is the trade wind season which results in not only currents that flow to the south between islands but also an offshore current that swings around the archipelago (Mittelstaedt, 1991), providing a connection between Tenerife and La Palma. The Canary Current has an estimated flow speed of 10–30 cm s^{-1} (Wooster *et al.*, 1976), suggesting that the offshore current would carry floating organic material deposited from the Orotava valley over the minimum distance of 120 km between the coast of La Orotava and the coast of La Palma in a period between four and 13 days.

Mega-landslide, or small raft?

Rafts of vegetation are recognized as an important mechanism for the arrival of species to oceanic islands from more distant continental source areas, and rafts of a similar nature are also likely to play a role in inter-island colonization. However, as highlighted by Gillespie *et al.* (2012), such rafts will be initiated from areas proximate to oceans (e.g. coastal areas, or upriver), and are thus more relevant for flora and fauna of coastal or riverine affinity. The *L. tessellatus* complex in Tenerife is typical of altitudes between 764 macsl and 1424 macsl (first and third quartiles of species distribution records), and is rarely observed below an altitude of 300 macsl (see Appendix S3), meaning that transportation by rafts, in the classical sense of coastal or freshwater origin, is improbable. In contrast, a landslide event on the scale of that forming the Orotava Valley would yield rafting organic matter from higher altitudes (Fig. 2). There are little direct data on what would happen to this organic matter once it enters the sea, but an important insight comes from the eruption of Mount St. Helens in May 1980. The eruption itself was preceded, and probably in part promoted, by a mega-landslide that carried tens of thousands of trees into Spirit Lake, where a giant log raft formed and persisted for years (Coffin, 1983; see Appendix S3). The behaviour of the Mount St. Helens landslide highlights the potential for large-scale

oceanic rafting of organic material derived from a mega-landslide. For the Orotava landslide, the estimated surface area 136 km^2 (Table S1.1 in Appendix S1), would have contributed many millions of individual plants and invertebrates to floating organic matter.

Mega-landslides, tsunamis and their consequences for island biogeography

Mega-landslides from volcanic island flank collapses are expected to directly deposit a large amount of organic material into the ocean (Fig. 2). An additional consequence of such landslide events is that they also trigger tsunamis when entering energetically into the sea (McGuire, 1996), and there are records of tsunamis from landslides in recent times (Evans *et al.*, 2006; Furukawa *et al.*, 2008 and references therein), as well as coastal deposits for more historical events (e.g. McMurtry *et al.*, 1999, 2004b; Pérez-Torrado *et al.*, 2006; Coello *et al.*, 2014; Ramalho *et al.*, 2015). The resulting tsunami waves are propagated both offshore and onshore (Didenkulova *et al.*, 2010; Sue *et al.*, 2011), and can reach heights of hundreds of metres, as recorded by coastal deposits (e.g. McMurtry *et al.*, 2004b: 240–356 m; McMurtry *et al.*, 2004a: 400 m; Pérez-Torrado *et al.*, 2006: 188 m; Ramalho *et al.*, 2015: 270 m). Thus, tsunamis not only wash up the coasts of islands and mainland areas in their trajectory but also the coast of the island suffering the landslide.

Given that there are both offshore and onshore tsunami waves propagating from a mega-landslide (Didenkulova *et al.*, 2010; Sue *et al.*, 2011), deposition of organic material into the ocean is also expected from (1) areas of the source island affected by the onshore tsunami, and (2) islands impacted by the offshore tsunami. Thus, mega-landslides are expected to promote the ocean deposition and rafting of significantly more organic material than that associated with the landslide itself, although the altitude of secondary deposition will be a function of the tsunami height. In the context of island biogeographical theory, for which colonization is a fundamental component (MacArthur & Wilson, 1963, 1967), mega-landslides may be an important driver of colonization, mediated by ocean currents and archipelago geomorphology.

Limitations and further considerations

A general limitation that applies to the present study is a lack of power to estimate the timing of colonization of mtDNA lineages, which are expected to be synchronous when driven by a mega-landslide event, and consistent with the timing of the mega-landslide event. This is because the estimation of colonization times of mtDNA lineages that are derived from coalescent mtDNA variation within a source population is subject to multiple sources of error, including unsampled or extinct haplotypes (see Figs 5 & 3 for a conceptual explanation), mean substitution rate uncertainty and high rate variance over a coalescent time-scale. We suggest that some of these challenges may be alleviated in future studies with reduced representation genome sequencing approaches, such as restriction site-associated DNA sequencing (RADseq). With access to geographically referenced patterns of relatedness across potentially thousands of nuclear loci, it may be possible to estimate demographic parameters such as the number of founding events, their timing, and their founding population size(s).

For a given mega-landslide event, ocean currents and archipelago geomorphology will influence the dispersal of organic material deposited into the ocean, potentially providing for model-based hypothesis testing. However, obtaining supporting evidence is expected to be challenging for older mega-landslide events. This is because lineage sorting will erode patterns of shared genetic variation across islands with time, until all individuals coalesce back to a single-source lineage. Thus, the older a landslide event is, the less likely it will be to find signatures of colonization involving multiple individuals. We therefore suggest that it will be advantageous to investigate mega-landslides of recent geological origin. Given the potential for mega-landslides to result in the synchronous colonization of a large number species to a neighbouring island, we also suggest sampling multiple species with distributions that could be explained by a mega-landslide. Taking a multi-species, multi-locus approach, with a focus on geologically recent mega-landslides should shed light on their general importance in oceanic island biogeography.

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SUPPORTING INFORMATION

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

Appendix S1: Landslides on the island of Tenerife.AUTHOR: Your paper contains Supporting Information. You should already have downloaded this from the e-proofing website when you collected your article proof. Please check that all legends and content are correct, including updating references where applicable. (Note that legends as provided with the Supporting Information itself should be full and complete, while those provided in the main article are shortened versions, where necessary.) Please ensure that line numbers are removed and that track-change edits are accepted so that they do not appear in the published version. If any changes are necessary, please ensure that you edit the files sent with the proof, as minor editorial changes may have been made to the files in the Editorial Office prior to manuscript export. Corrected Supporting Information files should be emailed to the Production Editor at the same time that you return your main article proof corrections, with a brief description of the changes made. If you have no corrections to your Supporting Information please inform the Production Editor, otherwise publication of your paper will be delayed.

Appendix S2 Sampling details, and Bayesian tree.

Appendix S3 Altitudinal data, and Mount St. Helens eruption.

DATA ACCESSIBILITY

The DNA sequence alignment reported in this paper, together with geographic and taxonomic details, has been archived in Dryad (doi:10.5061/dryad.503kg).

BIOSKETCH

The research team have complementary interests in the geology and biodiversity of oceanic islands, and the application of molecular data to understand the origin and maintenance of species and communities of species. This work is a synthesis of these different interests.

Author contributions: BCE, VGO and HL conceived and coordinated the study with input from JP, NA, AM, JCC and VS. BCE, VGO and HL undertook the fieldwork, with input from AMC. VGO carried out all laboratory procedures and data analysis, with input from BCE, HL and JP. VGO, HL and BCE wrote the paper with input from other authors.

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