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Abstract

Ongoing work shows that species richness patterns on volcanic oceanic islands are shaped by surface area changes driven by longer time scale (>1 ka) geological processes and natural sea level fluctuations. A key question is: what are the rates and magnitudes of the forces driving spatial changes on volcanic oceanic islands which in turn affect evolutionary and biogeographic processes? We quantified the rates of surface-area changes of a whole island resulting from both volcanogenic flows and sea level change over the last glacial–interglacial (GI) cycle (120 ka) for the volcanically active island of Terceira, (Azores, Macaronesia, Portugal). Volcanogenic activity led to incidental but long-lasting surface area expansions by the formation of a new volcanic cone and lava-deltas, whereas sea level changes led to both contractions and expansions of area. The total surface area of Terceira decreased by as much as 24% per time step due to changing sea levels and increased by 37% per time step due to volcanism per time step of 10 ka. However, while sea levels nearly continuously changed the total surface area, volcanic activity only impacted total surface area during two time steps over the past 120 ka. The surface area of the coastal and lowland region (here defined as area <300 m) was affected by sea level change (average change of 11% / 10 ka for 120–0 ka) and intra-volcanic change (average change of 17% / 10 ka for 120–0 ka). We discuss the biogeographic implications of the quantified dynamics, and we argue that surface area change is mainly driven by volcanic processes in the early stages of the island's life cycle, while during the later stages, area change becomes increasingly affected by sea level dynamics. Both environmental processes may therefore affect biota differently during the life cycle of volcanic oceanic islands.

Highlights

- We modelled the geospatial dynamics of both volcanic activity and sea level change on a volcanic island (Terceira, Azores) to map out how combined area change dynamics over 120 kyr could affect biogeographical and evolutionary processes.
- Volcanogenic and sea level dynamics have changed the surface area of the island to similar extents: volcanic dynamics mainly spasmodically added terrain, whereas sea level change both added and reduced terrain.
- A stable period of ca 40 kyr persisted over a glacial – interglacial cycle, potentially allowing for re-equilibration of species richness dynamics.
- The coastal-lowland area of Terceira appears to be the most affected area.
- Generalizing the Terceira dynamics to other settings suggests that although the identified geospatial dynamics will be qualitatively comparable for young stages of volcanic islands globally, they will all display different quantitative geospatial responses. For this reason, generalizing ontogenic histories for all islands may be fundamentally problematic.

Keywords: Azores, equilibrium theory, general dynamic theory, glacial sensitive theory, island biogeography, lava deltas, sea level change, species pump theory, volcanic oceanic islands.

INTRODUCTION

Volcanic oceanic islands represent important systems in biogeographical studies as they are geographically isolated, hold isolated populations, and are often of known geological age. This allows for comparative studies to analyze the effects of surface area change, isolation, and island age on the geographical distribution and evolutionary history of biotic systems (Borges and Hortal 2009, Losos and Ricklefs 2009, Warren et al. 2015, Otto et al. 2016, Whittaker et al. 2017). What makes volcanic oceanic islands especially relevant for biodiversity and evolutionary studies is their dynamism through their long-term life cycle from emergence to subsidence (Stuessy 2007, Ramalho et al. 2013, Ali and Aitchison 2014, Féraud et al. 2017). Our aim is to quantify how volcanic processes affect surface areas of islands over longer time scales and how that relates to climatic drivers of area and distance changes. Owing to increasing radiometric dating of volcanogenic rocks, crucial insights into their spatiotemporal dynamics can be obtained (e.g., Ramalho et al. 2013, Clague and Cherod

2014, Ricchi et al. 2018), thus linking the long-term geological dynamism of volcanic islands to bio-evolutionary processes. Such integrative island studies gave rise to the General Dynamic Model (GDM) of oceanic island biogeography (Whittaker et al. 2008), which states that present-day patterns of endemic richness can be explained by the dynamic geological life cycle of volcanic oceanic islands over millions of years (see also: Ziegler 2002, Stuessy 2007, Whittaker et al. 2008, 2017, Borges and Hortal 2009, Warren et al. 2015, Borregaard et al. 2017, Ávila 2018a, 2019, Lim and Marshall 2018).

On shorter time scales, over thousands of years, islands have often been considered as static land masses with biogeographic processes mainly driven by immigration and extinction based on present-day island configurations as hypothesized by the Equilibrium Theory of Island Biogeography (ETIB; MacArthur and Wilson 1963). However, during these shorter time scales, volcanic islands, when volcanically active, represent one of the most dynamic environments on the planet with high rates and magnitudes of surface area and archipelagic configuration changes, here denoted as geo-spatial changes. Volcanic activity affects evolutionary processes with repeated lava and pyroclastic flows generated by volcanic outbursts leading to the fragmentation of habitats, thereby reducing or disconnecting populations, hampering gene flow, or even inducing extirpations that ultimately may promote evolutionary processes (Carson et al. 1990, Vandergast et al. 2004, Gillespie and Roderick 2012). Volcanic island surface areas may be expanded by the emergence of new volcanos, pyroclastic flows, and lava flows that form lava-deltas along the coast, providing new habitats for species and influencing their distributions, species richness equilibria, and evolutionary dynamics (e.g., Ávila et al. 2018b). Inland volcanogenic flows temporarily isolate plant and invertebrate populations in “kipukas”, hampering gene flow and influencing speciation (Carson and Johnson 1975, Vandergast et al. 2004, Gillespie and Roderick 2014). For example, in the Azores, volcanogenic flows promoted the speciation of cave-adapted invertebrates (Borges and Hortal 2009). Superimposed on this purely volcanic dynamism, it has long been realized that Pleistocene sea level changes simultaneously affect islands and configurations of archipelagos and species distributions (e.g., Diamond 1972; Diamond and Gilpin 1983). The Glacial Sensitive Model (GSM; Fernández-Palacios et al. 2016) indicates that island surface areas and connectivity are not static as assumed by the ETIB (MacArthur and Wilson 1963), but instead fluctuate dynamically in response to Pleistocene climatic cycles. Moreover, recent studies suggest that the legacy of past changes are still detectable in present-day species richness patterns on islands and may have influenced evolutionary

processes (Warren et al. 2015, Fernández-Palacios et al. 2016, Borregaard et al. 2017, Simaiakis et al. 2017, Whittaker et al. 2017, Ávila et al. 2018a, b, 2019). During the last GI cycle (120 ka–present), global mean sea levels fluctuated between +10 m and -135 m and were on average 50 m below present-day sea level (Lambeck et al. 2014, Norder et al. 2019). Sea level fluctuations led to geospatial and connectivity changes within archipelagos and consequently to changes in species richness patterns and species distributions across archipelagos (Diamond 1972, Heaney 1986, Fernández-Palacios et al. 2016), also affecting endemic species richness patterns (Ali and Aitchison 2014, Rijdsdijk et al. 2014, Weigelt et al. 2016, Norder et al. 2018, 2019). Here we evaluate the combined effects of sea level and volcanic processes in the coastal and lowland insular habitat regions (<300 m) over the last GI cycle (120 ka ago until present). These lower elevation regions are directly exposed to both sea level change and volcanogenic flows flowing downhill and may be among the most dynamically changing environments in volcanic island settings.

As a study system, we selected the volcanically active island of Terceira (Azores archipelago, Macaronesia, Portugal) as its volcanic history is relatively well-known; volcanic deposits are radiometrically dated and their extents precisely mapped (Zbyszewski et al. 1971, Self 1976, Féraud et al. 1980, Nunes 2000, Calvert et al. 2006, Hildenbrand et al. 2014, Quartau et al. 2014). Terceira is volcanically active, representing a “young” island in the context of ontogenic states of the life cycle of volcanic oceanic islands, as defined by Ávila et al. (2019) and in accordance with the GDM (Whittaker et al. 2008), even though they are formed by a hotspot under a triple junction regime. As the triple junction setting is characterized by ultra-slow plate spreading (Vogt and Jung 2004, Quartau et al. 2014), Terceira can be considered as a useful analogy for a young active volcanic hotspot island in biogeographic studies. Given, however, the ongoing research on the diversity of volcanic oceanic islands and how their different geospatial dynamics may affect biogeographic processes differently (Ali 2017, Borregaard et al. 2017, Whittaker et al. 2017), our theoretical generalizations must still be considered with care.

We quantify for Terceira the change in both total surface area and coastal-lowland area (lower than 300 m, hereafter: “coastal area”) generated by the combined volcanogenic and sea level activity over the last 120 ka. We differentiate between volcanic activity that adds to the total surface area of the island (“volcanic”) and volcanic activity that occurs within the existing island perimeter; and therefore, this does not increase the total surface area (“intra-volcanic” or “intra-island volcanism”). Given what we know about the rates and durations of

environmental drivers on insular areas, we discuss how the combined volcanogenic and sea level dynamics affect intra-island species richness, gene flow patterns, genetic diversities, and species distributions for both the full island and the lowland coastal zone on Terceira. We first introduce the geographic factors and geological setting that may have affected the area change of Terceira. Then, we discuss the local sea level fluctuations that Terceira experienced over the timespan. After our analysis, we discuss the biogeographic implications of the area change effects on Terceira and place them in the wider context of biogeographic theories. In particular, we exploit our insights to evaluate how far the GDM and the GSM can be integrated.

SETTING

The Azores comprises nine volcanic oceanic islands situated near the Mid-Atlantic Ridge in the Atlantic Ocean (Fig. 1a). Terceira is a volcanically active remote island located about 1,520 km west of mainland Portugal, with a present surface-area of 401 km². It is the third largest island of the Azores archipelago. The summit of the most recent volcano, Santa Bárbara, reaches 1,021 m and is the highest point. Temperate climates prevail in the Azores, and Terceira is characterized by mild mean annual maximum summer temperatures (<18° to 23° C) and topography-controlled mean annual precipitation ranging from <1,000 mm/yr near the coast to 2,600 mm/yr in the uplands (Santos et al. 2004). The Azorean native vegetation comprises 210 species, of which 73 are endemic (Gabriel et al. 2014). The vegetation of the Azores is highly degraded at present; lowland laurel forests are very rare and coastal woodlands are greatly reduced, and in most cases invaded by *Pittosporum undulatum*. However, the pre-human communities would have comprised zonal laurel lowland and sub-montane forests (Dias 1996, Elias et al. 2016).

GEOLOGICAL FACTORS LEADING TO SURFACE AREA CHANGE

The Azores Islands emerge from the Azores Plateau, defined by the 2,000 m depth, formed by the interaction between the triple junction of the Eurasian, African, and North American plates and the Azores hotspot (Schilling 1975, Lourenço et al. 1998, Hildenbrand et al. 2014). Terceira lies on top of the 550 km extensive Terceira Rift, which corresponds to a dextral trans-tensional shear zone forming the Eurasian-African boundary (Lourenço et al. 1998). Terceira emerged ~400 ka along its eastern part by the Serra do Cume-Ribeirinha Volcanic

Complex, forming a shield volcano (Cinco Picos, Fig. 1b-A; Hildenbrand et al. 2014). The Serra do Cume-Ribeirinha Volcanic Complex is overlain by three overlapping and interstratified stratovolcanoes that decrease in age along the rift zone from east to west (Fig. 1b; Calvert et al. 2006, Quartau et al. 2014), although it should be noted that alternative views exist (Nunes, 2017). The Cinco Picos Volcano contains the largest caldera of the Azores (Calvert et al. 2006). This caldera is filled by pyroclastics and lavas from the younger Guilherme Moniz and Pico Alto volcanos, and the caldera floor contains active scoria cones and lava flows from the “Basaltic Fissures Area.” The Guilherme Moniz volcano is situated at the western flanks of the Cinco Picos Volcano and the volcanoclastics of these volcanos interdigitate (Nunes 2017). The Guilherme Moniz volcano reached its maximum subaerial extent around 270 ka and formed its caldera after 111 ka (Fig. 1b-B; Calvert et al. 2006). On the northern flank of the Guilherme Moniz volcano, the Pico Alto volcano formed and reached its maximum subaerial extent at 141 ka (Fig. 1b-C; Gertisser et al. 2010). The eruptions of the Pico Alto volcano continued until human settlement 500 years ago. The Pico Alto volcano comprises a chaotic assemblage of lava flows, domes, and several pyroclastic flows. The Santa Bárbara volcano is considered an actively expanding stratovolcano which emerged before 60 ka ago and is still active, with eruptions in the 18th and 19th centuries (Fig. 1b-D; Calvert et al. 2006, Hildenbrand et al. 2014). The Santa Bárbara volcano is surrounded by several small volcanic domes; its caldera formed after 30 ka ago and is filled with trachyte lavas (Self 1976, Hildenbrand et al. 2014). The Basaltic Fissural Area crosses the entire island in a WNW-ESE direction and is formed mostly by basaltic Hawaiian/Strombolian cinder cones and associated lava flows that started its activity at ~43 ka (Fig. 1b-E; Calvert et al. 2006). The flows form a thin volcanic unit a few tens of meters thick (Nunes et al. 2014), filling a depressed area between the Santa Bárbara volcano on the east and the Guilherme Moniz volcano and Pico Alto volcano on the West, and also covering a significant area of the Serra do Cume - Ribeirinha Volcanic complex (Fig. 1b-E, F).

Currently, Terceira is actively subsiding at rates of 1–5 mm/yr (Miranda et al. 2012, Marques et al. 2015), but these rates are not representative of the longer time spans of 1,000s of years we consider here (Quartau et al. 2014, 2016, Marques et al. 2015, pers. comm. Marques et al. 2016). Over a period of 370 ka, a mean subsidence rate of 0.25 mm/yr can be reconstructed based on the position of shelf breaks next to Cinco Picos and Guilherme Moniz volcanoes (Quartau et al. 2014). Localized subsidence or uplift within Terceira may also have affected areas over the last 120 ka. Two large, active normal fault bounded zones are present

on the island: the Lajes Graben in the NE and the Santa Barbara graben situated on the SE of the Santa Barbara stratovolcano (Fig. 1b- F; Madeira et al. 2015). However, the activity associated with these faults minimally modified total surface areas on Terceira over the last 120 ka. Large scale slope instabilities may also modify areas of islands, but no significant landslide scars affecting volcanic edifices have been identified in Terceira during the last 120 ka (Quartau et al. 2014, Marques et al. 2015).

SEA LEVEL CHANGE AT TERCEIRA

During sea level low-stands, the islands in the Azores were larger than they are today, whereas during sea level high-stands surface areas in the Azores were smaller (Rijsdijk et al. 2014, Norder et al. 2018). The differences in size are generated by exposure during glacial periods of the insular shelves that surround the islands and span from the present-day coastline to ~-130 m (Quartau et al., 2010, 2014, 2015a), and on some islands, (e.g., Flores, Graciosa or Santa Maria) it can exceed the subaerial area (Ávila et al. 2010, Quartau et al. 2015b, Ricchi et al. 2018). The global curve of mean sea level (MSL) change shows the rate of sea level variation on a global scale, but sea level varied differently across the planet, with large deviations from the mean nearby continents (Milne and Mitrovica 2008, Simaiaikis et al. 2017). For this study, a relative MSL curve for the Azores was reconstructed for the timespan of the last 120ka. In the Azores, the lowest sea level was at ca -108 m +/- 5% MSL, while the global eustatic sea level was at -135 m MSL (Lambeck et al. 2014).

DATA AND METHODS

To determine how sea level changes and volcanic phenomena have affected the island's surface area, we calculated two metrics for both the area of the whole island (total surface area) and the coastal-lowland area: 1) area change, which is the combined effect of sea level change, subsidence and volcanic activity, and 2) intra-island volcanic change, which is the amount of surface area within the existing island area that is influenced by volcanogenic flows (see Fig. 2 for workflow, Table 1 for data sources, supplementary Table S1 for calculated values, all raw data tabulated in an Excel sheet of supplementary Table S2). We calculated the area changes based on present day bathymetric data with corrections for changes in sea level, subsidence, landslide scars, and lava deltas (Fig. 2).

The areal effects were modelled over 120 ka, including one sea level rise and fall cycle, with time steps of 10 ka resulting in 13 time slices. We used ESRI ArcGIS 10.2.2 desktop software to create contours for each time slice and calculate area changes based on the differences between each time slice. We projected the maps in a Universal Transversal Mercator system, which led to minimal area distortions ($<1\%$) for the scale of our analysis ($<1\text{--}100\text{ km}^2$; Yildirim and Kaya 2008). All maps were georeferenced and collected in a geodatabase.

We first used bathymetric data to construct the present-day coastal contour of Terceira. Local sea level heights were combined with a bathymetric grid with a resolution of $1/8$ by $1/8$ arc-minutes (~ 32 by 32 m), which were obtained via the EMODnet portal (European Marine Observation and Data Network, 2016).

Since the LGM $\sim 22\text{ ka}$ ago, sea levels rose up to $\sim 130\text{ m}$ globally and caused disconnection of peninsular islands and partial drowning of continental, and some large oceanic islands that fragmented and shrunk in size. Numerical modelling of the palaeogeographic effects of sea level rise allows for quantifying timings and rates of connectivity loss, fragmentation, and area reduction over time steps of 1,000 years for one or more GI cycles. However, such a model must take into account all the interrelated physical mechanisms that compose the Glacial Isostatic Adjustment process: (i) the ice- and water-load induced solid Earth deformations, (ii) the change of mutual gravitational pull between continental ice sheets and ocean, and (iii) the movements of the Earth's rotational axis with respect to the surface in response to surface ice- and water-load changes. These factors give rise to regionally varying relative sea-level (RSL) changes that exponentially decay with time because of the viscous response of the Earth's mantle.

The ANICE-SELEN ice-sheet numerical model was used to model local relative sea levels taking into account the flexibility of the Earth's crust and the rheology of the mantle (De Boer et al. 2014; Fig. 3, Appendix S2). The model was based on the solution of the gravitationally self-consistent sea level equation and was used to reconstruct the RSL change for the Azorean region through the last four GI cycles (420 ka). In the ice-sheet model, it was assumed that ice melting in Greenland contributed $+2\text{ m}$ equivalent sea level (esl) between 127 and 116 ka and Antarctica $+5\text{ m}$ (esl) between 120 and 116 ka. Therefore, the eustatic highstand is a two-step feature. We constructed three curves with the ANICE-SELEN ice-sheet model that represent three realistic solutions based on different mantle viscosity profiles (MVP) with a fixed lithosphere thickness of 100 km .

We corrected the relative sea levels with a constant subsidence rate of 0.25 mm/yr, which represents an average rate of the subsidence of the insular shelves of the Cinco Pico Volcanos and Guilherme Moniz volcano over a period of 370 ka (Quartau et al. 2014). For this study, a relative MSL curve for the Azores was reconstructed for the timespan of the last 120 ka (Fig. 3, data in supplementary Table S2). The resulting relative sea level curve deviates from the global eustatic MSL curve due to local geophysical effects, which include (i) the ice- and water-load induced solid Earth deformations, (ii) the change of mutual gravitational pull between continental ice sheets and ocean, and (iii) the movements of the Earth's rotational axis with respect to the surface in response to surface ice- and water-load changes. These factors give rise to regionally varying relative sea-level (RSL) changes that exponentially decay with time because of the viscous response of the Earth's mantle.

For each time slice of 10 ka we compiled the maps of published radiometrically dated volcanogenic flows and their extents (Fig. 4). In our quantification of area changes we assumed that volcanic activity ceased between 120–90 ka, but there may be a data gap for this period. We used the -108m MSL contour of Terceira as a contour representative for the local maximum sea level lowering during the Last Glacial Maximum (LGM) 22 ka, when eustatic sea levels reached up to -135m globally (Lambeck et al. 2014). Volcanogenic additions (lava deltas) postdating 22ka were subtracted from the surface area. For the lowland coastal zone, we assumed the inland upland border of the coastal plant communities to have remained static over 120 ka at 300 m in elevation. The upper boundary most likely fluctuated in tandem with temperature changes during glacials and interglacials, and community zones expanded upwards with climatic warming and downwards with cooling (Fernández-Palacios et al. 2016). Hence, for this work, we mainly looked at areal effects of an elevational zone from prevailing sea level up to 300 m elevation, disregarding the altitudinal response of vegetation communities.

RESULTS

All calculated values referred to in this section are tabulated and presented in supplementary Table S1 and in Figure 4 and 5.

324 *VOLCANOGENIC CHANGE*

325 During the 120 ka timespan, the surface area of Terceira was only twice significantly affected
326 by volcanogenic flows and additions (Figs. 4 and 5). The most significant event was the
327 emergence of the Santa Bárbara volcano at around 60 ka, leading to a 37% increase in area
328 from 393 km² to 571 km² (Fig. 4). Later, between 30–20 ka, an increase of 1% in area
329 occurred by volcanogenic addition through eruptions by the Santa Bárbara volcano and the
330 Basaltic Fissures Area (Fig. 4). The two periods of increased volcanic activity affected major
331 parts of the interior of Terceira (Figs. 4, 5c). The first period was 8–50 ka when 18% to 37%
332 of the interior surface area was affected by volcanogenic flows, mainly from the active Santa
333 Barbára volcano. A second volcanically intense period occurred between 30 ka and present
334 times, when several volcanic systems were active. In this period, 22% to more than 50% of
335 the interior surface area was affected by volcanogenic flows (Fig. 5c, Table 2). The influence
336 of intra-island volcanic activity peaked in the coastal/lowland area at 31% 70–60 ka, and at
337 63% between 30 and 20 ka, coinciding with highest magnitudes and rates of sea level falls
338 (Figs. 5d, 5e).

339 *SEA LEVEL CHANGE*

340 Sea levels affected on average 6% of the area of Terceira, with a positive peak of 9% surface
341 increase between 70–60 ka, coinciding with a sea level fall of 25 m in 10 ka and the
342 emergence of the Santa Bárbara volcano (Figs. 4, 5b). The greatest surface area reduction of
343 24%, occurring between 20–10 ka, coincided with the steepest rise in sea levels of 70 m in 10
344 ka (Fig. 4, Table 2). Sea level changed in absolute terms on average 11% of the total coastal-
345 lowland area both positively and negatively, a factor two times lower than volcanogenic
346 activity (Table 2). Sea level changes affecting coastal-lowland areas peaked between 20–10
347 ka when sea level rise induced a reduction of 47% in coastal-lowland area, whereas a
348 maximum increase in coastal-lowland area of 13% occurred due to falling sea levels between
349 30–20 ka (Fig. 5e).

350 *COMBINED CHANGE*

351 As a result of combined volcanogenic and sea level change, Terceira's surface area changed
352 in size considerably over the last 120 ka, ranging between ca. 391 km² and ca. 589 km² (Table
353 2, Figs. 4 and 5). Although around 110 ka the caldera of Guilherme Moniz volcano was
354 created and sea level started to fall, until 70 ka, the total surface-area of Terceira remained

more or less constant around $385 \pm 10 \text{ km}^2$ (Fig. 5a). From 70 ka BP onwards, combined additions by pyroclastic flows and falling sea levels led to an increase of surface area of Terceira by 200 km^2 , reaching up to a maximum of 589 km^2 . The surface area varied minimally between $537\text{--}590 \text{ km}^2$ for ca. 40 ka between 70–20 ka. The maximum size of Terceira was reached between 30–20 ka, generated by the lowest sea level stand during the LGM. We can conclude that at Terceira falling sea levels from 70 ka led to a maximum total surface increase of ca. $\sim 9\%$ per 10 ka, representing one fourth of the incidental volcanogenic addition of landmass through the formation of the Santa Bárbara volcano ($\sim 37\%$) at around 60 ka (Fig. 5b). The coastal-lowland area fluctuated between the smallest value, at present of 119 km^2 , and the highest of 304 km^2 , which also was reached during the LGM period (30–20 ka ago; Table 2, Figs. 5d, 5e). This area remained more or less stable at ca. 200 km^2 between 120–70 ka but increased up to 50% (ca. 300 km^2) between 70–20 ka by volcanic activity and sea level change. Again, also in the lowlands, two phases of net volcanic additions of 31% occurred between 70–60 ka, due to the formation of the Santa Bárbara volcano, and 2% at 20 ka. On average, during active phases, 20% per 10 ka of the coastal-lowland surface area was affected by volcanic activity, confirming the highly dynamic character of this area (Table 2).

Interestingly, the interglacial areas of Terceira remained more or less unchanged at $\sim 400 \text{ km}^2$ during the last and present-day interglacials, in spite of the permanent addition of land mass generated by the formation of the Santa Bárbara volcano. However, the interglacial surface area of the coastal-lowland area decreased permanently as compared to the previous interglacial by 42% (from 203 km^2 to 119 km^2).

DISCUSSION

Based on the magnitudes and rates of geospatial change identified for Terceira, we discuss the hypothetical biogeographic and evolutionary effects on the terrestrial land locked biota of the geospatial change on active volcanic oceanic islands. Our major conclusions are summarized in Table 3. We are aware of other aspects of environmental change over glacial-interglacial cycles that influence biogeographic processes, including global warming and cooling, as well as changes in connectivity pathways by wind and water currents (Fernández-Palacios et al. 2016, Whittaker et al. 2017); but here we focus exclusively on discussing the implications of geospatial change mediated by volcanogenic and sea level changes.

IMPLICATIONS FOR THE GLACIAL SENSITIVE MODEL

The most significant expansion of the area of Terceira over the past 120 ka, from 393 to >530 km², was induced by the emergence of the Santa Barbara volcano around 60 ka (Figs. 4, 5). This volcanogenic area increase occurred synchronous with sea level fall; the combination of these two led to an area increase of 46% within 10 ka (Table S1). This large surface area continued to exist between 60 ka until 20 ka (Fig. 5a). Interestingly, the typical dominance of larger island size existing during glacial periods for more than 80% of the time (Norder et al. 2018) is barely noticeable at Terceira. The period of the smaller island size lasted ~50 ka, from 120 ka to 70 ka, and the period of the larger island size lasted ~40 ka, from 60 ka to 20 ka. All the net area gained by volcanism was negatively compensated by the long-term net subsidence of the island over this period. A key finding of this study is that volcanic additions are spasmodic but long-lasting or permanent, whereas sea level changes are repetitive and work on two directions over the Quaternary, inducing both periods of surface loss and surface gain (Table 3). These processes lead us to present the following testable hypotheses about how species richness may have been influenced by these changes, based on predictions from the ETIB.

Between ~60–20 ka, when the island had its largest surface area, the island could have hosted more species than before as immigration rates may have increased and extinction rates decreased during this period. The volcanogenic addition of extra area, after 60 ka, may have allowed a positive shift of equilibrium species richness, with increasing immigration rates and decreasing extinction rates that lasted some 40 ka (Fig. 6a; Table 3). Indigenous biota may have benefited from this 40 ka period by migrating and mixing their gene pools with the biota from other islands. This 40 ka period may thus have been sufficient for attaining a dynamic equilibrium in species richness (e.g., Fernández-Palacios et al. 2016). Perhaps this 40 ka period of larger surface areas was also sufficient to initiate speciation processes in some organisms (Table 3). In the period after 20 ka, due to sea level rise, the island shrunk by a third, attaining its present size of 401 km², while at the same time the inter-island distance increased (Rijsdijk et al. 2014). Both area contraction and distance increase may have raised extinction rates and generated extinction debts among some native species of Terceira (see Rijsdijk et al. 2014, Norder et al. 2018). In particular, species restricted to the coastal-lowland zone that expanded and contracted even more extremely (+87% to – 28% area change) were affected. Possibly, the extreme contraction after 20 ka may have left genetic bottleneck signatures still identifiable in the present-day native coastal-lowland species populations.

After 20 ka, the equilibrium species richness numbers may have shifted back downward to the last interglacial/early glacial levels. The coastal-lowland geospatial dynamics may have also promoted coastal species expansion to the interior of the islands as described in the taxon cycle theory (Wilson 1961). Species that may have established after prolonged periods of coastal expansion may then have been pushed into the adjacent uplands during coastal contraction phases, inducing increased species interactions, and perhaps these sea level rise periods coincided with inland genetic bottlenecks or anagenetic adaptation events.

At Terceira equilibrium processes may have occurred in tandem with the sea level cycles, as predicted by the Glacial Sensitive Model (Fernández-Palacios et al. 2016). Volcanic additions, however, which resulted in long-lasting land additions, may have shifted species equilibria towards higher levels over longer periods (>60 ka) than sea level rise periods, which pushed it downward over shorter periods (<20 ka) by decreasing areas (Table 3). Volcanic additions led to spasmodic increases of surface areas facilitating long-lasting increased opportunities of migrations and population expansions at Terceira occurring between 70-20 ka BP (Fig. 6a: right panel; Table 3). This period may have enticed recolonization events of species from adjoining islands, perhaps leading to increased interspecific competition and reinforcing speciation processes (Losos and Ricklefs 2009, Aguilée et al. 2011). Land loss by long-term subsidence, which at Terceira amounted to some 30 m over 120 ka, was compensated by volcanic additions. However, after the Holocene sea level rise, the coastal-lowland area decreased by 42% relative to its previous interglacial extent. Consequently, the coastal-lowland taxa had a much smaller area to inhabit and less refuge options compared to the last interglacial period and may have experienced higher extinction debts than during the previous interglacial state. This indicates that even over climatic cycles, the vacant area options for taxa differ and thus highlight the complexity of Glacial Sensitive Model assumptions over island area histories on volcanically active insular settings. Volcanism also affects the height of islands (Clague and Sherrod 2014, Ramalho et al. 2017) and topographic roughness (Seijmonsbergen et al. 2019), which also influence migration rates gene flow and habitat diversity (Lim and Marshall 2019), adding still more complexities that should be considered.

BIOGEOGRAPHIC CONSEQUENCES OF INTRA-ISLAND VOLCANISM

While the effects of volcanism in total area expansion of Terceira was mainly limited by the addition of the Santa Barbara Volcano at 60 ka, volcanic lava and pyroclastic flows were

active within the island over much of the past 120 ka. These volcanogenic flows covered major parts of the islands, reaching more than 50% between 30–20 ka (Calvert et al. 2006, Nunes et al. 2014). These flows sterilized vast areas, exceeding 60% of the coastal-lowland area between 29–20 ka. During and shortly after the eruptions, these flows isolated patches of vegetation known (in Hawaii) as “kīpukas”. The duration of the isolation periods of these kīpukas prior to their re-connection through colonization of the surrounding sterilized grounds must have depended on elevation, as biomass production rates associated with primary succession decreases with elevation, as shown in Big Island, Hawaii (Aplet and Vitousek 1994). Depending on the thickness of the lava flows, the top of the lava solidifies to a stony crust within hours, but it takes months to decades to fully solidify lava measuring meters to tens of meters thick (Helz and Thornber 1987). Regardless of the volcanic substrate type however within decades to centuries, providing climatic conditions are appropriate, rapid, and continued succession from early colonizer species to forest species take place (Whittaker et al. 1989, Kitayama et al. 1995, Elias and Dias 2004). Weathering rates of lavas and subsequent release of nutrients are positively related to mean annual temperature and influenced by net annual rain fall (Crews et al. 1995). For tropical islands this signifies that at lower elevations (<500 m), ca. 1 kg biomass/m² may be produced within a decade, whereas at 1,000 m this takes a century and at 2,000 m it may take several thousand years (Aplet and Vitousek 1994). As a consequence, the durations of geomorphic and genetic separation take longer and, therefore, the largest effects of genetic divergence are expected at higher elevations (Table 3). On the Azores, such genetic effects may be reduced due to the temperate climate; biomass production is probably lower at comparable heights for islands in the tropical realm, with not much differentiation between the higher and lower regions. Altogether, the time steps of 10 ka employed here exceed the ecological recovery and succession rates of the cooled lava flows by nearly an order of magnitude, making it less likely that genetic or diversity patterns have persisted over these time steps across the affected areas. However, genetic divergence between populations that were separated by lava flows is observed with increasing effects on older volcanoes (Gillespie and Roderick 2014). Although ecological recovery is faster, genetic divergence may accumulate at each separation, so that after several separation cycles, cumulative speciation is completed (Carson et al. 1990, Aguilée et al. 2011, Gillespie and Roderick 2014). Therefore, if lava flows were sufficiently frequent, they may have left a cumulative genetic imprint even on the time scale herein considered (Aguilée et al. 2009). An example of this process may be represented by the single island endemic beetle *Tarphius*

relictus, which currently occurs exclusively in an isolated forest fragment surrounded by a recent lava flow in which the Algar do Carvão lava tube is located (Borges et al. 2017).

IMPLICATIONS FOR THE GENERAL DYNAMIC MODEL

According to the species pump hypothesis, the combined full island and intra-island geospatial change may increase speciation events driven by both volcanic activity and sea level fluctuations (Vandergast et al. 2004, Roderick et al. 2012, Aguilée et al. 2013, Gillespie and Roderick 2014). Over an ontogenic cycle of a volcanic island, four stages can be identified that influence species equilibria conditions and speciation processes (young island, immature, mature, and old; see Table 2 of Ávila et al. 2019). The short-lasting early emergence stage (phase I, Fig 6b) of volcanic islands is characterized by the highest geospatial dynamics. Because surface areas are relatively small and heights relatively low, the influence of both sea level change and volcanic additions is initially high (Fig. 6b-I). This period is rapidly followed by the growing stage (phase II, which corresponds to the young/immature island stages) that is dominated by spasmodic volcanic additions as the volcanic island becomes larger and higher, and consequently the effect of sea level change on area relatively diminishes (Fig. 6b-II). The species richness dynamics is dominated by volcanogenic area additions, leading to increasing immigration and decreasing extinction rates. Growth of the island during its young and immature ontogenic states continues to push equilibria levels in a positive direction, facilitating species establishment, ecosystem development, and trophic network development (Fig. 6a). Frequent volcanic intra-island area changes are most pronounced and start to influence genetic signatures of settled populations. When an island becomes disconnected from the magma sources (phase III, which corresponds to the mature island stage; Fig. 6b-III), volcanism ceases and the island slowly erodes away while also subsiding on a still flexible but cooling crust (Clague and Cherrod 2014). During phase III, the island's surface is typically characterized by a rough terrain due to erosion (Seijmonsbergen et al. 2019). Later, in the post-eruptive stage of volcanic oceanic islands, the crust cools further and subsidence rates decrease, characterizing phase IV, which corresponds to the old island stage. Owing to the overall lowering of the island, the geospatial influence of sea level fluctuations relatively increased at this time (Fig. 6b-IV). This trend may explain why longer-lasting sea level stands left a signature on present-day endemic species (Norder et al. 2019). This would imply that endemism is promoted on relatively young and active volcanic islands due to the active volcanism and on old, inactive volcanic islands due to the greater influence of sea levels. Towards the final ontogenic stage of volcanic islands when

they are nearly completely submerged, increasing extinction rates lead to a net species loss (Whittaker et al. 2008). Emergent islands (phase I) are smoother, but (Seijmonsbergen et al. 2019) at least disallowing allopatric processes within the island (Borges and Hortal 2009). To evolve endemic species, time is a key requisite (Heaney 2000), and on the Azorean islands the most parsimonious model to explain single island endemism is mostly a linear product of area and time (Borges and Hortal 2009).

It should be noted that subsidence is not necessarily the ontogenic end stage of a volcanic island. Evidence from the oldest and volcanically inactive Azorean island, Santa Maria, shows that after a 3.5 Ma initial phase of subsidence, isostatic and tectonic conditions within the rift setting of the Azorean archipelago led to a prolonged phase of uplift of Santa Maria of 0.04–0.06 mm/yr lasting from 3.5 Ma ago until present (Ramalho et al. 2017, Ricchi et al. 2018). As a result, extensive marine platforms that were shaped during the last 3.5 Ma emerged, and ultimately led to a doubling in size of Santa Maria to its present 96.9 km² (Ávila et al. 2010, Quartau et al. 2016). Such late re-uplift stages are also recorded for some of the Hawaiian Islands with even faster vertical movements than the Azores, up to ~2 mm/yr over the past 200 ka (Huppert et al. 2015). These peculiarities in island dynamics demonstrate that island ontogenies and sea level histories should ideally be resolved on a per island basis (Rijsdijk et al. 2014, Borregaard et al. 2017, Ávila et al. 2019). It is clear, however, that the range in geospatial dynamics on different active volcanic oceanic islands generated by regional volcanogenic sea level and vertical motion dynamics can be considered as different modes of the species pump (in particular having different tempos) that have modified species richness patterns (Aguilée et al. 2018). Quantifying the geospatial dynamics as highlighted here provides a framework to test and assess how these different dynamic regimes are reflected in genetic- or in species-richness patterns (Table 3).

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Authors Contributions:

KFR and SB initiated and led the research, SB analysed the data, all authors contributed equally in discussions and writings. SS curated the data and workflow following the FAIR guidelines for transparent scientific practices <https://www.go-fair.org/fair-principles/>.

Data Accessibility

All GIS data produced for this paper is stored in a geodatabase in a publically assessable data repository:

https://uvaauas.figshare.com/articles/File_geodatabase_containing_Terceira_GIS_data/12230834.

Supplementary Materials:

The following materials are available as part of the online article from

<https://escholarship.org/uc/fb>:

Table S1. Area changes relative to the previous time slice of the total surface area of Terceira and the coastal-lowland area due to volcanism and sea level changes.

Table S2. Raw tabulated data and geospatial analysis results.

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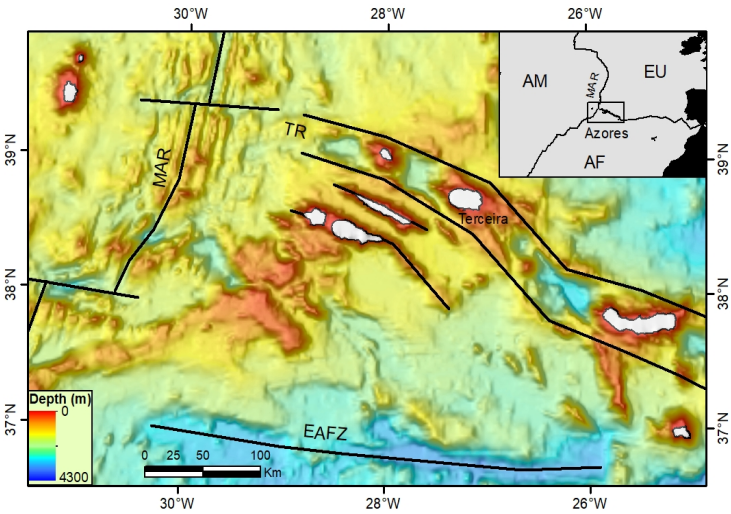
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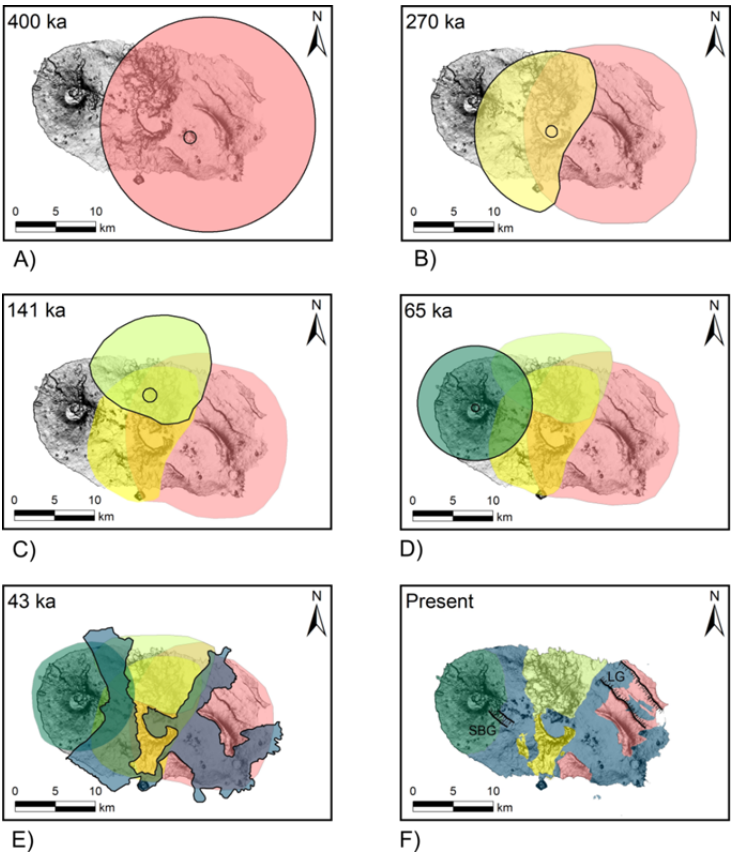
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Figure 1. a) Tectonic structures of the Azores archipelago (islands shown in white). Tectonic structures include Mid-Atlantic Ridge (MAR), the East Azores Fracture Zone (EAFZ), and the Terceira Rift (TR). Bathymetry of the Azores archipelago from Lourenço et al. (1998). Inset: Regional setting of the Azores archipelago within the North American (NA), Eurasian

852 (EU), and Nubian (NU) triple junction. b) Six stages of the development of Terceira, modified
853 after Quartau et al. (2014). The colors indicate relative age per time slice and the black lines
854 the two graben systems: Lajes Graben (LG) and Santa Bárbara Graben (SBG). A) At ~400 ka
855 the Cinco Picos volcano (pink) reached its maximum subaerial development. B) At ~270 ka
856 the Guilherme Moniz Volcano (yellow) emerged on the eastern flank of CPV. C) At ~141 ka,
857 the Pico Alto volcano (light green) emerged at the northern flank of the Cinco Picos volcano.
858 D) At ~65 ka, the Santa Bárbara volcano emerged at the eastern part of the island. E) At ~43
859 ka the Basaltic Fissural Area (blue) started its development and its associated volcanogenic
860 products affected much of the island. F) Current configuration of Terceira Island. See text for
861 further details.

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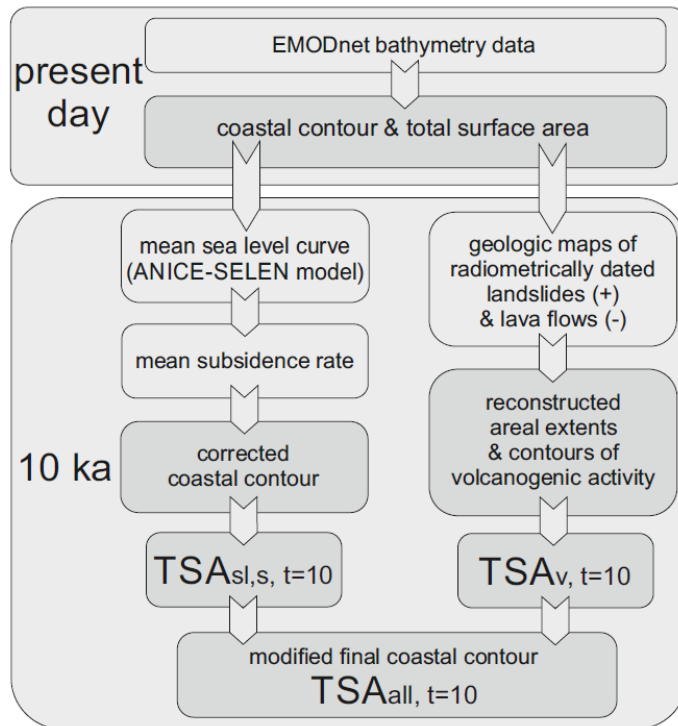


Figure 2. Workflow for the calculation of total surface area (TSA) per time step (t = time in ka before present, s = subsidence, sl = sea level). We corrected the present day coastal contour and surface area for sea level changes and subsidence and calculated the $TSA_{sl,s}$. We also used maps of volcanogenic activity to reconstruct contours for each time step and calculated TSA_v . Finally, we calculated the total surface area of the island after the combined effects of volcanogenic and sea level activity. Data sources and inputs used in this workflow are detailed in Table 1.

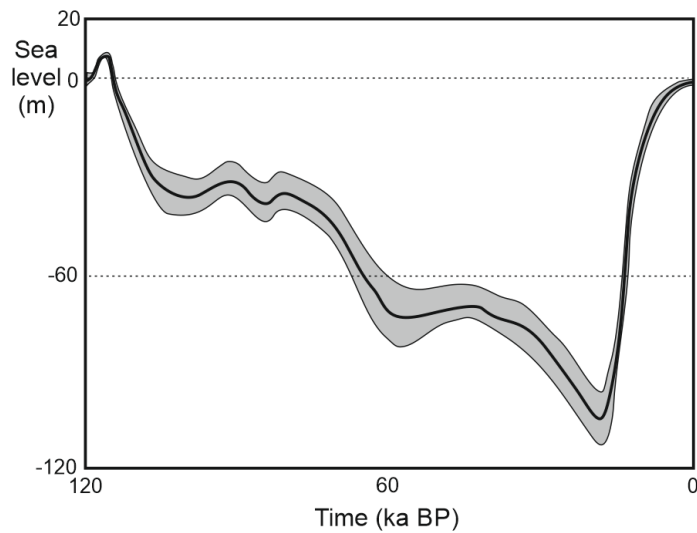
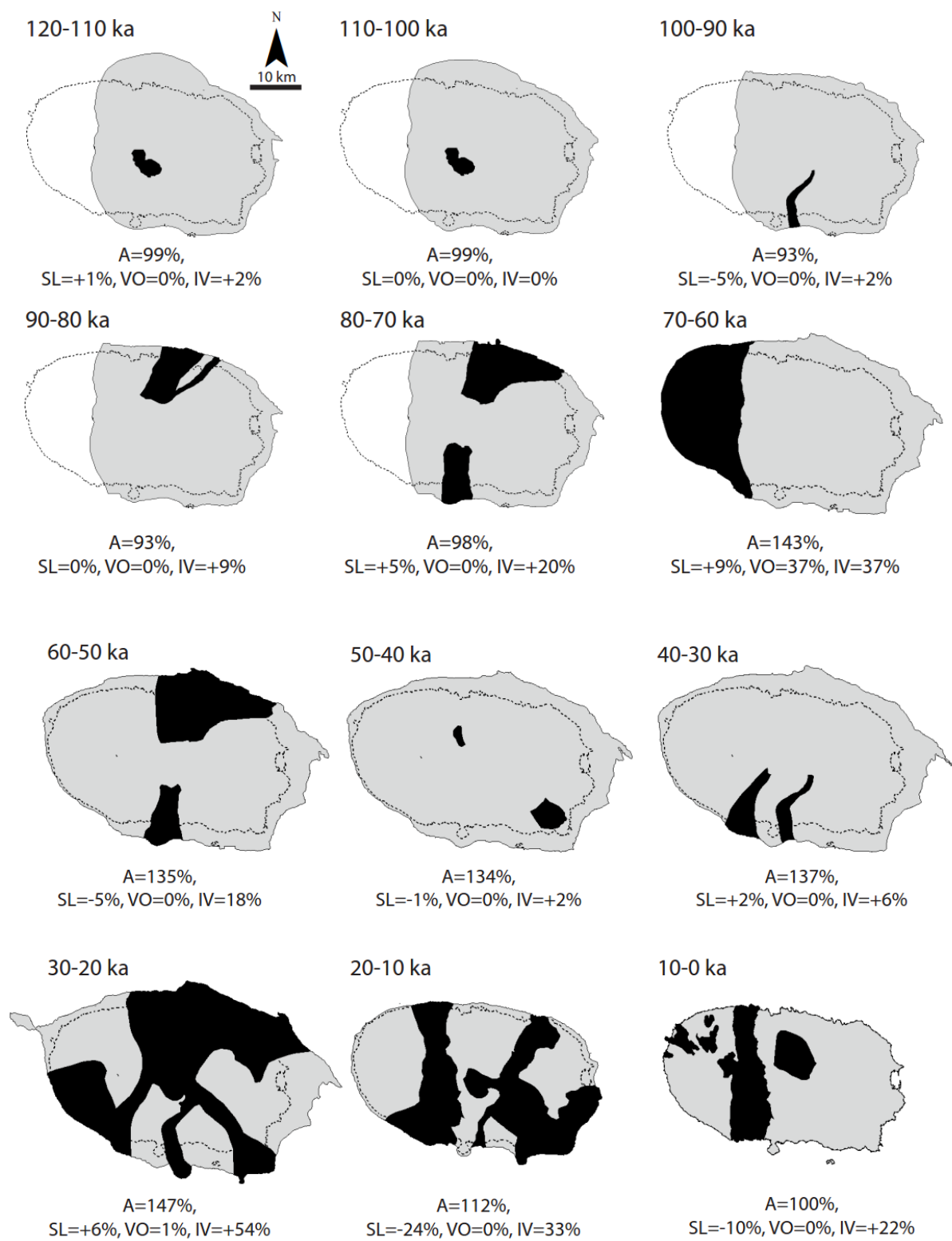


Figure 3. A relative mean sea level (MSL) curve for the Azores was reconstructed using the ANICE-SELEN model for the timespan of the last 120 ka (see Appendix S2). Based on different geophysical parameter settings realistic for the Azorean region, three scenarios for the regional MSL curve are modelled. The output represented by the middle black line is selected in this study as a mean solution. At the Azores, the relative MSL reached -108 m at its lowest point during the LGM period.



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Figure 4. Reconstructions of Terceira from 120 ka until present in time bins of 10 ka. The dotted line is the present-day extent of Terceira. North arrow and scale set in top left reconstruction of Terceira (120–110 ka) are valid for all time slices. The black polygons are

886 volcanogenic flows active during the 10 ka time bin. The area extents of the island are based
887 on published radiometrically dated volcanogenic expansions and flows, the height of relative
888 sea level, and the amount of subsidence (see Table 1 for sources). A = Area change relative to
889 present-day area (401 km²); ΔA_s is contribution of sea level change to total surface area since
890 the previous time bin; ΔA_v is contribution by volcanogenic flows to total surface-area since
891 the previous time bin. Red numbers are area decreases due to sea level rise; IV is percentage
892 of island covered by volcanogenic flows per time bin.

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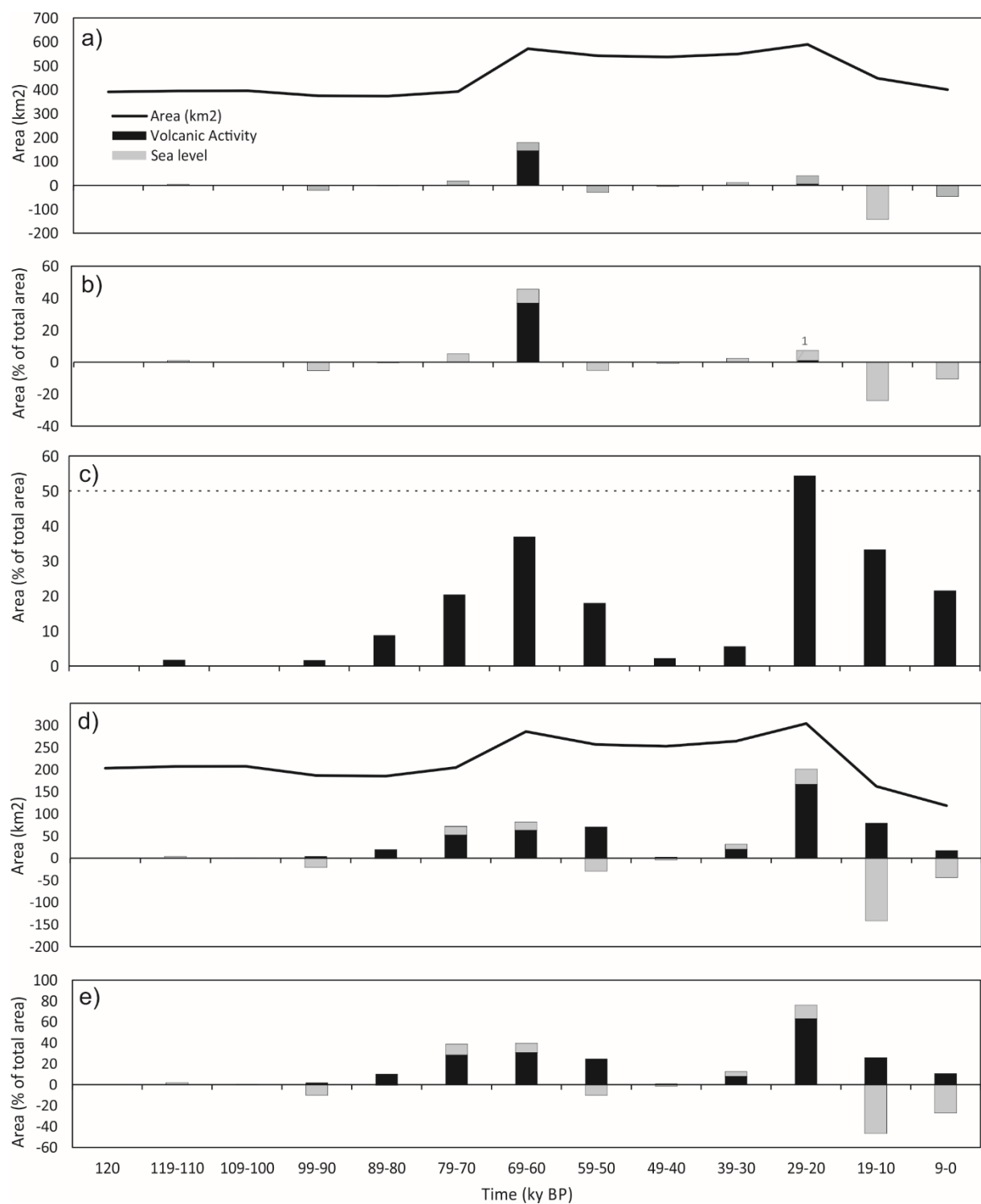


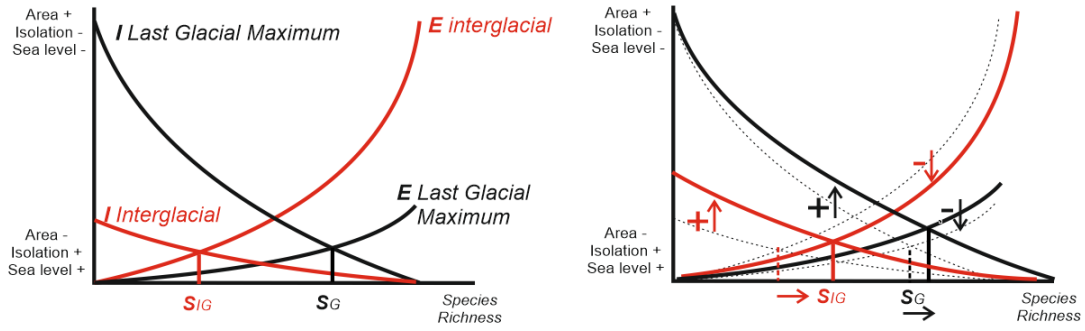
Figure 5. Effects of volcanogenic activity and sea level on total surface area (TSA) of the entire island and TSA of coastal and lowland areas. a) The solid line shows the interpolated net TSA (km²) of Terceira over the 120 ka time span. b) The percentage of total TSA affected by volcanogenic additions (black) and sea level change (gray) per 10 ka time slice. c) The percentage of intra-volcanic area change per 10 ka time slice. Dotted line is 50%. d) Influence

901 of volcanic activity (black) and sea level change (gray) on lowland-coastal areas (km²) per 10
902 ka time slice. e) Percentage of coastal areas influenced by volcanic activity (black) and sea
903 level change (gray) per 10 ka time slice. Area change is relative to the previous time slice.
904 Ages of time bins are truncated to integer numbers but each highest number in a bin includes
905 the rational number until the next integer number (e.g. 29–20 is equivalent to the interval [20,
906 30]).

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a)



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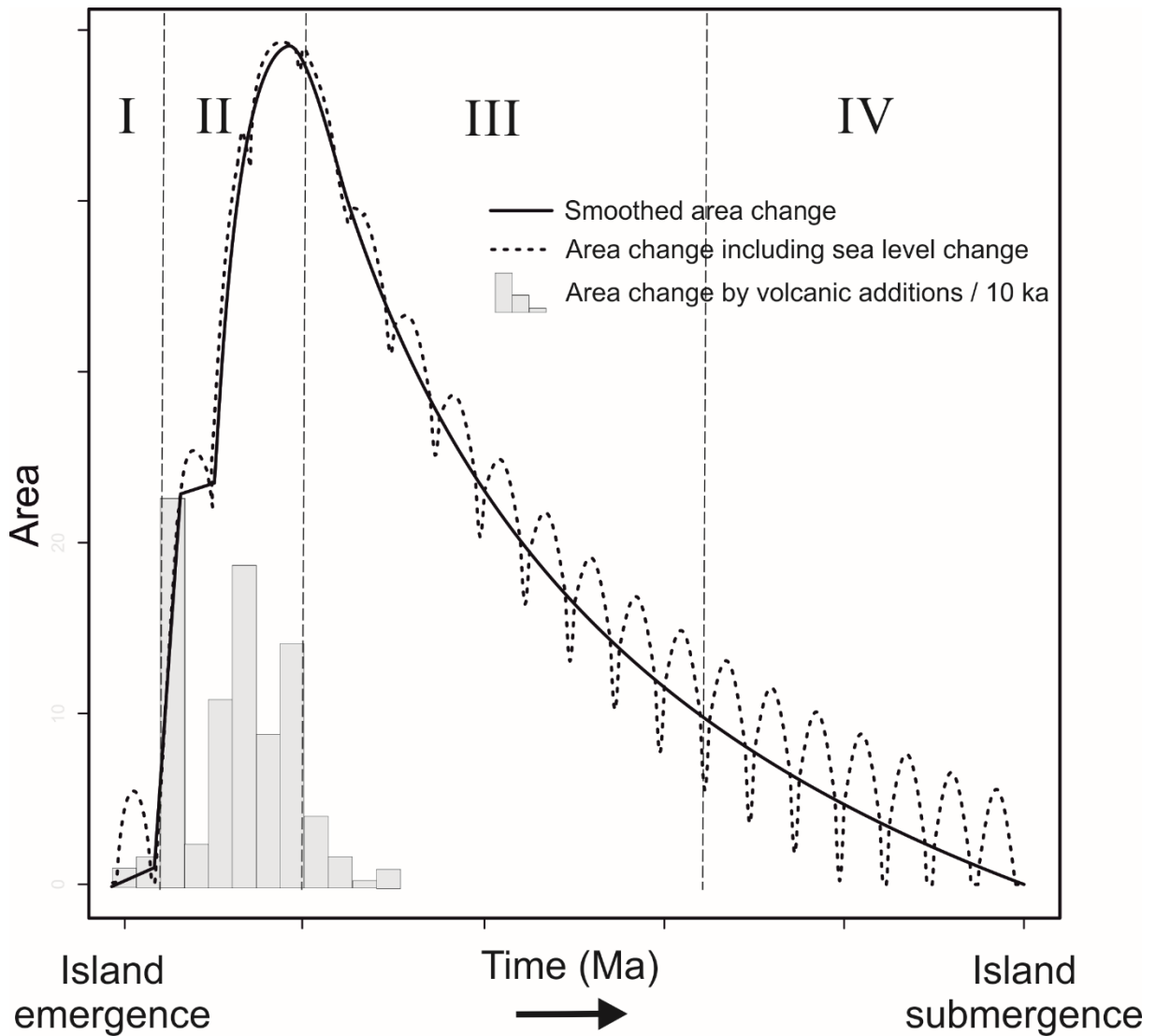


Figure 6. a) Hypothetical effects of volcanic land additions and sea level fluctuations on species richness equilibria, based on Fernández-Palacios et al. (2016). Left panel: species equilibria during interglacial (S_{IG}) and late glacial sea levels (S_G). Right panel: during

volcanic expansions, equilibria shift towards the right, leading to higher species richness during glacial and interglacial periods. Our analysis shows that the expansive period at Terceira Island lasted from 60–20 ka; before and after this period of time, the equilibria richness remained on the lower levels. b) Dynamics of area (and height) changing over time on a hypothetical volcanically active oceanic island. The order of magnitude and frequencies depicted of volcanogenic and sea level mediated surface change is based on values identified in this study. The continuous black line shows the area expansion over time. The dotted line showing asymmetrical sea level fluctuations, which for simplicity are considered unchanging in amplitude and frequency over Ma. The grey bars depict hypothetical volcanogenic additions on the island, some of which lead to area increase. During the earliest emergence stage (phase I) sea level change influences both area and height to a high degree in a similar way. As the island grows larger and higher, the relative influence of sea level decays over time. After decoupling from the magma plume, volcanism ceases and erosion and subsidence take place (phase III). As a result, the island becomes smaller and lower (phase IV), and the influence of sea level change increases over time. The roman numerals are related to the island's geological evolution [see text for discussion related to the island's ontogenic stages, as defined by Ávila et al. (2019)].

931 **Table 1.** Data input and sources used in this study.

Data	Resolution / SI unit	Method	Source
Bathymetric grid for Terceira	1/8 by 1/8 arc-minutes (32 m by 32 m)	EMODnet-portal	European Marine Observation and Data Network 2016
Relative mean sea level	See Figure 3	Output for Terceira of the ANICE-SELEN ice-sheet model	de Boer, Stocchi, and van de Wal 2014
Mean subsidence rate	0.25 mm/yr	Mean subsidence over 342 ka	Quartau et al. 2014
Volcanogenic paleogeography	Palaeo reconstructions based on geological field surveys	Digitizing palaeo-geographic maps of radiometrically dated volcanogenic flows and extents	Zbyszewski et al. 1971, Self 1976, Nunes 2000, Calvert et al. 2006, Hildenbrand et al. 2014, Quartau et al. 2014

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934 **Table 2.** Quantified surface area change of the entire island of Terceira and the coastal-lowland area for the study period (120-0 ka). See
935 supplementary Tables [S1 and S2 for all](#) surface area data.

Process	Rates in % per 10 ka	Total surface area change	Total intra- volcanic surface area change	Coastal-lowland surface area change	Coastal-lowland intra-volcanic surface area change
Volcanic	absolute mean rates	3%	17%	3%	17%
	max rates	37%	54%	31%	63%
	min rates	0-1%	0-2%	0	0-1%
Sea level	absolute mean rates	6%	-	11%	-
	max rates	-24% and +9%	-	-47% and +13%	-
	min rates	0-1%	-	0-1%	-
Combined	mean rates	9%	-	17%	-
	max rates	46%	-	+87% and -28%	-
	min rates	0-1%	-	0-1%	-

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937 **Table 3.** Hypothetical biogeographic and evolutionary effects of island change on terrestrial land locked biota. The relative contributions to
938 extinction, migration, and speciation rates of the geospatial changes are indicated by symbols: ++ high positive rates, + moderate positive rates, 0
939 no effect, - negative rates.

Processes and highest area change rates	Area effect and dynamics	Biogeographic consequences	Extinction rates	Migration rates	Speciation rates
Sea level rise A ~ 10% / 10 ka	Total surface-area reduction Dynamics variable over time; highest effect at the terminus of ice ages	As a result of area reduction, species in the coastal-lowland areas were most affected and may have become extinct or in a phase of extinction debt. Species richness equilibria shifted to lower species richness values. As a result of area reduction, migration rates reduced and range contractions occurred. This may have led to genetic imprints of biota that were affected by area contractions (bottlenecks). Smaller opportunities for allopatry. Decrease in speciation rates because of extinction of incipient species.	++	-	-
Sea level fall A ~25% / 10 ka	Surface-area increase Dynamics variable over time; highest effects during falls when entering maximum glacial extents	During sea level fall, surface areas increased leading to increased immigration rates; range expansions occurred. Extinction rates decreased, consequently speciation rates may have increased.	-	++	+
Sea level stability ~40 ka	Stable surface-area Stability during interglacials and stable periods during glacials	Periods of stable species richness equilibria, possibly modified by speciation events.	0	0	+
Volcanic additions A ~40% / 10 ka	Total surface-area increase Highest dynamics during young emergent stages of volcanic islands	Volcanic additions of the surface area of the island may have contributed to increased immigration rates and increased range expansions, leading to lower extinction and increased speciation rates.	-	++	+

Volcanic flows IA ~ 50% / ka	Sterilizing patches in flow pathways and isolate populations Continuous dynamics peaking during sea level fall and rise stages	Lava flows induced temporal isolation. Coastal-lowland regions were most affected. The duration of this isolation increases with altitude due to lower succession rates, hampering gene flow between vegetation communities for longer periods. This may be reflected by increased genetic divergence with altitude. In addition, repetitive cycles of isolation by volcanogenic flows may lead to accumulation of genetic divergence.	0	0	+
Subsidence	Total surface-area decrease Slow constant rates, although some fluctuations occur which are averaged out over 100 ka	No effect, subsidence of the island was too slow to incur surface area changes that are biogeographically meaningful. But the net effect on reducing the area of the coastal-lowland habitat relative to the pre-last interglacial may have led to conditions of lower equilibria species richness, and thus forced species into extinction that may have persisted during the Last Interglacial.	+	-	-
Volcano-tectonic activity	Creation of local calderas and tectonic basins	Increase of topographic roughness, isolation basins, barriers promoting intra-island population isolation and allopatric divergence. Basins persist but erode away after hotspot plume-detachment.	0	0	+

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Supplementary table S1. Area changes relative to the previous time slice of the total surface area of Terceira and the coastal-lowland area due to volcanism and sea level changes. Volc. = Volcanic, Int.-volc. = Intravolcanic.

Time bins (ka)	Total surface area changes of Terceira								Coastal and lowland area changes						
	Total area (km ²)	Total area (relative %)	Sea level area (km ²)	Volc. area (km ²)	Intra- volc. area (km ²)	Sea level area (%)	Volc. area (%)	Intra- volc. area (%)	Total area (km ²)	Total area (relative %)	Sea level area (km ²)	Volc. area (km ²)	Intra- volc. area (km ²)	Sea level area (%)	Volc. area (%)
10-0	401	100	-47	0	96	-10	0	22	119	100	-44	0	17	-27	0
20-10	448	112	-142	0	196	-24	0	33	162	137	-142	0	79	-47	0
30-20	589	147	34	6	299	6	1	54	304	257	34	2	167	13	2
40-30	549	137	12	0	30	2	0	6	264	223	11	0	20	4	0
50-40	537	134	-4	0	12	-1	0	2	253	213	-4	0	2	-1	0
60-50	541	135	-30	0	103	-5	0	18	257	217	-29	0	71	-10	0
70-60	571	143	34	145	145	9	37	37	286	241	19	31	63	9	31
80-70	393	98	19	0	76	5	0	20	205	173	19	0	53	10	0
90-80	373	93	-1	0	33	0	0	9	185	156	-1	0	19	-1	0
100-90	374	93	-21	0	7	-5	0	2	187	157	-21	0	4	-10	0
110-100	396	99	0	0	0	0	0	0	208	175	1	0	0	0	0
120-110	395	99	4	0	7	1	0	2	207	175	4	0	0	2	0
120	391	98	0	0	0	0	0	0	203	171	0	0	0	0	0
Averages (absolute)						6	3	17						11	3

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942 **Supplementary table S2.** All raw tabulated data and geospatial analysis results (see file).