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# **Title:** Beyond the Last Glacial Maximum: island endemism is best explained by long-lasting archipelago configurations

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**Biosketch:**

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Author contributions: KFR, SJN, RJW, KAT, JMFP, EvL, BHW, and WDK had the original idea. KP, KAT, MRA, AMdFM, RHC, CEP prepared the dataset on land snails. SJN and EvL developed the methodology and analysed the data. SJN coordinated the project and wrote the first draft of the manuscript. All authors contributed substantially to revisions and participated actively in discussions.

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**Short running title (max. 40 characters):** Palaeo-configuration shapes biodiversity

## ABSTRACT

**Aim:** To quantify the influence of past archipelago configuration on present-day insular biodiversity patterns, and to compare the role of long-lasting archipelago configurations over the Pleistocene to configurations of short duration such as at the Last Glacial Maximum (LGM) and the present-day.

**Location:** 53 volcanic oceanic islands from 12 archipelagos worldwide – Azores, Canary Islands, Cook Islands, Galápagos, Gulf of Guinea, Hawaii, Madeira, Mascarenes, Pitcairn, Revillagigedo, Samoa, and Tristan da Cunha.

**Time period:** The last 800 Kyr, representing the nine most recent glacial–interglacial cycles.

**Major taxa studied:** Land snails and angiosperms.

**Methods:** Species richness data for land snails and angiosperms were compiled from existing literature and species checklists. We reconstructed archipelago configurations at the following sea-levels: the present-day high interglacial sea-level, the intermediate sea-levels that are representative of the Pleistocene, and the low sea-levels of the LGM. We fitted two alternative linear mixed models for each archipelago configuration on the number of single-island endemic, multiple-island endemic, and native non-endemic species. Model performance was assessed based on the goodness-of-fit of the full model, the variance explained by archipelago configuration, and model parsimony.

**Results:** Single-island endemic richness in both taxonomic groups was best explained by intermediate palaeo-configuration (positively by area change, and negatively by palaeo-connectedness), whereas non-endemic native species richness was poorly explained by palaeo-configuration. Single-island endemic richness was better explained by intermediate archipelago configurations than by the archipelago configurations of the LGM or present-day.

**Main conclusions:** Archipelago configurations at intermediate sea-levels – which are representative of the Pleistocene – have left a stronger imprint on single-island endemic richness patterns on volcanic oceanic islands than extreme archipelago configurations that persisted for only a few thousand years (such as the LGM). In understanding ecological and evolutionary dynamics of insular biota it is essential to consider longer-lasting environmental conditions, rather than extreme situations alone.

**Keywords (6 - 10):** archipelago configuration, biotic interchange, endemism, flowering plants, glacial–interglacial cycles, land snails, late Quaternary, past environmental change, sea-level oscillations, volcanic oceanic islands.

## INTRODUCTION

Oceanic islands are among the most dynamic systems in the world: they emerge and submerge; they shrink and expand; and they split and merge. Changes in island geography and archipelago configuration are shaped by geological processes (e.g. plate tectonics, island ontogeny, and within-island volcanism) and sea-level fluctuations (Fernández-Palacios *et al.*, 2016). These sea-level fluctuations, driven by glacial–interglacial cycles over the Pleistocene, have influenced all archipelagos and their constituent islands simultaneously. During glacial periods, sea-levels were low and archipelago configurations were often very different: islands had larger surface areas than at present, with some islands fused into larger islands. For example, the Hawaiian islands of Maui, Molokai, and Lanai have repeatedly merged to form a single landmass (the Maui Nui complex; Price, 2004). Islands were also less isolated, with their larger areas reducing inter-island distance and with emerging sea mounts forming stepping stones for dispersal (Ali & Aitchison, 2014; Rijsdijk *et al.*, 2014; Pinheiro *et al.*, 2017). In contrast to these glacial periods, during interglacial high sea-level stands islands were smaller and further apart, as some islands were submerged and palaeo-islands fragmented. Glacial–interglacial cycles have followed a recurrent pattern over the Pleistocene with glacial periods spanning a much longer duration than interglacials (Fig. 1). Therefore, for most of the Pleistocene, sea-levels were lower than today, corresponding to larger and less isolated islands.

It has long been suggested that past archipelago configurations during lower sea-levels have influenced the distribution and evolution of insular biota (Mayr, 1944; Heaney, 1985). Recently, attempts have been made to quantify this relationship (Heaney *et al.*, 2005; Rijsdijk *et al.*, 2013, 2014; Ali & Aitchison, 2014; Fernández-Palacios, 2016; Weigelt *et al.*, 2016; Papadopoulou & Knowles, 2017). However, as Heaney *et al.* (2013) noted, emphasis has been on the relatively short-lasting configuration prevailing during the Last Glacial Maximum (LGM) (e.g. Weigelt *et al.*, 2016). The LGM refers to an exceptional and extreme situation (at approximately 21 ka) of maximum sea-level fall within only the most recent glacial–interglacial cycle of the nine cycles occurring over the last 800 Kyr. Even when summing up the duration of all glacial maxima over the last 800 Kyr, together they would constitute only about 2% of the time elapsed (Fig. 1). The duration of these glacial maxima may have been insufficient to shape the assembly of island biotas and especially their endemic component. Similarly, Porter (1989) asked whether short-lasting extremes such as the LGM and the current interglacial might have received undue attention, and recognized the important role of average Quaternary conditions in landscape evolution and geomorphology. The cyclic nature of Pleistocene sea-level fluctuations leads to alternating periods of island separation and connection, and of shrinking and expanding island areas. Some of these periods lasted longer than others, and some sea-level stands occurred for several instances while others were more exceptional (Fig. 1). Although Porter (1989) suggested the potential relevance of intermediate Pleistocene conditions for understanding biogeographic patterns, we are unaware of any study so far that has quantitatively analysed their relationship. Given that both LGM and current interglacial situations are exceptional and short lasting, it seems important to explore the extent to which present-day distributions of insular biota reflect past environmental conditions that are more representative of the Pleistocene.

Climatic and environmental fluctuations over the Pleistocene affected the extinction, speciation, fragmentation, merging, and population size of biota (Dynesius & Jansson, 2002; Hofreiter & Stewart, 2009; Blois *et al.*, 2013). However, the rates of biogeographical processes shaping island biota during Pleistocene climatic fluctuations varied over time and across taxa (Knowles, 2001b,a; Willis & Niklas, 2004; Shepard & Burbrink, 2009). To complicate matters further, the patterns of island endemism that we observe today might have been shaped by different biotic and abiotic processes which are difficult to distinguish in retrospect (Fig. 2). Despite the difficulty in making generalized statements about the prime response of biota to glacial–interglacial cycles, it is unambiguous that present-day biota consist of a large proportion of species (native and endemic) that have survived several glacial and interglacial periods (Webb & Bartlein, 1992; Hewitt, 2000). Present-day insular species richness might therefore be considered to be the cumulative outcome of varying biogeographical processes operating during different periods in the past (cf. Waldron, 2010; Dynesius & Jansson, 2014).

Volcanic oceanic islands are isolated from continental landmasses and therefore receive few colonists. The corresponding low rate of genetic exchange results in a relatively large number of endemic species confined to a single island (single-island endemics, SIE), or to several islands within the same archipelago (multiple-island endemics, MIE). This contrasts with (non-endemic) native species (N), which also occur outside the archipelago. There are two reasons to suggest that the effect of palaeo-configuration on extant species will be stronger for endemics (especially SIE) than natives (N). First, endemics differ from natives (non-endemic) in their adaptation to the insular environment and archipelagic setting; endemic species have frequently undergone a longer duration of *in situ* insular evolution (Whittaker & Fernández-Palacios, 2007; Warren *et al.*, 2015; Whittaker *et al.*, 2017) than non-endemic natives (N) and have therefore experienced glacial–interglacial cycles for a longer period (in the case of palaeo-endemics insular evolution was not the only process, but the idea of experiencing glacial–interglacial cycles for longer periods still applies). Second, taxa frequently exhibit high levels of endemism as a consequence of low levels of gene flow with neighbouring landmasses (Kisel & Barraclough, 2010). Further, low gene flow is often a consequence of a low dispersal capacity. Such poor-dispersing taxa may be expected to be impacted more profoundly by changes in the geographic configuration of archipelagos than good dispersers (cf. Borges & Hortal 2009). Such enhanced impact is due to the lower chances of successful colonization of another island and the narrower habitat availability within their dispersal range. However, the degree to which archipelago configuration influences patterns of endemic species richness probably differs among taxa (e.g. resulting from differences in dispersal capabilities (Claramunt *et al.*, 2012), number of life cycles (Comes & Kadereit, 1998), population sizes, and ecological requirements). Because of their isolated nature and high levels of endemism, volcanic oceanic islands are excellent study systems for understanding the role of long-term geographic processes on speciation and species richness, such as glacial–interglacial changes in archipelago configuration (Warren *et al.*, 2015).

Here, we explore to what extent the persistence and recurrence of different archipelago configurations have left an imprint on present-day species richness on oceanic islands of volcanic origin. Archipelago configuration refers to any combination of area and connectedness (or its antonym: isolation) of islands within the same archipelago (palaeo-configuration refers to an archipelago configuration in the past). We focus here exclusively on changes in archipelago configuration driven by sea-level fluctuations, which have affected all islands globally (Norder *et al.*, 2018). Although island bathymetry is also shaped by geological processes (such as volcanic eruptions, uplift, subsidence, and erosion), these are not the main focus of our analysis because they are highly island and archipelago specific (Whittaker *et al.*, 2008; Triantis *et al.*, 2016b). We restrict the analysis to volcanic oceanic islands to avoid the confounding effect of different abiotic conditions and archipelago configuration dynamics among other island types, such as archipelagos of atolls, land-bridge continental shelf islands and continental fragments (Whittaker & Fernández-Palacios, 2007; Warren *et al.*, 2010; Fernández-Palacios *et al.*, 2016; Ali, 2017). We focus on two contrasting taxa with generally good availability of data, land snails and angiosperms, because they differ in terms of dispersal capabilities, ecological requirements, and endemism level (which, on volcanic oceanic islands, is much higher for land snails than for angiosperms; Groombridge 1992; Whittaker & Fernández-Palacios 2007). Specifically, we test three hypotheses, that: 1) the signal of palaeo-configuration is stronger for SIE than for those that have wider distributions (i.e. MIE and N); 2) for SIE, palaeo-configurations that are more representative of the Pleistocene, associated with intermediate sea-levels, will have left a stronger signal than extreme configurations of a short duration (such as the Last Glacial Maximum); and 3) land snails will be more affected by past archipelago configurations than angiosperms because they have more restricted distributions and often have lower dispersal capabilities. We test all hypotheses against the classical expectation that present-day richness is best explained by current archipelago configuration.

## MATERIALS AND METHODS

### Islands and archipelagos

In total, 53 volcanic oceanic islands representing 12 archipelagos (Azores, Canary Islands, Cook Islands, Galápagos, Gulf of Guinea, Hawaii, Madeira, Mascarenes, Pitcairn, Revillagigedo, Samoa, and Tristan da Cunha) were included. Our criteria for inclusion of an island were: (i) species data were available for both land snails and angiosperms; (ii) islands are oceanic and of volcanic origin.

### Species richness data

Species richness data for land snails for each island of the dataset were compiled from existing literature and species checklists (references in Table S1 in Supporting Information). Infra-specific entities were grouped into their respective specific taxonomic rank. Species status was standardized based on MolluscaBase (2017; http://www.molluscabase.org). We considered only islands for which complete lists were available. Recorded extinct species were included in the data set, while species presumed to be introduced were excluded (Cameron *et al.*, 2013; Triantis *et al.*, 2016a). Land snails were classified according to chorotype (a group of species with their distribution restricted to a certain region; see Table 1 for an overview of chorotype acronyms) as: native non-endemic ($N_S$), multiple-island endemic ($MIE_S$), and single-island endemic ($SIE_S$).

Angiosperm richness data were obtained from Weigelt *et al.* (2016) for native non-endemics ($N_P$), and single-island endemics ($SIE_P$). Weigelt *et al.* (2016) also included angiosperm species endemic to past island units at a sea-level of -122m ($PIE_P$). In a similar way, land snail species endemic to past island units ($PIE_S$) at various sea-levels (see below) were initially calculated. However, for both land snails and angiosperms, the correlation between SIE and palaeo-island endemics (PIE) was $r > 0.99$, suggesting that for oceanic islands of volcanic origin, this distinction does not provide additional insights (Table S2 and S3 in Supporting Information). Therefore, we only consider present-day chorotypes (i.e. N, MIE and SIE classes, but not PIE) for further analysis.

### Palaeo-configuration data

We considered three archipelago configurations (Fig. 3; Table 1): 1) current configuration at the present-day high interglacial sea-level (hereafter: “highest”) with small island area and small connectedness (i.e. large isolation); 2) palaeo-configuration at intermediate sea-levels (hereafter:

“intermediate”) with intermediate island area and connectedness; 3) palaeo-configuration at minimum sea-level (hereafter: “lowest”) with largest island area and largest connectedness.

To represent long-term palaeo-configuration at intermediate sea-levels (SLI), we calculated two alternative summary measures: $SLI_{FREQ}$ for the most recurrent, and $SLI_{MED}$ for the most persistent sea-level. Both were calculated for the last nine full glacial–interglacial cycles using the estimated duration of interglacials from Tzedakis *et al.* (2012) and sea-level data from Bintanja *et al.* (2005). Over these nine glacial–interglacial cycles (between 787.9 ka and 11.2 ka), sea-levels between -90 m Mean Sea Level (MSL) and -80 m MSL occurred most frequently (16% of the time sea-levels were within this interval; Fig. 1). We used the central value (-85 m MSL) of this interval to represent the most frequent long-term sea-level stand ($SLI_{FREQ}$). For 32.5% of the time, MSL was below -85 m MSL. Over the same nine glacial–interglacial cycles, the median sea-level ($SLI_{MED}$) was -65m MSL (the mean is -64 m MSL). For 50% of the time, MSL was below -65 m MSL; for 9.5% of the time sea-levels were between -70 m and -60 m MSL (Fig. 1). To reconstruct palaeo-configuration during the lowest sea-levels (SLL) we used two sea-level stands: 1) the most recent estimate for the LGM low stand ($SLL_{GM}$) of -134 m MSL (Lambeck *et al.*, 2014); and 2) the sea-level low stand of -122 m MSL ($SLL_{-122}$) selected by Weigelt *et al.* (2016). To represent archipelago configuration at highest sea-levels (SLH), we used the present-day sea-level (although for 1.5% of the last ~800 Kyr sea-levels were higher; Fig. 1).

We obtained the palaeo-configuration of all islands at the respective sea-level stands ($SLI_{MED}$, $SLI_{FREQ}$, $SLL_{-122}$, and $SLL_{GM}$) from the Palaeo-Islands and Archipelago Configuration (PIAC) database (Norder *et al.*, 2018). For each palaeo-configuration, we calculated delta area (dA; km$^2$) for each reference sea-level as the log-transformed absolute difference between current area and palaeo-area. Palaeo-connectedness (PC) was calculated for each respective sea-level stand as the number of present-day islands that were connected within a single palaeo-island at a lower sea-level. For the highest sea-level we used the current area (CA) from the Database of Global Administrative Areas (GADM; http://www.gadm.org/version1), as reported in Weigelt *et al.* (2016). Current isolation (CI) was calculated as the distance to the nearest other island for which species data were available. Since island age is known to influence endemism patterns on individual islands and archipelagos (Peck, 1990; Whittaker *et al.*, 2008), we tested for correlation (herein Pearson’s correlation) between each of the aforementioned archipelago configuration variables and island age (island ages and sources in Table S4 in Supporting Information). All correlations were low and non-significant (Table S5 and Figure S1a-h in Supporting Information). This is unsurprising; although volcanic and erosional processes show some age-progressive trends (Whittaker *et al.*, 2008), it is problematic to stereotype the consequences of such trends for area and connectivity through sea-level fluctuations. The aim of the current study is to assess biotic responses to sea-level driven changes in archipelago configuration, which is a necessary in-between step towards an integrated understanding of the role of archipelago dynamics and complex island geologies in shaping island biodiversity (Borregaard *et al.*, 2017).

## Statistical analyses

All the statistical analyses conducted in this study were implemented within the R statistical programming environment (R Core Team, 2016). To test our first hypothesis ('H1: palaeo-configuration per chorotype') – that the role of palaeo-configuration is stronger for SIE than for MIE and N – we fitted linear mixed models separately for each chorotype. In each model, we used archipelago identity as a random effect (Bunnefeld & Phillimore, 2012; Cameron *et al.*, 2013) and used a Poisson error structure. Each of the models for palaeo-configuration consisted of the following fixed effects: current area (CA), delta area (dA), and palaeo-connectedness (PC) at either intermediate or lowest sea-levels. We adopted linear mixed models with archipelago identity as random effect to account for non-independence of data due to the underlying archipelagic structure (Bunnefeld & Phillimore, 2012; Triantis *et al.*, 2015; Borregaard *et al.*, 2017). For example, subsidence rates and erosion regimes (which are mainly climate-driven) vary greatly between archipelagos (Triantis *et al.*, 2016b). We fitted the models with the lmerTest R package, which is a wrapper around lme4 (Bates *et al.*, 2015).

To test our second hypothesis ('H2: intermediate configuration and SIE') – that the role of intermediate palaeo-configurations on SIE is stronger than extreme configurations – we included six alternative archipelago configuration models, including two for each of the three sea-levels considered (lowest, intermediate, highest; Fig. 3). For the intermediate, most representative, sea-level we fitted separate models for the median and most frequent sea-levels ($SLI_{MED}$, $SLI_{FREQ}$). For the lowest sea-level (corresponding to extreme configurations of short duration) we fitted separate models for -134 m MSL ($SLL_{GM}$, Lambeck *et al.* 2014) and a sea-level of -122 m MSL ($SLL_{-122}$, Weigelt *et al.* 2016). In addition to the models for intermediate and lowest sea-levels, we included two models for the present-day high sea-level. The first model ($SLH_{CA}$) consists of current island area (CA) as the only fixed effect. The second model ($SLH_{CACI}$) consisted of two fixed effects: current area (CA) and current isolation (CI). We have included this alternative model because those islands with large palaeo-connectedness might also be more proximate today.

To test our third hypothesis ('H3: palaeo-configuration per taxa') – that land snails are more affected by palaeo-configuration than angiosperms – we fitted the six models ($SLH_{CA}$, $SLH_{CACI}$, $SLI_{MED}$, $SLI_{FREQ}$, $SLL_{GM}$, $SLL_{-122}$) for each chorotype of land snails ($N_S$, $MIE_S$, and $SIE_S$) and angiosperms ($N_P$, $SIE_P$).

To make an informed decision about which archipelago configurations were most relevant in ecological terms, we adopted two complementary approaches to indicate which configuration had strongest statistical support: 1) we assessed for each model the total variance explained, and the proportion of variance explained by archipelago configuration; 2) we ranked significant models based on Akaike's Information Criterion corrected for sample size (AICc). For the first approach, we calculated the marginal and conditional $R^2$ (Nakagawa & Schielzeth, 2013) for each model per chorotype. We choose these metrics because they are appropriate within a linear mixed model framework (Nakagawa & Schielzeth, 2013). The conditional r-squared ($R^2_C$) provides a measure of the variance explained by the full model (fixed and random effects). The marginal r-squared ($R^2_M$) indicates the variance explained by archipelago configuration (fixed effects). The difference between marginal and conditional $R^2$ was calculated to reflect the variance explained by archipelago identity (see Ibanez *et al.* 2018 for a similar approach). For the second approach, we started by selecting those models for which all individual predictors were significant at $P < 0.05$ to arrive at a set of 'suggestive, but inconclusive' models (Murtaugh, 2014). The remaining models were ranked based on AICc. Although a cut-off rule of $\Delta$ AIC > 2 relative to the best model is often used, it is an arbitrary rule and models with a $\Delta$ AICc value between 2 and 7 should not be neglected (Burnham *et al.*, 2011). It should be noted that AICc is not an absolute measure of fit (Symonds & Moussalli, 2011) but is a metric that balances model complexity and model fit (Mundry, 2011). Therefore, Burnham et al. (2011) recommend inclusion of a metric to quantify how well models perform (we choose $R^2_C$ and $R^2_M$). To summarize, we calculated $R^2_C$ to assess goodness-of-fit of the full model, $R^2_M$ to assess the variance explained by archipelago configuration, and $\Delta$ AICc to assess model parsimony.

## RESULTS

### Description of the data

While all islands were larger than today during lowest and intermediate sea-levels, each island has a unique area change pattern in response to sea-level fluctuations (Fig. S2a-c in the Supporting Information). Consider, for example, these four islands, which today have a similar area of roughly 140 km$^2$: Socorro (Revillagigedo), Flores (Azores), Tutuila (American Samoa), and Príncipe (Gulf of Guinea). At $SLI_{MED}$ their sizes were respectively 179%, 154%, 224%, and 516% of the present-day. At $SLL_{GM}$, the respective values were 219%, 240%, 308%, and 951% (cf. Norder *et al.* 2018). Also palaeo-connectedness responded very differently across islands following the same amount of sea-level change. At the median and most frequent sea-levels ($SLI_{MED}$, $SLI_{FREQ}$) seven and eight of the 53 present-day islands were connected to another island within their archipelago, respectively. At a sea-level of -122 m MSL ($SLL_{-122}$) and the Last Glacial Maximum ($SLL_{GM}$), 12 and 13 islands were connected. Pearson's correlations of the predictor variables palaeo-connectedness and palaeo-area range from *r* = 0.28 to *r* = 0.55, with the highest values for palaeo-area and palaeo-connectedness at the same sea-level stand (Table S6). Palaeo-connectedness values at different sea-levels are strongly correlated, with lowest correlations between $SLI_{MED}$ and $SLL_{GM}$ (*r* = 0.67) and highest correlations between $SLL_{-122}$ and $SLL_{GM}$ (*r* = 0.97). The correlations between palaeo-area at different sea-levels show the same pattern: palaeo-areas at $SLI_{MED}$ and $SLL_{GM}$ are least correlated (*r* = 0.87), while the palaeo-areas at $SLL_{GM}$ and $SLL_{-122}$ can be considered identical (*r* > 0.99) for our dataset of 53 volcanic oceanic islands.

For land snails, our data represented 1903 species, including 1430 single-island endemics ($SIE_S$), 302 multiple-island endemics ($MIE_S$) and 171 native species ($N_S$). In total, 1627 single-island endemic angiosperms ($SIE_P$) were included in our dataset. Native species richness for angiosperms could not be calculated from the available data because we only had data on species richness per island but no species identities (see Weigelt *et al.* 2016). For land snails, the mean proportion of each chorotype across islands was 28.7% for $N_S$, 34% for $MIE_S$, and 37.2% for $SIE_S$. Mean inter-island chorotype proportion for angiosperms was 92.9% for $N_P$, and 7.1% for $SIE_P$.

### The role of archipelago configuration differs between chorotypes and taxa

We found that the variance in species richness that was explained by palaeo-configuration was larger for SIE than for species with a wider distribution, supporting H1 (palaeo-configuration per chorotype). The variance explained by palaeo-configuration ($R^2_M$ of $SLL_{GM}$, $SLL_{-122}$, $SLI_{FREQ}$, $SLI_{MED}$) was 30–47% for $SIE_S$ and 33–41% for $SIE_P$ (Fig. 4). For the more widespread chorotypes, the corresponding values were generally much lower: only 2–3% for $N_S$, 13–20% for $MIE_S$, and 22–27% for $N_P$. Comparing models in terms of AICc revealed a similar pattern. For $SIE_S$ and $SIE_P$ some palaeo-configuration models were within Δ AICc < 7, while for $MIE_S$, $N_S$, and $N_P$, there are no significant palaeo-configuration models within this range. These P-values were rather unrestrictive because consistent overdispersion was present across models. As a result, the subset of significant models initially included before AICc ranking was relatively broad.

The largest part of the variance in SIE richness for both taxa could be explained by palaeo-configuration at intermediate sea-levels, supporting H2 (intermediate configuration and SIE). Although for $SIE_S$, the model $SLI_{FREQ}$ had the lowest AICc, the largest part of the variance (73%) was explained by $SLI_{MED}$. Despite this model being outside Δ AICc < 7, it is the only model in which the variance explained by palaeo-configuration was larger than that explained by archipelago identity (47% and 26% respectively; Fig. 4). Also for $SIE_P$, the model $SLI_{MED}$ explained the largest part of the variance (86% of which 41% was explained by archipelago configuration and 45% by archipelago identity; Fig. 4). In addition, this model also had the lowest AICc. As expected, palaeo-configurations at intermediate sea-levels were able to explain a larger part of the variance than extreme configurations of a short duration. The performance of models for palaeo-configuration at lowest sea-levels was generally poorer. For $SIE_S$, the variance explained by palaeo-configuration at lowest sea-levels (32% for $SLL_{-122}$, 30% $SLL_{GM}$) was similar to $SLI_{FREQ}$ (33%) but lower than $SLI_{MED}$ (47%); the palaeo-configuration models at lowest sea-level were within Δ AICc < 7 (Fig. 4). Just as for $SIE_S$, the variance in $SIE_P$ explained by palaeo-configuration at lowest sea-level (34% for $SLL_{-122}$, 33% $SLL_{GM}$) was similar to $SLI_{FREQ}$ (34%), but lower than $SLI_{MED}$ (41%). However, for $SIE_P$, none of the models for palaeo-configuration at lowest sea-level was entirely significant.

The directionality of the relationships between the predictors in palaeo-configuration models (current area, CA; delta area, dA; palaeo-connectedness, PC) is consistent across taxa (Fig. 5): richness of $SIE_S$ and $SIE_P$ increases with current area and delta area, but decreases with palaeo–connectedness. However, the effect size of current area and delta area show opposing patterns for SIE angiosperms and land snails: current area has a larger effect on $SIE_P$, while delta area has a larger effect on $SIE_S$ (Fig. 5). This is partly in line with our expectation that land snails would be more affected by palaeo-configurations than angiosperms ('H3: palaeo-configuration per taxa'). The contrast in effect sizes of current area and delta area are consistent for other palaeo-configurations (Table S7 in Supporting Information).

## DISCUSSION

Our results are consistent with the hypothesis that palaeo-configurations at intermediate sea-levels – which are representative of the Pleistocene – have left a stronger imprint on single-island endemic land snail ($SIE_S$) and angiosperm ($SIE_P$) richness patterns on volcanic oceanic islands than extreme archipelago configurations. This suggests that the relatively short-lasting configurations that have prevailed during the Last Glacial Maximum (LGM) are not sufficient to explain endemism patterns on volcanic oceanic islands.

### Palaeo-configuration at different spatial scales of endemism

Our results conform to our first hypothesis that the signal of palaeo-configuration is stronger for SIE than for MIE and N. The proportion of the variance that could be explained by palaeo-configuration ($R^2_M$ at intermediate and lowest sea-level) was indeed larger for SIE than it was for MIE and N. Ranking significant models based on AICc shows that for SIE, both models with palaeo-configuration and current configuration are within the set of most parsimonious models. In contrast, for $MIE_S$, $N_S$ and $N_P$ the set of most parsimonious models only contains configurations at present-day (highest) sea-level. However, for these more widespread chorotypes, the variance explained by archipelago configuration was generally low (especially for $N_S$ and $MIE_S$). For all archipelago configuration models across chorotypes (except $SLI_{MED}$ for $SIE_S$), the largest part of the variation is explained by the identity of the archipelago (random effects in the model), suggesting that other factors besides archipelago configuration (e.g. climate, geological dynamics, distance from the mainland, island age, human impact, etc.) probably play an important role in shaping current diversity patterns on oceanic islands. These findings suggest that archipelago configuration is an important factor related to patterns of single-island endemics but less so for (non-endemic) natives. Furthermore, for SIE, those palaeo-configurations which are representative of the Pleistocene are more relevant than short-lasting configurations (Fig. 6).

**Persistence and recurrence of palaeo-configurations**

Palaeo-configuration at lowest (glacial maxima) sea-level had a weaker explanatory power on $SIE_S$ than intermediate configurations (noting the small Δ AICc between models for $SIE_S$), and a weak non-significant effect on $SIE_P$. This supports our second hypothesis that palaeo-configurations that are more representative of the Pleistocene, associated with intermediate sea-levels, have left a stronger signal than extreme configurations of a short duration. Our findings contrast those of Weigelt *et al.* (2016), who reported that the number of $SIE_P$ could be explained by palaeo-configuration at a sea-level of -122 m below today. The difference might be explained by the fact that we selected a subset of angiosperm data exclusively from volcanic oceanic islands, thus preventing confounding geological or genetic effects derived from mixing with islands of other geological origins (Whittaker & Fernández-Palacios, 2007; Ali, 2017). On continental fragments in particular, differences in bathymetry lead to dissimilar responses to cyclic sea-level fluctuations. The granitic Seychelles are a case in point illustrating the drastic area change and palaeo-connectedness of continental fragments (Warren *et al.*, 2010). However, the most important reason for the poor performance of models based on palaeo-configuration at lowest sea-levels compared to intermediate configurations is probably related to the short lasting and interruptive character of glacial maxima.

Intermediate palaeo-configurations were reconstructed at the median sea-level ($SLI_{MED}$) and the most frequent sea-level ($SLI_{FREQ}$). Palaeo-configuration at $SLI_{MED}$ explained most of the variance ($R^2_M$) for both $SIE_S$ and $SIE_P$. Also in terms of AICc intermediate palaeo-configurations performed best for SIE, however, for $SIE_S$, $SLI_{FREQ}$ had the lowest AICc, while for $SIE_P$, $SLI_{MED}$ had the lowest AICc. Although both $R^2_M$ and AICc suggest that it is worthwhile to consider palaeo-configurations at intermediate sea-levels for understanding present-day patterns of SIE richness, they do not provide conclusive evidence regarding the best choice of approach. We anticipate that future studies focussed on specific archipelagos (and other taxa) will shed more light on which sea-levels are most relevant in a particular archipelagic context. We hypothesize that the answer will depend on the sea-level thresholds at which island area and connectedness change significantly.

### Contrasting roles of palaeo-area and palaeo-connectedness across taxa

Sea-level fluctuations in the past have modified island area and isolation simultaneously. However, when considering these elements of archipelago configuration separately, it becomes clear that SIE richness of both land snails and angiosperms increases with current area and delta area, but decreases with palaeo-connectedness. Although current area and delta area both hold a positive relationship with SIE$_{S}$ and SIE$_{P}$ richness, delta area has a larger statistical effect on SIE$_{S}$, while current area is most important for SIE$_{P}$ (cf. Kreft *et al.* 2008). This finding is consistent with our third hypothesis that land snails will be more affected by palaeo-configuration than angiosperms. As already mentioned in our introduction, this pattern may be explicable in relation to general differences in speciation and dispersal between the two taxa; land snails tend to be able to speciate at smaller spatial scales than most angiosperms (Kisel & Barraclough, 2010). Hence land snails can produce more SIE in any given island area, and show stronger effects of island area being formerly larger than do angiosperms. Conversely, a greater mobility of plants could connect “would-be endemics” or replace them with fresh colonists and as such reduce the effect of area change. This reasoning seems in line with the chorotype proportions for SIE in our dataset, which are high for land snails and low for angiosperms. An interesting avenue for future research would be therefore to further explore the underlying mechanisms that might explain the differential response of both taxa to palaeo-area. Our results indicate a negative relationship between palaeo-connectedness and SIE richness of both taxa. The decreasing number of SIE$_{S}$ and SIE$_{P}$ with palaeo-connectedness might result from higher levels of gene flow, hindering diversification into distinct lineages (cf. Heaney *et al.* 2005). This agrees with a recent study on the Puerto Rico Bank where repeated connectedness and fragmentation impeded divergence and speciation of ground crickets (Papadopoulou & Knowles, 2017). Alternatively, elevated biotic interchange following climatic fluctuations and geographical rearrangements over the Pleistocene might have resulted in local extinctions (Vermeij, 1991). Weigelt *et al.* (2016) also found a negative relationship between palaeo-connectedness and SIE$_{P}$ and concluded that this result falsifies the species pump hypothesis, i.e. that repeated separation and connectedness drive speciation (Qian & Ricklefs, 2000; Gillespie & Roderick, 2014). However, it may also be explained by the fragmentation of a population of a SIE species on a palaeo-island into subpopulations, changing the chorotype from SIE to MIE as sea-levels rose towards the current interglacial high sea-level (Fig. 2).

Archipelago configuration models containing palaeo-connectedness as predictor performed better for SIE than those containing current isolation. This suggests that the actual fusion and splitting of islands may be more important as a moderating factor reducing numbers of SIE than the proximity of islands within an archipelago. Our findings correspond to Heaney *et al.* (2005) who found little genetic variation among mammal populations on Philippine islands that were merged during lower sea-levels, while populations on islands that were never connected (but sometimes in close vicinity) showed more genetic variation. A similar conclusion was reached by Rijsdijk *et al.* (2014) who found that the proportion of MIE/SIE plants shared between Fuerteventura and Lanzarote (which were joined in the palaeo-island Mahan) is significantly larger than all other Canary island pairs that were never connected.

### Island- and archipelago specific factors

Glacial–interglacial cycles over the Pleistocene have simultaneously influenced the geography of all islands globally. However, there are many regional factors shaping differences in insular biodiversity patterns among and within archipelagos. Islands commonly occur in archipelagos that exhibit biogeographical coherence, i.e. similar patterns, in species diversity as a result of shared climate, distance from the potential species pool, intra-archipelagic isolation and geological history (Heaney *et al.*, 2013; Triantis *et al.*, 2015; Ali, 2017). In our analyses archipelago identity explained a large part of the variance (random effect in linear mixed models), highlighting the importance of accounting for among-archipelago variation (Bunnefeld & Phillimore, 2012; Cameron *et al.*, 2013).

Regarding the within-archipelago differences, geological dynamics arguably have a large role in shaping island geography and archipelago configuration. For example, geological processes of plate tectonics, volcanism, subsidence and erosion may drive major changes in island geography and archipelago configuration (Gillespie & Roderick, 2002; Price *et al.*, 2002; Stuessy, 2007; Whittaker *et al.*, 2008; Gillespie & Clague, 2009; Carracedo, 2014; Borregaard *et al.*, 2017; Whittaker *et al.*, 2017). While general developmental trends may be identified for particular classes of oceanic islands (Whittaker *et al.*, 2008, 2017), in practice, island ontogeny and volcanic activity are island specific. For example, the eight main islands of the Hawaiian archipelago show linear age progression from east to west and range in age between 0.5 Ma (Hawaii Island) and 5.1 Ma (Kauai). Hawaii itself is the only island that is volcanically active, all others being disconnected from the hotspot and inactive for at least 0.75 Myr. This contrasts with the complex geological setting of the Azores, with a western group of two islands located on the North American plate, and a central and eastern group (of five and two islands, respectively) located at the junction between the Eurasian and Nubian lithospheric plate (Ramalho *et al.*, 2017), and no linear age progression from one side of the archipelago to the other (Ávila *et al.*, 2016). In addition, some islands in our dataset are younger than the last nine glacial–interglacial cycles (~800 ka) we used to calculate the most frequent and median sea-levels. However, due to the recurrent character of sea-level oscillations, later stages of these cycles will nonetheless have affected younger islands. Incorporating glacial–interglacial driven changes in island geography becomes challenging as longer timescales are considered because they overlap and interact with geological dynamics. For future studies it will be important to include greater detail on regional geological dynamics that have shaped archipelago configuration in the past.

## CONCLUSION

To our knowledge this is the first time that the effects of long- and short-lasting archipelago configurations on species richness patterns have been compared at a global scale across multiple archipelagos. Although we included in our study 53 volcanic oceanic islands with different geological histories, we still found a consistent pattern for the two taxa considered: palaeo-configurations at intermediate sea-levels have left a stronger imprint on single-island endemic richness patterns than extreme archipelago configurations of short duration, whereas non-endemic (native) species richness was generally poorly explained by palaeo-configuration. These findings support intermediate palaeo-configurations as most relevant for understanding present-day patterns of endemic biodiversity across volcanic oceanic islands. Further research is required to explore how these environmental dynamics may have influenced other archipelagos and taxa. Previous studies have acknowledged that islands were larger and less isolated in the past, but have generally overlooked the potential significance of the duration of different palaeo-configurations. Our results suggest that for understanding evolutionary dynamics of insular biota it is relevant to look beyond extreme palaeo-configurations that persisted for only a few thousand years (such as the LGM) and to test for biological legacies of alternative palaeo-configurations.

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Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: taking the long view of nature's laboratories. *Science*, **357**, eaam8326.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

Willis, K.J. & Niklas, K.J. (2004) The role of Quaternary environmental change in plant macroevolution: The exception or the rule? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 159–172.

## DATA ACCESSIBILITY STATEMENT

The authors confirm that, should the manuscript be accepted, the data supporting the results will be archived in ISLANDLAB (http://islandlab.uac.pt) and PANGAEA (https://www.pangaea.de/).

## TABLES

**Table 1** Description and sources of the chorotypes and archipelago configurations (palaeo-configurations and present-day configurations) used in this study.

| Acronym | Group | Description | Sources |
|---|---|---|---|
| *Chorotypes* | | | |
| $SIE_S$ | Land snails | Single-island endemic species richness | Table S1 in Supporting Information |
| $SIE_P$ | Angiosperms | Single-island endemic species richness | (Weigelt *et al.*, 2016) |
| $N_S$ | Land snails | Native (non-endemic) species richness | Table S1 in Supporting Information |
| $N_P$ | Angiosperms | Native (non-endemic) species richness | (Weigelt *et al.*, 2016) |
| $MIE_S$ | Land snails | Multiple-island endemic species richness | Table S1 in Supporting Information |
| *Archipelago configurations* | | | |
| $SLH_{CA}$ | Highest | Archipelago configuration model based on the present-day sea-level, consisting of only current area (CA) | (GADM; http://www.gadm.org/version1) |
| $SLH_{CACI}$ | Highest | Archipelago configuration model based on the present-day sea-level, consisting of current area (CA) and current isolation (CI) | (GADM; http://www.gadm.org/version1) |
| $SLI_{MED}$ | Intermediate | Archipelago configuration model based on the median sea-level of -65 m MSL, consisting of current area (CA), delta area (dA), and palaeo- | (Norder *et al.*, 2018) |

| | | | |
|---|---|---|---|
| | | connectedness (PC) | |
| SLI$_{FREQ}$ | Intermediate | Archipelago configuration model based on the central value of the most frequently occurring sea-level interval of -85 m MSL, consisting of current area (CA), delta area (dA), and palaeo-connectedness (PC) | (Norder *et al.*, 2018) |
| SLL$_{GM}$ | Lowest | Archipelago configuration model based on the last glacial maximum sea-level of -134 m MSL, consisting of current area (CA), delta area (dA), and palaeo-connectedness (PC) | (Lambeck *et al.*, 2014; Norder *et al.*, 2018) |
| SLL$_{-122}$ | Lowest | Archipelago configuration model based on the sea-level -122 m MSL, consisting of current area (CA), delta area (dA), and palaeo-connectedness (PC) | (Weigelt *et al.*, 2016) |

## FIGURES

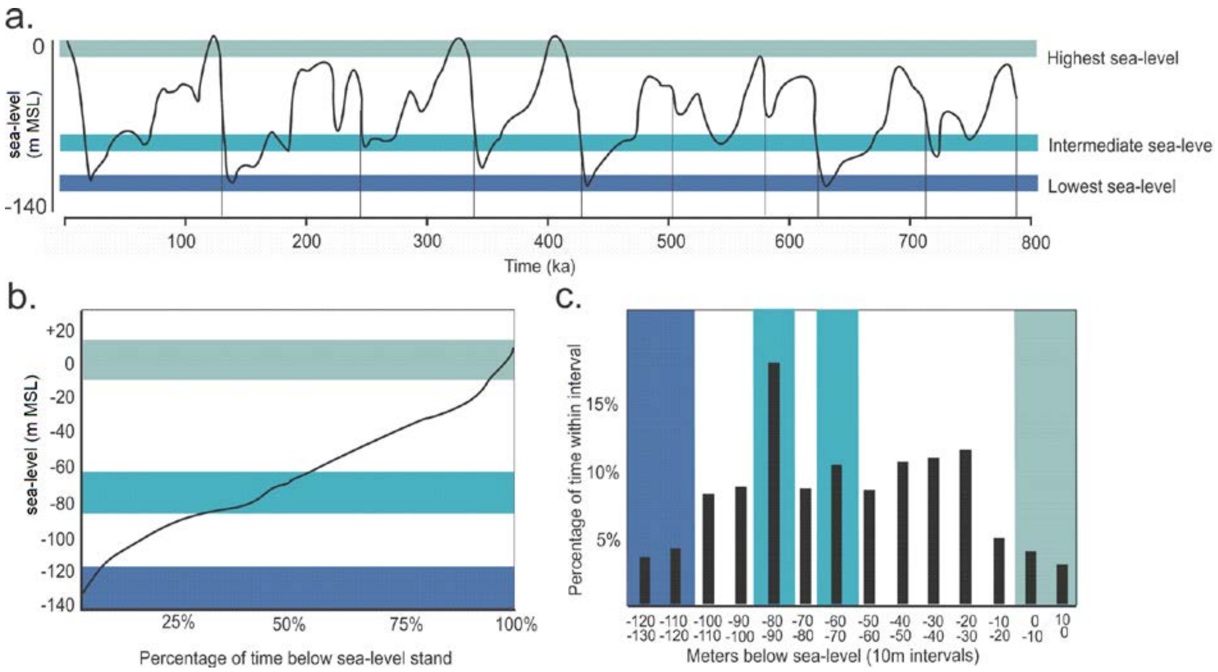

**Figure 1** Characterization of sea-level fluctuations over the last ~800 Kyr at highest, intermediate, and lowest sea-levels. (a) Sea-level fluctuations over the nine most recent glacial–interglacial cycles covering a period of the last ~800 Kyr. (b) The percentage of time over the last ~800 Kyr that the sea-level was below a certain sea-level. (c) The most frequently occurring sea-levels are quantified as the percentage of time over the last ~800 Kyr that sea-levels were within a certain interval (in 10 m bins, e.g. between -90 m MSL and -80 m MSL). The period of ~800 Kyr was chosen because it spans nine

full glacial–interglacial cycles (estimated duration of interglacials from Tzedakis *et al.,* 2012). All figures are based on data from Bintanja *et al.* (2005).

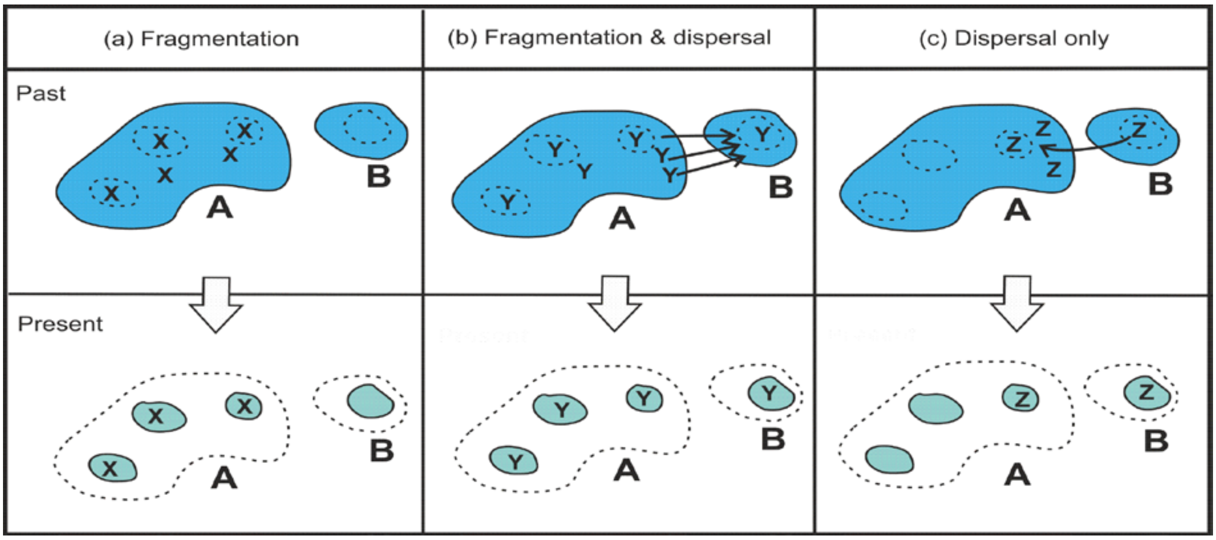

**Figure 2** Conceptual figure illustrating how observed present-day endemism patterns might result from fragmentation and/or dispersal. The chorotype of a species might change from single island endemic (SIE) to multiple island endemic (MIE) as a result of either of these processes (or a combination thereof). (a) SIE on palaeo-island A becomes MIE by fragmentation. (b) MIE shared by palaeo-islands A and B continues to be a MIE (but as a result of fragmentation and dispersal). (c) SIE on palaeo-island B becomes MIE by dispersal.

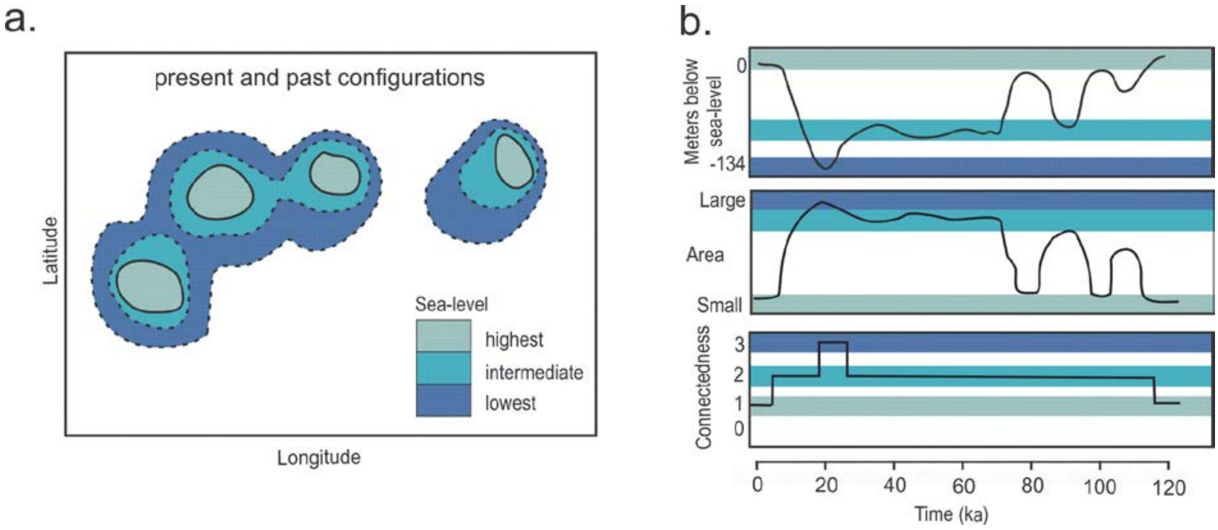

**Figure 3** Conceptual figure showing three archipelago configurations (highest, intermediate and lowest sea-level) that were used in this study, illustrated for one hypothetical sea-level cycle. (a) Conceptual illustration of how sea-level change affects archipelago configuration. (b) The three panels show how sea-level (top), area (middle) and connectedness (bottom) change for one specific island. Connectedness is quantified as the number of present-day islands connected in a palaeo-island. Archipelago configurations at intermediate sea-level are more representative of this cycle than the highest and lowest sea-levels, which both represent an extreme configuration of short duration.

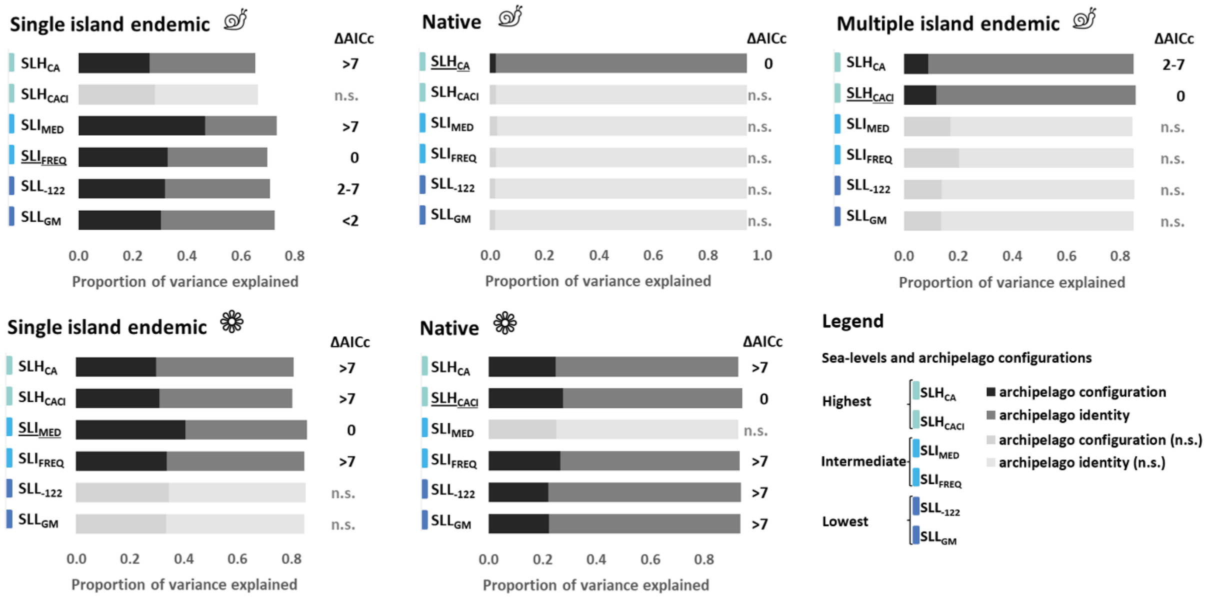

**Figure 4** Performance of different archipelago configuration models for 53 islands in 12 archipelagos for land snails and angiosperms. To explain species richness in both taxa, we considered archipelago configuration models at the following sea-levels: lowest (palaeo-configuration at -122 m MSL, $SLL_{-122}$; and at -134 m MSL, $SLL_{GM}$), intermediate (palaeo-configuration at the most frequent sea-level, $SLI_{FREQ}$; and at the median sea-level, $SLI_{MED}$), and highest (current area at present-day sea-level, $SLH_{CA}$; and current area and isolation at present-day sea-level, $SLH_{CACI}$). The size of each bar indicates the explained variance by archipelago configuration ($R^2_M$, darker shades) and archipelago identity ($R^2_C$ - $R^2_M$, lighter shades). The difference in Akaike's information criterion corrected for sample size (Δ AICc) is provided for those models for which all predictors are significant ($P < 0.05$), or marked 'n.s.' for models for which not all predictors are significant (the bars of these non-significant models are greyed out).

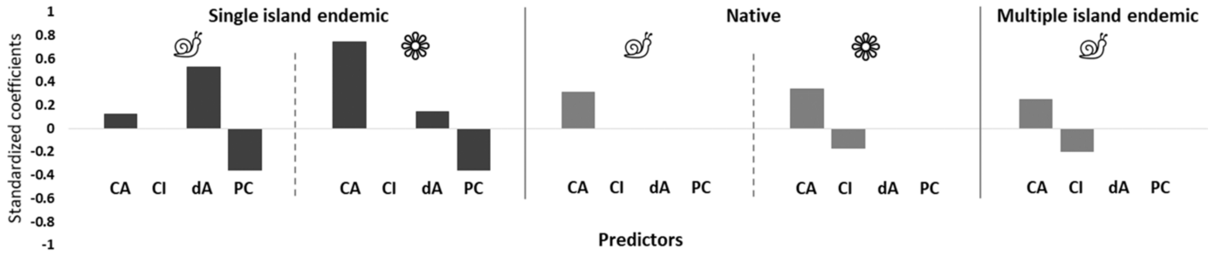

**Figure 5** Bars indicate effect size of parameters in the best archipelago configuration models for 53 islands in 12 archipelagos for land snails and angiosperms. Standardized effect size of significant parameters ($P < 0.05$) in the model with lowest Δ AICc (difference in corrected Akaike's information criterion). The colours of the bars represent archipelago configurations at intermediate (dark grey)

and highest (light grey) sea-levels. Each model contains a selection of the following predictors: current area (CA), delta area (dA), palaeo-connectedness (PC), and current isolation (CI).

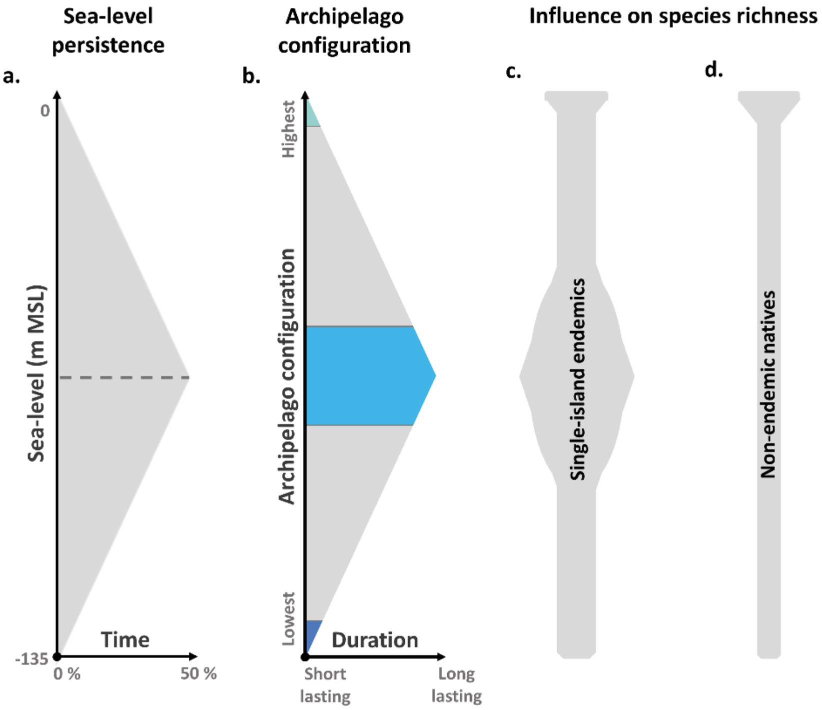

**Figure 6** Conceptual figure illustrating the influence of sea-level driven changes in archipelago configuration on species richness patterns of single-island endemics and non-endemic natives. (a) The percentage of time the sea-level was either above or below a certain level. (b) The duration of an archipelago configuration as shaped by sea-level fluctuations. (c, d) The width of the bars indicate the importance of an archipelago configuration (b) in shaping single-island endemic and non-endemic native richness.

## SUPPORTING INFORMATION

Table S1. Data sources for land snail data.

Table S2. Pearson correlation matrix of land snail chorotypes.

Table S3. Pearson correlation matrix of angiosperm chorotypes.

Table S4. Island ages and data sources per archipelago.

Table S5. Pearson correlation matrix of island age and archipelago configuration.

Table S6. Pearson correlation matrix for different archipelago configurations.

Table S7. Standardized coefficients for archipelago configuration models.

Figure S1 (a-h). Island age and elements of archipelago configuration.

Figure S2 (a,b,c). Current area and delta area for different palaeo-configurations.

## SUPPORTING INFORMATION

Table S1. Data sources for land snail data.

| **Archipelago** | **Sources** |
|---|---|
| Azores | Martins (2011), updated with unpublished data of A.M.F. Martins, R.A.D. Cameron and B.M. Pokryszko |
| Canary Islands | Núñez & Núñez (2010), updated by Vega-Luz & Vega-Luz (2008), Holyoak & Holyoak (2009), Neiber *et al*. (2011) and unpublished data of M.R. Alonso and M. Ibáñez |
| Cook Islands | McCormack (2007) |
| Galápagos Islands | Dall & Ochsner (1928), Smith (1966), Coppois (1985), Parent & Crespi (2006) and references therein, Miquel & Herrera (2014), Parent *et al*. (2014) |
| Gulf of Guinea | Angus (1994) |
| Hawaiian Islands | Cowie *et al*. (1995) and Cowie (1995), updated by reference to Pokryszko (1997) for *Lyropupa* |
| Madeira | Seddon (2008) with some corrections and minor modifications (following Goodfriend *et al*., 1996; Cameron *et al*., 2007) |
| Mascarenes | Griffiths & Florens (2006) |
| Pitcairn | Preece (1995) and Preece (1998) |
| Revillagigedo | Thompson (2011) |
| Samoan Islands | Cowie (1998) with additional records from Cowie (2001) and Cowie *et al*. (2002). |
| Tristan da Cunha | Holdgate (1965), Preece & Gittenberger (2003), Gittenberger *et al*. (2006) |

Table S2. Pearson correlation matrix for land snails for the following chorotypes: indigenous non-exotic ($S_S$), native non-endemic ($N_S$), endemic to single archipelagos ($END_S$), multiple island endemics ($MIE_S$), single island endemics ($SIE_S$). Total indigenous land snail richness ($S_S$) is dominated by endemic species. For our dataset of volcanic oceanic islands, the correlations between single island endemics and palaeo-island endemics were almost 100%. All correlations are significant at P < 0.001.

| | $S_S$ | $N_S$ | $END_S$ | $MIE_S$ | $SIE_S$ | $PIE_{MED}$ | $PIE_{FREQ}$ | $PIE_{MIN122}$ | $PIE_{GM}$ |
|---|---|---|---|---|---|---|---|---|---|
| $S_S$ | 1.000 | | | | | | | | |
| $N_S$ | 0.101 | 1.000 | | | | | | | |
| $END_S$ | 0.983 | -0.083 | 1.000 | | | | | | |
| $MIE_S$ | 0.816 | -0.060 | 0.829 | 1.000 | | | | | |
| $SIE_S$ | 0.973 | -0.085 | 0.990 | 0.741 | 1.000 | | | | |
| $PIE_{MED}$ | 0.972 | -0.090 | 0.990 | 0.744 | 0.999 | 1.000 | | | |
| $PIE_{FREQ}$ | 0.973 | -0.094 | 0.992 | 0.759 | 0.998 | 0.999 | 1.000 | | |
| $PIE_{MIN122}$ | 0.974 | -0.092 | 0.993 | 0.761 | 0.998 | 0.999 | 1.000 | 1.000 | |
| $PIE_{GM}$ | 0.974 | -0.094 | 0.993 | 0.764 | 0.997 | 0.998 | 0.999 | 0.999 | 1.000 |

Table S3. Pearson correlation matrix for angiosperms for the following chorotypes: indigenous species ($S_P$), native non-endemics ($N_P$), single island endemics ($SIE_P$), palaeo-island natives ($PN_P$), and palaeo–island endemics ($PIE_P$). Total indigenous angiosperm richness ($S_P$) is dominated by native (non-endemic) species. For our dataset of volcanic oceanic islands, the correlations between single island endemics and palaeo–island endemics, and between natives and palaeo-natives was almost 100%. All correlations are significant at P < 0.001.

| | $S_P$ | $N_P$ | $SIE_P$ | $PN_P$ | $PIE_P$ |
|---|---|---|---|---|---|
| $S_P$ | 1.000 | | | | |
| $N_P$ | 0.982 | 1.000 | | | |
| $SIE_P$ | 0.728 | 0.583 | 1.000 | | |
| $PN_P$ | 0.982 | 0.999 | 0.587 | 1.000 | |
| $PIE_P$ | 0.746 | 0.608 | 0.988 | 0.605 | 1.000 |

Table S4. Island ages (Myr) and data sources per archipelago. Where possible we used the subaerial age of the oldest geological formation on the island. When there was disagreement between sources we generally used the most recent source.

| Island | Age (Myr) | Archipelago | Sources |
|---|---|---|---|
| Corvo | 0.7 | Azores | Azevedo & Portugal Ferreira (2006), Calvert *et al*. (2006), Hildenbrand *et al*. (2014), Larrea *et al*. (2014), Sibrant *et al*. (2014, 2015a, 2015b), Ávila *et al*. (2016), Ramalho *et al*. (2017) |
| Faial | 0.85 | | |
| Flores | 2.16 | | |
| Graciosa | 1.057 | | |
| Pico | 0.27 | | |
| Santa Maria | 5.7 | | |
| São Jorge | 1.3 | | |
| São Miguel | 0.88 | | |
| Terceira | 0.39 | | |
| Fuerteventura | 23 | Canary Islands | Staudigel *et al*. (1986), van den Bogaard (2013) |
| Gran Canaria | 15 | | |
| El Hierro | 1.1 | | |
| La Gomera | 11 | | |
| La Palma | 1.7 | | |
| Lanzarote | 15 | | |
| Tenerife | 12 | | |
| Atiu | 10 | Cook Islands | Turner & Jarrard (1982), Clouard & Bonneville (2005) |
| Mangaia | 21.9 | | |
| Mauke | 6.3 | | |
| Mitiaro | 12.3 | | |
| Rarotonga | 3.6 | | |
| Española | 3.5 | Galápagos Islands | Poulakakis *et al*. (2012) |
| Fernandina | 0.07 | | |
| Floreana | 2.3 | | |
| Isabela | 0.8 | | |
| Pinzón | 1.7 | | |
| San Cristóbal | 4 | | |
| Santa Cruz | 2.3 | | |
| Santiago | 1.4 | | |
| Príncipe | 31 | Gulf of Guinea | Dunlop & Fitton (1979), Lee *et al.* (1994) |
| São Tomé | 15.7 | | |
| Hawaii | 0.6 | Hawaiian Islands | Ziegler (2002) |
| Kauai | 5.25 | | |
| Lanai | 1.6 | | |
| Maui | 1.75 | | |
| Molokai | 2.1 | | |
| Oahu | 4 | | |
| Madeira | 7 | Madeira | Ramalho *et al*. (2015), Ávila *et al.* (2016) |
| Porto Santo | 19 | | |
| Mauritius | 8.9 | Mascarenes | McDougall (1971), Duncan & Hargraves (1990), Thébaud *et al*. (2009), Moore *et al.* (2011), Torsvik *et* |
| La Réunion | 2.1 | | |

|  |  |  |  |
|---|---|---|---|
| Rodrigues | 15 |  | *al.* (2013), Warren *et al.* (2013) |
| Henderson | 0.2 | Pitcairn | Duncan et al. (1974), Clouard & Bonneville (2005), Neall & Trewick (2008), best estimate for Henderson (composed entirely of coralline limestone) |
| Pitcairn | 1 |  |  |
| Clarion | 4.5 | Revillagigedo | Bryan (1966), Farmer *et al.* (1993), Bohrson & Reid (1998), Triantis *et al.* (2016), best estimate for Socorro and Clarion. |
| Socorro | 1.7 |  |  |
| Ofu | 0.4 | Samoan Islands | Natland (1980), Clouard & Bonneville (2005), Cameron *et al.* (2013) |
| Olosega | 0.4 |  |  |
| Tutuila | 1.6 |  |  |
| Gough | 2.5 | Tristan da Cunha | Miller (1964), Mcdougall & Ollier (1982), Chevallier & Verwoerd (1987), Maund *et al.* (1988), Hicks *et al.* (2012) |
| Inaccessible | 6 |  |  |
| Nightingale | 18 |  |  |
| Tristan da Cunha | 0.2 |  |  |

Table S5. Pearson correlation matrix for island age and archipelago configurations at different sea-levels: highest (SLH$_{CA}$ and SLH$_{CACI}$), intermediate (SLI$_{MED}$ and SLI$_{FREQ}$), and lowest (SLL$_{-122}$ and SLL$_{GM}$). Each archipelago configuration consists of the following predictors: current area (CA), current isolation (CI), area change (dA), and palaeo–connectedness (PC). All correlations have a P value higher than 0.1 (significance levels: "." = P < 0.1, "*" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001).

|  | **Highest** |  | **Intermediate** |  |  |  | **Lowest** |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  | **SLH$_{CACI}$** |  | **SL$_{MED}$** |  | **SL$_{FREQ}$** |  | **SL$_{MIN122}$** |  | **SL$_{GM}$** |  |
|  | **CA** | **CI** | **dA** | **PC** | **dA** | **PC** | **dA** | **PC** | **dA** | **PC** |
| **Age** | **-0.03** | **0.21** | **0.20** | **0.02** | **0.16** | **-0.07** | **0.11** | **-0.17** | **0.10** | **-0.16** |

Table S6. Pearson correlation matrix for archipelago configurations at different sea-levels: highest ($SLH_{CA}$ and $SLH_{CACI}$), intermediate ($SLI_{MED}$ and $SLI_{FREQ}$), and lowest ($SLL_{-122}$ and $SLL_{GM}$). Each archipelago configuration consists of the following predictors: current area (CA), current isolation (CI), area change (dA), and palaeo–connectedness (PC). Significance levels: "." = P < 0.1, "*" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001.

| | | | **Highest** | | **Intermediate** | | | | **Lowest** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | **$SLH_{CACI}$** | | **$SL_{MED}$** | | **$SL_{FREQ}$** | | **$SL_{MIN122}$** | | **$SL_{GM}$** | |
| | | | **CA** | **CI** | **dA** | **PC** | **dA** | **PC** | **dA** | **PC** | **dA** | **PC** |
| **Highest** | **$SLH_{CACI}$** | **CA** | 1.00 | | | | | | | | | |
| | | **CI** | -0.16 | 1.00 | | | | | | | | |
| **Intermediate** | **$SLI_{MED}$** | **dA** | 0.74 *** | -0.11 | 1.00 | | | | | | | |
| | | **PC** | 0.03 | -0.25 . | 0.35 * | 1.00 | | | | | | |
| | **$SLI_{FREQ}$** | **dA** | 0.75 *** | -0.16 | 0.96 *** | 0.33 * | 1.00 | | | | | |
| | | **PC** | 0.13 | -0.24 . | 0.44 ** | 0.80 *** | 0.49 *** | 1.00 | | | | |
| **Lowest** | **$SLL_{-122}$** | **dA** | 0.79 *** | -0.20 | 0.87 *** | 0.28 * | 0.92 *** | 0.43 ** | 1.00 | | | |
| | | **PC** | 0.21 | -0.31 * | 0.37 ** | 0.70 *** | 0.50 *** | 0.88 *** | 0.54 *** | 1.00 | | |
| | **$SLL_{GM}$** | **dA** | 0.79 *** | -0.20 | 0.87 *** | 0.28 * | 0.92 *** | 0.43 ** | 1.00 *** | 0.54*** | 1.00 | |
| | | **PC** | 0.23 . | -0.33 * | 0.38 ** | 0.67 *** | 0.51 *** | 0.86 *** | 0.55 *** | 0.97*** | 0.54 *** | 1.00 |

Table S7. Standardized coefficients of linear mixed models for 53 volcanic oceanic islands in 12 archipelagos for land snails (SIE$_{S}$, N$_{S}$, MIE$_{S}$) and angiosperms (SIE$_{P}$, N$_{P}$). We fitted linear mixed models for archipelago configurations at different sea-levels: highest (SLH$_{CA}$ and SLH$_{CACI}$), intermediate (SLI$_{MED}$ and SLI$_{FREQ}$), and lowest (SLL$_{-122}$ and SLL$_{GM}$). SLH$_{CA}$ (current area only), CACI; current configuration (current area, current isolation), SL$_{MED}$; palaeo–configuration during median sea level, SL$_{FREQ}$; palaeo–configuration during most frequent sea level, SL$_{MIN122}$; palaeo–configuration at -122m MSL, SL$_{GM}$; palaeo–configuration at Last Glacial Maximum. Each model contains a selection of the following predictors: CA; current area, CI; current isolation, PC; palaeo–connectedness, dA; delta area. Significance levels: "." = P < 0.1, "*" = P < 0.05, "**" = P < 0.01, "***" = P < 0.001.

| **Archipelago configuration** | | | **SIE$_{S}$** | | **SIE$_{P}$** | | **N$_{S}$** | | **N$_{P}$** | | **MIE$_{S}$** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Highest** | **SLH$_{CA}$** | **CA** | 0.456 | *** | 1.010 | *** | 0.313 | ** | 0.453 | *** | 0.335 | *** |
| | **SLH$_{CACI}$** | **CA** | 0.375 | *** | 0.766 | *** | 0.269 | *** | 0.337 | *** | 0.248 | *** |
| | | **CI** | 0.003 | | -0.110 | * | 0.069 | | -0.171 | *** | -0.197 | * |
| **Intermediate** | **SLI$_{MED}$** | **CA** | 0.282 | *** | 0.744 | *** | 0.175 | . | 0.387 | *** | 0.255 | *** |
| | | **PC** | -0.311 | *** | -0.359 | *** | -0.237 | *** | -0.009 | | 0.021 | |
| | | **dA** | 0.418 | *** | 0.147 | * | 0.045 | | -0.047 | * | 0.167 | . |
| | **SLI$_{FREQ}$** | **CA** | 0.122 | * | 0.653 | *** | 0.199 | * | 0.431 | *** | 0.273 | *** |
| | | **PC** | -0.359 | *** | -0.312 | *** | -0.180 | * | 0.067 | *** | 0.036 | |
| | | **dA** | 0.525 | *** | 0.146 | * | 0.033 | | -0.105 | *** | 0.185 | . |
| **Lowest** | **SLL$_{-122}$** | **CA** | 0.121 | * | 0.663 | *** | 0.239 | * | 0.450 | *** | 0.297 | *** |
| | | **PC** | -0.375 | *** | -0.310 | *** | -0.114 | | 0.078 | *** | 0.074 | |
| | | **dA** | 0.504 | *** | 0.072 | | 0.010 | | -0.174 | *** | 0.052 | |
| | **SLL$_{GM}$** | **CA** | 0.194 | *** | 0.708 | *** | 0.250 | ** | 0.430 | *** | 0.287 | *** |
| | | **PC** | -0.358 | *** | -0.252 | *** | -0.103 | | 0.059 | *** | 0.070 | |
| | | **dA** | 0.496 | *** | 0.009 | | -0.005 | | -0.146 | *** | 0.052 | |

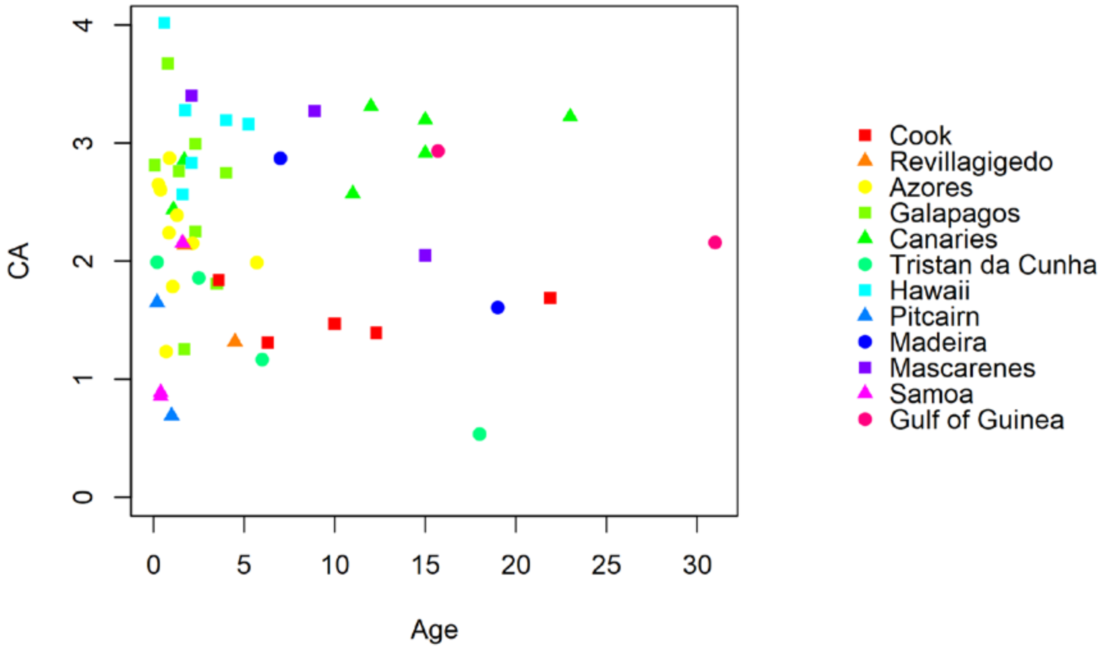

Figure S1a. Island age (Myr) and log-transformed current area (CA) for 53 islands in 12 archipelagos.

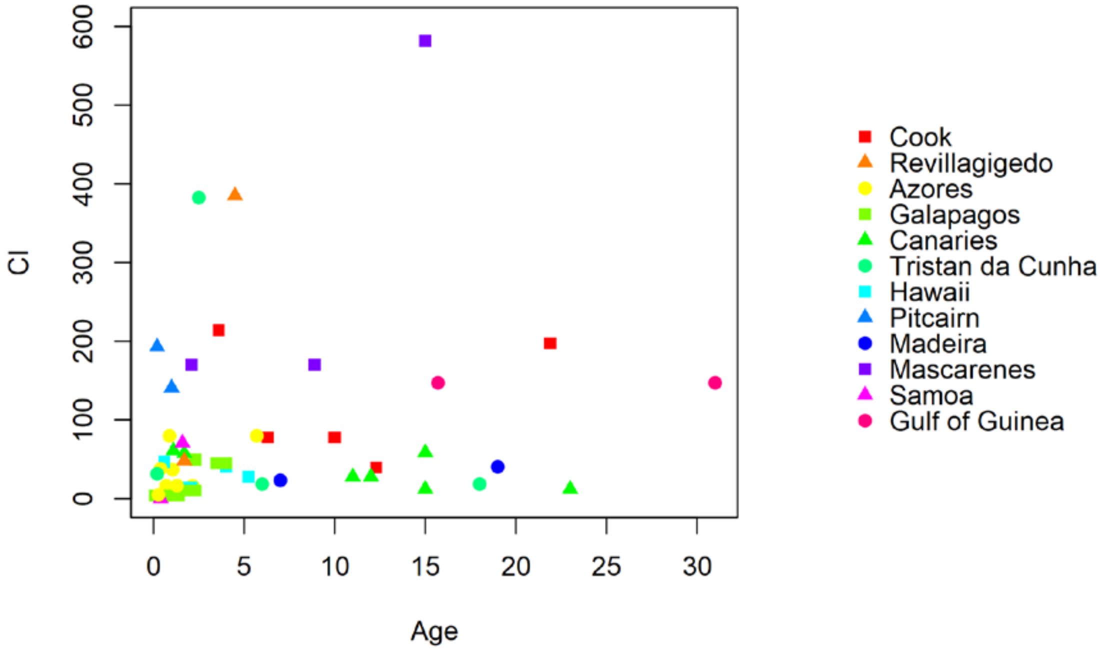

Figure S1b. Island age (Myr) and current isolation (CI) for 53 islands in 12 archipelagos.

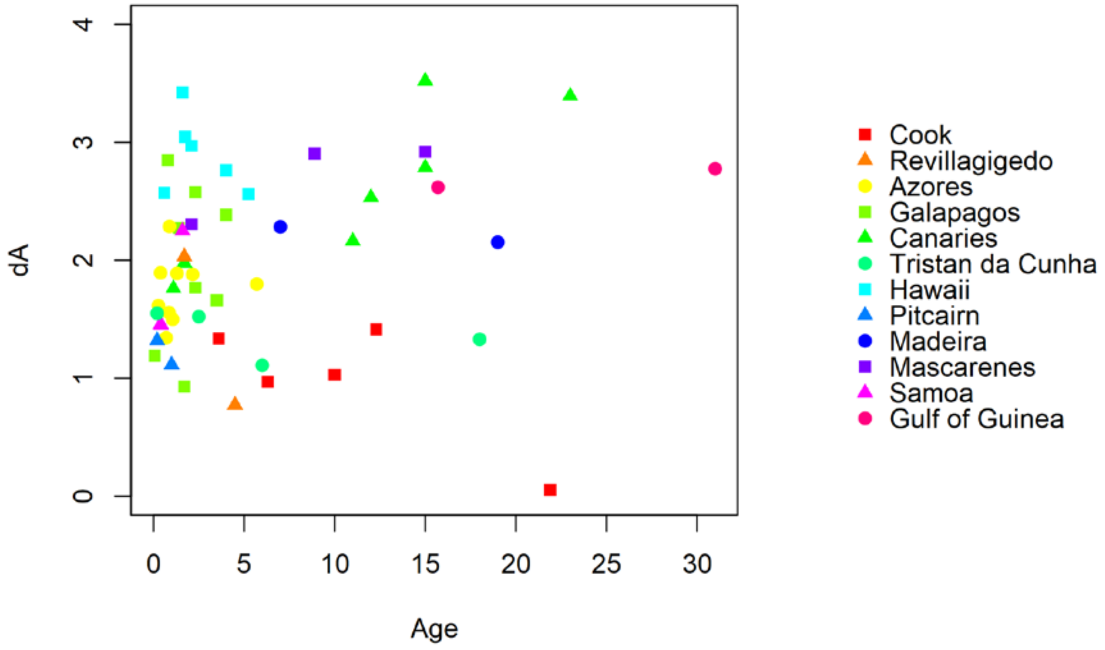

Figure S1c. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at $SLI_{MED}$.

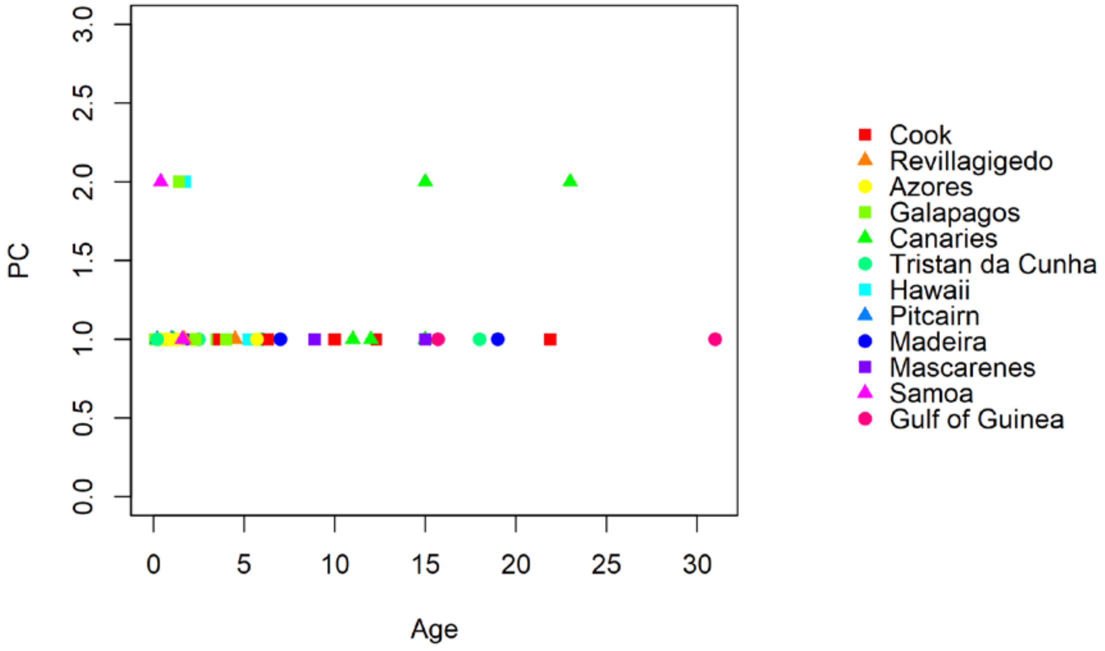

Figure S1d. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at $SLI_{MED}$.

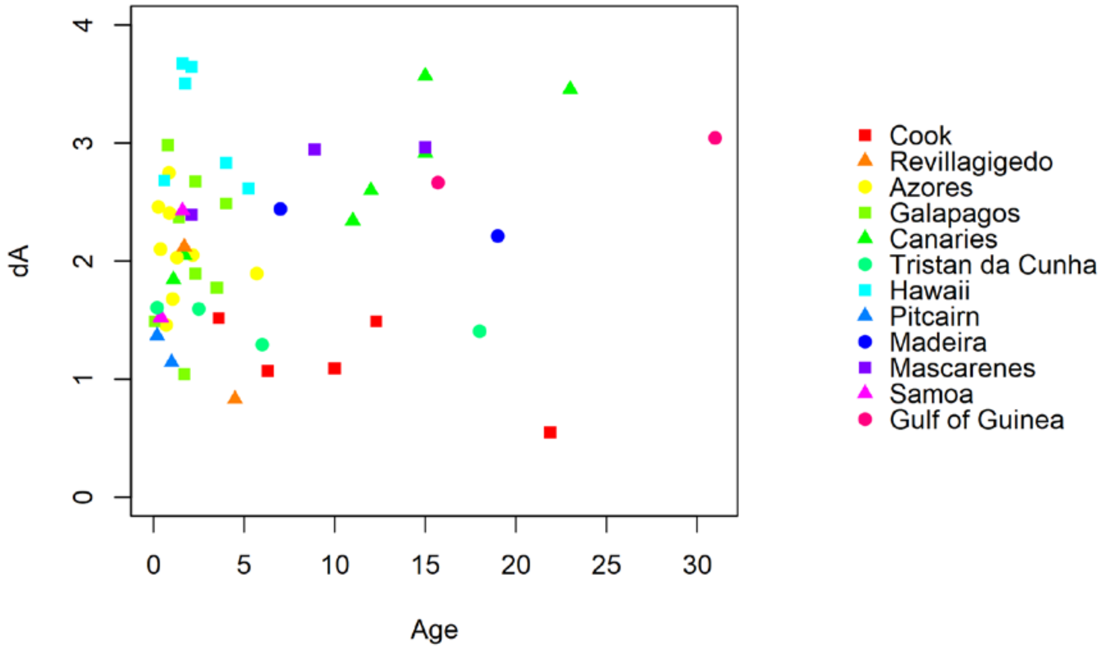

Figure S1e. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at $SLI_{FREQ}$.

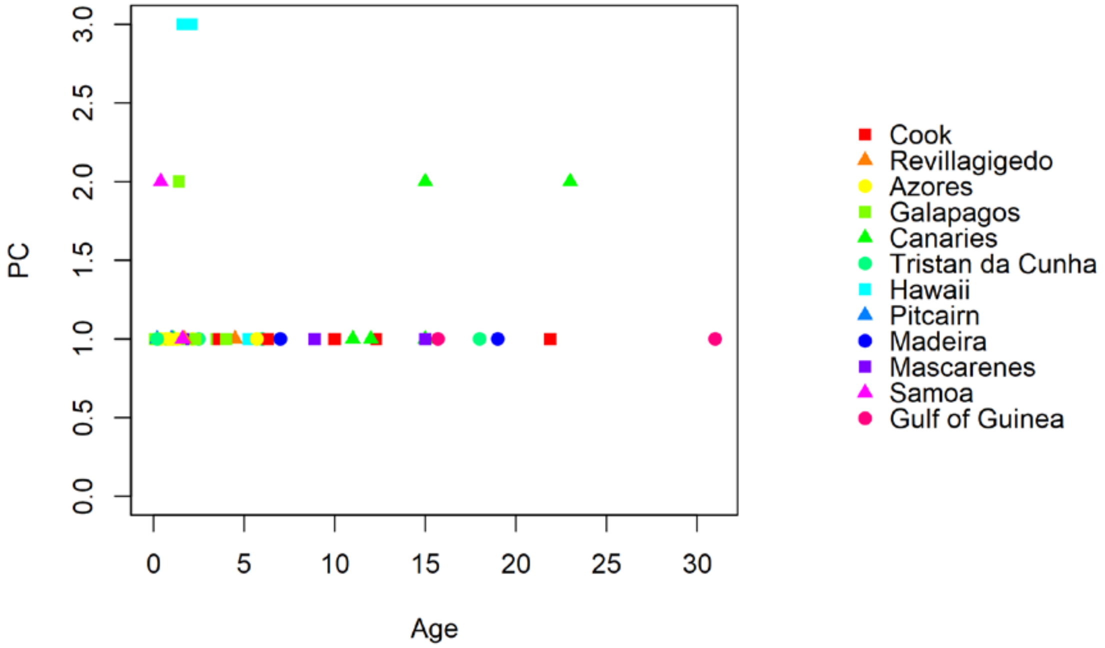

Figure S1f. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at $SLI_{FREQ}$.

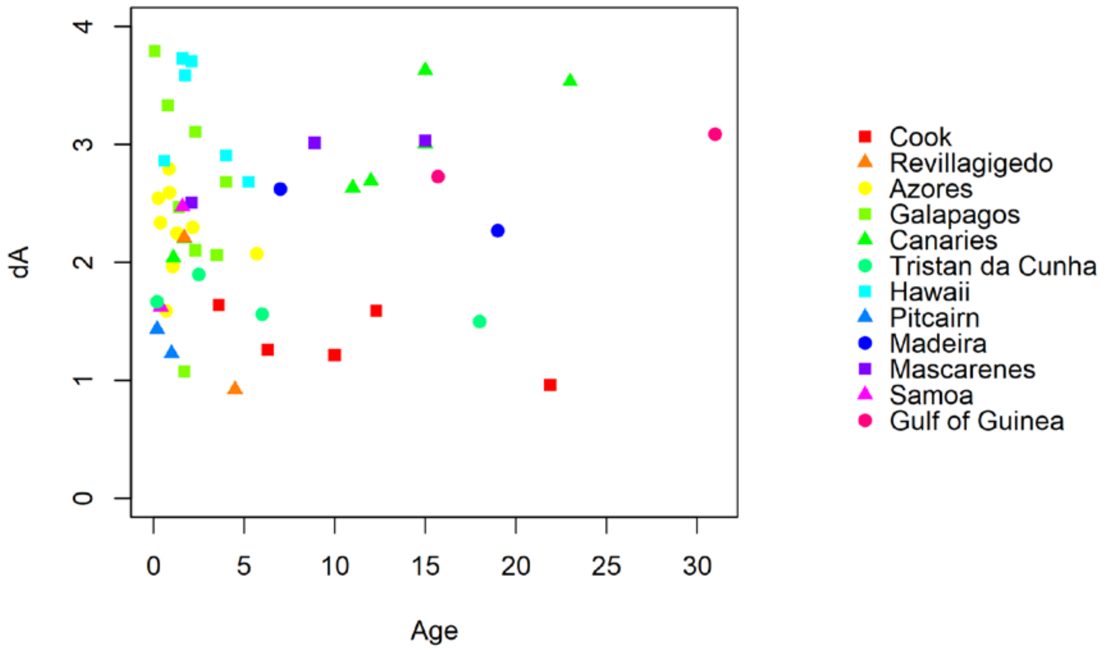

Figure S1g. Island age (Myr) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLL$_{GM}$.

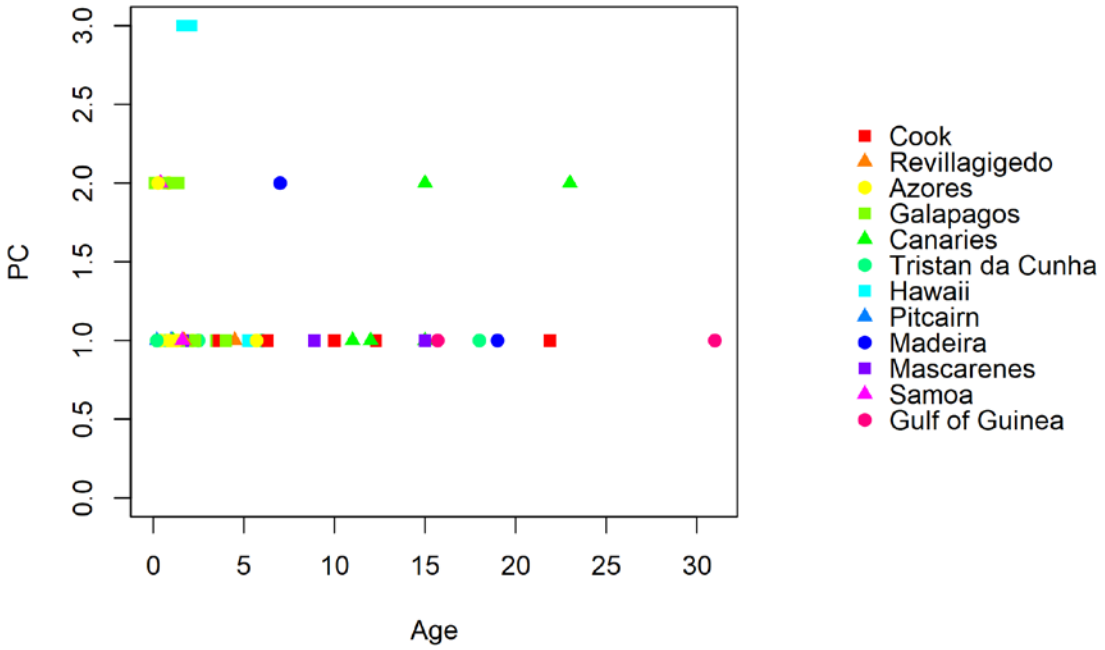

Figure S1h. Island age (Myr) and palaeo–connectedness (PC) for 53 islands in 12 archipelagos at SLL$_{GM}$.

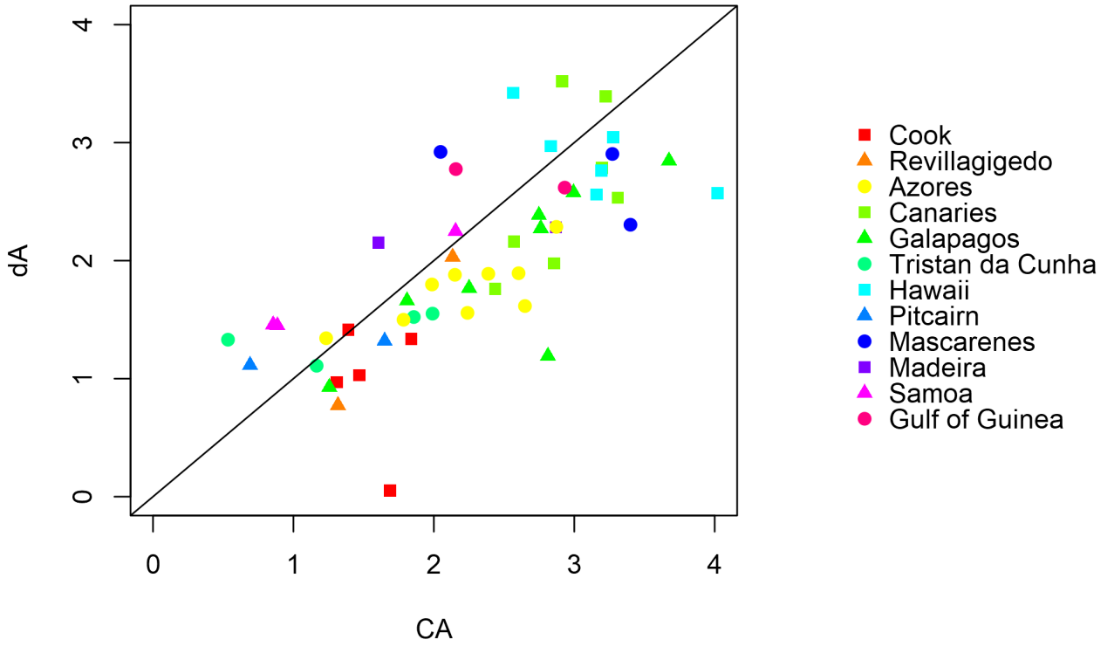

Figure S2a. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at SLI<sub>MED</sub>.

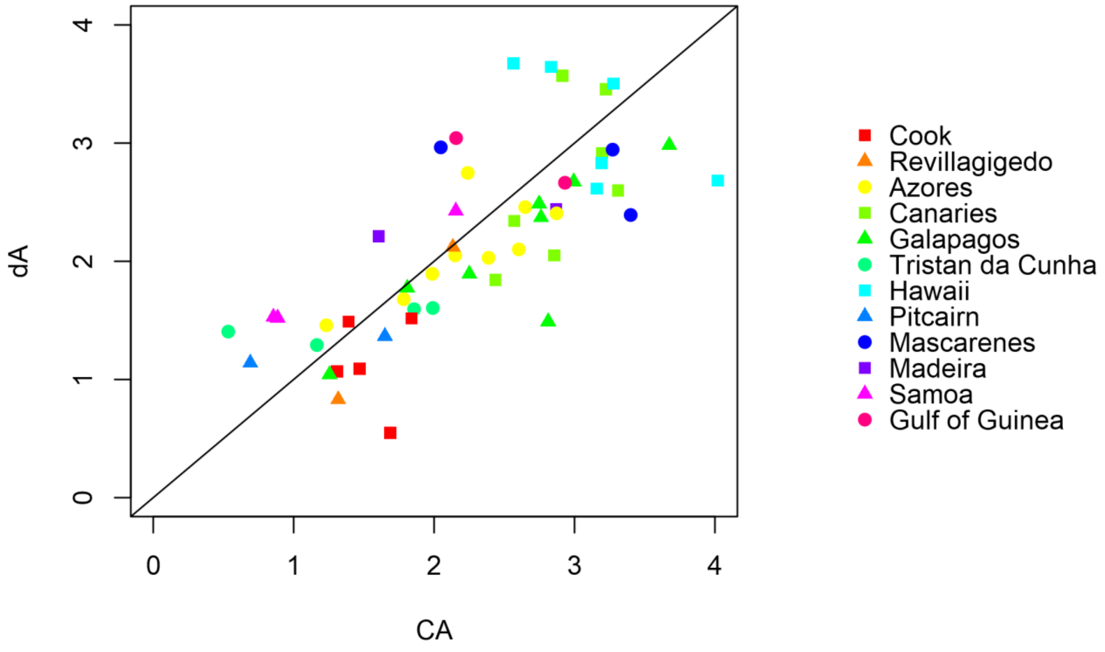

Figure S2b. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at $\mathrm{SLI}_{\mathrm{FREQ}}$.

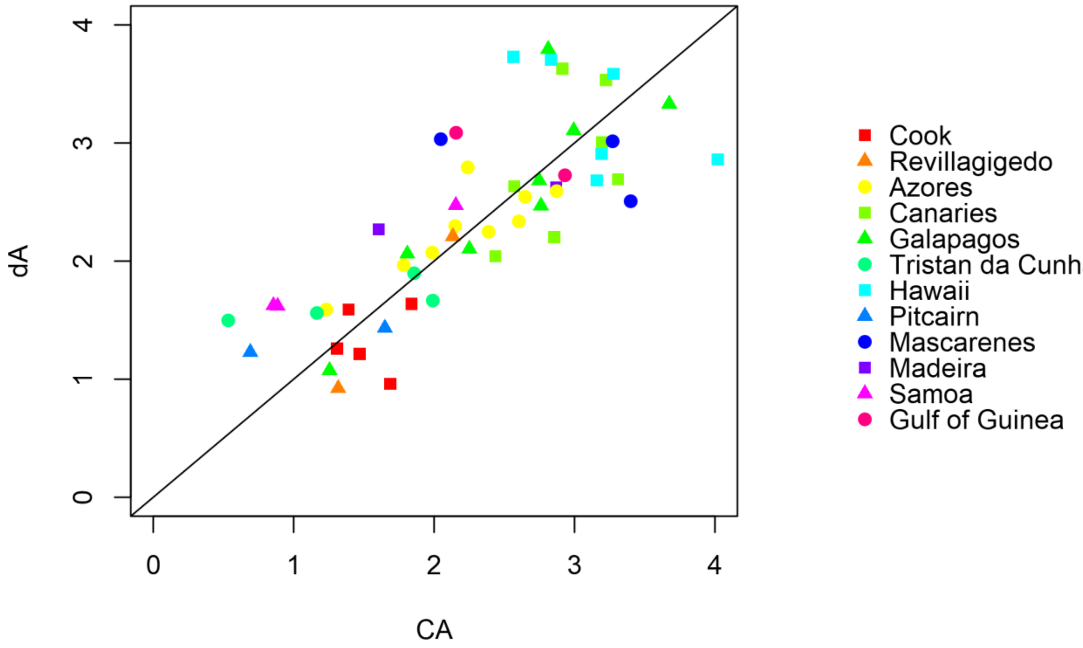

Figure S2c. Log-transformed current area (CA) and log-transformed area change (dA) for 53 islands in 12 archipelagos at $SLL_{GM}$.

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