Journal of Biogeography (*J. Biogeogr.*) (2016) **43**, 911–922

ORIGINAL ARTICLE

Transferring and implementing the general dynamic model of oceanic island biogeography at the scale of island fragments: the roles of geological age and topography in plant diversification in the Canaries

Rüdiger Otto[1,2,*], Robert J. Whittaker[3,4], Markus von Gaisberg[5], Christian Stierstorfer[6], Agustín Naranjo-Cigala[7], Manuel J. Steinbauer[8], Michael K. Borregaard[3,4], José Ramón Arévalo[1,2], Víctor Garzón-Machado[1], Marcelino del Arco[1] and José María Fernández-Palacios[1,2]

[1]Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, La Laguna 38206, Islas Canarias, Spain, [2]Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna, Tenerife, Canary Islands, Spain, [3]Conservation Biogeography and Macroecology Group, School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK, [4]Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen Ø, Denmark, [5]Pariser Str. 6, 10719 Berlin, Germany, [6]Dahlienweg 27, 93053 Regensburg, Germany, [7]Departamento de Geografía, Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria 35003, Islas Canarias, Spain, [8]Section Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, 8000 Aarhus, Denmark

*Correspondence: Rüdiger Otto, Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, La Laguna, Avda Astrofísico Francisco Sánchez, s.n., 38206 Islas Canarias, Spain.
E-mail: rudiger.otto@gmail.com

ABSTRACT

Aim The general dynamic model (GDM) of oceanic island biogeography integrates rates of immigration, speciation and extinction in relation to a humped trajectory of island area, species carrying capacity and topographic complexity through time, based on a simplified island ontogeny. In practice, many islands have more complex ontogenies, featuring surfaces of varying age. Here, we extend the GDM to apply at a local scale within islands, and test the predictions analytically within individual islands.

Location El Hierro, La Palma and Tenerife (Canary Islands).

Methods Following the GDM logic, we derive predictions for the distributions and richness of single island endemics (SIEs) across island landscapes of different age. We test these predictions by means of generalized linear models and binominal tests using gridded species occurrence data for vascular plant SIE species and a set of climatic, topographic and terrain age variables. We also examined phylogenetic divergence times for a subset of endemic lineages.

Results Geological age, in interaction with slope, and topographic variables, best explained SIE richness at the landscape scale. About 70% of SIEs had ranges strongly biased to, or largely restricted to old terrain. Available phylogenetic divergence times of SIEs of radiated plant lineages suggested an origin on the older parts of the islands. Metrics of anthropogenic disturbance and habitat availability were unrelated to the observed SIE pattern.

Main conclusions Our findings support the hypothesis that SIEs have evolved and accumulated on older and topographically complex terrain, while colonization processes predominate on the youngest parts. These results imply that evolutionary processes shape species distributions at the landscape scale within islands. This opens the perspective of extending the GDM framework to understand processes at a local scale within individual islands.

Keywords

Canary Islands, endemic plants, environmental heterogeneity, general dynamic model, island biogeography, island evolution, landscape diversity, oceanic islands, spatial autocorrelation, species richness patterns

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12684

INTRODUCTION

Volcanic activity on islands has long been recognized to affect population dynamics, extinction and immigration rates, and processes of evolutionary diversification (Carson *et al.*, 1990; Paulay, 1994), with implications for the interpretation of endemic species distributions (Juan *et al.*, 2000; Emerson, 2003; Price, 2004; Stuessy, 2007; Whittaker *et al.*, 2008).

Recently, Whittaker *et al.* (2007, 2008) developed the General Dynamic Model (GDM) of oceanic island biogeography, which relates the processes of immigration, speciation and extinction to the geological life cycle of an oceanic island (ontogeny *sensu* Stuessy, 2007). The model predicts that colonization will predominate in the early constructive phase of an island, followed by a quick increase of speciation due to the increasing availability of nonutilized ecological opportunity, related to availability of maximal resource space and environmental heterogeneity. This phase is followed by an increase in allopatric speciation, linked to increased topographic complexity and opportunities for geographical isolation of populations in the maturity stage. Finally, extinction overrides colonization and speciation, as the island enters and progresses through a diminishing old age where erosion (and subsidence) processes dominate.

The GDM represents a more comprehensive theoretical model for the biodiversity of oceanic islands of volcanic origin than previous models and has recently been empirically tested, statistically improved and examined by modelling (Cameron *et al.*, 2013; Steinbauer *et al.*, 2013; Valente *et al.*, 2014). However, the GDM is based on a highly simplified island ontogeny, and, in reality, even hotspot archipelago islands tend to progress through more complicated ontogenies, while other archipelago types may diverge considerably from the basic ontogeny, implying the need for modification to extend the applicability of the GDM (see e.g. Carracedo, 2011; Heaney *et al.*, 2013).

The spatio-temporal framework of the GDM

We set out here to transfer the GDM to a within-island scale. In evaluating the GDM, Whittaker *et al.* (2008) exploited the fact that hotspot archipelagos represent a wide array of island ages/stages at any given time. Here, we emphasize that each oceanic island itself is composed of distinct terrain units, representing different geological and evolutionary stages, with particular areas becoming rejuvenated, rebuilt or 'repaved' (Carson *et al.*, 1990). Hence, we may treat different terrain units ('fragments') as geological islands within the geographical island. Older, heavily eroded parts of an island represent the maturity stage of the GDM (showing highest topographic complexity), while younger parts remain in the initial or immaturity phase (e.g. evident in Maui (Hawaii), La Reunion (Mascarenes), Santo Antão (Cape Verde) or La Palma (Canaries; Fernández-Palacios *et al.*, 2014)). Often we may observe a mosaic of different 'island life cycle' stages across a single island.

The biological processes invoked by the GDM, when applied in this way, predict that older island fragments with high topographic complexity (which correspond to mature intermediate-aged islands in the original GDM) should have accumulated more single-island endemics (SIEs) through *in situ* speciation than have the younger areas. Many such SIEs have very narrow distributions and seemingly limited powers of dispersal, limiting their capacity to spread (Whittaker & Fernández-Palacios, 2007). However, over time, some SIEs that have arisen on older terrain units will spread to younger terrain or to neighbouring islands (thus becoming multi-island endemics, MIEs). Initial colonization of young surfaces within an older island will therefore include a mix of native but nonendemic species (NAT), MIEs and SIEs, mostly sourced from nearby older terrain. Enhanced rates of immigration of 'new' colonists from neighbouring islands may occur due to the availability of new environmental opportunities (micro-habitats, substrate geochemistry or texture, new climatic space), on these young island fragments. Where the younger terrain abuts older massifs we may also expect to find hybrid zones between closely related lineages (cf. Brochmann *et al.*, 2000). However, notwithstanding the relatively high rates of lineage diversification found in remote islands (Knope *et al.*, 2012), it is only with the passage of quite lengthy periods of time that these younger terrain units build-up their own stock of *in situ* endemics.

Empirical evaluation

To test specific predictions of the foregoing, we analyse vascular plant species distributions on the three youngest Canary Islands with recent volcanism – El Hierro, La Palma and Tenerife – using 1 × 1-km gridded data. We focus on SIE density, i.e. SIE number per km^2, as our index of diversity. For El Hierro, we also exploit reliable distributional data for NAT and MIE, by which means we calculate the proportion of SIEs (pSIE; as a fraction of indigenous species). Speciation in the fastest diversifying lineages on remote islands can be exceptionally rapid (Knope *et al.*, 2012), generating substantial numbers of new SIE species within 1–2 Myr, although, across whole assemblages, attainment of peak SIE richness may take longer (Whittaker *et al.*, 2008; Steinbauer *et al.*, 2013). The GDM predicts an overall hump-shaped relationship between SIE richness (or pSIE) and island age for entire islands, with maximum values at the maturity stage (prior to island decline in old age). As the three selected Canary islands harbour fragments representing the first half of the trajectory of island evolution, from the youngest stage (large areas of very young substrate aged 0.15–0.50 Ma are present on each island), over the late initial/early maturity stage (oldest parts of El Hierro and La Palma, 0.5–2 Ma, central building of Tenerife, 1–3 Ma) to the maturity stage (oldest parts of Tenerife, 5–11 Ma), an increase in SIE density at the landscape scale from the youngest to the oldest island fragments is expected. This prediction is based on the premise that the youngest terrain has provided too little time for extensive speciation to have occurred (whether through anagenesis or cladogenesis) and that many of the SIEs that have evolved on the older fragments of the islands will have been unable to spread across the whole island, due to dispersal limitation or competitive exclusion.

We test five hypotheses about the spatial distribution of SIEs within each of the three islands. Hypothesis 1 is that SIE density at a landscape scale increases with geological age and topographic complexity: hence both variables should be identified as strong drivers by models for SIE richness. Hypothesis 2 states that spatial distributions of individual SIEs should be strongly biased towards old substrates. Hypothesis 3 posits that analyses of available phylogenetic data of important plant lineages should show that divergence times of most SIEs are older than the defined young terrain, but younger than the maximum age of the island, indicating that they evolved on the older parts of the islands. Past research has shown that diversification rates within oceanic islands can vary between areas of different major ecosystem types (Zobel *et al.*, 2011; Steinbauer *et al.*, 2012), hence hypothesis 4 states: any observed relationship between terrain age and SIE diversity may be a by-product of differences in availability of the major ecosystem types between old and young terrain. Finally, it could be argued that current species distributions have been greatly influenced by human activities, and that reduced ranges of SIEs are a consequence of anthropogenic land use (de Nascimento *et al.*, 2009; Irl *et al.*, 2014). Hence, hypothesis 5 is that there will be a strong negative correlation of SIE richness with measures of human activity. If supported this would point to the possibility of an alternative mechanism for our observed patterns, weakening the argument for an evolutionary basis of SIE distribution patterns.

MATERIALS AND METHODS

Study area

El Hierro (EH; origin 1.1 Ma), in the south-west of the archipelago (27°37′ y 29°25′N and 13°20′ y 18°10′W), has a surface area of 285 km^2, while La Palma (LP; origin 1.8 Ma) provides the north-western extremity, with a surface area of 780 km^2 (Carracedo, 2011; Fig. 1). Tenerife (TFE; origin 11.9 Ma) is the biggest (2035 km^2) and highest Canary island (3718 m a.s.l.). Each island comprises older eroded terrain units and very young parts. Rapid growth and high levels of volcanic activity have been associated with instability, leading to a number of huge landslips, which have greatly influenced the size, shape and topography of these islands. On EH, the oldest geological series outcrops within the steep slopes of the collapse scarps of the ancient El Golfo volcano in the north and on the ancient Tiñor volcano in the east. Four giant landslips have occurred on EH, the most recent around 0.15 Ma (Carracedo, 2011).

The oldest part of LP was built by two shield volcanos (Garafía and Taburiente) in the north, which collapsed westwards 1.2 and 0.56 Ma respectively. The remainder of LP is covered by much younger lava flows and pyroclastics (< 150 ka). Tenerife has a more complex geological history: one scenario is that the island was formed from two or three palaeo-islands aged 5–11 Myr, which were joined together within the last 3 Myr by a huge central strato-volcano. An alternative scenario proposes that the central edifice has been present throughout the island's history, notwithstanding the young age of the existing central areas (Carracedo, 2011). At least three major landslips have formed the Güímar Valley (0.83–0.56 Ma), the Orotava Valley (0.56 Ma) and the Teide Caldera (0.17 Ma). The younger volcanic series III (< 0.5 Ma), and especially the post-caldera volcanism (< 0.17 Ma), cover extensive areas.

The climate is oceanic subtropical, influenced by north-easterly trade winds and characterized by warm, dry summers and rainfall mostly between October and March. The presence of the full array of major ecosystem types (lowland scrub, thermophilous woodlands, laurel forest, pine forest and summit scrub), as found on LP and TFE, requires a larger elevational range than found on EH, which lacks the summit scrub. The Canarian vegetation has been subject to anthropogenic alteration for at least 2000 years, but especially so following European conquest in the 15th century (Gaisberg, 2005; Stierstorfer, 2005; de Nascimento *et al.*, 2009). The resident populations of EH (10,000) and LP (87,000) are much smaller than TFE (900,000), where human impact on natural vegetation is more pronounced (Del Arco *et al.*, 2006).

Species and environmental data

For EH, plant presence/absence data were sourced from two detailed, systematic field surveys carried out between 1997 and 2003, following the 1 × 1 km² UTM grid (Gaisberg, 2005; Gaisberg & Stierstorfer, 2005; Stierstorfer, 2005; for nomenclature and floristic status see: Stierstorfer & Gaisberg, 2005). We distinguished three chorological groups: (1) single island endemics (SIE), (2) multiple island endemics (MIE, i.e. Canarian endemics), and (3) native species not endemic to the Canary Islands (NAT). For LP and TFE, we used the local government's ATLANTIS 3 database (www.biodiversidadcanarias.es/atlantis; accessed November 2013), which provides species distributions maps based on 500 × 500 m grid cells and includes all species in the most recent checklist for the Canary flora (Arechavaleta *et al.*, 2010). For LP and TFE, we used only distribution maps of SIEs because of known limitations of this database (Hortal *et al.*, 2007). The initial aim of this database was to compile herbaria and literature data focussed on species of interest, such as SIEs, but the most recent update included all species. Although the database has been reported to be spatially biased with regard to sampling effort (Hortal *et al.*, 2007), we consider that the SIE pattern is much less biased compared to the NAT or overall richness pattern (we checked this for the two data-

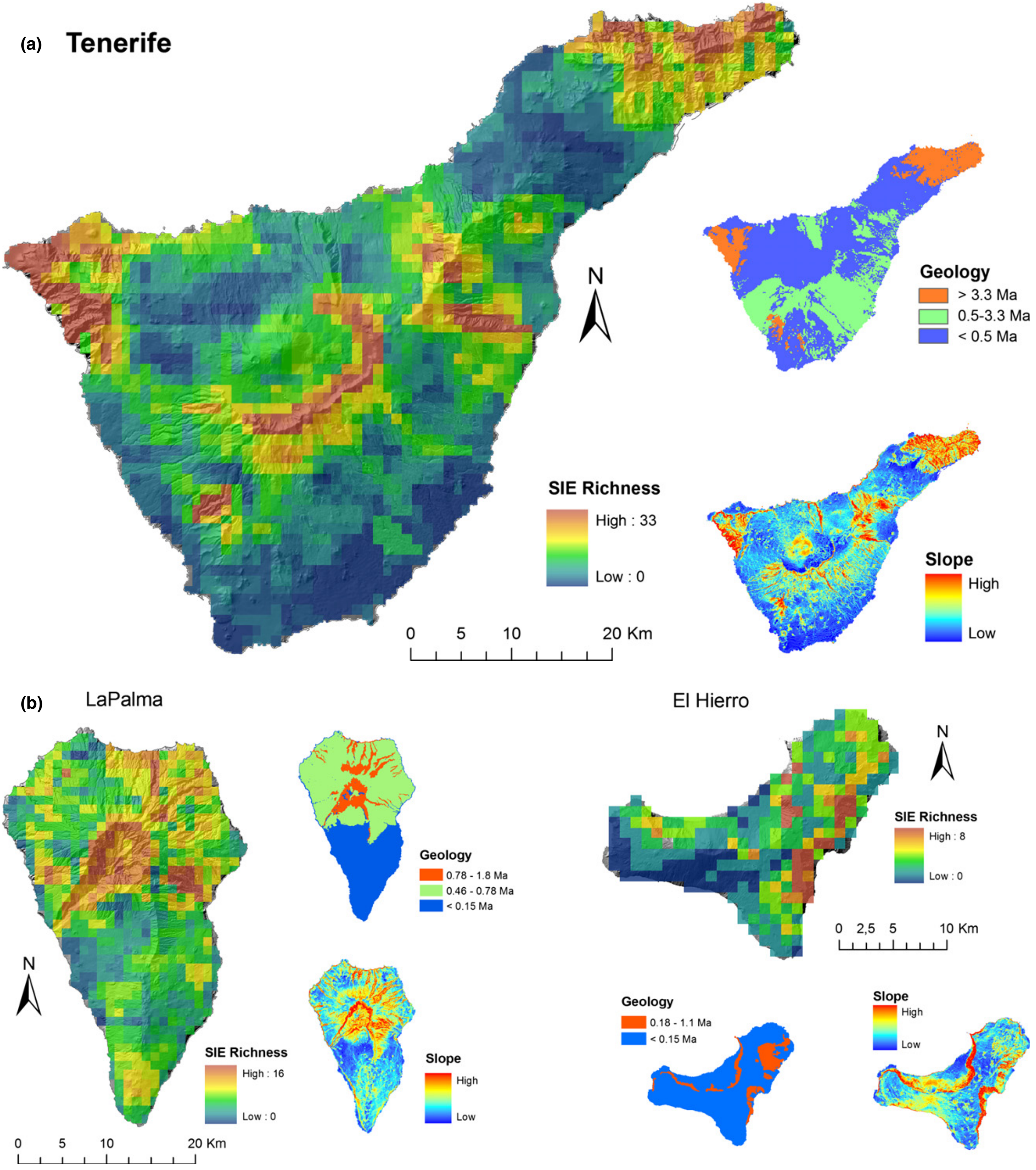

Figure 1 Within-island hotspots of richness of single island endemic plant species (SIE) for the three Canary Islands, El Hierro, La Palma and Tenerife, shown by grid-cell mapping with a resolution of 1 km^2. Additional information about geology and topography (mean slope) of each island is given.

bases available for El Hierro) as most previous studies focused on the endemic flora and the government additionally carried out numerous chorological studies on SIEs in recent decades, results from which were incorporated into the ATLANTIS 3 database. Data from LP and TFE were aggregated to grids of 1 × 1 km to provide a common scale of analysis to that for EH. For each island, we removed cells centred over or with > 50% ocean.

There have been many phylogenetic studies of Canarian plant lineages (e.g. Reyes-Betancort *et al.*, 2008), but few provide estimated divergence times based on molecular clocks (*Lotus*, Ojeda *et al.*, 2014; *Echium,* García-Maroto *et al.*, 2009; *Micromeria*, Puppo *et al.*, 2014). We made use of these data in testing hypothesis 3. These studies applied different clock models to estimate mean divergence times within the phylogenetic trees (penalized or maximum likelihood, Bayesian estimators). Phylogenetic trees were calibrated by the age of the most recent common ancestor of the Macaronesian lineage (subtribe Menthinae 23 Ma in the case of *Micromeria*) or by the maximum geological age of the archipelago (Fuerteventura, 20.6 Ma) for the Macaronesian lineages of *Lotus* and *Echium*. Mean values of divergence time estimates were given.

A recently developed database of phylogenetic lineages for the entire native Canary flora [J.P. Price *et al.*, unpublished data (J.P. Price, University of Hawai'i at Hilo)] was used to distinguish between SIEs belonging to cladogenetic lineages (many species in the same Canarian lineage) and SIEs representing anagenetic lineages (only one species per Canarian lineage).

Climatic, geological, topographical and land use data layers in digital raster or vector format were intersected with the 1 × 1 km grids using ArcGIS 10.2.2 (ESRI Inc., Redlands, CA, USA). Elevation, slope and aspect were obtained from a 25-m resolution digital elevation model (DEM). Aspect was transformed by applying a sine function to a lee/windward variable, ranging between −1 and 1 value (south-west to north-east). To account for topographic complexity we calculated mean values, ranges and standard deviations of the 1600 pixels within each 1 × 1 km cell for elevation, aspect and slope. Climate data were sourced from meteorological stations operated by the State Agencia Española de Meteorología and interpolated using multiple linear regression analysis followed by spatial interpolation of the regression residuals for EH and LP (see Garzón-Machado *et al.*, 2014) and, for TFE, using co-kriging.

Terrain age classification followed Carracedo (2011) (Fig. 1). For the richness models, we used three age classes for EH (Rift volcanism < 0.15 Ma, El Golfo volcano 0.56–0.8 Ma, Tiñor volcano 0.8–1.1 Ma), five for LP (youngest series < 0.15 Ma, Bejenado volcano 0.49–0.56 Ma, lower Taburiente 0.41–0.78 Ma, upper Taburiente 0.78–1.1 Ma, Garafía volcano 1.2–1.7 Ma) and three for TFE (youngest volcanism including the youngest series III and the post-caldera volcanism < 0.5 Ma, intermediate volcanism including pre-Teide volcanism and Dorsal series 0.5–3.3 Ma, old volcanism 3.3–11.9 Ma). For the random distribution models of SIEs and the habitat distributions, we used a binary code: 'young', the youngest geological series on each island (EH and LP < 0.15 Ma, TFE < 0.5 Ma) and 'old', the remainder. By this coding, old terrain comprises: TFE 1233 km^2 (60.7%), LP 468 km^2 (66.1%) and EH 99 km^2 (37.5%). Some areas of old terrain may once have been buried by younger volcanic deposits that have eroded again to reveal older terrain. Contrarily, other areas that are now 'young' occupy physical space that previously existed as older terrain units that have been destroyed and replaced (e.g. Sibrant *et al.*, 2015). Hence, recent volcanic and geomorphological dynamics may have impacted on the patterns of distribution analysed herein, leaving some palimpsest-like legacies. The present analyses assume that such legacies are negligible.

Land cover data in digital vector format (source: GRAFCAN, www.grafcan.es, accessed April 2012) were used to determine prevailing land use types, classified into semi-natural vegetation, sparse vegetation, forest plantation, abandoned fields, pastures, cultivated agricultural land and urbanized areas. Distances to nearest urban settlements were calculated for each grid cell in ArcGIS, as an index of human activity.

Statistical analysis

To model the relationship between species richness and explanatory variables, we used generalized linear models (GLM; McCullagh & Nelder, 1989) with Poisson distribution and log link function for all richness groups (Quinn & Keough, 2002). For EH island, we used NAT, MIE and SIE richness as dependent variables, but for LP and TFE we used only SIE richness (due to data availability – outlined above). For pSIE on EH, generalized linear models with binominal distribution were applied. The explanatory variables were standardized to zero mean and unit variance to enable direct comparison of regression terms (Quinn & Keough, 2002).

Generalized linear models were performed in R 3.0.0 (R Development Core Team, 2012). A best subset regression approach was applied where all combinations of predictor variables were modelled (Burnham & Anderson, 2002), using the function *dredge* of the R library 'MuMIn' 1.10.5 (Barton, 2014). First, we ran a best subset selection using a GLM model separately for each of the three groups of explanatory variables (climate, topography and anthropogenic influence), with richness as the dependent variable and all predictors within each group. We used the Akaike information criterion (AIC) corrected for small sample size (AICc) and the resulting models were ranked by AIC$_c$ weights. Those models with strongly collinear predictor variables, as assessed using the variance inflation factor (VIF; function *vif* of the library 'car'), were eliminated (Fox & Monette, 1992).

In a second step, a best subset selection was applied to a full GLM, including all the predictors of the candidate models selected during the first step. For the full approach, only the best models with ΔAIC$_c$ < 2 were selected and ranked by AIC$_c$ weights. Again, VIFs were calculated to check for possible collinearity and models with correlated predictors were eliminated. Therefore, final best models for each richness group only included noncorrelated predictors with coefficients of estimates significant at $P < 0.001$. Ecologically meaningful quadratic terms of predictors (mean annual precipitation; MAP) and interactions (slope x geological age) were included and tested in the final best subset modelling. Over-dispersion was checked for the best GLM model of each richness group (function *c-hat* of the library 'AICcmodavg'). Additionally, the adjusted McFadden Pseudo R^2 was calculated for the best GLM models (function *PseudoR2* of the library 'BaylorEdPsych' version 0.5; Beaujean, 2012), which reflects the deviance explained by the model.

To test for random distribution of SIEs in respect to terrain age, we applied the exact binominal test (function *binom.test* in R standard package stats), which assesses whether the percentage of a species' occurrences on old (or young) substrate is significantly higher than the percentage of area covered by old (or young) substrate on the island. The analysis was carried out for species distribution pattern at the 500 × 500 m grid level and repeated for each island. Of the species with significantly higher proportional occurrence on one of the two age classes we defined SIE as restricted to old (or young) substrate when > 90% of the grid cells occupied were of old (or young) terrain. To test if the distribution of the Canarian major ecosystem types might be biased in relation to age, we determined the proportion of these ecosystems of each island on old and young terrain by overlaying maps of terrain age and potential natural vegetation (Del Arco *et al.*, 2006).

We used Moran's *I* coefficient to investigate the spatial autocorrelation of the regression residuals (Diniz-Filho *et al.*, 2003). In all but one case these analyses showed an absence of spatial autocorrelation, with low and nonsignificant Moran's *I* coefficients (< 0.1) at the shortest distance classes (< 5 km). The exception was the SIE richness model for TFE, which exhibited significant spatial autocorrelation at the shortest distance (3.4 km) only (see Appendix S1). Because of the general absence of spatial autocorrelation, we concluded that there was no need to apply spatially explicit models. The software SAM 4.0 (Rangel *et al.*, 2010) was used for the analysis of spatial autocorrelation.

RESULTS

In the 264 grid cells of El Hierro, 284 indigenous vascular plant species were recorded: 179 (63.0%) native species (NAT) and 105 (37.0%) Canarian endemics; the latter subdivided into 12 (4.2%) SIEs and 93 (32.8%) MIEs. For La Palma, the distributions of 36 SIEs (8.9% of 416 indigenous species) were analysed for 706 grid cells. For Tenerife, 111 SIEs (17.7% of the indigenous flora) were analysed for 2030 grid cells. Of the total of 159 SIEs, 151 belong to lineages that have undergone speciation through cladogenesis, whereas 8 SIEs (all from TFE) represent mono-specific lineages. Of the latter group, probably only three might be relict, palaeo-endemics (Trusty *et al.*, 2005; J.P. Price *et al.*, unpublished data) and five can be termed anagenetic SIEs. Hence, the majority of the SIEs can be considered neo-endemic to the archipelago or archipelagic neo-endemics.

For each island, the highest densities of SIEs occur on steep slopes and old substrates (Fig. 1): on EH, on the steep slopes of the collapse scarps of the ancient El Golfo volcano in the north and east (Las Playas embayment) and on parts of the eastern slopes of the ancient Tiñor volcano; on LP, in the deep Taburiente crater and the highly eroded steep-sided valleys on the northern and north-eastern flanks; and on Tenerife in mountainous areas of the three palaeo-islands (Teno, Anaga and Adeje) and on the steep slopes of the central Teide crater and of the Güímar valley in the south-east.

For each island, the best GLM models for SIE richness, accounting for 40–45% deviance, found geological age or the interaction between geological age and mean elevational slope to be the best predictors, followed by precipitation (MAP^2 or MAP), after which the variables included differed (Table 1). Of the anthropogenic variables, only cover of pasture showed a significant but weak negative effect on LP, whereas cover of agricultural land, and of urban areas were included as weak (negative) effects for TFE. The results of the GLMs for pSIE on EH showed no important difference from the SIE richness model, with just slope deviation omitted from the pSIE model (Table 1).

When GLMs were carried out individually for the four most important predictors of SIE richness on each island (Table 2), geological age was the best single predictor on EH and LP, but second in importance on TFE, after mean slope.

Table 1 Results of generalized linear models (GLMs) for the three Canary Island of El Hierro (EH), La Palma (LP) and Tenerife (TFE), showing the best set of explanatory variables explaining richness of single island endemic plant species (SIEs). Akaike's Information Criteria (AIC_c) and AIC_c weights were used for best set selection. The Poisson distribution with log link function was chosen for all models. Adjusted McFadden's Pseudo R^2 (Adj. R^2) indicate the deviance explained in the model. Abbreviations: SLOPE = mean slope, AGE = geological age, MAP = mean annual precipitation (linear and quadratic term), SLOSD = standard deviation of slope, ASPSD = standard deviation of landscape aspect, CV = coefficient of variation of mean annual precipitation, SCRUB = cover of shrub vegetation, SPVEG = sparse vegetation, PAST = cover of pasture, AGR = cover of agricultural land, URB = cover of urbanized land. All selected predictors were significant at $P < 0.001$.

	EH SIE		*LP SIE*		*TFE SIE*	
	AICc w 0.12 (13)	Adj. R^2 0.44	AICc w 0.19 (10)	Adj. R^2 0.43	AICc w 0.53 (3)	Adj. R^2 0.43
Variable	Coeff.	*z*-value	Coeff.	*z*-value	Coeff.	*z*-value
SLOPE × AGE	0.32	5.61			0.38	37.12
AGE			0.13	8.74		
SLOPE			0.10	4.89		
MAP	0.25	4.40	0.03	1.52	0.21	15.24
MAP2	−0.23	−4.32	−0.10	−6.55	−0.32	−26.48
ASPSD	0.12	2.05			0.06	6.33
SLOSD	0.19	3.81				
CV	0.12	3.15				
SCRUB					0.11	10.08
SPVEG			0.06	5.01		
PAST			−0.05	−3.02		
AGR					0.09	−9.42
URB					−0.08	−3.75

However, for EH and TFE, the interaction term (i.e. the combined effect of geological age and slope) accounted for the highest amount of deviance explained in the full models (Table 1). In the case of EH, the best single predictors, although highly significant, only explained 17% of the overall deviance. Nonetheless, the full GLM accounted for 44% of the total deviance (Table 1), meaning that explained deviance was more equally distributed among predictors compared to TFE or LP.

Geological age was not included as a significant predictor for NAT or MIE richness on EH (Table 3). Instead, GLMs selected elevational range as the best predictor, followed by aspect (for MIE) and MAP^2 (for NAT). In contrast to SIE richness, anthropogenic variables such as cover of pasture and the distance to urbanization had a significant positive effect on NAT and MIE richness.

Binominal tests revealed a consistent pattern for all three islands, with most SIEs being more frequent on or restricted to old terrain (67% and 39% for TFE respectively; 69% and 44% for LP; and 73% and 33% for EH, Fig. 2). Very few SIE species showed higher proportional occurrences on young terrain (17 (15%) on TFE, 5 (14%) on LP and no species on EH). Within TFE, 11 of the 17 SIEs are components of the high-elevation summit scrub. Of the 159 SIEs across the three islands, only two (1.3%) were restricted to young terrain: *Carduus volutarioides* Reyes-Betancort, a recently described species, and *Kunkeliella subsucculenta* Kämmer, a rare endangered species, found on the northern slope or coast.

With the exception of the summit scrub, which is lacking from young terrain on LP, all of the major ecosystem types occur on both old and young terrain on each island (Fig. 3). Generally speaking, we can find the full array of habitats along the elevational gradient on both substrate age groups, although habitats are not distributed exactly in the same way. Coastal vegetation on TFE and laurel forest on LP and EH are more frequent on old terrain, whereas summit scrub on TFE, thermophilous woodland on LP and pine forest on EH are more common on young terrain.

Table 2 Deviance (%) explained by generalized linear models including only one single predictor for the three Canary Island of El Hierro, La Palma and Tenerife, showing the predictive power of individual explanatory variables selected in the multimodel inference approach (Table 1) explaining richness of single island endemics (SIE), proportion of SIE (pSIE), multiple island endemic (MIE) and native nonendemic plant species (NAT). The Poisson distribution with log link function was chosen for SIE models, and the binominal distribution for pSIE models. All single predictors were highly significant at $P < 0.001$. Abbreviations: AGE = geological age, SLOPE = mean slope, SLOPE:AGE = interaction between mean slope and geological age, MAP = mean annual precipitation (linear and quadratic term, MAP^2).

Richness	AGE	SLOPE	SLOPE:AGE	MAP + MAP^2
Tenerife SIE	19	29	33	17
La Palma SIE	32	29	30	9
El Hierro SIE	16	13	17	14
El Hierro pSIE	11	15	17	11
El Hierro MIE	6	32	29	9
El Hierro NAT	2	10	7	19

Table 3 Results of generalized linear models for El Hierro (EH), showing the best set of explanatory variables explaining richness of native nonendemic plant species (NAT), multiple island endemic plants (MIE) and proportions of single island endemics (pSIE). Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$) and $\mathrm{AIC_c}$ weights were used for best set selection. Poisson distribution with log link function was chosen in all models. Adjusted McFadden's Pseudo R^2 (Ajd. R^2) indicate the deviance explained in the model. The Poisson distribution with log link function was chosen for NAT and MIE models, and the binominal distribution for pSIE models. Abbreviations: SLOPE = mean slope, AGE = geological age, ELER = elevational range, MAP = mean annual precipitation (linear and quadratic term), SPVEG = sparse vegetation cover, ASP = mean value of landscape aspect, ASPSD = standard deviation of landscape aspect, CV = coefficient of variation of mean annual precipitation, PAST = cover of pastures, DUN = distance to urbanization. All selected predictor were significant at $P < 0.001$.

	EH NAT		*EH MIE*		*EH pSIE*	
	AICc w 0.19 (10)	Adj. R^2 0.30	AICc w 0.07 (27)	Adj. R^2 0.46	AICc w 0.20 (9)	Adj. R^2 0.32
Variable	Coeff.	*z*-value	Coeff.	*z*-value	Coeff.	*z*-value
SLOPE × AGE					0.28	4.96
ELER	0.08	6.03	0.24	17.31		
MAP	0.03	2.02	−0.07	−3.62	0.18	3.25
MAP^2	−0.07	−5.01			−0.21	−3.86
ASP			0.17	10.54		
ASPSD					0.15	2.88
CV					0.16	3.27
PAST	0.05	3.44				
DUN	−0.06	−4.00				

Estimated divergence times of all SIEs within the time calibrated plant lineages (*Lotus*, *Echium, Micromeria*), for 24 species (15% of SIEs), were older than the terrain defined as young (< 0.15 Ma for EP and LP and < 0.5 Ma for TFE), but younger than the maximum age of the island (see Appendix S2).

DISCUSSION

Within-island hotspots of SIEs and the importance of geological age and topography for diversification

Most SIEs on these islands belong to genera that provide excellent examples of adaptive (ecological) and/or allopatric (geographical) speciation in the Canary Islands (Gaisberg & Stierstorfer, 2005; Reyes-Betancort *et al.*, 2008), representing lineages that have undergone speciation within the archipelago through cladogenesis, thus forming archipelagic

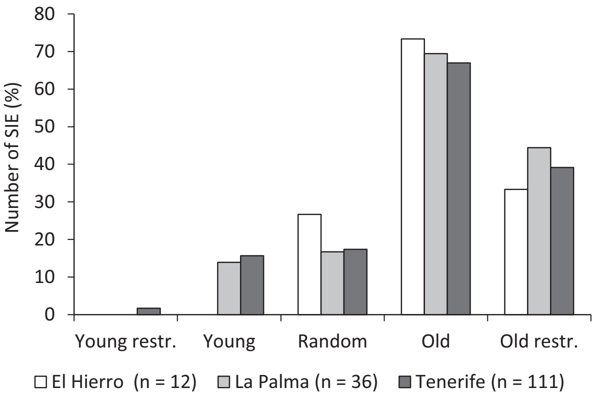

Figure 2 Distributions of single island endemic plants (SIE) in respect to geological age of substrate on El Hierro, La Palma and Tenerife. The random distribution of each species was tested applying a Binominal test. Random = random distribution with respect to substrate age, Old = nonrandom distribution with significant higher probability for occurrence on old substrate, Old restr. = nonrandom distribution with > 90% occurrence on old substrate, subgroup of class 'Old', Young = nonrandom distribution with significant higher probability for occurrence on young substrate, Young restr. = nonrandom distribution with > 90% occurrence on young substrate, subgroup of class 'Young'.

neo-endemics (including SIEs and MIEs). Estimated divergence times of these neo-endemics vary depending on the position in the phylogenetic tree of each lineage (García-Maroto *et al.*, 2009; Puppo *et al.*, 2014). Anagenetic SIEs (a category that may include palaeo-endemics) are very rare (5%) in our study. Hence, our assumption that SIEs generally evolved *in situ* is reasonable, although MIEs can, in principal, become SIEs by extinction from all but one island (Whittaker *et al.*, 2008).

Our analyses of SIE distribution and richness patterns are consistent with hypotheses 1 and 2 in finding that SIEs have accumulated predominantly on older and topographically complex terrain, but roughly half of them were also found on the extensive areas of younger terrain. Species restricted to young substrate were extremely rare. On each island, SIE richness was best predicted by geological age or by the combined effect of geological age and mean slope (Table 1). This indicates that topography can interact with geological age in favouring SIE richness, although both of these factors can independently act as strong drivers of SIE richness. This was further supported by the inclusion in the models of topographic complexity, expressed by standard deviation of landscape slope and aspect on EH and TFE (Table 1).

High topographic complexity represents not only environmental heterogeneity (microclimate, soil conditions), which is recognized as a strong driver of species richness from the regional to the global scale (Stein *et al.*, 2014), but also high geomorphological dynamism related to erosion on steep slopes. This combination of conditions prevents the formation of continuously closed forests or shrub communities where interspecific competition is high, and the reduced levels of competition creates opportunities for speciation for immigrated plant species (Kruckeberg, 2002; Silvertown, 2004). The positive correlations of shrub or sparse vegetation with SIE richness on TFE and LP, respectively, support this argument. Additionally, high topographic complexity at a local scale, if lasting long enough, may favour speciation through ecological and geographical isolation, as steep ravines and mountain crests can act as barriers for gene flow. Indeed, studies from continental settings (e.g. Cowling & Lombard, 2002; Garrick, 2011) have suggested that high endemism in topographically complex areas can arise from higher speciation rates and lower extinction. We postulate that this may hold true for oceanic islands where topographic complexity is linked to geological age (Whittaker *et al.*, 2008).

Divergence times of SIEs belonging to the time calibrated radiated lineages [*Lotus* (Ojeda *et al.*, 2014), *Echium* (García-Maroto *et al.*, 2009) and *Micromeria* (Puppo *et al.*, 2014)] indicate an origin of all species congruent with the age of the older parts of the host island, even for those species that are currently more abundant on very young terrain, or that show random distributions. Furthermore, molecular phylogenetic studies have indicated *Descurainia gilva* and *Pericallis multiflora* (SIEs from LP and TFE respectively) to be

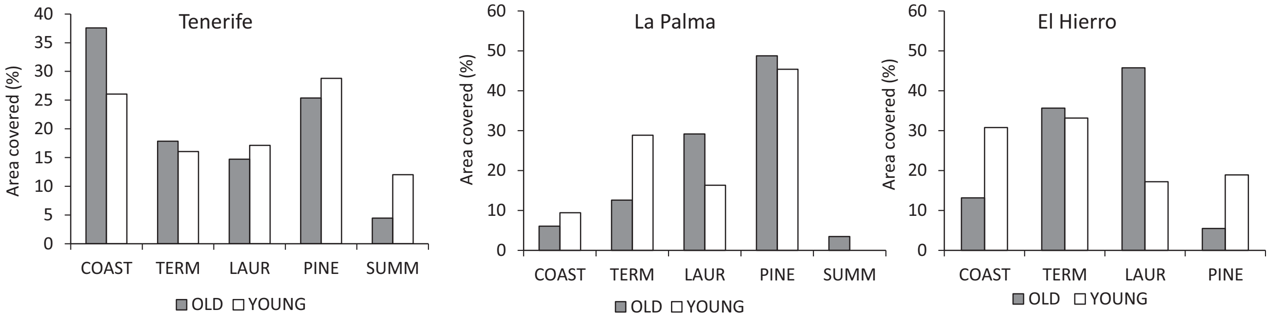

Figure 3 Distributions of major elevational ecosystems in respect to geological age of substrate on El Hierro, La Palma and Tenerife showing the area covered (%) by each major ecosystem on young and old substrate (COAST = coastal scrub, TERM = thermophilous woodlands, LAUR = laurel forest, PINE = pine forest, SUMM = summit scrub). Young terrain corresponds to the youngest geological series on each island (EH and LP < 0.15 Ma, TFE < 0.5 Ma) and the remainder is termed old terrain.

ancestral within their monophyletic lineages, indicating their speciation to have occurred early in the life of each island, notwithstanding that they are currently more frequent on young volcanic substrate (Swenson & Manns, 2003; Goodson *et al.*, 2006). In sum, the evidence strongly supports the hypothesis that most of the SIEs evolved relatively early in the island lifespan, although in some cases, particular species have spread onto younger terrain within the islands.

The role of ecological factors and habitat availability

Mean annual precipitation was found to be an important driver of SIE richness. A hump-shaped relationship with precipitation was also observed for NAT on EH, which is consistent with previous Canarian studies (Arévalo *et al.*, 2005; Otto *et al.*, 2013). The highest precipitation and species richness levels were documented at intermediate elevations on the Canaries, where hydrological and thermal stress are low and productivity is highest, consistent with the water–energy dynamics model (Field *et al.*, 2005). Similar elevation–richness patterns have been reported from other oceanic archipelagos and continents (Kessler, 2002; Price, 2004).

SIE distributions on old and young terrain were not simply explained by habitat availability, that is, SIEs are not more frequently found on old terrain because particular habitats that favour speciation are more abundant there. High proportions of endemism in plants have been assigned to the thermophilous woodland and the summit scrub and relatively lower diversification rates to the laurel forest (Zobel *et al.*, 2011; Steinbauer *et al.*, 2012). In our study islands, thermophilous woodland and the summit scrub are somewhat overrepresented on young terrain, and laurel forest towards old terrain, which is the opposite of what the habitat availability hypothesis would predict.

Processes of immigration, speciation and extinction at an intra-island scale

The GDM suggests that immigration is highest in the earliest phase of an oceanic island's development and that diversification rates are highest during island 'immaturity' (Whittaker *et al.*, 2008), contributing to attainment of peak richness prior to the phase when extinction dominates as the island shrinks. Following this logic, local species densities may be anticipated to continue to increase for much of the island's life span, particularly so in the most topographically complex areas. Interestingly, richness of NATs and of MIEs per grid cell on EH were found to be statistically independent of geological age, implying that these more widely distributed Canarian species generate local species density patterns that lack a significant historical legacy, and thus can be interpreted directly in relation to local environmental conditions.

Our data are largely supportive of a process of spillage of SIEs from older to younger substrates (intra-island progression rule; Funk & Wagner, 1995): a process which offers new opportunities for local adaptation and for hybridization between forms that have begun to, or have achieved, allopatric speciation (e.g. Brochmann *et al.*, 2000). Our findings support the importance of including geological dynamics in explanatory models of speciation processes within oceanic islands (Carson *et al.*, 1990; Gaisberg & Stierstorfer, 2005; Stuessy, 2007; Reyes-Betancort *et al.*, 2008). Further support for this idea comes not only from recent phylogenetic studies on plant lineages on the Canary islands included in this analysis (García-Maroto *et al.*, 2009; Ojeda *et al.*, 2014), but also from recent faunistic studies that show the imprint of geological history on within-island diversification (within genera and within species) on the Canary Islands (Juan *et al.*, 2000; Emerson, 2003; Macías-Hernández *et al.*, 2013) and on other oceanic archipelagos (Vandergast *et al.*, 2004).

The diversification rate on oceanic islands probably depends on the taxon, as well as on the climatic and geological history of the island and of the whole archipelago. Steinbauer *et al.* (2013) found that both number and proportion of SIEs on oceanic islands peaked at around 10 Myr, indicating that diversification can continue for spans far longer than either EH or LP have yet existed. The high number and proportion of SIEs on TFE might be explained by the much greater geological age, but probably also by the more complex geological history of the island. On TFE, supposedly two or three palaeo-islands existed for several million years before they coalesced into the contemporary island. These fragments, then aged 5-6 Myr, were not covered subsequently by more recent volcanic materials. As predicted by our downscaled GDM, these areas with the longest temporal windows for speciation and highest topographic complexity actually exhibit the highest concentration of SIEs of all three islands (Trusty *et al.*, 2005). However, we may also assume that the speciation process will be initiated on quite young substrates as some plant genera with very high diversification rates have been reported for the Canarian (*Echium* by García-Maroto *et al.*, 2009) and for the Hawaiian archipelago (e.g. *Bidens* by Knope *et al.*, 2012), with explosive speciation within < 1 Myr.

To summarize, our results are broadly consistent with our initial expectations and with the GDM and show that it may be possible to downscale the model to island fragments of different age. Our analyses are restricted to just three of the Canary Islands (El Hierro, La Palma and Tenerife), and thus capture only the beginning of the ontogenic trajectory, missing the over-mature and highly eroded old-age stage of flattened landscapes characteristic of Fuerteventura and Lanzarote. The issue of how the age of individual landscape units determines species distributions should be viewed within the GDM framework in relation to within-island patterns of migration, extinction and speciation, on the one hand, and between-landscape differences in carrying capacity. The latter is determined by properties such as topographic range (linked in turn to habitat and climatic diversity) and geochemical and hydrological properties of the soils. These factors can be anticipated to vary with terrain age but they will also be a function of the nature of the volcanism (e.g. chemical and physical properties of the lava) and the geomorphological processes that created the different sections of terrain in the first place. Thus, further empirical and theoretical work may be needed before a downscaled model of the GDM can be considered general.

Human influence

Variables related to anthropogenic activities and disturbance were not selected in the models of SIE richness, or of pSIE, for EH, and made only minor contributions to the SIE richness models for LP or TFE. Hence, we reject our last hypothesis of a strong negative effect of human disturbances on overall patterns of SIE richness.

We should caution that our approach to measure human influences is crude and may not adequately capture the effects of historical and pre-historical goat grazing, anthropogenic fire use and certain types of habitat transformation on islands that have been settled for possibly around 2,500 years (see e.g. de Nascimento *et al.*, 2009; Garzón-Machado *et al.,* 2010). For instance, topographically complex terrain can provide shelter for susceptible native plant species from non-native herbivores, the negative impacts of which have been demonstrated in several Canarian studies (e.g. Garzón-Machado *et al.*, 2010; Irl *et al.*, 2014). However, we regard it as implausible that most of the 112 SIEs (70%) that are currently more frequent on, or even restricted to, old terrain were once abundant on very young substrate and then completely or partly eliminated by animal browsing in the past. We argue that although such negative effects of non-native herbivores on SIE distributions might exist in particular cases, they do not depend on substrate age and, therefore, should not strongly bias our results. Fire disturbance, on the other hand, is only important in pine forest and rarely impacts the other Canarian ecosystems: hence fire also seems an unlikely general alternative hypothesis to explain the observed SIE pattern.

CONCLUSIONS

We have extended the spatio-temporal framework of the GDM, by down-scaling its dynamics to fragments with different geological histories within a single island. We consider our findings, although based on crude analyses, to be broadly consistent with the predictions of the core GDM. Our analyses illustrate the role of biogeographical processes within islands and the potential to develop a multiscalar theory of oceanic island biogeography. Hence, we argue that renewed attention should be given to analysing geological/geomorphological and evolutionary dynamics within islands, focussing on the frequency, intensity and extent of volcanic eruptions and other major landform-changing events (e.g. mega landslides), not merely on the maximum age of the island or archipelago.

ACKNOWLEDGEMENTS

We acknowledge the funding by the University Las Palmas of Gran Canaria and the University La Laguna of Tenerife within the framework of the program 'Programa Talento Tricontinental del CEI Canarias: Campus Atlántico Tricontinental'.

REFERENCES

Arechavaleta, M., Rodríguez, S., Zurita, N. & García, A. (2010) *Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres*. Gobierno de Canarias, Santa Cruz de Tenerife.

Arévalo, J.R., Delgado, J.D., Otto, R., Naranjo, A., Salas, M. & Fernández-Palacios, J.M. (2005) Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 185–202.

Barton, K. (2014) MuMIn: Multi-model inference. R package version 1.10.5.

Beaujean, A.A. (2012) BaylorEdPsych: R Package for Baylor University. Educational Psychology Quantitative Courses. R package version 0.5.

Brochmann, C., Borgen, L. & Stabbetorp, O.E. (2000) Multiple diploid hybrid speciation of the Canary Island endemic *Argyranthemum sundingii* (Asteraceae). *Plant Systematics and Evolution*, **220**, 77–92.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical–theoretic approach*, 2nd edn. Springer, New York.

Cameron, R.A.D., Triantis, K.A., Parent, C.E., Guilhaumon, F., Alonso, M.R., Ibáñez, M., de Frias Martins, A.M., Ladle, R.J. & Whittaker, R.J. (2013) Snails on oceanic islands: testing the general dynamic model of oceanic island biogeography using linear mixed effect models. *Journal of Biogeography*, **40**, 117–130.

Carracedo, J. C. (2011) *Geología de Canarias. Origen, evolución, edad y volcanismo*. Editorial Rueda, E.L., Madrid.

Carson, H.L., Lockwood, J.P. & Cradock, E.M. (1990) Extinction and recolonization of local populations on a growing shield volcano. *Proceedings of the National Academy of Sciences USA*, **87**, 7055–7057.

Cowling, R.M. & Lombard, A.T. (2002) Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. *Diversity and Distributions*, **8**, 163–179.

Del Arco, M.J., Wildpret, W., dePérez- -Paz, P.L., Rodríguez-Delgado, O., Acebes, J.R., García-Gallo, A., Martín, V.E., Reyes-Betancort, J.A., Salas, M., Bermejo, J.A., González, R., Cabrera, M.V. & García, S. (2006) *Mapa de Vegetación de Canarias*. GRAFCAN, Santa Cruz de Tenerife.

Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.

Emerson, B.C. (2003) Genes, geology and biodiversity: faunal and floral diversity on the island of Gran Canaria. *Animal Biodiversity and Conservation*, **26**, 9–20.

Fernández-Palacios, J.M., Otto, R., Thebaud, C. & Price, J.P. (2014) Overview of habitat history in subtropical oceanic island summit ecosystems. *Arctic, Antarctic and Alpine Research*, **46**, 801–809.

Field, R., O'Brien, E.M. & Whittaker, R.J. (2005) Global models for predicting woody plant richness from climate: development and evaluation. *Ecology*, **86**, 2263–2277.

Fox, J. & Monette, G. (1992) Generalized collinearity diagnostics. *Journal of the American Statistical Association*, **87**, 178–183.

Funk, V.A. & Wagner, W.L. (1995) Biogeographic patterns in the Hawaiian Islands. *Hawaiian biogeography: evolution on a hot spot archipelago* (ed. by W.L. Wagner and V.L. Funk), pp. 379–419. Smithsonian Institution Press, Washington, DC.

Gaisberg, M. (2005) Die Vegetation der Fußstufe von El Hierro (Kanarische Inseln). *Dissertationes Botanicae*, **395**, 1–364.

Gaisberg, M.V. & Stierstorfer, C. (2005) The significance of geological traits for the speciation of endemic angiosperms on El Hierro (Canary Islands). *Phytocoenologia*, **35**, 39–52.

García-Maroto, F., Mañas-Fernández, A., Garrido-Cárdenas, J.A., Alonso, D.L., Guil-Guerrero, J.L., Guzmán, B. & Vargas, P. (2009) Delta 6-desaturase sequence evidence for explosive Pliocene radiations within the adaptive radiation of Macaronesian *Echium* (Boraginaceae). *Molecular Phylogenetics and Evolution*, **52**, 563–574.

Garrick, R.C. (2011) Montane refuges and topographic complexity generate and maintain invertebrate biodiversity: recurring themes across space and time. *Journal of Insect Conservation*, **15**, 469–478.

Garzón-Machado, V., González-Mancebo, J.M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J.M., Del Arco-Aguilar, M. & Pérez-de-Paz, P.L. (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biological Conservation*, **143**, 685–2694.

Garzón-Machado, V., Otto, R. & Del Arco Aguilar, M.J. (2014) Bioclimatic mapping of a topographically complex oceanic island applying different interpolations techniques. *International Journal of Biometeorology*, **58**, 887–99.

Goodson, B.E., Santos-Guerra, A. & Jansen, R.K. (2006) Molecular systematics of *Descurainia* (Brassicaceae) in the Canary Islands: biogeographic and taxonomic implications. *Taxon*, **55**, 671–682.

Heaney, L.R., Balete, D.S. & Rickart, E.A. (2013) Models of oceanic island biogeography: changing perspectives on biodiversity dynamics in archipelagos. *Frontiers of Biogeography*, **5**, 249–257.

Hortal, J., Lobo, J.M. & Jiménez-Valverde, A. (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology*, **21**, 853–863.

Irl, S.D.H., Steinbauer, M.J., Messinger, J., Blume-Werry, G., Palomares-Martínez, Á., Beierkuhnlein, C. & Jentsch, A. (2014) Burned and devoured – introduced herbivores, fire, and the endemic flora of the high-elevation ecosystem on La Palma, Canary Islands. *Arctic Antarctic and Alpine Research*, **46**, 859–869.

Juan, C., Emerson, B.C., Oromí, P. & Hewitt, G.M. (2000) Colonisation and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology and Evolution*, **15**, 104–109.

Kessler, M. (2002) The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. *Journal of Biogeography*, **29**, 1159–1165.

Knope, M.L., Morden, C.W., Funk, V.A. & Fukami, T. (2012) Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). *Journal of Biogeography*, **39**, 1206–1216.

Kruckeberg, A.R. (2002) *Geology and plant life: the effects of landforms and rock types on plants*. University of Washington Press, Seattle, London.

Macías-Hernández, M., Bidegaray-Batista, L., Emerson, B.C., Oromí, P. & Arnedo, M.A. (2013) The imprint of geologic history on within-island diversification of woodlouse-hunter spiders (Araneae, Dysderidae) in the Canary Islands. *Journal of Heredity*, **104**, 341–356.

McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*. Chapman and Hall, London.

de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J. (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography*, **36**, 499–514.

Ojeda, D.I., Santos-Guerra, A., Oliva-Tejera, F., Jaen-Molina, R., Caujapé-Castells, J., Marrero Rodríguez, A. & Cronk, Q. (2014) DNA barcodes successfully identified Macaronesian *Lotus* (Leguminosae) species within early diverged lineages of Cape Verde and mainland Africa. *AoB Plants*, **6**, plu050; doi:10.1093/aobpla/plu050.

Otto, R., Arteaga, M.A., Delgado, J.D., Arévalo, J.R. & Fernández-Palacios, J.M. (2013) Road edge effect and elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). *Folia Geobotanica*, **49**, 65–82.

Paulay, G. (1994) Biodiversity on oceanic islands: its origin and extinction. *American Zoologist*, **34**, 134–144.

Price, J.P. (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *Journal of Biogeography*, **31**, 487–500.

Puppo, P., Curto, M., Velo-Antón, G., Pérez de Paz, P.L. & Meimberg, H. (2014) The influence of geological history on diversification in insular species: genetic and morphological patterns of *Micromeria* Benth (Lamiaceae) in Tenerife (Canary archipelago). *Journal of Biogeography*, **41**, 1871–1882.

Quinn, G.P. & Keough, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.

R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.Rproject.org.

Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography*, **33**, 46–50.

Reyes-Betancort, J.A., Santos Guerra, A., Guma, I.R., Humphries, C.J. & Carine, M.A. (2008) Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. *Anales del Jardín Botánico de Madrid*, **65**, 25–45.

Sibrant, A.L.R., Hildenbrand, A., Marques, F.O. & Costa, A.C.G. (2015) Volcano-tectonic evolution of the Santa Maria Island (Azores): implications for paleostress evolution at the western Eurasia-Nubia plate boundary. *Journal of Volcanology and Geothermal Research*, **291**, 49–62.

Silvertown, J. (2004) The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, **92**, 168–173.

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 866–880.

Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios, J.M. (2012) Increase of island endemism with altitude – speciation processes on oceanic islands. *Ecography*, **35**, 23–32.

Steinbauer, M.J., Dolos, K., Field, R., Reineking, B. & Beierkuhnlein, C. (2013) Re-evaluating the general dynamic theory of oceanic island biogeography. *Frontiers of Biogeography*, **5**, 185–194.

Stierstorfer, C. (2005) The vascular plant vegetation in the forest belt of El Hierro (Canary Islands). *Dissertationes Botanicae*, **393**, 1–375.

Stierstorfer, C. & Gaisberg, M. (2005) Annotated checklist and distribution of vascular plants of El Hierro (Canary Islands). *Englera*, **27**, 1–221.

Stuessy, T.F. (2007) Evolution of specific and genetic diversity during ontogeny of island floras: the importance of understanding process for interpreting island biogeographic patterns. *Biogeography in a changing world* (ed. by M.C. Ebach and R.S. Tangney), pp. 117–133. CRC Press, Boca Raton, FL.

Swenson, U. & Manns, U. (2003) Phylogeny of *Pericallis* (Asteraceae): a total evidence approach reappraising the double origin of woodiness. *Taxon*, **52**, 533–546.

Trusty, J.L., Olmstead, R.G., Santos-Guerra, A., Sá-Fontinha, S. & Francisco-Ortega, J. (2005) Molecular phylogenetics of the Macaronesian-endemic genus *Bystropogon* (Lamiaceae): palaeo-islands, ecological shifts and interisland colonizations. *Molecular Ecology*, **14**, 1177–1189.

Valente, L.M., Etienne, R.S. & Phillimore, A.B. (2014) The effects of island ontogeny on species diversity and phylogeny. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133227.

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

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J., Ladle, R.J., Araújo, M.B., Fernández-Palacios, J.M., Delgado, J.D. & Arevalo, J.R. (2007) The island immaturity – speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. *Ecography*, **30**, 321–327.

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

Zobel, M., Otto, R., Laanisto, L., Pärtel, M., Naranjo-Cigala, A. & Fernández-Palacios, J.M. (2011) The formation of species pools: historical habitat abundance affects current local diversity. *Global Ecology and Biogeography*, **20**, 251–259.

SUPPORTING INFORMATION

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

Appendix S1 Moran's *I* autocorrelation scores for best GLM model residuals.

Appendix S2 Divergence times of single island endemic plants from El Hierro, La Palma and Tenerife.

BIOSKETCH

Rüdiger Otto is a researcher at the Department of Ecology at La Laguna University (ULL) and member of the ULL Island Ecology and Biogeography Research Group. His research interests include island biogeography, forest dynamics and restoration, plant invasion and landscape ecology.

Author contributions: R.O., M.v.G. and C.S. conceived the idea; R.O., M.v.G., C.S., A.N., V.G., M.d.A. and M.S. compiled data; R.O. and M.S. performed the statistical analyses of the data; R.O., A.N. and V.G. carried out GIS analyses; R.O. and R.J.W. led the writing and all authors contributed to the writing process.

Editor: Hanno Schaefer