

Climate vs. topography – spatial patterns of plant species diversity and endemism on a high-elevation island

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Summary

1. Climate and topography are among the most fundamental drivers of plant diversity. Here, we assessed the importance of climate and topography in explaining diversity patterns of species richness, endemic richness and endemism on the landscape scale of an oceanic island and evaluated the independent contribution of climatic and topographic variables to spatial diversity patterns.

2. We constructed a presence/absence matrix of perennial endemic and native vascular plant species (including subspecies) in 890 plots on the environmentally very heterogeneous island of La Palma, Canary Islands. Species richness, endemic richness and endemism were recorded, interpolated and related to climate (i.e. variables describing temperature, precipitation, variability and climatic rarity) and topography (i.e. topographic complexity, solar radiation, geologic age, slope and aspect). We used multimodel inference, spatial autoregressive models, variance partitioning and linear regression kriging as statistical methods.

3. Species richness is best explained by both climatic and topographic variables. Topographic variables (esp. topographic complexity and solar radiation) explain endemic richness, and climatic variables (esp. elevation/temperature and rainfall seasonality) explain endemism. Spatial patterns of species richness, endemic richness and endemism were in part geographically decoupled from each other.

4. *Synthesis.* We identified several topography-dependent processes ranging from evolutionary processes (micro-refugia, *in situ* speciation, pre-adaptation to rupicolous conditions, dispersal limitations) to human-induced influences (introduced herbivores, fire, land use) that possibly shape the endemic richness pattern of La Palma. In contrast, climate mainly drives endemism, which is connected to ecological speciation and specialization to local conditions. We highlight the importance of incorporating climatic variability into future studies of plant species diversity and endemism. The spatial incongruence in hot spots of species richness, endemic richness and endemism emphasizes the need for an integrated conservation approach acknowledging different diversity measures to protect the complete spectrum of diversity. High-elevation islands such as La Palma are highly suitable to study drivers of diversity and endemism, as they offer environmental gradients of continental magnitude on the landscape scale of a single climatic *mini-continent* and a large array of *in situ*-speciated endemics.

Key-words: Canary Islands, climatic rarity, climatic stability, island ecology, landscape ecology, landscape scale, mini-continent, multimodel inference, spatial ecology

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Introduction

Species and species diversity are not distributed randomly in space (Rosenzweig 1995). Rather, they follow distinct spatial patterns (Orme *et al.* 2005; Stohlgren *et al.* 2005) or are distributed along differing environmental gradients (Hortal *et al.* 2013; Slaton 2015). In heterogeneous landscapes, often multiple overlapping and interacting gradients are influential, especially gradients based on topography and climate (Dewar & Richard 2007; Slaton 2015). This complexity results in a key task in ecology, biogeography and evolution: disentangling the major drivers of species distribution and biodiversity patterns from a diverse array of environmental factors.

In contrast to many other regions, oceanic islands harbour relatively low species richness but high endemism (Kier *et al.* 2009). Oceanic islands never had contact with other landmasses (Whittaker & Fernández-Palacios 2007); accordingly, most of their endemic species and especially single-island endemics (SIEs) are a result of *in situ* speciation (Whittaker, Triantis & Ladle 2008). The spatial distribution of endemism within a given oceanic island can thus give valuable information about origin and drivers of biodiversity patterns on the landscape scale and have important implications for conservation (Richardson & Whittaker 2010).

Landscape-scale studies on oceanic islands have a major advantage over comparable research on continental systems. The presence of a large share of species that have evolved *in situ* allows inferring general drivers of speciation from spatial patterns of diversity and endemism. In continental systems, endemism is less a product of *in situ* speciation but rather the result of range contractions of formerly widespread species (Tribsh & Schönswetter 2003; Orme *et al.* 2005). In addition, the mixing of species pools due to past species movement and immigration resulting from environmental fluctuations might impede the interpretation of emergent diversity patterns in the context of speciation on the continent (Kissling *et al.* 2012).

On oceanic islands, two distinctly different mechanisms related to speciation can be inferred from patterns of endemism. First, centres of endemism (i.e. endemic richness; Myers *et al.* 2000) show regions and/or environmental conditions to which most species from the regional species pool are adapted. Endemic richness thus can be used as a measure to identify biodiversity hot spots (Myers *et al.* 2000; Possingham & Wilson 2005). Secondly, and in contrast to richness patterns, the percentage of endemic species (i.e. endemism) is a measure of how strongly local species pools are derived from *in situ* speciation in comparison with immigration processes. High values of endemism thus indicate environmental conditions that make it necessary for colonizing species to adapt, which can lead to ecological speciation (Nosil 2012; Steinbauer *et al.* 2013a; Steinbauer, Irl & Beierkuhnlein 2013b).

On the regional scale, islands are characterized by relatively stable oceanic climate conditions (Whittaker & Fernández-Palacios 2007). However, traditionally, 'stability' is mainly acknowledged for island temperature regimes, whereas a large spatio-temporal variation in precipitation is a common

phenomenon within island archipelagos or even within a single island (Dewar & Richard 2007; Giambelluca *et al.* 2011). In addition, high intra-island precipitation variability increases the potential for adaptive evolutionary divergence within and among species, leading to adaptations to specific conditions within the island in focus (Mallet *et al.* 2014; Harter *et al.* in press). Thus, the concept of presumed stability (or variability) on islands might need a re-evaluation, as hot spots of neo-endemism tend to form in moderately variable conditions on the continent, indicating the importance of variability for speciation (Fjeldså *et al.* 1997).

Climatic conditions often show pronounced spatial patterns in the distribution of specific climatic features within a single island (Giambelluca *et al.* 2011; Garzón-Machado, Otto & del Arco Aguilar 2014). The commonness or rarity of these climatic conditions (i.e. their isolation in a spatial context) might affect the pattern of diversity and endemism by restricting immigration and enabling speciation under specific climatic conditions (Steinbauer *et al.* 2012). The concept of climatic rarity suggests that in a specific area, certain climatic conditions are less common than others (Ohlemüller *et al.* 2008). High climatic rarity is likely connected to spatially restricted selection pressure, which promotes adaptive differentiation processes (Nosil 2012). In this study, we transferred, for the first time, this concept to the landscape scale within a single island to take advantage of the continental-scale environmental gradients found on the landscape scale of a high-elevation island. This enabled us to relate these large-scale gradients to patterns of diversity and endemism of the complete species assemblage of this island at resolutions not feasible for continental systems.

Topographic complexity positively influences species richness patterns and speciation processes (Whittaker, Triantis & Ladle 2008; Hortal *et al.* 2009; Trigas, Panitsa & Tsiftsis 2013). Increasing topographic complexity (e.g. variation in slope inclination and aspect) increases habitat diversity, niche space available for niche partitioning and speciation and thus enables species coexistence (Hortal *et al.* 2009). Therefore, topographic complexity likely results in increased species richness (Hortal *et al.* 2009). In addition, complex topography offers micro-refugia during periods of environmental alterations (e.g. during past climatic fluctuations, or even during rare extreme weather events; Ashcroft *et al.* 2012). This can decrease extinction risks, consequently maintaining species richness and endemic richness over time (Mee & Moore 2014), which is crucial on isolated oceanic islands with low colonization rates. Thirdly, topographic complexity may cause gene-flow barriers among diverging populations, supporting reproductive isolation and hence local differentiation (Gillespie & Roderick 2014).

Our research aims were to assess how climatic and topographic variables individually contribute to explaining species richness, endemic richness and endemism at the landscape scale. Within this framework, we specifically focused on precipitation variability, climatic rarity and topographic complexity. We used the island of La Palma (Canary Islands) as a study system due to its strong elevational and ecological

gradients (Garzón-Machado, Otto & del Arco Aguilar 2014), very complex topography (Carracedo *et al.* 2002; Irl & Beierkuhnlein 2011) and large array of endemic plant species (Acebes Ginovés *et al.* 2010).

Materials and methods

STUDY AREA

La Palma is the north-westernmost island of the Canary Islands, located in the Atlantic Ocean off the coast of north-western Africa (Fig. 1). La Palma covers an area of 706 km²; its highest peak is Roque de los Muchachos (2426 m; Carracedo *et al.* 2002). La Palma has a subtropical–Mediterranean climate with humid winters and dry summers (Garzón-Machado, Otto & del Arco Aguilar 2014). However, climatic conditions differ considerably within the island. Annual precipitation ranges from about 170 mm to almost 1400 mm (excluding fog drip), annual temperature from about 9 °C on the island summit to around 22 °C at the leeward south-western coast (Irl & Beierkuhnlein 2011). Fog drip can locally lead to an increase of precipitation particularly relevant in summer (Marzol, Sánchez & Yanes 2011) but likely does not change the overall spatial pattern of precipitation because both fog drip and rainfall are largely linked to topography (Walmsley, Schemenauer & Bridgman 1996). The north-eastern trade winds create an elevation-associated climatic divide of the island in a humid windward and a dry leeward side. Above the trade wind-induced cloud zone exists a thermal inversion layer, generally exhibiting dry conditions with the possibility of snow and ice in winter (Garzón-Machado, Otto & del Arco Aguilar 2014).

La Palma is geologically divided into two parts. The northern older part is morphologically complex with steep valleys (so-called *barrancos*), coastal cliffs and the massive Caldera de Taburiente complex, which has almost vertical cliffs in its interior reaching 1000 m or more in elevation. The volcanic activity has ceased in the northern part, which is dominated by erosive processes (Carracedo *et al.* 2002). The younger, southern part is still subject to subaerial volcanic ontogeny (the last eruption on the southern tip of the island was documented in 1971) and has gentler slopes with volcanic cones and ash fields (Carracedo *et al.* 2002).

The zonal vegetation directly reflects the climatic conditions of the island (Garzón-Machado, Otto & del Arco Aguilar 2014). These zones range from halophytic communities in arid coastal areas to succulent scrub and thermophilic woodlands in semi-arid lower elevations, through the endemic Canary Pine forest in mid-elevations to a high-elevation summit scrub. On the windward side, a palaeo-endemic evergreen humid laurel forest and a slightly less humid tree heath *Erica arborea*–*Morella faya* forest exist at mid-elevations in the zone of the trade wind clouds instead of the Canary Pine forest (del Arco Aguilar *et al.* 2010; Garzón-Machado, Otto & del Arco Aguilar 2014). Endemic species are found in all natural vegetation zones (del Arco Aguilar *et al.* 2010). According to Acebes Ginovés *et al.* (2010), La Palma hosts 658 native vascular plant species (including species and subspecies; for simplification reasons, hereafter referred to as *species*), of which 193 are archipelago endemics (AEs, i.e. endemic to the Canary Islands). Of the AEs, 37 are SIEs.

SAMPLING METHOD

The presence and absence of endemic perennial vascular plant species (i.e. all SIEs and AEs) was recorded in 890 plots using a radial sampling approach with a 50 m radius (Fig. 1a; see Table S1 in

Supporting Information for a list of species; to access the data used in this study, see Irl *et al.* 2015). To cover all relevant gradients, we accessed sampling sites by all means possible (i.e. roads, tracks, hiking paths, backcountry, non-technical climbing, etc.). In a selected area, a random point was set as centre point of each plot. This centre point was recorded with a GPS device (Garmin Oregon 550). Our sampling approach covers all relevant environmental gradients on La Palma owing to the large number of plots and the good spatial coverage, even though plots were not randomly distributed (Fig. 1a). This sampling approach is very time-efficient, allowing for a large sample size, which is essential for differentiated high-resolution spatial analyses in the face of a variety of gradients (e.g. elevation, precipitation, geology, seasonality and solar radiation) and topographic complexity.

We focused on perennial vascular plant species including all woody species but excluding annuals. Perennials are valuable study objects for several reasons: (i) perennials are easy to identify in the field due to their relatively large growth (many are small- to medium-sized shrubs), whereas annuals can easily be underestimated as they produce above-ground biomass only for short time periods during the year. This might result in wrong absences for annuals if above-ground biomass is not present. (ii) Due to their longevity, perennials integrate over long-term environmental conditions (e.g. climate), while annuals react very strongly to short-term weather conditions, making their appearance dependent on stochastic events. (iii) Most endemics on the Canary Islands are perennials (93% according to Shmida & Werger 1992), whereas the relevance of annuals for the flora, especially the endemic flora, of the Canary Islands is limited. In addition, this sampling focus strongly increased sampling efficiency, resulting in exceptionally high spatial coverage, which is fundamental for our research objectives.

The numbers of remaining native perennial species (i.e. species that were not SIEs or AEs) were identified in the field and recorded without species' identities as our focus was on endemic diversity (i.e. endemic richness and endemism). We calculated total perennial species richness per plot (hereafter referred to as *species richness*, abbreviated as SR) by adding the number of recorded endemic perennial species to the remaining native perennial species.

The percentage of single-island endemics (pSIE) and the percentage of archipelago endemics (pAE) were calculated by dividing the number of single-island endemics (nSIE) and the number of archipelago endemics (nAE) through total species richness, respectively. Percentage indices are independent of richness gradients and are an indicator of taxonomic or, in our case, floristic uniqueness (Gillespie, Claridge & Roderick 2008). Nomenclature and endemic status follow Acebes Ginovés *et al.* (2010). Sampling took place in fall 2010 and in spring 2011, 2012 and 2013.

ENVIRONMENTAL DATA

Basic environmental data were derived from raster data sets provided by the Cabildo Insular de La Palma (2 × 2 m digital elevation model and geologic map). The resolution of the digital elevation model was resampled to a raster resolution of 100 × 100 m. All plots were recalculated as centroids of the 100 × 100 m raster. Plots that were located within the same raster cell were homogenized (i.e. species lists were added together). Elevation, slope angle, micro-aspect (northernness and easternness) and macro-aspect (mean aspect per grid cell within a 5 km radius) as well as mean annual solar radiation (using a standard diffuse atmosphere and based on latitude, elevation and slope aspect) were calculated for each plot.

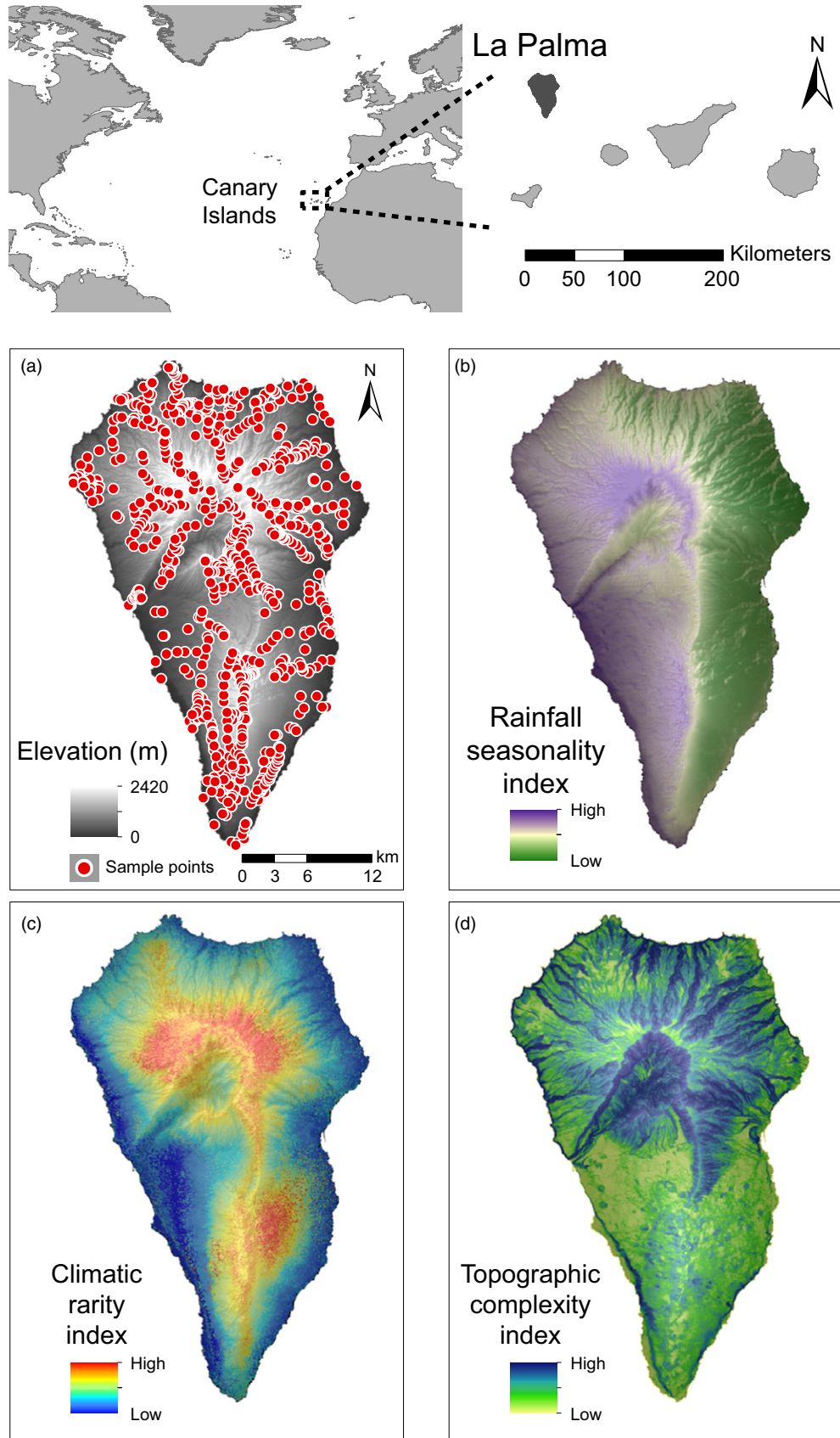


Fig. 1. Maps of La Palma within the Canary Islands showing the spatial distribution of (a) elevation (including the location of the sampled plots), (b) the rainfall seasonality index, (c) the climatic rarity index and (d) topographic complexity. The large number of sampled plots ($n = 890$) enabled to cover the whole island and all relevant environmental conditions.

Mean annual precipitation and mean annual temperature were interpolated using data collected from meteorological stations for the Canary Islands ($n = 214$ for mean annual temperature and $n = 288$ for mean annual precipitation; see Fig. S1). Linear regression kriging (R package *gstat*) was applied as interpolation method, with elevation, slope, island, micro-aspect and macro-aspect as covariables (for details on linear regression kriging, see Statistical analysis section). Three measures of precipitation variability were computed using monthly precipitation data from 47 meteorological stations from the Spanish Federal Meteorology Agency (AEMET) from the Canary Islands (time span: 1969 to 1998; see Fig. S1) and implementing the same linear regression kriging technique: (i) intra-annual variability represented by the 30-year mean of the annual coefficients of variation based on monthly precipitation sums, respectively, (ii) inter-annual variability represented by the coefficient of variation for annual precipitation over the 30-year time period, and (iii) rainfall seasonality represented by the rainfall seasonality index by Walsh & Lawler (1981); see the spatial distribution of the rainfall seasonality index for La Palma in Fig. 1a.

Climatic rarity was calculated following the method given by Ohlemüller *et al.* (2008) for two geographic entities: (i) based on the climate of the Canary Islands and (ii) based on the climate of La Palma. For both geographic entities, each climatic variable was divided into equal range classes. For mean annual temperature, we used a class size of 0.25 °C, and for mean annual precipitation, a class size of 25 mm. According to the temperature and precipitation conditions, each 100 × 100 m raster cell was assigned to a respective temperature and precipitation class (e.g. a combination of precipitation ranging from 300 to 325 mm and temperature from 20 to 20.25 °C). Then, all cells of each combined temperature and precipitation class on La Palma were summed up, resulting in a spatial index of climatic rarity based on area (in ha). Climatic rarity increases with decreasing index values (Fig. 1b).

Topographic complexity was estimated by calculating the ratio between the 3D and 2D surface area with the following equation (Fig. 1c; Jenness 2004):

$$\text{Topographic complexity index} = \frac{\sum_{100 \times 100 \text{ m}} (\text{Area}_{2 \times 2 \text{ m}} / \cos(\text{Slope}_{2 \times 2 \text{ m}}))}{\text{Area}_{100 \times 100 \text{ m}}},$$

where $\text{Area}_{2 \times 2 \text{ m}}$ is the area per grid cell from a 2 × 2 m digital elevation model (DEM), $\text{Slope}_{2 \times 2 \text{ m}}$ the slope of each grid cell from the same DEM in degrees, and $\text{Area}_{100 \times 100 \text{ m}}$ the area per grid cell from a 100 × 100 m DEM containing all 50 × 50 (i.e. 2500) grid cells from the 2 × 2 m DEM. This index increases with increasing topographic complexity (i.e. from 1 = absolutely flat surface to ∞).

The linear regression kriging method and all other statistical methods were implemented in R Statistics (version 3.0.1; R Core Team 2013). All other geo-information was calculated using ArcGIS® software by Esri (Redlands, CA, USA). A list summarizing all environmental variables used in this study is given in Table 1.

STATISTICAL ANALYSIS

First, the linear relationship between response and explanatory variables was assessed by bivariate correlations (Spearman's ρ ; see Table S2). To undergo a variable reduction for each response variable (species richness, nSIE, nAE, pSIE, pAE), explanatory variables with correlations $-0.1 \leq r \leq 0.1$ were excluded due to weak explanatory power (Fløjgaard *et al.* 2011). In a second step, collinearity was addressed by testing correlations for each possible pair of explanatory

variables. If $|r| > 0.7$, the explanatory variable performing poorer with the response variable was excluded (S2; see Dormann *et al.* 2013 for a discussion of collinearity). This resulted in a unique set of climatic and topographic variables for each response variable (see Table S3).

Nonlinear relationship between the independent and dependent variables can be accounted for in a regression framework using transformations. To select the appropriate transformation for each response variable, exploratory linear regression models were applied to each explanatory variable. The following transformations were separately tested to find the best model fit: untransformed, logarithmic, square root, quadratic (x^2) and hump-shaped ($x^2 + x$). Transformation selection was based on AICc values (i.e. second-order Akaike Information Criterion) of the respective regression models (Grueber *et al.* 2011; see Table S4). The best fitting transformation of each explanatory variable was implemented in a multiple linear regression (MLR). Table S5 displays the resulting MLR for species richness, nSIE, nAE, pSIE and pAE. Model fits of each MLR model were visually checked to ensure compliance with model assumptions.

The residuals of each MLR were tested for spatial autocorrelation using Moran's I to avoid potential parameter estimate bias and inflation of type I errors (Dormann *et al.* 2007). No spatial autocorrelation was detected in the residuals of the MLR for species richness ($I = -0.001$, n.s.) and nSIE ($I = -0.002$, n.s.), whereas nAE ($I = -0.007$, $P < 0.001$), pSIE ($I = -0.004$, $P < 0.001$) and pAE ($I = -0.003$, $P < 0.05$) resulted in significant spatial autocorrelation. To double-check the effect of spatial autocorrelation, simultaneous autoregressive models (SARs) with a spatially dependent error term were implemented based on the same set of explanatory variables as in the MLR. SARs account for spatial autocorrelation by using a neighbourhood matrix (Dormann *et al.* 2007). Results were compared with the respective MLR using Nagelkerke's pseudo- R^2 as correlation coefficient (Nagelkerke 1991; see S3). Performance of MLRs and SARs was comparable, even though Nagelkerke's pseudo- R^2 was consistently higher. For this reason and because the three significant Moran's I values are very close to zero, we conclude that spatial autocorrelation is therefore negligible for the following steps and is sufficiently covered by the explanatory variables in the respective MLR.

Variance partitioning using partial linear regression (R package *vegan*) was implemented to assess the overall importance of climate and topography following the guidelines of Legendre (2008). Variance partitioning quantifies the independent and/or joint explanatory power (adjusted R^2 as the goodness-of-fit measure) of different groups of explanatory variables by conducting MLRs always between a focal set of explanatory variables and the residuals of a regression between the dependent variable and all other explanatory variables (explained in Legendre 2008). Variance partitioning estimates the proportion of variation the response variable can be attributed exclusively to one set of explanatory variables once the effect of the other explanatory variables has been taken into account. All variables used in this study were pre-classified into being either climatic or topographic drivers (Table 1). The same set of variables as selected for the MLR and the SAR approach and their respective best fitting transformations were used for variance partitioning (see S3). Then, based on this set of variables, the independent, overlapping and total contribution of each class (i.e. topography or climate) was calculated based on adjusted R^2 values.

Multimodel inference (MMI) is an alternative approach to variance partitioning used to estimate the relative importance of each explanatory variable in relation to each response variable (R package *relaimpo* version 2.2-2). In contrast to traditional null-hypothesis

Table 1. List of all environmental variables and their abbreviations used in this study grouped into climate and topography

Environmental variables					
Class	Variable	Abbreviation	Unit	Min. value	Max. value
Climate	Climatic rarity for the Canary Islands	CR_CAN	ha	4	5311
	Climatic rarity for La Palma	CR_LP	ha	2	818
	Elevation	Elev	m a.s.l.	1	2392
	Intra-annual precipitation variability	INTRA_VAR	–	1.18	1.96
	Interannual precipitation variability	INTER_VAR	–	0.25	0.48
	Mean annual precipitation	MAP	mm	177	1331
	Mean annual temperature	MAT	°C	8.7	20.0
	Rainfall seasonality index	RSI	–	0.67	0.84
Topography	Annual solar radiation	ASR	Wh m ⁻²	63 650	189 110
	Easternness	Easternness	–	0	1
	Geologic age	Age	Ma	0.0005	4
	Macro-aspect	Macro	–	–0.925	0.899
	Northernness	Northernness	–	0	1
	Slope angle	Slope	°	1	55
	Topographic complexity index	TCI	–	1	2.97

Units and minimum and maximum values are given for each variable.

testing, MMI enables inference from more than one model (Johnson & Omland 2004) and has been proposed as a promising method in ecology and biogeography (Millington & Perry 2011). The relative importance and confidence intervals were calculated using bootstrapping ($n = 1000$) with all possible model combinations. As a result, the explained variation of the MMI for each response variable (indicated as adjusted R^2), and the relative contribution of each explanatory variable (i.e. % contribution to the R^2 of the respective MMI) and its confidence interval are given.

In a last step, the spatial interpolation of the response variables was conducted using linear regression kriging (R package *gstat*). Linear regression kriging uses a statistical approach (MLR) to infer the relationship of explanatory variables to the response variable and then interpolates the residuals into space (Garzón-Machado, Otto & del Arco Aguilar 2014). All explanatory variables used in the MLRs and their respective transformations according to each response variable were used as basis of direct spatial interpolation of species richness, endemic richness and endemism values.

Statistical significance is indicated in the following as ** for $P < 0.05$, *** for $P < 0.01$ and **** for $P < 0.001$. All correlation coefficients in MLRs, MMI and variance partitioning are given as number of variable-corrected adjusted R^2 .

Results

TOPOGRAPHY VS. CLIMATE

The large number of sampled points ensured a comprehensive and spatially dense coverage of the island, including all relevant environmental gradients (Fig. 1a), and a very high spatial density of plots on this scale (1.26 plots per km²). A total of 79 archipelago endemics were identified (44% of all perennial archipelago endemics of La Palma; Acebes Ginovés *et al.* 2010), 31 of which were SIEs (84% of all La Palma SIEs; Acebes Ginovés *et al.* 2010; see species list Table S1). Species richness ranged from 1 to 57 species per plot, nSIE from 0 to 8 species per plot, nAE from 0 to 24 species per plot, and pSIE as well as pAE from 0% to 100%. The overall

explanatory power of the MMI was good (species richness, pSIE and pAE) to moderate (nSIE and nAE); that is, a moderately large section of unexplained variance remained (Table 2).

Variance partitioning revealed that topography and climate both are more or less equally important for species richness (joint explained variation for climate: $R^2 = 0.41$ and topography: $R^2 = 0.34$, including a large share of overlapping contribution: $R^2 = 0.26$; Fig. 2a). However, endemic richness was dominated by the influence of topography for both nSIE (joint explained variation: $R^2 = 0.18$) and nAE (joint explained variation: $R^2 = 0.27$), whereas climate had very little influence on endemic richness (joint explained variation: $R^2 \leq 0.06$; Fig. 2b,c). Climate was very important in explaining endemism for both pSIE (joint explained variation: $R^2 = 0.42$) and pAE (joint explained variation: $R^2 = 0.45$; Fig. 2d,e). Moreover, the influence of topography was almost not separable from the explained variation of climate (independent explained variation for pSIE: $R^2 = 0.01$ and pAE: $R^2 = 0.02$; overlapping explained variation for pSIE: $R^2 = 0.15$ and for pAE: $R^2 = 0.22$). For all values of joint, independent, overlapping and total explained variation of each response variable resulting from variance partitioning, see Table S5.

ENVIRONMENTAL COMPONENTS OF TOPOGRAPHY AND CLIMATE

In the MMI, species richness was mainly explained by elevation, annual solar radiation, the rainfall seasonality index and the topographic complexity index (Fig. 2f, Table 2a), indicating the joint importance of climate (elevation, rainfall seasonality index) and topography (annual solar radiation, topographic complexity index). However, the relative contribution of each variable was relatively moderate (e.g. elevation as explanatory variable with the highest relative contribution only reaches 27%). Further climatic (climatic rarity, interan-

Table 2. Total explained variation and relative importance of each environmental variable in explaining (a) species richness, (b) endemic richness (nSIE = number of single-island endemics; nAE = number of archipelago endemics) and (c) endemicity (pSIE = percentage of single-island endemics; pAE = percentage of archipelago endemics). Total explained variation (given as R^2) results from multimodel inference (bootstrap $n = 1000$). '% of R^2 ' gives the relative contribution of the respective environmental variable to the total explained variation

(a) Species richness			(b) Endemic richness			(c) Endemicity		
SR	nSIE	nAE	nSIE	nAE	pSIE	pAE		
Total explained variation: $R^2 = 0.50$			Total explained variation: $R^2 = 0.20$			Total explained variation: $R^2 = 0.44$		
% of R^2	Dir.	Transf.	% of R^2	Dir.	Transf.	% of R^2	Dir.	Transf.
Elev	27	∅	TCI	50	Sqrt	Elev	50	Hump
ASR	20	∅	ASR	22	Hump	RSI	29	U
RSI	18	∅	Slope	16	Linear	ASR	13	Hump
TCI	9	+	INTRA_VAR	5	U	INTER_VAR	6	∅
CR_CAN	6	+	CR_LP	4	Log	Easterness	3	Linear
Easterness	6	U	INTER_VAR	4	Linear	INTRA_VAR	6	∅
INTRA_VAR	5	U				Age	4	Hump
INTRA_VAR	5	U						U
Slope	4	+						U
Total explained variation: $R^2 = 0.31$			Total explained variation: $R^2 = 0.48$			Total explained variation: $R^2 = 0.48$		
Total explained	variation:		Total explained	variation:		Total explained	variation:	
% of R^2	Dir.	Transf.	% of R^2	Dir.	Transf.	% of R^2	Dir.	Transf.
Elev	47	+	TCI	47	Sqrt	Elev	50	Hump
ASR	22	-	ASR	22	Sqrt	RSI	29	U
Slope	16	+	Slope	16	Quad	ASR	13	Hump
CR_LP	12	+	CR_LP	12	Log	INTER_VAR	6	∅
RSI	3	∅	RSI	3	Hump	Easterness	3	Linear

Explanatory variables are ordered by relative contribution and are grouped as either topographic (italics) or climatic variable (bold). The best fitting transformation is given in 'Transf.'. Tested transformations were as follows: linear, logarithmic, square root, quadratic and hump-shaped ($x^2 + x$). 'Dir.' indicates the direction of correlation ('+' = positive correlation, '-' = negative correlation; ∅ = hump; U = inverse hump). Abbreviations of variables are given in Table 1. For details, see the Materials and methods section.

nual precipitation variability, intra-annual precipitation variability) and topographic variables (easternness and slope) only played a subordinate role (Fig. 2f, Table 2a). Overall explained variation was high ($R^2 = 0.5$; Table 2a); however, half of the variation remained unexplained.

Endemic richness was best explained by different topographic variables, that is the topographic complexity index, annual solar radiation and slope for both nSIE and nAE (Fig. 2g,h, Table 2b). The topographic complexity index as largest contributor of relative importance reached 50% and 47% for nSIE and nAE, respectively. Climatic variables only had marginal influence of $\leq 5\%$ (i.e. intra-annual precipitation variability, interannual precipitation variability and the rainfall seasonality index), with the slight exception of climatic rarity for La Palma for nAE (12%; Table 2b). Overall explained variation was moderate for both nSIE and nAE and did not surpass $R^2 = 0.31$ (Table 2b).

Climatic variables had the highest explanatory power for endemism, whereas topographic variables were of minor importance (Fig. 2i,j). For pSIE, elevation and the rainfall seasonality index (both climatic variables) as well as annual

solar radiation (topographic variable) were the most important variables, ranging from 12% (annual solar radiation) to 50% relative importance (elevation; Table 2c). The climatic variables mean annual temperature (which is strongly linked to elevation; relative importance of 32%) and the rainfall seasonality index (relative importance of 31%) as well as to a certain degree also annual solar radiation (relative importance of 12%) had the highest relative importance for pAE (Table 2c). Other climatic (i.e. intra-annual precipitation variability and interannual precipitation variability) and topographic variables (i.e. geologic age and easternness) only had little additional explanatory power ($\leq 6\%$; Fig. 2i,j, Table 2c). Overall explained variation was high for both pSIE and pAE, almost reaching R^2 values of 0.5 for the latter (Table 2c).

SPATIAL DISTRIBUTION OF SPECIES RICHNESS, ENDEMIC RICHNESS AND ENDEMICITY

A complex pattern of species richness, endemic richness and endemism is visible for La Palma (Fig. 3). Species richness decreased with elevation and from northeast to southwest

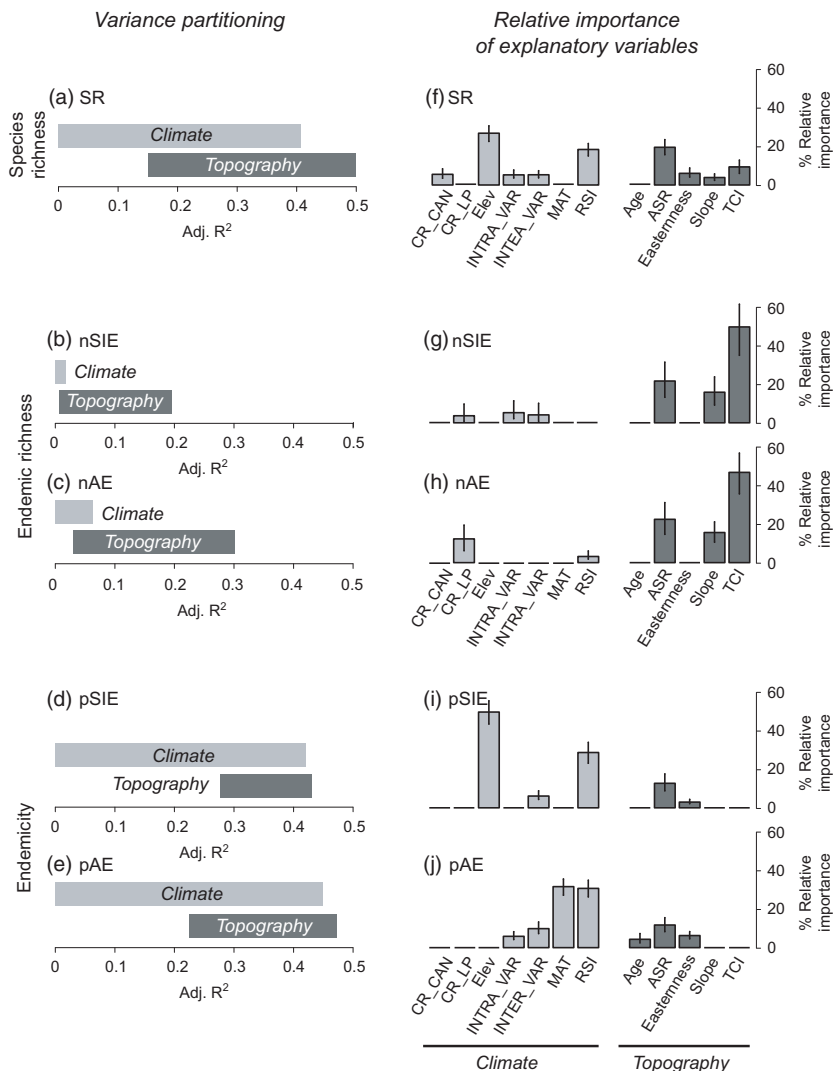


Fig. 2. Variance partitioning of the influence of climate and topography (a–d) and relative importance of explanatory variables (f–j) on species richness (SR), endemic richness (nSIE = number of single-island endemics; nAE = number of archipelago endemics) and endemism (pSIE = percentage of single-island endemics; pAE = percentage of archipelago endemics). Figures a–d show the independent and overlapping explained variation of climate and topography as portion of the total adjusted R^2 values. For values, see S5. Figures f–j display the relative importance of each explanatory variable calculated by the multimodel inference approach as per cent contribution to the R^2 for the respective response variable. Gaps indicate that these variables were removed due to collinearity or during the variable reduction process. Both variance partitioning and relative importance result from multiple linear regressions. For details on both methods, please see the Materials and methods section. Abbreviations of explanatory variables: Age, geologic age; ASR, annual solar radiation; CR_CAN, climatic rarity for the Canary Islands; CR_LP, climatic rarity for La Palma; Elev, elevation; INTER_VAR, interannual precipitation variability; INTRA_VAR, intra-annual precipitation variability; MAT, mean annual temperature; RSI, rainfall seasonality index; TCI, topographic complexity index.

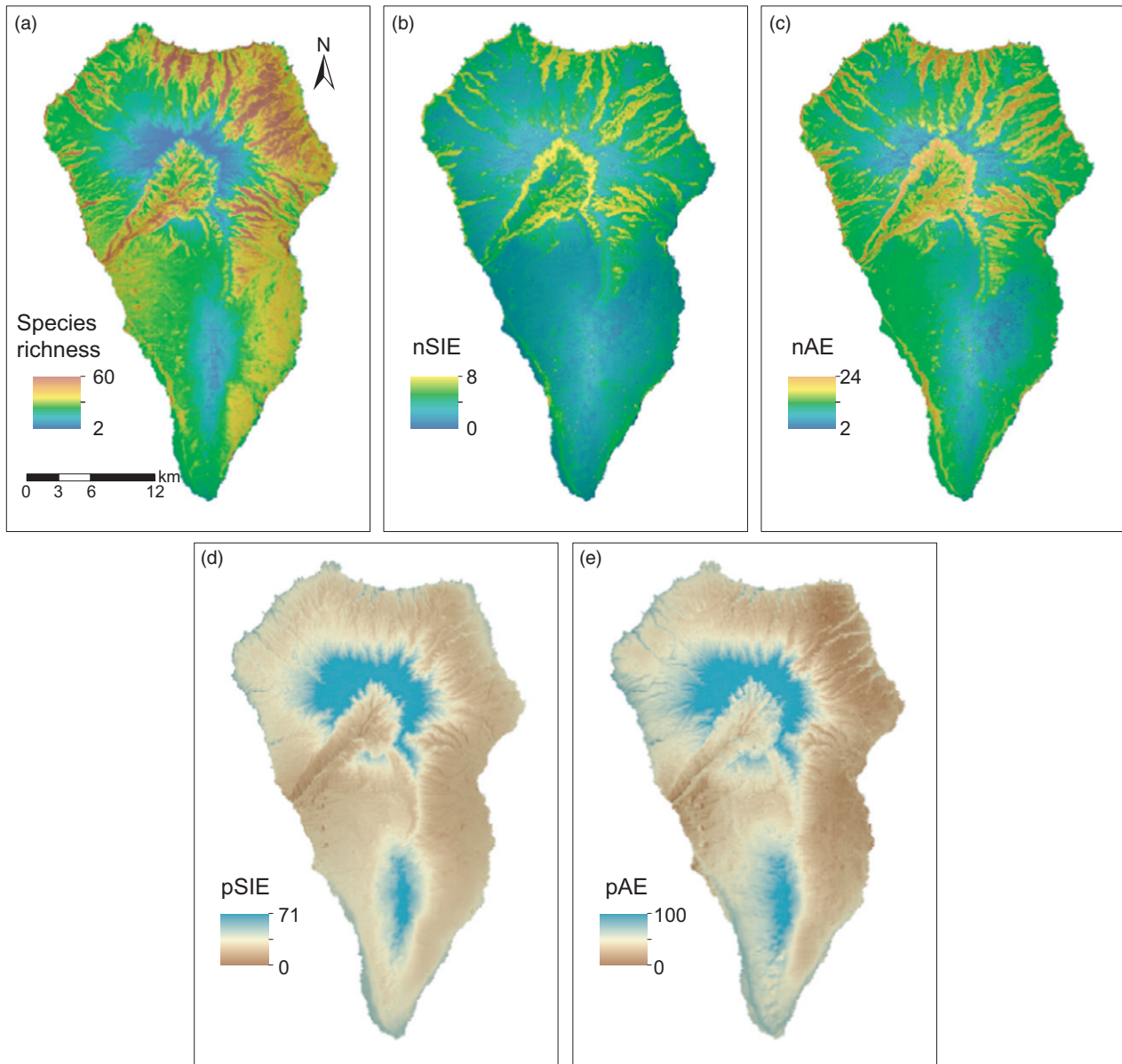


Fig. 3. Spatial interpolation maps of (a) species richness, (b) number of single-island endemics (nSIE), (c) number of archipelago endemics (nAE), (d) percentage of single-island endemics (pSIE) and (e) percentage of archipelago endemics (pAE).

(Fig. 3a). The highest values of species richness, however, reached values of around 60 species and were located in the steep barrancos and in the coastal cliffs on the northern part of the island, independent of island aspect. Endemic richness for both nSIE and nAE was highest in the steep barrancos of the north but also reached very high values in the inner cliffs of the Caldera de Taburiente complex (around 8 for nSIE and 24 for nAE; Fig. 3b,c). In general, endemic richness decreased with elevation but without the island aspect-driven asymmetry displayed by species richness. Endemicity for both pSIE and pAE strongly increases with elevation reaching values of 71% and around 100% at the highest elevations for pSIE and pAE, respectively (Fig. 3d,e). While strongly decreasing with elevation in eastern aspects, endemicity can reach quite high values (around 25% for pSIE and 75% for

pAE) in barrancos at lower elevations and coastal cliffs of the north, lowland areas of the south and western slopes at mid-elevations (esp. for pAE with values between 50% and 70%).

Discussion

EFFECTS OF TOPOGRAPHY AND CLIMATE

The present study shows that topography and climate are important drivers of species richness, endemic richness and endemicity on the landscape scale of the very heterogeneous oceanic island of La Palma. However, we find a shift in the overall importance of either topography or climate in explaining the distribution and spatial patterns of each response variable. The high-resolution spatial patterns of endemic richness

and endemism, which are mainly based on *in situ*-speciated species, allow us to make inferences about the biogeographic drivers important for patterns of evolution and speciation but also have major implications for species conservation on scales rarely targeted. Given the fact that endemic richness and endemism indicate quite different aspects, we discuss both patterns separately.

The current distribution of endemic richness on La Palma is likely shaped by adaptations to local environmental conditions, and recent human-mediated influence (i.e. introduced herbivores, fire and land use), a pattern probably relevant for most regions of the world. We suggest several possible evolutionary processes, which are not mutually exclusive, to be responsible for the strong positive impact of topography on endemic richness, which in our study is mainly influenced by the topographic complexity index.

First, a complex topography such as that found in this study likely renders a high diversity of different habitats and thus a large local niche space (Hortal *et al.* 2013; Steinbauer *et al.* 2013a) as well as an increase in area (Leutner *et al.* 2012). Secondly, high topographic complexity likely offers micro-refugia during periods of climatic fluctuation, thus reducing local extirpation probabilities (Médail & Diadema 2009) and possibly also increasing speciation (Mee & Moore 2014). Thirdly, the low influence of climate on endemic richness might indicate that the endemic species set (as a whole) is adapted to the complete range of climatic conditions on the island, as *in situ* speciation has happened in all climatic conditions on the island (esp. relevant for SIEs; Beard, Chapman & Gioia 2008). Fourthly, many endemic species are adapted to rupicolous conditions (del Arco Aguilar *et al.* 2010): conditions that are more likely to be present if topographic complexity is high. Finally, the loss of dispersal power is a common syndrome of evolution on islands (Whittaker & Fernández-Palacios 2007). Dispersal limitations within an island (i.e. gene-flow barriers) are expected to support speciation processes (Kisel & Barraclough 2010; Gillespie & Roderick 2014).

Like all islands world-wide, La Palma also is, to some degree, affected by anthropogenic influences (Caujapé-Castells *et al.* 2010). Therefore, we suggest that besides the mentioned evolutionary processes, several human-induced influences are present that can potentially explain the identified endemic richness pattern. On the one hand, steep and inaccessible areas might offer 'safe sites' for endemics from introduced herbivores (Irl *et al.* 2014a,b) because endemics are preferentially browsed by introduced herbivores (Garzón-Machado *et al.* 2010; Irl *et al.* 2012) due to lacking defence mechanisms (Bowen & Van Vuren 1997). On the other hand, endemics might experience lower fire frequencies (which have generally increased in recent decades; Climent *et al.* 2004) in topographic complex regions probably due to lower vegetation cover and lower productivity. Finally, human land use cannot occur, at least at high intensities, in areas of highly complex terrain. Thus, the presented pattern might be partially a result of the current land use distribution. However, further studies are needed to disentangle the independent effects of adaptive evolution and range retraction from human influence.

In contrast to endemic richness, climate has a stronger influence on endemism than topography on La Palma. Endemism stands for floristic uniqueness and the relative importance of endemics in a given area (Gillespie, Claridge & Roderick 2008) but is also interpreted as a measure of speciation (Emerson & Kolm 2005; Steinbauer, Irl & Beierkuhnlein 2013b). Climate and especially climatic changes directly influence speciation, for example through specific resource availability in terms of energy or water availability or by establishing specific selection pressures (Hua & Wiens 2013). For example, high-elevation ecosystems possess quite harsh conditions for plant growth; thus, selective pressure is very high (Anthelme & Dangles 2012). Idle resources, open niche space and potential isolation effects in high-elevation island ecosystems likely stimulate speciation processes (Steinbauer, Irl & Beierkuhnlein 2013b). As a result, endemism potentially indicates evolutionary *in situ* specialization to specific environmental conditions (i.e. past adaptive speciation processes), a phenomena which has been proposed to be relevant for all mountainous islands as well as isolated mainland peaks and mountain systems (Steinbauer, Irl & Beierkuhnlein 2013b).

PRECIPITATION VARIABILITY AND CLIMATIC RARITY

Precipitation variability, especially the rainfall seasonality index, contributed substantially in explaining species richness and endemism but not endemic richness on La Palma. The areas of La Palma with high precipitation variability host generally fewer species, while stable areas are mainly humid regions supporting relatively high species richness. High species richness likely results from high resource availability and low selective pressure for specialization, suitable for common (mesophytic) species communities (Stohlgren *et al.* 2005; Weigelt, Jetz & Kreft 2013). However, in aridity-prone regions, one of the essential resources for plant growth is very limited (i.e. water) and/or connected to a high temporal stochasticity, leading to less favourable growing conditions. This results in an increased importance of specialized endemics and thus a higher floristic uniqueness (i.e. endemism) but lower species richness in high-variability conditions (Dewar & Richard 2007). Several studies have shown that centres of endemic richness are connected to long-term climatic stability (Platts *et al.* 2013; Weber *et al.* 2014; Cook, Hardy & Crisp 2015), while endemic richness on La Palma is highest in variable conditions. However, our study used measures of climatic variability on a short-term scale (in the range of several decades), not accounting for stability on geologic time-scales. This might indicate that long-term stability and short-term variability are not mutually exclusive; thus, time-scales have to be considered for climatic stability analyses.

Although an intriguing concept due to its ability to integrate different climatic factors into a single parameter, climatic rarity only has negligible effects on both species richness and endemic richness. While climatic rarity has been shown to be a good indicator of species' range size and rarity on continental scales (Ohlemüller *et al.* 2008), it seems of

only minor importance for richness and endemism on the landscape scale of La Palma. Recent studies have shown that richness and species rarity have a complex relationship (e.g. Kreft, Sommer & Barthlott 2006; Hubbell 2013), which might not be as straightforward as previously assumed.

SPATIAL PATTERN OF SPECIES RICHNESS, ENDEMIC RICHNESS AND ENDEMICITY

The combined negative effect of both the elevation-temperature gradient and annual solar radiation indicates that high species richness is found in steep barrancos and coastal cliffs at low to mid-elevations because low temperatures and high solar radiation are stressful for plant growth (Körner 2003). The main drivers of endemic richness on La Palma are topographic complexity, annual solar radiation and slope. Similar to species richness, the highest values of endemic richness are found in the steep barrancos, coastal cliffs and inner cliffs of the Caldera de Taburiente (Fig. 3b,c), although without the trade wind-induced asymmetry shown for species richness. Earlier studies were not able to identify such small-scale differences in endemic richness on the Canary Islands (e.g. Reyes-Betancort *et al.* 2008).

Highest values of endemism are found at high elevations but also in the barrancos and coastal cliffs at low elevations on the western dry side of the island (Fig. 3d,e). High solar radiation at high elevations might select for adequate adaptation, while impeding the existence of most species that are adapted to conditions of lower radiation (Anthelme & Dangles 2012). This decreases general species richness and facilitates evolutionary adaptation processes, including ecological speciation of specialist endemics via UV-B radiation-induced mutagenesis (Flenley 2011). In addition, high UV-B radiation is responsible for the evolution of characteristic life-forms in the high-elevation ecosystems. On La Palma, this becomes obvious in the presence of giant rosette plants such as several representatives from the genus *Echium*, and morphological adaptations such as pubescence (e.g. *Genista benehoavensis*, *Echium wildpretii* subsp. *trichosiphon*, *Plantago webbii* or *Teline stenopetala* subsp. *sericea*).

Interestingly, hot spots of species richness, endemic richness and endemism are spatially decoupled on the landscape scale. In consequence, to conserve the whole spectrum of biological variation, it is obviously not enough to only focus on species richness as a measure of biodiversity on the continental scale (Orme *et al.* 2005; Daru, Bank & Davies 2015) or the island scale (Di Virgilio *et al.* 2014). Rather, it is important to employ conservation strategies for a wide range of different habitats and various definitions of 'hot spot' to adequately cover and preserve the total breadth of species diversity (Stohlgren *et al.* 2005; Daru, Bank & Davies 2015).

LOOKING BEYOND LA PALMA

While the isolation of oceanic islands has impeded the natural colonization of mammalian herbivores, there is virtually no oceanic island on the global scale without human-introduced

mammalian herbivores (Caujapé-Castells *et al.* 2010). Thus, the identified importance of topography for the identification of endemic hot spots may hint for a general importance of 'safe sites' within islands, protecting endemic species from introduced herbivores.

Similar to our results, highest percentages of endemic species on continental mountains are found in topographically complex areas (Verboom *et al.* 2015), often showing a strong increase of endemism with elevation (e.g. Vetaas & Grytnes 2002; Nogué, Rull & Vegas-Villarrúbia 2013). Thus, our results support a seemingly global pattern found in topographically complex regions, although we focus on the landscape scale of a single island. On continents, larger endemism in high elevations may, however, not only be driven by enhanced local evolutionary processes (e.g. elevation-driven isolation *sensu* Steinbauer *et al.* 2012), but also due to the survival of species widespread during times of colder climatic conditions (Tribusch & Schönswetter 2003). No matter what the underlying cause is, high-elevation areas should, as a consequence, be considered as high-priority sites for nature conservation both on islands and on the continent.

Conclusion

We suggest that future studies (e.g. using environmental niche modelling) need to acknowledge the effect of spatio-temporal climate variability but also the equally important effect of topography, especially on the distribution of species richness and endemic richness (Platts *et al.* 2013). On the one hand, the general use of long-term means in modelling of climatic envelopes in the face of climate change has recently been criticized (Letten *et al.* 2013). On the other hand, models only based on climate will likely perform poorer than models that also include topographic components, highlighting the importance of using both climate and topography. In addition, we argue that endemics might be more resilient towards ongoing climate change than previously thought because of their pre-adaptation to variable precipitation conditions. However, this needs to be investigated in future studies explicitly targeting climate change effects on islands (see Harter *et al.* 2015).

In general, high-elevation islands such as La Palma offer the opportunity to study continental-scale environmental gradients with high species turnover and clearly defined zonal ecosystems on the landscape scale of a single island. These so-called climatic *mini-continents* host a large array of endemic species, which mainly evolved *in situ* under island conditions (especially SIEs; Whittaker, Triantis & Ladle 2008). Thus, high-elevation islands are optimally suited to provide further insights into the fundamental drivers of diversity and endemism, even possessing the possibility to transfer the gained knowledge to non-island systems.

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Data accessibility

All data used in this article are accessible in the Dryad Digital Repository. For details, please see Irl et al. (2015).

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Supporting Information

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

Table S1. List of all species identified in this study.

Figure S1 Map of meteorological stations used for interpolating climate data.

Table S2. Bivariate correlation matrix of environmental variables.

Table S3. Table of best fitting transformations for MLR.

Table S4. Table of AICc values of transformations.

Table S5. Table of absolute values of variance partitioning.