

An island view of endemic rarity—Environmental drivers and consequences for nature conservation

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Abstract

Aim: Rarity—an important measure for conservation biogeography—can vary over many orders of magnitude. However, it is unclear which regional-scale abiotic conditions drive processes affecting rarity of endemic species on islands. To support conservation efforts, we (1) assess the main abiotic drivers of endemic rarity, (2) determine how well existing protected areas (PAs) coincide with hotspots of endemic rarity and (3) introduce and evaluate a new hypervolume-based rarity estimator.

Location: La Palma (Canary Islands).

Methods: We recorded all present endemic vascular plant species in 1,212 plots covering the entire island. We calculated endemic rarity (corrected range-rarity richness for endemics) using a rarity estimation approach based on kernel density estimations (hypervolume approach). We performed a sensitivity analysis based on multiple linear regressions and relative importance estimations of environmental drivers to estimate the performance of the hypervolume-based rarity estimation compared to standard methods (occurrence frequency, convex hulls, alpha hulls).

Results: Climate variables (mean annual temperature, climatic rarity, precipitation variability) best explained archipelago endemic (AE) and single-island endemic (SIE) rarity. Existing PAs covered the majority of AE and SIE rarity, especially national and natural parks as well as the Natura 2000 sites. In our study system, hypervolumes performed better than standard measures of range size.

Main conclusion: Both AE and SIE rarity on La Palma show a clear spatial pattern, with hotspots of endemic rarity found at high elevations and in rare climates, presumably owing to geographical and climatic constraints and possibly anthropogenic pressure (e.g., land use, introduced herbivores, fire). Areas of high rarity estimates coincide with the distribution and extent of PAs on La Palma, especially since the recent addition of the Natura 2000 sites. The hypervolume approach is a promising tool to estimate species range sizes, and can be applied on all scales where point/plot data are available.

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KEYWORDS

conservation biogeography, corrected weighted endemism, endemic plant species, evolutionary pattern, hypervolume, island ecology, Natura 2000, protected areas

1 | INTRODUCTION

Besides species richness, rarity is an important criterion of conservation value (Burlakova et al., 2011). Indeed, areas where rare species aggregate are often preferentially chosen as conservation areas (Crain, White, & Steinberg, 2011)—also because rare species contribute disproportionately to the functional structure of species assemblages (Leitão et al., 2016). Identifying hotspots of endemic rarity is of high importance in determining areas with high conservation value and priority, not only for local conservation efforts but also for preserving global biodiversity (Kier et al., 2009). Determining the fundamental drivers behind range sizes—and thus also rarity—enables to extrapolate the occurrence of rare species in space and time.

Species' range sizes vary over several orders of magnitude, even among related taxa (Brown, Stevens, & Kaufman, 1996). Besides phylogenetic effects (e.g., niche conservatism) and biogeographical history, environmental settings (e.g., climate, topography, disturbance regimes, species interactions) determine the range size of species (Brown et al., 1996). On high-elevation islands, which are often environmentally diverse but of small area, endemic species have evolved to realize niches in a wide range of habitats and environmental settings (Stuessy et al., 2006; Whittaker & Fernández-Palacios, 2007).

In terms of prioritization for conservation, isolated islands take a unique position as their high degree of endemism contributes significantly to global biodiversity (Kreft, Jetz, Mutke, Kier, & Barthlott, 2008). At the same time, island biota, and in particular island endemics, are highly threatened due to their usually small distribution area (Kier et al., 2009). Small distribution area and often small total population sizes make these species more sensitive to land use changes (Caujapé-Castells et al., 2010), neobiota (Kueffer et al., 2010) and climate change (Harter, Irl et al., 2015). To counteract this threat, most islands and archipelagos possess protected areas (PAs; Vera-Galván, Samarín-Bello, Delgado-Castro, & Viera-Ruíz, 2010), often with differing conservation priority as well as underlying legal framework. On the Canary Islands, for example, PAs fall under the local legal framework elaborated by the regional government (Martín-Esquivel, 1995), as well as under national and European Union (EU) jurisdiction (Vera-Galván et al., 2010), including the Natura 2000 network of protected areas. The European Natura 2000 network of protected areas has substantially contributed to increasing natural areas in the EU within the last decade (Kallimanis et al., 2015).

A wide spectrum of range size measures and of rarity has been proposed (reviewed in Kunin & Gaston, 1993). Most measures of rarity are based on range size maps or grid-based data. Yet, grid-based data represent a much coarser scale of species distribution than plot or point data, which can lead to scale-dependent effects regarding the environmental drivers of emerging patterns (Hurlbert & White, 2005). However, when using plot or point data, standard measures of rarity (such as range size

maps derived from grid-based data) are often not feasible, calling for alternative measures. Range-rarity richness, which is part of the “sum of inverse range sizes” family of rarity measures (see Guerin & Lowe, 2015 for details on a unification of rarity terminology), is frequently used in large-scale analyses of rarity estimations (e.g., Kier et al., 2009; Williams et al., 1996), as it can be directly derived from species' range maps or grid-based data (Gaston, 1994). However, on the landscape scale, such data are usually not available at appropriate resolutions. In this study, we introduce and evaluate an alternative method to calculate species' range sizes and rarity using kernel density estimations based on point data of species spatial occurrence by adapting the hypervolume approach of Blonder, Lamanna, Violle, and Enquist (2014).

We use the oceanic island of La Palma (Canary Islands) as case study, an island part of the Canary Island archipelago that is of high conservation value and is considered a hotspot of species radiations (Martín-Esquivel, 2010). La Palma is ideally suited to address questions regarding the distribution of species rarity owing to its spatial restriction by the surrounding ocean, strong environmental gradients, complex topography, large array of single island as well as archipelago endemics and only moderate human impact compared to other islands of the archipelago, which have experienced large alterations due to mass tourism and land use change (Fernández-Palacios, Arévalo, Delgado, & Otto, 2004).

We calculate endemic rarity using endemic species at the community level for both archipelago endemics (AEs) and single-island endemics (SIEs)—a measure that integrates information on all endemics within a given site, thereby eliminating species-specific idiosyncrasies. As a cumulative measure, endemic rarity is highly suited to identify environmental drivers and hotspots of rare endemics. Indeed, hotspots of rare endemics have a particular conservation value and should therefore be adequately covered by PAs. As a result, our research aims are (1) to identify the main environmental determinants of the spatial pattern of AE and SIE rarity, (2) to determine whether AE (and SIE) rarity, in comparison with AE (and SIE) richness, is reflected by regional, national and international conservation frameworks and (3) to evaluate how the kernel density estimation-based hypervolume approach of range size quantification performs compared to traditional measures of species range size.

2 | METHODS

2.1 | Study area

Located in the Atlantic Ocean, La Palma is the north-western-most island of the Canary Islands (Figure 1a and b). La Palma is a volcanic-oceanic island of medium age (1.7 Ma; Carracedo, Badiola, Guillou, de la Nuez, & Pérez-Torrado, 2001) and relatively small area (706 km²). The island reaches a maximum elevation of 2426 m a.s.l. at Roque de

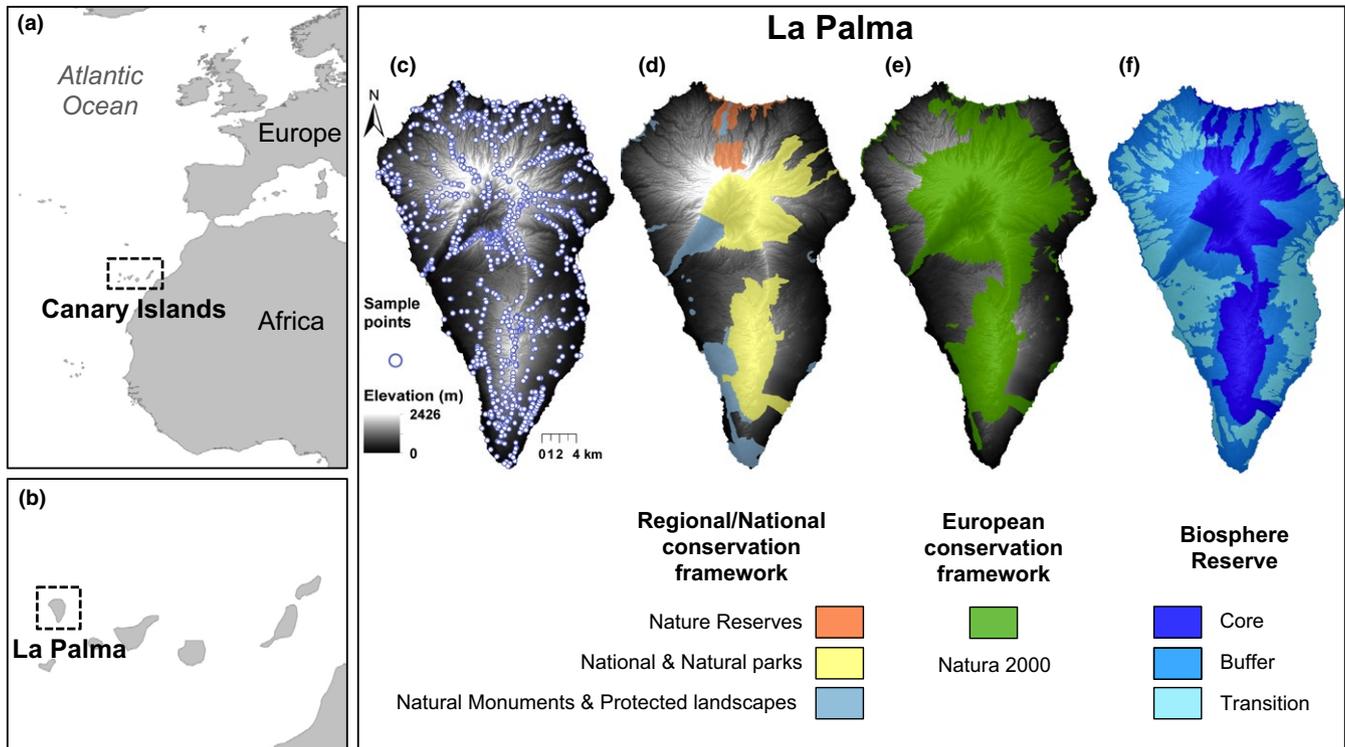


FIGURE 1 Map of the position of (a) Canary Islands and (b) La Palma in the Atlantic Ocean. (c) Map of La Palma showing elevation and the location of all sample points ($n = 1,212$). (d) Map of the three major regional and national conservation frameworks, (e) map of European Natura 2000 conservation framework (Special Areas of Conservation) and (f) map of the three different categories belonging to the Biosphere Reserve. Notice the large overlap of the core and the buffer areas of the Biosphere Reserve with already existing protection areas. [Colour figure can be viewed at wileyonlinelibrary.com]

los Muchachos. Complex topography with steep valleys, almost vertical coastal cliffs and the Caldera de Taburiente complex characterizes the northern and older part of the island, while the southern part has gentler slopes, recent volcanic cones and petrified lava flows, reflecting ongoing volcanic activity (Carracedo et al., 2001).

The mild subtropical Atlantic climate of the island is strongly modified by the complex topography (Garzón-Machado, Otto, & del Arco Aguilar, 2014). With high constancy, trade wind conditions transport moisture from the north-east. This leads to a climatic divide of the island: the northern to eastern areas experience relatively stable humid conditions and high cloud cover, while the western to southern regions are characterized by low and infrequent precipitation and high solar radiation. Above the trade wind inversion, cool and arid conditions prevail (Whittaker & Fernández-Palacios, 2007).

In total, La Palma possesses 193 archipelago endemics (including species and subtaxa, for simplification hereafter referred to as *species*; Acebes Ginovés et al., 2010). As a subgroup of archipelago endemics, La Palma hosts 37 single-island endemics (Acebes Ginovés et al., 2010). The nomenclature of all taxa in this study is based on Acebes Ginovés et al. (2010).

2.2 | Sampling design

We recorded the presence/absence of all endemic perennial vascular plant species (i.e., archipelago and single-island endemic) in 50-m radial

plots ($n = 1,212$; Figure 1c; see Table S1 in Supporting Information for a complete species list, Table S2 in Supporting Information for plot data and Table S3 for all per-plot occurrences of endemic species used for the analysis). The whole island was investigated using a high spatial coverage of sampling plots and attempting a random distribution of plots, with the exception of inaccessible areas on steep and unstable slopes. Settlements were avoided. Sampling took place in all years from 2010 to 2015 and in 2017, preferably in spring when vegetation was best developed.

We focused on perennial species because they are most important for the endemic flora of the Canary Islands (i.e., 93% of endemics are perennials, Shmida & Werger, 1992) and they are easy to detect in the field, ensuring a rapid sampling procedure. Also, due to their longevity, perennials are good indicators of climatic conditions, whereas annuals express a high stochasticity that is strongly dependent on short-term weather events. In this respect, annuals could lead to false absences, for example, if sampling took place during a time of year when annuals are dormant, potentially biasing range size calculations.

2.3 | Measures of endemic rarity and endemic richness

We develop and introduce a method to assess the range of a given species, where we quantify the spatial extent of a species' range by applying kernel density estimations on species occurrence probabilities on plot-based information of species spatial occurrences. As

a species' spatial occurrence is restricted to the island of La Palma by the surrounding ocean, we truncated the probability density of spatial occurrence estimated by the kernel density estimation to the shape of the study region. We therefore adapted the original *hypervolume()* command implemented in the *hypervolume-R* package developed by Blonder et al. (2014) (see Appendix S2 for commented R-script).

As species' spatial occurrences are usually not continuous, especially on the landscape scale, but characterized by patchy species distribution (there are unoccupied gaps within the overall distribution area), traditional approaches (e.g., convex hull methods) can strongly overestimate species' spatial occurrence within its range (Blonder, 2016). In contrast, our approach calculates species' range size based on spatial distribution and density of species occurrence and thus gives more realistic estimates of species' range sizes especially on regional scale, where species' distributions appear to be patchier than on large spatial scale (Gaston, 1994). In this approach, the probability of species occurrence is thereby modelled by a kernel density estimation applied on the actual points of species occurrence with longitude and latitude of the sampled species' occurrences as input variables. Probability of occurrence truncated by the spatial extent of the study region (i.e., area of La Palma) was then transferred into presence/absence used to quantify species spatial distribution by applying a threshold on the probability of occurrence (for more details, see the paragraph on sensitivity analysis). All recorded species with a minimum of three occurrence points were included in the analyses (for more details about the hypervolume approach and model calibration, see Blonder et al. (2014) as well as the commented R-scripts in Appendix S2).

Based on a unification of rarity terminology suggested by Guerin and Lowe (2015), we apply a rarity measure of the family of "sum of inverse range size" metrics to our data. To estimate what we call *endemic rarity*, we calculate corrected range-rarity richness (CRRR) per plot for pre-classified endemism categories (i.e., archipelago endemics and single-island endemics) as:

$$CRRR = \frac{\sum \frac{1}{rs_i}}{ER_j},$$

where ER_j is the endemic richness per plot j (i.e., the sum of all endemic species per plot; note: AE richness for archipelago endemics and SIE richness for single-island endemics) and rs_i is the estimated range size of species i . The inverted species-specific values of rs_i were then summed per plot and corrected for species richness effects (divided by ER_j), although we are aware that such a correction does not completely correct for species richness effects (Jetz, Rahbek, & Colwell, 2004). The hypervolume approach is a particularly suitable measure to estimate CRRR of single-island endemics (SIEs), as their global distribution is limited to a single island and is therefore entirely covered by our plot-based occurrence data. Therefore, we calculate endemic rarity for both archipelago endemics (i.e., for species endemic to the Canary Islands; AEs) and SIEs. Thus, we split endemic rarity up into *AE rarity* and *SIE rarity*. A list of each estimated rarity per species is given in Table S1. A list of CRRR per plot including additional geostatistical information is given in Table S2.

2.4 | Environmental and anthropogenic data

To correlate endemic rarity with local environmental conditions, we used a suite of environmental variables extracted from geoinformation layers provided by the local government of La Palma (i.e., digital elevation model and geologic age). Mean annual temperature (MAT) was interpolated from meteorological weather station data (for exact locations of the weather stations, see Irl et al., 2015), while monthly resolved precipitation data were used to calculate mean annual precipitation (MAP), interannual precipitation variability, intra-annual precipitation variability and the rainfall seasonality index (Walsh & Lawler, 1981). Climatic rarity as a measure of how common (or rare) specific combinations of climatic conditions are (i.e., MAT and MAP) was calculated according to Ohlemüller et al. (2008). For each plot, we calculated elevation, slope, northerness, easterness and macroaspect (mean aspect per plot in a 5 km radius) using the digital elevation model. Topographic complexity was calculated by dividing the 3D area by its 2D projection (Jenness, 2004). We calculated annual solar radiation based on latitude, elevation, slope and aspect.

Besides the environmental variables, we also included three anthropogenic variables to account for human-induced effects. We calculated distance to the nearest road and distance to the nearest city from road and urbanization maps, respectively (but see Irl, Steinbauer, Epperlein et al., 2014 for effects of roads on endemics). We developed a cultivation index that indicates whether a plot lies within the zone of cultivation (agriculture, settlements, etc.) or not (uncultivated).

For standardization purposes, we resampled all geoinformation layers to a resolution of 100 × 100 m for further analysis. For details on environmental variables and calculations, see Irl et al. (2015). Table 1 shows a list of all environmental variables. Values for AE and SIE richness were taken from Irl et al. (2015) for all years before 2014. Data collected in 2014, 2015 and 2017 can be found in Table S2.

2.5 | Protected areas

Besides being a World Biosphere Reserve since 2002 (San Blas, 2008), La Palma harbours a variety of protected areas (PAs) that differ in status and protective measures (Figure 1d and e), covered by conservation frameworks developed by regional, national and EU jurisdiction. On La Palma, six major categories are present at regional level. In the following, we list them according to their restrictiveness (Table 2, Martín-Esquivel, García-Court, Redondo-Rojas, García-Fernández, & Carralero-Jaime, 1995): (1) Natural Reserves are the strictest PAs declared to conserve the integrity of ecosystems and biological communities as well as individual species, habitats and geological and ecological processes; (2) National and Natural Parks were established to conserve their natural resources promoting the contact with humans (e.g., the Caldera de Taburiente National Park established in 1954; García-Canseco, 2009); (3) Natural Monuments and Protected Landscape are areas where geological structures and elements as well as aesthetical values support landscape beauty. In total, 20 different areas occupying 35.3% of the total island surface compose the La

Palma Network of PAs (Martín-Esquivel et al., 1995; Figure 1d; see Table S5). Note that Sites of Scientific Interest were excluded from the analysis because only four points were located in such PAs.

Regarding the areas of the Natura 2000 network on La Palma, 36 sites were declared Special Area of Conservation (SAC; Figure 1e), defined by the EU Habitat Directive (Vera-Galván et al., 2010). On La Palma, almost all PAs are also part of the Natura 2000 framework (Figure 1d and e). To enable a differentiation between conservation frameworks, in the following the term *Natura 2000* is only used for areas that are exclusively part of the Natura 2000 framework. We also keep this differentiation in our statistical analyses. Although all terrestrial areas and some adjacent marine areas of La Palma are World Biosphere Reserves, the areas that do not coincide with the core and buffer areas of existing PAs currently do not receive any active nature conservation and protection measures by the island authorities (see Transition areas; Figure 1f). Further on, these areas will be referred to as *unprotected*, even though they are theoretically part of the Biosphere Reserve framework.

TABLE 1 List of environmental variables and their respective units

Environmental variables	Unit
Annual solar radiation	Wh/m ²
Area of 100-m elevational bands	km ²
Climatic rarity	ha
Cultivation index	-
Easterness	-
Distance to nearest city	m
Distance to nearest road	m
Elevation	m a.s.l.
Geologic age	Ma
Intra-annual precipitation variability	-
Interannual precipitation variability	-
Macroaspect	-
Mean annual precipitation	mm
Mean annual temperature	°C
Northernness	-
Rainfall seasonality index	-
Slope angle	°
Topographic complexity index	-

Type	Area [Ha]	Framework	IUCN classification
Integral natural reserve	984.1	Local	I
Special natural reserve	1074.4	Local	I
National park	4690.0	Local/National	II
Natural park	12593.7	Local	II
Natural monument	1452.0	Local	III
Protected landscape	4107.7	Local	III
Natura 2000	12544.1	European union	IV

2.6 | Statistical tests and analysis tools

To quantify the main environmental drivers of endemic rarity, we performed multiple linear regression analyses. We determined the best explanatory variables using the *leaps()* command (*leaps*-R-package, version 2.9) under consideration of collinearity among the tested variables (Table 3 for best-model fits). For example, area and elevation are strongly collinear with MAT and were therefore both excluded from the analyses. Thus, when interpreting MAT in the model output, it is important to keep in mind that the effects of area, elevation and MAT are not statistically separable. Relative importance of the selected predictors was quantified by using partitioned R^2 -values from a multimodel inference analysis (*calc.relimp()* from the *relaimpo*-R-package; v. 2.2-2). The independent effect of a certain predictor on either AE or SIE rarity was accepted, when the bootstrapped 0.95 confidence intervals of the independent effect size did not include zero (*boot.relimp()* and *booteval.relimp()* command, 1,000 bootstraps). We decided to use this bootstrap approach instead of parametric estimations of confidence intervals as it is commonly known to be more robust against violations of the assumptions of parametric statistics (normally distributed sampling distribution, e.g., Briggs, Wonderling, & Mooney, 1997).

To interpolate AE rarity and SIE rarity into space, we applied a generalized linear model (GLM) with a Poisson-family distribution. The best-fit model from the multimodel inference analysis was used as basis for the GLM prediction. We quantified uncertainty of the spatial interpolation by running the GLM 1,000 times with a bootstrapped subset of the original data (two-thirds of the total data randomly selected with replacement after each model run). Based on 1,000 model runs, we calculated the standard deviation of the 1,000 estimates for each point as a measure of uncertainty (*sensu* Rocchini et al., 2011).

We tested differences in AE rarity and AE richness among the different categories of protected areas by using an ANOVA and a post hoc Tukey HSD test. We applied the same procedure for comparing SIE rarity and SIE richness. All analyses were performed in R (v.3.1.0, R Core Team, 2014) with a level of significance of $\alpha = .05$. For the spatial analysis implemented in the adjusted version of the hypervolume algorithm for species range size/rarity estimation and to evaluate the spatial coverage of species estimated occurrences by protected areas of different local, national and international nature conservation frameworks, we used the add-on R packages *sp* (v.1.2-3), *maptools* (v.0.8-40)

TABLE 2 Categories of conservation areas on La Palma, their total area, their respective legal framework and the IUCN classification scheme used for further calculations. For details on the legal framework, see text

and *raster* (v.2.5-8). Convex hull as well as alpha hull estimations of species range sizes were performed using the *EOO.computing()* command of the *ConR* add-on package (v.1.1).

2.7 | Sensitivity analysis for range size estimation methods

We compared the hypervolume approach to three standard approaches of species range size estimation: (1) we calculated the *occurrence frequency* of each species (i.e., the number of plots a species occurs in), which is roughly comparable with grid cell-based measure at larger scales (e.g., Williams et al., 1996) owing to the near-complete spatial coverage of plots. This approach assumes a positive relationship between range size and occurrence frequency. (2) We calculated *convex hulls* for each species, leading to a simple estimation of the geographical range size of species (Guerin, Ruokolainen, & Lowe, 2015; Romeiras et al., 2016). (3) We calculated *alpha hulls*, which are a kernel density-based approach and thus conceptually similar but less flexible than the proposed hypervolume approach. While hypervolumes, alpha hulls and the occurrence frequency represent area of occupancy, we also include convex hulls that measure the extent of occurrence (sensu Guerin et al., 2015), which is qualitatively a different aspect of range size but nevertheless often applied as measure of range size.

Whereas species range size estimation based on the occurrence frequency as well as the convex hull approach does not depend on model parameters, the probability of spatial occurrence estimated by the alpha hull and the hypervolume approach depends on a priori chosen thresholds. We therefore compared the performance of the four approaches for varying threshold parameters for the alpha hull and hypervolume approaches. For the alpha hull approach, we varied the parameter alpha between 0.2 and 3.0 in 30 steps. The spatial buffer added to the estimated alpha hulls was set to 0.01 decimal degrees. The range of tested threshold parameters for the hypervolume approach (bandwidths for longitude and latitude as the two modelled variables) was based on Silverman band width estimations that we conducted for all endemic species sampled with more than three points of occurrence. For all bandwidth estimations and the subsequent hypervolume estimations, we used standardized longitude and latitude values of species occurrences. The tested bandwidths for longitude thereby varied between 0.022 and 0.397, and between 0.004 and 0.603 for latitude (both with 30 values). To evaluate the

hypervolume approach in comparison with the three other standard measures, we calculated the portion of variation explained by the set of environmental variables from the best-fit multiple linear regression models selected by the *leaps()* command for each pair of bandwidths (for the adjusted hypervolume approach)/each alpha value (for the alpha hull approach). This set of selected environmental factors did not differ for the rarity measures based on occurrence frequency and convex hull but they changed with changing bandwidth/alpha values and, thus, changing hypervolume (CRRR) and alpha hull-based rarity measures. This resulted in four different sets of environmental parameters that were tested for each pair of bandwidths/each alpha value for each of the four rarity measures. Performance of the four different rarity measures was then quantified based on the adjusted R^2 values obtained for each rarity measure from multiple linear regressions with each of the four sets of environmental factors (see Figure 4).

3 | RESULTS

3.1 | Environmental drivers and endemic rarity

The high number of plots ($n = 1,212$) resulted in an average spatial coverage of 1.6 plots per km^2 . We recorded 110 endemic plant species on La Palma (57% of all endemic species of the island), which were used as basis for calculating AE rarity (CRRR; in Table S1). Of these, we used 34 single-island endemics (92%) for the calculation of SIE rarity (in Table S1).

The environmental variables used in this study were able to explain AE rarity (CRRR; adjusted $R^2 = .25$, $p < .001$, Tab. 3). MAT had a strong negative effect on CRRR (Figure 2a). Climatic rarity as the second most influential predictor had a significant positive effect on AE rarity with rare climatic conditions (i.e., cool and dry as well as cool and humid areas) apparently leading to AE rarity hotspots. Decreasing intra-annual precipitation variability, increasing topographic complexity and the presence of cultivated areas (the only relevant anthropogenic variable) had weak effects on AE rarity (Figure 2a). When interpolated using a GLM, AE rarity shows a clear spatial pattern (Figure 2b).

Around a third of the variance of SIE rarity was explained by environmental variables (CRRR; adjusted $R^2 = .34$, $p < .001$, Table 3). Again, MAT was the best explanatory variable (Figure 2c), followed by the rainfall seasonality index, climatic rarity and intra-annual precipitation variability. Anthropogenic variables had only little explanatory power;

TABLE 3 Best-fit multiple linear regression models used for linear regression kriging of AE rarity and SIE rarity in Figure 2b and d

Response variables	Model	Adjusted R^2	p-value
AE rarity	$\log(\text{MAT}) + \text{Intra-annual rainfall variability} + \log(\text{Climatic rarity}) + \text{Topographic complexity index} + \text{Cultivation index} + \text{Rainfall seasonality index} + \text{Distance to nearest road} + \text{Interannual rainfall variability}$.25	<.001
SIE rarity	$\log(\text{MAT}) + \text{Rainfall seasonality index} + \text{Climatic rarity} + \text{Intra-annual rainfall variability} + \text{Interannual rainfall variability} + \text{Northernness} + \text{Distance to nearest road} + \text{Topographic complexity index}$.34	<.001

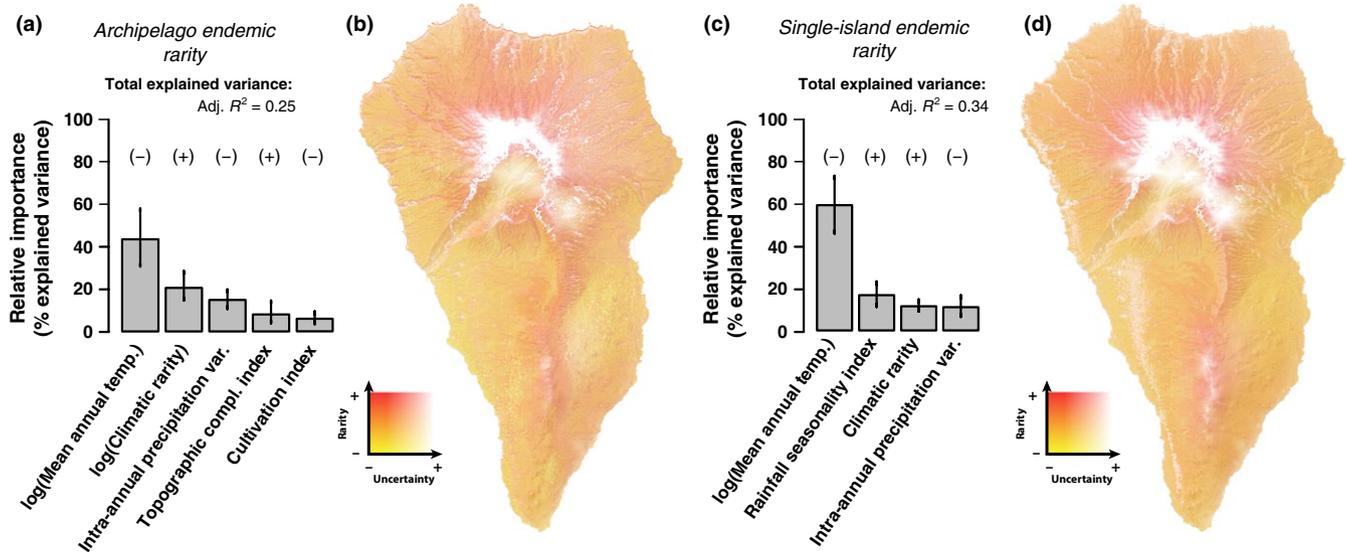


FIGURE 2 Relative importance of environmental variables in explaining archipelago endemic rarity and single-island endemic rarity as well as interpolated heat maps of rarity on La Palma. (a) Relative importance in explaining AE rarity of each environmental variable considered in the multimodel inference approach given as a fraction of the model's total explained variance (note: variables < 5% are excluded). Environmental variables are ranked according to relative importance. Whiskers show the bootstrapped 95% confidence interval. The direction of relationship of each environmental variable is given above each bar ("+" stands for positive correlation, and "-" for negative correlation). (b) Interpolated heat map of AE rarity using GLMs and including a measure of uncertainty. AE rarity increases from yellow to red. Uncertainty depicts the prediction quality (range: 0.02–0.83 SD). Areas of increasing uncertainty (i.e., decreasing prediction quality) become subsequently paler. (c) Relative importance of explaining SIE rarity. Configurations are the same as in (a). (d) Interpolated heat map of SIE rarity. Configurations are the same as in (b). [Colour figure can be viewed at wileyonlinelibrary.com]

for example, the addition of distance to nearest road only increased the adjusted R^2 from .32 to .34. A clear spatial pattern of SIE rarity, similar to that of AE rarity, can be seen in Figure 2d. Note that we excluded all explanatory variables with < 5% relative contribution from both graph 2 a) and c) to increase graph readability.

3.2 | Endemic rarity and conservation categories

We confirmed a good cover of AE and SIE rarity hotspots by the different conservation areas (see Figure 3b for AE rarity and Fig. S1 for SIE rarity). Two of three categories of conservation areas within the national conservation framework (i.e., Nature Reserves and National and Natural Parks) had significantly higher AE rarity than unprotected areas (Figure 3a), while for AE and SIE richness none of the PAs showed significantly higher values (Figure 3b, Appendix S1). National and Natural Parks covered sites with significantly higher AE rarity than Nature Reserves and Natural Monuments and Protected Landscapes. When comparing the national with the European conservation framework, study sites covered by Natura 2000 areas showed a tendency towards lower AE richness than sites that are under national protection. However, Natura 2000 study sites showed similarly high AE rarity as National and Natural Parks. Owing to their larger areas, National and Natural Parks as well as Natura 2000 areas are able to cover higher percentages of individual endemic species distribution areas than the smaller Nature Reserves and Natural Monuments and Protected Landscapes (Figure 3c). Our results show that a part of the range of every endemic used in this study is protected by at least one PA category.

3.3 | Sensitivity analysis for range size estimation methods

Correlations of the alternative rarity methods with the hypervolume approach ranged from strong to weak ($R^2 = .79$, $p < .001$, for occurrence frequency, $R^2 = .32$, $p < .001$, for alpha hulls and $R^2 = .09$, $p < .001$, for convex hulls) and for SIE rarity ($R^2 = .84$, $p < .001$, for alpha hulls, $R^2 = .74$, $p < .001$, for convex hulls and $R^2 = .68$, $p < .001$, for occurrence frequency). Correlations of the individual species rarity comparing the hypervolume approach to the alternative methods revealed similar results ($R^2 = .72$, $p < .001$, for occurrence frequency, $R^2 = .46$, $p < .001$, for alpha hulls and $R^2 = .34$, $p < .001$, for convex hulls). Nevertheless, a sensitivity analysis showed that the hypervolume approach outperforms all competing methods if bandwidths are sensibly chosen (Figure 4).

4 | DISCUSSION

4.1 | Possible drivers of endemic rarity

Climatic variables, especially mean annual temperature but also geographical constraints owing to decreasing area with elevation, govern endemic rarity on islands in general (Steinbauer, Irl, & Beierkuhnlein, 2013) but also on La Palma in particular (Steinbauer et al. 2017). This climate dependency of endemic rarity results in a clear spatial pattern on the island. Indeed, we find hotspots of endemic rarity (i.e., smallest mean range sizes) at high elevations above the trade wind inversion

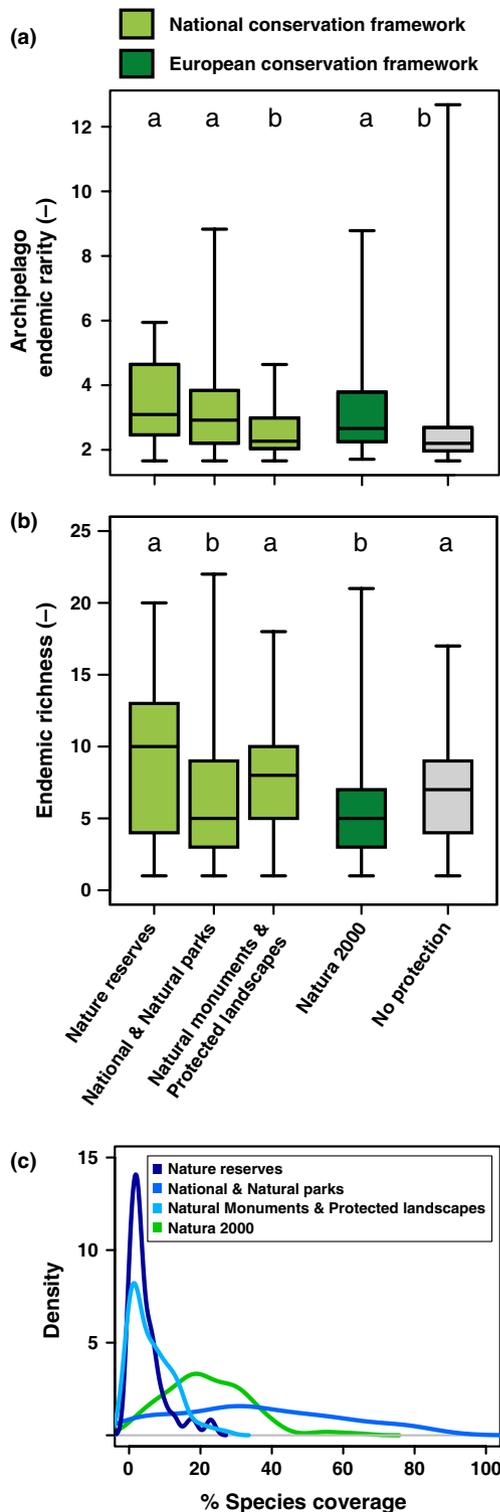


FIGURE 3 Coverage of (a) archipelago endemic rarity (measured as corrected range-rarity richness) and (b) archipelago endemic richness by existing protected areas (PAs). Light green PAs were developed under a national conservation framework and are grouped according to their conservation status. The Nature 2000 conservation framework (dark green) was elaborated under EU jurisdiction. The grey boxplot shows values without protection. Minor letters of each boxplot indicate significant groups ($\alpha = .05$). Whiskers extend to the extremes. (c) highlights the percentage of individual species coverage per PA type. The individual species coverages are shown as a density plot. [Colour figure can be viewed at wileyonlinelibrary.com]

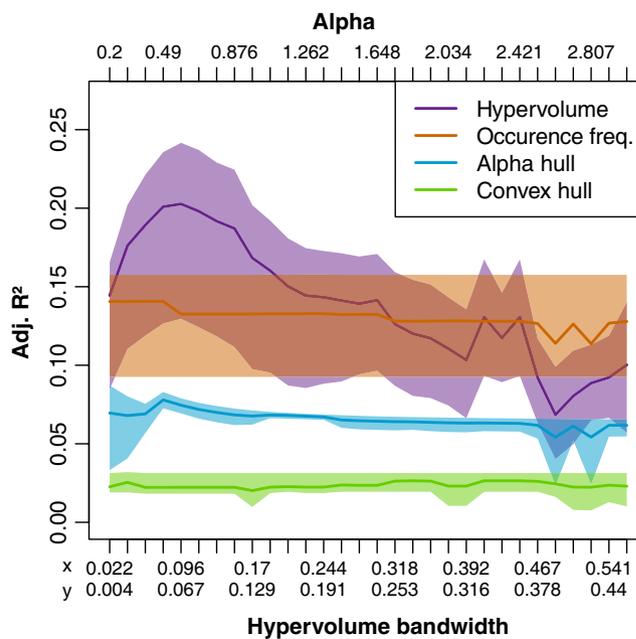


FIGURE 4 Evaluation of the hypervolume approach in comparison with three standard measures of species ranges size/rarity estimation. The hypervolume approach substantially outperforms the other measures (occurrence frequency and convex hull and alpha hull) in most of the tested cases. To test the performance of the different rarity measures, the proportion of variation explained by the set of environmental variables from the best-fit multiple linear regression models selected for each of the four rarity measures was calculated for each of the rarity measures (four sets of environmental factors for each rarity measure differing for each pair of hypervolume bandwidths, alpha values). Bold lines depict the average explanatory power (average adjusted R^2 from the four sets of environmental parameters tested by multiple linear regression), whereas the boundary of the shaded area depicts the minimum/maximum explanatory power for each rarity measure for each tested pair of hypervolume bandwidths/each tested alpha value (for more details about the sensitivity analysis, see Methods). [Colour figure can be viewed at wileyonlinelibrary.com]

and its related cloud layer for both AE and SIE rarity. Cold spots of endemic rarity are generally located in lowland and coastal areas, especially on the dry west coast—again a consistent pattern for both AE and SIE rarity. These areas also share climate characteristics with many neighbouring islands, indicating the wide geographical spread of AE lowland species.

High-elevation ecosystems tend to occupy smaller areas than coastal systems owing to decreasing area with elevation

(Fernández-Palacios, Otto, Thebaud, & Price, 2014; Steinbauer et al., 2016). Thus, high-elevation endemics might not be spatially restricted because of environmental constraints but due to area limitations, leading to smaller range sizes and subsequently higher rarity. Indeed, highly specialized and often strongly range-restricted endemics such as *Adenocarpus viscosus* subsp. *spartioides*, *Echium gentianoides*, *Echium wildpretii* subsp. *trichosiphon* or *Genista benehoavensis*

characterize the high-elevation ecosystem of La Palma (del Arco Aguilar, González-González, Garzón-Machado, & Pizarro-Hernández, 2010). As the mentioned species of the summit scrub above the tree line are single-island endemics on the species or the subspecies level (Acebes Ginovés et al., 2010), their global distributional range is restricted to an area of less than 20 km², highlighting their value for nature conservation and global biodiversity.

Our results show a positive climatic rarity–endemic rarity relationship, at least for AE rarity. Due to the subtropical position of La Palma, most of the island is dominated by warm and dry climate (del Arco Aguilar et al., 2010). Conditions other than that are restricted to small summit areas, for example, high-elevation zones (cool and dry), or mid-elevation zones of the windward side (cool and humid; Garzón-Machado et al., 2014). These climatic constraints result in a limited potential habitat for hygrophilous and cold-adapted endemics, whereas habitats of xeromorphic species are more widespread (del Arco Aguilar et al., 2010). On the continental scale, Ohlemüller et al. (2008) showed that range-restricted species are generally found under refugial conditions of rare climates. On La Palma, such unique conditions exist at the lower and upper extremes of both the temperature and humidity gradients, respectively.

Human-induced activities have been shown to threaten island endemics in high-elevation ecosystems (Irl et al., 2012; Irl, Steinbauer, Messinger et al., 2014) and adjacent systems (Garzón-Machado et al., 2010) on La Palma but also on other islands (Courchamp, Chapuis, & Pascal, 2003; Caujapé-Castells et al., 2010), thus likely increasing their rarity beyond the natural constraints these species already experience. Endemics on islands are often poorly adapted to introduced mammalian herbivores, for example, goats (*Capra hircus*), rabbits (*Oryctolagus cuniculus*) and the North African barbary sheep (*Ammotragus lervia*), because endemics evolved in the absence of their pressure (Bowen & Vuren, 1997). In addition, climatic alterations such as decreasing precipitation (Harter, Irl et al., 2015) in high-elevation island ecosystems might particularly threaten endemic specialists, for example, *Helianthemum juliae* on Tenerife (Marrero-Gómez, Oostermeijer, Carqué-Álamo, & Bañares-Baudet, 2007) or the iconic silverswords of Maui *Argyroxiphium sandwicense* subsp. *macrocephalum* (Krushelnicky et al., 2013). However, our analysis shows that adding anthropogenic variables to the model only marginally increased the model fit, indicating that environmental features likely are the main drivers of the observed pattern.

4.2 | Endemic richness, endemic rarity and current conservation areas

Existing PAs offer a good coverage of endemic rarity hotspots on La Palma, especially the recently adopted European Natura 2000 Habitat Directive as well as Natural Parks and National Parks. Indeed, our results show that the implementation of the Natura 2000 framework on La Palma in 2001 was a valuable addition to the previously existing regional and national conservation framework as Natura 2000 areas harbour—together with National Parks and Natural Parks—on average the highest endemic rarity on the island (both AE and SIE rarity). Thus, our detailed analysis of species range sizes is an important addition to evaluate the effectiveness of the Natura 2000 network.

Further conservation initiatives could be integrated into the wider framework of the La Palma World Biosphere Reserve (San Blas, 2008). Biosphere Reserves aim at bringing nature conservation, sustainable development and enterprises together, by designating nature conservation areas, which in the case of La Palma coincide with the already existing PAs, and areas, which foster economic and human development (UNESCO, 2015). Also, microreserves could be developed, aiming at protecting local- and small-scale hotspots of rarity (Laguna Lumbreras, 2001) either for specific rare species or for rarity at community scale. Microreserves seem a viable approach if larger PAs are politically or socially not feasible, also because they could be more easily moved if species migrate during ongoing climate change.

4.3 | Hypervolumes as a promising tool for range size estimation

We consider our kernel density-based method specifically suited to calculate range size (and subsequently rarity) in areas that have been previously poorly studied resulting in incomplete grid-based data coverage. As Blonder et al. (2014) provided a ready-to-use R package for hypervolume calculation, our approach to determine range sizes can be easily transferred to other point or plot data and any kind of geographical setting and scale (from local to continental).

Indeed, the hypervolume approach performed better than standard measures of range size, at least at the scale of our study. At this scale (~700 km²), species range sizes likely have very complex shapes and might be disjunct (c.f. Gaston, 1994), which seemingly cannot be grasped by less precise measures such as the occurrence frequency method and convex hulls; especially, convex hulls, which are widely applied in macroecology (e.g., Guerin et al., 2015; Leitão et al., 2016; Romeiras et al., 2016), might strongly overestimate range sizes by connecting and covering areas and environmental conditions that the species actually cannot inhabit (Blonder, 2016).

5 | CONCLUSION

Our case study illustrates that endemic rarity has a heterogeneous spatial distribution on a mountainous oceanic island such as La Palma, which differs from the spatial pattern of endemic richness. Thus, it is important to consider both endemic rarity and endemic richness for designing PAs. Areas of high endemic richness are also rich in other species but not necessarily the most threatened ones. Our approach is capable of supporting sound decision-making for future conservation areas and the process of developing effective conservation legislation for La Palma but also for other systems. However, La Palma is covered by an unusually large fraction of PAs (roughly 50%) and how PAs protect rare endemics on other islands or continental systems remains to be tested. Due to its heterogeneous climatic and topographic conditions (*climatic mini-continent*), La Palma can serve as a benchmark for other areas to achieve comparable PA coverage and protection of endemics.

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AUTHOR CONTRIBUTIONS

S.D.H.I., A.H.S. and F.M.M. conceived the ideas; C.B., S.D.H.I., D.E.V.H., A.J. and M.J.S. collected field data; J.M.F.P. and F.M.M. provided the environmental data; A.H.S. and S.D.H.I. analysed the data; and S.D.H.I. and A.H.S. led the writing with all co-authors contributing.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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