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RESEARCH ARTICLE

Evolutionary winners are ecological losers among oceanic island plants

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Abstract

Aim: Adaptive radiation, in which successful lineages proliferate by exploiting untapped niche space, provides a popular but potentially misleading characterization of evolution on oceanic islands. Here we analyse the respective roles of members of in situ diversified vs. non-diversified lineages in shaping the main ecosystems of an archipelago to explore the relationship between evolutionary and ecological 'success'.

Location: Canary Islands.

Taxon: Vascular plants.

Methods: We quantified the abundance/rarity of the native flora according to the geographical range (number of islands where present and geographical extent of the range), habitat breadth (climatic niche) and local abundance (cover) using species distribution data based on 500 × 500 m grid cells and 2000 vegetation inventories located all over the archipelago.

Results: Species of diversified lineages have significantly smaller geographic ranges, narrower climatic niches and lower local abundances than those of non-diversified lineages. Species rarity increased with the degree of diversification. The diversified Canarian flora is mainly comprised by shrubs. At both archipelagic and island level, the four core ecosystems (*Euphorbia* scrub, thermophilous woodlands, laurel forest and pine forest) were dominated by non-diversified lineages species, with diversified lineages species providing <25% cover. Species of diversified lineages, although constituting 54% of the archipelagic native flora, were only abundant in two rare ecosystems: high mountain scrub and rock communities.

Main conclusions: Radiated species, endemic products of *in situ* speciation, are mostly rare in all three rarity axes and typically do not play an important role in structuring plant communities on the Canaries. The vegetation of the major ecosystem types is dominated by plants representing non-diversified lineages (species that derive from immigration and accumulation), while species of evolutionarily successful lineages

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are abundant only in marginal habitats and could, therefore, be considered ecological losers. Within this particular oceanic archipelago, and we posit within at least some others, evolutionary success in plants is accomplished predominantly at the margins.

KEYWORDS
Canary Islands, colonization, community assembly, diversified lineages, ecological losers, island evolution, Rabinowitz rarity, vascular plants, vegetation plots

1 | INTRODUCTION

Oceanic islands are model systems for dissecting the interaction between evolutionary and ecological determinants of community assembly and composition (Emerson & Gillespie, 2008; Gillespie, 2004; Whittaker & Fernández-Palacios, 2007; Whittaker et al., 2017). The extreme isolation of most oceanic archipelagos limits the functional and phylogenetic variety of species able to colonize, opening evolutionary opportunities to diversify for those that do (Buira et al., 2020; Whittaker et al., 2017). Typically, in plants, a high proportion of species derives from the diversification of just a few colonists (Price et al., 2018; Price & Wagner, 2011). Such evolutionarily successful radiations are disproportionately derived from herbaceous colonists and include Hawaiian *Bidens*, silverswords (both Asteraceae) and lobeliads and Macaronesian *Aeonium* (Crassulaceae) and *Sonchus* (Asteraceae) (Borregaard et al., 2016; Knope et al., 2012; Whittaker & Fernández-Palacios, 2007). These clades can be considered evolutionary winners, often exhibiting speciation rates per unit area far above those observed in mainland settings (Borregaard et al., 2016). Such radiations are conventionally interpreted as a process of repeated specialization to the island environment, with species inhabiting novel niches and new geographic areas: implying that ecological and evolutionary success go hand in hand. But do these radiations really dominate the ecosystems of their constituent islands (Figure 1)?

Local communities, whether continental or insular, are typically dominated by just a few species, 'ecological winners' that impose their influence, in terms of demography, architectural structure, energy allocation, biomass production, water and nutrient cycling, on the majority of the species present (Lomolino et al., 2017; Ricklefs, 2009). The remaining species are rare in the community and mostly have less ecological and structural importance, although they can be fundamental to certain plant–animal interactions (Jain et al., 2014). Species rarity/success has been categorized by Rabinowitz (1981) into three main axes: (a) geographic range size, (b) abundance within communities locally, and (c) habitat breadth within the geographic range (which in turn influences site occupancy within the range). We might consider those species successful in at least two axes to qualify as ecological winners (Figure 1).

An early macroecological generalization is that large-ranged species tend to be locally abundant, while small-ranged (locally endemic) species are locally rare (Andrewartha & Birch, 1954; Lomolino et al., 2017) and associated with marginal habitats (Gaston et al., 2007): thereby placing these two groups of species at opposite

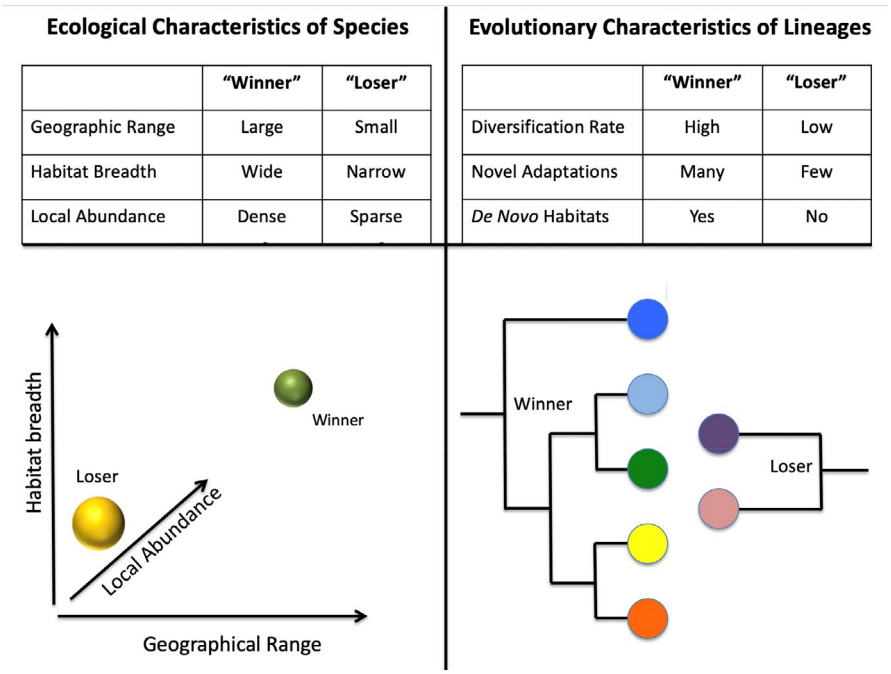

FIGURE 1 Characteristics of ecological and evolutionary winners and losers. Circles represent single species. Left: all combinations of "winner" and "loser" states for the three performance categories in the table above provide for eight states, seven of which are forms of rarity sensu Rabinowitz (1981), the most extreme of which are "loser" (yellow sphere) in all three senses and "winner" (green) in all three. Right: evolutionary success might be considered marked by combinations of high rates of diversification, the occupancy of novel habitats and the development of novel adaptations

corners of Rabinowitz's system. However, sometimes small-ranged endemics are locally abundant (Lesica et al., 2006), outperforming much larger-ranged congenerics. Additionally, species of limited geographical range are often found to be habitat specialists and thus may dominate in limited habitat patches within landscapes (Lavergne et al., 2004). Notwithstanding that different forms of rarity may not therefore always covary in a simple way, in general, the distribution of species along each rarity axis is strongly skewed toward rarity: this is also true of oceanic island biotas, including the Canary Islands (Martín, 2009).

The Canaries provide a uniquely suitable laboratory for analysing the relationships between evolutionary and ecological success, because (a) their flora is well studied and (b) a set of 2001 relevés provides standardized community composition data across islands and Major ecosystem types (METs). This has enabled us to distinguish members of non-diversified from diversified lineages (NDL vs DL) and to assess them quantitatively by life form (Table 1) and MET against Rabinowitz's (1981) three rarity axes: spatial range attributes (which we assess three ways: number of islands, spatial occupancy and maximum geographic extent of occupied grid cells), habitat breadth (hypervolume in standardized temperature/precipitation space) and local species cover (abundance in the six MET).

Here, we use a unique eco-evolutionary dataset of phylogenetic relationships, distributions, habitat associations and metrics of ecological dominance for Canarian plant species to test the following hypotheses: First, we used distribution and ecological trait data of all the native plants (Spermatophytes) of the Canary Islands to test if plant species from diversified lineages show, in general, higher degrees of rarity than those representing non-diversified lineages, following the concept of Rabinowitz's rarity dimensions (community abundance, ecological and spatial rarity) and if radiation is related to life forms. Then we test if species belonging to diversified lineages play, on average, an important role structuring the core plant communities by analysing 2000 vegetation plots located across this archipelago. Finally, we also evaluate the "refuge hypothesis," stating that human disturbance might determine the relative abundance of species of diversified lineages, restricting their prevalence to particular habitats.

TABLE 1 Life forms (%) of species in diversified lineages (diversification) and in non-diversified lineages (colonization). We use a modified Raunkiaer (1934) classification: trees (micro-, meso- and macrophanerophytes, height >4 m), shrubs (nanophanerophytes height: 0.25–4 m), dwarf shrubs (chamaephytes, which are mostly woody on the Canary Islands, height: <0.25 m), perennial herbs with bulbs or rhizomes (geophytes), perennial herbs (hemicryptophytes), annual herbs (therophytes). The last row percentages refer to the prevalence of both groups within the entire Canarian flora

Life form	Diversification, n (%)	Colonization, n (%)
Trees (>4 m)	2 (0.4)	32 (7.4)
Shrubs (0.25–4 m)	240 (47.5)	68 (15.7)
Dwarf shrubs (<0.25 m)	181 (35.9)	33 (7.6)
Perennial herbs	44 (8.7)	152 (35.0)
Annual herbs	38 (7.5)	149 (34.3)
Total	505 (53.8)	434 (46.2)

2 | MATERIALS AND METHODS

2.1 | Study area

The Canary archipelago is situated only 96 km off the hyper-arid coast of northwest Africa and belongs to the biogeographical region of Macaronesia (Azores, Madeira [also including the Savage Islands], Canary Islands, Cabo Verde). Despite the age of the older islands (21 Ma for Fuerteventura), unusually for a hotspot archipelago, all but La Gomera remain volcanically active. Over time new islands emerge, while existing islands are the subject of intensive and at times catastrophic erosive and/or volcanic episodes (Fernández-Palacios et al., 2011). The Pleistocene glaciation cycles have reiteratively doubled and halved the archipelago's area, with consequences such as the fusion of the islands of Lanzarote, Fuerteventura and satellite islets in a single landmass called Mahan, the emersion of several submarine banks and the diminution of the distance to the Africa. These profound changes have doubtless influenced colonization probabilities and the distribution of endemic species (Fernández-Palacios, 2016; Rijsdijk et al., 2014; Weigelt et al., 2016). Within the Canaries, there are more than 12,500 terrestrial and 5500 marine species in, or around, a land area of only 7500 km^2, from which about 3800 species and 113 genera are endemic (Arechavaleta et al., 2010). The endemics include many examples of spectacular plant radiations (e.g. within *Aeonium*, *Argyranthemum*, *Cheirolophus*, *Echium*, *Limonium*, *Lotus*, *Pericallis*, *Sideritis* and *Sonchus*).

The Canaries are affected by a Mediterranean-type climate and exhibit an outstanding ecosystem diversity. Steep climatic gradients occur, especially on the northern, more humid, slopes of the five higher islands (>1450 m), whereas the two eastern islands (Lanzarote, Fuerteventura) are lower and exhibit less environmental variation. Six major terrestrial ecosystem types (METs) have been described for the Canary Islands. Five form a zonal cline from coast to high mountain (del Arco et al., 2010; Fernández-Palacios, 1992; Fernández-Palacios & de Nicolás, 1995): sub-desert coastal *Euphorbia* scrub (found on all seven islands); thermophilous woodlands (seven islands); laurel forest (five islands); pine forest (five islands); summit scrub (three islands), and rock communities that can be found at any elevation. Other azonal vegetation types, such as coastal halophytic communities, sand dune habitats or wet habitat can be distinguished, but are too localized to be distinguished as separate entities for the present analyses. Short descriptions of each ecosystem can be found in del Arco et al. (2010) and Zobel et al. (2011). The full array of community types that comprise each MET is provided in Table S1. Natural vegetation has been severely disturbed by human activities, beginning with the first colonization of the archipelago by Berber tribes from North Africa ca. 2400–2200 yr BP

and intensifying after Castilian settlement in the 15th century (de Nascimento et al., 2020).

2.2 | Community inventories

To obtain information about species contributions to ecosystem assembly and structure, we collated 2001 vegetation plots covering all major habitats and islands, extracted from the online database SIVIM (Information System of the Iberian and Macaronesian Vegetation: http://www.sivim.info/sivi/). This database includes most of the published phytosociological surveys on the Canary Islands in the last 50 years. Some additional plot data from other published sources have been used (Cabrera, 2020; von Gaisberg, 2005; Méndez, 2010; Santos-Guerra, 1983; Stierstorfer, 2005). The common sampling protocol refers to the standard phytosociological methodology (Braun-Blanquet, 1964). Only the most natural vegetation types (phytosociological associations of potential vegetation series), but not secondary or substitution communities, were included, following the criteria of del Arco et al. (2010). Only associations with at least five plots were included in the analyses. Surveys of a number of different phytosociological associations were merged to the corresponding six METs (see Table S1). Other marginal azonal vegetation types, such as dunes or coastal marshes, were not taken into account. Following this approach, we obtained the mean proportion of the relative cover (details below) of all vascular plant species. Each species was categorized according to the degree of diversification of the colonizing lineage: non-diversified (1 species, either endemic or merely native status), moderately diversified (2–7 Canarian species in the lineage) or highly diversified lineages (>7 Canarian species per lineage). The plot data from the two easternmost islands, Lanzarote (45) and Fuerteventura (80) were combined, resulting in 125 inventories, because they were joined as a single island (Mahan) during extensive low-sea-level stands during the Pleistocene glacial periods (most recently until the early Holocene (Rijsdijk et al., 2014)) and being of low elevation and relatively degraded they are also ecologically simpler than the other islands.

Plots for phytosociological surveys (relevés) are subjectively selected in representative patches of the target communities (Braun-Blanquet, 1964), which leads to a certain bias towards well-preserved sites. However, this possible bias is countered, in our case, by the large number of plots representing accurately the composition and structure of the main vegetation types. The data for each site included: geographical characteristics (geographical coordinates, elevation, slope and area sampled), plus the cover for each species present, using a semi-quantitative index of its contribution. The so-called "abundance-dominance" index used in data collection, is based on the coverage, defined as the percentage of plot area covered by the projection of the aerial organs of a specific species within the plot. The index varies from r to 5, where: r = one individual with negligible coverage; + = more individuals, but a very low cover; 1 = up to 5% cover; 2 = 5–25% cover; 3 = 25–50% cover; 4 = 50–75% cover and 5 >75% cover). The phytosociological plots analysed vary in size (average: 260.5 m^2, range: 4–2000 m^2) depending on the type of vegetation and size of its species pool, although the proportion of species cover is not influenced by plot size or species richness.

The different METs have different overall levels of vegetation cover. For example, the laurel forest typically reaches 100% cover, but mature communities of coastal and summit shrublands, depending on the site, may have total cover values of 30–50% of the plot area. We calculated the relative cover of species of diversified lineages with respect to the total vegetation cover in the plot, which can exceed 100% in the case of sites with tree and shrub layers. For each phytosociological relevé and habitat type, we calculated separately the relative cover of all species within diversified and non-diversified lineages by substituting the relevé abundance code by the mean cover value of the abundance range (+, r = 1%; 1 = 5%, 2 = 15%, 3 = 37.5%, 4 = 62.5% and 5 = 87.5%). The rarest species are arguable slightly overrepresented by this approach, which therefore makes our analysis relatively conservative towards low-scoring species.

2.3 | Species data

In compiling our data, we used the most recent checklist of the vascular flora of the Canary Islands (Acebes Ginovés et al., 2010). Species of doubtful native origin were excluded following Price et al. (2018). Based on the most recent phylogenetic studies, each species of the entire native Canary flora was assigned to a putative colonist lineage following the approach used by Domínguez Lozano et al. (2010) and Price et al. (2018). Diversified lineages include species considered to be the product of in situ speciation within the Canarian archipelago through one or more diversification events of a common ancestor into two or more species (i.e. they are cladogenetic neo-endemics). Lineages that have diversified elsewhere in Macaronesia, but not in the Canaries (such as *Erica* or *Viburnum*) are considered non-diversified lineages in our analyses. Species belonging to non-diversified lineages may be divided into: (a) Canarian endemics, a group which comprises anagenetic neoendemic and palaeoendemic species); and (b) non-endemic-natives, which includes some Macaronesian endemics (species endemic to more than one Macaronesian archipelago, such as many laurel forest tree species shared by the Canaries and Madeira), plus those species with a wider distribution, occurring in, for example, North Africa, Sahara or Iberia. For present purposes, we considered all non-endemic natives to represent single colonization events and, therefore, as non-diversified lineages, with the exception of cases where phylogenetic studies support that there are also sister species that are endemic. Furthermore, each vascular plant species was assigned to a life-form following a modified version of Raunkiaer's (1934) approach: trees (micro-, meso- and macrophanerophytes, height >4 m), shrubs (nanophanerophytes height: 0.25–4 m), dwarf shrubs (chamaephytes, which are mostly woody on the Canary Islands, height: <0.25 m), perennial herbs with bulbs or rhizomes (geophytes), perennial herbs (hemicryptophytes), annual herbs (therophytes).

2.4 | Rarity dimensions

When analysing the rarity of diversifying vs. non-diversifying lineages we distinguished among three dimensions of rarity, following Rabinowitz (1981): (a) spatial or geographic rarity, that is, wide vs. narrow distribution; (b) local community abundance or demographic rarity, that is, abundant vs. scarce species, according to the cover which the species contribute to a given community and (c) habitat breadth or ecological rarity, that is, generalist vs. specialist species, here represented by the climatic niche width.

Spatial rarity was assessed by three different indices: the number of islands occupied, the geographic extent and the spatial occupancy across the Canaries, although in most analyses only the latter two were used. From the Canary Islands checklist of vascular plants (Acebes Ginovés et al., 2010), we extracted the number of islands a species is present on. Geographical extent and spatial occupancy were based on occupancy data across a grid of 500 × 500 m cells from the Canarian Government Atlantis 3 Biodiversity bank (Martín et al., 2005). The geographical extent for each species was calculated as the maximum linear Euclidean distance between the grid cells occupied by that species within an island for those species restricted to a single island, or, for all other species, within the archipelago, including the distance between islands, based on the UTM zone 28 coordinates of the mass centroids of the grid cells. Spatial occupancy was expressed by the total number of grid cells a species has been reported in. We used only those species occurrences with geo-referenced UTM coordinates or other accurate spatial information about the specific geographic location, in order to guarantee a high level of data quality, that is, the accuracy levels 1 and 2 in Martín et al. (2005).

The species community abundance value was defined as the maximum relative cover of the target species, expressed as the highest mean cover value recorded among all plots in a phytosociological association belonging to one of the selected six MET on any of the Canary Islands. First, we calculated the mean cover value, that is, the sum of cover values divided by the number of total plots in the association table, of the target species for every distinct phytosociological association on each island. Then we compared these values and chose the highest one to include as the species abundance value in further rarity analyses. For example, *Laurus novocanariensis*, the laurel tree, obtained its abundance value from one of the laurel forest associations (Table S1) of one of the five Canary Islands (H, P, G, T, C), where its mean cover value was highest. This value does not reflect the relative abundance of the species among all communities where it is present, but only the one where it is most abundant. Species not recorded in any inventory (410 species, or 43.7% of the flora) were considered to be very rare in the major vegetation types, although they might be locally abundant in certain rather rare variants of the six METs. They were allocated the lowest abundance value (i.e. 0.01% abundance) throughout the analyses.

Then, we calculated a two-dimensional climate niche width per species based on interpolated mean grid-cell temperature and precipitation values, the most important environmental factors affecting the distribution of plant species and communities on the Canary Islands (Fernández-Palacios, 1992). First, mean annual temperature and precipitation were interpolated from climate station data (N = 155 temperature, N = 305 precipitation) provided by Agencia Estatal de Meteorología de España (http://www.aemet.es). The interpolation was based on multiple linear regression for temperature and on boosted regression trees for precipitation (R-package dismo version 1.1-15, Poisson family error; 10-fold cross validation). Models were implemented with stepwise variable selection and included topography (elevation, aspect, slope), spatial information and rain shadow effects (calculated based on topography assuming a wind direction from 20°) as predictor variables.

For climate niche modelling, both mean annual temperature and annual precipitation were scaled between zero and one because multidimensional niche estimations are sensitive to the choice of units, scale and transformations (Petchey & Gaston, 2006). To provide a measure of the climatic niche width that is robust to extreme values and outliers, we calculated two-dimensional Gaussian hypervolumes with 95% quantiles applied to delineate the boundaries of the kernel density estimates, using the R package hypervolume v.2.011 (Blonder et al., 2014). The band width was fixed at the mean of all band widths estimated for the individual species based on the *estimate_bandwidth* function (Blonder et al., 2014).

The four rarity parameters (those listed above with the exception of number of islands) were standardized to a scale of 0–1 for purposes of comparison. Furthermore, a novel overall rarity index for each species was defined as the mean value of the four standardized rarity parameters, with the two spatial metrics (geographic range and spatial occupancy) each weighted by 0.5 and the rest by 1.

2.5 | Data analyses

Kernel density plots of species distributions were calculated for all four rarity parameters (geographic range, spatial occupancy, community abundance and climatic niche) and for overall rarity using the R (3.5.3) statistical software (R Development Core Team, 2009) and the R-package "ggplot2." Species were divided according to the degree of diversification between species of non-diversified, moderately and highly diversified lineages (1, 2–7 and >7 species per lineage, respectively) and with respect to life forms (first, all species including annuals and, second, only perennials). A Gaussian kernel function was selected for the smoothing of the histograms. The total area under the curve integrates to one. Community abundance and occupancy values were transformed (log, square root) to improve visual comparison. The differences of mean values of each rarity parameter between species of the three groups (highly, moderately and non-diversified lineages) were tested with the non-parametric Kruskal–Wallis rank sum test and the Wilcoxon test for differences between factor levels using the R-package "stats."

To test whether species belonging to diversified or non-diversified lineages play an important role in structuring the selected communities in which they participate we applied a

bootstrap approach (Crawley, 2007). We tested if the mean proportion of the relative cover of species belonging to diversified lineages in each MET on a certain island was significantly different from its proportion in the island's species pool, that is, if they are under- or overrepresented in the local community. We took 10,000 random samples with replacement from the total number of cover values for each species group and plant assemblage. Then, we calculated 95, 99 and 99.9% confidence intervals with lower and upper bounds of the cumulative probability distribution of the 10,000 bootstrapped mean values of the random samples. If the confidence interval lay below or above the value of the proportion of the island species pool, then the species group is deemed to be under- or overrepresented in the local community, respectively. The test was performed for each MET at the island and the archipelago level using the R-package "bootstrap."

To test for linear relationships between the proportion of relative cover of diversified species in community plots and plot elevation, slope and community tree cover, we applied generalized linear mixed models (GLMM) with a binomial error distribution, as recommended for continuous proportional data (Crawley, 2007).

We added geological age of the island as a proxy of evolutionary time, which is hypothesized to be a key determinant of overall island richness and endemism by the "General dynamic model of oceanic island biogeography," which postulates a humped relationship of these metrics with island age (GDM) (Whittaker et al., 2008). To visualize the effect of each variable on the distribution of diversified species in local communities we present partial residual plots of GLMMs on the scale of the original response after applying the inverse link function.

The proportion of plot cover of radiated species was introduced in the model as the dependent variable and elevation, slope, tree cover and island age (including a quadratic term) as independent variables. Island was treated as a random effect. Out of the total of 2001 plots, 1839 plots (92%) with information about slope, elevation and tree cover were used to perform the model. Model performance statistics such as generalized R^2-value and explained deviance are reported. Analyses were performed using the R-libraries "lme4," "MuMin" and "visreg."

3 | RESULTS

3.1 | Diversification and life forms

The Canarian native vascular flora comprises 939 species (Price et al., 2018): 434 (46%) belong to NDL and 505 (54%) to 85 DL (range 2–54, mean 5.94 species). Sixty-nine lineages with 2–7 species (moderately diversified) account for 218 species and 16 lineages of >7 species (highly diversified) a further 287 species. Within NDL there are 86 Canarian endemics and 348 native non-endemics (Price et al., 2018). Among DLs, the vast majority (83.4%) of species are shrubs, 16.2% herbs and 0.4% (2 species) trees, while NDLs are dominated by herbaceous species (69.3%), half of them annuals, followed by shrubs (23.3%) and trees (7.4%, 32 species; Table 1).

3.2 | Species rarity

For each rarity metric, whether considering the entire flora, or just perennials, a consistent pattern of greater rarity of DL species emerges (Figure 2, Table 2). The greatest differences are for aspects of geographical distribution, especially geographical range, which is strongly constrained by the geographical distribution of species among islands (Figure 2a,e,i). Notably, 11% of NDL species are single-island endemics, contrasting with 60% of DL species (44% for moderately diversified lineages, 71% for highly diversified lineages) (Figure 2i). The NDL group shows two peaks of island occupancy, for five islands (mostly species present in the five ecologically similar, topographically high, central/western islands) and seven islands (whole archipelago).

TABLE 2 Differences of mean values of each rarity type between species of non-diversified (1 species per lineage; n, 434 species = 434 putative colonist lineages), moderately diversified (2–7 species per lineage; m, 218 species in 69 lineages) and highly diversified lineages (>7 species per lineage; h, 287 species in 16 lineages) of the Canarian flora (939 species) were tested with the non-parametric Kruskal-Wallis rank sum test for all three groups together and the Wilcoxon test for differences between group levels

	All species					Perennials				
	Kruskal Wallis		Wilcoxon			Kruskal Wallis		Wilcoxon		
	Chi-square	*p* values				Chi-square	*p* values			
Rarity type			n-m	n-h	m-h			n-m	n-h	m-h
Overall rarity	85.1	<0.001	<0.001	<0.001	0.017	88.1	<0.001	<0.001	<0.001	0.024
Geographic range	309.3	<0.001	<0.001	<0.001	<0.001	229.8	<0.001	<0.001	<0.001	<0.001
Spatial occupancy	48.1	<0.001	<0.001	<0.001	0.079	48.0	<0.001	<0.001	<0.001	0.035
Local community abundance	0.4	0.527	>0.05	>0.05	>0.05	14.9	<0.001	0.004	0.002	>0.05
Climatic niche	10.8	0.003	0.302	0.002	0.302	21.5	<0.001	0.072	<0.001	0.072

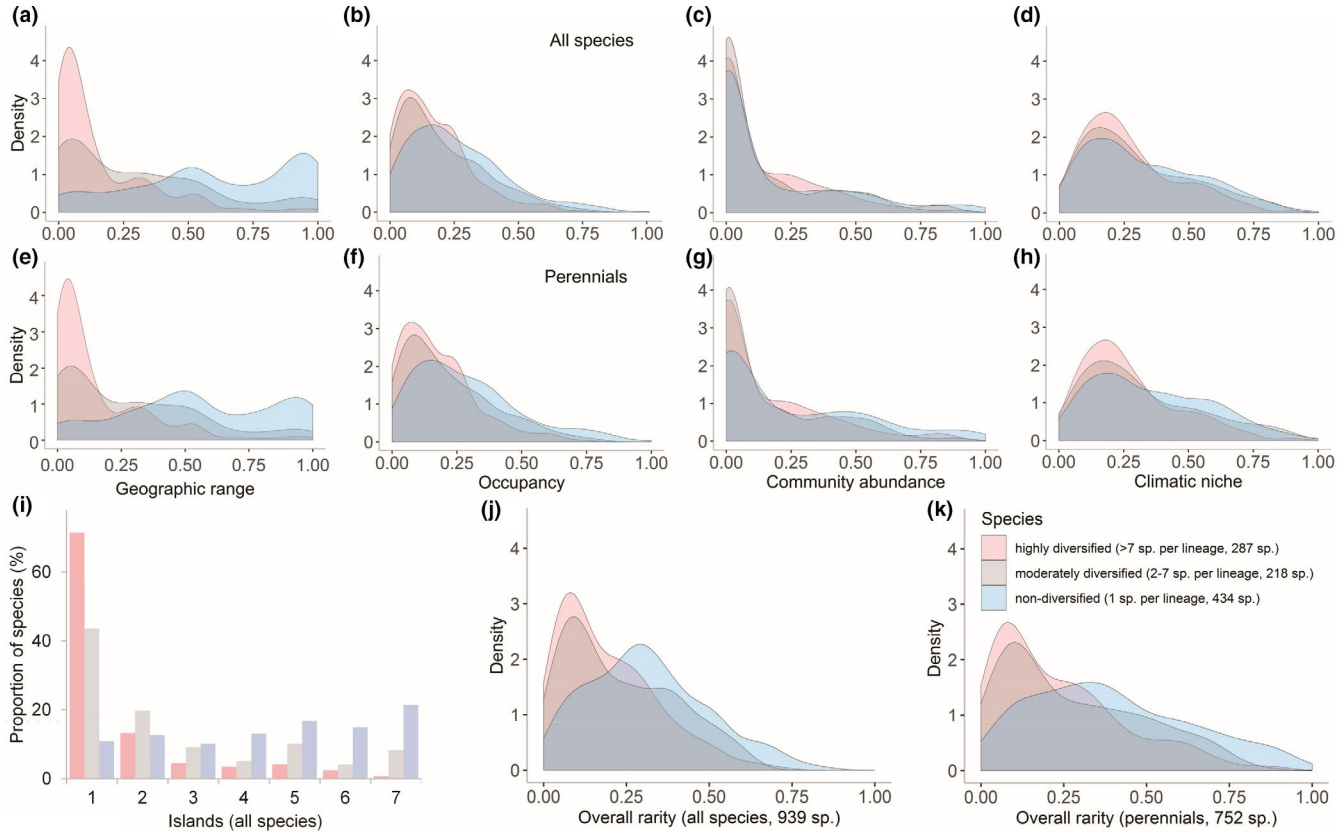

FIGURE 2 Canarian plant species distributions among five rarity parameters: geographic range (a, e), spatial occupancy (b, f), community abundance (c, g), climatic niche (d, h) and distribution among islands (i)) and overall rarity (mean value a-d and e-h, while a, b and e, f weighted 0.5). All species (panels a, b, c, d, i, j), and perennials only (e, f, g, h, k). Density plots generated with Gaussian kernel smoothing, where the total area under the curve integrates to one. Community abundance and occupancy values were transformed (log, square root) to improve visual comparison. Community abundance refers to the maximum cover a species obtains among all plots of one of the six selected METs. See Table S2 (and Methods) for statistical tests of group mean differences

Combining mean values of geographic range (weight 0.5), spatial occupancy (0.5), local abundance (1), and climatic niche (1) into a composite rarity index, we find that overall rarity also increases with the degree of diversification (Figure 2j,k, Table 2): the highly DLs are strongly skewed towards rarity, while the NDLs have a broad unimodal distribution encompassing the ecologically most successful species. Moderately diversified lineages are bimodally distributed, nonetheless tending to intermediate rarity. The distinction between DL and NDL species is enhanced when only perennials are considered (Figure 2a–h, Table 2).

3.3 | Community dominance

To further evaluate Rabinowitz's (1981) community abundance axis, we examined the relative dominance of diversified lineages within each of six METs. Four constitute the core Canarian habitats, originally covering 93% of the archipelago: (a) extensive coastal *Euphorbia* scrub, (b) the now much-depleted low-elevation thermophilous woodlands, (c) mid-elevation laurel forest, and (d) upper-elevation pine forest (Figure 3). The other two, much less extensive habitats, are (e) zonal summit scrub (restricted to the three highest islands), and (f) azonal rock communities, constituted by steep terrain of low vegetation cover.

At both archipelagic and island level, the communities of each of the four core METs are dominated by NDL species, with DL species providing <25% cover (range among habitats and islands: 8–33%) and showing lowest cover values for laurel forest and highest for thermophilous woodlands. DL species, although constituting 54% of the entire archipelagic native flora, are only abundant in the two rare METs: comprising 84% cover (range per island: 72–90%) of rock communities (4.3% of the archipelago area) and 73% cover (range 62–80%) of high mountain scrub (2.4% of the archipelago area) (Figure 3, Table 3).

Generalized linear mixed model (GLMM) showed that elevation and slope had a strong positive effect and tree cover a negative effect on abundance of species of diversified lineages in vegetation plots (Figure 4, Table S2). The GLMM also showed a (weak) humped relationship with the geological age of the island (i.e. time for speciation).

To test the "refuge hypothesis" that the high number of DL species in rock communities is ecologically equivocal, being the result of human disturbance, we applied non-parametric Wilcoxon tests which showed that non-native species are not

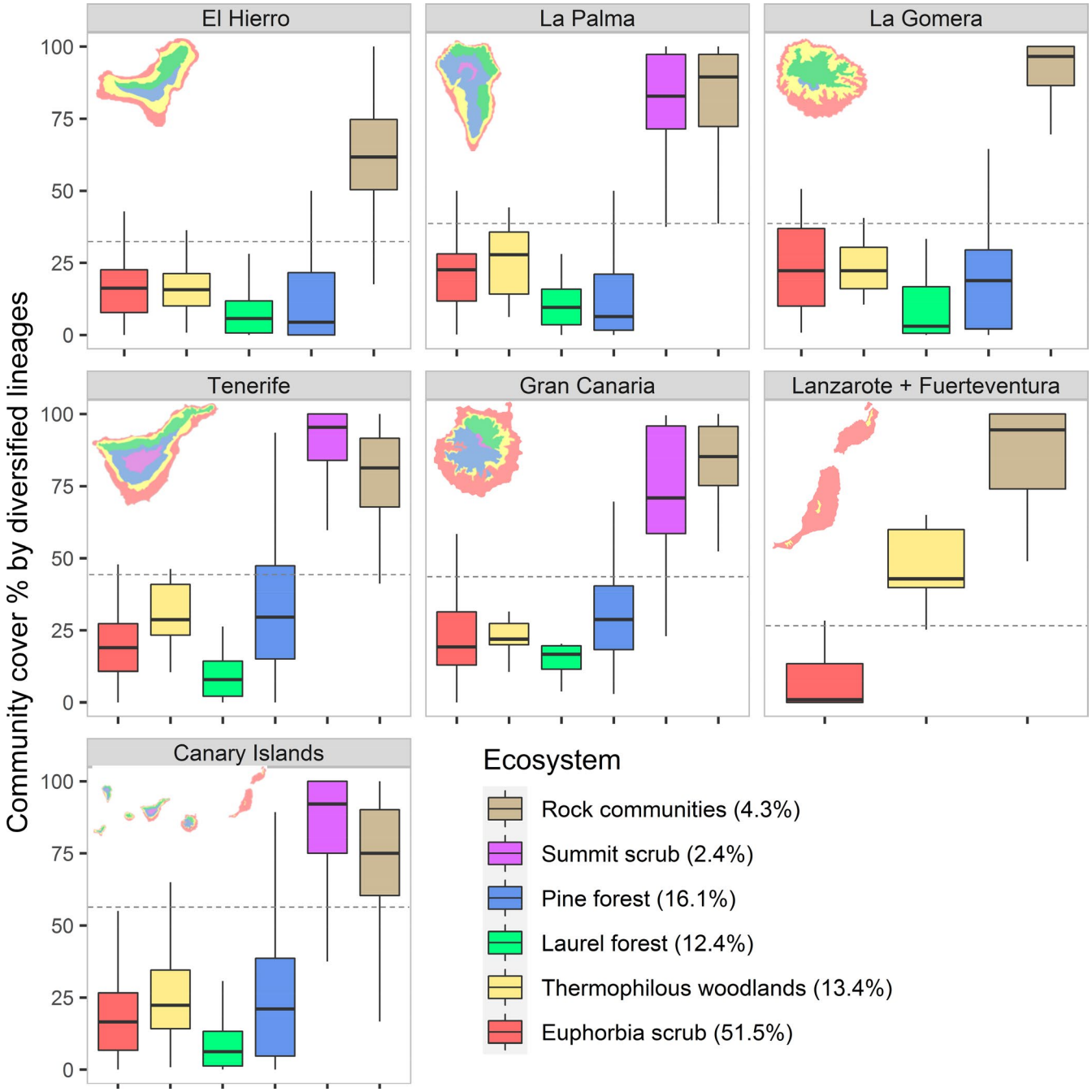

FIGURE 3 Importance of diversified plant species in community cover among Canarian major ecosystems types and islands. Dotted lines indicate the proportion of diversified species in the island/archipelago species pool. The METs are represented in each island map according to del Arco et al. (2010), with the exception of the rock communities, which may be found at any elevation. The proportion (%) of area for each MET across the whole archipelago is indicated in the legend. Boxplots represent the relative cover of diversified species in vegetation plots of each community. All communities revealed significantly lower or higher levels than expected by species pool proportions (see Table 3). Data for Lanzarote and Fuerteventura were merged because they formed a single island (Mahan) during extensive low-sea-level stands during the Pleistocene glacial periods

more common and threatened species are not less common in zonal ecosystems (*Euphorbia* scrub, thermophilous woodlands, laurel forest, pine forest, summit scrub) compared to rock communities (Proportion of non-native species per plot on all Canary islands: cover, Wilcoxon W = 249140, p = 0.819, number, W = 254140, p = 0.4; proportion of threatened species per plot on Tenerife: cover, W = 22912, p = 0.654; number, W = 22962, p = 0.706).

4 | DISCUSSION

The enigmas of oceanic island floras have long intrigued island biogeographers. Writing over 150 years ago, about the floras of Macaronesia, Joseph Dalton Hooker (1867) observed in respect to Madeira that "…the plants identical with those of Europe are both the most numerous in species, and the species are most numerous in individuals; then come the varieties – some are less scarcely

TABLE 3 Results of bootstrap tests comparing the contribution (plot cover%) of Canarian plant species of diversified lineages to community structure (CDC) with the proportion of the same species group in the island/archipelago species pool (PSP; %). 99.9% confidence intervals with lower and upper bounds of the cumulative probability distribution of the 10,000 bootstrapped mean values of the random samples of CDC are shown. If the interval of CDC is below or above PSP, then species of diversified lineages are under- or overrepresented in the local community (Lanzarote and Fuerteventura are combined as "Mahan" for analysis: see text for explanation).

		El Hierro		La Palma		La Gomera		Tenerife		Gran Canaria		Lanzarote and Fuerteventura		Canary Islands	
Species pool (%)		32.6		36.7		37		42.8		39.7		24.3		53.8	
Plot cover (%)	**n**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**	**Lower**	**Upper**
Euphorbia scrub	397	12.1	18.2	17.0	30.9	12.9	33.6	16.0	24.2	16.7	33.0	4.9	19.7	16.0	21.0
Thermophilous woodlands	160	11.2	18.1	18.6	32.3	16.4	31.2	19.6	41.2	17.7	30.5	36.3	59.8	21.0	29.2
Laurel forest	370	5.4	8.1	6.4	14.2	4.4	16.3	6.7	14.5	3.8	20.3	-	-	7.4	10.5
Pine forest	478	5.5	12.7	6.5	14.0	9.6	29.3	27.6	37.6	23.6	36.3	-	-	21.5	27.7
Summit scrub	259	-	-	62.6	84.3	-	-	84.6	91.7	54.5	89.3	-	-	79.4	87.9
Rock communities	337	50.5	62.0	69.0	89.3	73.5	99.9	69.8	80.3	76.3	90.8	63.4	96.2	69.8	77.0

perceptibly different from European plants, others constantly, and these are less numerous and less common. Then come the distinct species; of these some would be called varieties by many botanists, and others good species by all; these are still less common." Later in the article he noted: "The lofty mountains of the Canaries, though upwards of 11,000 feet high, contain no alpine plants, and as in the case of the Madeiran group, many of the most peculiar forms are extremely rare and local." Here, for "peculiar" we would today write "endemic." Summing up for the Atlantic islands as a whole Hooker stated "As a general rule, the species of the mother continent are proportionally the most abundant, and cover the greatest surface on the islands. The peculiar species are rarer, the peculiar genera rarer still." These excerpts serve to highlight that Hooker was aware of and thought noteworthy the existence of relationships between biogeographical distribution and local rarity that we quantify here and which we show to be related to in situ cladogenesis.

4.1 | Is rarity cause or consequence of diversification?

While the localized distribution of many island endemic plant species is well known (e.g. Barquín & Voggenreiter, 1988; Brochmann et al., 1997; Hooker, 1867; Price & Wagner, 2004), this is the first empirical demonstration that evolutionary winners are ecological losers using multiple dimensions and quantifications of rarity for the entire flora of an oceanic archipelago. This finding raises the further question: is diversification a cause or a consequence of rarity? If most DL species (evolutionary winners) are comparatively young, evolving within a rich flora, the new species may have had less time and opportunities to spread and become abundant compared to the early colonizers: implying species rarity as a consequence of diversification. Rare species inhabiting stressful habitats (ecological losers) may face low competition from other species and/or may diversify because they occur in patchy habitats with small, isolated populations that have limited between-patch genetic flux: implying diversification as a consequence of species rarity. A reciprocal interplay, whereby diversification is both a cause and consequence of different forms of rarity may reinforce the effects of these processes, as has been posited for the Hawaiian flora (Price & Wagner, 2004) and demonstrated for Samoan and Hawaiian National Parks, where local abundance is lower for species in larger lineages (Ibanez et al., 2021). In the Canaries, the direction of causality appears to vary among zones.

4.2 | Diversification and habitats

The lowland METs (Figure 3) have been filled mostly by colonization of NDL species from nearby NW Africa (including the so-called Rand Flora palaeoendemics: *Campylanthus*, *Ceballosia*, *Justicia*, *Kleinia*, *Neochamaelea*, *Plocama* (Pokorny et al., 2015)) or more recent colonizers, such as *Euphorbia balsamifera* or *E. canariensis* and, in some cases but mostly within the understory, by *in situ* radiation (*Argyranthemum*, *Lavandula*, *Sonchus*, *Euphorbia* sect. *Aphyllis*). By

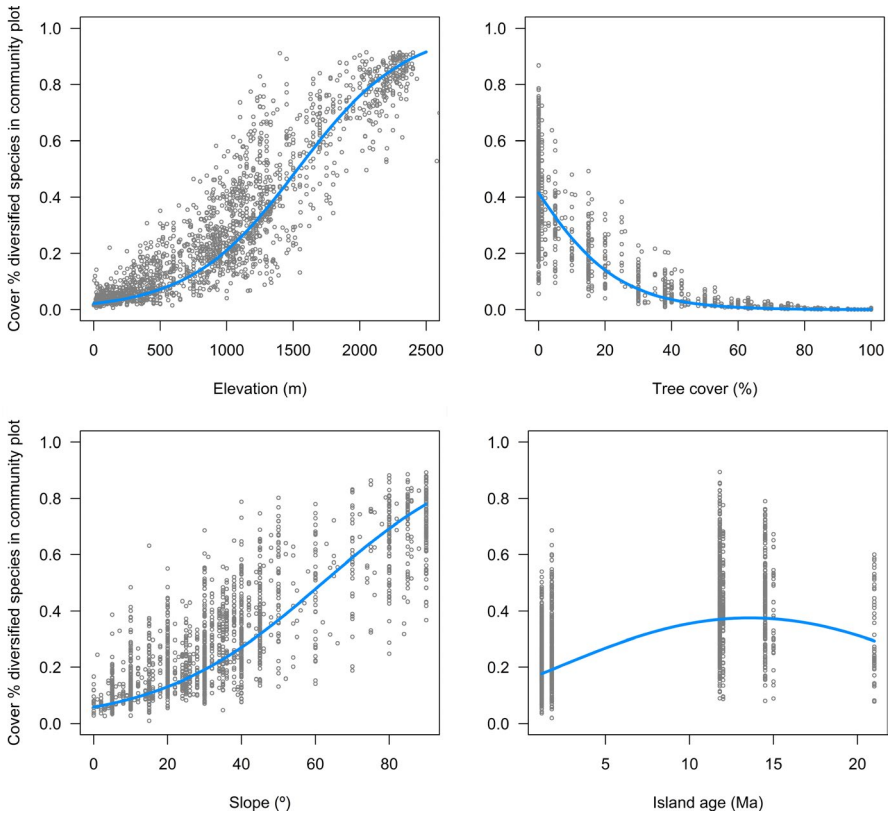

FIGURE 4 Partial residuals of a generalized linear mixed model with relative cover of species of diversified lineages in Canarian plant communities (plot cover %) as a function of plot elevation, tree cover, slope and island age (with a quadratic term) and island as a random factor (Model: number of plots = 1839, marginal R^2 = 0.77). The model is plotted on the scale of the original response after applying the inverse link function

contrast, the thermophilous woodlands (Figure 3) are a comparatively young MET of largely Mediterranean origin, dominated by NDL tree species (*Juniperus*, *Olea*, *Phoenix*, *Pistacia*) that probably colonized the archipelago contemporaneously or even later than the DL species found in the understory (*Hypericum*, *Globularia*). The dominant trees all have good dispersal abilities (mainly endozoochorous), showing wide distribution ranges and considerable genetic flux between island populations (*Olea*, *Phoenix*) (García-Verdugo et al., 2010), thus accounting for their limited *in situ* diversification.

Based on biogeographic and palaeogeographic studies (Fernández-Palacios et al., 2011), Canarian laurel and pine forests can be considered relict ecosystems (palaeo-habitats). Although high levels of diversification in arthropods and molluscs have been reported within these METs (Fernández-Palacios et al., 2019; Machado et al., 2017), especially in the laurel forests, strikingly, there is almost no signature of in situ plant diversification in these forests (Figure 3). When forest canopies are closed, especially within the laurel and humid pine forests, the canopy layer almost entirely comprises NDL species, the so-called Tethyan-Tertiary palaeoendemic trees: *Apollonias*, *Ilex*, *Laurus*, *Ocotea*, *Persea*, *Prunus*, *Visnea*, etc. in the laurel forest, or *Pinus canariensis* in the pine forest. We do not rule out plant diversification in older habitats, but suggest that this may have occurred predominantly within patchy open spaces, typically linked to steep slopes, where competition for resources is not that intense and species find ecological opportunity to diversify. This has been indicated as the possible origin of the so-called caulirosette habit group of opportunistic endemic species (Capelo et al., 2007; Fernández-Palacios et al., 2019), including *Echium pininana*, *Euphorbia mellifera*, *Hypericum fruticosum*, *Isoplexis* spp. or *Musschia wollastonii*, which thrive in Macaronesian laurel forest canopy gaps and belong to diversified lineages. Only in the open pine forests towards the upper elevations, do we find slightly elevated cover of some understory genera (*Cistus*, *Lotus*, *Micromeria*) that have diversified, although this is not evident in average cover values but in data distribution characteristics (note the boxplot widths in Figure 3).

Finally, the summit scrub seems an exception since it is the only zonal ecosystem dominated by DL endemics (Figure 3). Insular high mountains (sky islands), are known to be hotspots of endemism (Steinbauer et al., 2016). These habitats are ephemeral, very scarce and isolated in time and space with respect to environmental conditions and source regions (Fernández-Palacios et al., 2014). It is not colonization by pre-adapted species from similar environments from the mainland, but *in situ* speciation from sources originating at lower elevations that has dominated community assembly of the summit scrub. Although an azonal ecosystem and thus located across the elevational gradient, the rocky cliffs MET is consistently (and across all seven islands) characterized by DL species such as *Aeonium* and *Sonchus*, which dominate both species lists and community cover. These habitats, products of local erosion processes, are characterized by geomorphological dynamism and lack of soil: they are environmentally harsh and typically feature low levels of vegetation cover.

4.3 | Biogeographic and ecological aspects of diversification

Our findings challenge previous claims of niche pre-emption (Silvertown, 2004) or priority effects (Shaw & Gillespie, 2016), which posit that

lineages that colonize islands earlier have more possibilities to occupy space, diversify and potentially to dominate communities than those arriving later. But we need to distinguish the different METs in summarizing the key emergent outcomes. In general, it appears that the early-arriving (Miocene-Pliocene period) sub-tropical forest colonists became ecologically dominant, widespread and persistent: the large size, long life-spans, effective dispersal ability and tendency towards vegetative regeneration of the dominant trees have led to minimal *in situ* diversification in both laurel and pine METs (palaeo-habitats). By contrast, summit scrub and rock communities can be considered evolutionary young, *in situ* generated ecosystems (neo-habitats), filled with spectacular radiations, mostly within later-arriving lineages. Most of these diversified plant lineages are relatively young (crown ages 2.1 ± 2.4 Ma (García-Verdugo et al., 2019) compared to the age of the present emerged archipelago (21 Ma). This is consistent with the geodynamism and hence young biological age of the high elevation environments of Gran Canaria and especially Tenerife (effectively late-Pleistocene).

It is the open, steep rock habitats that have been the centres of Canarian plant speciation over the last few millions of years. Similar patterns have been reported for the Balearic archipelago, Iberian Peninsula, French Mediterranean region and Greek Islands, where endemics with small ranges preferentially occupy open, stressful habitats in which competition is relatively low (Buira et al., 2020; Kontopanou & Panitsa, 2020; Lavergne et al., 2004). This supports the idea that the availability of patchy ecological opportunities encourages diversification (Stroud & Losos, 2016). In the Canaries, rock communities are patchy in space and time and are distributed among all main ecosystems, covering the whole elevation gradient. They thus provide a network of ephemeral spaces across topographically complex landscapes encompassing diverse climatic conditions, permitting geographic and reproductive isolation, which drives speciation (Otto et al., 2016).

The successful diversification in the Canarian flora has mostly involved shrub life-forms (Lens et al., 2013). Moreover, several of the largest radiations involve the classic island pattern of continental herbaceous ancestors producing clades containing several derived (cladogenetic) woody descendants, often involving multiple evolutionary transitions (Lens et al., 2013). The origin of the secondary woodiness within the Canary flora is still debated, but might be related to the rocky, open, relatively competition-free habitats and the dominant Mediterranean climate (see e.g. Frankiewicz et al., 2020; Lens et al., 2013; Whittaker & Fernández-Palacios, 2007).

An alternative explanation is that the high number of DL species in rock communities is ecologically equivocal, being the result of human disturbance (refuge hypothesis). However, further analysis (Table S3) did not support this interpretation, as the core zonal ecosystems did not have higher cover of non-native species or fewer threatened plant species than steep rock habitats (Otto et al., 2016).

5 | CONCLUSIONS

We have shown that DL species, endemic products of within-archipelago diversification, are mostly rare in all three rarity axes (sensu Rabinowitz, 1981) and typically do not play an important role in structuring plant communities on the Canaries. It appears to be the rocky, high elevation, marginal and ephemeral habitats that have fostered much of the *in situ* diversification. Compared to NDL species, cladogenetic endemics show higher levels of rarity in geographic range, habitat affinity and local community abundance, which alongside other island plant syndromes (Burns, 2019) make them more susceptible to human extinction drivers such as habitat loss and alterations or climate change (Otto et al., 2017).

Only further research can establish the generality of the patterns we describe here. However, we consider that they will not be unique to these Macaronesian archipelagos and we postulate: evolutionary winners are *typically* ecological losers among island plants.

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DATA AVAILABILITY STATEMENT

Vegetation inventory data of the phytosociological associations assigned to the six major ecosystem types for each of the Canary Islands were obtained from the webpage "Sistema de Información de la Vegetación Ibérica y Macaronésica" (http://www.sivim.info/sivi/). The distributions of the Canarian native vascular plant species were obtained from the Canarian Government "Biodiversidad Canaria" webpage (https://www.biodiversidadcanarias.es/biota/especies). Finally, data of the Canarian meteorological stations were obtained from the "Agencia Española de Meteorología" webpage (http://www.aemet.es/es/portada). The maps of interpolated climate data and the input files for all statistical analyses are deposited in the DRYAD repository (https://doi.org/10.5061/dryad.qrfj6q5fs).Data will be released on 31th of May 2022.

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REFERENCES

Acebes Ginovés, J. R., León Arencibia, M. C., Rodríguez Navarro, M. L., del Arco, M. J., García-Gallo, A., Pérez de Paz, P. L., & Wildpret, W. (2010). Pteridophyta, Spermatophyta. In M. Arechavaleta, S. Rodríguez, N. Zurita, & A. García (Eds.), *Lista de especies silvestres*

de Canarias. *Hongos*, *plantas y animales terrestres* (pp. 119–172). Gobierno de Canarias.

Andrewartha, H. G., & Birch, C. (1954). *The distribution and abundance of animals*. Chicago University Press.

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

Barquín, E., & Voggenreiter, V. (1988). *Prodromus del Atlas Fitocorológico de las Canarias Occidentales* (volumes 1-7). Self Edition. 1316 pp.

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, *23*, 595–609. https://doi.org/10.1111/geb.12146

Borregaard, M. K., Amorim, I. R., Borges, P. A. V., Cabral, J. S., Fernández-Palacios, J. M., Field, R., Heaney, L. R., Kreft, H., Matthews, T. J., Olesen, J. M., Price, J., Rigal, F., Steinbauer, M. J., Triantis, K. A., Valente, L., Weigelt, P., & Whittaker, R. J. (2016). Oceanic island biogeography through the lens of the general dynamic model: Assessment and prospect. *Biological Reviews*, *92*, 830–853. https://doi.org/10.1111/brv.12256

Braun-Blanquet, J. (1964). *Pflanzensoziologie*, *Grundzüge der Vegetationskunde* (3rd ed.). Springer.

Brochmann, C., Rustan, Ø. H., Lobin, W., & Kilian, N. (1997). The endemic vascular plants of Cabo Verde. *Sommerfeltia*, *24*, 1–356.

Buira, A., Cabezas, F., & Aedo, C. (2020). Disentangling ecological traits related to plant endemism, rarity and conservation status in the Iberian Peninsula. *Biodiversity and Conservation*, *29*, 1937–1958. https://doi.org/10.1007/s10531-020-01957-z

Burns, K. C. (2019). *Evolution in isolation: The search for an island syndrome in plants*. : Cambridge University Press. https://doi.org/10.1017/9781108379953

Cabrera, F. (2020). Evolución de la sucesión primaria en la vegetación de costa de Cumbre Vieja en La Palma. PhD Thesis, University of La Laguna.

Capelo, J., Menezes de Sequeira, M., Jardim, R., & Mesquita, S. (2007). *Açores e Madeira. A floresta das ilhas*. In J. Silva-Sande (Ed.) (pp. 81-134). : Público.

Crawley, M. J. (2007). *The R book*. Wiley.

de Nascimento, L., Nogué, S., Naranjo-Cigala, A., Criado, C., McGlone, M., Fernández-Palacios, E., & Fernández-Palacios, J. M. (2020). Human impact and ecological changes during pre-historic settlement on the Canary Islands. *Quaternary Science Reviews*, *239*, 106322. https://doi.org/10.1016/j.quascirev.2020.106332

del Arco, M., González-González, R., Garzón-Machado, V., & Pizarro-Hernández, B. (2010). Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, *19*, 3089–3140. https://doi.org/10.1007/s10531-010-9881-2

Domínguez Lozano, F., Price, J., Otto, R., & Fernández-Palacios, J. M. (2010). Using taxonomic and phylogenetic evenness to compare diversification in two island floras. *Perspectives in Plant Ecology*, *Evolution and Systematics*, *12*, 93–106. https://doi.org/10.1016/j.ppees.2009.12.001

Emerson, B. C., & Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, *23*, 619–630. https://doi.org/10.1016/j.tree.2008.07.005

Fernández-Palacios, J. M. (1992). Climatic responses of plant species on Tenerife, The Canary Islands. *Journal of Vegetation Science*, *3*, 595–602.

Fernández-Palacios, J. M. (2016). Shaped by sea-levels shifts. *Nature*, *532*, 42–43. https://doi.org/10.1038/nature17880

Fernández-Palacios, J. M., Arévalo, J. R., Balguerías, E., Barone, R., de Nascimento, L., Elias, R. B., Delgado, J. D., Fernández-Lugo, S., Méndez, J., Naranjo-Cigala, A., Menezes de Sequeira, M., & Otto, R. (2019). *The laurisilva. Canaries*, *Madeira and Azores*. : Macaronesia.

Fernández-Palacios, J. M., de Nascimento, L., Otto, R., Delgado, J. D., García-del-Rey, E., Arévalo, J. R., & Whittaker, R. J. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography*, *38*, 226–246. https://doi.org/10.1111/j.1365-2699.2010.02427.x

Fernández-Palacios, J. M., & de Nicolás, J. P. (1995). Altitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science*, *6*, 183–190. https://doi.org/10.2307/3236213

Fernández-Palacios, J. M., Otto, R., Thébaud, C., & Price, J. P. (2014). Overview of habitat history in subtropical oceanic island summit ecosystems. *Arctic*, *Antarctic and Alpine Research*, *46*, 801–809. https://doi.org/10.1657/1938-4246-46.4.801

Frankiewicz, K. E., Oskolski, A., Banasiak, Ł., Fernandes, F., Reduron, J.-P., Reyes-Betancort, J.-A., Szczeparska, L., Alsarraf, M., Baczyński, J., Spalik, K. (2020). Parallel evolution of arborescent carrots (Daucus) in Macaronesia. *American Journal of Botany*, *107*, 394–412. https://doi.org/10.1002/ajb2.1444

García-Verdugo, C., Caujapé-Castells, J., & Sanmartín, I. (2019). Colonization time on island settings: Lessons from the Hawaiian and Canary Island floras. *Botanical Journal of the Linnean Society*, *191*, 155–163. https://doi.org/10.1093/botlinnean/boz044

García-Verdugo, C., Forrest, A., Fay, F. F., & Vargas, P. (2010). The relevance of gene flow in metatpopulation dynamics of an oceanic island endemic, *Olea europaea* subsp. *Guanchica*. *Evolution*, *64*, 3525–3536. https://doi.org/10.1111/j.1558-5646.2010.01091.x

Gaston, K. J., Davies, R. G., Orme, C. D. L., Olson, V. A., Thomas, G. H., Ding, T.-S., Rasmussen, P. C., Lennon, J. J., Bennett, P. M., Owens, I. P. F., & Blackburn, T. M. (2007). Spatial turnover in the global avifauna. *Proceedings of the Royal Society*, *Series B*, *274*, 1567–1574. https://doi.org/10.1098/rspb.2007.0236

Gillespie, R. (2004). Community assembly through adaptive radiation in Hawaiian spiders. *Science*, *303*, 356–359. https://doi.org/10.1126/science.1091875

Hooker, J. D. (1867). Insular Floras. Gardeners' chronicle and agriculture gazette, 6, 7, 27, 50, 51, 75 and 76.

Ibanez, T., Ainsworth, A., Gross, J., Price, J. P., Webb, E. L., & Hart P. J. (2021). Rarity patterns of woody plant species are associated with life-form and diversification rates in Pacific islands forests. *American Journal of Botany*, in press.

Jain, M., Flynn, D. F. B., Prager, C. M., Hart, G. M., DeVan, C. M., Ahrestani, F. S., Palmer, M. I., Bunker, D. E., Knops, J. M. H., Jouseau, C. F., & Naeem, S. (2014). The importance of rare species: A trait-based assessment of rare species contributions to functional diversity and possible ecosystem function in tall-grass prairies. *Ecology and Evolution*, *4*, 104–112. https://doi.org/10.1002/ece3.915

Knope, M. L., Morden, C. W., Funk, V. A., & Fukami, T. (2012). Area and the rapid radiation of Hawaiian *Bidens* (Asteraceae). *Journal of Biogeography*, *39*, 1206–1216. https://doi.org/10.1111/j.1365-2699.2012.02687.x

Kontopanou, A., & Panitsa, M. (2020). Habitat islands on the Aegean Islands (Greece): Elevational gradient of chasmophytic diversity, endemism, phytogeographical patterns and need for monitoring and conservation. *Diversity*, *12*, 33. https://doi.org/10.3390/d12010033

Lavergne, S., Thompson, J. D., Garnier, E., & Debussche, M. (2004). The biology and ecology of narrow endemic and widespread plants: A comparative study of trait variation in 20 congeneric pairs. *Oikos*, *107*, 505–518. https://doi.org/10.1111/j.0030-1299.2004.13423.x

Lens, F., Davin, N., Smets, E., & del Arco, M. (2013). Insular woodiness on the Canary Islands: A remarkable case of convergent evolution. *International Journal of Plant Science*, *174*, 992–1013. https://doi.org/10.1086/670259

Lesica, P., Yurkewycz, R., & Crone, E. E. (2006). Rare plants are common where you find them. *American Journal of Botany*, *93*, 454–459. https://doi.org/10.3732/ajb.93.3.454

Lomolino, M. V., Riddle, B. R., & Whittaker, R. J. (2017). *Biogeography* (5th ed.). Sinauer.

Machado, A., Rodríguez-Expósito, E., López, M., & Hernández, M. (2017). Phylogenetic analysis of the genus *Laparocerus*, with comments on colonisation and diversification in Macaronesia (Coleoptera, Curculionidae, Entiminae). *ZooKeys*, *651*, 1–77. https://doi.org/10.3897/zookeys.651.10097

Martín, J. L. (2009). Are the IUCN standard home-range thresholds for species a good indicator to prioritise conservation urgency in small islands? A case study in the Canary Islands (Spain). *Journal for Nature Conservation*, *17*, 87–98. https://doi.org/10.1016/j.jnc.2008.10.001

Martín, J. L., Zurita, N., Marrero Gómez, M. C., Izquierdo, I., Arechavaleta, M., Fajardo, S., & Valdivia, C. (2005). *El banco de datos de biodiversidad de Canarias*. Gobierno de Canarias.

Méndez, J. (2010). Análisis del impacto del fuego en la regeneración sexual del pino canario a lo largo de una cronosecuencia de incendios en la isla de La Palma (Canarias). PhD Thesis, University of La Laguna.

Otto, R., Garzón-Machado, V., del Arco, M. J., Fernández-Lugo, S., de Nascimento, L., Oromí, P., Báez, M., Ibáñez, M., Alonso, M. R., & Fernández-Palacios, J. M. (2017). Unpaid extinction debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands. *Diversity and Distributions*, *23*, 1031–1041. https://doi.org/10.1111/ddi.12590

Otto, R., Whittaker, R. J., von Gaisberg, M., Stierstorfer, C., Naranjo-Cigala, A., Steinbauer, M. J., Borregaard, M. K., Arévalo, J. R., Garzón-Machado, V., del Arco, M. J., & Fernández-Palacios, J. M. (2016). Transferring and implementing the general dynamic model of oceanic island biogeography at the scale of island fragments: The role of geological age and topography in plant diversification in the Canaries. *Journal of Biogeography*, *43*, 911–922.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*, 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Pokorny, L., Riina, R., Mairal, M., Meseguer, A. S., Culshaw, V., Cendoya, J., & Sanmartín, I. (2015). Living on the edge: Timing of Rand Flora pattern disjunctions compatible with ongoing aridification in Africa. *Frontiers in Genetics*, *6*, 1–15. https://doi.org/10.3389/fgene.2015.00154

Price, J. P., Otto, R., Menezes de Sequeira, M., Kueffer, C., Schaefer, H., Caujapé-Castelss, J., & Fernández-Palacios, J. M. (2018). Colonization and diversification shape species-area relationships in three Macaronesian archipelagos. *Journal of Biogeography*, *45*, 2027–2039. https://doi.org/10.1111/jbi.13396

Price, J. P., & Wagner, W. L. (2004). Speciation in Hawaiian angiosperm lineages: Cause, consequence, and mode. *Evolution*, *58*, 2185–2200. https://doi.org/10.1111/j.0014-3820.2004.tb01597.x

Price, J. P., & Wagner, W. L. (2011). A phylogenetic basis for species-area relationships among three Pacific islands Floras. *American Journal of Botany*, *98*, 449–459. https://doi.org/10.3732/ajb.1000388

R Development Core Team. (2009). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rabinowitz, D. (1981). Seven forms of rarity. In H. Synge (Ed.), *The biological aspects of rare plant conservation* (pp. 205–217). Wiley.

Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Oxford University Press.

Ricklefs, R. (2009). *The economy of nature* (6th ed.). Freeman & Co., Ltd.

Rijsdijk, K., Hengl, T., Norder, S. J., Otto, R., Emerson, B. C., Ávila, S. P., & Fernández-Palacios, J. M. (2014). Quantifying surfaces area changes of volcanic islands driven by Pleistocene sea level cycles: Biogeographic implications for Macaronesian archipelagos, Atlantic Ocean. *Journal of Biogeography*, *41*, 1242–1254. https://doi.org/10.1111/jbi.12336

Santos-Guerra, A. (1983). *Vegetación y flora de La Palma*. Interinsular Canaria.

Shaw, K. L., & Gillespie, R. G. (2016). Comparative phylogeography of oceanic archipelagos: Hotspots for inferences of evolutionary process. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 7986–7999. https://doi.org/10.1073/pnas.1601078113

Silvertown, J. (2004). The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, *92*, 168–173. https://doi.org/10.1111/j.1365-2745.2004.00853.x

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H. J. B., Borges, P. A. V., Cardoso, P., Chou, C.-H., De Sanctis, M., Menezes de Sequeira, M., Duarte, M. C., Elias, R. B., Fernández-Palacios, J. M., Gabriel, R., Gereau, R. E., Gillespie, R. G., Greimler, J., … Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, *25*, 1097–1107. https://doi.org/10.1111/geb.12469

Stierstorfer, C. (2005). *The vascular plant vegetation in the forest belt of El Hierro (Canary Islands)*. Cramer.

Stroud, J. T., & Losos, J. B. (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution and Systematics*, *47*, 507–532. https://doi.org/10.1146/annurev-ecolsys-121415-032254

von Gaisberg, M. (2005). *Die Vegetation der Fußstufe von El Hierro (Kanarische Inseln)*. Cramer.

Weigelt, P., Steinbauer, M. J., Cabral, J. S., & Kreft, H. (2016). Late Quaternary climate change shapes island biodiversity. *Nature*, *532*, 99–102. https://doi.org/10.1038/nature17443

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

Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. A., Borregaard, M. K., & Triantis, K. A. (2017). Island biogeography: Taking the long view of nature's laboratories. *Science*, *357*, eaam8326é. https://doi.org/10.1126/science.aam8326

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, *35*, 977–994. https://doi.org/10.1111/j.1365-2699.2008.01892.x

Zobel, M., Otto, R., Laanisto, L., Naranjo-Cigala, A., Pärtel, M., & Fernández-Palacios, J. M. (2011). The formation of species pools: Historical ecosystems commonness explain current diversity. *Global Ecology and Biogeography*, *20*, 251–259. https://doi.org/10.1111/j.1466-8238.2010.00593.x

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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