RESEARCH ARTICLE



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The late Pleistocene endemicity increase hypothesis and the origins of diversity in the Canary Islands Flora

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Abstract

Aim: We explore the idea that most pre-glacial non-endemic Canarian flora became endemic to the archipelago by the extinction of its mainland populations during the late Pleistocene glaciations, implying that the extant non-endemic flora is mostly post-glacial: the 'late Pleistocene endemicity increase hypothesis'.

Taxon: The native flora of the Canarian archipelago.

Methods: We statistically compare the distributions of 2087 Canarian endemic and native non-endemic plants across islands. We also carry out connectivity analyses using their dispersal paths, obtained by connecting all the islands of occurrence for each taxon.

Results: While the distribution of the endemic flora is strongly L-shaped (with a much higher proportion of Single-Island Endemics than Multiple-Island Endemics), that of the native non-endemics is U-shaped (i.e. similar prevalence of single-island taxa and taxa distributed on all islands). The native non-endemics have a significantly lower proportion of single-island taxa and a higher proportion of widespread taxa than the endemics. Most dispersal paths in the endemics connect the central and western islands, whereas they are extended across all islands in the native non-endemics.

Main conclusions: The contrasting distributional patterns of the endemics and the native non-endemics support an outstanding role of species diversification in the endemic flora, but a still negligible influence of the insular selective and stochastic pressures (including extinction) in the native non-endemic flora, arguably due to its recent origin. Our results suggest that the high endemicity levels of the extant Canarian flora can be explained by two complementary processes: (i) high diversification rates throughout the ontogeny of the archipelago, often from colonisers that attained a widespread distribution prior to speciation, and (ii) an 'endemicity increase' during the late Pleistocene glaciations, whereby most of the pre-glacial non-endemic Canarian flora became endemic due to the extinction of its mainland conspecific populations, thus emphasising the role of the Canaries as climatic refugia.

KEYWORDS

Canarian native Flora, climatic debt, conservation, distributional analyses, endemicity increase, late-Pleistocene glaciations, network connectivity

1 | INTRODUCTION

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Oceanic island systems offer analytical advantages over continental settings for reconstructing patterns of biotic assembly (i.e. small size, discrete geographical boundaries, geographical isolation), and they have frequently been deemed 'nature's test tubes' (Losos & Ricklefs, 2009). In geologically ancient archipelagos, the joint contribution of biotic and abiotic factors acting over a relatively small species number during the ontogeny of the islands, together with anthropogenic disturbance in more recent times, has increased the role of stochasticity in the composition and distribution of their biotas (e.g. Price & Clague, 2002). New integrative hypotheses on the assembly and evolution of insular floras have been posited recently, stimulated by the access to 'big data' (i.e. large-scale geographic and genetic datasets) and by multidisciplinary collaboration (e.g. Barajas-Barbosa et al., 2019; Caujapé-Castells et al., 2017; García-Verdugo et al., 2017; Schrader et al., 2021; Stuessy et al., 2014). These hypotheses highlight the complexity of insular assembly patterns, and the need to consider both stochastic (genetic drift, extinction, dispersal) and adaptive processes (colonisation of new habitats) in reconstructing the biogeographical history of insular biotas (Barrett & Schluter, 2007; Hoffmann & Sgrò, 2011; Morente-López et al., 2021; Price & Clague, 2002).

Molecular phylogenetic analyses have facilitated insight into the relationships among many insular endemics, and their evolutionary patterns and tempos (e.g. Curto et al., 2017; Kim et al., 2008; Romeiras et al., 2015). However, the usefulness of molecular phylogenies to inform colonisation patterns of insular biotas is limited at present because the DNA sequences employed usually do not contain enough polymorphism (especially in plants). Furthermore, in many oceanic island systems, the existing phylogenetic data are often restricted to a few DNA regions and focused on large radiations consisting of many Single Island Endemics (SIE; Williams et al., 2015; Curto et al., 2017; García-Verdugo et al., 2017; Jaén-Molina et al., 2020). By contrast, endemic species that show widespread distributions across an archipelago (Multiple Island Endemics, MIE) are typically underrepresented, or overlooked. Even less explored are species that are native to an archipelago but not endemic, that is, single or multiple island non-endemic species (SINE and MINE), that also comprise populations in the mainland (García-Verdugo et al., 2021; Kimura et al., 2022; Navarro-Pérez et al., 2015). Recently, our ability to reconstruct patterns of colonisation and diversification in insular organisms is improving significantly thanks to the use of genomic approaches (Mort et al., 2015; Villaverde et al., 2018). While we wait for these genetic data to accumulate and offer a clearer picture of phylogeographical patterns, several floristic distribution databases already provide valuable information to explore hypotheses on biotic assembly and insular evolution (e.g. Otto et al., 2016; Torre et al., 2019). One of them is the Biodiversity data bank of the Canary Islands (BIOTA, https://www. biodiversidadcanarias.es/biota/; see Methods).

The Canary Islands are an oceanic insular hotspot that belongs to the Macaronesian region and lies very close to the African mainland (Figure 1). The archipelago is formed by both very old (23 My) and very young (c. 1.1 My) islands (van den Bogaard, 2013) that harbour an endemic flora of more than 600 taxa (Martín et al., 2001). This flora is highly diverse taxonomically and genetically (Caujapé-Castells et al., 2017), and encompasses both relict and more modern lineages (Vargas, 2007). Inspired by the seminal works of Jaccard (1907) or Sørensen (1948), several authors have investigated the distributional patterns of Canarian and Macaronesian plant endemics to gain insight on the origin and assembly of their rich floristic diversity (e.g. Carine et al., 2009; Fernández-Palacios & Andersson, 1998; Humphries, 1979; Sunding, 1979; Torre et al., 2019).

Humphries (1979) was the first to analyse the distribution of the Canarian endemic SIE and MIE across islands. He found a strongly left-skewed (L-shaped) pattern, indicating that SIE are much more frequent than MIE. Humphries (1979) pointed out that this finding was closely related to the great ecological diversity of the Canaries, which imposes strong selective pressures on colonising taxa and results in large radiations of isolated, reproductively compatible species. Similar hypotheses have also been posited in other archipelagos by subsequent authors (Givnish, 1997, 2015; Losos & Ricklefs, 2009).

Paleoclimatic reconstructions indicate that the floras of regions with biogeographical links with the Canaries (e.g. Mediterranean Basin, southern Europe, northwest Africa) were affected by severe climatic events (Quézel, 1978). Because of their purported climatic stability during the Late Tertiary (Mairal et al., 2015; Maley, 1980; Rodríguez-Sánchez et al., 2009), the Canaries have often been considered as refugia for lineages that went extinct in the mainland during



FIGURE 1 Map of the Canarian archipelago in the Macaronesian region (1: Azores, 2: Madeira, 3: Canaries, 4: Cape Verde). Numeric values are estimated ages of the islands in My, according to van den Bogaard (2013). Note that Mahan is the single volcanic building to which Fuerteventura and Lanzarote belong. In the current geography of the Canaries, Fuerteventura and Lanzarote are separated by 11 km of sea through La Bocaina straits these highly adverse climatic episodes (Axelrod & Raven, 1978; Quézel, 1978; Sunding, 1979). Starting ca. 120 Kyr and ending ca. 23– 18 Kyr, the glacial and interglacial cycles of the late Pleistocene likely brought about the extinction of many of the continental populations that acted as diversity pools for the colonisation of the Canaries and other Macaronesian archipelagos (Hewitt, 2004). This suggests that many pre-glacial native non-endemic colonisers of the islands became Canarian endemics solely due to the extinction of their conspecific mainland populations. Exceptions are the taxa that colonised the islands before the glaciations and survived in mainland refuges (García-Aloy et al., 2017; Nieto-Feliner, 2011), and those that backcolonised the mainland from the Canaries (Caujapé-Castells, 2004, 2011; Durán et al., 2020; García-Verdugo et al., 2021).

These considerations suggest a 'late Pleistocene endemicity increase hypothesis' ('LPEIH' hereafter, represented in Figure 2) to help explain the high extant plant endemicity in the Canary Islands, which brings up a potentially important and so far not explicitly considered impact of the Pleistocene glaciations in the composition of this archipelago's flora. If the posited signature of the late Pleistocene mainland extinctions remains in the present composition of the Canarian flora, we would expect to observe significant differences between the distribution patterns of the endemic and the native non-endemic floras.

If the LPEIH holds, then the native non-endemic flora would be very recent (mostly post-glacial) so that the influence of extinction on its Journal of Biogeography WILEY

elements should be negligible in comparison with most of the endemic flora, which would be older overall and would have undergone for a much more prolonged time the insular selective and stochastic processes that fuel diversification, and to a greater number of SIE (García-Verdugo et al., 2015; Givnish, 1997, 2015; Humphries, 1979). Therefore, the most important evolutionary force acting so far on the native non-endemic flora would have been the recurrent inter-island dispersal and gene flow processes described for the Canaries (Caujapé-Castells, 2010; Caujapé-Castells et al., 2017; Curto et al., 2017; García-Verdugo et al., 2019; Hooft van Huysduynen et al., 2021; Jaén-Molina et al., 2020; Linder, 2008). Under these premises, we would expect that the native non-endemic flora had fewer single-island taxa and more widespread taxa than the endemic flora, fitting a distribution model similar to Figure 3a,b, or d.

If the LPEIH does not hold, then the native non-endemic flora would be relatively old. In this case, despite inter-island dispersal, its prolonged exposure to the insular selective and stochastic processes would have promoted a great number of extinctions (or endemisations) in many islands, resulting in a high proportion of SINE and a low proportion of widespread MINE. Thus, we would expect that the distribution of the native non-endemic flora was similar to that of the endemic flora (Figure 3e or f).

In addition to these spatial patterns, the LPEIH predicts predominantly pre-glacial colonisation times for the endemic flora, but mostly post-glacial colonisation times in the native non-endemic flora. This prediction may be tested using the available molecular dating



FIGURE 2 Schematic representation of the late Pleistocene endemicity increase hypothesis. (1) Pre-glacial Canarian endemic and native non-endemic floras evolve subjected to the same insular selective and stochastic conditions, but recurrent gene flow with the mainland prevents diversification in many native non-endemics. (2) Throughout the late Pleistocene glacial periods, the hypothesised endemicity increase of the Canarian flora takes place, as most pre-glacial native non-endemics become endemics due to the extinction of their mainland conspecific populations, save for some representatives of mainland lineages that survived in mainland refugia (white circles, see also Introduction). (3) After the late Pleistocene glacial native non-endemics colonise the vegetation areas where extinction had occurred, gene-flow with the Canaries is re-established, and post-glacial native non-endemics colonise the islands; many of them become widespread without differentiating, due to the recentness of these colonisations. For clarity, we only represent mainland extinction during the glaciations, but not extinction, secondary contact and introgression on the islands (see Caujapé-Castells et al., 2017 for further detail), or back-colonisation from the Canaries to the mainland



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FIGURE 3 Basic distributional trends for the native nonendemic Canarian flora (dashed lines) with respect to the expected L-shaped distribution of the endemic Canarian flora (solid line, after Humpries, 1979). In parentheses, we note the corresponding relationships between the proportions of SIE and SINE, and of widespread MIE (W-MIE) and widespread MINE (W-MINE). Asterisks indicate the distribution shapes that would support the LPEIH (see Introduction)

estimates for many Canarian plants, although they are still very scarce in the non-endemic native flora, and often associated with large uncertainty (García-Verdugo, Caujapé-Castells & Sanmartín, 2019).

In this study, we compare the distribution curves of the endemic and non-endemic floras using the detailed information on Canarian plant distributions contained in the BIOTA data portal to examine the support for the 'late Pleistocene Canarian endemicity increase hypothesis'. We also carry out network connectivity analysis (based on the routes traced by connecting all the islands of occurrence for each taxon) to better understand the spatial processes explaining their diversity, and the role of inter-island dispersal within the archipelago. Such comparisons provide a unique opportunity to gain insight into preradiation conditions in insular floras (Caujapé-Castells, 2004; Caujapé-Castells et al., 2017), because the native non-endemic taxa have not yet undergone the geographical isolation and diversification processes leading to endemisation, but they are otherwise subjected to the same insular stochastic and adaptive processes affecting island endemics.

2 | MATERIALS AND METHODS

2.1 | Data sources

The Biodiversity Data Bank of the Canary Islands (BIOTA henceforth, https://www.biodiversidadcanarias.es/biota/) is an information resource created by the Canarian Government to assemble all known distribution data of species across the archipelago. With more than 17,000 records of terrestrial taxa of flora and fauna (of which c. 3000 are vascular plants), it represents the most complete database on the composition and abundance of the Canarian Flora per island of distribution, and it incorporates increasingly precise abundance and taxonomic data, which are validated by expert researchers. Importantly, it allows for a reliable distinction among endemics, native non-endemics, and introduced and invasive taxa (File S1). Despite some existing caveats (File S1), BIOTA is fast becoming a widely used research tool to address unresolved questions in the study of the Canarian biodiversity (e.g. Irl et al., 2020; Patiño et al., 2017; Steinbauer et al., 2016). Therefore, this exhaustive database is likely the most reliable information source to substantiate the needed statistical comparisons between the distributions of endemic and native non-endemic Canarian flora.

We extracted the information on the distribution of all endemic and native non-endemic plants contained in BIOTA. The levels of precision employed for retrieving the data were from 1 to 4 (see https:// www.biodiversidadcanarias.es/biota/manual/Manual.pdf, only in Spanish). These encompassed from 'maximum precision' (precision level 1, i.e. records of occurrence with very detailed observations and/ or herbarium collections ascribed to guadrats of 500×500 m), to 'minimum precision' (precision level 4, i.e. more general records referred to one or various islands, without concrete geographical data beyond the presence on a given island). The details on the territories and data extraction and the assumptions made are given in File S1. Several records had to be removed from the analyses because no information was available about their insular distributions in the archipelago. The taxa obtained were classified according to four categories: SIE (Single-Island Endemics), SINE (Single-Island Non-Endemic Native taxa), MIE (Multiple Island Endemics) and MINE (Multiple Island Non-Endemic Native taxa). Within MIE and MINE, we distinguish ubiquitous taxa (i.e. those recorded in all the islands of the archipelago) from the rest.

From the resulting lists, we obtained the number of SIE, SINE and the number of multiple-island taxa shared exclusively by all possible combinations of n = 2 islands through n = 6 islands (see File S2). We also counted how many taxa, genera and families were represented in each distributional class for both endemic and non-endemic native

2.2 | Spatial distribution patterns and connectivity analyses

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To assess whether there are differences in the distribution of plants (and, separately, only Spermatophyta), we calculated and plotted the frequencies of each distributional class overall in the archipelago. All calculations were carried out for plant MIE and MINE independently, always excluding introduced and invasive species (see above). The Kolmogorov–Smirnoff statistic was calculated using XLSTAT© v. 2009.1.01 to test the differences between the frequency distributions of endemic and native non-endemic plants.

The distributions of endemic and native non-endemic plants were compared using the Index of Concentration at the Extremes (*ICE*, Krieger et al., 2018 and references therein), which in this case quantifies how the taxa in the Canarian flora are concentrated into the extremes of their insular distributions (SIE and SINE vs. ubiquitous MIE and MINE). The formula of the *ICE* is:

$$ICE_i = \frac{\left(E_i - U_i\right)}{T_i}$$

where

- E_i is the number of island-exclusive (SIE or SINE) taxa in category i;
- U_i is the number of ubiquitous taxa (MIE or MINE) in category *i*;
- T_i is the total number of taxa in category i.

The designation 'category' depends on the level of analysis and may refer to each island, or to sub-categories of interest (e.g. 'endemic taxa' or 'native non-endemic taxa' within a given family, see File S2). The possible value ranges of this parameter are -1 < ICE < 1, where high negative values indicate a J-shaped distribution (prevalence of ubiquitous taxa), values close to zero indicate a U-shaped distribution (prevalence of the extreme distributional classes), and high positive values indicate an L-shaped distribution (prevalence of island—exclusive taxa). The ICE was also calculated within each of the 47 Spermatophyta families where it could be estimated for both the endemic and the non-endemic subsets, and for the eight families that concentrate most taxa in the Canarian flora.

To spatially characterise within-archipelago colonisation patterns and explore eventual differences between non-ubiquitous MIE and MINE, the multiple-island migration paths were retrieved from the numbers of exclusive sharings of taxa among all possible combinations of islands (File S2, Figure S7). For the purposes of the paper, a migration path (or dispersal path) is any route in the archipelago that can be traced by connecting the islands where each of the taxa analysed is distributed. The *Z*-score parameter (Guimerà & Amaral, 2005) was used to estimate the 'network connectivity' of each island (Z_i), which in our case measures how well connected each island is to other islands in the archipelago. The formula for Z_i is:

$$Z_i = \frac{\left(k_i - \overline{k}\right)}{\sigma^2 k}$$

where

- k_i is the number of links of island *i* to other islands considered (computed as the total number of shared taxa between island *i* and the rest);

- \overline{k} is the average of k over all the islands;

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- $\sigma^2 k$ is the standard deviation of k.

Z-score values per island were estimated independently for MIE and MINE (and within each of these two groups for all Plantae and Spermatophyta). According to Guimerà and Amaral (2005), islands with higher Z-score values have a more important participation in the dispersal of the taxa analysed, and in the archipelago's connectivity structure, which can range from totally centralised (i.e. high Z-values are concentrated in only one or a few islands) to totally decentralised (i.e. all islands have similar connectivity).

3 | RESULTS

We analysed the distributions of 2087 Canarian plant taxa (species and subspecies) for which the data in BIOTA were most reliable (682 endemics and 1405 native non-endemics, of which, respectively, 672 and 831 were Spermatophyta). Figure 4 shows the distribution of endemics and non-endemic native species in the archipelago (see also File S2). The SIE represent 62.5% of all Canarian endemic plants (63.1% of Spermatophyta), and the ubiquitous MIE only 5.3% (5.1% of Spermatophyta). The SINE and the ubiquitous MINE are almost equally prevalent in the non-endemic native flora, representing, respectively, 22.5% and 24.6% of all plants (21.2% and 28.6% of Spermatophyta) with a slight excess of ubiquitous taxa. In Spermatophyta, the MINE contained c. 10-fold more ubiquitous taxa than the MIE (respectively, 238 vs. 34, Table 1); the proportion of ubiquitous MINE per island was also much higher than that of SINE and non-ubiquitous MINE (File S2).

The average ICE for endemic taxa indicates that their distribution is strongly L-shaped (ICE = 0.573 and ICE = 0.580 for all plants and only Spermatophyta, respectively; see Figure 4 and File S3). In contrast, the average ICE for non-endemic native taxa indicates a U-shaped distribution (ICE = -0.018 and *ICE* = -0.075 for all plants and Spermatophyta, respectively), albeit with a small prevalence of ubiquitous MINE that makes it slightly J-shaped (between Figure 3b, d). These differences were significant (Wilcoxon's test, p < 0.01) and were also detected in the eight botanical families that represent 70.5% of the Canarian endemic Spermatophyta; the average ICE per family for endemics and for native non-endemics (0.591 and -0.027, respectively) were also significantly different (Wilcoxon's test, p < 0.01, File S3 and Table S4).

The differences in the frequency distributions of the endemic and native non-endemic flora across islands of occurrence are statistically

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significant (Kolmogorov–Smirnoff's test, D = 0.259, p<0.05 for all plants and D = 0.232, p<0.1 for only Spermatophyta; Figure 4). Such significance was attributable to the differences between the two most extreme distributional classes, as the test was non-significant when excluding island-exclusive and ubiquitous taxa from the comparisons.

The analysis of data considering seven islands in the archipelago (i.e. with Fuerteventura and Lanzarote as individual islands rather than as parts of Mahan, the single insular edifice that they belong to) gave very similar results (File S2).

In Spermatophyta, the number of genera and families contained in each distribution class was significantly higher in the non-endemic than in the endemic flora (Wilcoxon's test, p < 0.05 in both cases, Table 1). Notably, the 424 SIE corresponded to 97 genera and 31 families, whereas the much lower number of SINE (176) corresponded to a much larger number of genera and families (121 and 44, respectively).

In the endemic Spermatophyta, 22 of the 97 genera represented in the SIE (Table 1) contained five or more taxa (the species-rich genera, encompassing 303 taxa overall), and 13 of these genera contained more than 10 taxa (explosive radiations). Of the remaining 76 genera with less than five taxa, 42 had only one taxon represented in the SIE. Within the SINE, only two of the 121 genera of Spermatophyta (Table 1) contained five or more taxa (*Silene* [Caryophyllaceae] and *Ranunculus* [Ranunculaceae]). Of the remaining 119 genera, 90 contained just one SINE.

The archipelago's connectivity network was not centralised (Figure 5): Tenerife had the highest overall Z-score, but three other islands also had considerably high values of this parameter (Gran Canaria, La Palma and La Gomera, in this order; see also Table S5). In line with the expectations of the LPEIH, there were many more dispersal paths exclusive of the MINE than of the MIE (respectively, 15 and two, File S2, Figure S7), and there were more MINE in the dispersal paths shared by MIE and MINE.

4 | DISCUSSION

4.1 | Single-island taxa, ubiquitous taxa and the origin of endemic lineages

The joint detection of (i) a significant overproportion of SIE than of SINE, and (ii) a significant excess of ubiquitous MINE with respect to the MIE (Figure 4 and File S2) supports the predictions of the LPEIH.



FIGURE 4 Distributional analyses of the endemic and native non-endemic Canarian flora (only Spermatophyta). Proportions of endemic and non-endemic taxa across (a) the number of islands of occurrence (1: Island-exclusive taxa, 6: Ubiquitous taxa); and (b) single islands and all multiple-island combinations. ICE: Index of concentration at the extremes (see Methods). The complete data and analyses with the ICE are given in File S3 and in Table S4

TABLE 1 Number of taxa (species+subspecies), genera and families represented in each distributional class of the Canarian endemic and non-endemic native flora (only Spermatophyta)

Distributional class	Таха	Genera	Families
Endemic flora			
SIE	424	97	31
2-island MIE	95	54	24
3-island MIE	45	35	23
4-island MIE	33	32	23
5-island MIE	41	38	22
Ubiquitous MIE	34	33	25
Native non-endemic flora			
SINE	176	121	44
2-island MINE	116	93	32
3-island MINE	100	81	32
4-island MINE	84	68	32
5-island MINE	117	97	43
Ubiquitous MINE	238	157	49

Note: The number of genera and families across distributional classes was significantly higher in the native non-endemic flora than in the endemic flora (Wilcoxon's test, p < 0.05). The detailed number of SIE/SINE for each island and of MIE/MINE and for each possible combination of two or more islands is given in Table S2.1.

Because the native non-endemic flora is subject to the same insular biogeographical, selective and stochastic factors as the endemic flora, if they were coetaneous, the proportion of ubiquitous MINE would have been much lower, and similar to that of ubiquitous MIE. The significantly higher number of genera and families in the native non-endemic flora than in the endemic flora (Table 1) also strongly suggests that the influence of selection and stochasticity have been comparatively negligible in the native non-endemic flora, feasibly because of its hypothesised much more recent colonisation of the archipelago (e.g. Menezes et al., 2017).

Given the hypothesised post-glacial colonisation origin of most of the native non-endemic flora, the excess of ubiquitous MINE suggests that dispersal of the native non-endemics within the archipelago has been rapid (see Introduction and Caujapé-Castells et al., 2017). Evidence of frequent gene flow with the mainland is given by the fact that 28 of the 121 genera represented in the SINE (23%) contain two or more congeneric taxa, and many of the MINE have 10 or 15 congeneric taxa, which strongly suggests multiple colonisations; notorious examples are *Galium* (Rubiaceae), with one SINE and nine MINE; or *Ononis* (Fabaceae), with three SINE and 12 MINE.

Because most Canarian endemics derive from lineages that were once non-endemic, these results further suggest that (i) many endemisation events in the Canarian flora may have started from widespread taxa, and (ii) a considerable proportion of the endemics may have originated after independent colonisations (see also Francisco-Ortega et al., 1999); this puts into question the presumed monophyly of most Canarian radiations (see also Caujapé-Castells et al., 2017; Herbén et al., 2005; Saunders & Gibson, 2005). Journal of Biogeography -WILEY-

Also in agreement with the expectations of the LPEIH, available estimates of divergence times show the confluence of considerably old and very recently diverged lineages in both (i) the genera with many SIE (i.e. the explosive diversifications and the most diverse radiations); and (ii) the genera with one or a few SIE, corresponding to either the last remnants of old radiations, or to incipient diversification processes. Many radiations analysed in Hooft van Huysduynen et al. (2021) comprise old lineages that diverged throughout the Miocene and early Pliocene (e.g. *Aeonium* (Crassulaceae), with 27 SIE; *Echium* (Boraginaceae), with 21 SIE; *Lavandula*, with nine SIE; or *Micromeria* (Lamiaceae), with 25 SIE); another example of such ancient lineages is *Cheirolophus* (Asteraceae), with 15 SIE (Vitales et al., 2014).

Furthermore, there are also lineages that gave rise to explosive diversification or to radiations but seem to have colonised the Canaries in the Pliocene and Pleistocene, as, for example, *Crambe* (Brassicaceae), with 11 SIE; *Sideritis* (Lamiaceae), with 27 SIE; *Sonchus*, *Pericallis*, *Argyranthemum* and *Gonospermum* (Asteraceae) (with, respectively, 17, 6, 25 and 5 SIE, all analysed in Hooft van Huysduynen et al., 2021); similar situations are also found in *Helianthemum* (Cistaceae), with 11 SIE (Albaladejo et al., 2021), or *Lotus* (Fabaceae), with 16 SIE (Jaén-Molina et al., 2020). Although these age estimates are subject to uncertainty (see e.g. García-Verdugo, Caujapé-Castells & Sanmartín, 2019), the latter cases exemplify that insularity can promote diversification very rapidly, so a higher number of SIE per genus cannot be equated with older colonisation times.

Another prediction of the LPEIH is a predominance of postglacial colonisation times in the native non-endemic flora. Unfortunately, this point remains uncertain because molecular dating studies available for the Canarian non-endemic native flora are very scarce, and some of the ubiquitous MINE examined by phylogeographical investigations have more complex patterns than expected. Hooft van Huysduynen et al. (2021) estimated a late Pleistocene colonisation of many lineages that contain native non-endemics, for example, Galium (Rubiaceae, with 10 taxa), Ononis (Fabaceae, with 15 taxa) or Trigonella (Fabaceae, with 3 taxa). However, in Periploca laevigata Aiton (Apocynaceae), García-Verdugo et al. (2017) found that the origin of some Canarian populations is post-glacial, but other populations are clearly preglacial. Likewise, the molecular dating of the most recent common ancestors of four Macaronesian-mainland clades in Scrophularia (Scrophulariaceae) give age estimates within the late Pleistocene, whereas other clades are much older (Navarro-Pérez et al., 2015). Thus, some of the presumably non-endemic MINE may contain congeneric taxa belonging to either (i) older lineages with overlooked endemics tentatively associated with the LPEIH or to (ii) post-glacial non-endemic natives that may maintain contemporary gene flow with their extant mainland relatives, and may even represent back-colonisations from the Canaries to the mainland, similarly as in Bituminaria bituminosa (L.) Stirton (Fabaceae) (García-Verdugo et al., 2021).

Overall, despite the utter scarcity of divergence time estimates for native non-endemic taxa preventing statistical assessments, our distributional analyses point out that the hypothesised endemicity



FIGURE 5 Connectivity among the Canarian islands based on the distribution of Spermatophyta. (a) and (b): Number of exclusive sharings of, respectively, endemic and non-endemic native Spermatophyta between island pairs. Numbers in circles are the taxa exclusively shared in each case, and the thickness of the connecting lines is proportional to the number of taxa shared. (c) Z-scores between each island and the other islands of the archipelago based on the total number of endemic Spermatophyta (solid coloured bars) and native non-endemic Spermatophyta (blank bars with coloured frames) (see also Table S3). The island and bar colours follow Caujapé-Castells et al. (2017)

increase on the islands, driven by extinction in the mainland during the late Pleistocene, could largely explain the singularity and richness of the extant Canarian endemic flora.

4.2 | The Canarian flora on the tracks: Nonubiquitous MIE and MINE

The connectivity analyses (Figure 5) support recurrent within- and among-island migration throughout the recent ontogeny of the archipelago (in agreement with e.g. Otto et al., 2016 or García-Verdugo et al., 2019). This is especially true for the MINE, which feature 15 exclusive paths (vs. only two exclusive in the MIE, see File S1 and Figure S6), and contain a significantly higher number of genera than the MIE in all the distributional classes (Table 1).

Based on the Z-score, which measures how well connected each island is to other islands in the archipelago, Tenerife is the most important inter-island floristic dispersal node for the extant Canarian flora, in line with Sanmartín et al. (2008). However, Gran Canaria holds the second highest Z-score and number of connections, suggesting that it plays a substantial role in the floristic dispersal between the eastern and the western islands. We should bear in mind that these patterns refer to the extant flora, and that connectivities have likely fluctuated throughout the archipelago's ontogeny; that is, those islands with higher altitudes in the past (e.g. Mahan, or Gran Canaria) probably had once greater connectivity values than at present. Within Spermatophyta, the close floristic relationship between Tenerife and Gran Canaria (63 MIE+MINE shared exclusively, Figure 5) can be explained by their large sizes, their short geographical distance and the similar ages of the oldest regions of each island (Ancochea et al., 1990).

Our analysis also indicates an important dispersal path connecting Tenerife and La Palma: they share exclusively 36 Spermatophyta (MIE+MINE, Figure 5, Table S5), which is considerably higher than the number of exclusively shared taxa between Tenerife and the much closer island of La Gomera (23 MIE + MINE), which is also much older (and smaller) than La Palma. This pattern may be explained by the close phylogenetic relationship detected between several congeneric SIE from Tenerife and La Palma (e.g. Curto et al., 2017 in Micromeria (Lamiaceae); Mort et al., 2015 in Tolpis (Asteraceae); Graham et al., 2021 in Echium (Boraginaceae); or Albaladejo et al., 2021 in Helianthemum (Cistaceae)). It also agrees with ecological evidence: La Palma is the second highest island after Tenerife, and they share similar alpine zones that the other islands lack at present; therefore, recent island hopping involving high mountain regions was only possible between Tenerife and La Palma; for example, Graham et al., 2021 in Echium; Marrero-Gómez et al., 2020 in Viola (Violaceae).

La Gomera lies in the area of the Atlantic Ocean where the deposition rates of African aerosol decrease abruptly (Goudie & Middleton, 2001), implying a lower probability of propagule impact. It is thus likely that the emergence of the whole building of

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the geographically adjacent and much bigger island of Tenerife contributed to increase plant colonisation in La Gomera. In support of this hypothesis, the number of taxa exclusively shared by La Gomera and Tenerife is far higher than those shared by La Gomera and any other single island (see Table S5). Furthermore, most MIE shared by La Gomera and two or more islands are also present in Tenerife (Figure S7).

A shortcoming of these analyses is that we only know which islands are involved in the dispersal paths, but we ignore the directions within them, or the ancestral habitats. Recent phylogeographical research suggests that many of these paths indeed represent different processes, encompassing (i) frequent reciprocal colonisation between the mainland and the eastern islands (e.g. García-Verdugo et al., 2019), (ii) back and forth colonisations among the central and western islands (e.g. in *Solanum* [Solanaceae], Gramazio et al., 2020) and from the eastern islands to the mainland (see Caujapé-Castells, 2004, 2011), or (iii) back-colonisations of the eastern islands from the western islands, for example, *Micromeria* (Lamiaceae, Curto et al., 2017, 2018) and *Kleinia neriifolia* Haw. (Asteraceae, García-Verdugo et al., 2019).

4.3 | A climatic extinction debt of the Canarian flora?

The LPEIH links the great diversity of the Canarian endemic flora to the much higher overall past climatic stability on the islands during the glaciations. This agrees well with the finding that hotspots of rare species are typically areas where the environmental risk of extinction has been low in the absence of human-induced perturbations (Enquist et al., 2019). It also introduces a possible contribution of recent, non-anthropogenic climate changes to the extinction debt of the extant Canarian endemic flora.

The growing human footprint in the Canaries since their human habitation (c. 1700 AD, de Nascimento et al., 2020) and the climatic projections for the next decades (IPCC, 2021) anticipate fast environmental shifts that pose an unprecedented threat for the endemic flora at large, through an 'anthropogenic extinction debt' (i.e. 'the time-lag between the reduction in habitat area and the eventual disappearance of the remnant populations', Triantis et al., 2010). However, the extant endemics involved in the LPEIH could be more at risk, especially those that colonised the islands shortly before the late Pleistocene glaciations. Prospectively, the adverse effects of contemporary anthropogenic pressures may exacerbate foreseeable future population extinctions linked with the action of nonanthropogenic insular diversification drivers on these taxa (see e.g. Ceballos et al., 2015).

The close relationship between high extinction rates and low species abundances (Rosindell & Harmon, 2013), and the fact that the Canarian taxa with a higher degree of threat and smaller population sizes are also significantly less diverse genetically (Pérez de Paz & Caujapé-Castells, 2013), especially threaten the SIE. Anthropogenic environmental changes are likely to promote the rapid extinction of most of these taxa, which generally have small population sizes, fast turnover and a shorter persistence of extinction debts (Cronk, 2016). The extinction of the SIE also may be influenced by the ontogenetic stage of the corresponding island; for example, many endemics of Mahan (the oldest Canarian island, Figure 1) are under high risk of extinction because of major habitat loss due to erosion, which is further aggravated by grazing by feral goats in the pristine habitats that still remain in the cliffs of Jandía and Famara (Gangoso et al., 2006). The case could be closely similar for the oldest SIE distributed in Tenerife's palaeoislands, whose most probable fate is extinction (Mairal et al., 2015).

Finally, many Canarian endemics likely originated from nonendemic taxa that attained widespread distributions, implying that many widespread endemics make an important part of the extinction debt of the flora. Hence, they also should be subject to urgent conservation actions to ensure the maintenance of the ongoing diversification processes that may beget future endemics.

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CONFLICT OF INTEREST

The authors declare they do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

The lists of species used were downloaded from the BIOTA data portal (https://www.biodiversidadcanarias.es/biota/) on June 2021 and are available in the Supplementary file entitled 'Lists of endemic and native non endemic taxa (Spermatophyta and all plants)' Comprehensive quantitative summaries of these data and details of the analyses carried out are given in other Supplementary Files.

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BIOSKETCH

JCC investigates the problems related to the origins, diversity and conservation of Macaronesian and other insular floras using multidisciplinary approaches that involve genetic information, and the integration of DNA banking and molecular data in taxonomic ID and biodiversity management. His research group participates in the formulation of science-based in situ and ex situ conservation objectives for the Cabildo de Gran Canaria (the local administration of this island), and the IUCN SSC Macaronesian Islands Plant Specialist Group. The other authors share one or several of these research interests, especially focusing on island biogeography and phylogeography (CGV, IS), evo-devo and genomics (JFA), taxonomy, phylogeny and conservation (CGV, MMR, JFA), biodiversity databasing (NZ), and bioinformatics (RN).

Author contributions: JCC conceived and developed the ideas, designed the research, carried out the data analyses, led the writing; CGV, IS, MR and JF furnished analytical suggestions, edited and revised the manuscript critically, NZP: facilitated raw data acquisition from BIOTA; RN: programmed the scripts to organise the data.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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