



Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands

Abstract

Subtropical islands are often viewed as refuges where Quaternary climatic shifts driving global episodes of extinction were buffered. Island biodiversity, however, may have been impacted by climatic fluctuations at local scales, particularly in spatially heterogeneous island systems. In this study, we generated a conceptual framework for predicting the potential impact of Pleistocene extinctions on the biogeographical pattern of the Canarian spermatophyte flora, with a focus on the easternmost Canarian islands (ECI). Then, we performed an exhaustive bibliographic revision (270 studies) to examine whether taxonomic, phylogenetic and phylogeographical data support our predictions. Although molecular information is limited for many lineages, the available data suggest that the majority of extant ECI plant taxa may be the result of relatively recent (<1 Ma) dispersal from surrounding insular and mainland areas. Different lines of evidence are compatible with the idea of a Pleistocene period of frequent lineage extirpation on ECI. Extinction may thus have provided new ecological opportunities for recent (re)colonization, with some cases of recent establishment mediated by facilitation. Considering background extinction on ECI, we describe five general patterns of colonization for Canarian plant lineages. In addition to factors related to island ontogeny and long-distance dispersal, we suggest that Pleistocene extinctions may have significantly contributed to extant biogeographical patterns in the Canarian archipelago, such as the biased distribution ranges of island plants and the low endemic richness on ECI. This new scenario provides testable hypotheses for future studies dealing with the phylogeography, taxonomy and conservation of terrestrial biodiversity on the Canarian islands, and possibly, on other near-shore islands.

1 | INTRODUCTION

Subtropical islands have been long considered as biodiversity refugia (Gibson et al., 2017; Hutsemékers et al., 2011; Sauer, 1969). Unlike most continental areas, climatic stability throughout the Pleistocene is hypothesized to have provided adequate conditions for long-term species persistence in these island systems (Jansson, 2003; Rodríguez-Sánchez & Arroyo, 2008). Extant patterns of biodiversity support this view. For instance, Tertiary continental fossils that strongly resemble living insular taxa (Erwin & Schorn, 2000; Kunkel, 1976) pinpoint the role of islands as climatic refugia. In addition, the levels of genetic and species diversity found within insular lineages

(Condamine, Leslie, & Antonelli, 2017; García-Verdugo et al., 2013; Kier et al., 2009) suggest that diversification greatly exceeded extinction over geological time. However, recent studies indicate that Pleistocene climatic oscillations may have locally impacted on the biota of subtropical archipelagos (Norder et al., 2019; Prebble et al., 2016; Weigelt, Steinbauer, Sarmiento Cabral, & Kreft, 2016). Thus, it is plausible that background extinction on islands could be related to recent climatic events, in addition to abrupt geological episodes (e.g. Marrero & Francisco-Ortega, 2001). If so, both processes may have played a fundamental role in the assembly of certain island biotas, although the incidence of extinction in space and time is often difficult to assess (Sanmartín & Meseguer, 2016).

The classical island literature depicts the Atlantic archipelagos of Macaronesia (Azores, Madeira, Selvagen, Canary Islands and Cape Verde) as prominent Quaternary refugia of by-gone continental floras (Bramwell, 1976; Cronk, 1997; Kunkel, 1976). Recent molecular approaches are, however, providing new perspectives on the tempo and mode of island colonization. Although previous studies confirm the long-term persistence of several plant lineages (reviewed in Fernández-Palacios et al., 2011; Vargas, 2007), there is mounting evidence that relatively recent (Quaternary) colonizers represent a substantial proportion of the endemic species pool of each archipelago (e.g. Désamoré et al., 2011; Franzke, Sharif Samani, Neuffer, Mummenhoff, & Hurka, 2017; García-Verdugo, Mairal, Monroy, Sajeve, & Caujapé-Castells, 2017; Jones, Reyes-Betancort, Hiscock, & Carine, 2014; Kondraskov et al., 2015). Positive correlations between the geological age of a given archipelago and lineage colonization time may be therefore restricted to very few cases (Kondraskov et al., 2015). Rather, molecular reconstructions indicate that multiple waves of island immigrants through time, hybridization and back-colonization are more common than initially thought (Caujapé-Castells et al., 2017; Emerson, 2002). The high rates of extinction and dispersal underlying such complex patterns are certainly opposed to the static view of islands as temples of relictualism or the end of colonization roads (Bellemain & Ricklefs, 2008; Caujapé-Castells, 2004; Patiño et al., 2015).

In the context of island colonization, it is remarkable that the potential effect of Pleistocene extinction has been rarely addressed in the Atlantic island floras. The few published studies dealing with this process at a regional scale have focused on the interpretation of palaeoenvironmental records (e.g. Genise & Edwards, 2003), and the potential implication of Pliocene episodes of biodiversity loss on Gran Canaria driven by geological events (Anderson, Channing,

& Zamuner, 2009; Emerson, 2003; Marrero & Francisco-Ortega, 2001). The impact of recent extinction, on the other hand, has been preferentially linked to human arrival to the islands (i.e. human-mediated biodiversity loss in the last few centuries; de Nascimento, Willis, Fernández-Palacios, Criado, & Whittaker, 2009; Illera, Spurgin, Rodríguez-Exposito, Nogales, & Rando, 2016; Terzopoulou, Rigal, Whittaker, Borges, & Triantis, 2015). To bridge this gap, the aim of this study is to address the hypothesis that Pleistocene episodes of background extinction may be largely responsible for the extant plant assembly of the oldest, near-shore Atlantic islands (see discussions in Sanmartín, van der Mark, & Ronquist, 2008).

Under equilibrium conditions, recent (Quaternary) colonization of old islands would be at odds with classical ecological thinking on island biogeography (reviewed in Whittaker & Fernández-Palacios, 2007). Predictions from the dynamic equilibrium model (MacArthur & Wilson, 1967), and two hypotheses coined in island systems such as the loss of dispersal potential (Carlquist, 1974; Cody & McOverton, 1996) and the niche-preemption (Silvertown, 2004), anticipate a slow pace of species turnover on old volcanic islands due

to ecological limitations for successful immigration: loss of dispersal power would reduce the ability of neighbouring island residents to reach the target island, whereas low ecological opportunity would hamper the establishment of external diaspores (Carlquist, 1974; Silvertown, 2004).

However, if an intense period of extinction locally impacts on an archipelago, the new non-equilibrium situation would open up a temporal window of recolonization due to the availability of previously occupied niche space (Carine, 2005). Such a scenario holds especially true if we consider two facts. First, the extent of the phenomenon of loss of dispersal ability has probably been generalized without too much empirical support. Evolution of dispersal potential on islands does not appear to follow an unidirectional pattern in plants, and some lineages may be unaffected, or even attain higher potential for dispersal, under insular conditions (García-Verdugo, Caujapé-Castells, Mairal, & Monroy, 2019; for conceptual discussions see Burns, 2018), thus increasing the likelihood of colonization from nearby islands less affected by extinction. Second, large islands close to source areas of potential immigrants are expected to act

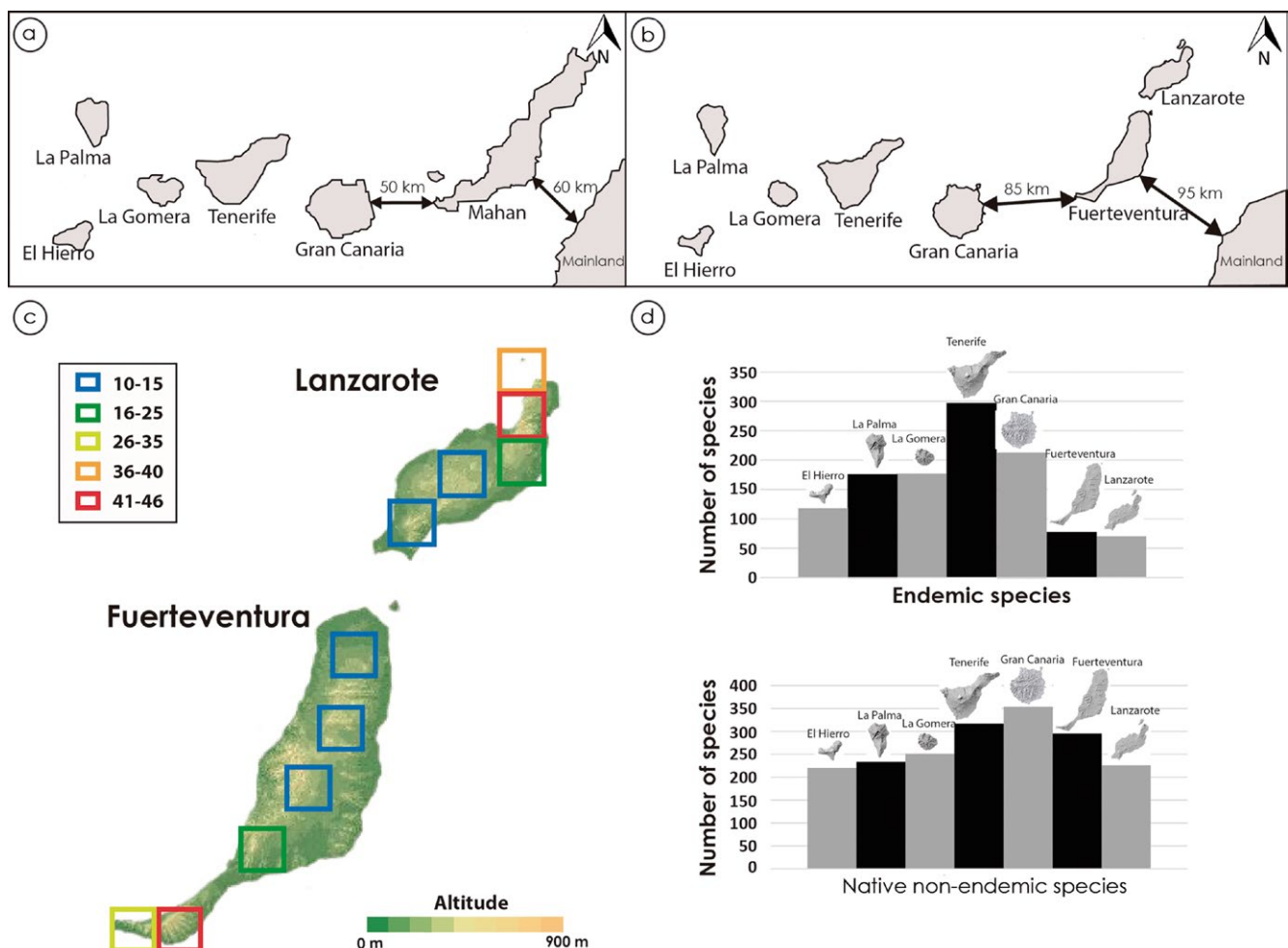


FIGURE 1 Comparison of the spatial configuration and emerged surface of the main Canarian islands at different times throughout the Quaternary (a: last glacial maximum, 20 kyr BP; b: at present), extant patterns of endemic plant species diversity across the two easternmost islands (following Reyes-Betancort et al., 2008) (c), and distribution of endemic versus native non-endemic plant species pools across the Canary Islands (d) [Colour figure can be viewed at wileyonlinelibrary.com]



as strong sinks of colonizers (MacArthur & Wilson, 1967). In sum, we postulate that, under a scenario of high extinction rates, species turnover on old islands should be a function of ecological opportunity for rapid colonization, a condition that Quaternary climatic fluctuations may have prompted on near-shore islands.

2 | CONCEPTUAL FRAMEWORK

2.1 | Overview of the study area

The Canary Islands are presently composed of seven main volcanic islands with an E-W linear arrangement and subaerial ages ranging from c. 20 to c. 1 Ma. However, they only correspond to six volcanic edifices, since the two easternmost Canarian islands (ECI), Lanzarote and Fuerteventura, represent emerged lands from the same geological building. In addition to their close geographical distance from the continent (they are located <100 km off the coast of mainland NW Africa), the ECI share some physical attributes that provide them with some peculiarities with respect to the western Canary islands (WCI). Thus, they are among the fourth largest islands in Macaronesia, and show the oldest geological age (>15 Ma in both cases), a xerophytic climate, and limited topographical complexity (for a detailed physical description of the islands, see Juan, Emerson, Oromí, & Hewitt, 2000; Illera, Díaz, & Nogales, 2006).

The ECI also have a particular ontogeny. Following Pleistocene oscillations, the fusion of these two islands and nearby islets throughout recurrent stadial periods resulted in an emerged surface area, known as Mahan, that was up to two times larger than at present (Figure 1a; see also Fernández-Palacios et al., 2016). The relatively low topological complexity of Mahan probably allowed plant and animal dispersal, providing genetic homogeneity across the extension of the currently separated islands (Caujapé-Castells et al., 2017). In addition, Mahan was much closer to neighbouring areas (mainland Africa and Gran Canaria) than the islands of Lanzarote and Fuerteventura are today (Figure 1a,b). According to biogeographical predictions, the physical attributes of Mahan (i.e. large emerged area and closeness to other sources of potential colonizers) could have offered high opportunities for island colonization (e.g. Fernández-Palacios et al., 2016).

The peculiar geology of the ECI is also reflected in their biotic composition. On floristic grounds, the ECI are considered as a different subprovince to that represented by the WCI (Reyes-Betancort, Santos-Guerra, Guma, Humphries, & Carine, 2008). Lanzarote and Fuerteventura share a significant proportion of their biodiversity, both in term of species and genetic variation (Reyes-Betancort et al., 2008; Sun, Li, Vargas-Mendoza, Wang, & Xing, 2016; Valtueña, López, Alvarez, Rodríguez-Riaño, & Ortega-Olivencia, 2016), and their distinctive flora has strong affinities with mainland SW Morocco (Médail & Quézel, 1999). It is also remarkable that their endemic richness is largely concentrated on the areas with higher topological complexity, mainly represented by the massifs of Jandía (south Fuerteventura) and Famara (north Lanzarote) (Figure 1c). Endemic plant richness of the ECI, however, is strikingly low when compared

to that of the WCI, both in terms of single- and multiple-island endemics (Acebes et al., 2010). Such a pattern raises some questions: Why are there so few ECI endemics and why do the figures for these islands match those observed on the youngest (c. 1–2 Ma) islands of La Palma and El Hierro? In other words, why do Canarian endemics mostly occur on the western islands? Previous biogeographical studies have explained this remarkable pattern by invoking the effects of island ontogeny (Caujapé-Castells et al., 2017; Whittaker, Triantis, & Ladle, 2008) but, to our knowledge, no attempts have been made to examine whether recent episodes of extinction followed by limited immigration may also represent a contributing factor (Sanmartín et al., 2008).

Low habitat heterogeneity, often associated with the advanced eroded stage of the islands and soil degradation, has been postulated as the major driver of the limited ECI endemism (Reyes-Betancort et al., 2008; Rodríguez Rodríguez, Mora, Arbelo, & Bordon, 2005). In addition, human impact is thought to have contributed to generate poor levels of taxonomic diversity on these islands (Illera et al., 2016; Reyes-Betancort et al., 2008). Unlike animal taxa (Gangoso, Donázar, Scholz, Palacios, & Hiraldo, 2006; Illera et al., 2016), human-driven extinction of Canarian plants has been rarely documented (Aedo, Medina, Barberá, & Fernández-Albert, 2015; Reyes-Betancort et al., 2008), but may have locally affected extant island distributions. Despite the potential implication of human impact, it is however interesting to make two observations with regard to the levels of plant diversity on the ECI. First, the pattern of distribution of native non-endemics (more recent colonizers) in the archipelago clearly does not match that of endemics (older colonizers) (Figure 1d), which appears to suggest that colonization time may also play a role. Second, while strong human-mediated pressure (including overgrazing by domestic ungulates) can affect plant abundance and recruitment (Gangoso et al., 2006), it has a more limited impact on the phylogeographical signal for extant lineages: regardless of their current abundance, recent phylogeographical studies are providing evidence that some ECI populations and taxa may have had a recent origin, either because they were the result of dispersal from the WCI or from mainland areas (Curto, Puppo, Kratschmer, & Meimberg, 2017; García-Verdugo et al., 2009; Stervander et al., 2015; Valtueña et al., 2016). A repeated signature across taxa of secondary colonization of the ECI without evidence of hybridization with putative old residents is compatible with the idea of broad-scale taxonomic extinction followed by recent immigration. Such a possibility, albeit frequently hypothesized (Cardoso, Arnedo, Triantis, & Borges, 2010; Caujapé-Castells et al., 2017; Sanmartín et al., 2008), has not been explicitly evaluated to date.

2.2 | Hypothesis and predictions

Our working hypothesis is that Pleistocene extinctions had a major impact on the biogeographical patterns of the plant species pool of the ECI. This hypothesis is framed within the spatio-temporal scenario provided by these islands during the last million of years. Although the Plio-Pleistocene transition (c. 2.6 Ma) is formally

recognized as the onset of the glacial period, there is general agreement that the “mid-Pleistocene transition” (MPT), starting at around 0.8 Ma, established a new stage of abrupt climatic shifts, with the strengthening and lengthening of the glacial-interglacial cycles (Loulergue et al., 2008; Lowe & Walker, 2015). Pleistocene cycles are thought to have had a profound impact on species distributions and survival rates across islands worldwide (Fernández-Palacios et al., 2016; Norder et al., 2019; Weigelt et al., 2016), and islands close to continental masses, as climatically marginal areas, might have experienced stronger impacts than more isolated climatically milder islands (Hardie & Hutchings, 2010).

Climatic, palaeontological and phylogeographical evidence indicate that both the near-shore ECI and mainland NW Africa were particularly impacted by climatic oscillations (García-Aloy et al., 2017; Meco et al., 2003; Ortiz et al., 2006). Since the performance of islands as refugia largely depends on the geographical extension and heterogeneity of their habitats (Condamine et al., 2017; Gillespie & Clague, 2009), the low topographical complexity of the ECI during the Quaternary likely offered very few micro-refuges for the

terrestrial biota, which concentrated on the Jandía and Famara masifs (Reyes-Betancort et al., 2008). Persistence was probably even more challenging for species with lower vagility, with specific habitat requirements or those relying on obligate biotic interactions (e.g. animal pollination; Brodie et al., 2014). Conversely, the ECI could have acted as sinks of immigrants throughout mesic periods, due to their larger emerged area, close geographical proximity to continental and island source areas and niche availability following extinction (Figure 1a; see also Fernández-Palacios et al., 2016). Considering these abrupt changes in environmental conditions and ecological opportunity over short evolutionary time, we anticipate that the ECI flora would have been subject to frequent extinction–(re)colonization events over the MPT.

In this study, we examine if extant distributions of native plants are associated with temporal patterns of island colonization driven by extinction. We expect that Quaternary background extinction may have left a detectable signature on measurable traits such as extant distributions and lineage colonization times. Thus, our predictions (Table 1) link extant distribution ranges to the biogeographical

TABLE 1 Predictions linking the distribution (WCI = western Canarian islands, ECI = easternmost Canarian islands) of extant endemic lineages, time of island colonization (time) and expected frequencies of plant endemic lineages (% lineages) under the hypothesis of Pleistocene extinction affecting the ECI. Colonization time is divided into two temporal windows (prior or after) with respect to the onset of the mid-Pleistocene transition (MPTo = 0.8 Ma)

Extant distribution		Predicted scenarios			
WCI	ECI	#Prediction	Time	% Lineages	Explanation for the expected % of lineages and references
X		P1	pre-MPTo	HIGH	WCI have had higher carrying capacities (larger total size and habitat diversity) than ECI during the Plio-Pleistocene. Therefore, they may have buffered MPT fluctuations more efficiently than ECI ⁽¹⁾ , resulting in old lineages with distributions affected by ECI extirpation ⁽²⁾
X		P2	post-MPTo	LOW	Because stepping-stone colonization from ECI to WCI is assumed to be the most plausible pattern ^(3,4) , most recent (post-MPTo) immigrants should be also present on ECI (unless affected by very recent extinction)
X	X	P3	pre-MPTo	HIGH	Assuming extinction, this scenario could be represented by two types of Canarian endemic lineages: those with old ECI taxa surviving extinction in situ ⁽⁵⁾ , and residents of neighbouring islands capable of recent back-colonization of ECI ⁽⁶⁾
X	X	P4	post-MPTo	LOW	Stepping-stone colonization from ECI to WCI is assumed to be the dominant pattern ^(3,4) , but extinction is expected to have resulted in extensive island extirpation of recent ECI immigrants
	X	P5	pre-MPTo	LOW	Old (pre-MPTo) island lineages with distributions restricted to ECI should be rare because these two islands have few areas qualifying as refuges ⁽⁷⁾ , and endemic lineages typically display multi-island distributions ⁽⁸⁾
	X	P6	post-MPTo	HIGH	Large island area, short dispersal distances from source areas and high carrying capacity (due to extinction-driven niche availability), enhance likelihood of successful colonization of immigrants that eventually differentiate from the source ^(9,10)

Notes. (1) Fernández-Palacios et al. (2016); (2) Caujapé-Castells et al. (2017); (3) Juan et al. (2000); (4) Shaw and Gillespie (2016); (5) Juan et al. (1998); (6) Curto et al. (2017); (7) Reyes-Betancort et al. (2008); (8) Price et al. (2018); (9) MacArthur and Wilson (1967); (10) Carine (2005).



imprint of Pleistocene extinctions. Floristic extirpations are expected to have shaped island lineages, regardless of whether these colonized the archipelago before or after the intensification of the glacial cycles (c. 0.8 Ma). Based on previous studies (Juan et al., 2000; Shaw & Gillespie, 2016) and the gradient in habitat complexity across the archipelago (Reyes-Betancort et al., 2008) we make two assumptions: (a) the most recurrent pattern of island colonization initially followed the progression rule (i.e. dispersal from mainland to ECI, and subsequent dispersal from ECI to WCI), (b) the WCI showed higher resilience to eventual climatic shifts than the ECI in the Pleistocene, due to larger habitat complexity and bigger extension. By comparing the available support for each set of predictions (Table 1), we aim at testing three spatio-temporal scenarios derived from the hypothesis of mid-Pleistocene extinction: (a) temporal filter of lineage dispersal to WCI (P1 + P2 predictions), (b) disruption of the progression rule (P3 + P4), and (c) driver of recent ECI immigration rates (P5 + P6). To further test the effect of colonization age on distribution patterns, we also predict that native, non-endemic lineages, unlike old island resident lineages, should display distribution patterns not affected by extinction filters (i.e. fully compatible with the progression rule).

2.3 | Literature survey

Our study focused on the spermatophyte flora of the Canarian archipelago. Some endemic-rich terrestrial groups have received considerable attention in biogeographical analyses centred on the Canary Islands (Illera et al., 2016; Juan et al., 2000; Sanmartín et al., 2008). However, information for Canarian plants far exceeds that available for animals, allowing lineage delimitation for the majority of plant taxa known to be native to the archipelago. Rather than focusing on recognized taxonomic species, we used island lineages as observational units (for similar approaches, see García-Verdugo, Baldwin, Fay, & Caujapé-Castells, 2014; Price et al., 2018; Valente et al., 2017). Island lineages were classified as endemic or native non-endemic following the rationale provided in Price et al. (2018). Briefly, endemic lineages were delimited using phylogenetic, taxonomic and/or population-level genetic studies that have identified groups of closely related Canarian species or populations strongly differentiated from mainland counterparts (see Appendix S1 in Supporting Information). Native non-endemic lineages were extracted from the most updated checklist of native, non-endemic Canarian species (Acebes et al., 2010), as we consider each of these species to represent independent colonization events of the islands without subsequent speciation. In this case, records were limited to those likely representing naturally occurring lineages ("nativo seguro" = native with certainty, and "nativo probable" = likely native) (Acebes et al., 2010).

In addition, the information included in the checklist of the vascular plants for the Canary Islands (Acebes et al., 2010) was used as a preliminary source for characterization of island distributions, even though it does not implement results from recent molecular studies. Then, we performed an exhaustive bibliographical search considering taxonomic, phylogenetic and phylogeographical studies on Canarian plant taxa. Data from 254 studies were analysed to identify

the number of island plant lineages as accurately as possible, and to obtain information on the biogeographical pattern of these lineages (see Appendix S1). Distribution data from the checklist of native lineages were updated. Thus, some native non-endemic lineages were treated in our study as island endemics, while other species/populations formerly regarded as native were treated as introduced when supported by data published after Acebes et al. (2010). When available, divergence time estimates between island lineages and closely related mainland taxa were used as a surrogate of island colonization. This latter approach bears, however, some limitations. First, age estimates of molecular divergence do not necessarily reflect colonization time accurately. Incomplete taxon sampling, either due to extinction of closer relatives or limited representation of continental and island species, and incomplete lineage sorting may result in poorly resolved or incorrect phylogenetic relationships, which lead to biased estimates of colonization times (see e.g. Emerson, 2002; Emerson, Oromi, & Hewitt, 2000; Stervander et al., 2015). To account for this source of uncertainty, we adopted the following approach. First, we estimated the most probable colonization time to be within the interval set by the stem (divergence from the continental relatives) and the crown age (diversification within the island setting) of the island lineage, when both estimates were provided. Second, because estimates of divergence times depend on the general rate of DNA substitution used, we also considered the confidence intervals generated in the studies. Lastly, we balanced the quality of the information provided by each study case, and the patterns inferred for lineages were classified into "strong" or "moderate". Thus, if studies provided divergence time estimates based on phylogenetic relationships resolved with high (i.e. >90% nodal bootstrap) support for the ECI taxa/populations, the pattern was classified as "strong". By contrast, inferences were deemed as "moderate" if divergence was based on levels of genetic differentiation and/or phylogenetic reconstructions with more limited support.

3 | SPATIO-TEMPORAL PATTERNS

Our literature survey allowed identification of 233 plant endemic lineages (see Appendix S1). We detected some endemic taxa for which assignment to clearly defined island lineages is still hypothetical due to the inconclusive information available to date. However, these only represented a small fraction (2.2%) of the total. On the other hand, after exclusion of cases that recent studies have redefined as endemic or human-introduced, native non-endemics were represented by 284 lineages.

We found significant associations between type of lineage (endemic vs. native non-endemic) and extant island distributions ($\chi^2 = 82.1$, $p < 0.001$; Table 2). Thus, endemic lineages preferentially occur on WCI (53.2% of cases), whereas a small fraction of this type of lineages (c. 10%) is restricted to ECI (Table 2). In contrast, recent colonizers represented by native non-endemic lineages preferentially occupy both ECI and WCI (70% of the total), and showed a small number of cases exclusively found on WCI (15.8%; Table 2).

TABLE 2 Contingency table of lineage (endemic vs. native non-endemic [Native NE]), and island distribution categories, with the number of observations followed by percentage of the total data (in parenthesis). Distributions representing the most abundant class within each type of lineage are highlighted in bold. ECI = easternmost islands, WCI = western islands, ECI+WCI = lineages spanning both island distributions

Lineage	Distribution			Total
	WCI	ECI+WCI	ECI	
Endemic	124 (53.2)	86 (36.9)	23 (9.9)	233
Native NE	45 (15.8)	199 (70.1)	40 (14.1)	284

Divergence time estimates were available for 42% of the endemic island lineages, but inclusion of cases with moderate support increased the proportion of endemic lineages up to 54%. Considering these cases, our predictions received different levels of support:

3.1 | Scenario 1: MPT as a temporal filter of dispersal to WCI

We found a substantial number of studies dealing with WCI lineages. This is most probably explained by the overrepresentation of this type of island distribution among endemic Canarian lineages (Table 2). In total, 51 study cases suggested that island colonization predated the onset of the MPT (P1), while three additional cases provided moderate support for this prediction (Figure 2). Notably, only one study documented an estimated age of island colonization within the MPT (P2), resulting in a 54(P1)/1(P2) ratio (i. e. strong support for scenario 1) (Figure 2). In most of the studies where divergence time estimates were available, confidence intervals did not overlap with the MPT threshold, whereas in 12 other cases, only a small fraction of the confidence interval (<5%–10%) overlapped with such a threshold (Figure 3a). Only three island lineages showed estimated divergence times from mainland relatives that did not fall within the Pliocene–Pleistocene period (mean of estimated island colonization age across lineages = 3.9 ± 3.1 Ma; Figure 3a).

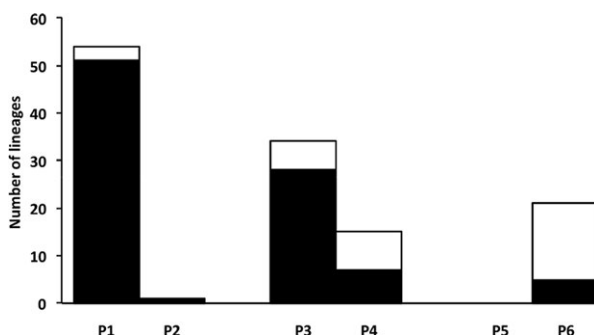


FIGURE 2 Number of study cases obtained from the literature that supports each of the six predictions of our study (see Table 1). Black bars represent studies providing strong support for each prediction whereas open bars represent cases providing moderate support

3.2 | Scenario 2: MPT as a disruptor of the progression rule

The number of lineages with ECI–WCI distributions and colonization ages older than the onset of the MPT (P3) was higher than those with younger colonization ages (P4), resulting in a 34(P3)/15(P4) ratio. These figures, however, should be taken with caution since we found a number of lineages for which large confidence intervals precluded unambiguous assignment to either of the two predictions (Figure 2). Within the set of studies providing support for P3, intra-lineage divergence estimates revealed two contrasting biogeographical patterns: all but two lineages (*Echium* and the *Aeonium* alliance) contained taxa that qualify as recent ECI colonizers (i.e. 95% confidence intervals virtually overlapping present time in all cases; Figure 3b). Excluding these two lineages, island colonization times were very recent (0.8 ± 0.6 Ma across ECI taxa). These figures did not support the progression rule, nor the analyses performed in the published studies recovered the ECI taxa as early divergent clades following archipelago colonization. In contrast, other studies conducted on lineages with limited taxonomic differentiation revealed young colonization ages (Figure 3c) and topological reconstructions among island populations that were congruent with the progression rule. In these cases, colonization times refer to the split between mainland and island populations, but divergence times between ECI and WCI populations are typically not reported.

3.3 | Scenario 3: MPT as a driver of recent ECI immigration rates

We could not find studies on ECI endemic plant lineages that revealed colonization ages that clearly predated the MPT. In contrast, the available information for lineages with this island distribution provided 21 cases of putative recent origin (P6, Figure 2), although colonization ages were only available for five of these (mean island colonization = 0.5 ± 0.3 Ma across lineages; Figure 3d). The available evidence suggests high rates of immigration from continental areas since the MPT.

4 | HYPOTHESIZED PATTERNS OF COLONIZATION

Taking the results for these scenarios together, we hypothesize five general patterns of island colonization for endemic plant lineages with a focus on the ECI (Table 3):

4.1 | Lineages with extant WCI distributions

Most of these lineages are expected to have reached the WCI prior to the MPT. The most plausible pattern is that they colonized ECI before dispersal to WCI, from which they went extinct at some point. The broad time span of island colonization ages inferred for this island

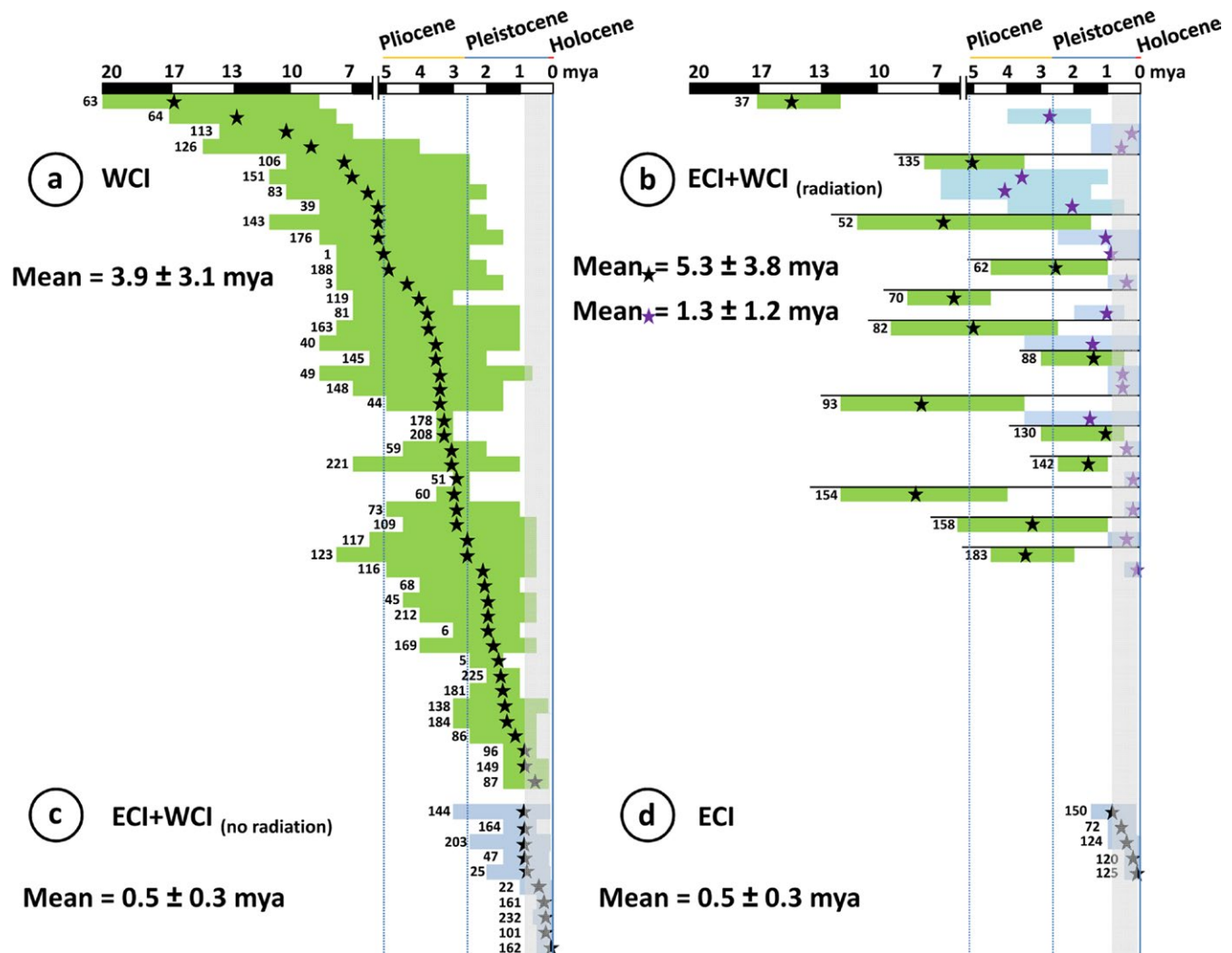


FIGURE 3 Estimated island colonization times obtained from the literature for Canarian plant lineages. Each estimate is represented with a mean value (star) and its confidence interval (colour bar). Lineages are divided into four classes (a–d), according to their extant distributions and taxonomic diversification. In (b), estimates of colonization times for ECI taxa are represented by purple stars. Numbers next to each estimate identify each lineage (see Appendix S1). The extent of the mid-Pleistocene transition is represented with a gray-shaded column, and mean values (\pm SD) across study cases are indicated for each lineage class [Colour figure can be viewed at wileyonlinelibrary.com]

distribution (Figure 3a) suggests that the hypothetical local extinction from ECI might have occurred at different times throughout the Plio-Pleistocene. However, the concentration of lineages with colonization times within the Pleistocene is suggestive of frequent island extirpation in recent times. Alternative patterns, such as introduction to the WCI via northern islands (e.g. Madeira) or direct long-distance dispersal from continental areas, would represent an exception to this general colonization pattern (i.e. no need to invoke ECI extirpation).

4.2 | Lineages with extant ECI-WCI distributions

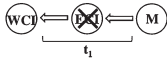
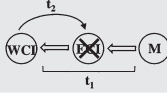
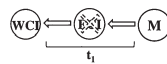
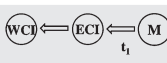
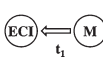
Under the scenario of extinction associated with MPT, the primary spatio-temporal sequence of the progression rule (i.e. dispersal from mainland to ECI followed by subsequent dispersal to WCI) could occur in the following two cases: (a) recent island colonizers, represented by lineages with limited

taxonomic diversification, and (b) old colonizing lineages that include some ECI surviving taxa, mostly related to the putative Pleistocene refugia of the Famara and Jandía massifs. In the latter case, lineages with extant ECI-WCI distributions and colonization times older than the MPT may have experienced extinction of all putative ECI taxa. In this particular subcase, and the case where ECI has experienced depauperation, back-colonization of ECI from WCI in recent times can account for their current distribution (which may extend to back-colonization of mainland areas).

4.3 | Endemic lineages to ECI

The available data indicate that most of the extant plant lineages endemic to ECI are the result of recent colonization from continental areas. Dispersal from other Macaronesian archipelagos (e.g.

TABLE 3 Hypothesized spatio-temporal patterns of colonization for Canary island plant lineages based on extant island distribution, degree of lineage diversification (low, high) and island colonization time. These patterns focus on ECI, but more complex scenarios are possible (see main text). Black cross = total island extirpation. "Dotted" cross = extinction causing biodiversity depauperation, but not total extinction, on ECI. Distribution: WCI = western Canary Islands, ECI = easternmost Canary Islands, M = source areas external to the Canary Islands (e.g. mainland Africa, Madeira)

Distribution	Lineage diversification (#ECI taxa)	Pattern	Divergence time (Ma)	Examples
WCI	Low/High (0)		$t_1 > 0.8$	<i>Ocotea</i> ⁽¹⁾ , <i>Cheirolophus</i> ⁽²⁾
ECI+WCI	Low/High (<3)		$t_1 > 0.8$ $t_2 < 0.8$	<i>Kleinia</i> ⁽³⁾ , <i>Micromeria</i> ⁽⁴⁾
ECI+WCI	High (≥ 3)		$t_1 > 0.8$	<i>Echium</i> ⁽⁵⁾ , <i>Aeonium</i> ⁽⁶⁾
ECI+WCI	Low (1)		$t_1 < 0.8$	<i>Rumex</i> ⁽⁷⁾ , <i>Phoenix</i> ⁽⁸⁾
ECI	Low (1)		$t_1 < 0.8$	<i>Periploca</i> ⁽⁹⁾ , <i>Euphorbia</i> ⁽¹⁰⁾

Notes. (1) Kondrakov et al. (2015); (2) Viales et al. (2014); (3) Sun and Vargas-Mendoza (2017) (4) Curto et al. (2017); (5) García-Maroto et al. (2009); (6) Pokorny et al. (2015); (7) Talavera, Navarro-Sampedro, Ortiz, and Arista (2013); (8) Saro et al. (2015); (9) García-Verdugo et al. (2017); (10) Bruyns, Klak, and Hanáček (2011).

Madeira, Selvagens) to ECI would represent an alternative source area of such recent colonizers.

5 | DISCUSSION

5.1 | Pleistocene extinction as a plausible driver of Quaternary biogeographical patterns in the Canary Islands

Our study revealed two general patterns that are well documented in the available literature of the Canary Island flora: (a) the origin of most island lineages that are absent from the easternmost islands predate the onset of the MPT, and (b) many taxa endemic to the easternmost islands appear to be the result of recent (MPT onwards) colonization. Without fossil evidence, the impact of extinction on a particular island lineage is hypothetical (Cardoso et al., 2010; Sanmartín & Meseguer, 2016). However, the intersection of these two patterns and the joint analysis of a significant proportion of the endemic Canarian flora allow us to describe a scenario in which Pleistocene extinction may have played a fundamental role in the floristic assemblage that we currently observe on the ECI.

The first pattern is congruent with Pleistocene ECI extirpation of extant WCI lineages (Figure 3a; Table 3), an explanation that has been frequently hypothesized in biogeographical studies (Arnedo, Oromí, & Ribera, 2000; Cardoso et al., 2010; Viales et al., 2014). In our study, comparisons of multiple lineages provide an upper bound for the occurrence of such a phenomenon around the mid-Pleistocene.

Notwithstanding the limitations of the approaches for linking divergence times to island colonization times (e.g. Pillon & Buerki, 2017), we argue that such a recurrent pattern adds a plausible explanation, in addition to direct dispersal to WCI from mainland, for some extant species distributions. Thus, recent extinction of ECI taxa (i.e. time constraints for recolonization) could explain why outstanding examples of island colonization and diversification, such as *Cheirolophus* (17 endemic species) or *Pericallis* (12), have no extant representatives on these islands, despite potential availability of suitable habitats (e.g. Viales et al., 2014). In turn, recent episodes of ECI colonization (second pattern; Figure 3b; Table 3) imply earlier extirpation, and would account for the limited ECI representation (one or two closely related species) of lineages with similar high colonization abilities (e.g. *Argyranthemum*, *Sideritis*, *Micromeria*) (Curto et al., 2017; Kim et al., 2008).

Our study showed that endemic Canarian lineages display a strong bias towards WCI distributions, thus suggesting a large number of candidates being affected by extirpation. Whether human-mediated extinction has a relevant implication in this pattern is uncertain, since well-documented cases of historic plant extinctions are restricted to WCI endemics (de Nascimento et al., 2009; Reyes-Betancort et al., 2008). For ECI extirpations apparently derived from background extinction, habitat loss related to island erosion has been often suggested as the main explanatory factor (Arnedo et al., 2000; Sanmartín et al., 2008). However, invoking erosion as a driver of extinction implicitly assumes geological processes that operate in a time-scale of Ma, which is not congruent with the second pattern revealed by our study (i.e. recent origin of ECI endemics). High immigration rates on ECI (Figure 3b–d) underlie a scenario



of frequent extinction within the last million of years, a temporal frame that could hardly imply profound habitat transformation associated with island ontogeny (for a temporal reconstruction of the islands, see Caujapé-Castells et al., 2017). Again, the impact of Pleistocene environmental shifts, albeit hypothetical, may satisfactorily explain a recent turnover of terrestrial biodiversity on the ECI (see e.g. García-Aloy et al., 2017; Haase, Greve, Hutterer, & Misof, 2014).

The view of the easternmost islands as areas of recent recolonization questions, to some extent, the idea of limited habitat heterogeneity as an explanatory factor for their low endemic richness. Habitat heterogeneity strongly correlates with species richness (Reyes-Betancort et al., 2008), and the ECI are geographically more homogeneous than the younger, western islands. However, several lines of evidence suggest that this factor alone cannot explain their low endemism. First, we found that 70% of extant native, non-endemic lineages currently occur on ECI plus another (most frequently, several) western island(s) (Table 2). This observation, linked with the high species diversity of non-endemics found on these islands (Figure 1d), indicates that habitat heterogeneity is sufficiently complex to act as source (or sink, depending on the colonization route) of recent immigrants to other islands. Second, several areas of the ECI, apart from the Jandía and Famara massifs (i.e. Ajaches, Betancuria, Montaña Cardón and Cuchillos de Vigán massifs), could have considerably increased habitat heterogeneity, at least before the introduction of goats hampered plant population survival in more recent times. Lastly, some species of endemic WCI lineages that have been deliberately introduced to the ECI in the last century (e.g. *Rumex*, *Salvia*) are currently under population expansion (Reyes Betancort, 1998), which provides evidence that habitats of putatively extirpated lineages are not necessarily lost. We propose that limitations not strictly related to habitat heterogeneity, but to recent island colonization, may also account for the pattern of low endemism of the ECI.

Our survey identifies a period that, rather than a temporal window of colonization (Carine, 2005; Kim et al., 2008), more specifically appears to have acted as a semi-permeable barrier of colonization and subsequent speciation. Some island lineages identified as recent ECI colonizers are composed of sister taxa displaying disjunct distributions within Lanzarote and Fuerteventura (Reyes Betancort, 1998; Sánchez, Caujapé-Castells, Reyes-Betancort, & Scholz, 2006). Thus, *Argyranthemum*, *Asteriscus*, *Bupleurum* and *Ferula* show populations mostly confined to the Famara and Jandía massifs. The central area of Mahan probably served as a dispersal corridor between both areas during favourable conditions in the Pleistocene, but geographically intermediate populations went extinct, probably due to Quaternary climate fluctuations and, more recently, to human-related pressures, including intense browsing by domestic herbivores. Such a biogeographical pattern has been supported by species displaying signatures of Quaternary population expansion on these islands (Juan, Ibrahim, Oromí, & Hewitt, 1998; Sun & Vargas-Mendoza, 2017).

This pattern ultimately reinforces the view of the north and south massifs of the ECI acting as efficient refugia, and underscores geographical isolation as a recent driver of speciation between eastern disjunct island populations.

5.2 | How representative are the proposed colonization patterns of other terrestrial groups?

We would expect that the main spatio-temporal patterns that we propose for the Canarian flora (Table 3) should be largely paralleled by terrestrial island elements tightly linked with plants, for example, highly specialized animal consumers. A cursory review of the literature published on animal taxa shows that phylogeographical studies often retrieve congruent patterns for species dependent on trophic interactions (Table 4). For instance, the idea that lineages with extant WCI distributions may have once occurred on the eastern islands, albeit hypothetical, receives further support by the fact that some animals and their obligate plant hosts appear to display a concordant spatio-temporal pattern (Hernández-Teixidor, López, Pons, Juan, & Oromí, 2016; Percy, Page, & Cronk, 2004). Colonization times of the WCI, in both plant and animal species, typically predate the MPT. If extinction of former ECI populations is excluded as a plausible option, we should invoke multiple events of direct dispersal from source areas to WCI for both plant and obligate animal consumers, which seems unlikely given the large distances involved and the limited dispersal abilities of most of these species. Progressive island hopping followed by Pleistocene extinction on the ECI appears to be a more likely explanation (e.g. Saura, Bodin, & Fortin, 2014). Quaternary ECI fossils of gastropod species in the genus *Theba*, which are currently represented by WCI populations (Haase et al., 2014), also provide insights into the incidence of Pleistocene extinction in the island distributions of extant species. Examples of immigration of animal-plant species pairs to ECI, either as a result of back-colonization or dispersal from mainland areas, can be also found in the literature (Table 4), and suggest that recent island colonization may be also mediated by facilitation (Bruno, Stachowicz, & Bertness, 2003).

Further evidence from the animal kingdom comes from studies inferring multiple colonization waves of conspecific taxa at different temporal windows. Such a recurrent pattern of island colonization is intrinsically consistent with the idea of extinction favouring arrival to islands previously colonized by relatives (Illera et al., 2016). In this context, placing extinction within a particular spatio-temporal background (i.e. Pleistocene, easternmost islands) is supported by the fact that ECI populations in these cases are often very recent (<1 Ma) (Bidegaray-Batista, Taiti, López-Hernández, Ribera, & Arnedo, 2015; Husemann, Depperman, & Hochkirch, 2014; Stervander et al., 2015). This pattern is in agreement with those revealed by recent plant studies using extensive population sampling of mainland and island regions (García-Verdugo et al., 2009, 2017; Valtueña et al., 2016).

In addition, some of the patterns receiving limited empirical support from the island plant literature may be supplemented

TABLE 4 Concordant phylogeographical patterns of plant (P)–animal (A) interactions obtained from independent studies. Abbreviations: WCI = western Canarian islands, ECI = easternmost Canarian islands, MPT = mid-Pleistocene transition

Distribution	P×A interaction	P	A	Phylogeographical pattern	Ref
WCI	Obligate host	<i>Euphorbia</i> spp (<i>Esula</i> subgen)	<i>Rhopalomesites</i> spp	The inferred colonization times for both the WCI beetle (3.2–7.6 Ma) and plant (2.8–4.4) lineages predate the MPT	1, 2
WCI	Obligate host	<i>Teline</i> spp	<i>Arytinnis</i> spp	The inferred colonization times for both the WCI lice (c. 2.5 Ma) and plant (c. 2.9 Ma) lineages predate the MPT	3, 4
WCI-ECI	Obligate larval host	<i>Euphorbia regis-jubae</i>	<i>Hyles tithymali</i>	Both animal and plant lineages initially colonized the archipelago before the MPT (>1 Ma), but independent analyses suggest WCI-to-ECI colonization in very recent times	5, 6, 7
WCI-ECI	Obligate host	<i>Pinus canariensis</i>	<i>Brachyderes rugatus</i>	Analyses suggest that the only known population of the beetle lineage on ECI is the result of a very recent human-mediated introduction of the plant host	8
WCI-ECI-mainland	Obligate host	<i>Euphorbia regis-jubae</i>	<i>Aphanarthrum affine</i>	Independent studies indicate a WCI-ECI-mainland colonization pattern for both lineages, and dating analyses in the host plant suggest that this pattern took place within the last Ma	9, 7
Mainland-ECI	Obligate larval host	<i>Lotus lancerottensis</i>	<i>Polyommatus celina</i>	Colonization time of ECI from mainland inferred for the butterfly species (0.1–0.3 Ma) corresponds with the recent colonization of the host species (0.0–1.18 Ma)	10, 11, 12
Mainland-ECI	Dispersal agent	<i>Olea</i> , <i>Phoenix</i> , <i>Pistacia</i>	<i>Sylvia</i> spp, <i>Corvus</i> , <i>Turdus</i>	Recent colonization time of some fleshy-fruited plant lineages (0.0–0.6 Ma) coincides with that inferred for the passerine island lineages acting as main dispersers (0.0–0.6 Ma)	13, 14, 15, 16

Notes. (1) Barres, Vilatersana, Molero, Susanna, and Galbany-Casals (2011), (2) Hernández-Teixidor et al. (2016), (3) Percy and Cronk (2002), (4) Percy et al. (2004), (5) Hundsdoerfer and Wink (2006), (6) Mende, Bartel, and Hundsdoerfer (2016), (7) Sun et al. (2016), (8) Emerson et al. (2000), (9) Jordal and Hewitt (2004), (10) Wiemers, Stradomsky, and Vodolazhsky (2010), (11) Dincă, Dapporto, and Vila (2011), (12) Ojeda et al. (2014), (13) Saro et al. (2015), (14) Nogales et al. (2015), (15) Valente et al. (2017), (16) C. García-Verdugo unpublished.

by well-documented cases of animal phylogeography. The oldest Canarian islands indeed may be home of a limited fraction of old plant lineages (that is, those which are hypothesized to have survived in Pleistocene refugia), but our survey only found two cases with strong support (*Aeonium* alliance and *Echium*). In animals, however, there are several species-rich lineages in which the signature of extinction in surviving ECI-WCI lineages can be inferred from phylogenetic (large branches and topological basal position) and demographic (Quaternary events of secondary cladogenesis) approaches dealing with ECI taxa (Bidegaray-Batista, Macías-Hernández, Oromí, & Arnedo, 2007; Juan et al., 1998). In agreement with our results for *Aeonium* and *Echium*, it is noteworthy that animal lineages qualifying as Pleistocene ECI survivors usually include several taxa endemic to ECI. We hypothesize that high ECI endemic richness within a given lineage may be indirect evidence of the expected effects of Pleistocene extinction. If Pleistocene extinction caused a dramatic reduction in ECI biodiversity levels, the processes promoting de novo speciation (i. e. dispersal, colonization, geographical/ecological isolation) are probably too recent to have allowed time for many new ECI taxa to emerge.

5.3 | Implications for future studies

Modern phylogeographical approaches have increased our ability to reconstruct complex biogeographical patterns by simultaneously testing alternative demographic scenarios (Curto et al., 2017; Saro, González-Pérez, García-Verdugo, & Sosa, 2015; Sun et al., 2016). Assuming the role of Pleistocene extinctions on the ECI provides a set of hypotheses linking extant island distributions with temporal windows of colonization (Table 3), which could be easily implemented in phylogeographical models.

Our findings also provide insights into the conservation and taxonomy of Canarian plant endemics. For instance, the restricted distribution of ECI endemics coupled with the detrimental effects of introduced herbivores anticipate an adverse scenario for long-term plant survival. However, most of the ECI endemics might not qualify as climate relicts due to their putatively recent origin. We could thus expect relatively quick population recovery in many cases, provided that perturbations caused by introduced herbivores are substantially attenuated. In addition, our study highlights that species with WCI distributions are typically associated with old (>1 Ma) colonization times. This opens an



interesting venue for taxonomic research, as populations of some native, non-endemic taxa currently displaying such distributions could have evolved under isolation for longer time than previously thought.

6 | CONCLUSIONS

The easternmost islands of Lanzarote and Fuerteventura represent a biogeographical cornerstone for explaining patterns of plant biodiversity in the Canarian archipelago. While their old volcanic origin and closeness to the continent postulated them as cradles of island biodiversity, they have probably been more affected by the consequences of island ontogeny and climatic fluctuations than more isolated, young islands. Thus, our study supports the idea that the impact of Pleistocene extinctions on these islands could explain some of the recurrent biogeographical patterns described in the region, such as the disruption of the progression rule (Juan et al., 2000; Shaw & Gillespie, 2016). This scenario also implies that tests of ecological hypotheses involving the ECI should consider detailed phylogeographical information for adequate data interpretation (García-Verdugo et al., 2019; Monroy & García-Verdugo, 2019).

The available evidence indicates that the Canary Island biota is assembled by lineages that colonized the archipelago at different geological times, but our findings strongly suggest that there is a significant component of young (<1 Ma) plant colonizers, especially on the ECI. Such a relatively recent origin of ECI elements appears to predate, in most cases, human arrival to the islands (i.e. before the last two millennia). We thus propose that considering estimates of lineage colonization ages may be more informative than surrogates based on island traits (i.e. subaerial ages) when testing for biogeographical predictions of terrestrial Canarian taxa.

In sum, we have outlined a spatio-temporal scenario where episodes of Pleistocene extinction may account, in addition to limited habitat heterogeneity, for the unique patterns of plant biodiversity of these islands. The peculiar spatial configuration of the Canary Islands (e.g. ECI closeness to continental masses and large emerged area) probably makes our predictions of limited applicability to more isolated archipelagoes (e.g. Hawai'i, Galápagos, Juan Fernández), but the biogeographical consequences anticipated by our conceptual framework might be mirrored by other terrestrial Canarian groups and, importantly, by land taxa occurring on other near-shore archipelagoes (e.g. Ryukyu, Izu, California Channel islands). Further studies with explicit assumptions on the imprint of Pleistocene extinction are needed to draw a general pattern of the factors affecting island terrestrial biodiversity within discrete temporal scales.

ACKNOWLEDGEMENTS

The development of ideas found in this manuscript has been possible thanks to many contributions made by all those colleagues who devoted their time to understanding the fascinating biodiversity of the Macaronesian islands. We also appreciate the insightful comments provided by three anonymous reviewers for

manuscript improvement. C. G.V. was funded by project SV-17-GIJON-BOTANICO. J.P. was funded by the MINECO through the Ramón y Cajal Program (RYC-2016-20506), and Marie Skłodowska-Curie COFUND, Researchers' Night and Individual Fellowships Global (MSCA grant agreement No 747238, 'UNISLAND').

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Keywords


background extinction, colonization patterns, glacial refugia, island biogeography, Mahan, Pleistocene climatic shifts

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How to cite this article: García-Verdugo C, Caujapé-Castells J, Illera JC, et al. Pleistocene extinctions as drivers of biogeographical patterns on the easternmost Canary Islands. *J Biogeogr.* 2019;46:845–859. <https://doi.org/10.1111/jbi.13563>