



# Inter-island colonization, and evolutionary processes in the Canarian endemic genus *Parolinia* Webb (Brassicaceae): implications for its conservation

Miguel Ángel González-Pérez<sup>1</sup> · Olga Fernández-Palacios<sup>1</sup> · Peter Beerli<sup>2</sup> · Antonio Díaz-Pérez<sup>3,4</sup> · Juli Caujapé-Castells<sup>1</sup>

Received: 11 July 2024 / Accepted: 26 November 2024  
© The Author(s), under exclusive licence to Springer Nature B.V. 2024

## Abstract

The Canary Islands are oceanic islands that encompass a wide diversity of geological ages, sizes, ecological regions, and orographic contexts that determine different isolation frameworks and provide a suitable geographical setting to address questions regarding genetic variation patterns and colonization processes. In the present study, we used nuclear microsatellites to quantitatively determine gene flow, colonization patterns, and geographical barriers in the Canarian endemic genus *Parolinia*, taking into account the dynamic geological ontogeny of the islands. Our genetic analyses showed a high number of shared alleles (68%) and low interspecific genetic differentiation, suggesting both a close relationship among the species of *Parolinia* and a likely recent origin of this Canarian endemic genus. MIGRATE analysis suggested a westward stepping stone colonization pattern from Gran Canaria to Tenerife, and then to La Palma and La Gomera. Supporting this hypothesis, *P. schizogynoides* (La Gomera Island) and *P. aridanae* (La Palma Island) clustered together in the STRUCTURE and PCoA analyses, and showed a high number of shared alleles and low genetic differentiation, which also suggests a recent migration from an ancestor from Tenerife Island. In addition, these analyses also point to *P. ornata* (Gran Canaria Island) as the genetically closest taxon to the putative ancestor of the genus. In view of the existence of genetic relationships within *Parolinia*, any population reinforcement programs should be carried out using genetic material with strict geographic and, when possible, genetic traceability to prevent anthropogenic hybridization. Translocations of individuals between different distribution areas should be avoided, and the most endangered species should be adequately represented in seed banks.

**Keywords** Colonization · Endemic species · Gene flow · Islands evolution · Speciation

## Introduction

Isolation is a key factor for the biological diversification processes on oceanic islands. Most factors that promote isolation are the consequence of natural geographical barriers that greatly favor the accumulation of genetic differences within and among populations, and eventually lead to the appearance of new taxa (Carson and Clague 1995; Caujapé-Castells et al. 2017; González-Pérez and Caujapé-Castells 2022). Yet, if geographical barriers disappear or are sufficiently permeable to allow dispersal, natural conspecific populations can constitute large metapopulations where genes may be exchanged between adjacent or nearby subpopulations (Kimura and Weiss 1964). A common outcome of such a situation is that the extent of gene flow does

✉ Miguel Ángel González-Pérez  
miguelglezprez@gmail.com

✉ Juli Caujapé-Castells  
julicaujape@gmail.com

<sup>1</sup> Jardín Botánico Viera y Clavijo-Unidad Asociada de I+D+i al CSIC (Cabildo de Gran Canaria), Camino del Palmeral 15, Las Palmas de Gran Canaria 35017, Spain

<sup>2</sup> Dept. of Scientific Computing, Florida State University, 400 Dirac Science Library, Tallahassee, FL 32306-4120, USA

<sup>3</sup> Gestión y Planeamiento Territorial y Medioambiental S. A., C. León y Castillo, 54, Las Palmas de Gran Canaria 35003, Spain

<sup>4</sup> Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela

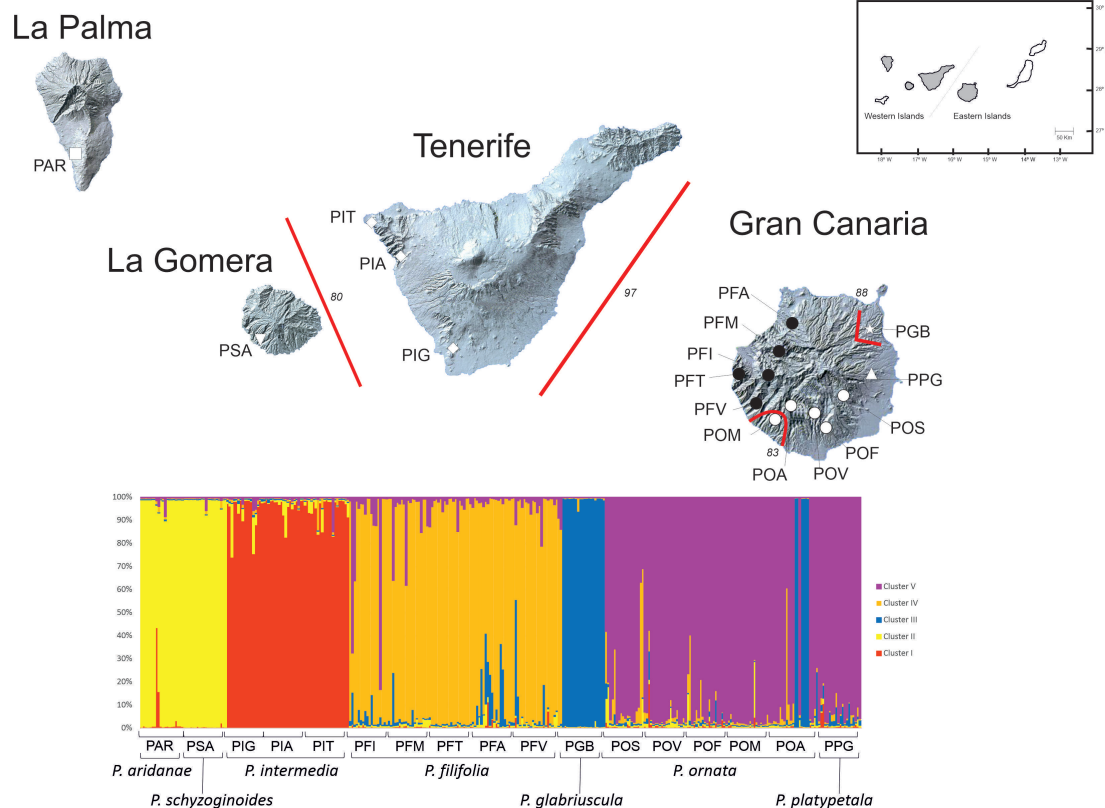
not exceed the distribution range of the subpopulations, thus preventing the formation of a single panmictic unit in the meta-population and producing a type of isolation called “isolation by distance” (Wright 1943; Kimura and Weiss 1964).

The natural isolation of oceanic archipelagos turns them into unique systems for studying evolutionary processes that promote speciation (Grant 1998; Losos and Ricklefs 2009), and for testing biogeographical models related to the origins and diversification of their biotas (Emerson 2002; Whittaker and Fernández-Palacios 2007; Sanmartin et al. 2008). Due to anthropogenic activities, oceanic islands are rapidly becoming models to study extinction, so the results of genetic investigations often help improve the conservation status of the most endangered taxa.

The Canary archipelago belongs to the Mediterranean biodiversity hotspot (Myers et al. 2000) and consists of seven major oceanic islands (Fig. 1) which host the most diverse flora in the Macaronesian region. The Canaries encompass a wide diversity of geological ages (spanning from 1.1 My of El Hierro and 23 My of Fuerteventura; van den Bogaard 2013), sizes, ecological regions and orographic contexts that determine different isolation frameworks, and

provide a suitable geographical setting to address questions about genetic variation patterns and colonization processes (Juan et al. 2000; Emerson 2002). Together with the biological features of the colonizing biota, the different geological ontogenies of the islands (Stuessy 2007; Caujapé-Castells et al. 2017), and their auspicious climatic conditions during the Pleistocene and Pliocene (Maley 1980; Rodríguez-Sánchez et al. 2009) have influenced the levels and distribution of population genetic diversity, and potentially affected the evolutionary ways of many lineages. Many of the extant Canarian endemic plants evolved locally from refuged taxa that avoided extinction during extremely dry and cold periods on the mainland throughout the Pleistocene glaciations (Bramwell 1979; Hewitt 2004; Caujapé-Castells et al. 2022). After colonization, diversification forces like stochasticity, migration, geographic isolation, or hybridization have also largely contributed to shaping the diversity of the endemic flora through gene flow levels between and within islands.

The population genetic diversity of the Canarian endemic flora is relatively high for an oceanic insular enclave (Francisco-Ortega et al. 2000; Pérez de Paz and Caujapé-Castells 2013), and its origins are still the subject of debate. While Silvertown et al. (2005) argue that most groups are



**Fig. 1** Geographical location of the sampled populations of *Parolinia*, and boundaries of genetic differentiation detected by BARRIER. The red lines and the numbers represent, respectively, the barriers and their statistical support (from 100 bootstrapped matrices). Each symbol represents a *Parolinia* taxon. The diagram below summarizes the

clustering results obtained with the Bayesian program STRUCTURE assuming five clusters (K = 5). Each individual is represented by a thin vertical line, which is partitioned into K coloured segments that represent the individual’s estimated membership fractions in K clusters. Populations are coded as in Table 1

monophyletic and multiple colonizations are prevented by competition with earlier colonizers (the ‘niche preemption hypothesis’), the ‘surfing syngamenon hypothesis’ (Caujapé-Castells et al. 2017) suggests that monophyly is mostly artifactual, because high migration rates from the mainland to the archipelago and among the islands likely facilitated secondary contact among lineages previously isolated in the mainland. According to this hypothesis, the high genetic diversity generated by admixture among these colonizers (see also Herben et al. 2005; Saunders and Gibson 2005) would have generated spurious monophyly, and favoured both lineage diversification and the colonisation of new areas (see also Crawford and Whitney 2010). Understanding the processes that underlie island colonization and diversification is important to suggest informed hypotheses on the origins of genetic diversity in the Canarian endemic flora, and its conservation.

*Parolinia* Webb (Brassicaceae) is a Canarian endemic genus that comprises seven species distributed in four of the seven islands of the archipelago (Fig. 1). These plants are woody perennials up to 2.5 m high occurring on dry and sunny slopes of the xerophytic Canarian zone from the coast to 1000 m a.s.l. All species are diploid ( $2n=22$ ) and have hermaphrodite flowers with homomorphic sporophytic self-incompatibility (Borgen 1969; Bramwell et al. 1972; Febles 1989; Fernández-Palacios 2010). Diverse insects (bees, wasps, etc.) visit the flowers and seed dispersal is anemochorous (Bramwell 1986; Hohmann et al. 1993).

Gran Canaria hosts four species (*Parolinia ornata* Webb, *P. platypetala* Kunkel, *P. filifolia* Kunkel, and *P. glabriuscula* Montelongo & Bramwell), and the other three islands of distribution harbour only one species each: *P. intermedia* Svent. & Bramwell occurs in Tenerife, *P. schizogynoides* Svent. in La Gomera, and *P. aridanae* Santos-Guerra in La Palma. Most of these species are protected by the Canarian catalogue of threatened species (*Ley 4/2010, de 4 de junio, del Catálogo de Especies Canarias*). According to the Red List of Spanish vascular flora (Bañares et al. 2010), two of them are critically endangered (*P. platypetala* and *P. glabriuscula*); one is endangered (*P. filifolia*), and two are vulnerable (*P. intermedia* and *P. schizogynoides*). *Parolinia aridanae* is considered critically endangered, especially after the very recent Tajogaite eruption in La Palma.

Previous investigations carried out with nuclear and chloroplastic DNA sequences (Jaén-Molina et al. 2007) revealed low phylogenetic differentiation among the seven species of the genus, which were resolved as monophyletic and closely related to the mainland African genera *Diceratella* and *Morettia*. ITS sequences gave a sister basal position to *P. intermedia* from Tenerife (Jaén-Molina et al. 2007) and Fernández-Palacios et al. (2004, 2006) and Fernández-Palacios (2010) hypothesized that *P. filifolia* is the taxon

genetically closest to the putative ancestor of the genus. Besides, these authors detected high micro-morphological and allozyme intra-population variation, but a low genetic inter-population differentiation. Although a more highly polymorphic molecular marker could better resolve the relationships and gene flow among the species. In this sense, González-Pérez and Caujapé-Castells (2022) carried out a genetic analysis of nuclear microsatellite loci in the four endemic species from Gran Canaria. These authors suggested that ancestral hybridization, vicariance and dispersal events linked to the complex ontogeny of the island may have been key factors to shape the current genetic diversity and structure of *Parolinia* in Gran Canaria.

We lack evidence of the relative antiquity of this endemic genus, but the low genetic differentiation detected among populations despite high intra-population genetic variation (Fernández-Palacios et al. 2004, 2006; Fernández-Palacios 2010; González-Pérez and Caujapé-Castells 2022), suggests that it could be a neoendemic, tentatively derived from extinctions of its closest mainland relatives during the late Pleistocene glaciations, as hypothesized in a recent phylogeographic investigation (Caujapé-Castells et al. 2022).

Thus, despite the research developed for *Parolinia*, there are still open questions on its genetic diversity and inter-island colonization which can be assessed by applying inferential statistical tools to genetic data. Nuclear microsatellites are hypervariable genetic markers that revealed a relevant role of past hybridization in the widespread *P. ornata* and *P. filifolia* from Gran Canaria (González-Pérez and Caujapé-Castells 2022), and may provide further clues to test different hypotheses about the patterns and tempos of colonization of the Canarian archipelago by *Parolinia*. Nuclear microsatellites also may contribute informed conservation strategies for these endemic species, most of them endangered (see above). Indeed, the distribution of genetic diversity in natural populations is one of the major concerns of conservation biology, given the degree to which it may affect the long-term evolutionary potential of species and populations (Ouborg 2010; González-Pérez et al. 2013).

In this investigation, we use eight nuclear microsatellites (González-Pérez and Caujapé-Castells 2014, 2022) on an exhaustive sampling of all the species of *Parolinia* to (1) propose an inter-island dispersal hypothesis for these species, (2) explore their populational genetic diversity, differentiation, and structure, (3) study barriers to gene flow and migration pattern within and among islands, and (4) inform the ongoing conservation strategies for the most endangered species.

## Materials and methods

### Plant material

In order to estimate the genetic diversity, differentiation and relationships among the seven species of *Parolinia*, an extensive and intensive population sampling was carried out representing 335 individuals from 17 populations (Table 1; Fig. 1). Using the distributional information available in the Banco de Datos de Biodiversidad de Canarias (Gobierno de Canarias, <https://www.biodiversidadcanarias.es/biota>), we surveyed and collected representative samples from a high percentage of all the extant populations of the genus (Table 1). These included the four endemic species of Gran Canaria (the only extant populations of *P. glabriuscula* and *P. platypetala*, and a comprehensive geographic representation of the more widespread *P. filifolia* and *P. ornata*); three populations of *P. intermedia* from Tenerife; the populations of *P. schizogynoides* from La Gomera; and the only known population of *P. aridanae* from La Palma. All sampling was conducted with prior permission from the Government of the Canary Islands (permit number 2017/6818).

### DNA isolation and microsatellite analysis

DNA was extracted following a slightly modified 2xCTAB protocol (Doyle and Doyle 1987) from silica-gel dried young leaves that were ground in a Mixer-Mill (RETSCH MM 301, Haan, Germany), with two glass balls in each micro-tube. About 150  $\mu$ l of each total DNA sample was purified using a Genelute PCR Clean-Up Kit (Sigma-Aldrich, St. Louis, MO, USA) for further analysis.

Forward and reverse primers specifically developed for *P. ornata* (González-Pérez and Caujapé-Castells 2014) were used to amplify eight polymorphic microsatellite loci. Polymerase Chain Reactions (PCR) were performed in a final volume of 12  $\mu$ L that contained approximately 20 ng of DNA, 10 pmol of each primer, and 7  $\mu$ L PCR Master Mix (Premix Taq, TaKaRa BIO INC., Otsu, Japan).

PCR products were detected using an ABI 3130XL Genetic Analyzer and fragment sizes were determined using GENEMAPPER v 4.0 (Applied Biosystems, Inc.), which allowed us to identify allele peak profiles at each locus, and to assign genotypes to each individual, considering their diploid nature.

**Table 1** Genetic diversity indices in the *Parolinia* species and populations sampled

Population	Code	Island	N°	A	NE	H <sub>o</sub>	H <sub>e</sub>	%P
<i>P. aridanae</i>								
El Remo	PAR	La Palma	20	2.63	0	0.342	0.328	62.50
<i>P. schizogynoides</i>								
Argaga	PSA	La Gomera	20	3.00	3	0.381	0.357	62.50
<i>P. intermedia</i>								
Teno	PIT	Tenerife	20	3.63	1	0.471	0.447	75.00
Guaza	PIG	Tenerife	20	3.50	1	0.275	0.343	87.50
Tamaimo	PIA	Tenerife	17	3.25	2	0.463	0.421	87.50
Overall <i>P. intermedia</i>			57	5.38	4	0.399	0.463	100
<i>P. glabriuscula</i>								
Bandama	PGB	Gran Canaria	20	2.63	0	0.443	0.417	100
<i>P. platypetala</i>								
Guayadeque	PPG	Gran Canaria	20	4.25	3	0.430	0.484	100
<i>P. ornata</i>								
Sorrueda	POS	Gran Canaria	20	4.75	2	0.394	0.495	100
Fataga	POF	Gran Canaria	20	4.13	0	0.506	0.523	100
Mogán	POM	Gran Canaria	20	3.88	2	0.453	0.464	100
Ayagaures	POV	Gran Canaria	19	4.88	2	0.447	0.499	100
Bco. Arguineguin	POA	Gran Canaria	20	5.13	1	0.463	0.648	100
Overall <i>P. ornata</i>			98	8.25	9	0.454	0.600	100
<i>P. filifolia</i>								
Inagua	PFI	Gran Canaria	20	5.00	1	0.500	0.533	100
Mesa Junquillo	PFM	Gran Canaria	20	4.50	2	0.504	0.514	100
Tasartico	PFT	Gran Canaria	19	4.00	4	0.467	0.494	100
Agaete	PFA	Gran Canaria	20	6.25	5	0.619	0.704	100
Veneguera	PFV	Gran Canaria	20	5.13	1	0.483	0.643	100
Overall <i>P. filifolia</i>			97	9.50	17	0.518	0.664	100

N° number of individuals analyzed, A: Average number of alleles per locus, NE: number of exclusive alleles, H<sub>o</sub>: Observed heterozygosity, H<sub>e</sub>: Expected heterozygosity, P: Polymorphic loci percentage

## Data analysis

The genotypic data matrix was entered into Transformer-4 v. 2.0.2 (Caujapé-Castells et al. 2013) which allowed us to export the data to different software programs. The standard within-population genetic diversity statistics were calculated with GENALEX v 6.5 (Peakall and Smouse 2006): mean number of alleles ( $A$ ), number of exclusive alleles ( $NE$ ), observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosity. The genetic differentiation coefficient ( $R_{ST}$ ) between all possible population pairs was estimated using SPAGeDi v 1.5 (Hardy and Vekemans 2002). As null alleles can overestimate  $F_{IS}$  values, the Bayesian program INEST 2.2 (Chybicki and Burczyk 2009) was used to simultaneously estimate the presence of null alleles and get corrected values of  $F_{IS}$ , with 50,000 burn-in cycles and 500,000 Markov Chain Monte Carlo (MCMC) iterations in total. To detect the potential existence of inbreeding effects in our dataset, INEST was run using the models 'nfb' (null alleles, inbreeding coefficients, and genotyping failures) and 'nb' (null alleles and genotyping failures).

To test the extent of genetic drift in the sampled populations, the occurrence of recent bottlenecks test was explored using INEST 2.2 software (Chybicki and Burczyk 2009), under the infinite allele model (IAM), the stepwise mutation model (SSM) and an intermediate, two-phased model (TPM).

An analysis of molecular variance (AMOVA; Excoffier et al. 1992) was performed using the software ARLEQUIN 3.0 (Excoffier et al. 2005), to calculate variance components and partitioning the variation 'between species', 'among populations within species' and 'within populations' for the entire data set. Subsequently, separate AMOVA models were analysed to test the distribution of genetic variance among and within populations of the species where/when? more than one population was analysed (*P. intermedia*, *P. filifolia* and *P. ornata*).

To represent the genetic relationships among populations, a principal coordinate analysis (PCoA) was made in GENALEX v 6.5 (Peakall and Smouse 2006) based on the allele frequencies of populations. The analyses of differentiation patterns were conducted following population-based approaches.

To investigate interspecific divergence, we first identified population structure, using the Bayesian clustering procedure STRUCTURE 2.2 (Falush et al. 2007) to infer the number of genetic clusters ( $K$ ), and to assign each sampled individual to one of them. The most likely value of  $K$  was assessed by comparing the likelihood of the data for different values of  $K$ . The algorithm uses Markov Chain Monte Carlo (MCMC) iterations to explore a parameter space considering individual memberships to the  $K$  clusters, ranging

from  $K=1$  (thus testing the null hypothesis of panmixia) to  $K=17$  (the total number of sites sampled). Each MCMC search was replicated 10 times for each  $K$ , with burn-ins of 100,000 and 1,000,000 replicates, and assuming an admixture model and correlated allele frequencies. Choosing a value of  $K$  that maximizes the posterior probability of the data (PPD) can be difficult to apply for complex data sets with many groups (Rosenberg et al. 2002). In the case of highly structured data, the most divergent groups separate first into distinct clusters as  $K$  is increased. Since the aim should be to find the smallest value of  $K$  that best captures the structure in the data, a second way to choose  $K$  is to consider the successive increase of the PPD for increasing values of  $K$ , which can be regarded as the increase in information at each addition of a set of allele frequencies. So, the optimum  $K$ , indicating the number of true clusters in the data, was also determined using the  $\Delta K$  criterion applying methods described by Evanno et al. (2005), and implemented in STRUCTURE HARVESTER (Earl & von Holdt, 2012). Populations and individuals were assigned to a particular cluster if their proportion of membership ( $q_i$ ) to that cluster was equal to or larger than an arbitrary threshold of 0.800.

To investigate the effects of geographical barriers on the distribution of genetic variability and population structure, we used the approach implemented in BARRIER 2.2 (Manni et al. 2004). The spatial organization of sub-populations was modelled by Voronoi tessellation, and a maximum-difference algorithm (Monmonier's algorithm) identified the borders between neighboring populations that exhibited the highest levels of genetic differences (Manni et al. 2004). One hundred permutations of pairwise matrices of population differentiation based on Nei's distance (Nei 1978) were used to assess the consistency of the boundaries detected by the algorithm. Only barriers with support > 70% were considered. The statistical significance of the relation between the genetic and geographic distances (isolation by distance) was assessed through a Mantel test using the IBD software (Bohonak 2002).

Historical gene flow was estimated using the Bayesian inference and Brownian motion approximation to the microsatellite ladder model implemented in the MIGRATE-n 5.0.4 software (Beerli and Felsenstein 2001). Nine evolutionary models were tested considering different clusters (islands, species, clusters inferred by STRUCTURE, etc.) and evolutionary processes (Table S4.). One long chain was run saving 50,000 generations with sampling increments of 100 generations after a burn-in period of 1,000,000 generations. Prior distributions were uniform with a range from 0.00 to 20.00 for Theta ( $\Theta$  which is  $4x$  the effective population size  $\times$  the mutation rate per locus) and for migration rate ( $M$  which is the mutation-scaled immigration rate). A static



heating scheme was applied with four temperatures of 1, 1.5, 3 and  $1 \times 10^6$  (Beerli and Palczewski 2010).

Contemporary rates of gene flow among species and migration directions were estimated with BAYESASS v 3.0 (Wilson and Rannala 2003). This program was run multiple times with different seeds, comparing the posterior mean parameter estimates for concordance, as recommended by the authors. In all cases, the runs consisted of 20,000,000 generations with a burn-in of 5,000,000 and sampling increments of 200. Parameters for migration rates, inbreeding coefficients, and allele frequencies were set to respectively 0.1, 0.3, and 0.2, to ensure adequate mixing and acceptance rates between 0.2 and 0.6 (Wilson and Rannala 2003).

## Results

### Genetic diversity

A total of 105 different alleles were observed in the eight polymorphic loci surveyed, ranging from six to 16 per locus. At the species level, the two more widespread species (*P. ornata* and *P. filifolia*, both from Gran Canaria) showed much higher genetic diversity values ( $H_e = 0.600$  and  $H_e = 0.664$ , respectively) than the more narrowly distributed species from Gran Canaria (*P. glabriuscula* and *P. platypetala*,  $H_e = 0.417$  and  $H_e = 0.484$ , respectively), from Tenerife (*P. intermedia*;  $H_e = 0.463$ ), from La Gomera (*P. schizogynoides*,  $H_e = 0.357$ ) and from La Palma (*P. aridanae*,  $H_e = 0.382$ ) (Table 1).

The AMOVA showed that the largest proportion of genetic variation (68.25%) was found within populations, and only 20.43% among species (Table S1). At the species level, the genetic variation within populations was similar for the three species with multiple populations (83% in *P. intermedia*, 87% in *P. ornata*, and 87% *P. filifolia*).

### Genetic differentiation among populations

We detected 30 private alleles (i.e. exclusive of one species) in all taxa except *P. aridanae* and *P. glabriuscula*. However, only in *P. intermedia*, *P. schizogynoides* and *P. filifolia* they did have frequencies higher than 5% (Table 1). All populations except PGB and PAR showed private alleles, with frequencies higher than 5% in six of them (PSA, PIT, PIA, PFM, PFT and PFA).

Overall, 71 alleles out of 105 (68%) were shared between different combinations of species. The highest numbers of shared alleles were detected within Gran Canaria (52 between *P. ornata* and *P. filifolia*, 11 of them exclusively), and between Tenerife and Gran Canaria (*P. intermedia* shared 30 and 31 alleles with *P. filifolia* and *P. ornata*,

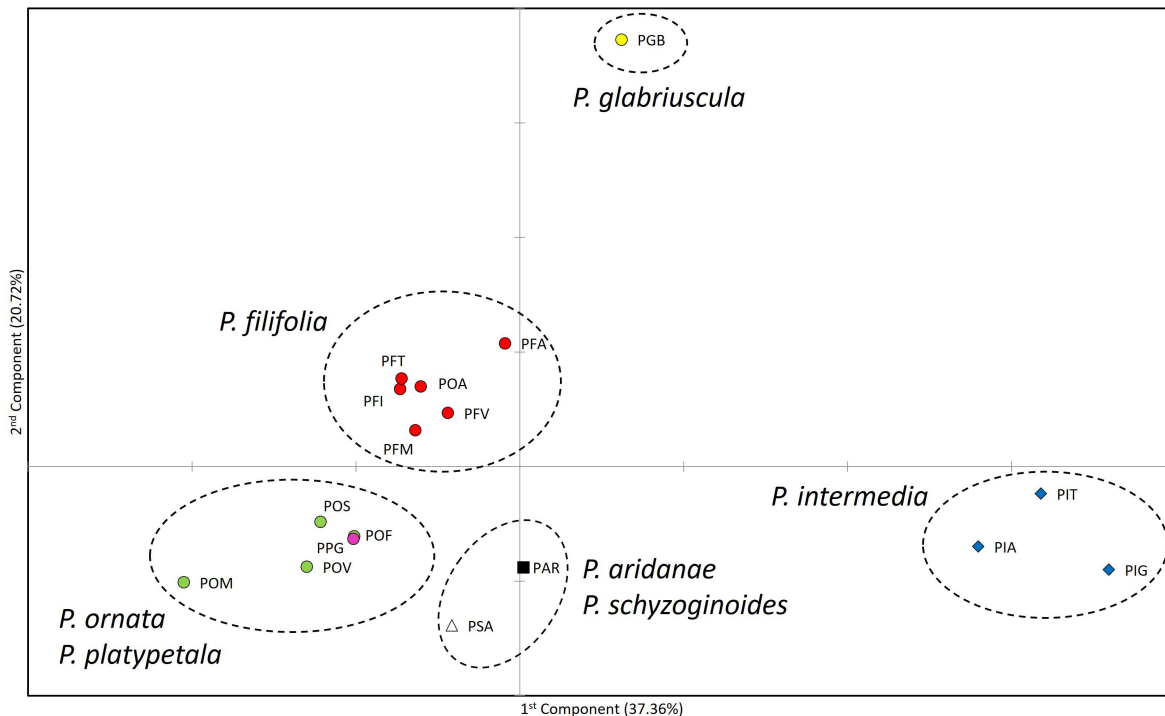
respectively, none of them exclusively). Finally, in Gran Canaria, *P. platypetala* shared 28 alleles with *P. filifolia* and *P. ornata*. *Parolinia aridanae* from La Palma and *P. schizogynoides* from la Gomera shared 11 alleles, none of them exclusively.

The values of the genetic differentiation coefficient ( $R_{ST}$ ) between population pairs (Table S2) ranged from  $R_{ST} = 0.005$  between PFV (*P. filifolia*) and POA (*P. ornata*), to  $R_{ST} = 0.872$  between PAR (*P. aridanae*) and POV (*P. ornata*). The high number of shared alleles between *P. filifolia* and *P. ornata* was also reflected in the moderate average pairwise  $R_{ST}$  between both species (0.297). The average value of  $R_{ST}$  between populations from the western islands and Gran Canariawas considerably high (0.745). However, the average  $R_{ST}$  among western island populations was 0.237, and among Gran Canaria populations was 0.249 (Table S2).

Our analyses with the INEST software concluded that inbreeding is a significant component of the model in three of the five populations of *P. filifolia* (PFI, PFM and PFT); in one of the five populations of *P. ornata* (POF), in one of the three populations of *P. intermedia* (PIA), and in the single existing population of *P. aridanae* (PAR). Null allele frequencies ranged from 0 to 0.14, and therefore the bias introduced by null alleles could be considered negligible (Dakin and Avise 2004). Wilcoxon tests implemented in the INEST 2.2 software detected heterozygosity excesses in POA, PGB, PFA, PFV, PIT and PSA under the IAM model, indicating recent bottlenecks in these populations (Maruyama and Fuerst 1985).

### Spatial patterns of genetic diversity

The rate of change of the likelihood function with respect to  $K$  in the STRUCTURE analysis using the total dataset (335 individuals, eight microsatellite loci, 17 populations) reached its maximum at  $K=5$  groups (Fig. 1, Fig. S1), corresponding to: all populations of *P. intermedia* (cluster I); *P. aridanae*+*P. schizogynoides* (cluster II); *P. glabriuscula*+some individuals of *P. ornata* from Arguineguín (cluster III); *P. filifolia* (cluster IV); and *P. ornata*, *P. platypetala*, and the remaining individuals of *P. ornata* from Arguineguín (cluster V). The two principal components of the PcoA analysis accounted for 58.08% of the total variance and was largely consistent with the STRUCTURE results (Fig. 2). *Parolinia intermedia* (Tenerife) and *P. glabriuscula* (Gran Canaria) occupied distant zones of the multivariate space. The overall shorter distances among the rest of populations indicated different degrees of species closeness; thus, the distributions of *P. ornata* and *P. filifolia* populations (both from Gran Canaria) showed a lower degree of overlap, whereas those of *P. aridanae* (La Palma) and *P. schizogynoides* (La Gomera) were more tightly clustered,



**Fig. 2** PCoA analysis are based on the allele frequency of eight scored microsatellite loci genotypes in the sampled *Parolinia* populations. The percentage of the explained variance of each axis is given in

and those of *P. platypetala* (from Gran Canaria) substantially overlapped with *P. ornata*.

The BARRIER software detected a primary order barrier that isolated Tenerife Island from Gran Canaria and La Gomera islands (Fig. 1). A further barrier to gene flow was identified within Gran Canaria Island between the *P. glabriuscula* population and the rest, and a secondary order barrier between population POM (*P. ornata*) and its neighbouring populations (Fig. 1). In accordance, Mantel test between genetic ( $F_{ST}$ ) and geographic distances detected significant IBD among the populations of *Parolinia* throughout the archipelago ( $r=0.704$ ;  $p<0.001$ ) (Fig. S2).

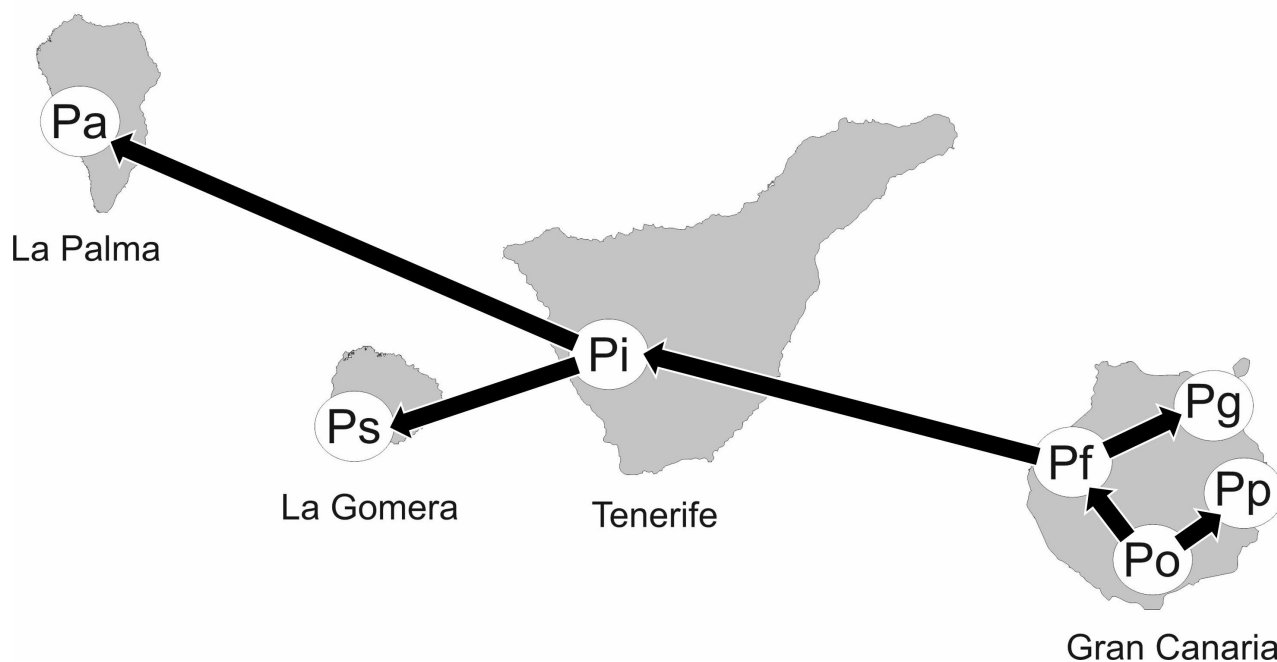
The most likely of the nine models tested in MIGRATE models assumed isolation of species units without migration events (Table S4). This model detected a split of *P. aridanae* and *P. schizoginoides* from *P. intermedia*. According to this model, *P. intermedia* and *P. glabriuscula* would have split from *P. filifolia*. Finally, *P. filifolia* and *P. platypetala* would have diverged from *P. ornata* (Fig. 3). However, BAYES-ASS detected significant contemporary migration from *P. ornata* to *P. platypetala* ( $m=0.259$ ) (Table S3).

parentheses. Populations are coded as in Table 1. Dashed circles represent the five clusters inferred by Bayesian cluster analysis

## Discussion

### Genetic diversity

Whereas genetic diversity detected in *P. intermedia* ( $H_e = 0.463$ ), *P. glabriuscula* ( $H_e = 0.417$ ), and *P. platypetala* ( $H_e = 0.484$ ) were similar to those reported for endemic species ( $H_e = 0.42$ ; Nybom 2004), *P. aridanae* ( $H_e = 0.328$ ) and *P. schizoginoides* ( $H_e = 0.357$ ) exhibited a lower genetic variation, in concordance with their hypothesized recent divergence from a common ancestor (Table 1). Furthermore, *P. filifolia* ( $H_e = 0.664$ ) and *P. ornata* ( $H_e = 0.600$ ) showed the highest genetic diversities, similar to those detected with nuclear SSRs in other Canarian endemic plant species: *Morella rivas-martinezii* ( $H_e = 0.56$ ; González-Pérez et al. 2009a, b), *Olea europaea* ssp. *guanchica* ( $H_e = 0.63$ ; García-Verdugo et al. 2010), *Sambucus palmensis* ( $H_e = 0.50$ ; Sosa et al. 2010) or *Juniperus phoenicea* ssp. *turbinata* ( $H_e = 0.60$ ; García et al. 2018). On the whole, higher genetic variability has been recorded in Canarian plant endemics than in those distributed in other oceanic islands (Francisco-Ortega et al. 2000; Caujapé-Castells and Pérez de Paz 2013).



**Fig. 3** Split model of the *Parolinia* species inferred by MIGRATE-n software. Pa: *P. aridanae*, Pf: *P. filifolia*, Pg: *P. glabriuscula*, Pi: *P. intermedia*, Po: *P. ornata*, Pp: *P. platypetala*, Ps: *P. schyzoginooides*

### Genetic relationships among species

As revealed by Bayesian cluster analysis, the 17 assessed populations are ascribed to five genetic pools which appear to have maintained their genealogical cohesiveness; three of these were localized in Gran Canaria and correspond to *P. glabriuscula*, *P. filifolia* and *P. ornata*-*P. platypetala* (Fig. 1). These findings may be correlated with ontogenetic events that generated geographical or ecological barriers to gene flow, or with the colonization of new distribution ranges as they became available (González-Pérez and Caujapé-Castells 2022).

A high number of shared alleles, the low interspecific genetic differentiation detected in the present study, and the scarce phylogenetic differentiation found with nuclear and chloroplastic DNA (Jaén-Molina et al. 2007) suggest a close relationship among the species of *Parolinia*, and likely a recent origin of this Canarian endemic genus; the latter possibility is also bolstered by the finding that the current

taxonomical separation of the seven species of *Parolinia* is not supported by DNA barcoding analyses (Jaén-Molina et al. 2014). Jaén-Molina et al. (2014) obtained an unresolved tree for *Parolinia ornata*, *P. filifolia* and *P. platypetala* using ITS1 and ITS2 DNA sequences. The high contemporary migration rate detected between *P. ornata* and *P. platypetala*, as well as the grouping of both species in STRUCTURE and PCoA analysis, support that *P. platypetala* represents the early stages of an incipient speciation process, as hypothesized by González-Pérez and Caujapé-Castells (2022).

Despite the overall phylogenetic closeness, our detailed MIGRATE analyses allow us to suggest a first colonization event of Gran Canaria from the mainland, followed by recent and rapid processes of (i) divergence of the four species currently known in this island, which sustain high levels of contemporary gene flow and hybridization (see González-Pérez and Caujapé-Castells 2022); and (ii) island hopping from Gran Canaria to Tenerife by the ancestor of *P. intermedia*. *Parolinia intermedia* has not yet diverged in Tenerife, but our data (Fig. 3) support that the current endemics



of La Palma and La Gomera, *P. aridanae* and *P. schizogynoides*, likely originated from a recent migration from an ancestor related to this species. Similar East-to-West inter-island colonization patterns have been described for other Canarian endemic lineages, e.g. *Descurainia* (Goodson et al. 2006), *Argyranthemum* (Asteraceae, Francisco-Ortega et al. 2000, 2001), or *Phoenix* (Arecaceae, Saro et al. 2015). Mantel test furnishes additional support for this hypothesis in *Parolinia* by detecting significant isolation by distance among the analyzed populations (Fig. S1). Thus, aligning with the tenets of the 'surfing syngamenon hypothesis' (Caujapé-Castells et al. 2017), it is feasible that the high levels of genetic variation attained through past and recent hybridization processes involving populations from Gran Canaria (González-Pérez and Caujapé-Castells 2022) may have facilitated rapid colonization of the Western islands where the genus is distributed. However, we cannot discard that the colonization of the archipelago was initially through the easternmost islands of Lanzarote and Fuerteventura, but because these islands are the oldest ones (15 and 23 Mya respectively; Van den Bogaard 2013) and the most eroded, the initial populations there could have gone extinct.

These results are at odds with the genetic and phylogenetic data available for the genus (Fernández-Palacios 2010; Jaén-Molina et al. 2007), which detected a sharp genetic diversity discontinuity between the island of Gran Canaria and the western group of islands (Tenerife, La Palma and La Gomera), and suggested that *Parolinia* may not have followed an east-to-west stepping-stone colonization, in line with other phylogenetic investigations, e.g. Curto et al. (2017) in *Micromeria* (Lamiaceae), White et al. (2020) in *Argyranthemum* (Asteraceae), García-Verdugo et al. (2021) in *Bituminaria* (Fabaceae).

Without natural selection and genetic drift, gene flow leads to genetic homogeneity among populations within a metapopulation (e.g. Kimura and Weiss 1964). *Parolinia intermedia* populations form a homogeneous and isolated group in the STRUCTURE and PCA analyses (Figs. 1 and 2), and this species is distributed in a wide ecological niche ranging up to 450 masl in the Western part of Tenerife. As indicated by the high migration rate within *P. intermedia* ( $m = 0.964$ , Table S3) and its moderate inter-population differentiation coefficient (average  $R_{ST} = 0.139$ ), considerable gene flow could exist among many of its areas of occurrence, largely limiting differentiation processes.

By contrast, a higher topographical complexity (with geographic barriers overcoming 1000 m asl) may have impeded gene flow and promoted rapid population divergence through geographic isolation in several zones of Gran Canaria. This possibility is consistent with the high pairwise overall genetic differentiation coefficient of the *Parolinia* populations within this island (average  $R_{ST} = 0.249$ ,

Table S2). Thus, the distribution range of *Parolinia* in Gran Canaria contains several genetic islands within its territory, in agreement with the suggestion that lineage diversification should be especially evident in insular regions with sharp ecological and geographical discontinuities (e.g. Caujapé-Castells et al. 2017). The habitats of the *Parolinia* species in Gran Canaria also encompass a wider ecological heterogeneity than in Tenerife. Together with the complex ontogenetic geological history and the older age of Gran Canaria, this factor could have stimulated the diversification of the genus on this island, aided by the greater genetic diversity attained through hybridization (González-Pérez and Caujapé-Castells 2022).

### Conservation guidelines

As is often the case in all oceanic archipelagos, the main threats to the conservation and proper scientific management of *Parolinia* species are anthropogenic; countering them poses great scientific challenges, as our genetic results often suggest contrasting actions. Considering the tight genetic relationship among the *Parolinia* species, conservation strategies should focus on facilitating and monitoring the conditions that allow the ongoing diversification processes in all the islands of distribution.

Different conservation strategies are thus possible according to genetic results. In the first place, seed dispersal in *Parolinia* is anemochorous (Bramwell 1986; Fernández-Palacios 2010), and therefore the natural connectivity among populations seems warranted, not requiring artificial translocation of individuals to maintain population diversity within and among zones of the islands of distribution where migration, colonization, and inter-specific hybridization are developing (Fernández-Palacios 2010; González-Pérez and Caujapé-Castells 2022). It could be the cases of the natural contemporary hybridization detected in Gran Canaria between the widespread *P. ornata* and the narrowly distributed *P. platypetala* (González-Pérez and Caujapé-Castells 2022 and this paper), or the colonization of Tenerife by *P. intermedia* from an ancestor related to the Gran Canarian *P. filifolia*.

A second strategy could be suggested for *Parolinia ornata* and *P. filifolia* from Gran Canaria which maintain widespread distributions in adjacent areas and are not especially endangered. Because we have not detected contemporary natural hybridization between them, translocations of individuals between their distribution ranges should be avoided, and any population reinforcement programs should be carried out using genetic material with strict geographic and, when possible, genetic traceability to prevent anthropogenic hybridization.

A third strategy is suggested in the narrowly distributed species of Gran Canaria (*P. glabriuscula* and *P. platypetala*), La Gomera (*P. schizogynoides*) and La Palma (*P. aridanae*), where extinction risk is a major issue making these species are more affected by diverse and severe threats that induce sharp population decline and fragmentation in all the species of the genus. Consequently, transformation of water-courses, tourism, introduced herbivores (mainly rabbits and feral goats), or invasive plants (e.g., *Cenchrus setaceus*) should be eradicated or mitigated to support the conservation of these species.

The known distribution ranges of all *Parolinia* species are consistently represented in the seed bank of the Botanic Garden Viera y Clavijo, with almost 50 accessions sampled from 1986 to the present, especially focussing on the most endangered species. However, the Canary Islands are very complex geographically, and hardly accessible areas in the known distribution ranges of many relatively widespread species often contain new populations or even taxa yet to be discovered, as illustrated by recent cases in many other lineages (*Lotus gomerythus*, Álvarez et al., 2019; *Thesium palmense*, Rodríguez-Rodríguez et al., 2022; *Cheirolophus barquinii*, Mesa-Coello 2023; *Helianthemum tibiabinae*, Marrero et al. 2023; *Ruta nanocarpa*, Mesa-Coello et al. 2023; or *Sideritis*, Marrero 2023). These considerations advise a thorough chorological review of *P. ornata*, *P. filifolia* and *P. intermedia* to discover potentially new populations or taxa, and to better represent their genetic diversity in our seed and DNA banks.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10592-024-01663-1>.

**Acknowledgements** In memoriam of David Bramwell, former director of the Jardín Botánico Viera y Clavijo and descriptor of *Parolinia glabriuscula*. This research was funded by the project ENCLAVES (MAC/3/C141). We thank the ‘Programa de Cooperación Transnacional Madeira-Azores-Canarias’ of the European Union for support.

**Author contributions** MAGP and JCC conceptualized and designed the research. MAGP, JCC and OFP coordinated fieldwork. Laboratory work was led by MAGP. MAGP, PB and ADP conducted the data analysis. MAGP wrote the manuscript with supervision of JCC. All the authors edited and reviewed the manuscript.

**Data availability** Genotypic data matrix that support results of this study have deposited in the web-site: <https://demiurge.nextgendem.eu/>.

## Declarations

**Competing interests** The authors declare no competing interests.

## References

- Álvarez AM, Martín-Carbajal González J, Reyes-Betancort A, Mesa-Coello RA (2019) *Gomerythusrythus* (Fabaceae-Loteae) Nova. *Bot Macaronés* 30:89–98
- Bañares Á, Blanca G, Güemes J, Moreno Jc OS (eds) (2010) Atlas y Libro Rojo de la Flora Vascular Amenazada de España. Adenda (2010) Dirección General de Medio Natural y Política Forestal (Ministerio de Medio Ambiente, y Medio Rural y Marino)-Sociedad Española de Biología de la Conservación de Plantas. Madrid, 170 pp
- Berli P, Felsenstein J (2001) Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. *Proc Natl Acad Sci* 98:4563–4568
- Berli P, Palczewski M (2010) Unified framework to evaluate panmixia and migration direction among multiple sampling locations. *Genetics* 185:313–326. <https://doi.org/10.1534/genetics.109.112532>
- Bohonak AJ (2002) IBD (isolation by Distance): a program for analyses of isolation by distance. *J Hered* 93:153–154. <https://doi.org/10.1093/jhered/93.2.153>
- Borgen L (1969) Chromosome numbers of vascular plants from the Canary Islands, with special reference to the occurrence of polyploidy. *Nytt Mag Bot* 16:81–121
- Bramwell D (ed) (1979) Plants and islands. Academy, London
- Bramwell D (1986) Contribución a la biogeografía de las islas Canarias. *Bot Macaroné* 14:3–34
- Bramwell D, Humphries CJ, Murray BG, Owens SJ (1972) Chromosome studies in the Flora of Macaronesia. *Bot Notiser* 125:139–152
- Carson H, Clague D (1995) Geology and biogeography of the Hawaiian Islands. In: Wagner WL, Funk VA (eds) Hawaiian biogeography: evolution on a hot spot archipelago. Smithsonian Institution, Washington
- Caujapé-Castells J, Castellano JJ, Ramos R, Henríquez V, Sabbagh I, Quintana-Trujillo FM, Rodríguez JF (2013) Transformer-4 version 2.0.1, a free multi-platform software to quickly reformat genotype matrices of any marker type, and archive them in the demiurge information system. *Mol Ecol Resour* 13:484–493. <https://doi.org/10.1111/1755-0998.12084>
- Caujapé-Castells J, García-Verdugo C, Marrero-Rodríguez A, Fernández-Palacios JM, Crawford DJ, Mort ME (2017) Island ontogenies, syngameons, and the origins of genetic diversity in the canarian flora. *PPEES* 27:9–22. <https://doi.org/10.1016/j.ppees.2017.03.003>
- Caujapé-Castells J, García-Verdugo C, Sanmartín I, Fuertes J, Romeiras MM, Zurita MN, Nebot R (2022) The late pleistocene endemicity increase hypothesis, and the origins of diversity in the Canary Islands Flora. *J Biogeogr* 49:1469–1480. <https://doi.org/10.1111/jbi.14394>
- Chybicki IJ, Burczyk J (2009) Simultaneous estimation of null alleles and inbreeding coefficients. *J Hered* 100:106–113. <https://doi.org/10.1093/jhered/esn088>
- Crawford KM, Whitney KD (2010) Population genetic diversity influences colonization success. *Mol Ecol* 19:1253–1263. <https://doi.org/10.1111/j.1365-294X.2010.04550.x>
- Curto M, Puppo P, Kratschmer S, Meimberg H (2017) Genetic diversity and differentiation patterns in Micromeria from the Canary Islands are congruent with multiple colonization dynamics and the establishment of species syngameons. *BMC Evol Biol* 17:198. <https://doi.org/10.1186/s12862-017-1031-y>
- Dakin EE, Avise JC (2004) Microsatellite null alleles in parentage analysis. *Hered* 93(5):504–509. <https://doi.org/10.1038/sj.hdy.6800545>

- Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem Bull* 19:11–15
- Earl DA, vonHoldt BM (2012) Structure harvester: a website and program for visualizing structure output and implementing the Evanno method. *Conserv Genet Resour* 4:359–361. <https://doi.org/10.1007/s12686-011-9548-7>
- Emerson BC (2002) Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Mol Ecol* 11:951–966. <https://doi.org/10.1046/j.1365-294x.2002.01507.x>
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software structure: a simulation study. *Mol Ecol* 14:2611–2620. <https://doi.org/10.1111/j.1365-294x.2005.02553.x>
- Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes—application to human mitochondrial DNA restriction data. *Genetics* 131:479–491. <https://doi.org/10.1093/genetics/131.2.479>
- Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol Bioinform Online* 1:47–50. <https://doi.org/10.1177/117693430500100003>
- Falush D, Stephens M, Pritchard JK (2007) Inference of population structure using multilocus genotype data: dominant markers and null alleles. *Mol Ecol Notes* 7(4):574–578. <https://doi.org/10.1111/j.1471-8286.2007.01758.x>
- Febles R (1989) Estudios de la flora Macaronésica: algunos números de cromosomas VI. *Bot Macaroné* 17:57–76
- Fernández-Palacios O (2010) Biodiversidad morfológico-reproductiva y genética del género endémico canario *Parolinia* Webb (Brassicaceae). PhD Thesis, Universidad de Las Palmas de Gran Canaria. Las Palmas de Gran Canaria
- Fernández-Palacios O, Pérez de Paz J, Febles R, Caujapé-Castells J (2004) Diversidad genética en *parolinia*: *P. Glabriuscula* Y *P. platypetala* (Brassicaceae: Matthioelae). *Bot Macaroné* 25:147–164
- Fernández-Palacios O, Pérez de Paz J, Febles R, Caujapé-Castells J (2006) Duplicaciones y diversidad genética de *parolinia ornata* (Brassicaceae: Matthioelae) endemismo de gran canaria en relación a Dos congéneres más restringidos y otros taxones isleños y continentales. *Bot Macaroné* 26:19–54
- Francisco-Ortega J, Santos-Guerra A, Kim SC, Crawford DJ (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. *Am J Bot* 87:909–919. <https://doi.org/10.2307/2656988>
- Francisco-Ortega J, Park SJ, Santos-Guerra A, Benabid A, Jansen RK (2001) Origin and evolution of Macaronesian endemic taxa of the Inuleae (Asteraceae): evidence from internal transcribed spacers of nuclear ribosomal DNA. *Biol J Linn Soc* 72:77–97. <https://doi.org/10.1111/j.1095-8312.2001.tb01302.x>
- García C, Guichoux E, Hampe A (2018) A comparative analysis between SNPs and SSRs to investigate genetic variation in a juniper species (*Juniperus phoenicea* ssp. *turbinata*). *Tree Genet Genomes* 14:87. <https://doi.org/10.1007/s11295-018-1301-x>
- García-Verdugo C, Forrest AD, Fay MF, Vargas P (2010) The relevance of gene flow in metapopulation dynamics of an oceanic island endemic, *Olea europaea* subsp. *guanchica*. *Evol* 64:3525–3536. <https://doi.org/10.1111/j.1558-5646.2010.01091.x>
- García-Verdugo C, Mairal M, Tamaki I, Msanda F (2021) Phylogeography at the crossroad: pleistocene range expansion throughout the Mediterranean and back-colonization from the Canary Islands in the legume *Bituminaria bituminosa*. *J Biogeogr* 48:1622–1634. <https://doi.org/10.1111/jbi.14100>
- González-Pérez MA, Caujapé-Castells J (2014) Development and characterization of nuclear microsatellite markers for *Parolinia Ornata* Webb (Brassicaceae), and cross-species amplification in all species described in the Canary Islands. *Conserv Genet Resour* 6:705–706. <https://doi.org/10.1007/bf02712670>
- González-Pérez MA, Caujapé-Castells J (2022) Gene flow, barriers, speciation and hybridization in *Parolinia species* (Brassicaceae) endemic to Gran Canaria. *Bot J Linn Soc* 198:403–416. <https://doi.org/10.1093/botlinnean/boab069>
- González-Pérez MA, Sosa PA, Rivero E, González-González EA, Naranjo A (2009a) Molecular markers reveal no genetic differentiation between *M. Rivas-Martinezii* and *M. Faya* (Myricaceae). *Ann Bot* 103:79–86. <https://doi.org/10.1093/aob/mcn222>
- González-Pérez MA, Lledó MD, Lexer C, Fay M, Marrero M, Bañares A, Carqué E, Sosa PA (2009b) Genetic diversity and differentiation in natural and reintroduced populations of *Bencomia exstipulata* and comparisons with *B. caudata* (Rosaceae) in the Canary Islands: an analysis using microsatellites. *Bot J Linn Soc* 160:429–441. <https://doi.org/10.1111/j.1095-8339.2009.00986.x>
- González-Pérez MA, Batista F, Sosa PA (2013) Conservation genetics in two endangered endemics from the Canary Islands, *Helianthemum Gonzalezferreri* Marrero (Cistaceae) and *Kunkeliella subsucculenta* Kämmer (Santalaceae): different life histories that involve different management strategies. *Pl Syst Evol* 299:1981–1990. <https://doi.org/10.1007/s00606-013-0852-4>
- Goodson BE, Santos-Guerra A, Jansen RK (2006) Molecular systematics of *Descurainia* (Brassicaceae) in the Canary Islands: biogeographic and taxonomic implications. *Taxon* 55(3):671–682. <https://doi.org/10.2307/25065643>
- Grant PR (1998) Pattern on islands and microevolution. En: Grant, P.R. (ed.). *Evolution on Islands*. pp. 1–17. Oxford Univ. Press, Oxford
- Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol Ecol Notes* 2:618–620. <https://doi.org/10.1046/j.1471-8286.2002.00305.x>
- Herben T, Suda J, Munclinger P (2005) The ghost of hybridization past: niche pre-emption is not the only explanation of apparent monophyly in island endemics. *J Ecol* 93:572–575. <https://doi.org/10.1111/j.1365-2745.2005.01005.x>
- Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. *Philos Trans R Soc Lond B Biol Sci* 359:183–195. <https://doi.org/10.1098/rstb.2003.1388>
- Hohmann H, La Roche F, Ortega G, Barquin J (1993) J Plantas alimenticias y sus visitantes. *Abejas, avispas y hormigas de las Islas Canarias (Insecta: Hymenoptera: Aculeata)*. Vol. Band II. *Veröffentlichungen aus dem Übersee-Museum Bremen (Naturwissenschaften)*. 591–712
- IUCN (2012) IUCN red list of threatened species. Version 2012.1. World Conservation Union. <http://www.iucnredlist.org>
- Jaén-Molina R, Caujapé-Castells J, Fernández-Palacios O, De Pérez J, Febles R, Bramwell D (2007) Filogenia molecular del género *Parolinia* (Brassicaceae) basada en secuencias ITS. III Congreso De Biología De La Conservación De Plantas. Puerto De La Cruz. Tenerife: 153. [https://descargas.grancanaria.com/jardincanario/documentosweb/publicaciones%20de%20biodiversidad%20Molecular/2007/Jaen%20Molina%20et%20al\\_%202007\\_%20poster%20Parolinia.pdf](https://descargas.grancanaria.com/jardincanario/documentosweb/publicaciones%20de%20biodiversidad%20Molecular/2007/Jaen%20Molina%20et%20al_%202007_%20poster%20Parolinia.pdf)
- Jaén-Molina R, Marrero-Rodríguez A, Reyes-Betancort A, Santos-Guerra A, Naranjo Suárez J, Caujapé-Castells J (2014) Molecular taxonomic identification in the absence of a barcoding gap: a test with the endemic flora of the canarian oceanic hotspot. *Mol Ecol Resour* 15:42–56. <https://doi.org/10.1111/1755-0998.12292>
- Juan C, Emerson BC, Oromi P, Hewitt GM (2000) Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *TREE* 15:104–109. [https://doi.org/10.1016/S0169-5347\(99\)01776-0](https://doi.org/10.1016/S0169-5347(99)01776-0)

- Kimura M, Weiss GH (1964) The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* 49:561–576. <https://doi.org/10.1093/genetics/49.4.561>
- Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. *Nature* 457:830–836. <https://doi.org/10.1038/nature07893>
- Maley P (1980) Les changements climatiques de la fin du Tertiaire en Afrique: leur conséquence sur l'apparition du Sahara et de sa végétation. In: Faure H, Williams M (eds) *The Sahara and the Nile*. A. A. Balkema, pp 63–86
- Manni F, Guerard E, Heyer E (2004) Geographic patterns of (genetic, morphologic, linguistic) variation: how barriers can be detected by using Monmonier's algorithm. *Hum Biol* 76:173–190. <https://doi.org/10.1353/hub.2004.0034>
- Marrero A (2023) El complejo de *Sideritis dasygnaphala* de la isla de Gran Canaria (Islas Canarias) ¿Una especie única o Un complejo de viejos taxones, algunos en vías de extinción? *Bot Macaroné* 32:175–230
- Marrero A, Díaz-Bertrana M, Scholz S (2023) *Helianthemum Tibiabiniae* Marrero-Rodr., Díaz-Bertrana & S. Scholz sp. Nov., (Cistaceae) nueva especie para Fuerteventura, Islas Canarias. *Bot Macaroné* 32:95–108
- Maruyama T, Fuerst PA (1985) Population bottlenecks and non equilibrium models in population genetics. II. Number of alleles in a small population that was formed by a recent bottleneck. *Genetics* 111:675–689
- Mesa-Coello RA (2023) Revisión corológica De *Cheirolophus Webbianus* (sch. Bip.) Holub Y descripción De *Cheirolophus barquini* sp. nova (Asteraceae, cardueae), De La Isla De Tenerife (Islas Canarias). *Bot Macaroné* 33:3–18
- Mesa-Coello RA, Álvarez AM, Martín-Carbajal González J, Reyes-Betancort A (2023) *Ruta nanocarpa* (Rutaceae), una nueva especie para la isla de La Gomera (Islas Canarias, España) y tipificación de *Ruta microcarpa* svent. In Agulló *Bot Macaroné* 32:109–124
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89:583–590. <https://doi.org/10.1093/genetics/89.3.583>
- Nybom H (2004) Comparison of different nuclear DNA markers for estimating intraspecific genetic diversity in plants. *Mol Ecol* 13:1143–1155. <https://doi.org/10.1111/j.1365-294X.2004.02141.x>
- Ouborg NJ (2010) Integrating population genetics and conservation biology in the era of genomics. *Biol Lett* 6:3–6. <https://doi.org/10.1098/rsbl.2009.0590>
- Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol Ecol Notes* 6:288–295. <https://doi.org/10.1111/j.1471-8286.2005.01155.x>
- Pérez de Paz J, Caujapé-Castells J (2013) Review of the allozyme dataset for the Canary Island endemic flora: causes of the high genetic diversity levels, implications for conservation. *Ann Bot* 111:1059–1073. <https://doi.org/10.1093/aob/mct076>
- Rodríguez-Rodríguez P, Fernández de Castro AG, Pérez de Paz PL, Curbelo L, Palomares Á, Mesa R, Acevedo A, Sosa PA (2022) Evolution and conservation genetics of an insular hemiparasitic plant lineage at the limit of survival: the case of *Thesium* sect. *Kunkeliella* in the Canary Islands. *Am J Bot* 109(3):419–436. <https://doi.org/10.1002/ajb2.1830>
- Rodríguez-Sánchez F, Guzmán B, Valido A, Vargas P, Arroyo J (2009) Late neogene history of the laurel tree (*Laurus* L., Lauraceae) based on phylogeographical analyses of Mediterranean and macaronesian populations. *J Biogeogr* 36:1270–1281. <https://doi.org/10.1111/j.1365-2699.2009.02091.x>
- Rosenberg NA, Pritchard JK, Weber JL, Cann HM, Kidd KK, Zhivotovskiy LA, Feldman MW (2002) Genetic structure of human populations. *Science* 298(5602):2381–2385. <https://doi.org/10.1126/science.1078311>
- Sanmartín I, van der Mark P, Ronquist F (2008) Inferring dispersal: a bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *J Biogeogr* 35:428–449. <https://doi.org/10.1111/j.1365-2699.2008.01885.x>
- Saro I, González-Pérez MA, García-Verdugo C, Sosa PA (2015) Patterns of genetic diversity in *Phoenix canariensis*, a widespread oceanic palm (species) endemic from the canarian archipelago. *Tree Genet Genomes* 11:815. <https://doi.org/10.1007/S11295-014-0815-0>
- Saunders NH, Gibson DJ (2005) Breeding system, branching processes, hybrid swarm theory, and the humped-back diversity relationship as additional explanations for apparent monophyly in the macaronesian island flora. *J Ecol* 93:649–652. <https://doi.org/10.1111/j.1365-2745.2005.01027.x>
- Silvertown J, Francisco-Ortega J, Carine M (2005) The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *J Ecol* 93:653–657. <https://doi.org/10.1111/j.1365-2745.2005.01038.x>
- Sosa PA, González-Pérez MA, Moreno C, Clarke JB (2010) Conservation genetics of the endangered endemic *Sambucus palmensis* link (Sambucaceae) from the Canary Islands. *Conserv Genet* 11:2357–2368. <https://doi.org/10.1007/s10592-010-0122-8>
- Stuessy TF (2007) Evolution of specific and genetic diversity during ontogeny of island floras: the importance of understanding process for interpreting island biogeographic patterns. In: Ebach MC, Tangney RS (eds) *Biogeography in a changing World*. CRC, New York, pp 117–133
- van den Bogaard P (2013) The origin of the Canary Island Seamount Province - New ages of old seamounts. *Sci Rep* 3:2107. <https://doi.org/10.1038/srep02107>
- White OW, Reyes-Betancort JA, Chapman MA, Carine MA (2020) Geographical isolation, habitat shifts and hybridisation in the diversification of the Macaronesian endemic genus *Argyranthemum* (Asteraceae). *New Phytol* 228:1953–1971. <https://doi.org/10.1111/nph.16980>
- Whittaker RG, Fernández-Palacios JM (2007) *Island biogeography, ecology, evolution and conservation*. Oxford University Press, 416 p
- Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163:1177–1191. <https://doi.org/10.1093/genetics/163.3.1177>
- Wright S (1943) Isolation by Distance. *Genetics* 28:114–138. <https://doi.org/10.1093/genetics/28.2.114>

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.