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Review

# Island ontogenies, syngameons, and the origins and evolution of genetic diversity in the Canarian endemic flora

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## ABSTRACT

We use the molecular data available for the plant genera currently distributed in the Canaries to propose a hypothetical framework that updates the Surfing Syngameon Hypothesis (SSH) to explain the origins of the high genetic diversity of this flora in connection with the General Dynamic Model of Island Ontogeny and the available knowledge on the geology of the islands. Based on our review, we propose that (i) secondary contact and subsequent gene flow among genotypes previously confined to the mainland or to other insular regions generated syngameons across the archipelago, whose temporal extent and distribution were influenced by the ontogenetic stages of each island; and (ii) the resulting high levels of genetic variation were critical to the successful colonization of many other regions in the Canaries, especially those where more complex geographical and ecological features promoted gene flow cessation, drift, and/or eventual selection processes leading to species radiations. Under the updated SSH, the colonizing contingents of the islands would not necessarily have low genetic variation, because multiple colonizations followed by secondary contact among different genotypes would enhance genetic diversity through introgressive hybridization. As with other theories, the SSH contends that the monophyly detected in a large proportion of its lineages is artifactual. However, the SSH further differs from past hypotheses in (i) suggesting a spatio-temporal sequence of events giving rise to syngameons in different islands and island regions, (ii) showing that the ontogenetic mismatch among the Canarian islands should be largely responsible for similar levels of population genetic diversity in many congeneric endemics distributed in several islands, (iii) hypothesizing a substantial role for both allopolyploid and homoploid hybridization in the origins of the Canarian flora, and (iv) positing that, in many cases, the admixture processes in the syngameons formed at different stages of the islands' ontogeny made possible the rapid colonization of multiple environments, and the generation of the current floristic diversity.

## 1. Introduction

Natural hybridization is recognized as a major evolutionary force in genomic and organismal evolution (Anderson and Stebbins, 1954; Arnold, 1997, 2006; Mallet, 2005; Baack and Rieseberg, 2007; Soltis and Soltis, 2009; Arnold et al., 2012). Recent empirical evidence also shows compellingly that most extant plant lineages have undergone either allopolyploidy (Symonds et al., 2010) or homoploid hybrid speciation (Coyne and Orr, 2004) throughout their evolutionary history, indicating an overall high degree of reticulate evolution processes (Soltis and Soltis, 2009). Specifically, hybridization is proven to have facilitated major ecological transitions in plants (Rieseberg et al., 2003), eventually leading to lineage diversification and adaptive evolutionary change (Arnold et al., 2012; Abbott et al., 2013; but see Servedio et al., 2013).

Several investigations (e.g. Stebbins, 1959; Arnold et al., 2012; Chester et al., 2012) further suggest that evolution mediated by hybridization must be rapid, because the effect of combining genomes from different lineages produces many unique genotypes simultaneously, thereby allowing them to rapidly explore heterogeneous

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ecological spaces and expand their niche, a situation similar to what has been described in exotic species (Vandepitte et al., 2014). Such a dynamic genetic landscape may have important implications in the evolution of biodiversity on oceanic islands, where ecological opportunity stimulates adaptation and speciation (Losos and Ricklefs, 2009), and where the barriers to hybridization between congeneric endemic species are usually weak (Carr, 1985; Crawford et al., 1987).

Experimental data in insular endemics across the world bolster the importance of hybridization processes in the colonization of these environments. In the Hawaiian archipelago, Barrier et al. (1999) identified two to three mainland tarweed lineages that contributed to the origin of the endemic silversword alliance, confirming an allopolyploid hybrid speciation event at the base of this adaptive radiation. Harbaugh (2008) found evidence for six independent polyploid events in the history of *Santalum* (Santalaceae) in the Pacific islands, plus hybridization between two tetraploid Hawaiian clades that produced the Bonin Islands endemic *S. boninense*. Ecological studies, on the other hand, have provided some evidence that hybrids of closely related species display novel variation associated with the colonization of new habitats (Baldwin and Robichaux, 1995; García-Verdugo et al., 2013). Molecular and morphological analyses also revealed bidirectional multiple hybrid origins in *Prunus yedoensis* (Rosaceae), endemic to the island of Jeju in South Korea (Cho et al., 2014). Similarly, at least two independent colonization events from different source areas followed by admixture account for the origins of *Scrophularia takesinensis* (Scrophulariaceae) in Ulleung Island, also in South Korea (Gil et al., 2016).

The Canary Islands are one of the best-known oceanic archipelagos of the world in terms of the characterization of the flora (Emerson and Kolm, 2005), and there are published genetic diversity and phylogenetic/phylogeographic data for the lineages that most significantly contribute to its current makeup (see Table 1, and below). Thus, they provide one of the best possible scenarios to discuss the causes that underlie the origin of plant endemism.

The Canaries are situated less than 100 km off the Atlantic coast of Africa, and an important difference with respect to other hostspot oceanic archipelagos like Hawai'i and the Galápagos is their much closer proximity to the nearest mainland, and their considerable geological antiquity, spanning from ca. 21 Mya in one of the easternmost islands (Fuerteventura) to barely 1 Mya in the westernmost island (El Hierro) (Carracedo et al., 2002).

The isolation among the different islands, their overall great topographic ruggedness, their high elevation gradients, and their relative climatic stability during Quaternary glacial/interglacial periods (e.g. Rodriguez-Sanchez and Arroyo, 2008), have stimulated the generation of an extremely rich flora that currently includes ca. 610 recognized endemic species, most of which are single island endemics (SIE) (Izquierdo et al., 2001; A. Santos-Guerra, unpubl. data).

The earliest review of genetic data for the Canarian flora (Francisco-Ortega et al., 2000) detected unexpectedly high levels of (presumably neutral) population genetic diversity, and construed them as due to a major influence of both the old geological age of the islands, and their close proximity to the nearest continent. Statistical tests carried out in the most updated review (Pérez de Paz and Caujapé-Castells, 2013) also confirmed the prevalent influence of a short distance to the mainland (along with comparatively more important biotic factors) in promoting such high levels of population genetic diversity. Based on their meta-analysis, Pérez de Paz and Caujapé-Castells (2013) concluded that the taxa best suited to diversify in the Canaries are those with high basic chromosome numbers, polyploidy, partial or total self-incompatibility, and long-distance seed dispersal. Another recent review (García-Verdugo et al., 2015) suggests that, when markers potentially affected by selection are identified and removed, the expectation of low genetic diversity (Frankham, 1997) should not be generalized to island populations. All these lines of evidence indirectly support a highly dynamic history of colonization and admixture in the origins of the Canarian endemic flora.

Despite the wealth of molecular data for a wide range of endemic taxa, the causes underlying such high genetic diversity are still insufficiently understood. Indeed, the convergence between high levels of genetic diversity and the recurrent detection of topological monophyly in most phylogenetic reconstructions has been largely viewed as a paradox, if not an enigma. As suggested by Crawford et al. (2008), the large genetic diversity in insular populations would represent a dilemma for Baker's law (Baker, 1955), because we would expect self-compatible and highly selfing colonizers to give rise to populations with low genetic diversity, which could limit subsequent evolution (Stuessy et al., 2012).

In an attempt to explain the frequent resolution of oceanic island lineages as monophyletic, Silvertown (2004) and Silvertown et al. (2005) argued that because dispersal barriers to islands are weak, the first successful colonization should inhibit the establishment of later arrivals through interspecific competition. However, other authors (namely Herben et al., 2005, and Saunders and Gibson, 2005) contended that the pattern of monophyly resolved in many Canarian plant radiations was more apparent than real, and largely attributable to hybridization/admixture following multiple colonizations of the islands. According to these researchers, later colonizers would have made only limited contributions to the gene pools of their lineages before dying off or being dilluted into the hybridizing swarm, thus leading to the topological monophyly patterns detected in most phylogenetic reconstructions based on molecular data.

More recently, the "surfing syngameon hypothesis" (SSH henceforth, Caujapé-Castells, 2011) contends that high migration rates to suitable areas in the Canaries facilitated secondary contact among lineages previously isolated in the mainland, and the high genetic diversity generated by repeated hybridization among these colonizers (and with their sibs) would have favoured lineage diversification. The latter is especially true in insular regions with abrupt ecological and geographical discontinuities, where persistence requires the ability to adapt rapidly to local habitats. Both open and ecologically more complex habitats have been variously available for the formation of syngameons throughout the ontogeny of each island in the Canarian archipelago (see below).

In agreement with Herben et al. (2005) and Saunders and Gibson (2005), the SSH challenges the prevalent monophyly in the Canarian flora, but it adds a conceptual twist to the earlier explanatory theories by further suggesting that, especially in the last few million years, (i) the much older and eroded easternmost Canary Islands may have been key physical grounds for hosting generalized admixture processes among genetically close propagules from different mainland areas that established secondary contact on the islands, and (ii) multiple migrations from the resulting syngameons could have been important for the rapid exploration and successful colonization of different ecological spaces, where allopatric and peripatric speciation triggered evolutionary divergence conducive to the generation of new species.

Although the possible reasons for the recurrent detection of spurious monophyly in the Canarian flora can be various, we suggest that they mainly stem from the low resolution furnished by the DNA sequence markers employed to date, along with the use of largely unrepresentative sampling strategies in many published phylogenetic studies (reviewed in Caujapé-Castells, 2011). As underscored by Seehausen (2004) in another geographical and biological context, most genealogies of Canarian plant lineages would be based on DNA sequences which cannot distinguish between an origin from a single species (true monophyly), or an origin from a "hybrid swarm" involving the combination of parental genotypes from differentiated mainland populations (spurious, simply topological monophyly). The latter possibility was assumed to be highly unlikely in the Canarian flora; however, recent *in silico* experiments (Currat et al., 2008; Petit and Excoffier, 2009) and empirical evidence (see below, and Table 1) do enforce the role of admixture in rapidly generating a monophyly pattern, thus largely supporting the compatibility between multiple

**Table 1**
Genera in the Canarian flora where hybridization is likely to have played an evolutionary role. We distinguish among groups where evidence for hybridization in the Canarian taxa can be considered robust (INFORMED CASES) from those where the potential role of hybridization is not yet sufficiently supported in the Canarian taxa or is available only for other taxa in the corresponding genus (OTHER CASES). Although evidence of hybridization exists in some other lineages (see e.g. Francisco-Ortega and Santos-Guerra, 2001), we only consider here the genera for which some molecular data are available. C: Hypothesized colonization pattern of the Canaries inferred in the published molecular evidence (M: Multiple colonizations, S: single colonization,?: undetermined). PMS: Predominant mating system (SELF: predominant selfer, OUTC: obligate or predominant outcrosser, −: unknown) NT: total number of taxa known in the Canaries (species + subspecies + varieties), following Acebes-Ginovés et al. (2009); NE: number of Canarian endemic taxa, following Acebes-Ginovés et al. (2009); *2n*: chromosome numbers known in the genus (the superscript indicates the corresponding literature source, if other than in column "References" see Table footer); PL: Ploidy levels known in the genus. REFERENCES: scientific literature supporting diagnoses of hybridization and mating system. For chromosome numbers, ploidy levels and breeding systems see also Pérez de Paz et al. (2012); and Pérez de Paz and Caujapé-Castells (2013).

| GENUS/CASE | FAMILY | C | PMS | NT | NE | *2n* | PL | REFERENCES |
|---|---|---|---|---|---|---|---|---|
| INFORMED CASES | | | | | | | | |
| *Aeonium* | Crassulaceae | S | SELF/OUTC | 33 | 33 | $36^{1}$ | 4 | Santos-Guerra (1983), Mes et al. (1997), Mort et al. (2002) |
| *Aichryson* | Crassulaceae | S | SELF/OUTC | 14 | 14 | $30,34^{2}$ | ≥2 | Santos-Guerra (1983), Mes et al. (1997), Mort et al. (2002) |
| *Androcymbium* | Colchicaceae | S | SELF/OUTC | 2 | 2 | $18,20^{3}$ | 2 | Del Hoyo and Pedrola-Monfort (2010) |
| *Andryala* | Asteraceae | ? | OUTC | 2 | 5 | $18^{2}$ | 2 | Fehrer et al. (2006) |
| *Argyranthemum* | Asteraceae | S | OUTC | 32 | 32 | $18^{4}$ | 2 | Francisco-Ortega et al. (1996), Brochmann et al. (2000), Fjellheim et al. (2009) |
| *Atalanthus* | Asteraceae | S | – | 6 | 6 | $18^{6}$ | 2 | Kim et al. (1996). |
| *Babcockia* | Asteraceae | S | OUTC | 1 | 1 | $18^{8}$ | 2 | Artificial crossing experiments and observations in nature (and Lee et al., 2005) |
| *Bencomia* | Rosaceae | S | OUTC | 4 | 3 | $28^{9}$ | 4 | (Helfgott et al. (2000), González-Pérez et al. (2009) |
| *Brassica* | Brassicaceae | S | OUTC | 3 | 1 | $18^{11}$ | 2 | Lannér-Herrera et al. (1996), Lázaro and Aguinagalde (1998) |
| *Chrysoprenanthes* | Asteraceae | S | – | 2 | 2 | $18^{6}$ | 2 | Lee et al. (2005) |
| *Chamaecitysus* | Fabaceae | ? | OUTC | 4 | 4 | $48^{2}$ | 4 | Cubas et al. (2002) |
| *Cistus* | Cistaceae | S | OUTC | 14 | 11 | $18^{12}$ | 2 | Dansereau (1940), Guzmán and Vargas (2005), Civeyrel et al. (2011) |
| *Convolvulus* | Convolvulaceae | M | OUTC | 16 | 10 | $30^{2}$ | 6 | Carine et al. (2007) |
| *Dactylis* | Poaceae | M | – | 5 | 2 | $14,28^{13}$ | 2,4 | Sahuquillo and Lumaret (1995, 1999) |
| *Descurainia* | Brassicaceae | S | – | 7 | 7 | $14^{2}$ | 2 | Goodson et al. (2006) |
| *Echium* | Boraginaceae | S | OUTC (?) | 31 | 29 | $16,24,32^{2}$ | 2 | Mora-Vicente et al. (2009), Bramwell (1972) |
| *Euphorbia* | Euphorbiaceae | M | OUTC (?) | 33 | 9 | $20^{2}$ | 2 | Molero et al. (2002) |
| *Genista* | Fabaceae | S | OUTC | 1 | 1 | $48^{2}$ | 4 | Pardo et al. (2004) |
| *Greenovia* | Crassulaceae | S | SELF/OUTC | 4 | 4 | $36^{2}$ | 4 | Santos-Guerra (1983), Mes et al. (1997), Mort et al. (2002) |
| *Hedera* | Araliaceae | M | – | 2 | 0 | $48^{14}$ | 4 | Vargas et al. (1999), Valcárcel et al. (2003) |
| *Helichrysum* | Asteraceae | S | – | 4 | 3 | $42^{17}$ | 4 | Galbany-Casals et al. (2009) |
| *Hypericum* | Hypericaceae | M | SELF/OUTC | 8 | 2 | $40^{2}$ | 4 | Dlugosh and Parker (2007) |
| *Hypochaeris* | Asteraceae | ? | SELF/OUTC | 4 | 1 | $6^{2}$ | 2 | Cerbah et al. (1998), Samuel et al. (2003) |
| *Ilex* | Aquifoliaceae | M | OUTC | 3 | 2 | $40?^{18}$ | 2 | Manen et al. (2010) |
| *Lactucosonchus* | Asteraceae | S | OUTC | 2 | 2 | $18^{10}$ | 2 | Kim et al. (1996) |
| *Laurus* | Lauraceae | S | OUTC | 1 | 1 | $36,48^{14}$ | 4 | Rodríguez-Sánchez et al. (2009) |
| *Lobularia* | Brassicaceae | M | OUTC | 7 | 4 | $22^{2}$ | 2, 4 | Borgen (1996) |
| *Lolium* | Poaceae | ? | OUTC | 11 | 1 | $14^{15}$ | 2 | Charmet and Balfourier (1994), Catalán et al. (2004) |
| GENUS/CASE | FAMILY | C | | NT | NE | *2n* | PL | SUMMARY AND REFERENCES |
| *Lotus* | Fabaceae | M | OUTC | 25 | 17 | $14,28^{16}$ | 2,4 | Oliva-Tejera et al. (2005), Ojeda et al. (2012) |
| *Matthiola* | Brassicaceae | M | OUTC | 5 | 1 | $12^{19}$ | 2 | Jaén-Molina et al. (2009) |
| *Micromeria* | Lamiaceae | M | – | 23 | 23 | $30^{2}$ | ≥2 | Puppo et al. (2015) |
| *Monanthes* | Crassulaceae | S | – | 11 | 11 | $36,72^{2}$ | 4,8 | Santos-Guerra (1983), Mes et al. (1997), Mort et al. (2002) |
| *Olea* | Oleaceae | M | OUTC | 2 | 1 | $46^{20}$ | 2,4,6 | Besnard et al. (2007), García-Verdugo et al. (2009, 2010) |
| *Pericallis* | Asteraceae | S | OUTC | 12 | 12 | $60^{2}$ | 6 | Swenson and Manns (2003), van Hengstum et al. (2012), Jones et al. (2014) |
| *Phoenix* | Arecaceae | S | OUTC | 2 | 1 | $36^{2}$ | 2 | Greuter (1967), Wrigley (1995), González-Pérez et al. (2004), Henderson et al. (2006) |
| *Senecio* | Asteraceae | M | OUTC | 13 | 4 | $20\text{-}60^{2}$ | 4,6 | Comes and Abbott (2001), Pelser et al. (2012) |
| *Sideritis* | Lamiaceae | M | OUTC | 27 | 27 | $36,38,40,42^{2}$ | 4 | Barber et al. (2007) |
| *Silene* | Caryophyllaceae | ? | SELF/OUTC | 29 | 8 | $24^{2}$ | 2 | Rautenberg et al. (2010) |
| *Sonchus* | Asteraceae | S | OUTC | 24 | 18 | $18^{2}$ | 2 | Lee et al. (2005) |
| *Helispartocitysus* | Fabaceae | ? | OUTC | 2 | 2 | $48^{23}$ | 4 | Cubas et al. (2002) |
| *Sventenia* | Asteraceae | S | OUTC | 1 | 1 | $18^{10}$ | 2 | Lee et al. (2005) |
| *Teline* | Fabaceae | M | OUTC | 17 | 16 | $48^{2}$ | 4 | Percy and Cronk (2002) |
| *Tolpis* | Asteraceae | M | OUTC | 8 | 7 | $18,36^{24}$ | 2,4 | Gruenstaeudl et al. (2012), Soto-Trejo et al. (2013) |
| *Viola* | Violaceae | M | SELF | 8 | 3 | $64^{25}$ | 8 | Yockteng et al. (2003) |
| OTHER CASES | | | | | | | | |
| *Arrhenatherum* | Poaceae | ? | – | 2 | 1 | $28^{5}$ | 4 | Quintanar et al. (2007) |
| *Avena* | Poaceae | ? | – | 9 | 1 | $14,28,42^{7}$ | 2,4,6 | Drossou et al. (2004), Li et al. (2000). |
| *Brachypodium* | Poaceae | M | OUTC | 4 | 1 | $10,20,30^{10}$ | 2,4,6 | Shiposha et al. (2016) |
| *Bryonia* | Cucurbitaceae | ? | OUTC | 1 | 1 | $20^{2}$ | 2 | Volz and Renner (2008) |
| *Bupleurum* | Umbelliferae | S | SELF | 5 | 2 | $32^{2}$ | 4 | Neves and Watson (2004) |
| *Bystropogon* | Lamiaceae | M | – | 5 | 5 | $42^{2}$ | 6 | La Serna-Ramos (1984), Trusty et al. (2005) |
| *Carex* | Cyperaceae | ? | – | 11 | 3 | $68^{8}$ | 4 | Molina et al. (2015) |
| *Dendropoterium* | Rosaceae | S | – | 2 | 2 | $28^{9}$ | 4 | Helfgott et al. (2000). |
| *Lavatera* | Malvaceae | M | OUTC | 5 | 1 | 42 | 6 | Escobar-García et al. (2009) |
| *Limonium* | Plumbaginaceae | M | OUTC | 23 | 18 | $12,14^{2}$ | 2 | Morgan et al. (1998) |
| *Luzula* | Juncaceae | M | – | 3 | 1 | $12^{2}$ | 2 | Drábková et al. (2003) |
| *Marcetella* | Rosaceae | S | – | 1 | 1 | $28^{2}$ | 4 | Helfgott et al. (2000) |
| *Morella* | Myricaceae | ? | OUTC | 2 | 1 | $16^{19}$ | 2 | Batista et al. (2004) |
| *Pancratium* | Amaryllidaceae | ? | – | 2 | 1 | $n = 9,10,11,12,23^{21}$ | 2,4 | Castro et al. (2014) |
| *Phalaris* | Poaceae | M | – | 6 | 0 | ? | ? | Voshell and Hilu (2014), Quintanar et al. (2007) |

(continued on next page)

**Table 1** *(continued)*

| GENUS/CASE | FAMILY | C | | NT | NE | *2n* | PL | SUMMARY AND REFERENCES |
|---|---|---|---|---|---|---|---|---|
| *Reseda* | Resedaceae | M | – | 4 | 2 | 30[2] | ≥ 2 | Martin-Bravo et al. (2007) |
| *Rhamnus* | Rhamnaceae | M | OUTC* | 4 | 2 | ? | ? | Bolmgren and Oxelman (2004) |
| *Salvia* | Lamiaceae | M | SELF/OUTC | 9 | 2 | 22[2] | 2 | Will and Classen-Bockhoff (2014) |

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colonizations and topological monophyly.

In close connection with the above, the use of more polymorphic DNA sequences for phylogeographic reconstruction associated with intensive population sampling in the Canaries and mainland source areas is increasingly revealing complex colonization patterns of the archipelago. Notably, the most recent results also encompass the detection of hitherto overlooked colonization routes (and taxa) in a diversity of endemic plant lineages, either widespread or narrowly distributed (e.g. *Tolpis* [Asteraceae, Gruenstaeudl et al., 2012; Mort et al., 2014]; *Olea* [Oleaceae; García-Verdugo et al., 2009]; the Canarian species of *Ruta* [Rutaceae, Soto, 2016; Soto et al. in prep.]; and *Dorycnium broussonettii* (Choisy ex DC.) Webb & Berthel. [Fabaceae, Jaén Molina et al., 2015], or in native taxa considered non-endemic to date (e.g. *Periploca laevigata* Aiton [Asclepiadaceae, García-Verdugo et al., under review]; *Scrophularia arguta* Aiton [Scrophulariaceae, Valtueña et al., 2016]). All of these results provide additional support to the hypothesis that the proximity of the African mainland fostered the frequent colonization of the Canaries by reproductively compatible propagules from different geographical regions, potentially setting the stage for the generation of high levels of genetic diversity on the islands.

Nevertheless, the current hypotheses on the origins of the Canarian flora do not account for the influence of the complex spatial and temporal context of the archipelago's ontogeny in the generation of the genetic diversity patterns that may explain the high species diversity in the archipelago (but see Marrero and Francisco-Ortega, 2001a, 2001b). Capitalizing on the abundance of genetic data for the Canarian flora, we use the present knowledge on the geological history of the islands in this archipelago (Carracedo, 2011) in the context of the theory of the General Dynamic Model of oceanic islands (Whittaker et al., 2007, 2008), to update and expand the original tenets of the SSH.

## 2. Conceptual background

### 2.1. The surfing syngameon hypothesis

The concept of "syngameon" will be used extensively throughout the paper in a way that differs slightly from its classical definition (i.e., "a group of individuals that are able to cross successfully", Lotsy, 1931). Our use of the term will refer to a population that originated from genetically close colonizers (belonging to the same or different taxonomic species) from diverse geographic origins that meet in a given insular space, where they reproduce and give rise to viable progeny. Similar uses of this concept (not always circumscribed to insular territories) can be found in Van Oppen et al. (2001) or in Seehausen (2004, 2013) who used the designation "hybrid swarm".

The "surfing syngameon hypothesis" (SSH, Caujapé-Castells, 2011) argues that (i) secondary contact and subsequent gene flow in insular habitats among genotypes that may have been previously isolated in the mainland (or in other insular regions) generated syngameons in certain island regions; and (ii) the resulting high levels of genetic variation were critical to the successful colonization of many insular regions, especially those where more complex geographical and ecological features promote gene flow cessation, drift, and/or eventual selection processes leading to radiations. Thus, unlike the general theory of founder events, the colonizing contingents would not necessarily have low genetic variation, because secondary contact among different genotypes would have enhanced genetic diversity (see also García-Verdugo et al., 2015; or Dlugosh and Parker, 2007, 2008 about high levels of genetic diversity on insular populations).

A central concept for the SSH is that of "introgressive hybridization" (or simply introgression), defined as the transfer of alleles from one lineage into the gene pool of another lineage via hybridization and backcrossing (Anderson and Hubricht, 1938; Harrison and Larson, 2014). The SSH intimates that evolutionary change in the syngameons that form in open island areas should be slowed down by introgression following high levels of gene flow among the colonizing individuals/populations. However, on ecogeographically more complex island regions, the prevalent influence of selection, gene flow cessation, and/or drift would tend to rapidly diminish the levels of population genetic variation and exacerbate the differences with respect to syngameons in other regions. Thus, under the SSH eventual adaptation and competition would happen after the hybridization processes, not before; indeed, it is precisely the genetic diversity in syngameons that would promote adaptations.

The SSH differs from Herben et al. (2005) and Saunders and Gibson (2005) in that the contributions of subsequent waves of island colonizers would not have been necessarily limited. However, it agrees with those investigations in that (i) a 'hybridization past' could help explain the high genetic diversity of the current Canarian flora and the diversification of many of its endemic lineages (Table 1), and (ii) the monophyly inferred for most of the Canarian endemic flora would be more the exception than the rule. The latter point is being increasingly confirmed by recent research on well-sampled lineages with multiple cpDNA markers or NGS (e.g. in *Tolpis*, where Mort et al. (2014, 2016) further improve the resolution of phylogenetic hypotheses for the Canarian endemics with respect to earlier works on the same taxa (Moore et al., 2002; Archibald et al., 2006; Mort et al., 2007; Gruenstaeudl et al., 2012) (see Table 1).

The most important biotic factor for the SSH is that sufficient reproductive compatibility should exist among the colonizers to allow the generation of high genetic diversity levels through hybridization. In such context, the adaptive potential of introgression stems from the fact that "natural selection is presented not with one or two new alleles but with segregating blocks of genic material belonging to entirely different adaptive systems" (Anderson and Stebbins, 1954). The process entails the transfer of adaptations present in one of the hybridizing lineages through transgressive segregation, whereby some phenotypes of later-generation hybrid progeny may exceed the phenotypic range of the parental species (Rieseberg et al., 1999; Bell and Travis, 2005) but also, in many cases, develop novel adaptations due to recombination between divergent genomes (Fritz et al., 1999; Arnold et al., 2012; Feldman et al., 2012).

With multiple colonizations of the islands, Baker's law would be of limited concern, because compatible mates would be introduced in any case. Preliminary data indicate that over 40% of the 27 lineages examined in the Canaries originated from self-incompatible (SI) ancestors (Crawford et al., 2013). Detailed studies in the genus *Tolpis* (Asteraceae) find that "obligately" SI species in fact exhibit various levels of selfed seed (Crawford et al., 2008). Five of the six largest radiations in the Canaries have SI members, and likely originated from SI or Pseudo Self-Compatible (PSC) ancestors (Greg Anderson et al. unpubl. data). Also, because propagules from continental source areas would probably have come from outcrossing populations in most cases, each seed would have higher genome-wide heterozygosity compared to propagules from highly selfing populations. Table 1 illustrates that most Canarian lineages where evidence for hybridization is documented are obligate or predominant outcrossers.

However, we emphasize that Baker's law and hybridization are not mutually exclusive. Mating systems may fluctuate over evolutionary time, so that SC colonizers capable of selfing might have established a lineage following Baker's law. Notably, selection after establishment is less likely to be characterized by mate limitation, so that mechanisms for outcrossing may then be favored (Pannell et al., 2015), and may later promote hybridization when other species of that lineage arrived. Also importantly, several factors may cause the breakdown of genetic SI systems (e.g. polyploidization, or environmental influence), resulting in the ability to set seed by selfing (see e.g. Mable et al., 2005).

Notably, speciation involving polyploidization in Angiosperms is estimated to be about 15% overall (Wood et al., 2009), but recent results for the Canarian flora reveal that at least 40% of 104 Angiosperm species surveyed are of polyploid origin (Suda et al., 2003). Taking into account that only a few Monocots were examined in the latter investigation, probably the proportion of putative polyploids is in fact much higher, thus adding up to the substantial role of hybridization in the evolution of the present Canarian flora. This does not entail that the origin of all these species was via polyploidization (i.e., when the continental ancestors were already polyploids). Furthermore, not all polyploid species are allopolyploids (Barker et al., 2016); in many cases, the hybridizing individuals would be genetically very close, and they would rather have given rise to 'homoploid hybrid' or 'recombinational' species (Rieseberg, 1997; Coyne and Orr, 2004). Homoploid hybrids are harder to detect, but instances have been reported, e.g. in Canarian endemic *Argyranthemum* (Asteraceae, Brochmann et al., 2000; Fjellheim et al., 2009).

The very close proximity of the Easternmost Canary Islands to the African mainland, their low geographic and ecological complexity since the last 5 My, and the different wind regimes that have affected the archipelago, have created very favorable conditions for the dispersal of propagules from many different geographic enclaves. This situation is bound to have provided a variety of sources for admixture in the islands, although population genetic diversity is indeed influenced by many other biotic and abiotic factors (see the review by Pérez de Paz and Caujapé-Castells, 2013).

Recent results (Harbaugh et al., 2009; García-Verdugo et al. under review) also show that, at least in some lineages, the post-colonization dispersal capabilities of plants endemic to Hawai'i and the Canary islands could be much higher than contended by the so-called "low dispersal hypothesis on islands" (LDHI, see e.g. Carlquist, 1966; Kudoh et al., 2013). According to this empirical evidence, island-island or mainland-island gene flow would not be as limited by dispersal ability as the LDHI anticipates.

### *2.2. Island ontogeny, admixture, 'single colonization events' and 'radiations'*

The "ontogenetic mismatch" among the different Canary Islands (i.e. the radically different ontogenetic stages of the different islands) also determines a variable likelihood of occurrence of patterns and processes of spatial colonization and diversification (Fig. 1). Thus, similarly as discussed by Stuessy (2007), the ontogenetic stage of an oceanic island influences the levels and distribution of population genetic diversity in the biota that it hosts, potentially affecting the evolutionary fates of many lineages.

The relationship between island ontogeny and genetic diversity may vary in strength depending on the biotic traits of each colonizing lineage and extrinsic factors, such as the characteristics of the abiotic conditions where colonization occurs. This is so because they are both determinants for the successful dispersal episodes necessary for subsequent colonization and diversification: without adequate habitat availability, no establishment can occur, irrespective of whether the biotic traits of the colonizing organisms are optimally suited for that purpose.

Also by virtue of such "ontogenetic mismatch", high genetic diversity levels would have been rapidly generated in a first stage in some island areas through secondary contact and further recombination among alleles from parental populations from other regions. In open, geologically stable island areas, this scenario would describe a diversification landscape analogous to anagenesis, whereby the founding population accumulates genetic variation and changes (genetically and morphologically) over time through mutation and recombination (Stuessy et al., 2014; Takayama et al., 2015). In the case of the SSH, however, the generation of genetic diversity would have been faster, and mediated by secondary contact and introgression. As noted by Crawford et al. (2008, 2009), the much higher proportion of self-incompatible taxa in the Canarian endemic flora than in other oceanic archipelagos is a salient reproductive characteristic (and an exception to Baker's law), that likely contributed to the swift generation of higher genetic diversity levels.

In a second stage, such admixture would have produced more genotypes for selection to facilitate the exploration of the different ecological conditions, ultimately resulting in radiation events and the rapid evolution of reproductive isolation among the populations subjected to different selective forces (Sweigart and Willis, 2012; Seehausen, 2013; Calhoun et al., 2016; see also Rieseberg et al., 1999 or Brothers et al., 2013 for empirical discussion in other contexts). This

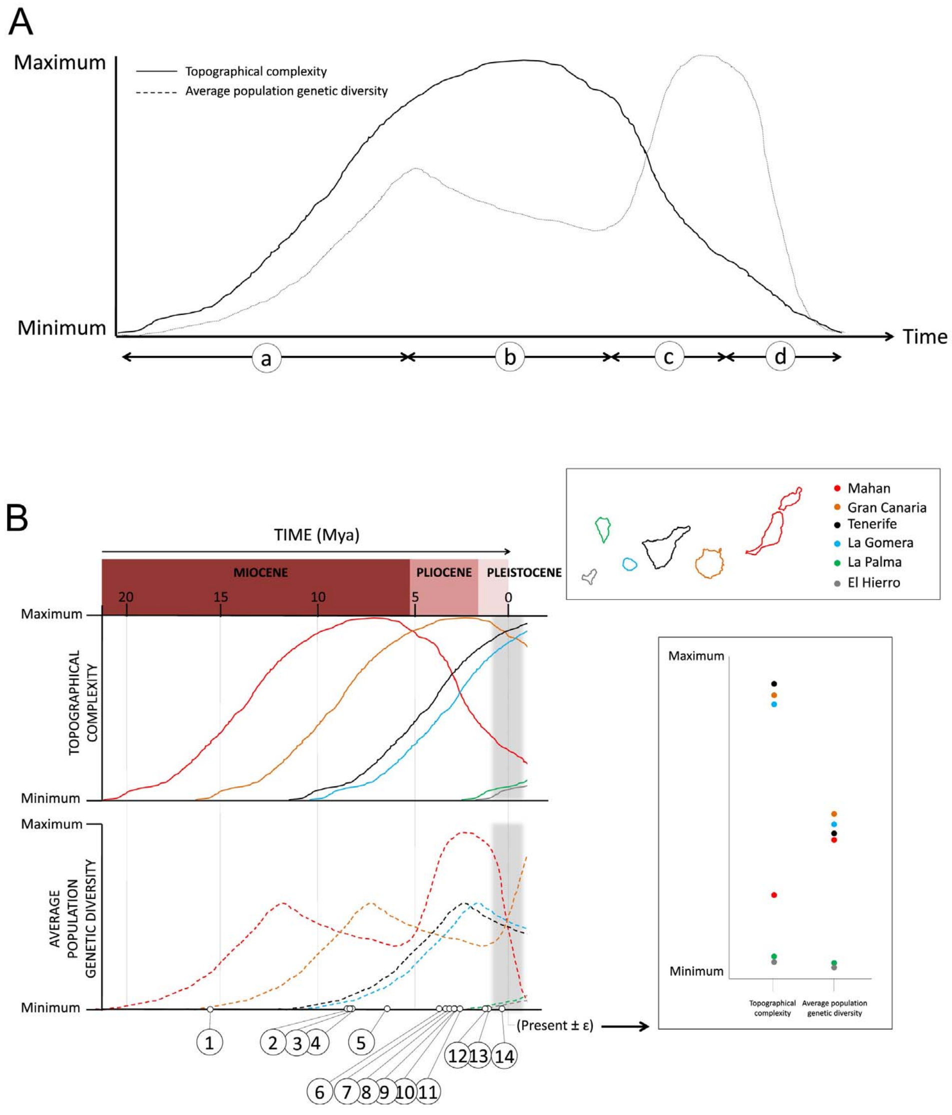

**Fig. 1.** Representation of the ontogenetic mismatch among the Canary Islands. A) Comparison between the evolution of an oceanic island's topographical complexity (adapted from Whittaker et al., 2008) and the hypothesized evolution of the average population genetic diversity through geological time (i.e., considering the islands as 'genetic diversity sinks', sensu Caujapé-Castells, 2011 and Sanmartin et al., 2008). (a) The first syngameons form due to inmigration from out of the island, and population genetic diversity increases until it reaches a local maximum (some isolation by distance may develop); (b) the island's increasing geographic and ecological complexity drives natural fragmentation, and gene flow cessation. As a result, most syngameons reduce their size and genetic diversity, and give rise to radiations; (c) as the island's geographic and ecological complexity decreases, there is an upward surge of population genetic diversity because some populations previously isolated in different island spaces make secondary contact, and the island keeps receiving colonizers from other areas. Unless there are interfering external factors, we hypothesize that these secondary syngameons should be more genetically diverse than the first ones because there would be more contributing sources of genetic diversity (see text); (d) erosion, downcutting, subsidence, and mega-landslips determine the rapid reduction of population sizes and genetic diversity until the island disappears below the sea level. B) Contrasts between the topographical complexity and the hypothesized average population genetic diversity of the Canary Islands through time. The origin of the lines is placed at the estimated age of the oldest rocks dated on each island (Carracedo, 2011). The time-span of the island cycles is subjective, and we consider it the same for all islands in the archipelago: the subsidence of the Canaries is determined by marine erosion and absence of rejuvenation because, unlike Hawai'i, they are grounded on an old, thick and rigid lithosphere (Francisco Pérez-Torrado, pers. comm.). The framed graph compares the level of differentiation between topographical vs population genetic diversity among the Canary Islands at time 'present ± ε', taking as a reference the intersection of the lines representing each island with time "0". The circled numbers below pinpoint the estimated colonization dates of several endemic lineages in the Canarian endemic flora for which molecular datings exist (see paper text). 1: the *Aeonium* alliance; 2: the *Sonchus* alliance; 3: genus *Micromeria*; 4: genus *Crambe*; 5: *Bystropogon* Sect. *Canariense*; 6: genus *Lotus* (Central and Eastern islands); 7: genus *Lotus* (central and western islands); 8: genus *Echium*; 9: genus *Pericallis*; 10: genus *Sideritis*; 11: genus *Androcymbium*; 12: genus *Cheirolophus*; 13: genus *Canarina*; 14: genus *Cistus*.

process is analogous to speciation by cladogenesis, whereby genetically closely related species are generated with much lower genetic variation within and among populations than in anagenetic assemblages (Stuessy et al., 2014). Thus, although not all cladogenetic processes should be adaptive and many of them should be mediated by geographic isolation only, anagenesis and cladogenesis are interlinked in the context of the SSH, as anagenesis likely paves the way for further cladogenesis in some lineages.

The intensity of the "surfing" of genetic variation through time across the archipelago would have been affected by the degree of ontogenetic mismatch among the different islands at each epoch (Fig. 1), which illustrates that the evolution of population genetic diversity in each island is quite complex. At present, despite the great differences in topographical complexity among the Canary Islands (Figs. 1 and 2), the expected average population genetic diversity per island would be very similar in most of them, except for the much younger El Hierro and La Palma (Fig. 1B). This fact partly explains the difficulty of detecting a progressive reduction of average population genetic diversity from older to younger islands, as the original formulation of the SSH contended (Caujapé-Castells, 2011). Furthermore, cogent with the finding that population genetic fragmentation in many lineages the Canarian endemic flora is much lower than had been assumed (Caujapé-Castells, 2010), the most recently founded populations should still contain high genetic variation because drift and/or selection have not acted yet, thus generating a "population genetic diversity debt" (i.e. the genetic variation that will be lost after the action of drift and/or selection), especially in the younger and geographically or ecologically more complex island regions.

In view of these considerations, a "single colonization event" is better conceived as the introduction (via one or more dispersal episodes) of a variable number of viable propagules, not necessarily from geographically close areas, but sufficiently related genetically to (i) hybridize and give rise to viable offspring, and (ii) retrieve a monophyletic origin with the DNA sequences currently used for phylogenetic reconstruction. If the SSH holds, the advent of NGS techniques will probably determine the detection of patterns of multiple colonizations in many Canarian lineages currently assumed to be monophyletic, provided a throrough sampling strategy is employed.

In this paper, we refer indistinctly to 'adaptive radiation', 'radiation' and 'explosive species diversification' as "the rise of a diversity of ecological roles and attendant adaptations in different species within a lineage" (Givnish, 1997; but see Givnish, 2015 for fine distinctions among these terms).

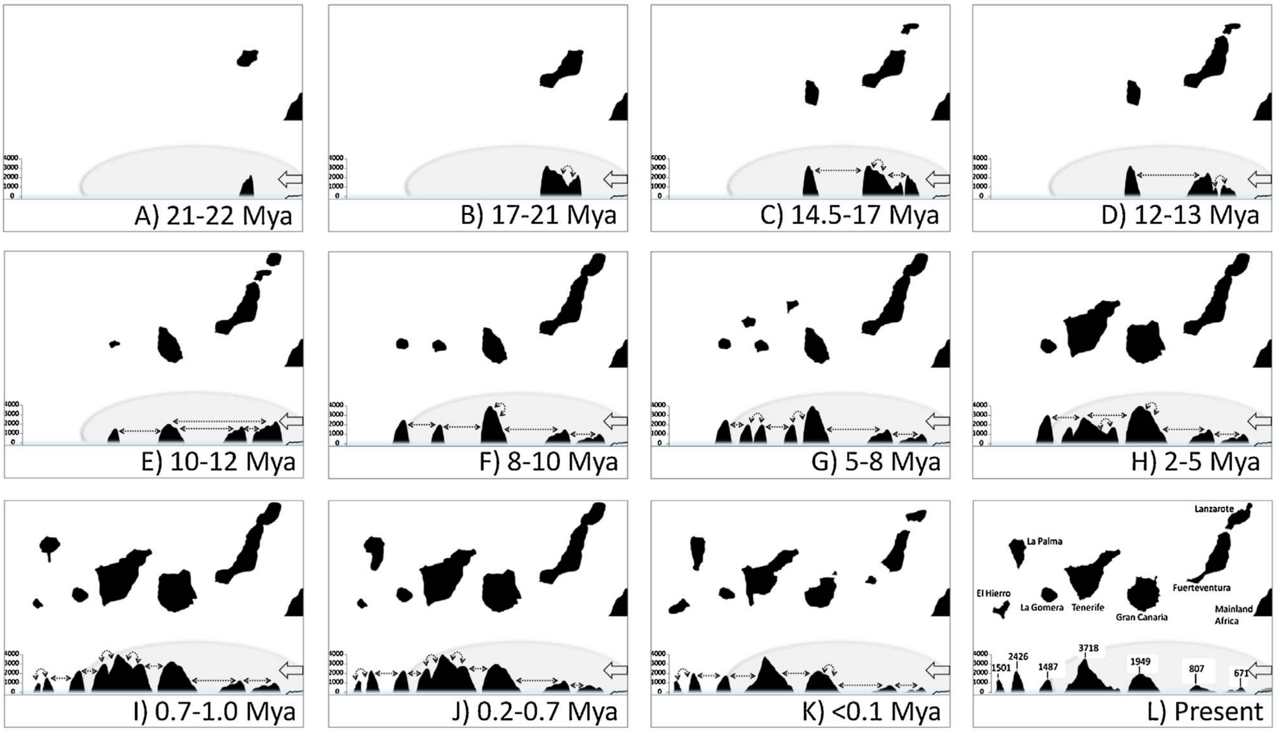

**Fig. 2.** Conceptual simplification of the ontogeny of the Canary Islands throughout geological time (see text). The solid arrow indicates founder events from outside the archipelago. Bidirectional arrows indicate some possibilities of inter- and intra-island migration in different epochs. The numbered scale to the left is in meters; numbers at the summits of the islands in L) are the present maximum heights. The gray cloud encompasses the regions where biodiversity interchange from the mainland to the islands is more probable, according to dust deposition rates in Goudie and Middleton (2001). During a time-window in the Holocene, the westerlies (Rognon and Coude-Gaussen, 1996) determined a higher probability of colonization from the islands to the mainland that is not represented in the figure, for simplicity (see paper text and Caujapé-Castells 2011). Only the emerged parts of the islands are depicted. The figure is not scaled.

## 3. WHEN, AND WHERE?

### 3.1. *Simplified geological ontogeny of the Canaries*

As argued by Marrero and Francisco-Ortega (2001a, 2001b), hypothesizing the colonization processes that may have driven organismic evolution on the Canaries requires a basic understanding of the dynamic geology of the archipelago throughout its history. Below, we provide a simplified chronology of the main events that shaped the current geology of the seven islands, adapted from Carracedo and Day (2002), Carracedo et al. (2002), and Carracedo (2011), unless otherwise specified. This background (illustrated in Fig. 2) will set the stage for the considerations in Sections 2 and 3.

Geologically, Fuerteventura and Lanzarote are two parts of a single volcanic edifice presently separated by a 3 Km straits (La Bocaina, less than 50 m deep). However, they were connected above sea level during glacial lowstands, forming an emerged macro-island called Mahan, to which we will refer as needed.

The most ancient volcano in Fuerteventura formed south of Betancuria (near the central region of the island) in the early Miocene (some 21-22 Mya), and it could have reached more than 3000 m asl, according to the upslope projection of the lava flows on the remnants of its flanks (Stillman, 1999). Throughout the next 10 million years, two more shield volcanoes formed in the island: one in Jandía (to the South, with the oldest rocks dated ca. 19 Mya, which ceased activity about 17-15 Mya), and one in the north, which ceased activity about 14-12 Mya. Upslope projections on the curved western face of the Jandía peninsula suggest that its volcano could have also reached ca. 3000 m in height, and its summit would have been well to the west of the current southwestern shore of the island. Avalanche deposits on the deep ocean floor along the western coast of the island indicate the collapse of this ancient volcano. Shield volcanism on Fuerteventura ended ca. 12 Mya, and was followed by a long period of erosion (lasting about seven million years) before intermittent basaltic volcanism began again, about 5 Mya, including several eruptions in the Pleistocene.

Lanzarote originated through two independent shield volcanoes: one in the Ajaches and the other in Famara, respectively to the South and the North of the current island. The main shield-building stage of the Ajaches volcano developed from ca. 14.5 to ca. 13.5 Mya (although an apparently questionable radiometric aging dated the most ancient lavas much earlier, ca. 19 Mya, Carracedo and Day, 2002). This volcano is just 14 Km in diameter and 608 m in height today, but it probably covered most of the southern half of the island in the past, just until post-erosive dismantling started from ca. 13.5 Mya to ca. 5.7 Mya. The Famara shield volcano started its activity some 10.2 Mya, and finished ca. 3.8 Mya; today, only the western half of this volcano remains, which forms a 600 m-high cliff that probably represents the eroded side of a giant gravitational collapse. The latest episodes of post-erosional volcanism on Lanzarote seem to have developed throughout the Pleistocene. According to recent dating, Holocene eruptions have been only occasional, and they may limit to the historical records in the 18th and the 19th centuries.

Gran Canaria is a geologically complex island that shows two main phases of volcanic activity, one in the Miocene, and the other in the Pliocene-Holocene. These have overlapped with intense erosion before and during post-erosional volcanism, which has continued to the present. The remnants of the oldest shield volcanos of Gran Canaria (Hogarzales and Güigüí, dated ca. 15.5 and ca. 8 Mya, respectively) are situated in the central west of the island, and overlap in space with other old volcanoes. Unlike those in Mahan, these do not show evidence of lateral collapses, except for the suggestive forms of the steep curved cliffs north-west of the island. Some 14 Mya, the stratovolcano in the west of Gran Canaria collapsed, forming Tejeda's caldera (Pérez-Torrado, 1997). From ca. 5.5 to ca. 2.7 Mya, the centre of Gran Canaria was occupied by a large stratovolcano (the Roque Nublo), with a height that may have reached more than 3,000 m. The Roque Nublo stratovolcano was subject to at least three moderate sized collapse events in the south and the west separated by periods of scarp erosion and volcano regrowth. Following a large collapse in the south flank ca. 3.5 Mya (Funck and Schmincke, 1998) debris filled many ravines in that area, but not large neighboring ridge environments (Mehl and Schmincke, 1999). These collapses, characterized by giant avalanches and landslips, transported materials more than 20 km from their origin, and together with Plio-Pleistocene volcanic activity (Pérez-Torrado, 2000), shaped the ravines and deposits in the southern and western side of the island

Tenerife first consisted of three independent edifices in the Miocene, now known as the paleo-islands: the area surrounding the Roque del Conde massif in Adeje (11.9–8.9 Mya), Teno (ca. 6.1–5.1 Mya), and Anaga (ca. 4.9–3.9 Mya). Despite controversies with regard to the dating of the main geological events, it seems that the shaping of Tenerife as a single island started only some 3.5 Mya (Carracedo and Pérez-Torrado, 2013), as continued volcanism accompanied the development of the central Las Cañadas volcano. From ca. 5 Mya till ca. 3 Mya (perhaps with a break in volcanic activity from ca. 4 Mya), the effusive activity of the central edifice settled down, opening an erosive period which feasibly destroyed the upper part of the Cañadas edifice in central Tenerife. The renewal of volcanic activity some 2.5–2 Mya refilled this edifice (Araña and Carracedo, 1978), which colapsed again forming the current Las Cañadas caldera about 170–200 ky ago, when the present Teide-Pico Viejo stratovolcano (currently reaching 3718 m asl) started its construction (Carracedo and Pérez-Torrado, 2013). Further erosion developed until recently, although the island is now at about the peak stage of its ontogeny.

La Gomera is a shield volcano unrelated to those of Tenerife, despite the short distance that separates both islands (only 28 km between their closest points). La Gomera developed predominantly in the Miocene (the oldest geological formation appears in the northwest of the island, and the most reliable estimates date its age at around 9.4 Mya). Between the shield and post-erosional stages, a northward-trending giant landslide may have occurred, and volcanism ceased completely ca. 2.9 Mya.

La Palma is a volcanically very active island characterized by two distinct shield structures: the Pliocene-Pleistocene northern shield (Garafía and Taburiente volcanoes), and the Pleistocene-Holocene southern shield (the Bejenado and the Cumbre Vieja Volcano). With an inferred age of ca. 1.7 Mya, the Garafía volcano is the oldest subaerial volcano on the island (though it is almost totally covered at present by the overlying Taburiente volcano), and it is estimated to have been 23 km in diameter and ca. 2500–3000 m in height. Its southern flank collapsed into the sea ca. 1.2 Mya, but continuing volcanic activity progressively spilled lavas over the northern flank which ended up forming the 3000 m-high Taburiente Volcano. In the final stages of development of the Taburiente volcano (ca. 0.8–0.7 Mya), a concentration of eruptions in the Cumbre Nueva rift zone formed a north-south elongated dorsal which may have reached ca. 2500 m asl. Deep shield erosion starting ca. 0.6 Mya has carved spectacular canyons. Subsequently, the small post-collapse Bejenado volcano, active from ca. 0.5 to 0.2 Mya, defined the SE wall of the Caldera de Taburiente (1854 m in height at present). At the end of the growth of the Bejenado, the island possibly entered a period of quiescence until 0.13 Mya, when the 1950 m-high Cumbre Vieja ridge was rapidly formed. Activity along its rift enlarged the island considerably, especially to the south. At least six eruptions have occurred since the colonization of the island by the Castilians (ca. 1493).

El Hierro forms with La Palma a dual line of volcanoes at the western end of the Canaries, and both islands may have had some "on-off" connection in their magma source at least in the past 700,000 years, whereby intense volcanism in one island corresponds to volcanic quiescence in the other. The oldest surface lavas dated in El Hierro are ca. 1.2–1.5 my old (Carracedo, 1999). The island seems to have grown rapidly by the superposition of three main volcanic edifices separated by gravitational collapses: Tiñor (in the North East of the island), El Golfo (in the North West, whose edifice is estimated to have reached ca. 2000 m), and the Rift volcanism which, unlike the previous two, has not yet produced a conspicuous edifice. The formation of the El Golfo embayment (maybe just 80,000 years ago, León et al., 2016) was accompanied by the sliding into the ocean of a high volume of rocks, which probably produced a huge tsunami that affected at least the Canary Islands. Historical records also show a seismic crisis in 1793, and a recent one in the seafloor facing the southern part of the island started in 2011.

## 4. Predictions of the SSH during the Canarian Miocene

Geological evidence indicates that, till the early Pliocene, Mahan and Gran Canaria may have reached between 2500 and 4000 m in height (Fuster et al., 1968; Ancochea et al., 1993; Stillman, 1999; Acosta et al., 2003), thus hosting several ecological altitudinal zones. The first waves of mainland colonizers could have reached these islands from similar areas in Western Africa, and/or from more remote northern regions using the stepping stones represented by the chain of now-submerged seamounts and guyots north of the Canaries and Madeira (Fernández-Palacios et al., 2011), that were still high islands when Betancuria's shield volcano was formed, some 22-21 Mya.

The geological upheavals concomitant to the episodes of shield formation in these islands likely drove many of the early colonizers to extinction, as the forming volcanoes underwent radical (and apparently rapid) lateral collapses. However, some of the founding lineages probably succeeded; e.g. the origin of the Canarian circumscription of the *Aeonium* alliance is dated ca. 15.3 Mya (Kim et al., 2008) (Fig. 1B).

In Mahan, the ca. 7 million-year window of post-shield erosion and relative volcanic quiescence in the Miocene (from ca. 12 Mya to ca. 5 Mya) was probably auspicious for hosting further colonization waves with a much higher rate of success. Throughout this epoch, Mahan (and also Gran Canaria) could have furnished more opportunities for secondary contact among evolutionary lineages that had undergone variable periods of geographic isolation in the mainland, and perhaps even evolutionary divergence. The origin of some species in the Canarian Laurel forest is dated in this epoch by Kondraskov et al. (2015): *Prunus lusitanica* (Rosaceae, ca. 11.46 Mya), *Ixanthus viscosus* (Gentianaceae, ca. 9.40 Mya), *Bystropogon* Sect. *Canariense* (Lamiaceae, ca. 6.41 Mya, see Fig. 1B) or *Picconia excelsa* (Oleaceae, ca. 5.20 Mya).

If the founder propagules were self-incompatible, the expected increase in diversity would have been extremely high (Fig. 1A), as they originated in geographically separated mainland populations. If the founder propagules were self-compatible, multiple colonizations would equally have promoted a high degree of outcrossing, thereby creating higher diversity than if founders came from just one or a few propagules from a single mainland region/population. While data are still limited, the emerging picture in some Canarian plants is that pseudo-self-compatible (PSC) island colonizers may be more common than previously thought (Crawford et al., 2008), entailing a higher likelihood that populations will be outcrossing rather than selfing (outcross pollen will outcompete self-pollen, Levin, 1996), which thereby should generate a large amount of genetic variation in the first colonization stages.

Thus, multiple colonizations may have given rise to considerably high genetic diversity levels, as the foreseeable effect of stochasticity would have determined a heterogeneous genetic composition in the colonizing stocks (Ellstrand and Schierenbeck 2000; Dlugosh and Parker, 2007, 2008). As hypothesized by Borgen (1996) based on the allozyme polymorphism detected in *Lobularia canariensis* (DC.) L. Borgen (Asteraceae) "multiple colonizations may have brought much variation to the archipelago, and this may explain some of the genetic variation observed today". Similarly, Diaz-Perez et al. (2008) suggested that *Festuca agustinii* Linding. may have colonized a single island several times from relative different genetic pools, possibly of different evolutionary origins. According to the SSH, such high levels of genetic diversity could have facilitated in these and many other cases the successful colonization of open spaces and of the altitudinal ecological zones that existed in Mahan and in other islands from the mid-Miocene on (see "Background" above).

During this period of maximum topographic complexity, and before the start of the dismantling processes of the Betancuria, Jandía, Ajaches, Hogarzales and Güigüí shield volcanoes in Mahan and Gran Canaria, the lineages in the different altitudinal zones could have colonized (or have received colonizers from) areas with a similar ecology in other islands. Although the first emerged parts of Tenerife and La Gomera formed respectively about 11 Mya and 9.5 Mya, most such "island-hopping" processes in the mid-late Miocene must have proceeded between Mahan and Gran Canaria. The exchange of migrants between Tenerife and La Gomera and other regions was probably lower in this epoch because of their relatively small sizes, and their higher distance to the mainland and easternmost islands (annual aerosol deposition rates over the North Atlantic indicate an abrupt downward slump in La Gomera, Goudie and Middleton, 2001; see Fig. 2).

According to molecular datings in Kim et al. (2008) the origin of the radiations of the *Sonchus* alliance (Lamiaceae) and *Crambe* (Brassicaceae) happened within this time interval (respectively ca. 8.5 Mya and ca. 8.2 Mya). Puppo et al. (2015) also date the origin of *Micromeria* (Lamiaceae) some 8.4 Mya, which was followed by a radiation burst originating in the central islands some 6.4 Mya (Fig. 1B).

Till the mid-Pliocene, only the three regions known as the 'palaeo-islands' existed in the territory of Tenerife. The geological processes that filled the gap between these three palaeo-islands and gave rise to the volcanic edifice of Tenerife as we know it at present only appeared between ca. 3.5 and 2.5 Mya (Carracedo and Pérez-Torrado, 2013). Thus, the colonization of Tenerife from Mahan or Gran Canaria during the Miocene could have affected only the very small area occupied by the paleo-islands, and not the present altitudinal zones of the island, that started to develop much later. Hence, as discussed by Marrero and Francisco-Ortega (2001a), the older Canarian islands not only offered variably large target areas for the impact of propagules throughout the Miocene, but also potential colonization bridges to other islands.

## 5. Predictions of the SSH during the Canarian Pliocene and Pleistocene

In the Pliocene and Pleistocene, the geological history of the Canaries was dominated by sea-level changes. During extremely low stands, the sea was 120–130 m below the present level, and Fuerteventura and Lanzarote were connected by a landbridge, thus widening the terrestrial area available to plant colonizers. During high-stands in the last 5 My, the sea level was about 25 m higher than at present (Root Routledge, https://www.e-education.psu.edu/earth107/node/901), entailing the filling of La Bocaina straits, the separation of Fuerteventura and Lanzarote, the flooding of many insular territories (provoking the extinction of populations), and the availability of a much smaller target area for eventual founders. In the last 2 Mya (Pleistocene) sea levels underwent extreme oscillations. Sea levels dropped at least 100 meters below modern sea level on at least 4 occasions during the last 600,000 years, thereby bringing about cycles of enlargement and contraction of the emerged area of Mahan (Fernández-Palacios et al., 2016). In the latest interglacial (Eemian) the sea level was some 8 m above the present one.

The progressive dismantling of the North-Fuerteventura and the Famara shield volcanoes in Lanzarote is estimated to have started ca. 5 Mya, and it may have been conducive to the formation of further syngameons that promoted admixture also among genotypes that occurred in the earlier ecological altitudinal zones in the Jandía, Betancuria and Ajaches volcanoes. The syngameons in the Pliocene may have even entailed a further increase of the population genetic diversity in some lineages through the admixture of conspecific populations (or close congeneric species) that were previously separated by geographic barriers. We must also bear in mind that colonizers from external areas would have kept arriving, potentially increasing population genetic diversity.

Thus, all lineage-dependent factors being equal, these secondary syngameons should be overall more genetically diverse than the initial ones (Fig. 1) because there would be more contributing sources of genetic diversity. We emphasize, however, that genetic diversity is determined and fine-tuned by a complex combination of many variables (see e.g. Pérez de Paz and Caujapé-Castells, 2013), so that the shape of the population genetic variation curve may vary across lineages.

About 5 Mya, the central part of Gran Canaria was dominated by the Roque Nublo volcano, so that island-hopping was still possible between similar altitudinal zones in Mahan and in Gran Canaria. Although the main volcanic edifice of central Tenerife was already in place some 3.5 Mya, its upper part was first destroyed by erosion and subsequently refilled by a second peak of volcanic activity ca. 2.5 Mya (Araña and Carracedo, 1978). This means that most island-hopping phenomena resulting in successful colonization of central Tenerife may have been possible only about 2.5–2 Mya.

In this epoch, the filling of the gap that separated the three paleo-islands of Tenerife in the Pliocene represented (1) a much more sizeable target for colonizers from older islands, and (2) a potential stepping stone for propagules coming from other regions, thereby increasing the expected frequency of new colonizers to and from La Gomera. Such may be the case of *Periploca laevigata* (Asclepiadaceae, García-Verdugo et al. under review), where the levels of genetic diversity and the distribution of sub-lineages in the archipelago consistently suggest that Tenerife was recently colonized from La Gomera. It could also explain the patterns of haplotype sharing between the East of La Gomera and the Northwest of Tenerife detected in *Olea cerasiformis* Rivas-Mart. & del Arco (Oleaceae, García-Verdugo et al., 2010).

As represented in Fig. 1B, the radiation of *Lotus* (Fabaceae) in the Canaries entails multiple colonizations and is estimated by Ojeda et al. (2012) to have started in the Pliocene between ca. 4.3 Mya (in the Eastern and central islands) and ca. 3.71 Mya in the Central and Western islands. According to the datings in Kim et al. (2008), the origin of the radiations of *Echium* (Boraginaceae, ca. 3.7 Mya) and *Sideritis* (Lamiaceae ca. 3.3 Mya) also fall within the same time frame (approximately coinciding with the maximum geographic complexity of Gran Canaria and the forming of the pre-Teide volcano in Tenerife). Similarly, the divergence time estimates by Jones et al. (2014) place the origin of the radiation of *Pericallis* (Asteraceae) in the late Pliocene, some 3.5 Mya, and the colonization of the Canaries by *Androcymbium* (Colchicaceae) took place less than 3.5 Mya, according to Del Hoyo and Pedrola-Monfort (2010). Notably, this genus is distributed at present in all the Canarian islands save for Tenerife and Gran Canaria, so that the volcanic events from the last 3.5 million years may have brought about the extinction of its populations in these two islands.

Some authors (e.g. Araña and Carracedo, 1980) contend that all the vegetation of Gran Canaria went extinct as a consequence of the collapse of the big stratovolcano that generated the 'Caldera de Tejeda' (some 14 Mya), and of the three events that collapsed the Roque Nublo stratovolcano (starting about 3.5 Mya), but this seems unlikely (Navascués et al., 2006; Anderson et al., 2009). The time between collapses should have allowed for vegetation survival and recovery, although part of the flora of the island during these epochs must certainly have been threatened, and in many cases probably survived in mosaic habitats (Anderson et al., 2009). Marrero and Francisco-Ortega (2001a) estimate that if these events happened today, they would entail the extinction of respectively 80% and 50% of the insular flora.

Further dismantling and erosion of the Roque Nublo volcano about 2 Mya created both (i) new open areas in the South and East of Gran Canaria, and (ii) deep ravines in the central and western regions of the island. Throughout geological time, these spaces must have been suitable for hosting further processes of genetic admixture followed by strong genetic isolation in some cases. Colonizers of these territories may have originated from (a) the western half of Gran Canaria, (b) Mahan, (c) some of the seamounts north of the Canaries that were emerged during the Pleistocene, or (d) the mainland. According to molecular age datings, *Cheirolophus* (Asteraceae) experienced an explosive diversification in the Canaries starting ca. 1.74 ± 1.19 Mya (Vitales et al., 2014); Mairal et al. (2015) estimate that *Canarina canariensis* (L.) Vatke (Campanulaceae, now present in all the Canary Islands save for Mahan) started to colonize the Canaries ca. 1 ± 0.75 Mya, coinciding with the advanced erosive phase of Mahan and the dismantling of the last big volcanoes in Gran Canaria (Fig. 1B). The splitting date of the Canarian circumscription of *Cistus* (Cistaceae) occurred much more recently (0.33 ± 0.14 Mya) according to the datings in Guzmán and Vargas (2010). According to Kondraskov et al. (2015), 14 species in the Canarian laurel forest originated between ca. 4.56 Mya and 0.68 Mya.

Also importantly, the formation of the 'El Golfo' embayment in El Hierro brought about giant landslips and avalanches into the ocean (maybe just 80,000 years BP, León et al., 2016), which likely generated a giant tsunami that must have provoked mass extinctions in many Canarian regions. Given that Mahan had been in its advanced dismantling phase since ca. 5 Mya, and a large part of the Eastern side of Gran Canaria was also formed by open, flat spaces, this tsunami very likely affected especially most of the plant diversity of the lower altitude regions in Mahan and Gran Canaria (perhaps with the exception of the heights of Famara, Jandía, and the remnants of the Hogarzales, Güigüí and Roque Nublo volcanoes), and the other islands in the archipelago. Thus, apart from erosion, recurrent recent volcanism, and hybridization phenomena in the last 5 My, this recent tsunami (León et al., 2016) may be an important added factor to explain the currently low endemic plant diversity on Mahan. Notably, this would be just the last of a long list of tsunamis linked to catastrophic landslides that ocurred throughout the formation of the Canaries. For instance, the landslide of Güímar valley in Tenerife (ca. 0.8 My BP) originated a tsunami that reached 100 m asl in Agaete, on the NW of Gran Canaria (Carracedo et al., 2009).The prevalence of the Westerlies (Rognon and Coude-Gaussen, 1996) in several epochs of the late Pleistocene (ca. 18,000 years BP) probably determined colonization waves from the Western islands to Eastern islands (e.g. as in the case of *Micromeria rupestris* [Lamiaceae] endemic to Lanzarote, Puppo et al., 2015), and from the islands to the mainland (see Caujapé-Castells 2004, 2011).

## 6. Concluding remarks

Classical theories (Mayr 1942; Dobzhansky 1951) contended that hybridization retards speciation because hybrids are less fit than their parents, and it certainly can be so in highly eroded islands where open habitats are frequent and there are scarce environmental stimuli for selection to act. However, that earlier monolithic view is also changing, because hybrid speciation is now much better documented (Buerkle and Rieseberg, 2008; Abbott et al., 2013), and hybridization appears to be particularly common in the most species-rich and rapidly diversifying groups of organisms (Schwarzer et al., 2012).

In recent geological times (the last 2 My), the formation of syngameons in the Canaries could have been especially favored when Mahan and the Eastern part of Gran Canaria attained a certain geological stability, and their geographic complexity was largely reduced by either (i) advanced erosion, or (ii) the dismantling of old volcanoes. However, at different times since the Miocene, diverse factors likely contributed to promote genetically highly diverse syngameons through secondary contact and admixture among previously isolated genotypes across the archipelago (see Fig. 1B).

Although the dismantling of Mahan may not have been incompatible with the survival of many endemics and the formation of syngameons, the relatively recent eruptions, the much older age of this island, and possibly the effects of the tsunami provoked by giant landslips in El Hierro must have entailed the extinction of a high number of populations from lineages which are now only present in other islands of the archipelago. All of these factors contribute to the much lower present biotic makeup of Mahan. Consequently, many Canarian lineages that may have originated from syngameons in Mahan either do not have already extant representatives in this island, or were retro-colonized from other islands by their descendants.

The earlier assumption of the SSH that a sustained decrease of population genetic diversity should be detected from the older to the younger Canary islands (Caujapé-Castells, 2011) was an over-simplification. Given the heterogeneous impacts of the dynamic ontogeny of the Canaries on their biota, such a decrease could only be detected in lineages that have colonized the islands very recently in an East-to-West direction, and provided that extinction has not had a significant impact on their current distribution. Furthermore, the fact that the expected average population genetic diversity should be quite similar among most islands at present (Fig. 1B), and that recently founded populations in the younger, geographically more complex islands should host transiently higher levels of genetic variation (the 'genetic diversity debt', see above) would make the distinction statistically difficult even in such cases.

At present, Fuerteventura and Lanzarote should be regarded as mainly "anagenetic" regions, where species do not originate through radiation but via the accumulation of genetic variation (Stuessy et al., 2014; Takayama et al., 2015); however, they were probably "cladogenetic" in many stages of their earlier ontogeny, coinciding with their maximum geographic complexity throughout the Miocene (see above). A difference with respect to Stuessy et al. (2014) is that anagenesis under the SSH would in general be attained more rapidly, via multiple introductions followed by hybridization, rather than only by the progressive accumulation of genetic variation through time.

As the geological ontogeny of the archipelago continues, the relentless dismantling and erosion of Gran Canaria, Tenerife, and La Gomera may give rise to further secondary syngameons, from which colonizations to the much younger La Palma and El Hierro may occur. Hence, similar processes to those associated with the discussed 'hybridization past' context will probably promote a 'hybridization future' that may entail introgression among many lineages that consist of different species at present, until the islands eventually cannot host more terrestrial biodiversity in the last stage of their ontogeny above sea level.

### 6.1. Current and future research

Detailed experimental data demonstrating the relationship between hybridization and the origin of adaptive radiations are still in short supply, but when they exist, they compellingly suggest rapid adaptive evolution through natural hybridization (e.g. Barrier et al., 1999; Rieseberg et al., 2003; Martin et al., 2006; Grant and Grant, 2010; Whitney et al., 2010; Brothers et al., 2013).

Likewise, in the Canarian flora there are very few works that address the roles of hybridization with comprehensive multi-disciplinary data (perhaps the single exception to date would be the works with *Tolpis* referred to throughout the paper), but molecular investigations that do suggest a substantial role of hybridization abound. Table 1 shows that hybridization may have played a role in the evolution of 62 genera that contain about 400 Canarian endemic taxa (44 genera and 354 endemics if only considering 'informed cases').

As highighted by Hochkirch (2015), the integration of interdisciplinary information on natural model systems is a fundamental objective for the study of hybridization and introgression processes; however, the number of adaptive radiations that have been extensively studied is very small (Gavrilets and Losos, 2009). Certainly, molecular data can provide substantial insight, but the thorough assessment of the SSH also entails tests of reticulate evolution, and chromosomal analyses

(FISH and GISH) in selected groups.

To mitigate the major drawback posed by extinction in the distant and recent past, a feasible strategy is to address the study of relatively widespread Canarian endemics that still have numerous congeneric populations in the mainland (Jaén-Molina et al., 2009; García-Verdugo et al., 2015). Although the current geo-ecological conditions of the Canaries are different from those that fostered the formation of syngameons in different past epochs, possibly these distribution patterns are the only viable approach to attain almost fully representative population and taxon sampling to reconstruct pre-radiation conditions in the Canarian flora. However, even in these cases, the human settlement on the islands at some point within the first millennium BC (del Arco et al., 1997; Rando et al., 1999) started to influence the distribution of biodiversity elements, which dramatically and swiftly changed since the Castilian conquest of the Canaries between 1402 and 1496 (see e.g. Fernández-Palacios et al., 2011). These recent historical perturbations have increased in the last decades with the threats posed by invasive species, and may warp the thorough testing of many hypotheses.

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