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The extension of the taxon cycle model to island plants: insights from the Canarian vascular flora

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ABSTRACT

Taxon cycle models describe eco-evolutionary patterns of lineage colonization, diversification, and decline across archipelagos, inferring an important role for competition amongst ecologically similar taxa in driving concurrent niche changes. Hitherto described in detail only for animal taxa (notably ants and land birds), we extend the application of taxon cycle analysis to the flora of the Canary Islands, in the process describing several variants on the classic model. Our analysis is based on the premise that taxon cycle dynamics are driven by interactions within closely related species, represented here by congenerics. We compiled distributional and phylogenetic data for 556 species (59% of the native vascular flora), enabling us to allocate the members of each colonist lineage to one of five taxon cycle distributional stages (colonization and range expansion, diversification, range contraction and further diversification, becoming threatened, and extinction). We then grouped the genera into six models: classic taxon cycle (23% of flora), intra-lineage taxon cycle (39%), spontaneous taxon cycle (22%), incomplete taxon cycle (4%), evolutionary stasis (5%), and no taxon cycle (6%). We discuss the drivers that may be shaping these distributions and evaluate how well they conform to the taxon cycle paradigm. We also highlight the use and limitations of stem and crown ages as a tool to test or refine taxon cycle attributions. Our analyses demonstrate that the taxon cycle provides a plausible framework for the analysis of the flora of an oceanic archipelago, while highlighting that both its general applicability and the mechanisms responsible for it will require further independent verification.

Key words: Canary Islands, diversification, eco-evolutionary pathway, ecological opportunity, endemism, evolutionary stasis, island biogeography, native vascular plants, taxon cycle stages, taxon cycle models.

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I. INTRODUCTION

Island taxon cycles were first described by Edward O. Wilson in a seminal series of papers describing the eco-evolutionary pathways followed by the Melanesian ponerine ants (Wilson, 1959, 1961). Based on distributional data and phylogenetic relationships, he inferred that, within a particular taxon, reiterative waves of mainland colonizers would displace the earlier island colonizers from coastal to interior forested habitats and, in doing so, they would become isolated and would diversify taxonomically. Over time, these species would become restricted in distribution, leading to eventual stochastic extinction (reviewed by Whittaker, Fernández-Palacios & Matthews, 2023). Initially subdivided by Wilson into three stages, subsequent work on Caribbean land birds by Ricklefs & Cox (1972) found it useful to distinguish four phases, the last of which represents highly localized endemic species. In his later application of the taxon cycle framework to the Hawaiian honeycreepers, Ricklefs (2017) showed the practical relevance of the model by demonstrating a link between the taxon cycle and historical extinction prevalence. Specifically, Ricklefs (2017) showed that late-stage species were especially prone to anthropogenic population extinctions. In applying the model to contemporary oceanic island settings, we may therefore differentiate a fifth stage, whereby anthropogenic extinction of a stage-four species has occurred (Table 1).

Classic taxon cycle explanations infer a significant role for interactions between ecologically similar species in driving biogeographical patterns. Within Wilson's (1959, 1961) ponerine ant model, recent colonists are hypothesized to have a competitive advantage over the products of earlier colonizations. Within the Caribbean birds system Ricklefs and colleagues described how new colonists initially benefit from ecological release but, as they progress through the cycle, the local biota 'counter-adapt' to them (Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002). This contributes to the colonists' increasing specialization to more localized distributions and their vulnerability in the face of subsequent colonists that may successfully attempt to occupy similar niche space. It is important to note that within the island biogeographical literature, inferences of the past effects of competition as drivers of contemporary distributions have generated much controversy (reviewed in Whittaker *et al.*, 2023). More recent work on the taxon cycle has tended to confirm its value as a general framework, while highlighting the roles of other evolutionary mechanisms (e.g. niche shifts, island syndromes such as loss of dispersiveness) alongside competition (Economo *et al.*, 2015; Matos-Maraví *et al.*, 2018) and a need to modify the original models to accommodate system-specific features (e.g. Liu *et al.*, 2020).

Although the idea of taxon cycles has been considered in non-insular contexts (e.g. Rull, 2023), in its original form, as an island biogeographical model, analyses to date have focused exclusively on animal taxa, principally birds, lizards, and ants. The approach presupposes a dominant source region and a series of recipient islands comprising a well-defined archipelago, or meta-archipelago (as exemplified in Table 2). Thus far, the only applications to plants of which we are aware are non-insular and/or represent relatively limited tests based on, for example, diversification rates (e.g. Rull, 2023; Keppel, Nge & Ibanez, 2024): they nonetheless suggest that the model may have applicability to plant as well as animal taxa.

Here, our aim is to apply and evaluate the taxon cycle framework for the flora of an oceanic archipelago. We have selected the Canaries as its flora is well studied and includes several genera that have radiated *in situ*, involving a mix of single or multiple colonization events from outside the archipelago. Our approach involves a number of theoretical assumptions, paramount within which are that: (*i*) competitive interactions occur within the flora that influence niche shifts, niche occupancy and ultimately geographical distributions of members of evolving lineages within the archipelago; and (*ii*) consideration of these interactions can be reduced, for present purposes, to a focus on closely related congeneric

Table 1. Taxon cycle stages, drawing from Wilson (1961), Ricklefs & Cox (1972), and Ricklefs (2017) and criteria used in this work to allocate species to a given stage.

Taxon cycle stage	Characteristics	Criteria used to allocate a species to a given stage
Early Stage 1	Colonization of an archipelago by a mainland species, spreading across the closer islands and occurring mainly within disturbed habitats, as such species are typically generalists with good dispersive ability. There is no or little differentiation initially between mainland and island forms.	Non-endemic native (NEN) species scarcely distributed in the archipelago, despite existing non-colonized islands possessing suitable habitats.
Late Stage 1	The colonization of the archipelago has been completed and all the suitable islands have been occupied.	Non-endemic native (NEN) or palaeoendemisms widely distributed in the archipelago.
Early Stage 2	The colonist may then expand its niche, invading other habitats, displaying more patchy distributions as selection against mobility reduces gene flow.	Widely distributed anagenetic multiple island endemic (MIE) (i.e. a species that has evolved from the ancestor until achieving a new species identity, without radiating).
Late Stage 2	Gradually, local forms evolve, restricted to a subset of the islands, and as they are out-competed in their original colonizing niche by later colonists, their niches narrow and they become restricted to interior forest habitats.	Non-threatened multiple island endemic (MIE) present in two or more islands.
Stage 3	Continuing this process, species become highly differentiated and are found as scattered endemic forms.	Non-threatened single island endemic (SIE).
Stage 4	Highly differentiated endemic species persists as a relict on several islands or a single island, with high vulnerability to stochastic extinction processes.	Species included in IUCN *Red List* with a threat category (Vulnerable, Endangered or Critically Endangered).
Stage 5	Prehistoric/historic phase of anthropogenic change processes (habitat loss, introduction of non-native species, etc.) lead to their final extinction.	Species included in the list of extinct species given by Orihuela-Rivero *et al.* (2025).

Table 2. Illustrative selection of insular studies that have attempted to apply the logic of the taxon cycle model.

Authors	Islands/ archipelagos	Taxa
Wilson (1961)	Melanesia	Ponerine ants
Ricklefs & Cox (1972)	Caribbean	Land birds
MacLean & Holt (1979)	Virgin Islands	*Sphaerodactylus* lizards
Jones *et al.* (1987)	Madeira and Canaries	Landbirds and butterflies
Roughgarden & Pacala (1989)	Caribbean	Anoline lizards
Losos (1992)	Caribbean	Anoline lizards
Ricklefs & Bermingham (2002)	Lesser Antilles	Landbirds
Cook *et al.* (2008)	Caribbean	Freshwater decapod shrimps
Economo & Sarnat (2012)	Fiji	Ants
Jønsson *et al.* (2014)	Indo-Pacific	*Pachycephala* passerines
Ricklefs (2017)	Hawaii	Honeycreepers
Matos-Maraví *et al.* (2018)	Indo-Pacific	Ants
Pepke *et al.* (2019)	Wide	Corvoid birds

species. The rationale for this focus is that, as a general proposition, species of the same genus (and especially those most closely related) typically share many traits that can lead to them competing for largely overlapping niche space, potentially leading to negative associations between them within specific habitats, notwithstanding that they may also interact and compete with many other species that share adaptations to the same habitat(s) (e.g. Sanderson, Diamond & Pimm, 2009; Park *et al.*, 2020).

Our working hypothesis is that diversifying lineages within the Canarian flora are shaped over evolutionary time by taxon cycle dynamics, resulting – as a by-product – in increased vulnerability to anthropogenic extinction processes. We also occasionally refer to lineages that span other archipelagos within Macaronesia in addition to the Canaries. Our approach is to use distributional and phylogenetic data for the native flora to classify the members of each genus and distinct colonist lineage into the five stages outlined in Table 1. Based on this first step, we then develop a series of alternative scenarios proposing generalized variants of the taxon cycle model to which we assign exemplar cases. We thereby aim to establish the viability of the taxon cycle model as a general model for the analysis of the evolutionary dynamics of an oceanic island flora. Testing our inferences is for future work.

II. STUDY AREA

The Canaries archipelago (Fig. 1 and Table 3) is made up of seven major islands (Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Palma, La Gomera and El Hierro), and four minor islands (Alegranza, Montaña Clara, and La Graciosa, to the north of Lanzarote and Lobos Island to the north of Fuerteventura). These islands conform with a

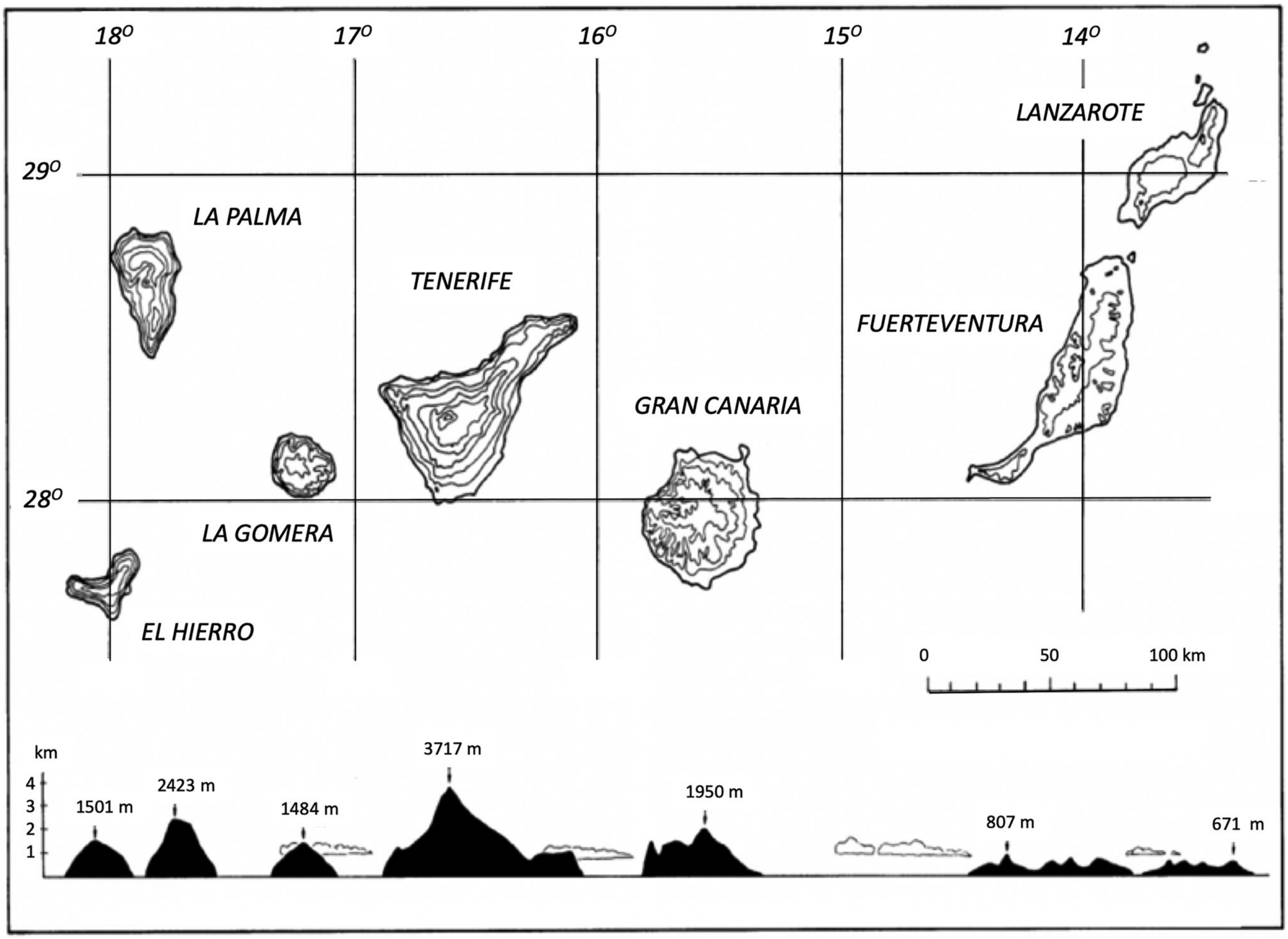

Fig. 1. Map of the Canaries, including the topographic profile of the major islands and the incidence of the sea of clouds (depicted only in Tenerife and La Gomera for simplicity, but also extending to Gran Canaria, La Palma and El Hierro), providing the higher central and western islands with a climatic refugium where the laurel forest can withstand the summer aridity of the predominant mediterranean-type climate. Source: Machado (1992).

hotspot (volcanic, oceanic) model of formation and have never had a land connection to Africa, although the easternmost Canaries are only 96 km from the hyper-arid northwestern African coast. The major islands formed between <2 million years ago (Ma) and *c*. 24 Ma (Table 3) and mostly remain volcanically active, with the most recent eruption being of Tajogaite volcano on La Palma in 2021. The Pleistocene glacial–interglacial cycles had a pronounced effect on the geography of these islands, repeatedly increasing and decreasing their surface area, as well as joining the easternmost islands (Lanzarote, Fuerteventura and their satellite islets) into a single insular entity (Mahan) (Fernández-Palacios *et al.*, 2016).

There are more than 12,500 terrestrial species and 5,500 marine species in or around the Canaries, of which approximately 4,000 species and 120 genera are endemic (Banco de Datos de Biodiversidad de Canarias, n.d.). Among them are some outstanding examples of explosive radiation, both within invertebrates (*Attalus*, *Dolichoiulus*, *Dysdera*, *Hemicycla*, *Laparocerus*, *Napaeus*, etc.) and within the vascular plants (*Aeonium*, *Argyranthemum*, *Crambe*, *Cheirolophus*, *Echium*, *Limonium*, *Lotus*, *Pericallis*, *Sideritis*, *Sonchus*, etc.). The Canaries are subject to a largely mediterranean-type climate and have a great diversity of ecosystems that vary zonally from the semi-desert scrub of the coasts to thermophilous mediterranean-type forests, mid-elevation cloud forests, pine forests and the shrublands of the summits.

The Canaries are the only Macaronesian islands that had indigenous inhabitants at the time of European colonization in the 15th century. The Romans were active in the Canaries around the start of the Common Era but did not settle. Archaeological and genetic evidence indicates that ethnic Amazigh Berbers, who became the archipelago's first indigenous communities, first settled in 200–400 CE (Mitchell, 2024; Santana *et al.*, 2024). They introduced goats, sheep, pigs, dogs in addition to wheat, barley, fava beans, peas, lentils, figs and the practice of transforming forests into pasture by the use of fire. They did not create written records and thus human modification of the landscape precedes written chronicles (de Nascimento *et al.*, 2020). The Norman–

Table 3. Geographic data for individual Canarian islands and for the entire Canaries archipelago. Note that the geological ages vary slightly among sources. Source: Fernández-Palacios *et al.* (2017).

Island	Area (km^2)	Elevation (m)	Distance from the continent (km)	Age (million years)
Tenerife	2034	3718	288	11.5
Fuerteventura	1655	807	96	24
Gran Canaria	1532	1949	199	15
Lanzarote	805	671	127	16
La Palma	708	2.423	416	2
La Gomera	370	1487	337	12
El Hierro	269	1501	384	1.5
La Graciosa	29	266	152	0.05
Alegranza	10.3	289	169	0.035
Lobos	4.6	122	123	?
Montaña Clara	1.5	256	160	0.039
Canaries	7450	3718	96.0	24

Castilian conquest and the subsequent European settlement began in the 15th century. Today, about 2.2 million people live in the archipelago and more than 15 million tourists visit per year (Whittaker *et al.*, 2023).

III. ENDEMISM AND DIVERSIFICATION WITHIN THE CANARIAN FLORA

Current assessments indicate that the Canarian native vascular flora comprises 939 species (excluding species of uncertain origin), of which 434 (46%) belong to non-diversified lineages (hereafter, NDLs) and 505 (54%) belong to 85 diversified lineages (hereafter, DLs) which each contain between two and 54 species (mean 5.94 species) (Fernández-Palacios *et al.*, 2021). From the latter, 69 moderately diversified lineages (2–7 species) account for 218 species, whereas 16 highly diversified lineages (>7 species) account for 287 species. Within NDLs there are 86 Canarian endemics and 348 non-endemic natives (hereafter, NENs). Among DLs, the vast majority (83.4%) of species are shrubs, 16.2% herbs and 0.4% (two species) trees. NDLs are dominated by herbaceous species (69.3%), half of them annuals, followed by shrubs (23.3%) and trees (7.4%, 32 species, mainly palaeoendemics or NENs) (Fernández-Palacios *et al.*, 2021). The term palaeoendemic refers to an island form that appears to be essentially unchanged from its ancestral mainland form, where the species has become extinct in the mainland portion of its distribution.

It has been argued that taxonomic classification can overestimate the contribution of *in situ* cladogenesis within the assembly of oceanic floras, and that modern phylogenetic assessments are required to identify endemics that result either from anagenesis or from palaeoendemism (Igea *et al.*, 2015). While this potential source of error may be applicable to some Canarian plant taxa, there are modern phylogenetic models available for many larger Canarian lineages, permitting the distinguishing of single from multiple archipelagic colonization events within most putative radiations.

IV. METHODS

We compiled data on the distribution of 556 (59%) of the 939 native vascular plant species of the Canaries from several updated checklists of Canarian species (Banco de Datos de Biodiversidad de Canarias, n.d.; Schönfelder & Schönfelder, 2018; Sauerbier, Cabrera Calixto & Muer, 2023). For each, we extracted data on the number of 0.5 × 0.5 km grid cells and the islands occupied. We then calculated three dimensions of rarity, following Rabinowitz (1981): (*i*) spatial or geographic rarity, (*ii*) local community abundance, and (*iii*) climatic niche. Spatial rarity was assessed by three different indices: the number of islands occupied, the geographic range, and the number of grid cells occupied across the Canaries [accuracy levels 1 and 2 in Martín *et al.* (2005)]. The geographic range for each species was calculated as the maximum linear Euclidean distance between the grid cells occupied by that species within the archipelago including, where relevant, the distance between islands. The species community abundance value was calculated as the maximum relative cover of each species among all plots in a phytosociological association belonging to one of the six elevational ecosystems of the Canaries (for further details see Fernández-Palacios *et al.*, 2021). Finally, a two-dimensional niche model was performed to estimate climatic niche width per species based on interpolated mean grid cell annual temperature and precipitation values, applying two-dimensional Gaussian hypervolumes with 95% quantiles using the function 'hypervolume_gaussian' in the R package *hypervolume* v.2.011 (Blonder *et al.*, 2014; bandwidth fixed at 0.05). Temperature and precipitation are the most important environmental variables affecting the distribution of plant species and communities on the Canary Islands (Fernández-Palacios, 1992). Mean annual temperature and precipitation data were obtained from meteorological stations ($N = 155$ for temperature, $N = 305$ for precipitation) maintained by the Agencia Estatal de Meteorología de España (http://www.aemet.es). Temperature values were interpolated using multiple linear regression, whereas precipitation values were modelled with boosted regression trees (function 'gbm.step' of the R package *dismo* v.1.1–15, Poisson family error; 10-fold cross-validation) including elevation, aspect, and slope as topographic predictors (see also Fernández-Palacios *et al.*, 2021). The four rarity parameters were standardized to a scale of 0–1, and a novel overall rarity index for each species was defined as the mean value of the four standardized rarity parameters.

To determine the threat status of the endemic vascular plant species, we consulted the IUCN *Red List* (n.d.), a widely recognized and regularly updated source, for assignment to the following categories: critically endangered (CR; 45 species for the Canarian vascular flora, of which 39 are included within our data set); endangered (EN; 42 species, of which 36 are included); and vulnerable (VU; 25 species, of which 18 are included). The extinct species list (EX; six species, all included) was obtained from Orihuela-Rivero *et al.* (2025) because the IUCN *Red List* does not currently provide this information.

In addition, for each genus we searched for the most recently published phylogeny so that we could differentiate between monophyly (all native Canarian species stem from a single colonizer) and polyphyly (the native Canarian species derived from two or more different colonizers), which is crucial for determining the biogeographical dynamics of each genus within the archipelago (Igea *et al.*, 2015).

These data permit us to determine the distributional properties, aspects of the environmental niche, rarity and threat status of each species, and also to assess their place within the sequence of colonization and diversification that has unfolded within each genus.

V. TAXON CYCLE STAGES

In order to classify each species into the five stages of the taxon cycle described in Table 1, we generated the following guidelines. We emphasize from the outset that these descriptions invoke a particular dynamic interpretation for the distributional patterns observed, for which we draw on available published phylogenies. Key abbreviations used are: SIE, single-island endemic; MIE, multi-island endemic; NEN, non-endemic native; palaeoendemic, a species that has become endemic to the Canaries (or to the Canaries plus one or more other Macaronesian archipelagos) due to extinction from its original mainland range, and without having evolved distinguishing features *in situ*; anagenetic species, a species that has evolved from the ancestor until achieving a new species identity within an island or archipelago, without further cladogenesis *in situ*.

Stage 1: *colonization and range expansion*, which can be subdivided into (*i*) *Early Stage 1*, initial archipelagic colonization (where only one or few islands have been colonized) by a NEN; and (*ii*) *Late Stage 1*, completed archipelagic colonization by a NEN or a palaeoendemic. This stage implies that only very limited genetic diversification has taken place. The 'completed' archipelagic colonization of a given species is determined with reference to the availability of the habitat for that species within the archipelago. For instance, coastal scrub and thermophilous woodland species occur within all the Canarian Islands, but laurel forest species are restricted to the five highest (central and western) islands (see Fig. 1), pine forest species are restricted to Gran Canaria, Tenerife, La Palma and El Hierro, and summit scrub species are limited to La Palma and Tenerife (Fernández-Palacios, 1992; del Arco & Rodríguez-Delgado, 2018).

Stage 2: *diversification*, when a species diversifies taxonomically from its ancestor. This stage can be subdivided into: (*i*) *Early Stage 2*, a widely distributed anagenetic MIE species; and (*ii*) *Late Stage 2*: a more restricted, but not-yet threatened, MIE.

Stage 3: *range contraction and further diversification*, when a species that is part of an *in situ* archipelagic radiation has a non-threatened (SIE) status (see Table 1).

Stage 4: *species becomes threatened with extinction* as a result of its limited distribution and is considered CR, EN or VU by the IUCN. Many endemic Canarian plant species are classified as threatened, including not only SIEs, but also MIEs, which we interpret as resulting from anthropogenic extinction drivers (habitat loss, overgrazing, competition with non-natives, etc.) overlaying the natural processes of the taxon cycle to reduce range and population sizes.

Stage 5: *extinction* (including extinction in the wild), when there is no reasonable doubt that the last individual of a species has already disappeared after exhaustive efforts have been made to search their known or expected habitats within their known historic distribution (IUCN, 2012). We include this stage largely for completeness as, in contrast to the analysis of Hawaiian honeycreeper taxon cycles by Ricklefs (2017), the fossil record for plants is insufficiently well resolved to have a high likelihood of detection of pre-historical cases of extinctions of localized endemics. Stage 5 species identified herein are thus restricted to the comparatively few plant species that have gone extinct following scientific description (Orihuela-Rivero *et al.*, 2025).

In applying the above guidelines, it became evident that, although some taxa fitted into this classic model, others suggested alternate pathways. We therefore present in Section VI.2 a series of alternative taxon cycle model hypotheses for the Canarian flora based on the classification of species into the five stages.

VI. RESULTS

(1) Attribution to taxon cycle stages

We have classified 556 species, more than half of the native Canarian vascular flora, into the four extant phases of the taxon cycle (as defined in Section V). Figure 2 summarizes the distributional characteristics of the species in each stage. Unsurprisingly, given that the taxon cycle stages are mainly determined on distributional grounds, both geographical range (Fig. 2A) and number of grid cells occupied (Fig. 2B) show a general decline with taxon cycle stage. The same pattern applies for local community abundance (Fig. 2C) and for climatic niche (Fig. 2D). Finally, when three aspects of rarity are combined into a single metric (Overall rarity; Fig. 2E), each stage is statistically distinct, with rarity increasing from Stage 1 to Stage 4.

(2) Taxon cycle models

Within the vascular Canarian flora, we have grouped taxa into six different models of colonization–diversification (A to F). Each of these models is represented by multiple taxa.

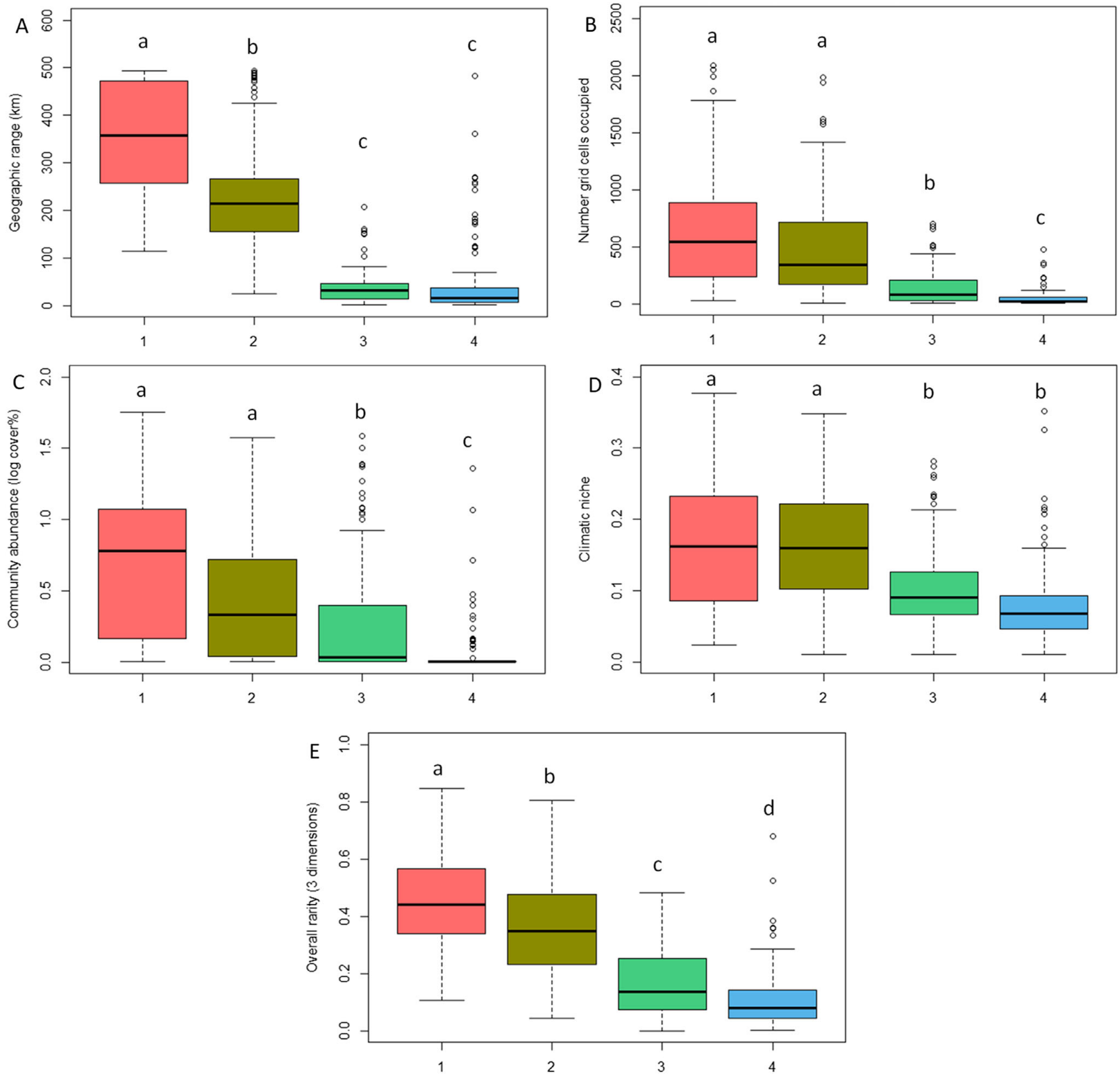

Fig. 2. Box plot diagrams showing the distributional properties of 556 species of the native vascular plants of the Canaries, subdivided into the four (1–4) extant taxon cycle stages (see Table 1 and Section V for details). Different letters indicate significant differences among stages using Kruskal–Wallis test with *post-hoc* Dunn tests. (A) Geographical range. (B) 0.5 × 0.5 km grid cell occupancy. (C) Local community abundance. (D) Climatic niche width (habitat breadth). (E) Overall rarity, calculated as mean of the normalized scores for the metrics geographic range, community abundance, and climate niche. Box plots: The horizontal line inside the box marks the median (50th percentile). The box spans from the first quartile Q1 (25th percentile) to the third quartile Q3 (75th percentile), and the whiskers extend from the box to the most extreme observed values that are still within 1.5 × interquartile range (Q3–Q1). Dots represent outliers.

(*a*) *Model A: classic taxon cycle*

This model applies when two (or more) different lineages per genus (or clade) coexist in the archipelago, and in which one older lineage(s) comprises many species of restricted distribution, and one younger lineage is represented by a single generalist species with a large distribution (NEN or MIE). We term this the classic taxon cycle (Fig. 3).

The model is initiated (Early Stage 1) by colonization of an island within the archipelago by a member of a given genus (first lineage colonization, L1), with eventual expansion to occupy the whole archipelago without diversification (Late

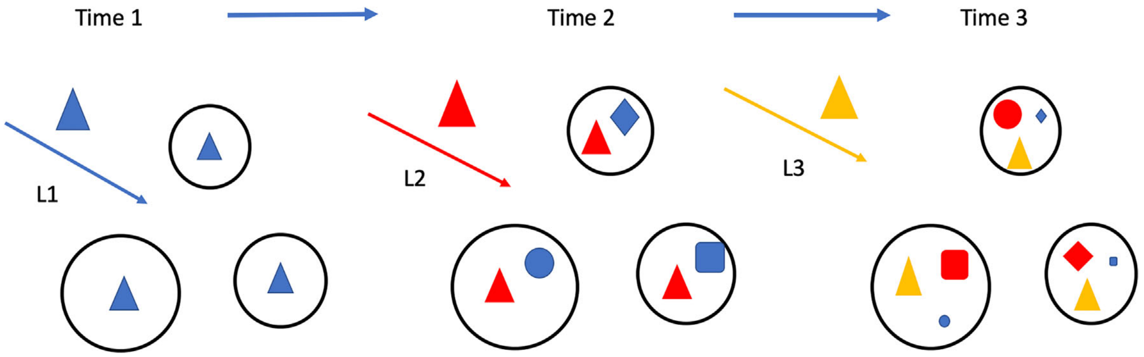

Fig. 3. Model A: schematic representation of a classic taxon cycle, with three distinct colonization events (blue, red and orange) by related species (e.g. congenerics) occurring at three well-separated points in time within an archipelago of three islands (black circles), showing the consequent dynamics. The different shapes with the same colour imply diversification; small sizes represent high extinction threat. Different colours represent different lineages (L1, L2 and L3). We designate this variant the classic taxon model, due to its obvious similarities with the model defined for animal taxa (Table 1). Time 1: blue colonist expansion (Stage 1); Time 2: red colonist expansion (Stage 1), blue colonist range contraction and diversification (stages 2 and 3); Time 3: orange colonist expansion (Stage 1), red colonist range contraction and diversification (stages 2 and 3), blue colonist extinction threat (Stage 4).

Stage 1). After colonization by a separate lineage (second lineage colonization, L2), the insular populations of the original lineage diversify (stages 2 and 3) and, in time, become reduced in distribution such that, following human engagement in the system, the species is threatened with extinction (Stage 4). A third lineage (L3) may colonize even later and, if so, the same processes will affect the species of the second lineage. To match this model, second lineage generalist species have to be spontaneous colonizers (*Secure Native* category in Banco de Datos de Biodiversidad de Canarias, n.d.).

Lineages within the native vascular flora analysed that correspond to this model include *Asparagus*, the *Bencomia* alliance (*Bencomia*, *Dendriopoterium* and *Marcetella*), *Cistus*, *Convolvulus*, *Helianthemum*, *Hypericum*, *Limonium*, *Lotus*, shrubby Malvaceae, *Polycarpaea*, *Scrophularia*, and *Teline* (Table S1).

In *Limonium* there appear to have been as many as six colonization events to the archipelago. The assumed order of arrival of those lineages are: the section *Limoniodendron* lineage, with a single, very restricted and threatened La Gomera SIE (*Limonium dendroides*) unrelated to all the other Canarian sea-lavenders; a second lineage that includes all the 15 endemic *Limonium* within the section *Pterocladus* subsection *Nobilia* lineage, all of them with restricted distributions (the majority being SIEs); and finally, a series of lineages that are considered to have colonized recently, many shared with other Macaronesian islands or the African mainland, whose representative species are *L. pectinatum*, *L. ovalifolium*, *L. tuberculatum* and *L. lobatum* (Koutroumpa *et al.*, 2018).

Limonium dendroides, the single species within the section *Limoniodendron* of the subgenus *Limonium*, is sister to all the Mediterranean *Limonium* species, thus demonstrating that it has a very old origin. Within our analysis, we infer it to be the single survivor of a very early colonization of the Canaries by sea lavenders. It is a Critically Endangered species with distribution restricted to a few ravines in La Gomera (Argaga, El Cabrito and Guarimiar) (Stage 4), away from the seashore, which is the likely habitat of its ancestor. The second lineage colonizing the archipelago (or at least, the one colonizing after the *Limoniodendron* section ancestor) was the ancestor of section *Pterocladus* subsection *Nobilia*, within which up to 15 endemic Canarian species belong (Table S1). Many of these diversified species are either MIE (Stage 2), or SIE (Stage 3), and five of them are considered threatened (hence being classed herein as Stage 4). Some of them occupy new interior habitats rather than the classic seashore habitat of *Limonium*, from which we can infer that they are following the taxon cycle. This classic taxon cycle (Model A) within *Limonium* can be viewed as being triggered by the arrival of several later colonizing lineages containing species occupying the seashore and not yet endemic to the Canaries (they are shared either with other Macaronesian archipelagos, northwest Africa, or both), but that are either beginning to expand across the islands' seashore environments, such as *L. papillatum* or *L. tuberculatum* (Early Stage 1), or they have already done so, such as the abundant *L. pectinatum* (Late Stage 1). The fact that within *L. pectinatum* up to four different varieties can be recognized already (var. *pectinatum*, in Gran Canaria, Tenerife, El Hierro and Selvagens; var. *corculum* in Gran Canaria and Tenerife; var. *divaricatum* in Tenerife, and finally, var. *solandri* in Tenerife, La Palma, La Gomera and El Hierro) (Banco de Datos de Biodiversidad de Canarias, n.d.) is taken to indicate that this species is already transiting to Stage 2.

(*b*) *Model B: intra-lineage taxon cycle*

This variant applies where only one colonization has occurred in the past (monophyletic generic lineage) and one (or a few) of the species of the lineage maintain a generalist distribution, whereas the rest are displaced to specific habitats, diversifying and becoming threatened (Fig. 4). Lineages of the native vascular flora corresponding with this model include *Adenocarpus*, the *Aeonium* clade, *Argyranthemum*, *Athamanta*, *Bystropogon*, *Carduus*, *Carlina*, *Ceropegia*, *Echium*, shrubby

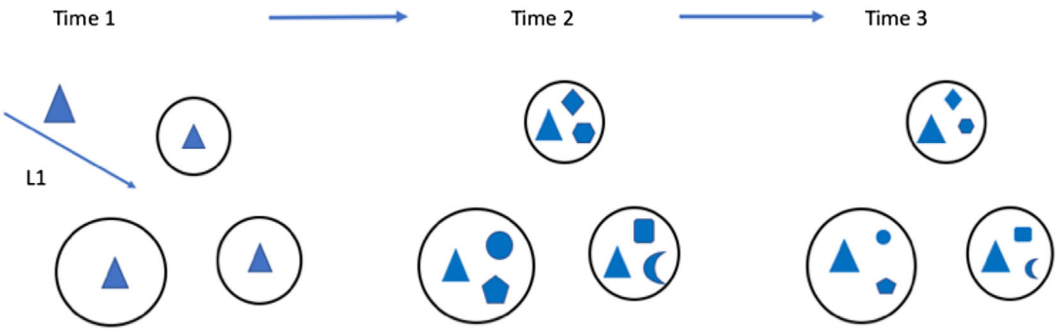

Fig. 4. Model B: schematic representation of the intra-lineage taxon cycle, with one unique colonization event and its consequences for the native species produced over time within the lineage. Time 1: expansion (Stage 1); Time 2: generalist species range stability with anagenetic differentiation and later evolutionary stasis (Stage 2), specialist species range contraction and diversification (Stage 3); Time 3: generalist species range stability with anagenetic differentiation and later evolutionary stasis (Stage 2), specialist species extinction threat (Stage 4). See Fig. 3 legend for further explanation.

Euphorbia, *Globularia*, *Gonospermum*, *Gymnosporia*, *Isoplexis*, *Pericallis*, *Pterocephalus*, *Rubus*, *Sonchus* clade, *Spartocytisus*, *Tolpis* and *Vicia* (Table S1,S2).

The endemic genus *Argyranthemum*, the Macaronesian daisies, is a paradigmatic example of this intra-lineage taxon cycle model, where two species of the 24 (20 in the Canaries, three in Madeira and one in Selvagens) generated by this impressive radiation event conform to the ecological profile of a generalist species and are widely distributed across the archipelago. These two species are the two MIEs of this genus (Stage 2): the coastal daisy (*A. frutescens*, present in all the islands except Fuerteventura) and the forestal daisy (*A. adauctum*, present in Gran Canaria, Tenerife, La Palma and El Hierro). In addition, 16 species are Stage 3 SIEs, and two more are Stage 4 SIEs (*A. lidii* and *A. winteri*). Until very recently, a third *Argyranthemum* species (*A. broussonetii*) was considered a MIE of Tenerife and La Gomera laurel forest, but recent genetic work (White *et al*., 2021) recognized its polyphyletic origin and the species was split accordingly (*A. broussonetii* for Tenerife and *A. callichrysum* subsp. *gomerensis* for La Gomera). Interestingly, for each of the two generalist species (*A. frutescens* and *A. adauctum*), seven subspecies have been recognized across the archipelago, showing that they are already in transition from Stage 2 to Stage 3. *A. adauctum* is polyphyletic, with three subspecies distributed in Gran Canaria, two in Tenerife, one in La Palma and the last in El Hierro. It can be anticipated that further taxonomic work on these taxa will increase the recognized diversity of this genus (White *et al*., 2020). There is a representative of *Argyranthemum* in all the major zonal ecosystems of the Canaries, several of them within a single island.

(*c*) *Model C: spontaneous taxon cycle*

Where only one colonization has occurred (monophyletic generic lineage) and there is no current widely distributed generalist (occupying more than one habitat in more than one island), but within the clade the transitions across the different stages have still taken place, we can consider this to be an apparently spontaneous taxon cycle. In this situation all the species of the lineage have become dwellers of interior habitats and are threatened, despite the apparent lack of a generalist species competing with them (Fig. 5). It seems that not all the specialized SIEs have generalist ancestors, and the generalist may only be present on one or a few islands. Lineages of the native vascular flora analysed that correspond to this model include *Atractylis*, *Cheirolophus*, *Crambe*, *Descurainia*, *Dracaena*, *Micromeria*, *Parolinia*, *Pimpinella*, *Ruta*, *Sideritis*, *Silene*, and *Thesium* (Table S3).

The genus *Cheirolophus* is a paradigmatic example of this taxon cycle model. *Cheirolophus* is present in the western Mediterranean area, including Iberia, Southern France, the Balearic Islands, Corsica, Sicily and Malta. However, it is most species rich in Macaronesia, where there are 18 species, 17 of them endemic to the Canaries (Vitales *et al*., 2014) (Table S3). With the exception of *C. teydis* (Stage 2), which is restricted to the summit scrub of Tenerife and La Palma, the rest of the species are SIEs of the central (Gran Canaria and Tenerife) and western (La Palma, La Gomera and El Hierro) islands (16 species). Eight of these SIE species are not included in the IUCN *Red List* (i.e. they are Stage 3), whereas the other eight are included (Stage 4) (Table S3). In other words, almost half of the Canarian *Cheirolophus* species are threatened with extinction.

(*d*) *Model D: incomplete taxon cycle*

An incomplete cycle is when the taxon cycle has progressed no further than Stage 2, i.e. the formation of a generalist, widely distributed anagenetically formed neoendemic species (which may nonetheless show phylogeographical structure across the archipelago). Such a distribution could still be compatible with the taxon cycle if the species concerned is a relatively recent colonist (Fig. 6). Lineages of the vascular flora assigned to this model include *Bosea*, *Caralluma*, *Ceballosia*, *Cedronella*, *Chamaecytisus*, *Chrysojasminum*, *Euphorbia balsamifera*, *Forsskaolea*, *Gesnouinia*, *Kleinia*, *Neochamaelea*, *Olea*, *Phillyrea*, *Phoenix*, *Retama*, *Rutheopsis*, *Salsola*, *Sambucus*, *Sideroxylon*,

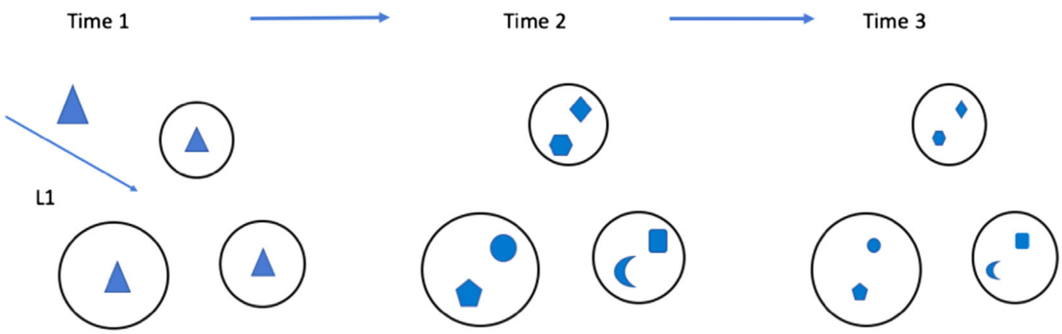

Fig. 5. Model C: schematic representation of a spontaneous taxon cycle, with one unique colonization event and its consequences for the native species produced over time within the lineage. Time 1: expansion (Stage 1); Time 2: generalist species range contraction and diversification (stages 2 and 3); Time 3: specialist species extinction threat (Stage 4). See Fig. 3 legend for further explanation.

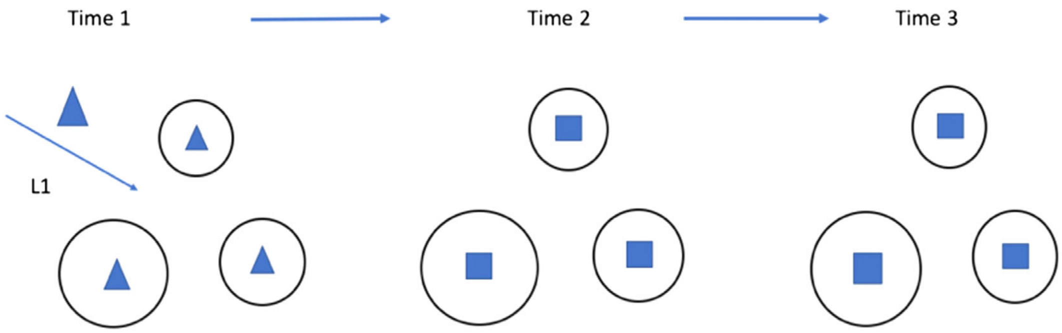

Fig. 6. Model D: schematic representation of an incomplete taxon cycle, with one unique colonization event and its consequences for the native species produced over time within the lineage. Time 1: expansion (Stage 1); Times 2 and 3: anagenetic diversification, range stability and evolutionary stasis (Stage 2). See Fig. 3 legend for further explanation.

Teucrium, *Viburnum*, and *Volutaria* (Table S4). These lineages each exhibit the same profile: a wide distribution across the archipelago (Stage 2), and a lack of other species within the genus with a more restricted distribution.

(*e*) *Model E: evolutionary stasis due to lack of second colonization*

This model applies when no *in situ* diversification to species level has occurred following colonization (Fig. 7). In contrast to Model D, the colonizing species remains taxonomically undifferentiated from the mainland source population. This results either in a NEN (*Arthrocnemum*, *Astydamia*, *Bituminaria*, *Cakile*, *Crithmum*, *Culcita*, *Daphne*, *Diplazium*, *Euphorbia paralias*, *Heliotropium*, *Hyparrhenia*, *Lycium*, *Osyris*, *Periploca*, *Prunus*, *Ranunculus*, *Traganum*, *Vandenboschia*, *Woodwardia*), or in the case of continental extinction, in a species that is designated a palaeoendemic, either belonging to the Tethyan-Tertiary European Palaeotropical Geoflora (*Ixanthus*, *Laurus*, *Morella*, *Ocotea*, *Picconia*, *Pinus*, *Pleiomeris*, *Visnea*) (Fernández-Palacios *et al*., 2017) or to the African Rand flora (*Campylanthus*, *Canarina*, *Euphorbia canariensis*, *Plocama*) (Pokorny *et al*., 2015) (Table S5). Within the logic of the taxon cycle, this absence of differentiation might be attributed to the lack of colonization by a second, related lineage, although that explanation is hard to apply to species of *Euphorbia*, given that other lineages have colonized (see Tables S2 and S4). Maintenance of effective dispersal within the archipelago is also likely to characterize this group.

(*f*) *Model F: no taxon cycle*

Finally, we recognize cases that do not comply with key requirements of the taxon cycle or of the variants described above. In this model (Fig. 8), despite the arrival of later related lineages, the first and second (and third, and so on) colonist species co-occur in the same island and (usually) habitat without subsequent diversification. In the case of NEN ancestors, they may undergo an anagenetic diversification, differentiating themselves from the continental ancestor after some period of isolation (*Erica platycodon*, *Juniperus canariensis*) or not (*Asplenium*, *Caroxylon*, *Ephedra*, *Frankenia*, *Pistacia*, *Suaeda*, *Tetraena*). In the case of palaeoendemics (*Ilex* and *Persea*), they remain taxonomically undifferentiated from now-extinct continental populations (Table S6).

There could be several explanations for cases where, despite the temporally separate colonization by two related species, there is no indication of either demonstrating taxon cycle dynamics. One scenario is where the two species occupy

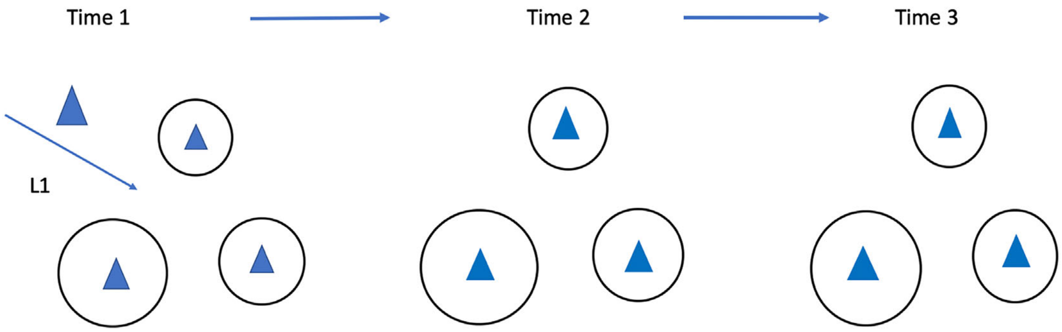

Fig. 7. Model E: schematic representation of an evolutionary stasis due to lack of second colonization, with one unique colonization event without diversification. Time 1: expansion (Stage 1); Times 2 and 3: range stability and evolutionary stasis (Stage 1). See Fig. 3 legend for further explanation.

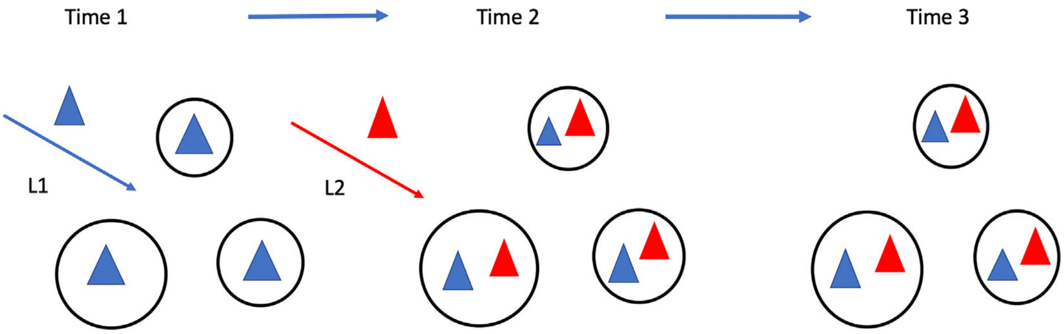

Fig. 8. Model F: schematic representation of cases not complying with any form of taxon cycle, with two different colonization events of related taxa, separated in time, but resulting in the co-occurrence of both taxa on the same island and (usually) habitat. Time 1: blue lineage expansion (Stage 1); Time 2: red lineage expansion (Stage 1), blue lineage range stability and evolutionary stasis (Stage 1); Time 3: blue and red lineages range stability and evolutionary stasis (Stage 1). See Fig. 3 legend for further explanation.

distinct habitats and therefore do not compete. This may apply to the two species of *Juniperus*, with *J. cedrus* occupying the laurel forest and summit scrub, and *J. canariensis*, thriving in the thermophilous woodlands. Another possibility could be that even where the two species do occupy the same habitat, they differ in some other critical niche dimension. For instance, two species each of *Erica* (*E. arborea* and *E. platycodon*), *Ilex* (*I. canariensis* and *I. perado*), and *Persea* (*P. barbujana* and *P. indica*) thrive in the laurel forest, and both *Pistacia* (*P. atlantica* and *P. lentiscus*) species inhabit the thermophilous woodland. In each case they exploit different regeneration niches, thereby enabling their coexistence.

Furthermore, up to three species of *Ephedra* (*E. altissima*, *E. fragilis* and *E. nebrodensis*) belonging to different lineages coexist in Tenerife and several species of different *Asplenium* lineages (*A. anceps*, *A. aureum*, *A. hemionitis*, *A. filare*, *A. onopteris*, and *A. trichomanes*) coexist in several Canarian laurel forests. Finally, *Suaeda* (*S. maritima* and *S. vera*) and *Tetraena* (*T. fontanesii* and *T. gaetula*) each feature two species in the coastal scrub. At least for these last taxa, it seems that their high dispersibility (spores and seeds dispersed *via* anemochory and hydrochory) have not only permitted the arrival of different lineages to the Canaries, but also the persistence of genetic flow with their continental populations.

VII. DISCUSSION

Our analyses have been undertaken within an analytical framework that implicitly accepts the taxon cycle concept (e.g. Wilson, 1961) as a reasonable overarching theory of biogeographical dynamics in island lineages. We assume that competitive effects are a key element in driving evolutionary change in plants and that these effects are manifested by (and signified by) very closely related taxa, essentially congenerics or in cases conspecifics. In order to accommodate cases differing from the original model, we have developed six alternative taxon cycle models (the original, four variants, and no taxon cycle). Analysing the island distributions and threatened status of 556 native vascular plant species, we have been able to assign each species to one of the five taxon cycle stages (Table 4) and each lineage to one of the six taxon cycle models (Table 5). We are reasonably confident that our framework can accommodate the majority of the Canarian lineages that have not been included in this analysis and that overall our analyses support the application of the taxon cycle concept to many Canarian plant lineages.

Nevertheless, we recognize that a variety of other speciation mechanisms have been put forward to explain diversification within Canarian plant lineages, with varying degrees

Table 4. Summary of the allocation to the different taxon cycle stages (1–5) (see Table 1) of the studied species, according to their distributional characteristics and threatened status.

	Stage 1 (NEN or palaeoendemic)	Stage 2 (non-threatened MIE)	Stage 3 (non-threatened SIE)	Stage 4 (threatened in IUCN Red list)	Stage 5 (extinct)
Number of species	80	143	235	92	6
% of species considered	14.4	25.7	42.3	16.5	1.1

of compatibility with the above models. For instance, it is a realistic scenario that, when closely related plant species come into secondary contact, they hybridize, sometimes leading to species formation (see e.g. Caujapé-Castells *et al.*, 2017; White *et al.*, 2020; Jackson, Carine & Chapman, 2023). Mismatches among chloroplastic and nuclear DNA in several Canarian phylogenies support this scenario. Indeed, hybridization has been invoked to play a significant role in *Argyranthemum* (White *et al.*, 2020), *Cheirolophus* (Vitales *et al.*, 2014), *Descurainia* (Jackson *et al.*, 2023), *Micromeria* (Curto, Puppo & Meimberg, 2025) and *Sideritis* (Barber *et al.*, 2007), mostly involving lineages we have assigned to Model C. The recognition of the role of hybridization, allopolyploidy and autopolyploidy within insular floras (Whittaker *et al.*, 2023) may complicate assessment of taxon cycle dynamics, perhaps requiring further modifications of the models proposed.

Furthermore, the models outlined above do not preclude the description of yet more variants. For instance, the genus *Rhamnus* (Rhamnaceae) in the Canaries is represented by three different lineages (Table S6) each containing one endemic species: (*i*) *R. crenulata* (all over the archipelago, inhabiting thermophilous woodlands), (*ii*) *R. glandulosa* (in the five highest islands and Madeira, member of the laurel forest) and (*iii*) *R. integrifolia* (only in Tenerife, with two different ecotypes, one occurring in the thermophilous woodland and one in the summit scrub). Thus, in Tenerife, three different *Rhamnus* species belonging to three different lineages have been able to colonize and persist by specializing in three different ecosystems (e.g. Hand, Grossmann & Lauterbach, 2017). Conversely, in the genus *Volutaria* (Asteraceae), two species coexist in the archipelago in the coastal scrub but occupy different islands: *V. bollei* (in the eastern islands) and *V. canariensis* (in the central and western islands) (Table S4). In all these cases there is coexistence of different lineages and different anagenetic neoendemics within an island (*Rhamnus*) or archipelago (*Volutaria*), thus, illustrating a mixture between models D and F.

(1) How can evolutionary stasis be interpreted?

The first piece of evidence that seems to counter the generality of classic taxon cycle dynamics is the apparent evolutionary stasis demonstrated by many taxa (models D, E and F). The lack of diversification with time in particular colonists appears to be related either to: (*i*) the lack of later-arriving generalist species within the same or related lineages (a consequence of the geographical isolation of the archipelago from relevant source regions) and, thus, the lack of competitive pressure from closely related species; (*ii*) the high dispersibility of the species concerned, which may hamper differentiation; or (*iii*) the combination of a highly competitive species with medium–high dispersibility, which also limits chances of diversification. These traits characterize those species described by Fernández-Palacios *et al.* (2021), as 'ecological winners', which generally do not diversify. Examples include *Euphorbia balsamifera*, *Euphorbia canariensis*, *Juniperus*, *Laurus*, *Olea*, *Pinus*, etc. We suggest that there are four different scenarios for understanding the lack of *in situ* taxonomic differentiation (Table 6).

(*a*) *Scenario 1: high dispersibility*

According to this scenario, the focal species maintains its NEN status, despite having colonized up to several million years ago, due to it possessing and maintaining a high dispersal capacity, providing for high rates of gene flow within the archipelago, and even between the archipelago and the mainland. Examples include trees such as *Erica arborea* (Desamoré *et al.*, 2011a), or ferns such as *Culcita macrocarpa* (Suárez Santiago *et al.*, 2024) and *Vandenboschia speciosa* (Ben-Menni *et al.*, 2022). In some cases, this pattern reflects retro-colonization (i.e. back colonization) from Macaronesia to Europe, such as the ferns *Diplazium caudatum* (Ben-Menni *et al.*, 2021) and *Woodwardia radicans* (Santos *et al.*, 2026).

(*b*) *Scenario 2: recent colonization*

In our second scenario, the species retains NEN status reflecting the recentness of its colonization and that, despite the lack of gene flow with mainland source populations, insufficient time has passed for marked diversification to emerge. In these cases, there will be insufficient genetic structure to warrant the application of specific status in the absence of morphological differences. Examples include species such as *Bituminaria bituminosa* (García-Verdugo *et al.*, 2021), *Cistus monspeliensis* (Fernández-Mazuecos & Vargas, 2011) or *Periploca laevigata* (García-Verdugo *et al.*, 2017), all of which feature exclusive Canarian haplotypes, but are considered NENs by taxonomists. In the case of *Daphne gnidium*, exclusive haplotypes have not yet been discovered in the Canaries, suggesting a recent natural colonization (Ramos-Capón *et al.*, 2024). In the case of *Cistus monspeliensis* (Fernández-Mazuecos & Vargas, 2011), it is notable that there is more genetic structure among the Canarian populations on their path to

Table 5. Summary of the eco-evolutionary paths recognized for each taxon cycle stage in the native Canarian vascular flora (Tables S1–S6), with the number of lineages and species fitting each model for the 556 species analysed, comprising more than half of the native Canarian flora.

Model	Name	Description	Paradigmatic taxa fitting the model	No. of lineages analysed fitting this model	No. of species analysed fitting this model	% of analysed species that fit this model
A	Classic taxon cycle	Two (or more) different lineages per genus coexist in the archipelago in which one (or more) older lineage(s) include many species of restricted distribution, and one younger lineage comprises one (or a few) generalist species with large distribution range.	*Asparagus*, *Bencomia* clade, *Cistus*, *Convolvulus*, *Helianthemum*, *Hypericum*, *Limonium*, *Lotus*, shrubby Malvaceae, *Polycarpaea*, *Scrophularia*, *Teline*	27	127	22.8
B	Intra-lineage taxon cycle	Although only one colonization has occurred, one (or several) of the species of the lineage remain(s) widespread generalists, whereas the rest have been restricted to specific habitats, diversifying and becoming threatened.	*Adenocarpus*, *Aeonium* clade, *Argyranthemum*, *Athamanta*, *Bystropogon*, *Carduus*, *Carlina*, *Ceropegia*, *Echium*, shrubby *Euphorbia*, *Globularia*, *Gonospermum*, *Gymnosporia*, *Isoplexis*, *Pericallis*, *Pterocephalus*, *Rubus*, *Sonchus* clade, *Spartocytisus*, *Tolpis*, *Vicia*	21	217	39.0
C	Spontaneous taxon cycle	Although only one colonization occurred, and notwithstanding the absence of a generalist species in the contemporary flora, the transitions across the different taxon cycle stages can nonetheless be detected.	*Atractylis*, *Cheirolophus*, *Crambe*, *Descurainia*, *Dracaena*, *Micromeria*, *Parolinia*, *Pimpinella*, *Ruta*, *Sideritis*, *Silene*, *Thesium*	12	124	22.3
D	Incomplete taxon cycle	The taxon cycle has proceeded no further than the formation of a generalist, widely distributed anagenetically formed neoendemic species.	*Bosea*, *Caralluma*, *Ceballosia*, *Cedronella*, *Chamaecytisus*, *Chrysojasminum*, *Euphorbia balsamifera*, *Forsskaolea*, *Gesnouinia*, *Kleinia*, *Neochamaelea*, *Olea*, *Phillyrea*, *Phoenix*, *Retama*, *Rutheopsis*, *Salsola*, *Sambucus*, *Sideroxylon*, *Teucrium*, *Viburnum*, *Volutaria*	24	24	4.3

(Continues on next page)

Table 5. *(Cont.)*

Model	Name	Description	Paradigmatic taxa fitting the model	No. of lineages analysed fitting this model	No. of species analysed fitting this model	% of analysed species that fit this model
E	Evolutionary stasis due to lack of second colonization	Evolutionary stasis, perhaps attributable to the lack of a second colonizing lineage within the genus	*Arthrocnemum*, *Astydamia*, *Bituminaria*, *Cakile*, *Campylanthus*, *Canarina*, *Chrithmum*, *Culcita*, *Daphne*, *Diplazium*, *Euphorbia canariensis*, *Heliotropium*, *Hyparrhenia*, *Ixanthus*, *Laurus*, *Lycium*, *Morella*, *Ocotea*, *Osyris*, *Periploca*, *Picconia*, *Pinus*, *Pleiomeris*, *Plocama*, *Prunus*, *Ranunculus*, *Traganum*, *Vandenboschia*, *Visnea*, *Woodwardia*	30	31	5.6
F	No taxon cycle	Despite the arrival of a later, second related lineage, both species co-occur in the same island and (usually) the same habitat without subsequent diversification.	*Asplenium*, *Caroxylon*, *Ephedra*, *Erica*, *Frankenia*, *Ilex*, *Juniperus*, *Persea*, *Pistacia*, *Rhamnus*, *Suaeda*, *Tetraena*	33	33	5.9
Total				147	556	100

Table 6. Possible scenarios to understand evolutionary stasis (models D, E and F) within particular colonist lineages within the native Canarian vascular flora.

Scenario	Example	Reference
1 (high dispersibility)	*Culcita macrocarpa*	Suárez Santiago *et al.* (2024)
	Erica arborea	Desamoré *et al.* (2011a)
	Vandenboschia speciosa	Ben-Menni *et al.* (2022)
2 (recent colonization)	*Bituminaria bituminosa*	García-Verdugo *et al.* (2021)
	Daphne gnidium	Ramos-Capón *et al.* (2024)
	Periploca laevigata	García-Verdugo *et al.* (2017)
3 (palaeoendemism)	*Laurus novocanariensis*	Betzin *et al.* (2016)
	Ocotea foetens	Trofimov *et al.* (2022)
	Pinus canariensis	Climent *et al.* (2007)
4 (anagenetic diversification)	*Euphorbia canariensis*	Coello *et al.* (2024b)
	Kleinia neriifolia	Sun & Vargas-Mendoza (2017)
	Ranunculus cortusifolius	Williams *et al.* (2015)

diversification than is observable in the Mediterranean region, which nonetheless provides a unique haplotype and occupies a basal position in the phylogeny. The Mediterranean populations span a wide distribution (from Portugal to Cyprus), and their limited genetic structure is thought to reflect a population bottleneck linked to Pleistocene glaciations.

The possibility that *Bituminaria bituminosa* was introduced to the Canaries by the Guanche people from North Africa to provide fodder for their ovicaprid herds has long been considered. However, García-Verdugo *et al.* (2021) have recently demonstrated that the Canarian populations of this very widely distributed species (Portugal to Palestine), feature six exclusive haplotypes, confirming on the one hand its native status, and on the other, its path towards diversification. *Periploca laevigata*, an NEN species in the Canaries, also shows a phylogeographical signal in the form of many exclusive haplotypes in the Canarian populations, contrasting with very few in the Mediterranean area. This profile again points towards limited morphological change despite the existence of many exclusive haplotypes in the Canarian populations (García-Verdugo *et al.*, 2017).

(*c*) *Scenario 3: palaeoendemism*

Our third scenario is where the ancestral mainland populations of highly dispersive species have already vanished from the continent, so the island form becomes a palaeoendemic species. But, as these species maintain significant levels of gene flow among islands or archipelagos, this precludes their *in situ* diversification. Examples of this pattern include *Pinus canariensis* (Climent *et al.*, 2007), and several laurel forest tree genera, such as *Persea*, *Pleiomeris*, *Ocotea*, and *Visnea*, among others (Fernández-Palacios *et al.*, 2017). In the case of *Pinus canariensis*, fossil seeds and strobili have been found in early Pliocene deposits on the Iberian Mediterranean coast, from where it later vanished (Morla *et al.*, 2003). It is currently extant only in the Canaries, where it has been present since at least 4–3 Ma (Góis Marques *et al.*, 2024). It occurs naturally in five of the islands, which share the majority of haplotypes, with only a few being restricted to a number of very tiny populations (Climent *et al.*, 2007).

(*d*) *Scenario 4: anagenetic diversification (incomplete cladogenesis)*

Our final scenario is anagenetic diversification, where the species has been insular long enough to differentiate from the mainland, but where inter-island gene flow is sufficient to preclude insular morphological differentiation to species level. Examples include anagenetic neoendemics such as *Euphorbia canariensis* (Coello *et al.*, 2024b), *Kleinia neriifolia* (Sun & Vargas Mendoza, 2017; Rincón-Barrado *et al.*, 2023) or *Ranunculus cortusifolius* (Williams *et al.*, 2015). *Ranunculus cortusifolius* is a candidate for this scenario at archipelagic level. Williams *et al.* (2015) recently demonstrated that, although the species is endemic to Macaronesia and present in Azores, Madeira and the Canaries, it does not share any haplotypes between the archipelagos, pointing towards ongoing diversification.

(2) **Correlation is not causation**

Although we have analysed the eco-evolutionary trajectory of a significant fraction of the Canarian vascular plant lineages, comprising a majority of the existing plant biodiversity, our approach has not demonstrated causation. We have not proved that competitive interaction with more recent colonists (of a closely related lineage) is instrumental in the retreat to particular (generally interior) habitats and the consequent diversification and population reduction of members of earlier colonist lineages. The general question arises: is diversification related to competition with phylogenetically related species (i.e. a 'pushing factor'), or to other drivers such as reproductive isolation due to dispersal limitation, exploitation of unfilled ecological opportunity (vacant niche space), or species characteristics such as phenotypic plasticity? Put another way, how confident can we be that it is indeed colonization by a new, related, more generalist species, as has been postulated in the case of animal taxon cycles

(Wilson, 1961; Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002), that drives the taxon cycle, or is this simply a consequence?

If the effect is causational (classic taxon cycle scenario), then new colonizing generalist species have an important role in 'pushing' the earlier colonists into increasingly specialist, interior habitats, promoting their diversification *via* population isolation, range and population reduction and, eventually their extinction. This 'pushing' would occur through the higher competitive ability of new colonists and/or by changing pest or pathogen load experienced by the species over the course of their progression through the taxon cycle (Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002).

Alternatively, if the arrival of new colonists is a consequence, not the cause, then the taxon cycle is driven by the availability of habitats and niches that promote ecological opportunity. Spontaneous range contraction and diversification processes impact insular species due to: (*i*) low mobility (which may be selected for in islands); (*ii*) landscape topographic complexity, coupled with constant renewal of habitat availability driven by the geo-environmental dynamism of volcanic island systems; (*iii*) the availability of vacant niche space in particular microhabitats that select for novelty, especially in the case of early-arriving colonists, drawing them repeatedly into local diversification within interior habitats (see Fernández-Palacios *et al.*, 2021; Whittaker *et al.*, 2023). Steinbauer *et al.* (2016) questioned the role of competitive displacement due to climatic requirements in defining species distributions within six highly diverse clades (*Aeonium*, *Argyranthemum*, *Descurainia*, *Echium*, *Lotus* and *Sonchus*) of the Canarian vascular flora. Inherent to this scenario is that subsequent colonization of disturbed habitats by new generalist species within the same or similar lineages may repeat this process to the degree permitted by factors (*i*)–(*iii*).

From our eco-evolutionary analyses, it seems that both options (cause and consequence) may co-occur within the Canarian vascular flora. For instance, models A, D and E seem to be consistent with the classic taxon cycle model. In lineages following models D and E, these colonization waves seem to have not yet arrived.

On the other hand, models B, C, and F fit less clearly with the classic scenario: either the taxon cycle progresses without the need for a new immigrant (models B and C) or, when subsequent colonization events have happened (Model F), both species continue to coexist in the same ecosystem. In his essay on radiation within the Canarian flora, Silvertown (2004) argued that the prevalence of monophyly within large endemic groups supports an important role for niche preemption by early colonists, preventing subsequent colonization events by the same ancestral species or closely related forms. This argument may be particularly relevant to Model C, while also allowing that subsequent colonization by congenerics may become easier over time. It is also entirely reasonable to expect that progression of particular colonists along the taxon cycle pathway has occurred owing to interactions with ecological competitors that share intersecting niches but that are not congenerics, giving rise to patterns here classed under models B and C.

Within the classic faunistic insular taxon cycles, it is largely assumed that later colonization by generalist species is a key driver of niche shifts in the members of earlier colonist lineages, either *via* direct competition or indirectly *via* change over time in the pest (pathogen or parasite) load of the focal species (Ricklefs & Cox, 1972; Ricklefs, 2011). While this hypothesis of initial escape from pests/pathogens followed by a phase of 'counteradaptation' is intuitively attractive, even for birds it has proven challenging to test (but see Soares, Latta & Ricklefs, 2017; Inumaru *et al.*, 2024). For plants, linking taxon cycle dynamics to changing susceptibility to plant pests, browsers, etc. is certainly no less challenging to test. There are multiple cases of plant pests and pathogens that have been transported by humans and have caused the collapse of populations of species of trees [examples including ash die back (Carroll & Boa, 2024), acute oak decline (Denman *et al.*, 2014), rapid 'Ōhia'a death (Perroy *et al.*, 2021), Dutch elm disease (Santini & Faccolo, 2015)] or sometimes groups of species (e.g. jarrah dieback in Western Australia; Anderson *et al.*, 2010), but such cases are far from being restricted to islands. We are also not aware of evidence for a significant role for plant pathogens/pests in relation to the Canarian flora, although the case of rapid 'Ōhia'a death in Hawaii illustrates that species within oceanic island floras can be significantly impacted by changing pest or pathogen loading (Perroy *et al.*, 2021).

Another possibility is that the path of diversification and isolation occurs effectively autonomously within early colonist lineages, as they lose dispersal powers (Whittaker *et al.*, 2023) and as they respond to the topographic complexity of volcanic island systems. Moreover, the repeated, intermittent devastation through volcanic action of large areas within hotspot oceanic islands is also likely to be relevant to generating new opportunities for intra-island and inter-island colonization throughout the active lifespan of such islands (Machado *et al.*, 2017; Whittaker *et al.*, 2023). This will leave opportunities in the dynamic landscapes provided by these islands for new colonists to establish, thus reinitiating the cycles stochastically over time without the need to invoke competition between closely related species and, for that matter, without ruling out roles for competition with other, less-closely related species that happen to occupy similar microhabitats. A further variation of the classic taxon cycle would include a pattern where the early generalist species does not necessarily spread to most of the archipelago's islands, but instead specializes into different habitats, first on a large island with high habitat diversity, then subsequently colonizing similar habitats as a specialist on other islands followed by allopatric speciation on each. We hypothesize that this scenario may apply within the Canaries to the lineage *Helianthemum* (see Albaladejo *et al.*, 2020).

(3) Analyses of stem and crown ages

At least for the classic taxon cycle (model A), an approach towards supporting its existence would be to compare the stem age (reflecting colonization timing) of lineage 2 with the crown age (reflecting start of the radiation process) of lineage 1 (see García-Verdugo, Caujapé-Castells & Sanmartín, 2019). Timings consistent with the taxon cycle would be supportive (but not proof) of the model, while timings inconsistent with the hypothesized sequence could refute the model. Table 7 compiles some relevant evidence, where five cases for which stem and crown ages of consecutive arriving lineages are available.

Martín-Hernanz *et al.* (2023) provided stem and crown ages for the two endemic lineages of *Asparagus* coexisting in the Canaries, although some of the species are shared with the Selvagens and Madeira (Table S1). The *A. umbellatus* clade (including *A. arborescens* and *A. fallax*) has a crown age of 1.78 (0.62–2.70 Ma), whereas the *A. scoparius* clade (including *A. nesiotes* and *A. plocamoides*) has a colonization age of 1.65 (0.72–2.38 Ma). Interestingly, this second lineage has also diversified, perhaps due to the presence of the two NEN lineages (*A. horridus* and *A. pastorianus*). The very close age estimates and the broad confidence intervals do not permit us to determine which lineage colonized first, and thus to conclude whether or not this case supports Model A.

The stem age of the Canarian endemic *Cistus symphytifolius* lineage is 1.23 ± 0.25 Ma, whereas its crown age is 0.33 ± 0.14 Ma (Guzmán & Vargas, 2010). The stem age of the widespread native non-endemic *C. monspeliensis* is 0.93–0.22 Ma (Fernández-Mazuecos & Vargas, 2011), meaning that we cannot discard the hypothesis that colonization by *C. monspeliensis* triggered the diversification of the *C. symphytifolius* lineage. Nevertheless, the fact that *Cistus monspeliensis* is already diversifying (Fernández-Mazuecos & Vargas, 2011) without a generalist competitor of the same genus, would suggest spontaneous diversification (Model C).

The crown age of the shrubby Canarian endemic *Euphorbia* (section *Aphyllis*, subsection *Macaronesicae*) is 7.48 ± 2.55 Ma (Sun *et al.*, 2016), meaning that this clade had probably already diversified before the arrival of *E. balsamifera*, a species with a stem age of 3.7 (1.80–5.65 Ma) (Rincón-Barrado *et al.*, 2024), in which case we could not attribute this diversification event to competition with *E. balsamifera*.

Lotus glinoides (with pink flowers) belonging to section *Chamaelotus*, is a NEN species in the Canaries and is considered to be a secure native, having colonized this archipelago *c.* 0.32 (0.08–0.75 Ma), without having diversified (Jaén-Molina *et al.*, 2021). On the other hand, section *Pedrosia* colonized the Canaries twice *c.* 1.28 Ma and diversified into clade A *c.* 0.29 (0.06–0.51 Ma) and clade B *c.* 0.27 (0.13–0.47 Ma), respectively (Jaén-Molina *et al.*, 2021), thus likely post-dating the colonization of *Chamaelotus*, and leading to the formation of 23 endemic species. Finally, section *Canaria* (ex *Dorycnium*) colonized around 2.6 Ma, but diversified only 0.19 Ma, resulting in three new species (Jaén-Molina *et al.*, 2021). It seems that the most reasonable scenario for fitting these dates would have been an early colonization of the section *Canaria* lineage, followed by the colonization of the section *Pedrosia* lineage, with each of these lineages diversifying after the arrival of the section *Chamaelotus* lineage. This scenario with three consecutive lineage colonizations, is similar to the case of *Limonium* (see Section VI.2*a*). Unfortunately, the broad range of the confidence intervals means that no firm conclusions are possible.

Scrophularia arguta, a widespread herbaceous species considered a secure native in the Canaries, seems to have colonized

Table 7. Canarian vascular plant lineages in which compatibility with the classic taxon cycle (Model A) was investigated. Diversification age refers to crown age of the first-arriving lineage, whilst colonization age refers to the stem age of the second-arriving lineage. Shrubby *Euphorbia* (Model B) and *E. balsamifera* (Model D) have also been included although they are inconclusive in relation to Model A. Ma, million years ago.

Case	Lineage 1 diversification age	Lineage 2 colonization age	Compatibility with classic taxon cycle	References
Asparagus	*A. umbellatus* clade 1.78 (0.62–2.70) Ma	*A. scoparius* clade 1.65 (0.72–2.38) Ma	Inconclusive	Martín Hernanz *et al.* (2023)
Cistus	Canarian endemic *Cistus symphytifolius* clade (0.33 ± 0.14 Ma)	*Cistus monspeliensis* (0.22–0.93 Ma)	Yes, but see section VII (3)	Guzmán & Vargas (2010); Fernández-Mazuecos & Vargas (2011)
Euphorbia	Canarian endemic shrubby *Euphorbia* (sect. *Aphyllis* subsect. *Macaronesicae*) clade (7.48 ± 2.55 Ma)	*Euphorbia balsamifera* 3.7 (1.80–5.65) Ma	No	Sun *et al.* (2016); Rincón-Barrado *et al.* (2024)
Lotus	Canarian endemic *Lotus* sect. *Canaria* (0.19 Ma) and *Lotus* sect. *Pedrosia* clade A 0.29 (0.06–0.51) Ma and clade B 0.27 (013–0.47) Ma	*Lotus glinoides* 0.32 (0.08–0.75) Ma	Inconclusive	Jaén-Molina *et al.* (2021)
Scrophularia	Canarian endemic *Scrophularia smithii* clade 3.37 (1.30–5.84) Ma	*Scrophularia arguta* (2.7–5 Ma)	Yes	Navarro-Pérez *et al.* (2015); Valtueña *et al.* (2016)

the Canaries twice during the Pliocene (5–2.7 Ma) (Valtueña *et al.*, 2016). It appears to comprise two cryptic species (Western Canaries and Mahan), and a later, unrelated, arrival (perhaps introduced from North Africa) to Gran Canaria. On the other hand, the stem age of the Canarian endemic *Scrophularia smithii* clade is 5.95 Ma and its crown age is 3.37 (1.30–5.84 Ma) (Navarro-Pérez *et al.*, 2015). These timings appear compatible with the classic taxon cycle, although the resulting inference is of a later herbaceous colonist helping to drive diversification in an earlier arriving but woody lineage, which seems questionable.

These cases illustrate that crown/stem ages typically have a large error margin and, if they involve different islands, may be misleading as to the degree to which members of the two lineages actually interacted within the archipelago (whether in terms of potential competition, or potential gene flow). For instance, the crown age refers to the moment of diversification based on extant species. We do not know if diversification started earlier and the early-diversified species already went extinct, which actually would fit the spontaneous taxon cycle, meaning that the extant species of the radiation of a lineage might represent only part of the entire radiation process that included many more species. Moreover, as the events we are inferring took place deep in the past, we should be wary that the contemporary biogeography of the lineages concerned may be misleading as to the past sequence of evolutionary development in a given lineage. It also seems entirely likely that the competitive milieu for any given lineage would be set by whatever species happen to co-occur on the same island or massif, share habitat and occupy a broadly similar niche, not only by those that happen to be similar because they are phylogenetically closely related. Nonetheless, the sheer number of lineages that can plausibly be described as fitting within one of our taxon cycle model variants lends credence to the proposal that taxon cycle models, including that corresponding with the classic zoogeographical model system, can reasonably be applied to Canarian plant lineages. Overall, phylogenetic data support a general taxon cycle process for the Canarian flora, but with uncertainty as to the drivers, and the relevance of alternative variants on the classic taxon cycle model.

Another important consideration in interpreting the distributional and phylogenetic data for the flora is that the archipelago is a dynamic platform, as captured in the general dynamic model of oceanic island biogeography (Whittaker, Triantis & Ladle, 2008). As highlighted in Table 3, the islands range greatly in area, and many of the lineages analysed herein colonized the archipelago prior to the emergence of the youngest islands, with many lineages following the progression rule (i.e. with a dominant pattern of colonization from old to young islands). Being volcanically active over extended durations, the islands are subject to repeated destructive and constructive episodes, as well as eventual decline of area and elevation with extreme age. Plant and animal taxa respond to opportunities as they are presented and particular localized species suffer extinction through volcanism, flank collapse and other destructive processes, leaving no trace of their existence but doubtless involving the loss of many late taxon-cycle stage species in the past, long before human interference in the archipelago. The large areas of new habitats reiteratively created within each island by their ongoing volcanism may be particularly significant, not only in destroying earlier evolutionary products, but also in enabling phases of colonization (e.g. Machado *et al.*, 2017), including by new colonists that drive the taxon cycle. It is perhaps all the more remarkable that the general patterns described herein are so clearly evidenced.

(4) Limitations of the approach

The data we have collated provide many cases that conform with a classic taxon cycle in which species have colonized fairly open lowland habitats, which themselves are widespread, allowing these species to become widespread, multi-island occupants, which then are in a position to exploit other niche spaces within each island. Typically, this involves the formation of localized endemics in the interior, including at higher elevations. Nevertheless, we have indicated certain limitations of our approach in Sections VII.2 and 3. It is important to consider others. One is the general supposition of the classic taxon cycle model (Wilson, 1959, 1961) that newly arrived species typically occur in marginal, coastal habitats. Although this would be the case for plant species colonizing by floatation in the sea, species dispersed by zoochory or anemochory may be adjusted to and be deposited into interior habitats from the very beginning (likely the case for species dispersed by, for example, granivorous forest birds or migratory ring ouzels that visit the mountains of Tenerife). Island summits can be considered islands within islands, due to their species impoverishment, thus offering empty niches that can be filled by newcomers, either from the lower elevations within the same island or from other more distant insular or continental summits, as applies to some endemic species of the highest mountain habitats (*Erigeron*, *Genista*, *Nepeta*, etc.) (Fernández-Palacios *et al.*, 2014). These ecological opportunities have led to the Canarian summits being the insular areas with the highest rates of diversification and plant endemism (Steinbauer *et al.*, 2012).

Another point of note for evaluation of our taxon cycle hypotheses is that plant fossils are not very commonly found in oceanic islands. Although some fossil species have been identified in the Canaries [i.e. *Tetraclinis articulata* from Gran Canaria, currently extant in Northern Africa (Anderson, Channig & Zamuner, 2009), and *Ruta museocanariensis* from Gran Canaria, which is globally extinct (Marrero-Rodríguez *et al.*, 2023)], the fossil data lack the quantity or resolution to provide a means of testing the models we have constructed. Ideally, we would like to be able to disentangle, for example, if a given taxon is: (*i*) a palaeoendemic, where the focal species is the same (or very similar) to the colonizer, or (*ii*) an anagenetic diversification from the original colonist, when it has been progressively transformed *in situ* until achieving taxonomic differentiation from the original colonist. This problem has evident consequences regarding the ascription of lineages to either models D or E. Herein, we have mainly followed the existing published phylogenies, analysing the antiquity of the focal species' stem age to support allocation to either anagenetic neoendemism (Model D) or palaeoendemism (Model E).

Also interesting is the ecological role of palaeoendemics. One of the core elements of the classic, original taxon cycle theory is the need for available 'empty' (or at least unsaturated) interior habitats to which the species of open, marginal habitats can move after the pressure exerted by a new colonization wave. If those interior habitats are already occupied by older, palaeoendemic species that have not diversified, which is the case in the mid-elevations of the western Canaries with the existence of closed evergreen laurel forests dominated by palaeoendemic trees, it may be extremely difficult for species originally of open habitats to invade. In this case, the displaced species should find alternative non-occupied interior habitats, where they may thrive and diversify. Indeed, there is evidence that the proportion of endemism is generally greater at higher elevations within the Canaries, with many species of diversified lineages specializing in rocky and high mountain habitats (Steinbauer *et al.*, 2012; Fernández-Palacios *et al.*, 2021). The evergreen, mid-elevation forests, dominated by palaeoendemic evergreen trees, thus feature fewer plant radiations (and fewer members of them) than the more open lowland and higher elevation habitats. On the contrary, in more open woodlands, such as the pine forest and the thermophilous woodlands, shrubs or herbs may have an opportunity to radiate, as is the case for *Cistus* and *Micromeria* lineages (which diversified mostly within the pine forest belt).

Finally, our analyses are predicated to some degree on the validity of the genus as a taxonomic level within botany. Existing plant genera vary both in size and in the rationale historically used for their delimitation, with those represented in the Canarian flora ranging from the monotypic endemic *Vieria*, through genera such as *Cheirolophus* with around 25 species globally to *Euphorbia*, with >2000 species globally. Hence, it could be argued that congeneric colonizations from within a very large genus may be equivalent to colonizations representing two closely related small genera. While phylogenetic distance within a monophyletic group may be a preferable way of distinguishing a genus going forward, it remains challenging to determine the threshold at which to cut the phylogeny (Humphreys & Linder, 2009).

(5) Reaching stages 4 and 5 of the taxon cycle: natural or anthropogenic drivers?

Species belonging to stages 4 (threatened) and 5 (extinct) could have achieved this status due to natural dynamics. But those doing so within the last one and a half millennium are mostly attributable to anthropogenic factors (Santana *et al.*, 2024). Disentangling which is the ultimate cause of their precarious status (or even their demise) is challenging in the absence of historical records or fossils. Although the very first 'complete' species lists of Canarian vascular plants did not appear until Webb & Berthelott's (1835–1850) *Histoire Naturelle des îles Canaries*, several pre-Linnean accounts pre-dated this milestone, for example: Leonard Plukenet's work, published from 1691 to 1705; James Cuninghame, who visited La Palma in 1698 and whose findings were later published by James Petiver from 1698 to 1713; and Louis Feuillée (1724), who visited Tenerife and El Hierro (Herrera-Piqué, 1982; Francisco-Ortega, Santos-Guerra & Jarvis, 1994; Francisco-Ortega & Santos-Guerra, 1999; Santos-Guerra *et al.*, 2011). At this point in time, humans and the animals introduced by them (goats, sheep, pigs, dogs, cats and mice) had already been roaming across the islands for more than one and a half millennia, undoubtedly transforming ecosystems and impacting the original vegetation and flora (de Nascimento *et al.*, 2020). Following the arrival of the Castilians in around the 15th century, these commensals were joined by rabbits, rats, cow, horses, donkeys and camels. It is easy to understand that many plant species that evolved in the absence of mammals [except, on particular islands, the lava mouse (*Malpaisomys insularis*) and a giant rat (*Canariomys* sp.)], were not prepared for the new wave of herbivory that arrived alongside humans.

Since all Canarian vegetation types suffered from human impact and no virgin sites exist on this archipelago, we may infer that both natural and anthropogenic factors have jointly shaped the current spatial distribution of species. In some cases, we believe that species were already quite rare before human arrival and human pressure only pushed the species a little more towards the brink of extinction. Examples might be drawn from lineages including *Cheirolophus*, *Helianthemum*, *Limonium*, *Lotus*, etc. But there are also examples where we can be confident that human activity has greatly reduced the distributions of once very common insular species, in some cases moving MIEs from Stage 2 to 4 or 5. Indeed, previous work has shown that the number of endangered species per habitat is correlated in the Canaries with the degree of past anthropogenic habitat loss (Otto *et al.*, 2017). Thus, it should be expected that human activity has inflated the number of species included in stages 4 and 5, forcing the lineages affected by taxon cycle dynamics to proceed further and faster towards extinction than natural causes would have allowed.

VIII. CONCLUSIONS

(1) Taxon cycles have hitherto only been studied for island fauna, but it seems that some island vascular plant lineages may also follow the biogeographical and evolutionary pathways encapsulated in the taxon cycle framework.

(2) Owing to its high richness, endemism and fragmentation across an oceanic island archipelago, the Canarian native vascular flora constitutes a perfect model system for exploring the relevance of the taxon cycle framework in plants.

(3) We have described and exemplified six eco-evolutionary pathways, all but one matching, to varying degrees, the precepts of the taxon cycle.

(4) We are unable to validate the causal pathways that we infer, but suggest that the evidence compiled for multiple Canarian plant lineages supports further work to explore the relevance for other systems (e.g. Hawaii, Mascarenes, Galápagos, Cabo Verde) of the scenarios we have outlined and to attempt critical tests of the models presented herein.

(5) The extent to which taxon cycles are driven by interactions with closely related species, as opposed to interactions with other competitors, or being consequences of other insular evolutionary syndromes, colonization biases and the non-random distribution of ecological opportunities within oceanic islands remains to be determined.

(6) Finally, the incorporation of a measure of extinction threat and realized anthropogenic extinction into the analysis has enabled us to differentiate five distributional stages of the taxon cycle, with our analyses underlining the implications of insular evolution for contemporary conservation.

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X. DATA AVAILABILITY STATEMENT

Data compiled in this study are available in the Tables in the Supporting Information. Data used to generate Fig. 2 are deposited in the DRYAD repository (https://doi.org/10.5061/dryad.qrfj6q5fs).

XI. REFERENCES

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XII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Model A: clades of the Canarian native vascular flora that correspond to the classic taxon cycle.

Table S2. Model B: clades of the Canarian native vascular flora that correspond to the intra-lineage taxon cycle.

Table S3. Model C: clades of the Canarian native vascular flora that correspond to the spontaneous taxon cycle.

Table S4. Model D: clades of the Canarian native vascular flora that correspond to the incomplete taxon cycle.

Table S5. Model E: clades of the Canarian native vascular flora that correspond to evolutionary stasis due to lack of second colonization.

Table S6. Model F: clades of the Canarian native vascular flora that do not correspond to any of the taxon cycle models A to E.

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