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Life history traits and patterns of diversification in oceanic archipelagos: a meta-analysis

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Ecological conditions, such as high habitat diversity and the absence of competitors, have been proposed as key determinants of the patterns of speciation observed in oceanic island floras. However, the relationship between plant traits and lineage diversification has received less attention. Here, we review 120 published phylogenetic and population genetic studies of three well-studied oceanic archipelagos (Canary Islands, Galápagos and Hawai‘i) to investigate potential associations between life history characters (growth form and fruit type) and patterns of diversification. The available data suggest that the phenotypic syndrome ‘herbaceous-dry fruited’ was predominant among ancestors of species-rich lineages, although the Hawaiian flora also shows a substantial proportion of ‘woody-fleshy fruited’ ancestors. Growth form, unlike fruit type, is shown to be a labile character strongly selected for woodiness, particularly in radiating lineages. Dry fruits, although representative of diverse dispersal modes and efficacies, are generally associated with a low incidence of inter-island colonization, and the analysis of population genetic data confirms strong genetic differentiation among islands for dry fruited species of radiating lineages. In contrast, fleshy fruited species of monotypic lineages typically show widespread distributions coupled with extensive gene flow among islands, which probably impedes speciation. Our analyses suggest that fruit types associated with limited evidence of dispersal promote recurrent speciation within lineages, although particular character states related to speciation appear to be context dependent. This study reinforces the idea that plant traits associated with island colonization and population persistence are, in addition to ecological conditions, important factors in understanding the patterns of diversification on islands. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **174**, 334–348.

ADDITIONAL KEYWORDS: adaptive radiation – colonization ability – dispersal – fleshy fruits – island endemics – lineage diversification – speciation – woodiness.

INTRODUCTION

The exceptional levels of biological diversity found on oceanic islands have been the focus of scientific research since the 19th century (Bory de

Saint-Vincent, 1803; Darwin, 1839; Mann, 1869). The vast majority of oceanic islands are of volcanic origin and were never part of continental landmasses, unlike other types of islands; terrestrial biotas on oceanic islands are therefore generally the result of long-distance dispersal, often followed by *in situ* speciation, a condition that has stimulated numerous hypotheses in biogeography, systematics

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and evolutionary ecology (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007; Bramwell & Caujapé-Castells, 2011). Many studies have investigated factors that may account for the remarkable number of endemic species occurring in these relatively small geographical areas. For instance, island age and area, environmental heterogeneity and geographical isolation have been pointed out as major factors determining species diversity on islands (for recent syntheses, see Whittaker & Fernández-Palacios, 2007; Gillespie & Baldwin, 2009). However, because most biogeographical models consider total species number, the conclusions drawn from such studies are somewhat biased by the large contribution of those island lineages that experienced dramatic episodes of diversification (i.e. radiating lineages). Oceanic island floras also harbour a remarkable number of endemic lineages for which variation across populations does not support the occurrence of multiple speciation events (i.e. those that originated by anagenesis; Stuessy *et al.*, 2006). Contrasting levels of diversification among island plant lineages are, in part, probably the result of processes associated with intrinsic traits (Price & Wagner, 2004; Herben, Suda & Munclinger, 2005; Levin, 2006; García-Verdugo, Friar & Santiago, 2013b), which, in addition to ecological opportunity (Silvertown, 2004; Carine, 2005), may explain the patterns of diversification in these areas.

Fruit type and growth habit are two life history characters that have been the subject of considerable attention with regard to their relationship with speciation (Tiffney & Mazer, 1995; Dodd, Silvertown & Chase, 1999; Smith, 2001; Givnish, 2010). Having an herbaceous growth habit may promote diversification rates in plant lineages because of short generation times or high fecundity (Ricklefs & Renner, 1994; Dodd *et al.*, 1999). High rates of molecular evolution in herbaceous taxa relative to woody plants also support this idea (Smith & Donoghue, 2008). In contrast, other studies relate woodiness to high species diversity, as woody species may experience lower extinction rates than herbaceous lineages (Tiffney & Mazer, 1995). Fruit type is typically associated with the way in which seeds are most effectively dispersed, which is also expected to affect diversification rates. The frequency and range of seed dispersal may have a significant role in species cohesion, particularly in those species inhabiting areas with strong physical barriers, such as oceanic islands (Givnish, 2010; Kisel & Barraclough, 2010). Fleshy fruits of island species are probably dispersed by frugivorous vertebrates, mostly birds, which may enhance rates of gene flow among populations as a result of frequent consumption and animal mobility. Results from population genetic studies in some fleshy fruited species are

apparently congruent with this expectation (García-Verdugo *et al.*, 2009, 2010a; Moura, Silva & Caujapé-Castells, 2013). Broader comparative studies of the Hawaiian flora, however, indicate that fleshy fruits may favour lineage diversification and high species diversity in some lineages (Carlquist, 1966a; Price & Wagner, 2004; Givnish *et al.*, 2009).

In this study, we review the recent literature on oceanic island floras to investigate potential associations between life history traits and speciation in island plant lineages. By separating lineages into two contrasting patterns of diversification (species-rich vs. monotypic), we aim to identify those traits more closely related to diversification within archipelagos. We use published phylogenetic reconstructions of ancestral character states to identify which particular traits were predominant among early colonizers that gave rise to species-rich lineages. Species distribution data are also used to infer whether colonization ability could be related to certain trait combinations or type of lineage. Lastly, we review the available molecular evidence to investigate whether fleshy fruits are generally associated with species cohesion in oceanic archipelagos, and consider possible explanations for contrasting levels of diversification of fleshy fruited lineages in different insular settings.

MATERIAL AND METHODS

SELECTION OF ISLAND SYSTEMS

Our survey focused on the floras of those oceanic archipelagos for which abundant information from phylogenetic and population genetic studies was available. Archipelagos comprising several islands, not single-island systems, were chosen because multiple islands offer opportunities to analyse the effect of colonization ability on diversification patterns across lineages (e.g. Price & Wagner, 2004). In addition, oceanic rather than continental archipelagos were selected because the former generally display a higher diversity of lineages, thus providing robust sample sizes for statistical analysis. The high levels of endemism on oceanic islands also present ideal circumstances for the analysis of factors related to speciation. Three archipelagos (Canary Islands, Galápagos and Hawaiian Islands) satisfied all these conditions and were used for further analyses. It should be noted that, although the selected archipelagos share a number of characteristics useful for our analyses (high levels of endemism, multiple islands), some other attributes, particularly distance to mainland source areas and climatic conditions, are markedly different. Such differences help to explain the level of endemism of each archipelago (e.g. c. 90% for the Hawaiian Islands, the most remote from conti-

mental sources), and provide a good opportunity to investigate whether similar patterns of plant diversification can be found despite geographical differences among archipelagos.

DATA COLLECTION

During the last two decades, numerous phylogenetic studies have investigated the origin and evolution of oceanic island plant groups that comprise multiple endemics (for recent reviews, see Baldwin & Wagner, 2010; Tye & Francisco-Ortega, 2011). Population genetic studies at the species level have been comparatively less abundant, although increased accessibility and resolution of molecular markers have led to more studies in recent years (Caujapé-Castells, 2011; Pérez de Paz & Caujapé-Castells, 2013). We surveyed 120 published molecular studies and a few complementary taxonomic treatments to extract phylogenetic and population genetic information for lineages of each archipelago (see Supporting Information, Tables S1–S3). Lineages were established on the basis of current taxonomic and phylogenetic information (i.e. on the condition of monophyly). In order to analyse differences between contrasting modes of diversification, lineages were classified as ‘species-rich’ (more than two extant endemics constituting a clade; for a similar classification, see Pérez de Paz & Caujapé-Castells, 2013) or ‘monotypic’ (those with a single endemic species). Lineages with two extant endemic species were not considered, to ensure that patterns of diversification among types of lineages were markedly different (i.e. high vs. no diversification). Lineages with two endemics represent only a small fraction of the total endemic species pool of each archipelago (< 5%, on average), which means that our analyses covered the endemic flora of each archipelago almost entirely. A few studies have identified some genera for which the pool of species is the result of independent colonization events (e.g. Harbaugh & Baldwin, 2007; Andrus *et al.*, 2009), and the type and number of lineages in these cases were determined using the most updated taxonomic and molecular information. Recent reviews with a focus on phylogenetic inference on oceanic island lineages were also considered to obtain synthetic information, particularly for Hawai‘i (Baldwin & Wagner, 2010; Keeley & Funk, 2011) and Galápagos (Tye & Francisco-Ortega, 2011).

For species-rich lineages, phylogenetic reconstructions from published studies were used to gather information on the character states of fruit type and growth habit inferred for ancestors of these lineages, as is typically included in this type of study (e.g. Lowrey, Whitkus & Sykes, 2005; Andrus *et al.*, 2009; Givnish *et al.*, 2009). For the few radiating lineages

for which phylogenetic information has not yet been generated, character states of ancestors were either inferred from taxonomic treatments of island and mainland species (when the study character, i.e. habit or fruit type, was not variable among species) or excluded from the analyses (see Tables S1–S3). In the case of population genetic studies, data on the distribution of genetic variation among hierarchical levels for a given species (among islands, among populations within islands and within populations) were extracted from each publication, typically presented as analysis of molecular variance (AMOVA) results, or re-analysed with this method from information provided by the corresponding author on request (see Table 1). Data collection in this case was restricted to woody island taxa to avoid potential biases in the distribution of genetic variance within groups as a result of the inclusion of different growth forms (Nybom, 2004; García-Verdugo *et al.*, 2010a). Only species with widespread distributions were selected to investigate the effect of multiple island colonization on population genetic structure. To reach a reasonable sample size for each type of lineage, we broadened our search to other oceanic archipelagos, with a few examples from the Azores and Cape Verde Islands being included for this analysis.

STUDY GROUPS AND ASSUMPTIONS

Our study focused almost entirely on angiosperms as they represent the most diverse plant group of oceanic island floras. Nevertheless, three gymnosperm lineages (*Pinus* L. and two lineages of *Juniperus* L.) were also considered for the Canary Islands because of their wide distributions. Because the aim of the study was the analysis of factors related to speciation, only endemics were considered, thus avoiding potentially recent introductions (i.e. native, but not endemic, species). For the Canary Islands, monotypic lineages also included those for which populations have been documented from other Macaronesian islands, but are not found on the mainland.

One of the potential biases of our approach is that the number of endemic species might not accurately represent the pattern of diversification of a given lineage, for example (1) if extant monotypic lineages were more diverse on the islands in the past, but experienced extinctions; or (2) if species with former island–mainland distributions went extinct in mainland areas and thus are not island endemics that originated by *in situ* speciation. Because fossil records are scarce for oceanic islands, and the potential bias caused by species extinctions is thus difficult to address, we followed the simple approach adopted in most analytical studies (e.g. Price & Wagner, 2004; Stuessy *et al.*, 2006) of assuming that monotypic

Table 1. Partitioning of genetic variation at three hierarchical levels (among islands, A-ISL; among populations within islands, A-POP; within populations, W-POP) as obtained from analysis of molecular variance (AMOVA) in published population genetic studies of woody island endemics, grouped here according to the type of lineage (M, monotypic; S, species rich). Main modes of dispersal for each taxon as indicated in the literature (AN, animal; WA, water; UN, unassisted/unknown) and number of populations (pops) and islands considered in each study are detailed

Family	Taxon	Type of lineage	Archipelago	Seed dispersal	# islands (pops)	AMOVA				Reference
						A-ISL	A-POP	W-POP		
Oleaceae	<i>Picconia azorica</i> (Tutin) Knobl.	M	Azores	AN	7 (17)	1.9	14.1	84.0	1*	
Oleaceae	<i>Olea cerasiformis</i> Rivas-Mart. & del Arco	M	Canary Islands	AN	4 (9)	2.5	20.5	77.0	2	
Myricaceae	<i>Myrica faya</i> (Aiton) Wilbur	M	Canary Islands	AN	3 (8)	5.7	1.8	92.5	3	
Adoxaceae	<i>Sambucus palmensis</i> Link	M	Canary Islands	AN	3 (5)	8.0	15.0	77.0	4	
Cupressaceae	<i>Juniperus brevifolia</i> (Seub.) Antoine	M	Azores	AN	5 (18)	10.8	32.2	57.0	5	
Adoxaceae	<i>Viburnum treleasei</i> Gand.	M	Azores	AN	4 (8)	11.9	24.5	63.6	6	
Arecaceae	<i>Phoenix canariensis</i> Chabaud	M	Canary Islands	AN	4 (9)	17.9	40.6	41.5	7*	
Cistaceae	<i>Cistus symphytifolius</i> Lam.	S	Canary Islands	UN	2 (4)	15.3	9.6	75.1	8*	
Plantaginaceae	<i>Plantago pachyphylla</i> A.Gray	S	Hawai'i	UN†	4 (8)	21.7	16.5	61.8	9*	
Boraginaceae	<i>Echium stenosphon</i> Steud. ex Webb	S	Cape Verde	UN	3 (10)	29.7	9.8	60.5	10	
Asteraceae	<i>Scalesia affinis</i> Hook.f.	S	Galápagos	UN	3 (7)	33.6	10.0	56.4	11	
Caryophyllaceae	<i>Schiedea globosa</i> H.Mann	S	Hawai'i	UN-WA	4 (10)	33.7	7.1	59.2	12	
Asteraceae	<i>Dubautia laxa</i> Hook. & Arn. subsp. <i>hirsuta</i> (Hillebr.) G.D.Carr	S	Hawai'i	UN†	3 (4)	46.1	3.2	50.7	13	
Rosaceae	<i>Bencomia exstipulata</i> Svent.	S	Canary Islands	UN†	2 (4)	59.7	4.0	36.3	14	

*Data are re-analysed from information shown in the reference or provided by the corresponding author.

†Bird dispersal has been reported as incidental for these taxa.

References: 1, Ferreira *et al.* (2011); 2, García-Verdugo *et al.* (2010a); 3, González-Pérez *et al.* (2009a); 4, Sosa *et al.* (2010); 5, Silva *et al.* (2011); 6, Moura, Silva & Caujapé-Castells (2013); 7, González-Pérez, Caujapé-Castells & Sosa (2004); 8, Batista *et al.* (2001); 9, Dunbar-Co & Wiczorek (2011); 10, Romeiras *et al.* (2007); 11, Nielsen (2004); 12, Wallace *et al.* (2009); 13, McGlaughlin & Friar (2011); 14, González-Pérez *et al.* (2009b).

lineages are more parsimoniously explained by anagenetic events of speciation rather than cladogenesis followed by multiple extinctions.

LIFE HISTORY TRAITS

Two qualitative characters (fruit type and growth form) associated with diversification rates and species richness in several studies (Smith, 2001; Price & Wagner, 2004; Givnish, 2010) were chosen for the present study. We chose qualitative rather than quantitative traits because the former are readily available from the large number of phylogenetic studies of island lineages including this type of data (e.g. Givnish *et al.*, 2009; Baldwin & Wagner, 2010; Tye & Francisco-Ortega, 2011), and thus can be generated for large taxon sample sizes. In addition, qualitative data provide a straightforward way to test for associations between particular trait combinations (phenotypic syndromes hereafter) (Dodd *et al.*, 1999; Price & Wagner, 2004).

To assign a character state to extant species, we followed the taxonomic descriptions compiled in the most comprehensive island floras of each archipelago: Wiggins & Porter (1971) for Galápagos; Wagner, Herbst & Sohmer (1999) for the Hawaiian Islands; and the compilation by Bramwell & Bramwell (2001) for the wild flora of the Canary Islands. For 'growth form' (character state = woody vs. herbaceous), the 'woody' condition included trees, shrubs, subshrubs, woody vines and other arborescent or suffrutescent plants. Previous studies have employed a phylogenetic context to analyse evolutionary shifts in growth habit between extant island endemics and their ancestors, but such cases were restricted to particular lineages (e.g. Böhle, Hilger & Martin, 1996; Andrus *et al.*, 2009; Baldwin & Wagner, 2010 and references therein) or to a given island system, e.g. Macaronesia (Carine *et al.*, 2010). In this study, we aimed to compare the information available from phylogenetic analyses among the three selected archipelagos. We followed the rationale of earlier studies analysing the evolution of growth form: woodiness (including suffrutescent habit) is associated with relatively long generation times and other factors that could have an effect on speciation patterns (Tiffney & Mazer, 1995; Dodd *et al.*, 1999; Andreasen & Baldwin, 2001; Smith & Donoghue, 2008). Scoring of character states in each case followed the descriptions provided in each phylogenetic study, where suffrutescent plants are typically regarded as woody (e.g. Böhle *et al.*, 1996; Mort *et al.*, 2001). For 'fruit type', two character states were considered: fleshy fruit (FF) vs. dry fruit (DF). FFs included drupes and berries, drupaceous and berry-like structures (e.g. aggregate of drupelets in *Rubus* L. or berry-like cones in *Juniperus*), and

fruits enclosed by fleshy receptacles or calyces (e.g. *Touchardia* Gaudich.). In a few cases, seeds attached to fleshy tissues, such as arils, were also regarded as FFs (e.g. *Alphitonia* Reissek ex Endl.). DFs, however, included achenes, capsules, pods and nutlets. Fruits were classified into these two categories on the understanding that not all fruits of each character state are alike, and may vary in physical characteristics (size, form, colour) and dispersal vectors. For example, DFs of some species include propagules that may be dispersed widely and frequently by abiotic means (e.g. oceanic drift), whereas those of other species have features favouring vertebrate dispersal (e.g. barbs, hooks or viscid exudate). By grouping fruits into the two broad categories of DF and FF, we primarily aimed to test the hypothesis that FFs are generally related to species cohesion and limited diversification, notwithstanding important exceptions.

COLONIZATION ABILITY

Potential for island colonization was estimated as the number of islands on which each endemic species occurred (realized colonization ability), following the most comprehensive bibliographic information on species distribution for each archipelago: Acebes-Ginovés *et al.* (2010) for the Canary Islands; Jaramillo Díaz *et al.* (2010) for Galápagos; and Wagner *et al.* (1999) with modifications from Wagner *et al.* (2012) for Hawai'i. This variable accounts for the occurrence of at least one successful event of inter-island dispersal for the establishment of new populations, with self-incompatible or dioecious plants representing simultaneous or separate dispersal of multiple individuals. We appreciate that the lack of occurrence of some species on particular islands may have as much or more to do with historical or extrinsic factors, such as niche pre-emption by earlier colonists, than with dispersal-related traits of the plants in question (see Discussion), and that differences in timing of arrival on islands will be important to include in future studies, as such data, which are especially lacking for monotypic lineages, become more widely available. For Canarian monotypic lineages with populations on other Macaronesian islands, analysis of distributional data was restricted to populations found in the Canary Islands. Other Macaronesian islands (mainly Madeira and Salvage Islands) show clear floristic affinities with the Canary Islands, but this latter archipelago is considered as a biogeographical unit for the purpose of the present study. Because monotypic lineages with populations in other Macaronesian areas are widespread in the Canaries (e.g. *Jasminum* L., *Prunus* L., *Ranunculus* L., *Ilex* L.), the omission of populations outside the Canaries should not affect our analyses on

colonization ability (see below). To analyse potential differences between lineage and fruit types in colonization ability, a mean range size across constituent species was calculated for each species-rich lineage, following Price & Wagner (2004).

STATISTICAL ANALYSES

Potential associations between life history characters (growth form and fruit type) and between phenotypic syndromes and levels of realized colonization ability were evaluated with contingency tables. To investigate the distribution of different phenotypic syndromes among ancestors of species-rich lineages, the association between life history traits was assessed with 2×2 contingency tables computed with Statistica 5.0 (Statsoft, Inc, Tulsa, OK, USA). A similar analysis was conducted for life history traits of monotypic lineages. All analyses were performed for each archipelago separately.

Monotypic lineages were then classified according to three classes of colonization ability: low (species reported on one or two islands), medium (three or four islands) and high (five islands or more). To analyse the potential association between realized colonization ability and phenotypic syndromes (herbaceous-FF, herbaceous-DF, woody-FF, woody-DF), 3×4 contingency tables were computed for each type of lineage with Statistica 5.0. Analyses were performed considering each archipelago separately. Differences in realized colonization ability were further evaluated with a two-way analysis of variance (ANOVA) using the total pool of lineages for each archipelago and including fruit type (two levels: FF vs. DF) and lineage type (monotypic vs. species-rich) as fixed factors. For species-rich lineages, the mean species range size was used for this analysis (Price & Wagner, 2004). The distribution of data for 'lineage type' was right skewed for the Canary Island and Hawai'i datasets, and so a logarithmic transformation was applied. After transformation, data for this factor remained skewed in both cases (Bartlett test, $P < 0.05$), but deviation from homoscedasticity was less severe (see also Price & Wagner, 2004). The interaction factor 'type of lineage \times fruit type' was not considered for the Galápagos dataset because of insufficient sample size for species-rich lineages with FFs.

Lastly, information from population genetic studies extracted from AMOVA for each species (Table 1) was compared between the two main types of lineage (monotypic vs. species-rich) using Mann-Whitney U -tests. The proportion of genetic variance for each hierarchical level (among islands, among populations within islands and within populations) was analysed separately.

RESULTS

GENERAL OBSERVATIONS

Our literature review allowed the inference of ancestral character states for the majority of species-rich lineages from the three oceanic archipelagos ($N = 16$, Galápagos; $N = 46$, Canary Islands; $N = 63$, Hawai'i). The number of monotypic lineages considered was $N = 62$ for Galápagos, $N = 113$ for the Canary Islands and $N = 81$ for Hawai'i (for detailed descriptions of all lineages, see Tables S1–S3). As a general pattern, growth habit was shown to be a highly variable character; an 'herbaceous' state was inferred for 60% of ancestors of species-rich lineages (average across archipelagos), but 80% of extant species of this type of lineage displayed a 'woody' state. In contrast, shifts between fruit types (i.e. between DF and FF conditions) since the arrival of early colonizers appeared to be rare in species-rich lineages, and were found only in six Hawaiian lineages (e.g. lobelioids and mints) and one Canarian lineage (*Bencomia* Webb & Berthel. alliance) (see Tables S1–S3).

LIFE HISTORY TRAITS AND TYPE OF LINEAGE

Results from contingency tables revealed significant associations between pairs of traits in ancestors of species-rich lineages for Galápagos (χ^2 , d.f. 1 = 6.86, $P < 0.01$), the Canary Islands (χ^2 , d.f. 1 = 4.78, $P < 0.05$) and Hawai'i (χ^2 , d.f. 1 = 20.32, $P < 0.001$). The most frequent phenotypic syndrome among inferred ancestors of species-rich lineages was 'herbaceous-DF', although this syndrome was found in different proportions depending on the archipelago: 75% of the species-rich lineages analysed for Galápagos, 70% of Canary Island lineages and 43% of Hawaiian lineages (Fig. 1). A lower proportion of inferred 'herbaceous-DF' ancestors in Hawai'i than that obtained for the other archipelagos was accompanied by a high proportion (33%) of 'woody-FF' ancestors of species-rich lineages (Fig. 1). On average, herbaceous-DF ancestors represented 58% of cases across all lineages considered ($N = 125$) (Fig. 1). Analyses of phenotypic syndromes of monotypic lineages also showed significant trait associations for Galápagos (χ^2 , d.f. 1 = 10.84, $P < 0.001$), the Canary Islands (χ^2 , d.f. 1 = 17.00, $P < 0.001$) and Hawai'i (χ^2 , d.f. 1 = 36.33, $P < 0.001$). For monotypic lineages, however, the proportion of 'woody-FF' species was similar to that of 'herbaceous-DF' species, particularly for the Canary Islands and Hawai'i (Fig. 2).

COLONIZATION ABILITY

Analyses of realized colonization ability in monotypic lineages showed significant associations of this attribute with phenotypic syndromes for the Canary Island

(χ^2 , d.f. 6 = 26.08, $P < 0.001$) and Hawaiian (χ^2 , d.f. 6 = 10.7, $P < 0.05$) lineages, but tests were only marginally significant for Galápagos (χ^2 , d.f. 6 = 7.46, $P < 0.10$). Thus, monotypic lineages with a high realized potential for colonization were most frequently represented by ‘woody-FF’ syndromes in all archipelagos (20% of monotypic lineages in Galápagos, 24% in the Canary Islands and 26% in Hawai‘i; Fig. 3). Conversely, low realized colonization ability was most frequently observed among ‘herbaceous-DF’ species (13% of monotypic lineages in Galápagos, 16% in the Canary Islands and 15% in Hawai‘i; Fig. 3).

Species in radiating lineages were associated with a limited realized ability for inter-island colonization, as < 50% of lineages had mean range sizes of more than two islands and only 14% had mean range sizes

of more than three islands (Supporting Information, Fig. S1). In line with these results, ANOVA showed that monotypic lineages and species of radiating lineages differed significantly in realized colonization ability, as did FF vs. DF lineages (Table 2). Monotypic lineages had wider distributional ranges than species in radiating lineages in Hawai‘i (monotypic, 4.3 ± 0.2 ; species in radiating lineages, 2.2 ± 0.1), the Canary Islands (monotypic, 4.0 ± 0.2 ; species in radiating lineages, 2.2 ± 0.1) and Galápagos (monotypic, 5.0 ± 0.4 ; species in radiating lineages, 4.3 ± 0.5), but the differences were statistically significant only for Hawai‘i and the Canary Islands (Table 2). Conversely, FF lineages had wider distributional ranges than DF lineages in Hawai‘i (FF = 4.0 ± 0.3 ; DF = 3.0 ± 0.2), the Canary Islands (FF = 5.1 ± 0.2 ; DF = 2.9 ± 0.2) and Galápagos (FF = 6.0 ± 0.6 ; DF = 4.4 ± 0.4), but again significant differences were only detected for Hawai‘i and the Canary Islands (Table 2).

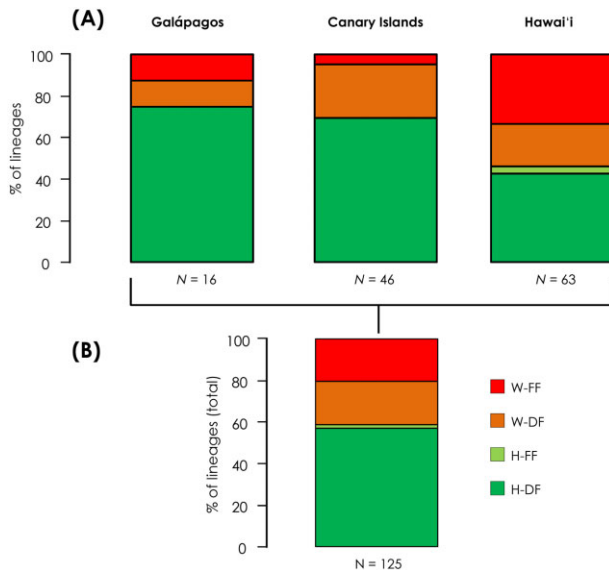


Figure 1. A, Percentage of ancestors of species-rich island lineages classified according to their inferred phenotypic syndromes (W, woody; H, herbaceous; FF, fleshy fruited; DF, dry fruited). B, Values averaged across all three archipelagos.

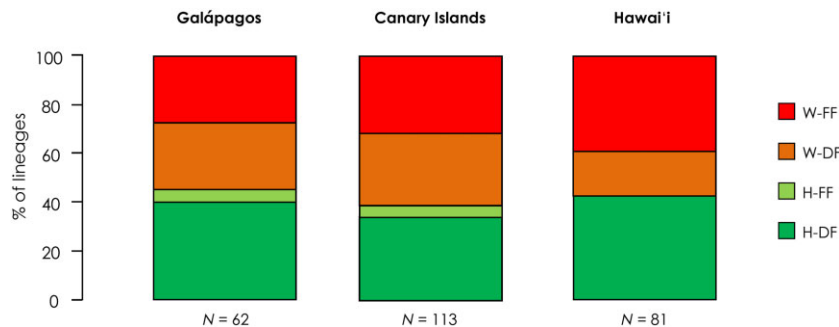


Figure 2. Percentage of oceanic island endemics of monotypic lineages classified according to their phenotypic syndromes (W, woody; H, herbaceous; FF, fleshy fruited; DF, dry fruited).

PARTITIONING OF GENETIC VARIATION AND TYPE OF LINEAGE

The analysis of levels of genetic variance obtained from AMOVA showed that widespread species of monotypic lineages displayed significantly lower differentiation among islands than that typically reported for species of radiating lineages (Mann–Whitney U -test, $P < 0.01$; Fig. 4). Indeed, levels of genetic variance for this hierarchical level were close to zero in monotypic lineages, suggesting a virtual lack of differentiation among islands (Fig. 4). Differences between types of lineage for the distribution of genetic variance ‘among populations within islands’ and ‘within populations’ were not or only marginally significant (Mann–Whitney U -test, $P = 0.05$ and $P = 0.08$, respectively).

DISCUSSION

LIFE HISTORY TRAITS AND DIVERSIFICATION

Analyses of data obtained from phylogenetic reconstructions and population genetic studies support the

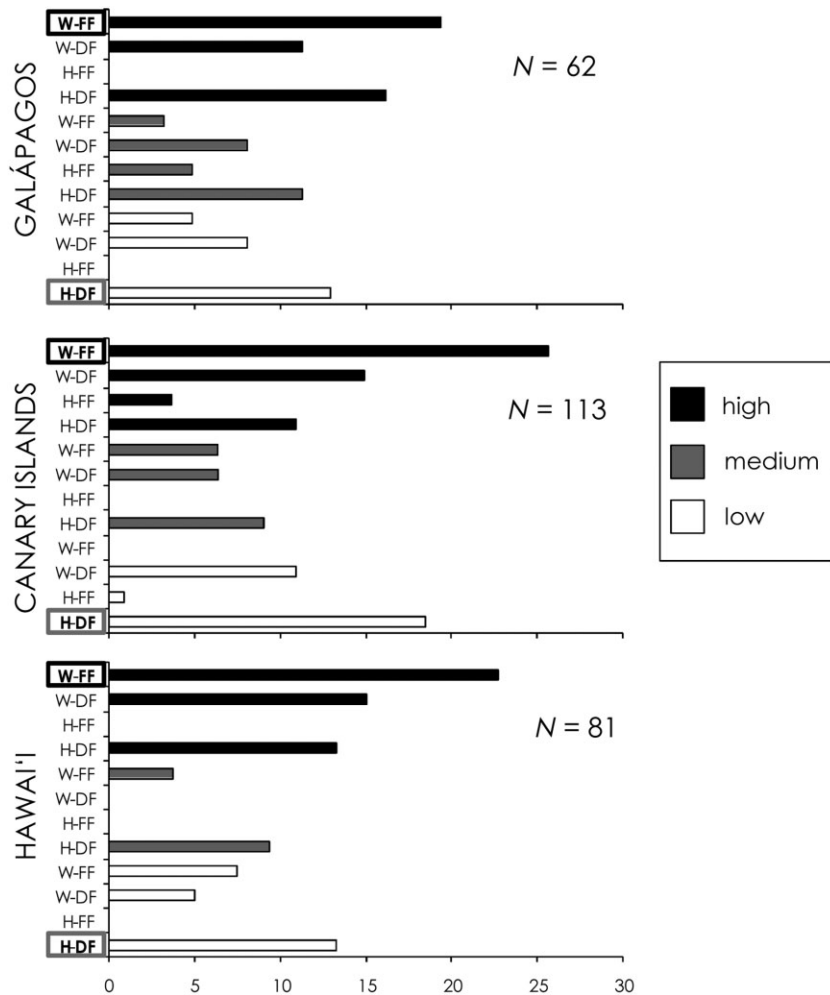


Figure 3. Number of monotypic lineages of each archipelago classified according to colonization ability (low, one or two islands; medium, three or four islands; high, more than five islands) and phenotypic syndromes (W, woody; H, herbaceous; FF, fleshy fruited; DF, dry fruited). Phenotypic syndromes showing the highest number of cases for low and high colonization ability are highlighted.

Table 2. *F* ratios and significance from the two-way analysis of variance (ANOVA) used to analyse the differences in species distributional range between types of lineage (species-rich vs. monotypic), types of fruit (fleshy vs. dry) and their interaction. Interaction factor in Galápagos was excluded because of insufficient sample size for fleshy fruited, species-rich lineages

Archipelago	Lineage type (L)	Fruit type (F)	L × F
Hawai'i	$F_{1,140} = 33.4^*$	$F_{1,140} = 6.6^\dagger$	$F_{1,140} = 0.2$ ns
Canary Islands	$F_{1,158} = 6.5^\dagger$	$F_{1,158} = 9.2^\dagger$	$F_{1,158} = 0.5$ ns
Galápagos	$F_{1,75} = 0.6$ ns	$F_{1,75} = 0.7$ ns	NA

* $P < 0.001$.

† $P < 0.01$.

ns, non-significant; NA, not applicable.

idea that certain phenotypic traits are related to the diversification of island lineages. The analysis of character states obtained from published phylogenetic studies revealed that some trait combinations were

particularly frequent among ancestors of extant species-rich lineages on oceanic archipelagos. Thus, the phenotypic syndrome 'herbaceous-DF' was the most common among colonizers that subsequently

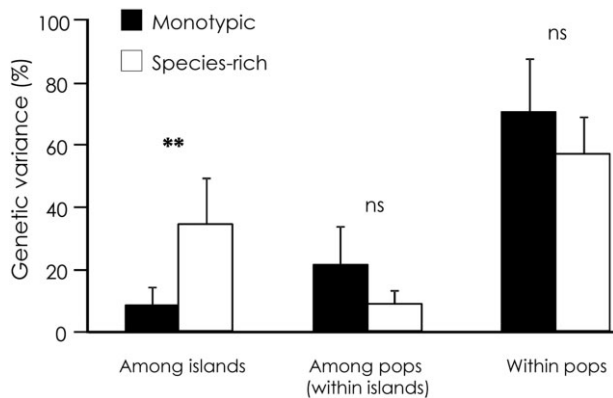


Figure 4. Comparison of levels of hierarchical genetic variance for species of two types of lineage (monotypic vs. species-rich) as obtained from analysis of molecular variance (AMOVA) using population genetic data of woody island endemics. **Significant differences ($P < 0.01$) according to Mann–Whitney U -test; ns, non-significant difference for that hierarchical level.

underwent diversification (Fig. 1). In addition, population genetic and distributional data indicate that geographical isolation in lineages with only limited dispersal among islands has been an important pattern of diversification, as suggested by previous phylogenetic studies (e.g. Baldwin *et al.*, 1998). In a recent review of the genetic diversity of the Canarian flora, Pérez de Paz & Caujapé-Castells (2013) found that levels of genetic differentiation in species-rich lineages (as inferred from G_{ST}) were significantly higher than those obtained for monotypic lineages. Similarly, we found that the colonization of several islands by DF species of radiating lineages typically leads to strong genetic differentiation among these geographically separated populations (Fig. 4). Oceanic barriers often impose limits to gene flow, particularly when seeds are not efficiently dispersed (Bittkau & Comes, 2005; García-Verdugo *et al.*, 2013a), and ultimately provide the conditions for allopatric speciation to occur (Johnson, Adler & Cherry, 2000; Kisel & Barraclough, 2010). Distributional ranges of species illustrate the importance of geographical isolation in lineage diversification, insofar as most species of radiating lineages are confined to one or a few islands and sister species are often allopatric (Price & Wagner, 2004; Acebes-Ginovés *et al.*, 2010; Fig. S1). Inter-island colonization of species with poor dispersal abilities may thus have promoted allopatric speciation in some cases, although multiple factors, including major ecological shifts, have been implicated in both among- and within-island differentiation of extensively diversified lineages (e.g. Baldwin *et al.*, 1998), as is probably reflected by frequent parapatry of sister species in Hawai'i (Price & Wagner, 2004). Thus, mechanisms of

speciation acting at the island level (e.g. ecological divergence across habitats, geographical isolation within islands, sympatric speciation, hybridization between closely related species) may be of greater or lesser importance in the complex pattern of differentiation observed in most radiating island plant groups (Price & Wagner, 2004; Gillespie & Baldwin, 2009; Papadopulos *et al.*, 2011; García-Verdugo *et al.*, 2013a).

Although the available evidence seems to suggest a significant association between particular traits and speciation events, it often proves difficult to infer causality, because shifts in a given trait could be either the consequence or the cause of speciation (Chown, 1997; Dodd *et al.*, 1999). Stasis in a given character with a suspected effect on speciation could indicate a causal relationship, because the possibility of phenotypic shift as an evolutionary consequence can be ruled out. In the present case, each of the analysed life history characters showed a different pattern. Growth habit was shown to be labile during the course of lineage diversification. For instance, many island radiations illustrate that the herbaceous condition of the first colonizers shifted to woodiness early in the process of diversification, as all phylogenetically derived species display a woody condition in these groups [e.g. silverswords (*Argyroxiphium* DC. and relatives), *Silene* L. and *Geranium* L. in Hawai'i or *Sideritis* L. and *Argyranthemum* Webb in the Canary Islands]. The high proportion of extant woody species (80% across species in radiating lineages), when compared with the inferred herbaceous condition of most (60%) putative ancestors, supports the idea that woodiness was strongly selected for in the island setting (Carlquist, 1974; Jorgensen & Olesen, 2001; Carine *et al.*, 2010). In contrast, phylogenetic studies of some plant groups suggest that the herbaceous condition is derived in some species of radiating lineages, thus showing that reversals in habit also occur during the evolution of species-rich lineages (Böhle *et al.*, 1996; Mort *et al.*, 2001; Swenson & Manns, 2003). In the case of growth form, it is therefore difficult to discern whether shifts in character states were consequences of speciation or, alternatively, were involved in lineage divergence. A different pattern is shown by fruit type, as broadly defined here to include two character states: FF and DF. With relatively few exceptions, including the Hawaiian lobelioids and mints (Lindqvist & Albert, 2002; Givnish *et al.*, 2009) and the *Bencomia* alliance in the Canary Islands (Pérez de Paz, 2004), fruit types have not undergone dramatic change between these states during the evolutionary history of most radiating island lineages. Unlike growth form, comparison of inferred character states in ancestors and those observed in the descendant species-rich lineages sug-

gests that relative stasis in fruit type since island colonization has been the rule for most of these lineages. Carlquist (1966a, b) noted that Hawaiian species often show modifications in fruits and seeds when compared with their mainland relatives, however, with changes related to quantitative characters apparently involved in dispersibility (i.e. fruit and appendage sizes). Our broad categorization of fruits as DF or FF fails to capture such important distinctions. Notwithstanding the generality of our trait categorization, high levels of diversification in certain oceanic island lineages appear to be mainly associated with remarkable phenotypic differentiation in vegetative rather than fruit characters (for a review, see Jorgensen & Olesen, 2001), probably because the genetic architecture of vegetative characters makes them more easily adaptable to environmental shifts, and phylogenetic constraints for these characters are therefore weak (Jorgensen & Olesen, 2001; Levin, 2006).

Our estimates of ancestral characteristics, however, should be considered with caution. Because ancestral states of species-rich lineages were obtained from inferences of phylogenetic analyses, these estimates are subject to the same caveats that potentially affect any phylogenetic approach. The extinction of closely related species and the limited sampling of mainland relatives (for a further discussion, see Caujapé-Castells, 2011) might affect the accuracy of ancestral character state reconstructions typically reported in phylogenetic studies. For example, increased sampling of mainland taxa in a molecular phylogenetic analysis of the endemic *Pericallis* D. Don in Macaronesia suggested that the ancestral life form was woody rather than herbaceous, although the heterogeneity in growth form in this genus complicated an accurate inference of the ancestral state for the island group (Panero *et al.*, 1999; Swenson & Manns, 2003). However, fruit type represents a different case for character state reconstructions. Because this character has apparently been phylogenetically constrained since island colonization in most lineages, limitations imposed by phylogenetic inferences probably do not have a substantial effect on our conclusions in this case (Schluter *et al.*, 1997). Furthermore, population genetic data provide an alternative line of evidence to that obtained from phylogenetic inference (Fig. 4), which also suggests that fruit type, in addition to other (e.g. ecological) factors, is relevant to the diversification of extant species-rich lineages.

FLESHY FRUITS AND SPECIATION ON ISLANDS: A CONTEXT-DEPENDENT RELATIONSHIP

Our analyses showed that FFs are generally associated with a high potential for inter-island colonization

(Fig. 3, Table 2). Although rare events of dispersal to distant islands would probably lead to population divergence and eventual speciation (Johnson *et al.*, 2000; Price & Wagner, 2004), population genetic data suggested that most species with FFs readily overcome oceanic barriers and show weak population genetic structure across islands (Fig. 4). Extensive gene flow across islands associated with FFs suggests that this fruit type represents a trait favouring species cohesion in fragmented landscapes (García-Verdugo *et al.*, 2010a; Ferreira *et al.*, 2011; Moura *et al.*, 2013).

Our conclusions drawn from population genetic data seem to be at odds with studies on Hawaiian lineages for which high species diversity has been linked to limited dispersal of FFs (Price & Wagner, 2004; Givnish *et al.*, 2009). These contradictory results are most probably explained by the different habitats in which Hawaiian vs. Galápagos and Canary Island lineages of FF species evolved. According to the previous studies, Hawaiian FF lineages that have undergone extensive diversification mostly occur in moist forests, where limited dispersal by sedentary birds, in some instances because of increased seed or fruit size (Carlquist, 1966a), could have promoted speciation (Givnish *et al.*, 2009). Hawaiian tropical moist forests currently cover an area of 6700 km² (World Wildlife Fund, 2013), which is substantially larger than the estimated potential area for densely forested zones (subtropical forests) in the drier Canary Islands (926 km²; Guimarães & Olmeda, 2008) and Galápagos (Hamann, 1979), especially if we take into consideration the fact that human impact has significantly reduced the original area of moist forests in Hawai'i. Thus, high species number as a consequence of limited bird dispersal in forested areas (Smith, 2001) is a more plausible explanation for Hawaiian lineages than for the other archipelagos. In addition to the high availability of forested areas on the Hawaiian Islands, other factors may account for the substantial proportion of 'woody-FF' ancestors inferred for this archipelago (Fig. 1). For instance, trait evolution on other Pacific islands prior to the colonization of Hawai'i may have promoted the acquisition of a woody habit under insular conditions, as suggested for *Tetramolopium* Ness (Lowrey *et al.*, 2005). In summary, differences in patterns of character evolution and speciation among archipelagos can be attributed to context-dependent conditions for lineage diversification (Herrera, 1989), although common trends across archipelagos also occur (Figs 1–3).

LACK OF SPECIATION ON OCEANIC ARCHIPELAGOS

Phylogenetic studies have demonstrated that oceanic archipelagos have promoted the *in situ* diversification

of many plant lineages. In this sense, oceanic islands could also represent a framework in which to address questions about the opposite pattern: i.e. what factors are responsible for a lack of speciation in certain (monotypic) lineages? Excluding the Hawaiian lineages mentioned previously, our analyses suggest that FFs could be one intrinsic factor involved in species cohesion. FFs are generally linked to high colonization ability and extensive gene flow among islands (Figs 3, 4), which may, at least in part, explain why this type of fruit is often displayed by monotypic lineages (Fig. 2). Nevertheless, lack of speciation in extant oceanic lineages is obviously not limited to FF species. DF species also represent a substantial proportion of monotypic lineages (Fig. 2). Several factors, most also applicable to FF, monotypic lineages, may account for this fact. Because the colonization of oceanic archipelagos could have been constrained to discrete temporal windows (Carine, 2005), some of these lineages may have found opportunities for colonization only in recent times, so that there has not been sufficient time for recurrent speciation. In turn, it is also plausible that earlier colonizers had more opportunities for *in situ* diversification. In line with this argument, niche pre-emption by earlier colonizers may have hindered adaptation to novel environments (Silvertown, 2004), limiting opportunities for speciation. Such a possibility could be further tested by the analysis of habitat differentiation among populations of monotypic lineages with DFs showing widespread distributions (Fig. 3). Another complementary explanation is that some DFs are frequently dispersed over large distances (e.g. by oceanic drift), and thus recurrent gene flow among populations would be expected to reduce the likelihood of speciation, as discussed previously for FFs. Molecular studies on *Phylica arborea* Thouars, for example, indicate that this tree species overcame distances of up to 8000 km during the colonization of multiple oceanic islands around southern Africa despite its DF condition (Richardson *et al.*, 2003). A final point for consideration is that the actual number of monotypic lineages might be conditioned by taxonomic uncertainty in those plant groups in which limited taxonomic research or cryptic speciation obscures the real pattern of diversification. Further interdisciplinary research, including taxonomic, molecular and ecological data, is needed to identify the most important factors related to lack of speciation in monotypic lineages.

Lastly, although poorly studied on islands, other intrinsic factors affecting patterns of diversification include those characters related to habitat colonization and population persistence that are induced by environmental cues (Pfennig *et al.*, 2010). For instance, the architectural organization of trees and

shrubs favours phenotypic plasticity across canopy layers, allowing persistence and reproduction even under stressful conditions (e.g. García-Verdugo, 2011). In addition, resprouting ability is thought to be another key trait for population persistence (Bond & Midgley, 2001). Recent ecological studies on widespread island taxa, such as *Pinus canariensis* C.Sm. ex DC. (López, Climent & Gil, 2010), *Olea cerasiformis* Rivas-Mart. & del Arco (García-Verdugo *et al.*, 2010b; García-Verdugo, 2011) and *Croton scouleri* Hook.f. (Castillo *et al.*, 2013), have indicated that phenotypic plasticity and resprouting ability play a significant role in habitat colonization across broad environmental gradients in Macaronesia and Galápagos. These studies support the idea that not only fruit dispersal traits, but also specialized life history strategies involved in population establishment and persistence, may be important in the successful colonization of remote areas and subsequent patterns of diversification of colonizing lineages (e.g. Christenhusz & Chase, 2013). Further studies using a plant trait perspective may help us to understand the implications of intrinsic factors for lineage diversification.

CONCLUDING REMARKS

Although the present study suffers from typical constraints of meta-analyses (e.g. lack of consistency in methods among published studies, limited sample sizes), it constitutes, to our knowledge, the first attempt to summarize the inferences drawn from molecular studies on three paradigmatic oceanic archipelagos. Despite clear differences in physiography and geographical isolation, our analyses revealed some similar patterns among these island systems. Thus, phylogenetic reconstructions of character states suggest that ancestors of species-rich lineages in these archipelagos were predominantly herbaceous and with DFs. Island environmental conditions apparently selected for a shift from an herbaceous to a woody habit in most lineages. In contrast, fruit type (i.e. DF or FF) appears to be strongly phylogenetically constrained, which may have promoted speciation in DF lineages because of generally limited dispersal ability compared with FF lineages. The complexity of the evolutionary processes and biotas considered here, including diversity in fruit morphologies relevant to dispersal ability and dispersal vectors, places limits on the applicability of these patterns. For instance, our analyses suggest that the relationship between high species diversity and FFs indicated by previous studies could be a particular outcome for plant groups that evolved in moist forests, such as those found in Hawai'i. Traits related to frequent dispersal (particularly FFs), in combination with

those favouring population persistence (phenotypic plasticity, resprouting ability), probably play a significant role in species cohesion and thus contribute to prevent speciation in some lineages. Although further phylogenetic research with new molecular markers is resolving complex evolutionary patterns in radiating lineages (e.g. Marcussen *et al.*, 2012), ecological and population genetic studies on islands, particularly those focusing on monotypic lineages, are still critically needed to allow a broader picture to be developed of how evolution works on oceanic archipelagos.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Mean species range size of each species-rich lineage based on the number of islands where extant species have been reported. Only archipelagos with high sample sizes (Canary Islands and Hawai'i) are represented.

Table S1. Description of Hawaiian lineages included in the study, showing the number of constituent endemic species (# end), growth form (habit), fruit type (DF, dry fruit; FF, fleshy fruit) and mean range size across species (for species-rich lineages) or distribution range (for monotypic lineages) (D). Inferred character states of putative ancestors in growth form and fruit type were based on published studies (see reference list below). Each lineage is typically designated by its genus name (together with the authority at first mention). Abbreviations for fruits: ACH, achene; ACH-cy, cypsela; ACH-ca, caryopsis; ANT, anthocarp; BER, berry or berry-like; CAP, capsule; DRU, drupe; FOL, follicle; NUC, nucule, nutlet; POD, pod; SIL, silicula, siliqua; SCH, schizocarp, mericarp; UTR, utricle; ???, unknown state for putative ancestor.

Table S2. Description of Canarian lineages included in the study, showing the number of constituent endemic species (# end), growth form (habit), fruit type (DF, dry fruit; FF, fleshy fruit) and mean range size across species (for species-rich lineages) or distribution range (for monotypic lineages) (D). Inferred character state of putative ancestors in growth form and fruit type was based on published studies (see reference list below). Each lineage is typically designated by its genus name (together with the authority at first mention). Abbreviations for fruits are the same as in Table S1.

Table S3. Description of Galápagos lineages included in the study, showing the number of constituent endemic species (# end), growth form (habit), fruit type (DF, dry fruit; FF, fleshy fruit) and mean range size across species (for species-rich lineages) or distribution range (for monotypic lineages) (D). Inferred character state of putative ancestors in growth form and fruit type was based on published studies (see reference list below). Each lineage is typically designated by its genus name (together with the authority at first mention). Abbreviations for fruits are the same as in Table S1.