



Plant colonization across the Galápagos Islands: success of the sea dispersal syndrome

PABLO VARGAS^{1*}, MANUEL NOGALES², PATRICIA JARAMILLO³, JENS M. OLESEN⁴, ANNA TRAVESET⁵ and RUBEN HELENO^{5,6}

¹*Real Jardín Botánico de Madrid (RJB-CSIC), 28014 Madrid, Spain*

²*Island Ecology and Evolution Research Group (IPNA-CSIC), 38206 La Laguna, Tenerife, Canary Islands, Spain*

³*Charles Darwin Foundation, Puerto Ayora, Santa Cruz, Galápagos, Ecuador*

⁴*Department of Bioscience, Aarhus University, Aarhus, Denmark*

⁵*Institut Mediterrani d'Estudis Avançats (UIB-CSIC), 07190 Esporles, Mallorca, Balearic Islands, Spain*

⁶*Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, Coimbra, Portugal*

Received 21 November 2013; revised 10 December 2013; accepted for publication 13 December 2013

A new approach for investigating evidence for the capacity of plant colonization between islands and the success of plant morphological traits associated with seed dispersal is presented. As colonization is the result of dispersal and establishment, oceanic archipelagos provide an ideal spatio-temporal system in which to analyse plant dispersal traits related to current distributions of species across islands. The Galápagos archipelago comprises 12 islands > 10 km² that harbour 403 native angiosperms, of which 313 native species occupy lowland habitats that are present on all islands. We inferred the minimum number of colonization events within the archipelago for the species (289 lowland species) present on more than one island (floristic analysis). The distribution (number of islands) of species across the islands was slightly left-skewed, with 58% of all lowland species being present on one to six islands. The success of dispersal syndromes (i.e. morphological trait sets of the diaspores associated with dispersal) favourable to inter-island dispersal (medium-distance dispersal, MDD) was also analysed (syndrome analysis). In particular, the 289 lowland species were classified into four dispersal groups (syndromes): sea (thalassochory), wind (anemochory), and animal interior (endozoochory) or animal exterior (epizoochory). Most species ($N = 174$, 55.6%), however, displayed no traits related to MDD (unspecialized diaspores). Analyses of the distribution of syndrome traits across the 289 lowland native species and 12 islands revealed that: (1) species with one or more of the four MDD syndromes did not have broader distributions than those with unspecialized diaspores; (2) species with sea dispersal traits were the most broadly distributed; and (3) a net loss of dispersability for diaspore traits (from non-endemic natives to endemic species) was not supported for the whole flora by our analyses. In summary, our analyses showed that species with sea-drifting diaspore traits were significantly associated with the success of plant colonization across the Galápagos Islands. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, ••, ••–••.

ADDITIONAL KEYWORDS: anemochory – endozoochory – epizoochory – hydrochory – island biogeography – plant dispersal syndromes – seed dispersal – unspecialized diaspores.

INTRODUCTION

Colonization is the combined result of dispersal and establishment, which are best analysed within the

spatio-temporal limits furnished by oceanic islands (Thornton, 2007). Dispersal is conditioned by the characteristics of the mainland source (diaspore traits, dispersal agents) and the geographical distance to islands, whereas establishment of new organisms depends primarily upon local conditions (habitat

*Corresponding author. E-mail: vargas@rjb.csic.es

suitability, mutualism, antagonism) (Gillespie & Clague, 2009). Likewise, current species distributions across an archipelago reflect the success of colonization as a result of dispersal events, establishment, and persistence since islands were formed, with or without further speciation.

Generally, the actual means of long-distance dispersal (LDD) causing the colonization of the present island floras is a matter of speculation (Vargas *et al.*, 2012). In contrast, testing whether particular diaspore traits have been favourable in the formation of a flora can provide an evolutionary framework. In other words, success of particular morphologies (diaspore specializations) acquired in the evolutionary history of the angiosperms can be tested for LDD to islands (Nogales *et al.*, 2012). Most oceanic islands, such as the Galápagos Islands, are shield volcanoes built up from the sea floor that have never been connected to the mainland, offering an ideal framework to test plant colonization by LDD (Klein *et al.*, 2005; Poulakakis *et al.*, 2012). Similar proportions of sets of LDD traits (categorized as syndromes) favourable to sea-water (thalassochory 19%), animal interior (endozoochory 16%), animal exterior (epizoochory 16%), and wind (anemochory 13%) dispersal were found for early colonists of the Galápagos Islands (Vargas *et al.*, 2012). In addition, a fifth category (unspecialized diaspores) not related to any LDD syndromes accounted for an unexpectedly high proportion (36%) of the flora. Although plants with traits associated with LDD appeared to be better represented as a whole (64%) in the flora of the Galápagos Islands than plant traits unrelated to LDD, the question remains as to whether the success (high proportion) of the five categories stays the same when studying the dispersal of species among the Galápagos Islands.

During the development of an archipelago, continental immigrants have the opportunity to further colonize islands after succeeding in LDD from the mainland (MacArthur & Wilson, 1967). Once the new species establishes a population in the archipelago, it can start colonizing the other islands. In principle, nearby islands are expected to be more easily colonized, and thereafter, because of fewer dispersal limitations imposed by inter-island sea barriers than by mainland–archipelago distances (Gillespie & Clague, 2009). Distance is critical in the process of dispersal (Lomolino *et al.*, 2010; Weigelt & Kreft, 2013). In biogeography, dispersal is considered worldwide (LDD), in contrast to dispersal within and between ecological zones where distances are shorter and barriers are expected to be weaker. Remote oceanic archipelagos, such as the Galápagos, Hawai'i, the Azores and the Canary Islands, offer the opportunity to consider three biogeographical scales on which dispersal operates: (1) LDD over considerable distances

between the mainland and remote archipelagos; (2) medium-distance dispersal (MDD) among islands of the same archipelago; and (3) short-distance dispersal (SDD) within an island. SDD is comparable to distances within the same mainland ecosystem. Accordingly, a study of different distance barriers imposed by sea bodies offers the opportunity to build up a reliable framework for the colonization theory of island biogeography (Gillespie *et al.*, 2011).

The present study was focused upon the MDD of angiosperms across the Galápagos Islands and addressed the following objectives: (1) to review the distributions (chorology) of plant species across the islands; (2) to assign each species to one or more of the five dispersal syndrome categories; and (3) to evaluate to what extent the presence of the five dispersal categories is a good estimator of the distribution of species across the 13 larger islands. Distance limits plant island dispersal and distribution, and thus species with specialized traits for LDD and MDD are expected to be more favoured for dispersal (Nathan, 2006). Indeed, a majority of plants in the Galápagos archipelago had to overcome the almost 1000 km that separates the islands from the South American mainland (Vargas *et al.*, 2012). In this paper, the general hypothesis to be tested was that organisms displaying specialized traits for inter-island dispersal have been more favoured in colonizing a higher number of Galápagos Islands than those lacking those traits.

MATERIAL AND METHODS

NUMBER OF COLONIZATION EVENTS

The distribution of the native species over the 13 larger islands (> 10 km²) was taken from the dataset of the Charles Darwin Foundation (<http://checklists.datazone.darwinfoundation.org/vascular-plants/>; see also Jaramillo & Guézou, 2011). However, we considered only 12 islands in the analyses because Santa Cruz and Baltra formed a single island until recently (Poulakakis *et al.*, 2012).

The following complementary steps were taken: (1) we used the species as the operational starting unit; (2) only native taxa were considered; (3) nomenclatural and systematic changes were revised; (4) the list of native species was additionally amended with six species from palaeobotanical records (palaeobotanical correction) (van Leeuwen *et al.*, 2008); (5) a single ancestor was adopted for the origin of each species from the mainland as long as there is no phylogenetic evidence for multiple colonizations of the same species (phylogenetic correction); and (6) molecular evidence was revised from the literature to infer multiple colonizations of the same island (phyloge-

graphical correction) (see more details in Vargas *et al.*, 2012). The rationale supporting the phylogenetic and phylogeographical corrections is that a monophyletic group of the same plant group (typically species) indicates a single colonization from the dispersal source, and that two or more independent lineages of the same plant group (i.e. unrelated individuals) are interpreted as the arrival of two or more colonists from different source populations. Some examples of the importance of these corrections can be found in Andrus *et al.* (2009) and Appelhans *et al.* (2014).

Given that native species arrived in the archipelago by natural means, we assumed that they had the same opportunities for inter-island colonization. Admittedly, here we did not consider the importance of dispersal per se and island age, inter-island distances, island size, and time of species arrival to the archipelago, which also influence the distribution of each species (see Castro *et al.*, 2010). Instead, we focused on actual colonization in our analysis of the geographical structure of the Galápagos flora. In addition, habitat suitability was controlled by analysing species occurring below 300–400 m (dry zone) to include ecological conditions present in all islands. We initially assumed that each species present on two or more islands is the result of one or more colonization events, and consequently the number of islands on which a species is present informs us about the minimal number of colonization events (number of islands – 1). Accordingly, presence of a species on only a single island indicates failure in colonization of the other islands, and thus no colonization events recorded. In contrast, the presence of a species on multiple islands is indicative of successful MDD. Thus, a maximum of 11 colonization events across the 12 islands can be inferred for each species, although detailed phylogeographical studies could increase this number (see Vargas *et al.*, 2012, for discussion).

A presence/absence matrix of species on the 12 islands (species/no. of islands matrix) was assembled and analysed. We had the opportunity to improve the species/no. of islands matrix qualitatively and quantitatively during four expeditions (2010–2013) across the 12 islands.

FLORISTIC ANALYSES

The species/no. of islands matrix (403 species, 12 islands) was converted into a new matrix (313 species, 12 islands) including only the species occurring in the dry zone (below 300–400 m; lowland species). As this zone is found on all the larger islands, the success of species colonization was calculated based on native, lowland species ($N = 289$) that have been found on two or more islands (colonization

events). We used Pearson's correlation to evaluate if there was an association between each species distribution (from one to 12 islands) and the frequency of species distributions, i.e. if only a few species were present on many islands and if most species were present on few islands. Likewise, the effect of plant endemism on plant distribution was statistically explored by contrasting the number of endemic and non-endemic species with their distribution across islands. This made it possible to describe patterns of colonization after local speciation (reflected by endemic species), i.e. acquisition of new traits, following further colonization or permanence on the same island.

DISPERSAL SYNDROME ANALYSES

MDD is here understood in a biogeographical sense, i.e. plant connections between islands within the same archipelago. The same diaspore morphologies used to assess successful LDD were also considered for MDD (see Vargas *et al.*, 2012), which also express specialization in assisting diaspores in dispersal over inter-island sea barriers. Plant diaspore traits of infrutescences, fruits, seeds, and vegetative parts were classified into four syndromes (Vargas *et al.*, 2012): dispersal by wind (anemochory), sea water (thalassochory), animal ingestion (endozoochory), and animal adhesion (epizoochory) (Fig. 1). All traits related to short-range plant dispersal (e.g. myrmecochory, barochory, autochory, ballistic) were coded into a fifth category (unspecialized) as these syndromes are not considered particularly favourable in promoting inter-island colonizations. Previous flora descriptions (Wiggins & Porter, 1971), field observations (2010–2013) and analysis of herbarium specimens (CDS, MA) were used for diaspore characterization and classification (van der Pijl, 1982). For some species, three scientific web search engines (<http://www.info.scopus.com>, <http://www.scholar.google.com>, and <http://www.isiknowledge.com/WOS>) were needed because of limited herbarium information. The resulting table is available from the authors upon request.

Each species present in the archipelago was assigned a colonization probability of 1. For plants with more than one syndrome, the probability of each syndrome associated with the colonization of the archipelago was assigned a fraction of 1. As there are no experimental data for Galápagos species to express a probabilistic value for two or more syndromes, an aprioristic approach was adopted. For example, for a species in which two syndromes were identified, each syndrome was assigned a value of 0.5 to reflect a 50% probability of being responsible for the number of colonization events. As a result, a matrix of species and syndromes (species/syndrome matrix) was



Figure 1. Species classified into the five categories of long-distance dispersal to islands based on morphological traits: A, fruit pappus related to anemochory in *Pectis tenuifolia* (DC.) Sch.Bip. (Asteraceae); B, fleshy fruit related to endozoochory in *Castela galapageia* Hook.f. (Simaroubaceae); C, glabrous seeds, but hairy loment (fruit) related to epizoochory in *Desmodium procumbens* (Mill.) Hitchc. (Fabaceae); D, cork-like fruits related to thalasochoy in *Hippomane mancinella* L. (Euphorbiaceae); and E, unspecialized fruit of *Scalesia affinis* Hook.f. (Asteraceae).

assembled and analysed (289 lowland species, five syndrome categories). The total probability of each MDD syndrome category (the dependent variable used in the analyses) was obtained by the summation of proportions of the syndrome category from each species divided by the number of lowland species for the flora of the Galápagos Islands. These proportions of dispersal syndromes were considered the starting point for plant colonization, i.e. the proportions of trait sets displayed by all the species in the archipelago, irrespective of the number of islands subsequently colonized.

The most successful species distributions across the Galápagos Islands were investigated by considering syndrome proportions (dependent variable) and geographical distribution (independent variable) for each species. To estimate the contribution of each syndrome to the colonization of the islands, the species/no. of islands matrix was transformed into a species syndrome/no. of islands matrix (289 lowland species, five syndrome categories, 12 islands). Summation of each species syndrome distribution for all species provides information about the success of each syndrome across the flora.

The two syndrome matrices (species/syndrome matrix and species syndrome/no. of islands matrix) were used for the dispersal syndrome analyses. In particular, six main analyses were performed to contrast: (1) the relative importance of species syndrome proportions for the archipelago (species/syndrome matrix) versus species syndrome proportions for the 12 islands (species syndrome/no. of islands proportions) to detect differences in the case of intra-island colonization; (2) the proportion of the five dispersal syndrome categories exclusively present on one island (no colonization events) versus those of species distributed over two or more islands (at least one MDD

event) to associate syndrome categories and failure in further colonization; (3) the mean distributions of species with unspecialized diaspores versus the mean distributions of species with dispersal syndromes to quantify the success of having dispersal attributes; (4) the mean distributions of species bearing a single MDD syndrome versus those with two or more MDD syndromes to evaluate the success of multiple dispersal specialization; (5) the distributions of species with epi- and/or endozoochory (zoochory) versus those of the species without these syndromes; and (6) the proportion of unspecialized diaspores in the non-endemic native flora versus the proportion of unspecialized diaspores in the endemic flora to evaluate if endemic plants show a trend to lose dispersal traits as a result of speciation.

Contingency analyses (G tests) were used to determine if there were significant differences in the proportions of the frequencies of the assigned MDD syndrome diaspore categories (analyses 1, 2, and 6), and generalized linear models (GzLM) with a log-linear link-function were used to evaluate which syndromes (presence/absence: binary predictors) affect species distributions (number of islands: Poisson distributed response) (analyses 3–5). All data were analysed using SPSS (v.19.0) software.

RESULTS

SUCCESS OF SPECIES COLONIZATION

After surveying the previous species/no. of islands matrix (Jaramillo & Guézou, 2011) during four expeditions (2010–2013) across the 12 studied islands, only nine new species records were added to the original list: *Batis maritima* L. and *Opuntia megasperma* Howell on Española; *Commicarpus tuberosus*

Table 1. Number of native (including endemic and non-endemic) plant species, on one or more islands (maximum of 12 major islands) in the dry zone of the Galápagos archipelago (see text); proportions of unspecialized diaspores over proportions of the other four syndrome categories for endemics and non-endemics are also shown

No. of islands	No. of native species	No. of endemic species	No. of non-endemic species	Percentage unspecialized endemics	Percentage unspecialized non-endemics
1	25	19	6	63.2	40.0
2	26	12	14	50.0	57.7
3	31	18	13	60.0	53.8
4	30	10	20	60.0	47.5
5	31	13	18	46.1	60.5
6	39	13	26	38.5	51.9
7	30	16	14	43.7	78.6
8	26	10	16	32.0	46.4
9	21	7	14	57.1	57.1
10	24	10	14	30.0	26.9
11	16	7	9	57.1	50.0
12	14	8	6	68.7	58.3
Total	313	143	170	–	–

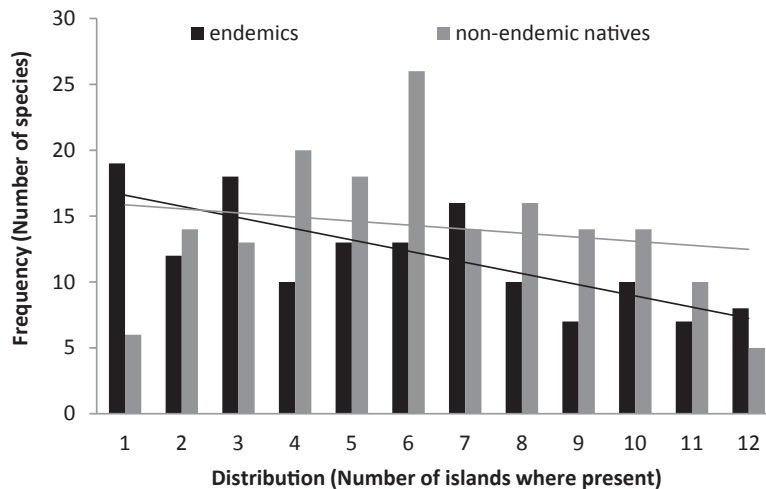


Figure 2. Number of native species of the dry zone (313 native species) distributed between one and the 12 large islands of the Galápagos archipelago. Lines indicate tendency slopes for endemic and non-endemic species.

(Lam.) Standl. and *Cyperus elegans* L. on Genovesa; *Conocarpus erectus* L. and *Plumbago zeylanica* L. on Marchena; and *Croton scouleri* Hook.f., *Scutia spicata* (Humb. & Bonpl. ex Willd.) Weberb., and *Vallesia glabra* (Cav.) Link on Pinzón. The species have very different distributions, ranging from 24 species exclusively present on one island to 19 species distributed across all 12 (Table 1). The distributions of the 313 native species occurring in the dry zone were inversely proportional to the number of islands (i.e. a greater number of species are present on a lower number of islands) (Fig. 2). Regardless, 288 species are distributed on two or more islands, which

led us to interpret success in multiple colonization events. The distribution of native species across the islands was slightly left-skewed ($r_p = -0.601$, $P < 0.039$), with 58% species only on six or fewer islands. In addition, significant results were obtained for the 143 endemics ($r_p = -0.755$, $P = 0.004$) but not for the 170 non-endemics ($r_p = -0.193$, $P = 0.547$).

SUCCESS OF SYNDROME COLONIZATION

Presence of syndrome traits across the 313 lowland species of the Galápagos archipelago (colonization starting point) is as follows: anemochory (14.9%),

Table 2. Contingency tables of dispersal traits for (A) syndrome proportions for the 313 lowland species occurring in the Galápagos archipelago (species/syndrome matrix) and across the 12 islands (species syndrome/no. of islands matrix) and (B) syndrome proportions (species syndrome/no. of islands matrix) of species present on one island and distributed over two or more islands

	ANE	ENDO	EPI	THA	UNS
(A) Distribution of species syndromes					
Archipelago syndrome proportions (%) ($N = 313$)	6.9	15.8	12.2	15.5	49.6
12-island syndrome proportions (%) ($N = 3756$)	8.0	14.8	10.9	14.1	52.2
(B) Distribution of species syndromes					
On one island (%) ($N = 24$)	12.0	8.0	16.0	4.0	60.0
On two or more islands (%) ($N = 289$)	7.6	15.4	10.4	15.0	51.6

ANE, anemochory; ENDO, endozoochory; EPI, epizoochory; THA, thalassochory; UNS, unspecialized.

Table 3. Effect of the presence or absence of each particular syndrome on the distribution (i.e. number of islands) of lowland, native plants across the Galápagos Islands

Syndrome	Mean island distribution without each syndrome	Mean island distribution with each syndrome	Wald statistics	d.f.	<i>P</i>
Anemochory	6.06	5.20	2.903	1	0.088
Endozoochory	5.89	6.41	1.967	1	0.161
Epizoochory	5.93	6.26	1.738	1	0.187
Thalassochory	5.84	6.54	4.637	1	0.031

Differences across the mean distributions have been explored with a multivariate generalized linear model (GzLM) with a loglinear link function. Cases in which presence of a specific syndrome were significantly related to plant distribution ($\alpha = 0.05$) are highlighted in bold.

endozoochory (19.3%), epizoochory (9.9%), and thalassochory (4.8%). Therefore, we failed to find any trait related to MDD in 51.1% of the cases.

The analysis of the contingency table of MDD syndromes revealed only small deviations between the initial syndrome proportions (proportions in the archipelago) and the distribution of syndrome proportions across the 12 islands ($G_4 = 0.624$, $P = 0.96$; Table 2A). The proportions of species present on a single island differ from those present on more than one island ($G_4 = 21.71$, $P < 0.001$; Table 2B). The species with one of the four syndromes had a tendency to have a wider distribution than species with unspecialized diaspores (see García-Verdugo *et al.*, 2014), but this difference was not significant (mean \pm SE unspecialized species = 5.7 ± 0.26 islands; specialized species = 6.2 ± 0.25 islands; Wald chi-square₁ = 2.81; $P < 0.094$). The contribution of each syndrome to successful colonization was significantly different for the flora of the Galápagos Islands as a whole. The GzLM revealed that only thalassochory was significantly related (Wald chi-square₁ = 4.64, $P = 0.031$) to broad species distributions within the Galápagos Islands, even if moderately, whereas none of the other syndromes (anemochory, endozoochory,

and epizoochory) appears to contribute significantly to intra-island dispersal (Table 3). It was not, however, possible to analyse species with two or more syndromes because of their low frequency (20 species) in the Galápagos flora.

Our floristic approach indicates similar proportions of endemic and non-endemic species with unspecialized diaspores ($G_1 = 0.567$, $P = 0.452$) (Table 4A). Therefore, we failed to find significant dispersal trait shifts in the course of speciation in the flora of the Galápagos Islands. Nevertheless, the proportion of traits related to inter-island dispersal was underrepresented in endemic species ($G_1 = 20.09$, $P < 0.001$; Table 4B). The prevalence of endozoochory ($G_1 = 4.39$, $P = 0.036$) and anemochory ($G_1 = 57.24$, $P < 0.001$) was higher among endemic than among non-endemic natives, supporting new dispersability traits for particular syndromes.

DISCUSSION

The flora of the Galápagos Islands consists of species transported by LDD. However, it is intriguing that most (c. 58%) of the lowland species are present on only six or fewer of the 12 islands analysed in this

Table 4. Contingency analysis (*G*-test) of differences in proportions of endemic and non-endemic species with (A) specialized (endozoochory, epizoochory, anemochory, thalassochory) and unspecialized diaspores and (B) total number of species and the four specialized syndromes

	Endemics (observed)	Non-endemic natives (expected no loss of dispersability)	Statistical analyses
(A)			
With any specialized syndromes	76 (53%)	85 (50%)	$G_1 = 0.567, P = 0.452$
Unspecialized syndromes	67 (47%)	85 (50%)	
(B)			
Total number of species	143	170	
Anemochory	26 (18%)	4 (2%)	$G_1 = 57.24, P < 0.001$
Endozoochory	29 (20%)	22 (13%)	$G_1 = 4.39, P = 0.036$
Epizoochory	19 (13%)	24 (14%)	$G_1 = 0.063, P = 0.802$
Thalassochory	13 (9%)	47 (28%)	$G_1 = 20.09, P < 0.001$

Values for each syndrome category are given in parentheses (see text). Distributions significantly broader than $\alpha = 0.05$ are highlighted in bold.

study (Table 1), but managed to overcome the considerable sea barrier (c. 1000 km) between the Galápagos Islands and the American continent (Darwin, 1859; Wiggins & Porter, 1971). This implies significant difficulties for recurrent plant colonizations despite the relatively short distances between islands. Indeed, the geographical distributions of both endemic (143) and non-endemic (170) species were inversely proportional to the number of islands. This pattern has already been described for Pacific archipelagos, in contrast to floristic homogenization in the Atlantic (Castro *et al.*, 2010). Distribution patterns of insular plants are not only affected by distance but also by local conditions such as the area of surrounding landmasses, prevailing winds, direction of ocean currents, and climatic similarity between islands (Weigelt & Krefl, 2013). Therefore, distance and local conditions, coupled with the biology of each species, have historically been considered the major factors that drive colonization patterns on oceanic islands (MacArthur & Wilson, 1967). The question remains as to which plant dispersal syndromes are more related to the colonization of the Galápagos Islands in the same geographical area (Galápagos) and similar habitat conditions (dry zone).

SUCCESS OF SEA DISPERSAL TRAITS

The Galápagos flora is the result of 372 early colonists, as inferred by the taxonomic and phylogenetic analyses of plant genera (Vargas *et al.*, 2012). These ancestors show a high frequency of diaspore attributes related to LDD, as revealed by a high proportion (64%) of specialized diaspores grouped into anemochory (13.3%), endozoochory (16.4%), epizoochory (15.7%), and thalassochory (18.6%). The species-level

analysis performed here revealed that a high proportion (51.1%) of lowland species displayed no syndromes related to MDD across the Galápagos Islands. In addition, the four syndromes were found in different proportions in the Galápagos archipelago: anemochory (14.9%), endozoochory (19.3%), epizoochory (9.9%), and thalassochory (4.8%). Despite this low proportion, traits related to sea dispersal were significantly more widely distributed across the islands than any others (Table 3). Such events are often observed as stranded plant material along island coasts (Guppy, 1906; Ridley, 1930). Indeed, during our four expeditions we recorded some fruits and seeds belonging to species that were not always present on the islands (e.g. fruits of *Rhizophora mangle* L. and *Hippomane mancinella* L. on Marchena). Comparative analyses of tropical floras (Carlquist, 1967), albeit with no consideration of unspecialized diaspores, led to the opinion that thalassochory is well represented in oceanic island floras, particularly on atolls (Fenner & Thompson, 2005).

Although plant traits associated with MDD by vertebrates (primarily birds) are common in the archipelago (29.2% of epi- and endozoochory), they appeared to have not been particularly well distributed across the islands (25.6%), which is an unexpected result. The study of bird diet on two islands (Santa Cruz and San Cristobal) showed high dispersal activity of seeds by Galápagos birds (Heleno *et al.*, 2013). Almost 10 000 intact seeds from 58 plant species were recovered from the droppings of 15 bird species. Indeed, some medium- and large-sized birds (including insectivores) frequently broaden their diet to include fruits and seeds on oceanic islands, a phenomenon known as 'niche expansion' (Wright, 1980). A remarkable example is that of the abundant

and ubiquitous endemic small-ground finch (*Geospiza fuliginosa*), that despite being mostly granivorous (i.e. seed predator) was shown to disperse the seeds of at least 21 plant species actively, of which 17 are lowland species (Heleno *et al.*, 2013). Unfortunately, there are few bird phylogeography studies (Browne *et al.*, 2008; Nietlisbach *et al.*, 2013) that could help in answering whether relatively narrow inter-island distributions of endozoochorous species are related to limited colonization of Galápagos Islands by birds.

LOSS OF DISPERSABILITY

Carlquist (1966a) formulated the hypothesis of loss of plant dispersability as a result of evolution in the Hawaiian Islands (Thorne, 1963). Morphological characters of the flora of Hawai'i were carefully studied and taxonomic comparisons performed on genera of 27 families of angiosperms, in which a tendency toward gigantism in fruit size was related to decreased dispersability (Carlquist, 1966a). Although 'precise statistical expressions of loss of dispersability' were not undertaken, Carlquist concluded that some dramatic evolutionary changes, such as gigantism in habit and diaspores, can be observed on oceanic islands. Comparisons of putative relatives based on taxonomy have recently become possible by phylogenetic reconstructions, and the sister-group principle has been used to infer some characteristics of the most recent common ancestor of endemic species (Vargas, 2007). Unfortunately, there are only a few phylogenetic analyses of Galápagos plant groups available to address this issue, and those with a reliable sample do not show any tendency to loss of dispersability (Sánchez-del Pino, Motley & Borsch, 2012; Vargas *et al.*, 2012; see also Trusty *et al.*, 2012). A lineage-by-lineage reconstruction of sister-group relationships is needed on a considerable number of plant groups to test diaspore shifts.

An alternative approach is presented here, in which the whole flora of the Galápagos Islands is analysed to explore if there is any significant sign of a loss of dispersability after speciation (i.e. an increase in the proportion of unspecialized diaspores of endemic plants) in the archipelago. Indeed, most endemic species tend to be distributed across only a few islands (Fig. 2). However, the analysis of endemic species versus non-endemic species both with unspecialized diaspores, which are expected to increase when related to *in situ* loss of dispersability, did not document a pattern of general syndrome shifts (Table 4). Nevertheless, a certain loss of dispersability was observed for sea-water dispersal traits, whereas wind-dispersal showed the opposite trend. Regardless, loss of dispersability appears to be closely related to particular plant groups (Carlquist, 1966b;

Cody & Overton, 1996). An analysis of wind-dispersed shifts showed two opposite tendencies towards gain (*Epilobium* L.) and loss (*Cirsium* Mill.) of anemochory on temperate islands (Fresnillo & Ehlers, 2008). Nevertheless, the predominantly dry habitats of the Galápagos Islands, which are those analysed in our study, have been claimed to be responsible for only a slight dispersability change in Asteraceae (Carlquist, 1966b). By contrast, an experimental study of sea-water dispersal demonstrated loss of seed buoyancy in *Hibiscus glaber* Matsum. ex Nakai (endemic to the Bonin Islands), in contrast to the high seed buoyancy of the widespread Pacific *H. tiliaceus* L., which is also found in the Galápagos Islands (Kudoh, Takayama & Kachi, 2013). It is intriguing that thalassochory is significantly more common among species present on two or more islands (Table 2B), despite the predominant trait loss of this syndrome in endemic species (Table 4B). Both patterns need further investigation using empirical experimentation for dispersal potential, molecular markers for arrival time estimates and accurate number of colonization events, and niche modelling for determining finer habitat suitability. Therefore, the hypothesis of dispersability loss is still a challenge for each plant group of any flora, specifically for those species potentially increasing in diaspore size, rather than losing flying and floating structures, which have not been analysed in our study (Carlquist, 1966a).

CONCLUSIONS

Floristic analyses can generate new hypotheses to be tested within the theory of island biogeography. In particular, our approach can be performed for any oceanic archipelago once detailed information about floras and species distributions is available. In addition, inference of multiple colonizations of the same island by the same species using molecular markers can substantially help reconstruct a more realistic colonization process. With 313 lowland angiosperm species distributed across a high number of large islands (12), the Galápagos Islands are an ideal system in which to study plant colonization. Our results suggest that MDD syndromes do not necessarily increase species distribution. The Galápagos flora has a relatively low proportion (48.9%) of species with MDD syndromes, of which species with thalassochorous traits appear to have been the most successful in the colonization history across this archipelago.

ACKNOWLEDGEMENTS

This study is framed within a biodiversity project in the Galápagos Islands, financed by the Spanish Min-

istry of Economy and Competitivity (CGL2012-38624-C02-01). We thank all botanists since Darwin who have collected plants in this archipelago, because a comprehensive floristic database could not otherwise have been analysed without numerous botanical explorations. In particular, we appreciate the generosity and assistance of the Herbarium staff (Charles Darwin Foundation; Puerto Ayora, Galápagos) in our work with syndrome coding. Both the Charles Darwin Foundation and the Parque Nacional de Galápagos offered essential logistics to our research. R.H. was funded by the Marie Curie action FP7-2012-CIG-321794, and J.M.O. by the Danish National Science Foundation.

REFERENCES

- Andrus N, Tye A, Nesom G, Bogler D, Lewis C, Noyes R, Jaramillo P, Francisco-Ortega J. 2009.** Phylogenetics of *Darwiniothamnus* (Asteraceae: Astereae) – molecular evidence for multiple origins in the endemic flora of the Galápagos islands. *Journal of Biogeography* **36**: 1055–1069.
- Appelhans MS, Wen J, Wood KR, Allan GJ, Zimmer EA, Wagner WL. 2014.** Molecular phylogenetic analysis of Hawaiian Rutaceae (*Melicope*, *Platydesma* and *Zanthoxylum*) and their different colonization patterns. *Botanical Journal of the Linnean Society*. doi: 10.1111/boj.12123.
- Browne RA, Elizabeth C, Anderson DJ. 2008.** genetic structure of Galápagos populations of the Yellow Warbler. *The Condor* **110**: 549–553.
- Carlquist C. 1966a.** The biota of long-distance dispersal. III. Loss of dispersability in the Hawaiian flora. *Brittonia* **18**: 310–335.
- Carlquist C. 1966b.** The biota of long-distance dispersal. II. Loss of dispersability in Pacific Compositae. *Evolution* **20**: 30–48.
- Carlquist C. 1967.** The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club* **94**: 129–162.
- Castro SA, Daehler CC, Silva L, Torres-Santana CW, Reyes-Betancort JA, Atkinson R, Jaramillo P, Guezou A, Jaksic FM. 2010.** Floristic homogenization as a teleconnected trend in oceanic islands. *Diversity and Distributions* **16**: 902–910.
- Cody ML, Overton JM. 1996.** Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* **84**: 53–61.
- Darwin C. 1859.** *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- Fenner M, Thompson K. 2005.** *The ecology of seeds*. Cambridge: Cambridge University Press.
- Fresnillo B, Ehlers BK. 2008.** Variation in dispersability among mainland and island populations of three wind dispersed plant species. *Plant Systematics and Evolution* **270**: 243–255.
- García-Verdugo C, Baldwin BG, Fay MF, Caujapé-Castells J. 2014.** Life history traits and patterns of diversification in oceanic archipelagos: a meta-analysis. *Botanical Journal of the Linnean Society*. doi: 10.1111/boj.12127.
- Gillespie RM, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK. 2011.** Long-distance dispersal: a framework for hypothesis testing. *Trends in Ecology and Evolution* **27**: 47–56.
- Gillespie RM, Clague DA. 2009.** *Encyclopedia of islands*. Berkeley, CA: University of California Press.
- Guppy HB. 1906.** *Observations of a naturalist in the Pacific between 1896 & 1899. Vol. 2. Plant dispersal*. London: Macmillan.
- Heleno RH, Olesen JM, Nogales M, Vargas P, Traveset A. 2013.** Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proceedings of the Royal Society B* **280**: 20122112. doi: 10.1098/rspb.2012.2112.
- Jaramillo P, Guézou A. 2011.** *Charles Darwin Foundation Galápagos species checklist*. Puerto Ayora: Charles Darwin Foundation. Available at: <http://www.darwinfoundation.org/datazone/checklists/vascular-plants/> Last updated 23 July 2012.
- Klein EM, Smith DK, Williams CH, Schouten H. 2005.** Counter-rotating microplates at the Galapagos triple junction. *Nature* **433**: 855–858.
- Kudoh H, Takayama K, Kachi N. 2013.** Loss of seed buoyancy in *Hibiscus glaber* on the oceanic Bonin Islands. *Pacific Science* **67**: 591–597.
- van Leeuwen JFN, Froyd CA, van der Knaap WO, Coffey EE, Tye A, Willis KJ. 2008.** Fossil pollen as a guide to conservation in the Galápagos. *Science* **322**: 1206.
- Lomolino M, Riddle BR, Whittaker RJ, Brown JH. 2010.** *Biogeography*. Sunderland, MA: Sinauer Associates.
- MacArthur RH, Wilson EO. 1967.** *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Nathan R. 2006.** Long-distance dispersal of plants. *Science* **313**: 786–788.
- Nietlisbach P, Wandeler P, Parker PG, Grant PR, Grant BR, Keller LK, Hoeck PEA. 2013.** Hybrid ancestry of an island subspecies of Galápagos mockingbird explains discordant gene trees. *Molecular Phylogenetics and Evolution* **69**: 581–592.
- Nogales M, Heleno R, Traveset A, Vargas P. 2012.** Evidence for overlooked mechanisms of long-distance seed dispersal to and between oceanic islands. *New Phytologist* **194**: 313–317.
- van der Pijl L. 1982.** *Principles of dispersal in higher plants*. Berlin: Springer-Verlag.
- Poulakakis N, Russello M, Geist D, Caccione A. 2012.** Unravelling the peculiarities of island life: vicariance, dispersal and the diversification of the extinct and extant giant Galápagos tortoises. *Molecular Ecology* **21**: 160–173.
- Ridley HN. 1930.** *The dispersal of plants throughout the world*. Ashford: L. Reeve & Co.
- Sánchez-del Pino I, Motley TJ, Borsch T. 2012.** Molecular phylogenetics of *Alternanthera* (Gomphrenoideae, Amaranthaceae): resolving a complex taxonomic history caused by different interpretations of morphological characters in a

- lineage with C4 and C3–C4 intermediate species. *Botanical Journal of the Linnean Society* **169**: 493–517.
- Thorne RF. 1963.** Biotic distribution patterns in the tropical Pacific. In: Gressitt JL, ed. *Pacific Basin biogeography*. Honolulu: Bishop Museum Press, 311–350.
- Thornton I. 2007.** *Island colonization: the origin and developments of island communities*. Cambridge: Cambridge University Press.
- Trusty JL, Tye A, Collins TM, Michelangeli FA, Madriz P, Francisco-Ortega J. 2012.** Galápagos and Cocos Islands: geographically close, botanically distant. *International Journal of Plant Sciences* **173**: 36–53.
- Vargas P. 2007.** Are Macaronesian islands refugia of relict plant lineages?: a molecular survey. In: Weiss SJ, Ferrand N, eds. *Phylogeography in southern European refugia: evolutionary perspectives on the origins and conservation of European biodiversity*. Dordrecht: Springer, 297–314.
- Vargas P, Heleno R, Traveset A, Nogales M. 2012.** Colonization of the Galápagos Islands by plants with no specific syndromes for long-distance dispersal: a new perspective. *Ecography* **35**: 33–43.
- Weigelt P, Kreft H. 2013.** Quantifying island isolation – insights from global patterns of insular species richness. *Ecography* **36**: 417–429.
- Wiggins IL, Porter DM. 1971.** *Flora of the Galápagos Islands*. Stanford, CA: Stanford University Press.
- Wright SJ. 1980.** Density compensation in island avifaunas. *Oecologia* **45**: 385–389.