



0 Colonization of the Galápagos Islands by plants with no specific syndromes for long-distance dispersal: a new perspective 53

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15 Since nobody has witnessed the arrival of early plant colonists on isolated islands, the actual long-distance dispersal (here-
after LDD) has historically been a matter of speculation. In the present study, we offer a new approach that evaluates
whether particular syndromes for LDD (i.e. the set of traits related to diaspore dispersal by animals, wind and sea cur-
rents) have been favourable in the natural colonization of the Galápagos Islands by plants. Dispersal syndromes of the 251
20 native genera (554 angiosperm species) presently acknowledged as native were carefully studied, combining data from
floristic lists of the Galápagos Islands, diaspore traits, characteristics of continental relatives and our own observations. We
used these genera (and occasionally infrageneric groups) as the working units to infer the number of introductions and
colonists. A final number of native plants was inferred and analysed after correcting by pollen records of six species from
six genera previously considered exotic (palaeobotanical correction). The number of early colonists was also corrected by
incorporating information from the few ($n = 12$) phylogenetic studies of genera from both the Galápagos Islands and
25 the Americas (phylogenetic correction). A total of 372 colonization events were inferred for the native flora using the
latest check-list. The proportions of native colonists grouped into five categories were: endozoochory 16.4%, epizoochory
15.7%, hydrochory 18.6%, anemochory 13.3%, and unassisted diaspores 36.0%. These figures did not vary significantly
on analysing only the 99 genera that include endemic species in order to rule out any human-mediated introductions.
Irrespective of the roles of the different agents involved in LDD, diaspores with no special syndrome for LDD (unas-
sisted diaspores), such as many dry fruits, have been successful in reaching and colonizing the Galápagos archipelago. This
30 finding leads us to suggest that unpredictable and so far unknown LDD mechanisms should be further considered in the
theory of island biogeography. 65

35 Islands are ideal models to study long-distance plant dis-
persal (hereafter LDD) (Gillespie and Clague 2009). Seed
dispersal is often the first step for plants to colonize new
territories and thus is crucial to understanding species com-
position, range expansion and genetic structure (Cain et al.
2000, Nathan 2006). Traditionally, taxonomic and floristic
40 data have provided the basic tool to infer the geographic
origin of flowering plants on oceanic islands (Hooker 1847,
Carlquist 1967, MacArthur and Wilson 1967). Given their
relatively recent origin from the sea-floor in comparison to
continental areas, researchers have focused on the bioge-
45 ography of LDD events in oceanic islands. The number of
taxa (mainly genera) has been widely used to estimate the
number of colonization events. In addition, description of
the vegetative and diaspore structures of plants has aided
in categorising them into four main groups of diaspores
50 related to dispersal by: wind (anemochory), water (hydro-
chory), internally by animals (endozoochory), and exter-
nally by animals (epizoochory) (Carlquist 1967). The lure
of reconstructing the colonization history of each archi-
pelago has led scholars to infer, and often speculate, about
actual vectors responsible for the presence of plant groups
on remote oceanic islands. Wagner et al. (1990) calculated
for the Hawaiian flora that the ca 1000 native species arose
90 from 270–280 colonists. According to Carlquist (1967),
Hawaiian colonists were dispersed by birds (73%), oceanic
drift (23%) and wind (4%). For the Galápagos flora (436
native species), Porter (1983) also suggested that a large
proportion (60%) of all flowering plants had been intro-
95 duced by birds, a lower fraction by wind (31%), and the
rest by ocean drift (9%).
Which dispersal agent was responsible for the presence
of a plant group in an archipelago is a matter of specu-
lation, because fruits and seeds may have arrived on an
island by unpredictable means (Higgins et al. 2003). Rather
than speculating on the colonization vector, a more test-
able exercise would be to evaluate the relative presence of
100 different plant dispersal syndromes occurring on islands,
105

0 regardless of how the first propagules actually arrived (Vargas 2007). Previous authors, however, claimed for a high number of seeds accidentally introduced by mud adherence (41 colonists) for the Galápagos Islands (Porter 1983), even if there is no solid evidence for such events. 5 Direct observations of the arrival of new diaspores are unlikely and inferences of means of dispersal used by early founders cannot be reliably tested. In contrast, the contribution of various dispersal syndromes of plants that have colonized remote archipelagos (like the Galápagos) can be estimated. 10

In order to correctly assess whether the four LDD syndromes have been favourable in the natural colonization of oceanic islands, it is necessary to control for some factors obscuring correct inferences. The most confounding factor is colonization by plants brought by humans and therefore not attributable to natural dispersal. The Galápagos have been continuously colonized since their formation (subaerial volcanic rocks of <6 Ma, Geist 1996). This period is considered long enough for the islands to receive natural introductions that may have differed into morphological varieties (endemic taxa). Thus, the endemic (and then native) status of these taxa is simply identified using morphological characters. For non-endemic taxa, natural *vs* human-mediated introductions are often difficult to tell apart (Tye 2006). Nevertheless, pollen records predating the first human arrival (1535) can help determine natural introductions (van Leeuwen et al. 2008). 15 20 25

The appropriate unit to test the success of LDD syndromes is the number of colonizations itself, which is unknown. Initial working units for the number of introductions are genera, assuming an independent origin for each. However, a single genus can be the result of more than one introduction, particularly large genera including infrageneric taxa. Therefore, multiple dispersal events from the same plant group (genus, subgenus, species, lineage) may greatly increase the number of successful dispersal events undetected by morphology. In addition to morphological inferences, phylogenetic and phylogeographic methods are essential tools at the species and population levels, inasmuch as they provide precise reconstructions of lineage relationships for Galápagos and continental plants (Andrus et al. 2009). In particular, phylogenetic methods aid in evaluating the number of colonization events (testing monophyletic groups), geographical sources of origin (inferring sister-group relationships) and shifts of ancestral syndromes related to LDD (reconstructing ancestral characters) (Vargas 2007). On the other hand, phylogeographic methods allow us to determine the unique genotypes of particular areas (endemic genotypes), which equally support the native origin of populations followed by genetic differentiation (Avice 2009). 30 35 40 45 50

The specific objectives addressed in this paper were to: 1) review the literature of floristic data, including those distinguishing between native and introduced floras; 2) perform a categorization of the LDD syndromes of native plant groups using results from previous studies complemented with our own *in situ* observations; 3) analyse the distribution of LDD syndromes across the native and endemic floras. The ultimate goal was to evaluate the frequency of different dispersal syndromes in the Galápagos native flora. 55 60

Materials and methods 61

Number of colonization events

A full list of native plant genera of angiosperms from the Galápagos Islands was taken from an annotated checklist of angiosperms by Lawesson et al. (1987). An additional floristic list (Porter 1983) was also analysed for comparison. Floristic data were systematically evaluated along the following complementary steps: 1) we used genera as operational starting units (Table 1); 2) only native taxa indicated in floristic studies were considered; 3) the initial list of the native species was amended according to recent palaeobotanical evidence (palaeobotanical correction) (Table 2); 4) more than one ancestor was adopted for genera containing multiple taxonomic groups (subgenera, sections, subsections); and 5) the inferred number of original colonists was corrected by phylogenetic evidence (phylogenetic correction), in which each independent, monophyletic group accounts for a single origin. Fossil records and phylogenetic reconstructions (including phylogeography) are two powerful tools to inform hypotheses of island colonization. We used published findings of fossil pollen and plant remains preserved in sedimentary deposits to adjust previous assumptions of nativeness of the Galápagos plants (van Leeuwen et al. 2008). We assume that every single Galápagos lineage originates from a mainland lineage. A minimal number of introductions can, however, be inferred from phylogenetic and phylogeographic topologies as long as a significant sample from the Galápagos and the mainland is provided: 1) a monophyletic group only involving island species of the same plant group indicates a single colonization; 2) two or more independent clades of the same genus (i.e. unrelated species) are interpreted as the arrival of two or more colonists from different mainland lineages; 3) two or more independent clades of the same species (i.e. unrelated individuals) are interpreted as the arrival of two or more colonists from different mainland lineages. Accordingly, the number of inferred colonizations was re-assessed by considering the most recent common ancestors between Galápagos and mainland groups, for which clade topologies were used to correct the number of colonists (Vargas 2007). 65 70 75 80 85 90 95 100

We followed previous approaches as much as possible in testing the number of native species and number of natural introductions (Porter 1983, Lawesson et al. 1987). Major difficulties have arisen in inferring natural vs human-mediated introductions in the Galápagos (see different figures in Wiggins and Porter 1971, Porter 1983, Lawesson et al. 1987, as discussed by Tye 2006). First, we used the native criteria implemented in the check-lists of Lawesson et al. (1987) and Porter (1983) (putatively native flora approach). Both datasets were partly amended according to the results of the studies reporting pollen records and fossil fragments in sediments (e.g. van Leeuwen et al. 2008) to ensure the native status of species in the analysis. In addition, we applied a complementary strategy, considering only genera containing at least one endemic taxon (species, subspecies, variety) to reduce the likelihood of including human-mediated introductions (endemic flora approach). This is a conservative approach as it might exclude recent 110 115 121

0 Table 1. List of the 251 native genera considered for the Galápagos Islands (Porter, 1983 and Lawesson et al. 1987), including information on the taxonomic family, origin (End, endemic; Int, introduced by humans; Nat, native; cultivated species and genera with only introduced species were excluded), fruit type, coding of dispersal syndromes (in brackets, syndromes unrelated to LDD), and dispersal vectors as assigned by Porter (1983). Bibliographic references in Supplementary material (Appendix 1). Codes for dispersal syndromes are: UNA–unassisted; ENZ–endozoochory; EPZ–epizoochory; HYD–hydrochory; ANE–anemochory; MYR–myrmecochory, AUT–autochory and VEG–vegetative. Syndromes observed by the authors in the wild are marked with an asterisk after these codes. 61

Genera (no. introductions)	Family	Origin	No. spp. (endemic spp. in Galápagos)	Fruit type	Dispersal syndromes	References	Dispersal vector (Porter 1983)	
10	<i>Abutilon</i> (1)	Malvaceae	End	1 (1)	Schizocarp	UNA	65	Drift
	<i>Acacia</i> (3)	Leguminosae	End/Int	4 (1)	Pod	UNA*, HYD, (AUT)	65, 29, 25, 18	Drift
	<i>Acalypha</i> (1)	Euphorbiaceae	End	4 (4)	Capsule	UNA, (AUT), (MYR)	65, 29, 63, 17	Interior
	<i>Acanthospermum</i> (1)	Compositae	Nat	1	Achene	EPZ	50, 65	–
15	<i>Acnistus</i> (1)	Solanaceae	End	1 (1)	Berry	ENZ*	65	Interior
	<i>Ageratum</i> (1)	Compositae	Nat	1	Achene	EPZ*	65	Interior
	<i>Alternanthera</i> (4)	Amaranthaceae	End	11 (6)	Utricle	UNA*	15	Mud
	<i>Amaranthus</i> (2)	Amaranthaceae	End	8 (3)	Utricle	UNA, ENZ, EPZ*	65, 63	Interior, Mud
	<i>Anredera</i> (1)	Basellaceae	Nat	1	Drupe	ENZ	65	Interior
	<i>Apium</i> (2)	Umbelliferae	Nat	2	Schizocarp	UNA, HYD	50, 65	–
20	<i>Aristida</i> (1)	Gramineae	End	4 (4)	Caryopside	EPZ*, ANE	65	Exterior
	<i>Astrephia</i> (1)	Valerianaceae	Nat	1	Achene	UNA	50	–
	<i>Atriplex</i> (1)	Chenopodiaceae	Nat	1	Utricle	ENZ, HYD	65	Mud
	<i>Avicennia</i> (1)	Avicenniaceae	Nat	1	Capsule	HYD*	65, 29, 9	–
	<i>Baccharis</i> (2)	Compositae	End	2 (1)	Achene	ANE*	65, 39, 14, 34	Wind
	<i>Bastardia</i> (1)	Malvaceae	Nat	1	Schizocarp	EPZ*, ANE	65, 39	Mud
25	<i>Batis</i> (1)	Batidaceae	Nat	1	Drupe-like	HYD	65	Drift
	<i>Bidens</i> (2)	Compositae	Nat/Int	3	Achene	EPZ*	65, 39, 63	Exterior
	<i>Blainvillea</i> (1)	Compositae	Nat	1	Achene	EPZ*	65	Exterior
	<i>Blechnum</i> (1)	Acanthaceae	Nat	1	Capsule	UNA	65	Exterior
	<i>Blutaparon</i> (1)	Amaranthaceae	Nat	1	Achene	UNA	15	–
	<i>Boerhaavia</i> (2)	Nyctaginaceae	Nat/Int	3	Achene	EPZ*, HYD	65, 39	Interior, Mud, Exterior
30	<i>Borreria</i> (1)	Rubiaceae	End	6 (5)	Capsule	UNA*	65	Interior
	<i>Bouteloua</i> (1)	Gramineae	Nat	1	Caryopside	EPZ	50, 65, 31	–
	<i>Bowlesia</i> (1)	Umbelliferae	Nat	1	Schizocarp	UNA, EPZ	13, 14	Exterior
	<i>Brachycereus</i> (1)	Cactaceae	End	1 (1)	Berry	ENZ*	65	Interior
	<i>Brickellia</i> (1)	Compositae	Nat	1	Achene	ANE	50	–
35	<i>Buddleja</i> (1)	Loganiaceae	Nat	1	Capsule	ANE	65, 39	–
	<i>Bulbostylis</i> (1)	Cyperaceae	Nat	1	Achene	UNA	65	Interior, Mud
	<i>Bursera</i> (1)	Burseraceae	End	2 (1)	Drupe	ENZ*	65	Interior
	<i>Caesalpinia</i> (1)	Leguminosae	Nat	1	Pod	HYD, (AUT)	65, 32, 58, 25, 61	Drift
40	<i>Cacabus</i> (1)	Solanaceae	Nat	1	Berry-like	ENZ*	65	–
	<i>Calandrina</i> (1)	Portulacaceae	End	1 (1)	Capsule	UNA	65, 8, 27	Interior
	<i>Calceolaria</i> (1)	Scrophulariaceae	Nat/Int	2	Capsule	UNA	65, 8	Mud
	<i>Callitriche</i> (1)	Callitrichaceae	Nat	1	Capsule	UNA	50, 65	–
	<i>Canavalia</i> (1)	Leguminosae	Nat	1	Pod	HYD	50, 65, 43	Drift
	<i>Canna</i> (1)	Cannaceae	Nat/Int	2	Capsule	UNA, HYD	50, 65, 41	Internal
45	<i>Capraria</i> (2)	Scrophulariaceae	Nat	2	Capsule	UNA, EPZ*	65, 39	Mud
	<i>Capsicum</i> (1)	Solanaceae	End/Int	1 (1)	Berry	ENZ*	65, 20, 29	Interior
	<i>Cardiospermum</i> (1)	Sapindaceae	End	2 (1)	Capsule	HYD, ANE	50, 65	Interior
	<i>Castela</i> (1)	Simaroubaceae	End	1 (1)	Drupe	ENZ*	65, 39	Interior
	<i>Castilleja</i> (1)	Scrophulariaceae	Nat	1	Capsule	UNA	65, 14	Wind
	<i>Cenchrus</i> (1)	Gramineae	End	2 (1)	Caryopside	EPZ	65	Exterior
50	<i>Centella</i> (1)	Umbelliferae	Nat	1	Schizocarp	UNA	13, 65	Interior, Mud
	<i>Ceratophyllum</i> (1)	Ceratophyllaceae	Nat	1	Achene	ENZ, HYD	65	Mud
	<i>Chamaesyce</i> (1)	Euphorbiaceae	End	11 (8)	Capsule	UNA, EPZ, (AUT), (MYR)	65, 39, 17	Interior
	<i>Chiococca</i> (1)	Rubiaceae	Nat	1	Drupe	ENZ*	65	Interior
55	<i>Chloris</i> (4)	Gramineae	Nat	4	Caryopside	EPZ, ANE*	50, 65, 16	–
	<i>Chrysanthellum</i> (1)	Compositae	End	2 (2)	Achene	UNA	65	Exterior
	<i>Cissampelos</i> (2)	Menispermaceae	End	2 (1)	Drupe	ENZ, EPZ*	65, 29, 39	Interior
	<i>Cissus</i> (1)	Vitaceae	Nat	1	Berry	ENZ	65, 20, 2, 29, 47, 25	Interior
	<i>Clerodendron</i> (1)	Verbenaceae	End	1	Drupaceous	ENZ, HYD	65	Interior

(Continued)

	Genera (no. introductions)	Family	Origin	No. spp. (endemic spp. in Galápagos)	Fruit type	Dispersal syndromes	References	Dispersal vector (Porter 1983)	
5	<i>Commelina</i> (1)	Commelinaceae	Nat	1	Capsule	UNA	65, 34	Interior	65
	<i>Commicarpus</i> (1)	Nyctaginaceae	Nat	1	Achene	EPZ*, HYD	65, 39	Exterior	
	<i>Conocarpus</i> (1)	Combretaceae	Nat	1	Drupe-like	HYD*	39	–	
	<i>Convolvulus</i> (1)	Convolvulaceae	Nat	1	Capsule	HYD	65	Drift	70
	<i>Conyza</i> (1)	Compositae	Nat/Int	2	Achene	ANE*	63, 66	–	
	<i>Corchorus</i> (1)	Tiliaceae	Nat	1	Capsule	UNA	65	Mud	
10	<i>Cordia</i> (3)	Boraginaceae	End/Int	6 (4)	Drupe	UNA, ENZ*, EPZ, HYD, ANE	65, 20, 29, 25	internal	75
	<i>Coronopus</i> (1)	Cruciferae	Nat	1	Capsule	UNA	60	–	
	<i>Cranichis</i> (3)	Orchidaceae	End	2 (1)	Capsule	ANE	50, 65	Wind	
	<i>Crassula</i> (1)	Crassulaceae	Nat	1	Capsule	UNA	5	–	80
	<i>Cressa</i> (1)	Convolvulaceae	Nat	1	Capsule	UNA	3	–	
15	<i>Crotalaria</i> (2)	Leguminosae	Nat/Int	3	Pod	UNA*	65	Interior	
	<i>Croton</i> (1)	Euphorbiaceae	End	1 (1)	Capsule	UNA, ENZ*, (AUT), (MYR)	65, 29, 25, 17, 59, 34, 35	Interior	85
	<i>Cryptocarpus</i> (1)	Nyctaginaceae	Nat	1	Achene	HYD	65	Mud	
20	<i>Cuphea</i> (1)	Lythraceae	Nat	3	Capsule	HYD	65	–	
	<i>Cuscuta</i> (2)	Convolvulaceae	End	2 (2)	Capsule	UNA	65	Interior	90
	<i>Cyperus</i> (14)	Cyperaceae	End	14 (3)	Achene	UNA*, HYD	65, 63	Interior, Mud	
	<i>Dalea</i> (1)	Leguminosae	End	1 (1)	Pod	UNA	65	Interior	
	<i>Darwiniothamus</i> (2)	Compositae	End	3 (3)	Achene	EPZ*, ANE	65, 39	Wind	95
	<i>Desmanthus</i> (1)	Leguminosae	Nat	1	Pod	UNA*	65	Interior	
25	<i>Desmodium</i> (4)	Leguminosae	Nat	4	Pod	EPZ	65	Exterior	
	<i>Dichondra</i> (1)	Convolvulaceae	Nat	1	Capsule	UNA	65	Interior	100
	<i>Dicliptera</i> (1)	Acanthaceae	Nat	1	Capsule	UNA	65	Exterior	
	<i>Digitaria</i> (2)	Gramineae	Nat/Int	3	Caryopsid	UNA, EPZ*, ANE, (AUT)	50, 65, 45	–	
30	<i>Diodia</i> (1)	Rubiaceae	Nat	1	Capsule	HYD, (VEG), (MYR)	65, 35	–	105
	<i>Distichlis</i> (1)	Gramineae	Nat	1	Caryopsid	UNA, (VEG)	6, 40	–	
	<i>Dodonaea</i> (2)	Sapindaceae	End	1 (1)	Capsule	HYD, ANE	50, 65, 29	Interior	
	<i>Drymaria</i> (3)	Caryophyllaceae	End	3 (1)	Capsule	UNA, EPZ	65, 63	Interior	110
	<i>Duranta</i> (3)	Verbenaceae	Nat	3	Drupe-like	ENZ*	65	Interior	
35	<i>Eclipta</i> (1)	Compositae	Nat	1	Achene	EPZ	65	Interior, Mud	
	<i>Elaterium</i> (1)	Cucurbitaceae	Nat	1	Capsule	UNA	65	Drift	115
	<i>Eleocharis</i> (6)	Cyperaceae	Nat	6	Achene	UNA, HYD	65	Interior, Mud	
	<i>Elvira</i> (1)	Compositae	End/Int	3 (2)	Achene	ANE	65	–	
	<i>Encelia</i> (1)	Compositae	End	1 (1)	Achene	EPZ	65, 39	Wind	120
	<i>Enydra</i> (1)	Compositae	Nat	1	Achene	UNA	65	Interior, Mud	
40	<i>Epidendrum</i> (1)	Orchidaceae	End	1 (1)	Capsule	ANE*	50, 65, 39	Wind	
	<i>Eragrostis</i> (4)	Gramineae	Nat	5	Caryopsid	UNA, HYD, ANE*, (AUT)	65, 63	Interior	125
	<i>Eriochloa</i> (1)	Gramineae	Nat	1	Caryopsid	EPZ*	65	Interior	
	<i>Erythrina</i> (1)	Leguminosae	Nat	1	Pod	ENZ, HYD, ANE	50, 65, 29, 25, 33	Interior	
45	<i>Erythrodes</i> (1)	Orchidaceae	End	1 (1)	Capsule	ANE	50, 65	Wind	130
	<i>Eupatorium</i> (1)	Compositae	Nat/Int	2	Achene	ANE	50, 18	–	
	<i>Euphorbia</i> (1)	Euphorbiaceae	End	1 (1)	Capsule	UNA, (AUT), (MYR)	65, 8, 63, 17	Interior	
	<i>Evolvulus</i> (2)	Convolvulaceae	Nat	2	Capsule	UNA*	65	Interior	135
	<i>Fimbristylis</i> (2)	Cyperaceae	Nat	2	Achene	UNA, HYD, ANE	65, 34	Interior, Mud	
50	<i>Fleurya</i> (1)	Urticaceae	Nat	1	Achene	EPZ	65	Interior	
	<i>Froelichia</i> (1)	Amaranthaceae	End	2 (2)	Utricle	ANE	65	Wind	140
	<i>Galium</i> (2)	Rubiaceae	End	2 (1)	Schizocarp	EPZ*	65, 8, 30	Interior	
	<i>Galvezia</i> (1)	Scrophulariaceae	End	1 (1)	Capsule	UNA*	65	Mud	
	<i>Galactia</i> (2)	Leguminosae	Nat	2	Pod	UNA	50, 37	Interior	145
	<i>Geoffroea</i> (1)	Leguminosae	Nat	1	Pod	UNA, HYD	50, 51, 7	–	
55	<i>Gnaphalium</i> (2)	Compositae	Nat	2	Achene	ANE	50, 65, 63, 14, 12	–	
	<i>Gossypium</i> (2)	Malvaceae	End	2 (1)	Capsule	HYD, ANE	49, 65	Drift	150
	<i>Govenia</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	
	<i>Grabowskia</i> (1)	Solanaceae	Nat	1	nutlet	ENZ*	65	Interior	

(Continued)

	Genera (no. introductions)	Family	Origin	No. spp. (endemic spp. in Galápagos)	Fruit type	Dispersal syndromes	References	Dispersal vector (Porter 1983)	
5	<i>Habenaria</i> (3)	Orchidaceae	Nat	3	Capsule	ANE*	50, 65, 39	Wind	65
	<i>Heliotropium</i> (4)	Boraginaceae	End	5 (1)	Nutlet	UNA, HYD	65	Interior, Mud	
	<i>Hemicarpha</i> (1)	Cyperaceae	Nat	1	Achene	HYD	50, 38, 23, 65	–	
	<i>Herissantia</i> (1)	Malvaceae	Nat	1	Schizocarp	UNA	65	Interior	
	<i>Hibiscus</i> (1)	Malvaceae	Nat/Int	3	Capsule	UNA*	65	Drift	
	<i>Hippomane</i> (1)	Euphorbiaceae	Nat	1	Drupe-like	ENZ*, HYD*	65, 17	Drift	70
10	<i>Hydrocotyle</i> (1)	Umbelliferae	End	1	Schizocarp	UNA	13, 65	Interior, Mud	
	<i>Hypericum</i> (1)	Haloragaceae	Nat	1	Capsule	UNA*	65	Interior, Mud	
	<i>Hypoxis</i> (1)	Hypoxidaceae	Nat	1	Capsule	UNA	65	Interior	
	<i>Hyptis</i> (2)	Labiatae	End/Int	5 (1)	Nutlet	UNA, EPZ	65, 34	Exterior	
	<i>Ichnanthus</i> (1)	Gramineae	Nat	1	Caryopside	UNA	65	–	
	<i>Ionopsis</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	75
15	<i>Ipomoea</i> (6)	Convolvulaceae	End/Int	9 (3)	Capsule	HYD, ANE	65, 25	–	
	<i>Jaegeria</i> (1)	Compositae	End	1 (1)	Achene	UNA	65	Mud	
	<i>Jaltomata</i> (1)	Solanaceae	End	1 (1)	Berry-like	ENZ	1	–	
	<i>Jasminocereus</i> (1)	Cactaceae	End	1 (1)	Berry	ENZ*	65	Interior	
	<i>Juncus</i> (1)	Juncaceae	Nat	1	Capsule	HYD	52	–	
20	<i>Justicia</i> (1)	Acanthaceae	End	3 (1)	Capsule	UNA	65	Exterior	80
	<i>Kallstroemia</i> (1)	Zygophyllaceae	End	1 (1)	Mericalp	ENZ, HYD	65, 54	Interior, Exterior	
	<i>Koanophyllon</i> (1)	Compositae	Nat	1	Achene	ANE	28	Wind	
	<i>Laguncularia</i> (1)	Combretaceae	Nat	1	Drupe-like	HYD*	65	Drift	
	<i>Lantana</i> (1)	Verbenaceae	End/Int	2 (1)	Drupaceous	ENZ*	65, 25, 34	Interior	85
25	<i>Lecocarpus</i> (1)	Compositae	End	3 (3)	Achene	EPZ, ANE	65, 39	Exterior	
	<i>Lemna</i> (1)	Lemnaceae	Nat	1	Utricle	UNA	65	Exterior, Mud	
	<i>Lepidium</i> (1)	Cruciferae	Nat	1	Silicua	UNA, ENZ, EPZ	65, 63, 42, 14	–	
	<i>Leptochloa</i> (2)	Gramineae	Nat	2	Caryopside	ENZ	65, 14	–	
	<i>Lindernia</i> (1)	Scrophulariaceae	Nat	1	Capsule	UNA	65	Mud	
	<i>Linum</i> (1)	Linaceae	End	2 (2)	Capsule	UNA	65, 57	Exterior	90
30	<i>Liparis</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	
	<i>Lippia</i> (2)	Verbenaceae	End	4 (2)	Drupaceous	UNA	65	Interior, Mud	
	<i>Lithophila</i> (1)	Amaranthaceae	End	2 (2)	Utricle	UNA	65	Wind	
	<i>Lobelia</i> (1)	Lobeliaceae	Nat	1	Capsule	UNA, ENZ	50, 65	Mud	
	<i>Ludwigia</i> (3)	Onagraceae	Nat	3	Capsule	HYD	65, 44	Interior, Mud	
	<i>Luffa</i> (1)	Cucurbitaceae	Nat	1	Capsule	HYD	65	Drift	95
35	<i>Lycium</i> (1)	Solanaceae	End	1 (1)	Berry	ENZ	65	Interior	
	<i>Lycopersicum</i> (1)	Solanaceae	End	1 (1)	Berry	ENZ*	65, 39	Interior	
	<i>Macraea</i> (1)	Compositae	End	1 (1)	Achene	ANE	65, 39	Exterior	
	<i>Maytenus</i> (1)	Celastraceae	Nat	1	Capsule	ENZ*	65, 20, 2, 29	Interior	
	<i>Mecardonia</i> (1)	Scrophulariaceae	Nat	1	Capsule	UNA	65	Mud	100
40	<i>Mentzelia</i> (1)	Loasaceae	Nat	1	Capsule	UNA, EPZ*,	65, 39	Exterior	
	<i>Merremia</i> (1)	Convolvulaceae	Nat/Int	2	Capsule	HYD	65	Drift	
	<i>Miconia</i> (1)	Melastomataceae	End	1 (1)	Berry	ENZ*	65, 20, 59, 34, 48	Interior	
	<i>Mollugo</i> (2)	Molluginaceae	End	5 (4)	Capsule	UNA	65	Interior, Mud	
45	<i>Muhlenbergia</i> (1)	Gramineae	Nat	1	Caryopside	UNA, EPZ	65, 63	Exterior	105
	<i>Najas</i> (2)	Najadaceae	Nat	2	Nutlet	UNA	65, 46	Interior, Exterior	
	<i>Nama</i> (1)	Hydrophyllaceae	Nat	1	Capsule	UNA	65, 63, 14	Interior	
	<i>Neptunia</i> (1)	Leguminosae	Nat	1	Pod	UNA	65	Interior	
	<i>Nicandra</i> (1)	Solanaceae	Nat	1	Berry	ENZ	65	–	
	<i>Nicotiana</i> (1)	Solanaceae	Nat/Int	2	Capsule	UNA	65, 14,	–	110
50	<i>Nolana</i> (1)	Nolanaceae	End	1 (1)	mericalp	HYD	65	Drift	
	<i>Ombrophytum</i> (1)	Balanophoraceae	Nat	1	Achene	UNA, HYD, (MYR)	26	Interior	
	<i>Oplismenus</i> (1)	Gramineae	Nat	1	Caryopside	UNA	36	–	
	<i>Opuntia</i> (2)	Cactaceae	End	6 (6)	Berry	ENZ*	65, 25	Interior	
55	<i>Oxalis</i> (2)	Oxalidaceae	Nat/Int	4	Capsule	UNA, ANE	63, 25	Exterior	115
	<i>Panicum</i> (7)	Gramineae	End	7	Caryopside	UNA, ENZ, ANE	65, 14, 34	Mud, Interior	
	<i>Parietaria</i> (1)	Urticaceae	Nat	1	Achene	UNA, EPZ	65	Interior	
	<i>Parkinsonia</i> (1)	Leguminosae	Nat	1	Pod	HYD	65, 11, 19	Drift	
	<i>Paspalum</i> (3)	Gramineae	End/Int	9 (2)	Caryopside	UNA, EPZ*, ANE	35	Mud, Interior	
	<i>Passiflora</i> (3)	Passifloraceae	End	3 (1)	Berry	ENZ*	65, 20, 29	Interior	

	Genera (no. introductions)	Family	Origin	No. spp. (endemic spp. in Galápagos)	Fruit type	Dispersal syndromes	References	Dispersal vector (Porter 1983)	
5	<i>Pectis</i> (2)	Compositae	End	3 (2)	Achene	ANE*	65, 39	Exterior	65
	<i>Pennisetum</i> (1)	Gramineae	End/Int	1 (1)	Caryopsid	UNA, ANE*	65	Exterior	
	<i>Peperomia</i> (3)	Piperaceae	End	6 (4)	Drupe-like	EPZ	65, 2	Exterior	
	<i>Pernettya</i> (1)	Ericaceae	End	1 (1)	Berry	ENZ	65	Interior	
	<i>Phaseolus</i> (3)	Leguminosae	End	4 (1)	Pod	UNA	65	Interior	
	<i>Philoxerus</i> (1)	Amaranthaceae	End	1 (1)	Achene	UNA, HYD	65	Wind	70
10	<i>Phoradendron</i> (1)	Viscaceae	End	1 (1)	Drupe	ENZ*	65, 39, 14	Interior	
	<i>Phyla</i> (1)	Verbenaceae	Nat/Int	2	Dry	UNA	65	–	
	<i>Phyllanthus</i> (1)	Euphorbiaceae	Nat	1	Capsule	UNA, (AUT)	65, 29, 17	Interior	
	<i>Physalis</i> (3)	Solanaceae	End	4 (1)	Berry	ENZ*, HYD	65, 1	Interior	
	<i>Phytolacca</i> (1)	Phytolaccaceae	Nat	1	Berry-like	ENZ*	65	Interior	
15	<i>Pilea</i> (2)	Urticaceae	End	3 (1)	Achene	UNA	65	Interior, Mud	75
	<i>Piscidia</i> (1)	Leguminosae	Nat	1	Pod	ANE*	65, 39	Wind	
	<i>Pisonia</i> (1)	Nyctaginaceae	End	1 (1)	Achene	EPZ	65, 29, 39	Exterior	
	<i>Plantago</i> (1)	Plantaginaceae	End/Int	2 (1)	Capsule	UNA, EPZ	65, 8, 39	–	
	<i>Pleuropetalum</i> (1)	Amaranthaceae	End	1 (1)	Capsule	ENZ	65	Interior	
	<i>Plumbago</i> (2)	Plumbaginaceae	Nat	2	Capsule	EPZ	65	Exterior	80
20	<i>Polygala</i> (1)	Polygalaceae	End	2 (2)	Capsule	UNA	65, 8, 34	Interior	
	<i>Polygonum</i> (4)	Polygonaceae	End	4 (1)	Achene	UNA, ENZ, EPZ, HYD, ANE	65, 8	Interior, Mud	
	<i>Ponthieva</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	
	<i>Portulaca</i> (3)	Portulacaceae	End/Int	3 (1)	Capsule	UNA, HYD	65	Interior	
	<i>Potamogeton</i> (1)	Potamogetonaceae	Nat	1	Drupe-like	ENZ	65, 10	Interior, Exterior	85
25	<i>Prescottia</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	
	<i>Prosopis</i> (1)	Leguminosae	Nat	1	Pod	ENZ, HYD	65, 14	Drift	
	<i>Psidium</i> (1)	Myrtaceae	End/Int	2 (1)	Berry	ENZ*	65	Interior	
	<i>Psychotria</i> (1)	Rubiaceae	End	2 (2)	Berry-like	ENZ*	65, 20, 29, 17, 59, 34, 18	Interior	90
30	<i>Ranunculus</i> (1)	Ranunculaceae	Nat	1	Achene	UNA*	53	–	
	<i>Rhizophora</i> (1)	Rhizophoraceae	Nat	1	Berry	HYD*	65, 29	Drift	
	<i>Rhynchosia</i> (1)	Leguminosae	Nat	1	Pod	UNA	65	Interior	
	<i>Rhynchospora</i> (5)	Cyperaceae	Nat/Int	6	Achene	HYD	65	–	
	<i>Rivinia</i> (1)	Phytolaccaceae	Nat	1	Berry	ENZ	65	–	
	<i>Rorippa</i> (1)	Cruciferae	Nat	1	Capsule	UNA	–	–	95
35	<i>Ruellia</i> (1)	Acanthaceae	Nat	1	Capsule	UNA	65	Exterior	
	<i>Ruppia</i> (1)	Ruppiales	Nat	1	Nutlet	UNA	50, 65	Interior, Exterior	
	<i>Salicornia</i> (1)	Chenopodiaceae	Nat	1	Utricle	HYD	65	Drift	
	<i>Salvia</i> (2)	Labiatae	End	4 (3)	Nucule	UNA, EPZ	65, 63, 14, 34	Exterior	100
40	<i>Sapindus</i> (1)	Sapindaceae	Nat	1	Schizocarp	ENZ*, HYD	50, 65, 20, 29, 39	Interior	
	<i>Sarcostemma</i> (1)	Asclepiadaceae	End	1 (1)	Follicle	ANE	65, 39	Wind	
	<i>Scaevola</i> (1)	Goodeniaceae	Nat	1	Drupe	ENZ*, HYD	65, 39	Drift	
	<i>Scalesia</i> (1)	Compositae	End	15 (15)	Achene	UNA, EPZ	65	Exterior	
	<i>Scleria</i> (2)	Cyperaceae	Nat	2	Achene	UNA, ENZ	50, 65	Internal	105
45	<i>Sclerothrix</i> (1)	Loasaceae	Nat	1	Capsule	UNA	65	Exterior	
	<i>Scoparia</i> (1)	Scrophulariaceae	Nat	1	Capsule	UNA	65	Mud	
	<i>Scutia</i> (1)	Rhamnaceae	Nat	1	Nutlet	ENZ*	50, 65, 39	Interior	
	<i>Senna</i> (3)	Leguminosae	Nat/Int	6	Pod	UNA*, HYD, (AUT)	65, 32	Interior	
50	<i>Sesuvium</i> (2)	Aizoaceae	End	2 (1)	Capsule	UNA	65	Drift	110
	<i>Setaria</i> (2)	Gramineae	End/Nat	3	Caryopsid	UNA	50, 22	Interior/ Exterior	
	<i>Sicyocaulis</i> (1)	Cucurbitaceae	End	1 (1)	Capsule	UNA	65	Exterior	
	<i>Sicyos</i> (1)	Cucurbitaceae	End	1 (1)	Capsule	EPZ	65	Exterior	
	<i>Sida</i> (5)	Malvaceae	Nat/Int	10	Schizocarp	ENZ, EPZ	65, 34	Exterior	
	<i>Sisyrinchium</i> (1)	Iridaceae	End	1	Capsule	UNA	65	Interior	115
55	<i>Solanum</i> (2)	Solanaceae	End	2	Berry	ENZ*	65, 20, 29, 39, 1, 34	Interior	
	<i>Soliva</i> (1)	Compositae	Nat	1	Achene	EPZ	50	–	
	<i>Spermacoce</i> (1)	Rubiaceae	Nat	1	Capsule	UNA	65	–	
	<i>Spilanthes</i> (1)	Compositae	End/Int	2 (1)	Achene	EPZ	65	Exterior	

(Continued)

	Genera (no. introductions)	Family	Origin	No. spp. (endemic spp. in Galápagos)	Fruit type	Dispersal syndromes	References	Dispersal vector (Porter 1983)	
5	<i>Sporolobus</i> (3)	Gramineae	Nat	3	Caryopside	UNA, HYD	50, 65	Interior, Exterior, Drift	65
	<i>Stemodia</i> (1)	Scrophulariaceae	Nat	1	Capsule	UNA	65	–	
	<i>Stenotaphrum</i> (1)	Gramineae	Nat	1	Caryopside	HYD	50, 65	Mud, Interior	
	<i>Stictiocardia</i> (1)	Convolvulaceae	Nat	1	Capsule	HYD	65, 4	Drift	
	<i>Stylosanthes</i> (1)	Leguminosae	Nat	1	Pod	UNA	65	Drift	70
10	<i>Talinum</i> (1)	Portulacaceae	Nat	1	Capsule	UNA, (AUT)	65	–	
	<i>Tephrosia</i> (1)	Leguminosae	Nat	1	Pod	UNA*	50, 65	Interior	
	<i>Tetramerium</i> (1)	Acanthaceae	Nat	1	Capsule	UNA	65	Exterior	
	<i>Teucrium</i> (1)	Labiatae	Nat	1	Nutlet	EPZ	65, 39	Exterior	
	<i>Tillandsia</i> (1)	Bromeliaceae	End	1 (1)	Capsule	UNA, ANE	65, 35	Wind	
	<i>Tiquilia</i> (2)	Boraginaceae	End	4 (4)	Drupaceous	ENZ, HYD	65	Interior	75
15	<i>Tournefortia</i> (2)	Boraginaceae	End	3 (2)	Drupe	ENZ*, HYD	65, 29	Interior	
	<i>Trema</i> (1)	Ulmaceae	Nat	1	Drupe	ENZ*	62, 24	–	
	<i>Trianthema</i> (1)	Aizoaceae	Nat	1	Capsule	UNA	65	Drift	
	<i>Trichoneura</i> (1)	Gramineae	End	1 (1)	Caryopside	UNA	65	Exterior	
	<i>Trisetum</i> (1)	Gramineae	End	1 (1)	Caryopside	EPZ	65	Exterior	80
20	<i>Tropidia</i> (1)	Orchidaceae	Nat	1	Capsule	ANE	50, 65	Wind	
	<i>Tribulus</i> (2)	Zygophyllaceae	Nat	2	Schizocarp	EPZ*	50, 65	–	
	<i>Triumfetta</i> (1)	Tiliaceae	Nat	1	Capsule	EPZ*	50, 65	–	
	<i>Turnera</i> (1)	Turneraceae	Nat	1	Capsule	UNA	65	–	
	<i>Uniola</i> (1)	Gramineae	Nat	1	Panicle	HYD	65, 21	Drift	
	<i>Urera</i> (1)	Urticaceae	Nat	1	Achene	UNA, ENZ	50, 64	–	85
25	<i>Urocarpidium</i> (1)	Malvaceae	End	1 (1)	Schizocarp	EPZ	65	Interior	
	<i>Utricularia</i> (1)	Lentibulariaceae	Nat	1	Capsule	UNA	65	Mud	
	<i>Vallesia</i> (1)	Apocynaceae	End	1 (1)	Drupe	ENZ*	65	Interior	
	<i>Verbena</i> (2)	Verbenaceae	End/Int	4 (3)	Schizocarp	EPZ	65	Interior, Mud	
	<i>Vigna</i> (1)	Leguminosae	Nat	3	Pod	UNA, HYD	50, 65	Interior	
	<i>Waltheria</i> (1)	Sterculiaceae	Nat	1	Capsule	UNA, ENZ	50, 65	Interior	90
30	<i>Zanthoxylum</i> (1)	Rutaceae	Nat	1	follicle	ENZ*	65, 29, 55, 56	Interior	
	<i>Zinnia</i> (1)	Compositae	Nat	1	Achene	EPZ	50	–	
	<i>Zornia</i> (1)	Leguminosae	Nat/Int	2	Pod	EPZ	50, 65	–	

[AQ1] Synonyms: for *Achyranthes* see *Alternanthera*; for *Brugmansia* see *Datura*; for *Delilia* see *Elvira*; for *Cassia* see *Senna*; for *Exedeconus* see *Cacabus*; *Varronia* is included in *Cordia*.

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natural introductions from the analysis (those with no morphological differentiation into taxa), but ensures only including introductions that occurred before humans colonized the islands. The datasets of native and endemic floras were accordingly analysed using a contingency analysis (likelihood ratio test). All data were analysed with the SPSS (v. 15.0) software.

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45 Dispersal syndromes

Long-distance dispersal is herein understood in a biogeographical sense, i.e. transoceanic dispersal between the Galápagos Islands and the American continent (ca 1000 km) (Wiggins and Porter 1971). Diaspore morphologies (infrutescences, fruits, seeds and vegetative tissues) were initially classified into seven major syndromes (van der Pijl 1982). Of these, we only considered syndromes associated with LDD by: wind (anemochory), sea water (hydrochory), animal ingestion (endozoochory) and animal adhesion (epizoochory) (Ridley 1930). All other syndromes unrelated to LDD were coded as unassisted, including dispersal syndromes associated to short distances (in a biogeographic context), such as ant dispersal (myrmecochory) or self-dispersing mechanisms (autochory). We initially used information on

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diaspore morphologies from Wiggins and Porter (1971) and dispersal syndromes listed by Porter (1983). This was supplemented by inferring LDD characteristics of Galápagos plants and related mainland genera using results found in three scientific web search engines <www.info.scopus.com> <www.scholar.google.com> and <www.isiknowledge.com/WOS> (Supplementary material Appendix 1). Searches for characteristics of native Galápagos species were done first. In the case of unavailable information of such species, data on morphological attributes of their morphologically closest relatives were collected. In addition, observations of plants in the herbarium of the Charles Darwin Station (CDS) and in the field allowed us to confirm and refine previous estimates (Tye and Francisco-Ortega 2011; Table 2).

As a result, our new perspective includes features essential for analysing the contribution of particular dispersal syndromes in colonization, which were not considered in previous analyses: phylogenetic and palaeobotanical corrections, a multiple-syndrome based analysis (Table 2), and the negligible role of mud adherence and natural rafts as dispersal syndromes – even though they might have played an important role in actual plant dispersal. This is because Porter's (1983) approach was intended to infer probable means of dispersal, whereas our study estimates occurrence of plants bearing a particular syndrome for LDD.

0 Table 2. Results of the phylogenetic correction analysis. This is a first attempt to infer number of introductions and dispersal syndromes of Galápagos colonists based on phylogenies of a reliable sample size. Genera with asterisks indicate a significant contribution of the phylogenetic analyses. 61

5	Genus (species number)	No. Galápagos taxa (studied taxa from Galápagos)	No. inferred dispersals/ no. previous estimates (Porter 1983)	Inferred ancestor diaspore syndrome	Reference	65
	<i>Acalypha</i> (ca 500 spp.)	4 (4)	1/1	unassisted (myrmecochory, autochory)	Seberg (1984)	
	<i>Cordia</i> * (incl. <i>Varronia</i>) (ca 350 spp.)	6(6)	3/2	unassisted, endozoochory, epizoochory, hydrochory, anemochory	Weeks et al. (2010)	70
10	<i>Cuscuta</i> (145 spp.)*	2(2)	2/?	unassisted	Stefanovic (2007)	
	<i>Darwinothamnus</i> * (3 spp.)	3(3)	2/1	epizoochory	Andrus et al. (2009)	
	<i>Encelia</i> (15 spp.)	1(1)	1/1	epizoochory	Fehlberg and Ranker (2007)	
	<i>Euphorbia</i> (ca 2000 spp.)	1(1)	1/1	unassisted	Steinmann and Porter (2002)	75
15	<i>Galvezia</i> (4 spp.)	3(3)	1/1	unassisted	Vargas et al. (unpubl.)	
	<i>Gossypium</i> (39 spp.)*	2(2)	2/2	anemochory, hydrochory	Wendel et al. (2009)	
	<i>Lecocarpus</i> (3 spp.)	3(1)	?/1	epizoochory, anemochory	Rauscher (2002)	
	<i>Lycopersicon</i> (7 spp.)	2(2)	1/1	endozoochory	Peralta and Spooner (2001)	80
20	<i>Macraea</i> (1 spp.)	1(1)	1/1	anemochory	Panero et al. (1999)	
	<i>Nolana</i> (18 spp.)	1(1)	?/1	hydrochory	Tu et al. (2008)	
	<i>Phaseolus</i> (1 spp.)	3(1)	?/3	unassisted	Delgado-Salinas et al. (2006)	
	<i>Polygala</i> (ca 500 spp.)	5(2)	1/1	anemochory (myrmecochory)	Forest et al. (2007)	
	<i>Tiquilia</i> (27 spp.)	4(3)	1/1	unassisted	Moore et al. (2006)	85
25	Total		at least 20 dispersal events from 15 tested groups			

30 We initially assumed that each plant group is the result of a single colonization event. Accordingly, colonization of a plant group with a single LDD syndrome was assigned the value 1. Nevertheless, some plants had multiple dispersal syndromes that summed up to a total of 1. For example, in a plant group for which two LDD syndromes were identified, the assigned value of each one was 0.5 to reflect a probability of 50% of being responsible for the original colonization. The total probability of each LDD syndrome (the variable used in the analyses) was obtained by multiplying the proportion of each syndrome for each plant group by the number of inferred introductions containing that particular syndrome (Table 1). The proportion of introductions unrelated to any of the four LDD syndromes was also included in the analysis as one more category (unassisted). Contingency analyses (likelihood ratio tests) were used to evaluate the frequencies of assigned LDD syndromes and unassisted diaspores in plant colonization. 90

50 Results

The 509 native species and 251 genera forming the flora of the Galápagos Islands (Lawesson et al. 1987) were considered to be the result of 372 natural introductions (Table 2). These figures are higher than those of previous estimates: 431 angiosperm species resulting from 291 natural introductions in Porter (1976) and 436 species from 306 introductions in Porter (1983). Palaeobotanic and phylogenetic corrections contributed to clarify the status of early colonists as follows. Six genera (*Ageratum*, *Diodia*, *Brickellia*, *Cuphea*, *Hibiscus* and *Ranunculus*) previously considered as introduced by humans (Wiggins and Porter 1971, Lawesson et al. 1987, Tye 2006) were, however, herein considered as containing native species after van Leeuwen et al. (2008). Phylogenetic and phylogeographic reconstructions of 15 genera were used to establish a minimum number of 20 introductions, whereas previous estimates based on morphology rendered a lower number (17) (Porter 1983). Of the 372 natural introductions, 207 (55.6%) correspond to plant groups displaying a single LDD syndrome, 74 (19.9%) to plant groups with multiple syndromes, and 91 (24.5%) showed no evidence of any LDD syndromes. This last group was categorized as unassisted diaspores (UNA) (Table 2), and consists primarily of reproductive structures unrelated to the four LDD syndromes. They are included in 54 botanical families and defined as pods, schizocarps, some types of achenes, and dehiscent capsules with no special LDD traits. In addition, the phylogenetic reconstructions indicate sharing of diaspora structures by early colonists and mainland relatives (Table 1). 95

We obtained the following different proportions of dispersal categories in the native Galápagos flora (Lawesson et al. 1987): endozoochory 16.4%, epizoochory 15.7%, hydrochory 18.6%, anemochory 13.3% and unassisted 36.0%. When we considered exclusively genera with at least one endemic species, the proportions changed only slightly: endozoochory 20.2%, epizoochory 14.9%, hydrochory 14.5%, anemochory 15.3% and unassisted 35.1% (Fig. 1A). In both datasets the frequency of the four LDD syndromes was not statistically different (genera containing native species $G = 0.9$, $DF = 3$, $p = 0.830$; genera containing 110

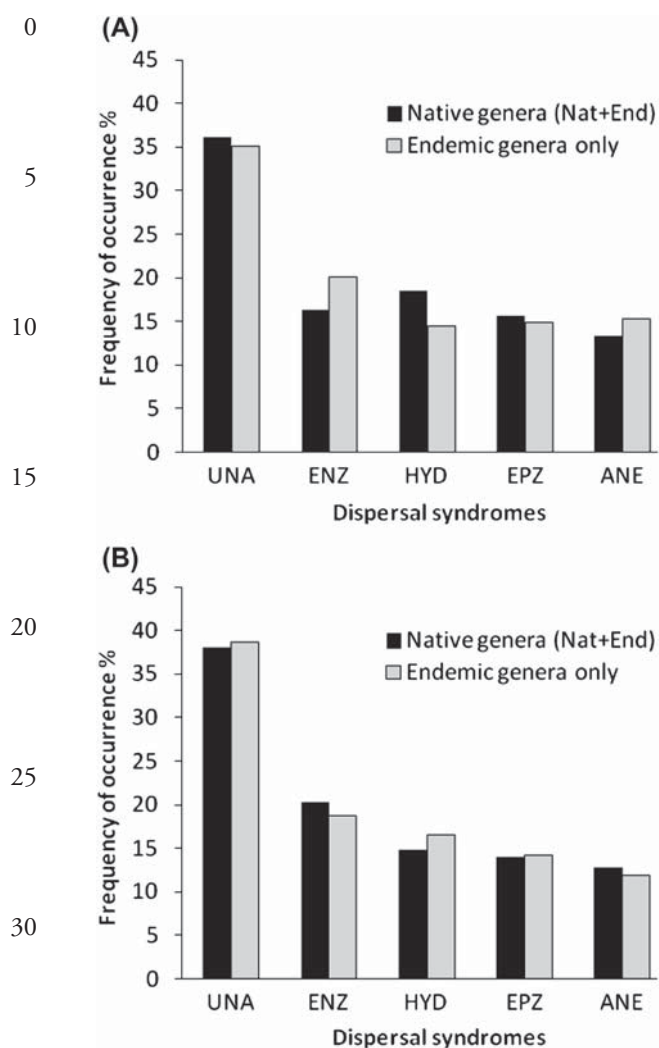


Figure 1. Frequency of occurrence (%) of the five LDD categories: EPZ epizoochory, ANE-anemochory, HYD-hydrochory, ENZ-endozoochory and UNA-unassisted. Proportions based primarily on floristic data from (A) Lawesson et al. (1987) and (B) Wiggins and Porter (1971).

endemic infraspecific taxa $G = 1.2$, $DF = 3$, $p = 0.751$). When including the frequency of unassisted diaspores in the analysis, this was significantly higher than that of the four syndromes associated with LDD (genera containing native species $G = 14.8$, $DF = 4$, $p = 0.005$; genera containing endemic infraspecific taxa $G = 13.6$, $DF = 4$, $p = 0.009$). Comparable proportions were obtained when considering number of natural introductions from the floristic account of Porter (1983) in our analysis: endozoochory 20.3%, epizoochory 14.0%, hydrochory 14.8%, anemochory 12.8% and unassisted 38.1%. When we considered exclusively the endemic genera, the proportions were comparable: endozoochory 18.7%, epizoochory 14.2%, hydrochory 16.5% and anemochory 11.9% and unassisted 38.7% (Fig. 1B). No significant differences were found between the two data sets (endemic vs. native species) in each of the five syndrome categories ($G = 0.46$; $DF = 4$; $p = 0.977$). In agreement with these results, we found no significant differences between the datasets taken from the taxonomic treatments of Porter (1983) and Lawesson et al. (1987) for the native

flora ($G = 2.0$, $DF = 4$, $p = 0.731$) and exclusively for the endemic flora ($G = 1.7$, $DF = 4$, $p = 0.804$). This means that the higher number of native species (68 spp.) interpreted from the annotated checklist of Lawesson et al. (1987), followed in the present study, does not affect the general result of a high proportion of unassisted diaspores. In summary, neither differences between the two floristic accounts used for raw data nor the analysis of native vs. endemic datasets rendered significant results.

Discussion

Several studies have investigated many aspects of the colonization history of Galápagos plants (Carlquist 1967, Porter 1983). They were based on floristic accounts and circumstantial evidence of dispersal. Given the practical impossibility of determining the actual number of dispersal events, new estimates have to rely on the number of colonizations as inferred from the floristic, taxonomic, palaeobotanic, LDD syndrome category and phylogenetic (and phylogeographic) data.

The phylogenetic correction in analysing island colonization

No syndrome shifts within a plant group have been reconstructed from the phylogenies available, i.e. Galápagos plants and relatives share similar diaspore types. We predict that syndrome constancy after colonization may indeed be a general pattern, as observed in the analysis of the Canarian flora (Vargas 2007), because this archipelago has been available for differentiation since at least 15 million yr earlier (but see Givnish et al. 2009 for Hawaiian lobeliads). The phylogenetic approach is also a powerful tool to infer the number of introductions. One case has recently been shown for the origin of the endemic genus *Darwiniothamnus*, in which its three Galápagos species form a non-monophyletic assemblage resulting from two independent colonization events from the Americas (Andrus et al. 2009). Unfortunately, very few phylogenies have been published to date and this phylogenetic correction is limited to 12 plant groups (Table 1). Further phylogenetic (species level) and phylogeographic (population level) reconstructions are certainly needed to find out the number of lineages accounting for the flora of the Galápagos Islands and therefore the number of successful colonizations. An increase in the number of angiosperm colonists has been estimated in the last decades based primarily on floristic and taxonomic accounts: 291 in Porter (1976), 306 in Porter (1983) and 372 in this paper. In agreement with this tendency, we envision that, as more phylogenetic, phylogeographic and palaeobotanical studies become available, the number of inferred original introductions will increase, as already shown for the Canarian flora (Vargas 2007).

Syndromes favourable to long-distance dispersal

Distant archipelagos provide us with some of the best indirect evidence of the effectiveness of angiosperms over long

0 distances (Stewart 1911, Carlquist 1967, Porter 1976,
Bramwell 1985, Wagner et al. 1990). Plant morphology
indicates that mechanisms unrelated to LDD are abundant
in the Galápagos flora. We showed that a large number of
5 plant groups display no special morphological adaptations
for LDD (36.0% for the native flora and 35.1% for the
endemic flora) reached the Galápagos Islands prior to human
colonization. A similar approach used for the Canarian flora
also showed a large fraction (somewhat lower than a third)
10 of unassisted diaspore (Vargas 2007). Unassisted diaspores
appear to have been widely successful in the colonization of
the Galápagos Islands in contrast to syndromes historically
considered to be specialized in long-distance colonization,
such as endozoochory (16.4% of native genera and 20.1%
15 of endemic genera). Our analysis showed rather similar figures
(not significantly different) between the proportions of
the four main LDD syndromes (endozoochory, epizoochory,
anemochory and hydrochory), whereas the proportion of
unassisted diaspores significantly exceeded that of each syndrome.
20 Nevertheless, the percentage of zoochory (32.1%),
i.e. endozoochory (16.4%) and epizoochory (15.7%) considered
together, parallels that of the unassisted category.

The successful colonization by plants ($n = 68$) bearing
capsules and small seeds is puzzling (Table 2). To account
for this, Porter (1976, 1983) alleged that mud attached to
25 animals was responsible for 41 (13.4%) dispersal events.
A similar percentage (ca 14%) for Galápagos colonists was
also assigned by Carlquist (1967, 1974) to mud adherence.
Therefore, it appears that a large number of plants with no
specific mechanism for long-distance dispersal were considered
30 as 'mud dispersed'.

Long distance dispersal is a rare phenomenon often difficult
to detect and quantify (Higgins and Richardson 1999,
Nathan 2006). We argue that a more evolutionary, practical
exercise would be to analyse the dispersal syndrome spectra.
35 In other words, have adaptations for LDD been favoured in
the colonization of the Galápagos archipelago? To infer this,
performing a contrast analysis between the floras of Galápagos
and source areas (typically the Americas) is needed.

Stochastic and deterministic processes can be difficult to
40 tell apart in biology. Flower syndromes are more evolutionarily
constrained than dispersal syndromes (Whitney 2009),
and have been considered when formulating theoretical models
of evolution of flower shifts (Barrett 2008). Yet, analyses
of dispersal syndromes gain particular significance in certain
45 circumstances. As herein shown, remote floras, like that of the
Galápagos Islands, have a great deal of mechanisms related to
LDD (64% of endozoochory, epizoochory, anemochory and
hydrochory altogether). The observed consistency of high
syndrome proportions provides further, albeit circumstantial,
50 evidence that deterministic forces play a strong role in
LDD. Equally significant is the high proportion of flowering
plants (between a third and a quarter) involved in the colonization
of the Galápagos despite the absence of specific LDD
mechanisms (i.e. unassisted), which suggests that stochastic
55 processes may have also been involved.

Despite our arguing that unspecific diaspores account for
a large number of successful colonizations of the Galápagos
Islands, caution should be exercised in assigning all cases of
'unassisted diaspores' to stochastic processes. In the same
60 way that the presence of a particular LDD syndrome does

not necessarily imply that this was responsible for the actual
arrival of the propagules, neither does the fact that many successful
colonizers lack special dispersal syndromes allow us to assume
dispersal favoured by stochastic or rare events. It may simply
65 mean that LDD is not as clearly attributable to particular
mechanisms as previously thought, and we need to analyse
additional causes to understand highly complex and non-standard
dispersal processes (Nogales et al. 1999, 2001, 2007 Higgins et al. 2003,
Guerrero and Tye 2009).

In this paper we claim that a new perspective is needed
70 to realistically understand successful colonizations related to
plant dispersal syndromes. Testing whether particular diaspore
traits have been favourable in the formation of a flora gives us
the opportunity to: 1) refine our understanding of successful
syndromes in the colonization of islands, 2) provide an evolutionary
75 framework in which particular morphologies acquired in the
evolutionary history of angiosperms have been competitive for
LDD, and 3) evaluate the role of stochastic processes in plant
colonization.

We suggest that the speculative exercise of inferring actual
80 dispersal to remote archipelagos should be discouraged. Instead,
analyses of mechanisms favouring LDD generate explicit hypotheses
to be tested within the theory of island biogeography. The results
of this paper support the thesis that a significant number of
ancestors arrived in the Galápagos Islands through so far
85 unpredictable or unknown events. The question remains as to
whether unassisted diaspores have indeed been favoured, on
contrasting Galápagos plants and the source flora.

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50 Supplementary material (Appendix E6980 at <www.oikosoffice.lo.se/appendix>). Appendix 1.

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