Research

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

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Since nobody has witnessed the arrival of early plant colonists on isolated islands, the actual long-distance dispersal (hereafter 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 currents) have been favourable in the natural colonization of the Galápagos Islands by plants. Dispersal syndromes of the 251 native genera (509 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 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 (unassisted diapores), such as many dry fruits, have been successful in reaching and colonizing the Galápagos archipelago. This finding leads us to suggest that unpredictable and so far unknown LDD mechanisms should be further considered in the theory of island biogeography.

Islands are ideal models to study long-distance plant dispersal (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 composition, range expansion and genetic structure (Cain et al. 2000, Nathan 2006). Traditionally, taxonomic and floristic 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 biogeography 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 related to dispersal by: wind (anemochory), water (hydrochory), internally by animals (endozoochory), and externally by animals (epizoochory) (Carlquist 1967). The lure of reconstructing the colonization history of each archipelago 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 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 introduced 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 speculation, 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 testable exercise would be to evaluate the relative presence of different plant dispersal syndromes occurring on islands,

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. 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.

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).

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 syndrome morphologies 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 (Avise 2009).

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 the four 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.

Materials and methods

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); 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 (Table 2). 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 of each Galápagos and mainland groups, for which clade topologies were used to correct the number of colonists (Vargas 2007).

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 (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 natural

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.

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

(Continued)

Table 1. *(Continued)*.

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

Table 1. *(Continued)*.

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

(Continued)

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Table 1. *(Continued)*.

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

(Continued)

Table 1. *(Continued)*.

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

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

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.

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 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.

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.

Genus (species number)	No. Galápagos taxa (studied taxa from Galápagos)	No. inferred dispersals/ no. previous estimates (Porter 1983)	Inferred ancestor diaspore syndrome	Reference
Acalypha (ca 500 spp.)	4 (4)	1/1	unassisted (myrmecochory, autochory)	Seberg (1984)
Cordia (incl. *Varronia*) (ca 350 spp.)	6(6)	3/3	unassisted, endozoochory, epizoochory, hydrochory, anemochory	Weeks et al. (2010)
Cuscuta (145 spp.)*	2(2)	2/?	unassisted	Stefanovic (2007)
Darwiniothamnus (3 spp.)*	3(3)	2/1	epizoochory	Andrus et al. (2009)
Encelia (15 spp.)	1(1)	1/1	epizoochory	Fehlberg and Ranker (2007)
Euphorbia (ca 2000 spp.)	1(1)	1/1	unassisted	Steinmann and Porter (2002)
Galvezia (4 spp.)	3(3)	1/1	unassisted	Vargas et al. (unpubl.)
Gossypium (39 spp.)	2(2)	2/2	anemochory, hydrochory	Wendel et al. (2009)
Lecocarpus (3 spp.)	3(1)	?/1	epizoochory, anemochory	Rauscher (2002)
Lycopersicon (7 spp.)	2(2)	1/1	endozoochory	Peralta and Spooner (2001)
Macraea (1 spp.)	1(1)	1/1	anemochory	Panero et al. (1999)
Nolana (18 spp.)	1(1)	?/1	hydrochory	Tu et al. (2008)
Phaseolus (36 spp.)	3(1)	?/3	unassisted	Delgado-Salinas et al. (2006)
Polygala (ca 500 spp.)	5(2)	1/1	anemochory (myrmecochory)	Forest et al. (2007)
Tiquilia (27 spp.)	4(3)	1/1	unassisted	Moore et al. (2006)
Total		at least 20 dispersal events from 15 tested groups		

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.

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 1). 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 11 genera were used to establish a minimum number of 15 introductions (Table 2), whereas previous estimates based on morphology rendered a lower number (14) (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 1), 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 diaspore structures by early colonists and mainland relatives (Table 2).

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
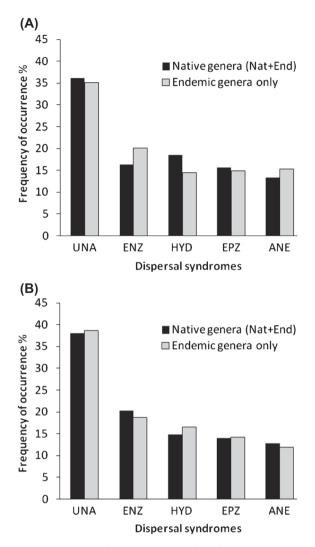
(A)

(B)

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) Laweson 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 reliable in 11 plant groups (Table 2). 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

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 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) 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% 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. 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 1). To account for this, Porter (1976, 1983) alleged that mud attached to 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 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. 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 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 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, 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 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 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 events. It may simply 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 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 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 dispersal to remote archipelagos should be discouraged. Instead, analyses of syndromes and 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 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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