

Contrasting patterns of plant evolution in the Canarian and Galápagos islands: the origin of dispersal and colonization

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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. The number of taxa (mainly genera) has been widely used to estimate the number of colonisation events. In addition, description of the vegetative and reproductive structures of plants has aided in categorising them into four main groups of diaspores related to dispersal by: wind (anemochory), sea (hydrochory), internally by animals (endozoochory), and externally by animals (epizoochory) (van der Pijl 1982). The lure of reconstructing the colonisation 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.

In the case of the Canary Islands, Bramwell (1985) estimated that the extant flora was generated by 186 founders (c. 1500 species), of which 63 (34%) were considered endozoochorous, 35 (19%) epizoochorous, 48 (26%) anemochorous, 8 (4%) hydrochorous and 32 (17%) uncertain. For the Galápagos flora (c. 500 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 different unpredictable means (Higgins et al. 2003). Rather than speculating on the colonisation 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 with 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 and the Canary Islands) can be estimated.

In order to correctly assess whether the four LDD syndromes have been favourable in the natural colonisation of oceanic islands, it is necessary to control for some factors obscuring correct inferences. The most confounding factor is colonisation by plants brought by humans and therefore not attributable to natural dispersal. The Galápagos (subaerial volcanic rocks of < 6 Ma, Geist 1996) and Canary (subaerial volcanic rocks of < 21 Ma Carracedo et al. 2002) islands have been continuously colonized since their formation. This period is considered long enough for the islands to receive natural introductions that may have differed into morphological varieties (endemic taxa). Thus, the native (and endemic) 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).

The appropriate unit to test the success of LDD syndromes is the number of colonisations 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 oceanic islands and continental plants (see Andrus et al. 2009). In particular, phylogenetic methods aid in evaluating the number of colonisation 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).

In this study we contrasted the proportion of syndromes that have been favourable in the colonization of the Canarian and Galápagos archipelagos. We used floristic data and a new approach that proposed explicit assumptions and corrections to find out the contribution of four diaspore syndromes to the colonization history of oceanic archipelagos. A fifth category was considered in the analysis for diaspores displaying no specific traits for LDD.

Material and methods

The colonization of a new territory entails four essential phases: dispersal from the source flora, arrival on the new land, establishment in particular habitats, and in situ differentiation and further distribution. The origin of floras from ancient and dynamic continental plates has historically been difficult to be reconstructed. In contrast, oceanic islands are relatively new territories where spatial and temporal frameworks are simplified. In any case, the complete reconstruction of this process for a whole flora is unfeasible using testable data because nobody has witnessed the arrival of early plant colonists. However, it can be tested whether particular plant features have significantly contributed to the success of plants in the colonization. A new approach herein presented focuses on three essential aspects needed to infer whether particular diaspore traits have been favourable: plant diversity, colonist and syndrome estimates.

Floristic diversity estimates

Floristic data were systematically evaluated along the following complementary steps:

- 1) Analysis of only native taxa as considered from floristic studies.
- 2) Use of lists of the native species that were amended using palaeobotanical evidence (palaeobotanical correction).
- 3) Additional analysis of only endemics (flora endemic approach) to prevent from including human-mediated introductions.
- 4) Comparable analyses from multiple floristic accounts differing in number of all the species and in number of native species.

Early colonist estimates

The number of early colonists is inferred from the native and endemic flora. There are, however, some assumptions to consider in order to reliably estimate the number of colonizations that brought about the current flora:

- 1) One colonization result in a lineage that either differentiated or not.
- 2) Genera are used as operational starting units.
- 3) More than one ancestor was adopted for genera containing multiple taxonomic groups (subgenera, sections, subsections).
- 4) The inferred number of original colonists was corrected by phylogenetic evidence (phylogenetic correction), in which each independent, monophyletic group accounts for a single origin. This correction implies the analysis of species and population levels using phylogenetic and phylogeographic methods, respectively.

Dispersal syndrome estimates

A testable, evolutionary analysis relies on plant features of the extant flora. Only traits related to LDD in the colonization are used to categorise the inferred colonists. The following considerations are used for the analysis:

- 1) Syndromes unrelated to LDD were not considered, i. e. myrmecochory, autochory and ballistic.
- 2) Four LDD syndromes related to LDD dispersal by: water (hydrochory), wind (anemochory), internal animals (endozoochory) and external animal (epizoochory).
- 3) One more category is analysed for plants with no specific mechanism for LDD: unassisted.
- 4) Probability of one colonization event is calculated depending on species displaying one or more syndromes.
- 5) Syndrome coding of the early colonists as revealed by morphologies of the extant species from the oceanic island and closely-related taxa from the continent. Result searches were performed with three scientific web search engines (Scopus, ISI, Google).

Results

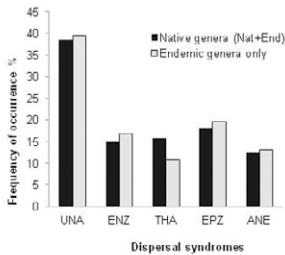
We did not find noticeable differences between the two floristic accounts used to analyze the number of colonists in the Galápagos Islands (Fig. 1). They basically differed in number of species (68 more species in Laweson et al. 1987) and consideration of native vs. non-native species. Once corrected by means of the fossil pollen and phylogenetic information available to date, we obtained the following different proportions of dispersal categories in the native Galápagos flora: endozoochory 16.4%, epizoochory 15.7%, hydrochory 18.6%, anemochory 13.3% and unassisted 36.1%. When we considered exclusively genera with at least one endemic species, the proportions changed only slightly: endozoochory 20.1%, epizoochory 14.9%, hydrochory 14.5%, anemochory 15.3% and unassisted 35.1% (Fig. 1). 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 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 $G = 13.6$, $df = 4$, $p = 0.009$).

The use of the same approach on a subset (38) of plant groups from the Canary islands reveals the following results: endozoochory (34%), epizoochory (10.5%), anechory (8%),

hydrochory (16%), unassisted (21%) and uncertain (10.5%) (Vargas 2007). Interestingly, these results are similar to previous estimates using a different approach. Bramwell (1985) estimated that 186 founders generated the extant flora of the Canary Islands, of which 63 (34%) were endozoochorous, 35 (19%) epizoochorous, 48 (26%) anemochorous and 8 (4.3%) hydrochorous. It is difficult to interpret the category of 32 (17%) uncertain plant groups (Bramwell 1985), but this figure may include both the unassisted category considered in our study plus plants with diaspores of uncertain classification into the four LDD syndrome categories.

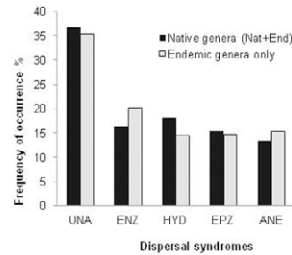
Syndrome estimates for the Galápagos Islands

- Number of species included: 436
- Number of inferred colonists: 306



Using floristic list from Wiggins & Porter (1971)
"Flora of the Galápagos"

- Number of species included: 509
- Number of inferred colonists: 375



Using floristic list from Lawesson et al. (1987)
"An updated check-list of the vascular plants of
the Galapagos Islands"

Figure 1

Discussion

As the actual the arrival of early plant colonists to isolated islands cannot be tested, the actual means of long-distance dispersal (LDD) have historically been a matter of speculation. Given the practical impossibility of determining the actual number and vectors of dispersal events, estimates of the number of colonisations have to rely on taxonomic data, LDD syndrome categories and phylogenetic reconstructions.

We showed that a large number of plant groups with no special morphological adaptations for LDD (36.1% of the native flora and 35.4% of the endemic flora) may have reached the Galápagos Islands prior to human colonisation. Unassisted diaspores appear to have been successful in the colonisation of the Galápagos Islands and represent a proportion even higher than diaspores with syndromes historically considered to be successful in long-distance colonisation, such as endozoochory (16.4% of native genera and 20.1% of endemic genera). The same is true for the estimates of the origin of the Canarian flora. No

special morphological adaptations for LDD were needed to reach the Canarian archipelago in nearly 20% of the cases, and possibly in some of the 10% more categorized as uncertain (Vargas 2007). These figures are even more striking given that the Galápagos and Canary archipelagos share few characteristics (similar land area). In fact, many dissimilar features considered essential in the theory of island biogeography do not meet in the Galápagos and Canary islands, respectively: location (Pacific and Atlantic oceans), proximity to the continent (c. 100 vs. 1000 Km), age of subaerial volcanic rocks, number of habitats (highest elevation of 3742 m vs. 1710 m). A preliminary analysis of a subset of the Hawaiian flora, of which there are reliable phylogenies published, revealed that also about 30% of colonists lacked any special mechanism to LDD (Vargas 2007; z et al., unpublished). Therefore, the question remains as to why most of the world's oceanic archipelagos were colonised by a successful group of plants (between 20 and 40%) with unassisted diaspore.

In summary, we suggest that the speculative exercise of inferring actual dispersal to remote archipelagos should be discouraged. Instead, analyses of sets of traits favouring LDD generate explicit hypotheses to be tested within the theory of island biogeography.

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