

LETTER

Habitat filtering not dispersal limitation shapes oceanic island floras: species assembly of the Galápagos archipelago

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Abstract

Remote locations, such as oceanic islands, typically harbour relatively few species, some of which go on to generate endemic radiations. Species colonising these locations tend to be a non-random subset from source communities, which is thought to reflect dispersal limitation. However, non-random colonisation could also result from habitat filtering, whereby only a few continental species can become established. We evaluate the imprints of these processes on the Galápagos flora by analysing a comprehensive regional phylogeny for ~ 39 000 species alongside information on dispersal strategies and climatic suitability. We found that habitat filtering was more important than dispersal limitation in determining species composition. This finding may help explain why adaptive radiation is common on oceanic archipelagoes – because colonising species can be relatively poor dispersers with specific niche requirements. We suggest that the standard assumption that plant communities in remote locations are primarily shaped by dispersal limitation deserves reconsideration.

Keywords

Dispersal, flora, Galápagos, habitat filtering, oceanic islands, phylogenetic structure, species assembly.

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INTRODUCTION

Island systems have provided the inspiration for many key theories in ecology and evolution (Warren *et al.* 2015), including natural selection (Darwin 1859; Wallace 1869), community assembly (Diamond 1975) and island biogeography (MacArthur & Wilson 1967). In studies of island systems, particular emphasis has been placed on how biogeographical processes (e.g. immigration, extinction, speciation) and island characteristics (e.g. area, isolation, age) influence patterns of species diversity (e.g. Hamilton *et al.* 1963; Johnson & Raven 1973; Losos & Schluter 2000; Whittaker *et al.* 2008). However, ecological and evolutionary features of potential colonisers might additionally impact island community assembly (Lomolino 2000; Gillespie 2016). In this study, we attempt to disentangle the relative importance of dispersal, environmental filtering and speciation in shaping the Galápagos flora.

The Galápagos flora has been characterised as a disharmonic species assemblage (Darwin 1859; Porter 1983). Disharmony, a prominent pattern for oceanic island biotas, refers to a distinct taxonomic composition relative to continental source regions; i.e. an overrepresentation of some groups and an underrepresentation of others (Gillespie *et al.* 2012). This pattern suggests the action of a strong dispersal filter, such that species composition is primarily determined by isolation from the mainland (about 1000 km for the Galápagos). Most of the Galápagos flora was thought to have colonised the archipelago because they possessed traits that facilitated long-

distance dispersal (e.g. Hooker 1847; Carlquist 1967; Porter 1983). However, dispersal is only the first step in the colonisation process. Evidence showing that an important proportion of native colonisers have no obvious mechanism for long-distance dispersal (Vargas *et al.* 2012), and that some species having long-distance dispersal mechanisms show relative restricted distributions within the archipelago (Vargas *et al.* 2014) suggest that factors other than dispersal potential can limit species establishment.

Environmental conditions might provide an additional filter to species establishment on oceanic islands (Carlquist 1965). For example, the Galápagos archipelago has desert and subtropical environments (Palmer & Pyle 1966), which could have favoured establishment by some species over others (Porter 1983). Previous work has suggested that plant species composition on the Galápagos is correlated with island habitat diversity, particularly the availability of wet and dry environments, which are associated with island area and elevation (Hamilton *et al.* 1963; Johnson & Raven 1973; Hamann 1981; Van Der Werff 1983). However, few studies have directly evaluated the relative importance of dispersal vs. environmental filtering in structuring insular plant assemblages. The Galápagos archipelago provides an excellent system to explore these relationships due to its oceanic origin, geographical isolation and its close relationship with adjacent continental biotas (Hooker 1847; Svenson 1946; Porter 1984).

Here, we evaluate the role of biogeographical factors in structuring the species composition of the Galápagos

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archipelago by examining the phylogenetic structure of plant assemblages. Phylogenetic approaches for ecological inference have most commonly been applied at the community level (Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012), but they can also be applied to larger spatial scales, where they might capture the signature of historical biogeography and diversification (Emerson & Gillespie 2008; Davies & Buckley 2012; Baeten *et al.* 2015). While recent work by Vargas *et al.* (2014) and Nogales *et al.* (2016) has integrated evolutionary and ecological information to examine species dispersal on the Galápagos, our study is the first to directly test the relative importance of dispersal vs. habitat filtering.

First, we analysed the phylogenetic structure of the Galápagos flora relative to potential continental species pools. We might expect strong filtering to generate phylogenetic clustering (i.e. species more related than expected by chance), assuming key ecological traits show phylogenetic conservatism (Webb *et al.* 2002). Second, to disentangle the effect of dispersal vs. habitat filtering, we examined the ecological characteristics of successful colonisers, and tested whether species dispersal strategies vs. environmental niche preferences better predict colonisation success. Third, we assessed the processes driving phylogenetic structure across different islands within the archipelago. If habitat filtering is the primary determinant of species composition, we might expect greater phylogenetic overdispersion (species less related than expected by chance) on larger islands because they encompass multiple habitat types (Cavender-Bares *et al.* 2004), and greater phylogenetic turnover between islands that are most dissimilar in their abiotic environments rather than between islands that are more geographically distant.

We show that the native Galápagos flora is a phylogenetically clustered subset of the continental pool of potential colonisers. We also provide new evidence that indicates habitat filtering was more important than dispersal limitation in determining species composition on the archipelago, as well as across individual islands within the archipelago. Last, we show that speciation influences the phylogenetic structure of plant assemblages by increasing phylogenetic clustering on the archipelago, and increasing phylogenetic overdispersion on individual islands.

MATERIAL AND METHODS

Source areas and phylogenies

To explore the processes shaping the Galápagos flora, we first identified the most likely geographical source pool from which native flowering plants could have originated. Using plant checklists, public databases and literature (see Appendix S1 in Supporting Information), we compiled a list of the 216 native, non-endemic species present in the archipelago and annotated their presence/absence in 15 surrounding regions including South America (mostly partitioned by country), Mesoamerica (Mexico and Central America), the West Indies and North America. For each of the 15 putative source regions, we estimated: (1) a similarity index (SI) based on the proportion of the native, non-endemic, Galápagos species found in that region and (2) the probability that any given native,

non-endemic, species found in the archipelago originated from that region (P_i), following Papadopoulos & Baker 2011 (see Appendix S1).

Next, we used the above floristic indices to define three potential regional species pools according to their likely contribution to the Galápagos flora: a large species pool (38 905 species) including Mesoamerica, Venezuela, Colombia, Ecuador and Perú; a medium species pool (25 486 species) including Colombia, Ecuador and Perú; and a small species pool (6465 species) restricted to the continental region of Ecuador (Fig. 1). Species names were standardised to The Plant List 1.1 <<http://www.theplantlist.org/>> using the taxonstand 1.7 R package (Cayuela *et al.* 2012). Unmatched names were rechecked using the The Taxonomic Name Resolution Service <<http://tnrs.iplantcollaborative.org/>> (Boyle *et al.* 2013). Higher taxonomic membership was corrected to the APG III (Angiosperm Phylogeny Group 2009).

Phylogenetic relationships were reconstructed based on the comprehensive species-level phylogeny of vascular plants generated by Zanne *et al.* (2014) and updated by Qian & Jin (2016). This phylogeny includes 30 193 angiosperm species and was used as a backbone onto which we placed additional species. From the species present in our species pools (38 905), 5196 matched directly to those sampled by Zanne *et al.* (2014), and the remainder were added as polytomies at the root node for their genus membership using the merge tool implemented in the R package pez. 1.1 (Pearse *et al.* 2015). Species within genera that were not represented on the backbone tree (4601 species) could not be included; we thus generated an additional tree placing taxa as polytomies at the root node for their families to favour species completeness.

Phylogenetic structure of the Galápagos flora

We used the R package picante 1.6 (Kembel *et al.* 2010) to calculate two commonly used indices of phylogenetic structure: Faith's (Faith 1992) phylogenetic diversity (PD) and the mean pairwise phylogenetic distances (MPD). To test the significance of the observed patterns and calculate standardised effect size of these metrics (SES.PD and SES.MPD), we compared observed PD and MPD values to null expectations generated by drawing species at random (999 runs) from each species pool (large, medium and small). Positive SES values indicate phylogenetic overdispersion, whereas negative SES values indicate phylogenetic clustering. Here, we place more emphasis on the metric of MPD because our interest was in measuring phylogenetic divergence rather than phylogenetic richness (Tucker *et al.* 2016), and the greater sensitivity of SES.PD to more terminal structure makes it better suited for exploring assembly processes working at finer temporal and spatial scales (Mazel *et al.* 2015). To examine the importance of speciation in driving archipelago phylogenetic structure, we recalculated each metric excluding species that were endemic to the Galápagos (156 species considered here) under the assumption that endemic species are more likely to be the products of *in situ* speciation.

Phylogenetic signal in colonisation was estimated using the D statistic (Fritz & Purvis 2010), as implemented in the R package caper 0.5.2 (Orme *et al.* 2013), on the binary matrix

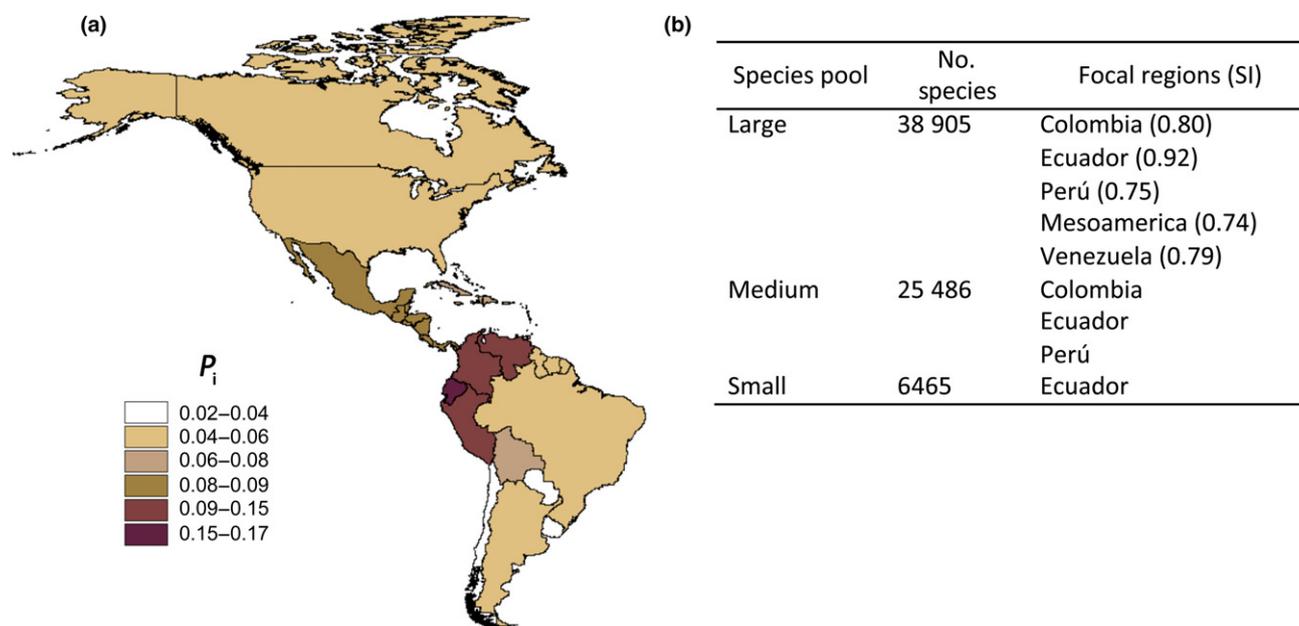


Figure 1 Potential species source pools for the Galápagos flora. (a) Map showing focal regions shaded by p_i , the probability of each area being the unique source of origin of any given native, non-endemic, Galápagos species (see Appendix S1). (b) Size (number of species) and focal regions of selected species pools. Similarity index (SI) measured as the proportion of native, non-endemic, angiosperms from the Galápagos present in each region.

of presences/absences in the Galápagos for each species pool. The D statistic allows us to test if the presence of flowering plants in the Galápagos is independent from phylogeny ($D = 1$), or if it follows the distribution expected under a Brownian motion model of evolution ($D = 0$). D values close to 0 would be expected if traits associated with colonisation success (e.g. long-distance dispersal ability, vegetative propagation, long flowering periods) are tightly conserved on the phylogeny.

Dispersal and habitat filtering

We evaluated the importance of dispersal and environmental filtering in determining the composition of the Galápagos flora by fitting a phylogenetic logistic regression (Ives & Garland 2010) with species presence/absence on the Galápagos archipelago as response, and species dispersal strategy and climatic suitability as predictors. For this analysis, we considered all species present in the medium regional pool, which we determined as the most likely source pool for Galápagos species based on our analyses of indices of floristic similarity and geographical distance.

We compiled information on species dispersal (see Appendix S2) and classified species as possessing or lacking a long-distance dispersal strategy. Species having zoochory (animal dispersal), anemochory (wind dispersal) or hydrochory (water dispersal) dispersal were classified as long-distance dispersers (except species that use insects as vectors). Species with unassisted dispersal, seeds that drop to the ground close to or beneath the parent plant or seeds actively dispersed by the parent plant by an explosive mechanism were classified as lacking a long-distance dispersal strategy (Willson 1993; Gómez & Espadaler 1998; Thomson *et al.* 2010). For species without a documented dispersal mechanism, we used

descriptions of diaspore morphology from the literature to assign most likely strategy (Ridley 1930; Van der Pijl 1982; Willson *et al.* 1990; Hughes *et al.* 1994, see details in Appendix S2). In total, we were able to obtain dispersal information for 4339 species (data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.43b1t>).

To estimate of climatic suitability of the Galápagos for potentially colonising species, we quantified the distance between each species' continental climatic niche and the climatic space available on the Galápagos Islands. For this, we first compiled distribution data from the Global Biodiversity Information Facility (GBIF; <<http://www.gbif.org/>>) using the R package `rgbif` 0.9.3 (Chamberlain *et al.* 2016), then for each species' spatial location recorded within the putative source region (i.e. Colombia, Ecuador and Perú), we extracted 19 climatic variables from WorldClim at a resolution of 30 arc-seconds (Hijmans *et al.* 2005; <<http://www.worldclim.org/>>). Species with fewer than five localities were excluded from the analyses to avoid potential bias associated with small sample sizes, leaving a total of 11 934 included species. Species' continental climatic niches were summarised as the first three components of a principal component analysis on the 19 climatic variables. Next, we used the same WorldClim variables to characterise the climatic space of the Galápagos archipelago. We then calculated two climatic suitability metrics for each species. The first metric, niche dissimilarity (ND), was derived using the `hypervolume` package in R (Blonder *et al.* 2014), and represents the euclidean distance between each species' hypervolume centroid and the centroid for the climatic hypervolume represented by the Galápagos archipelago. The second metric, niche overlap (NO), was calculated in the `nicheROVER` 1.0 package (Swanson *et al.* 2015), and represents the probability that a randomly drawn point from a given species' climatic niche space falls within

the Galápagos Islands climate space, using 1000 Monte Carlo draws.

We tested whether long-distance dispersal strategy and/or higher climatic suitability better explain species' presence on the Galápagos archipelago by fitting phylogenetic logistic regression models in the R package *phylolm* 2.3 (Ho & Ané 2014). The predictor variables were a binary categorisation that scored each species for long-distance dispersal strategy (LDD), niche dissimilarity (ND) and niche overlap (NO). Because we were not able to obtain data on dispersal strategy and climatic suitability for all species, for model comparisons, we fit models only using species that had data on both dispersal and climatic suitability (3029 species). Model comparisons were performed using Akaike information criterion (AIC). Given the imbalance in our data set (162 species present and 2867 absent from the archipelago), we also evaluated statistical relationships across 1000 subsets of 162 species randomly drawn from the set of species absent from the archipelago. For each subset, we fit and compared three models: one with LDD as the predictor variable, the second with ND as the predictor variable and the third including both as predictor variables. In addition, we fit models separately for dispersal and climatic suitability including all species in the data set, and used an alternative categorisation of species' dispersal strategy based on the number of long-distance dispersal strategies to evaluate whether having multiple strategies was also a predictor of colonisation success (Vander Wall & Longland 2005; Vargas *et al.* 2015).

Phylogenetic structure of islands within the archipelago

To evaluate community composition on individual islands, we examined the association between phylogenetic structure, island geography and climate. First, we pruned the regional phylogeny to just the species considered native to the archipelago (217 native non-endemics plus 156 endemics) for which we had data on distributions among islands (fourteen main islands) (Wiggins & Porter 1971; Jaramillo Díaz *et al.* 2015); this species set was considered to be the new regional source pool. Second, for each island assemblage, we estimated SES.PD and SES.MPD (see above), using random draws from the regional species pool as our null. See Appendix S3 for species list and geographical distributions.

Statistical relationships were assessed by fitting multivariate linear models with phylogenetic structure (SES.PD and SES.MPD) as the response variables and four key island characteristics as predictors: area (km²), annual mean temperature (°C) and annual precipitation (mm) obtained from Weigelt *et al.* (2013), and island isolation (km), measured as the mean distance from each island to all the other main islands within the archipelago. Minimum distance between each pair of islands was obtained from Bisconti *et al.* (2001) and Hamilton & Rubinoff (1967). To evaluate the importance of speciation on phylogenetic structure, we (1) recalculated each SES metric excluding species that were endemic to the archipelago and compared results between the two analyses, and (2) included the degree of island endemism, calculated as the proportion of endemic species present on each island, as an additional predictor. Also, we fitted an additional model including the

estimated minimum geologic age (million years) for each island, from Parent *et al.* (2008), to control for the effect of island ontogeny. All predictor variables were log transformed and standardised to a mean of 0 and a standard deviation to 1 prior to analysis. We did not detect significant multicollinearity among predictors, as assessed by variance inflation factors (all VIFs < 10; Quinn & Keough 2002). We thus generated the set of all possible additive models using the *MuMIn* 1.15.6 R package (Bartón 2016), and then calculated standardised coefficients for each predictor using model averaging with corrected $\Delta\text{AIC}_C < 4$ (Burnham & Anderson 2004).

Last, we calculated phylogenetic beta diversity (βMPD) among island assemblages using the R package *picante* 1.6 (Kembel *et al.* 2010), and examined the association between βMPD and differences in island environment and geographical distance separating islands using partial Mantel tests in *vegan* 2.3–3 (Oksanen *et al.* 2015). Both mantel partial correlations were conditioned on area. Environmental differences among islands were calculated as euclidean distances of combined island annual mean temperature (°C), annual precipitation (mm), minimum values of annual mean temperature range (°C) and the coefficient of variation in monthly precipitation, from Weigelt *et al.* (2013).

RESULTS

Archipelago assembly from continental floras

The Galápagos flora represents a highly phylogenetically clustered subset of the potential colonisers that are present in continental America. Species that are found on the archipelago are more closely related than expected by chance according to both phylogenetic structure metrics SES.PD and SES.MPD (Table 1, Fig. 2). Clustered patterns were consistent across all three putative continental source pools (small, medium and large). Stronger clustering was found using the largest source pool (SES.PD = -6.87; SES.MPD = -9.34, both $P \ll 0.05$), but remained significant even when assuming the small pool of potential colonisers (SES.PD = -5.90; SES.MPD = -8.16, both $P \ll 0.05$). Of the three species pools, the regions of Ecuador, Perú, Colombia, Venezuela plus Mesoamerica (large pool) showed the greatest similarity with the Galápagos flora (SI $\gg 0.70$), whereas Ecuador, Perú plus Colombia (medium pool) had the highest probability of being the unique source

Table 1 Phylogenetic clustering of the Galápagos archipelago estimated using three potential source pools (small, medium and large)

	Species pool	SES.PD	SES.MPD
Small	Native species	-5.90*	-8.16*
	Native species, non-endemics	-3.99*	-3.54*
Medium	Native species	-6.72*	-8.52*
	Native species, non-endemics	-4.49*	-3.79*
Large	Native species	-6.87*	-9.34*
	Native species, non-endemics	-4.75*	-6.19*

Standard effect sizes of phylogenetic diversity (SES.PD) and mean pairwise distances (SES.MPD) calculated from 999 random draws from the phylogeny. Negative values indicate phylogenetic clustering. Significant patterns relative to the null model are marked with an asterisk (*).

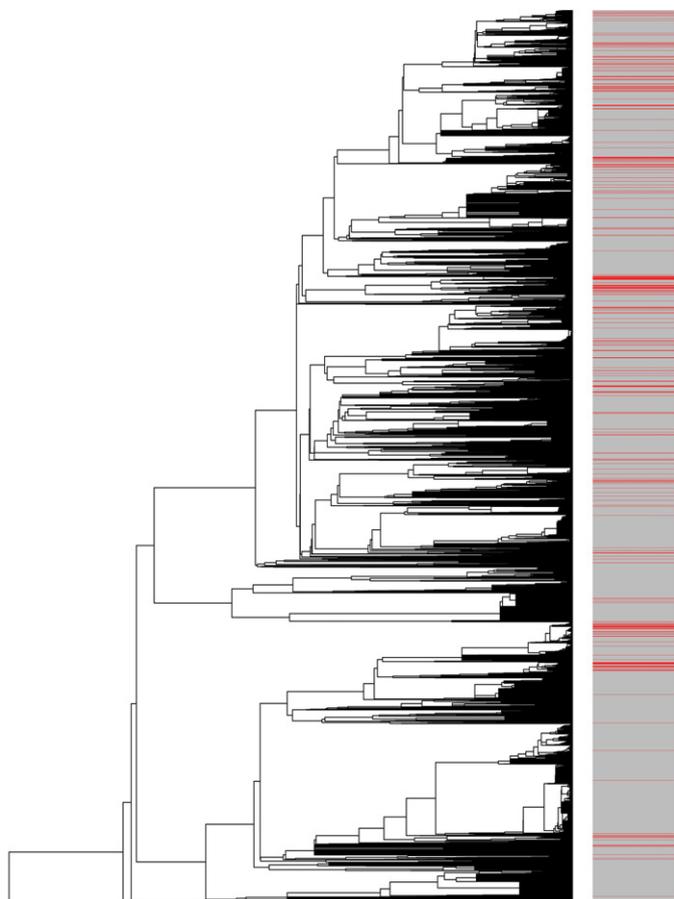


Figure 2 Phylogenetic structure of the Galápagos flora. Phylogeny of species within the medium size pool (Colombia, Ecuador, and Perú); red bars indicate species native to the Galápagos Islands and grey bars continental species. Native species to the archipelago are more closely related than expected by chance according to the standard effect sizes of phylogenetic diversity (SES.PD) and mean pairwise distances (SES.MPD) (SES.PD = -6.72 , $P = 0.001$; SES.MPD = -8.52 , $P = 0.001$).

of origin for species in the archipelago ($P_i = 0.17$, $P_i = 0.11$, and $P_i = 0.10$, respectively). However, more than 90% of the native non-endemic Galápagos angiosperms are found in the smallest and closest continental pool, the flora of Ecuador (Fig. 1, Appendix S1).

Phylogenetic clustering was stronger when endemic species were included in the analysis (Table 1), revealing the importance of macroevolutionary processes, such as speciation, in shaping regional patterns of phylogenetic structure. Lower values of SES.MPD than SES.PD suggest that clustering occurs deep in the phylogeny, as SES.MPD is more sensitive to structure towards the root of the tree (Webb *et al.* 2002; Mazel *et al.* 2015). Similar patterns were observed using the reduced phylogeny with greater tip resolution (see methods above and Appendix S4).

We found a highly significant phylogenetic signal in colonisation, although D values ($D = 0.87$, 0.84 and 0.76 for the large, medium and small pools, respectively) were significantly greater than Brownian motion expectations ($D > 0$; $P < 0.001$). We suggest that this likely reflects a tendency for closely related species to share similar key traits related to dispersal and

probability of establishment. Colonisation success was correlated with species' climatic suitability (Table 2), with the top-ranked model by AIC including niche dissimilarity (ND) as the only predictor variable. Successful colonisers tend to have continental distributions encompassing climates that are similar to the Galápagos (e.g. niche dissimilarity [ND]: $z = -13.247$; $P < 0.001$). In contrast, long-distance dispersal (LDD) explained no additional variance ($\Delta\text{AIC} = 1.66$), and the model including only LDD had low support ($\Delta\text{AIC} = 215.86$). We found no association between having multiple dispersal strategies and colonisation success (see Appendix S5), and niche dissimilarity was always a better predictor of colonisation success than the number of long-distance dispersal strategies. Repeating models across balanced subsets of data (equal number of species present and absent from the archipelago) produced broadly comparable results: models including both predictors (ND and LDD) did not show a better fit (AIC mean \pm SD; 320.75 ± 16.44) to the data than the models including ND only (AIC = 319.76 ± 16.98). Models fit separately for dispersal strategy and climatic suitability including all species are included in Appendix S5.

Phylogenetic structure of islands within the archipelago

Island assemblages showed mixed patterns of phylogenetic structure (Fig. 3a). Among the fourteen islands, four showed significant phylogenetic structure, with Española (SES.MPD = -2.89 , $P = 0.005$), Floreana (SES.MPD = -1.81 , $P = 0.032$) and Pinzón (SES.MPD = -2.34 , $P = 0.023$) demonstrating phylogenetic clustering, and Santa Cruz demonstrating phylogenetic overdispersion (SES.MPD = 2.59 , $P = 0.001$). Equivalent results for SES.PD are reported in the supplemental material (Appendix S6). When endemic species were excluded from the analysis, all islands showed an increased trend towards clustering (Fig. 3a).

Averaged multivariate models showed that SES.MPD is significantly associated with island area ($z = 0.583$; $P = 0.022$) and annual precipitation ($z = 0.569$; $P = 0.030$), and weakly associated with island annual mean temperature ($z = 0.522$; $P = 0.056$), but it is not correlated with island isolation ($z = -0.464$; $P = 0.094$) or degree of endemism ($z = -0.409$; $P = 0.224$). Larger islands, with higher precipitation and mean annual temperature have assemblages that tend to be more phylogenetically overdispersed, whereas smaller islands, with lower annual precipitation and mean annual temperature tend to be more phylogenetically clustered (Table 3, Fig. 3b). Full models are presented in Appendix S7. Including island ontogeny (age) did not appreciably alter the relationship between phylogenetic structure and the other predictor variables (Appendix S7).

The analysis of phylogenetic turnover among islands revealed that geographically close islands were no more similar in phylogenetic composition than geographically distant islands ($r = 0.12$, $P = 0.25$), but turnover was lower between islands with similar climates ($r = 0.43$, $P = 0.001$).

DISCUSSION

The native flora of the Galápagos is a phylogenetically clustered subset of the regional continental species pool, with

Table 2 Phylogenetic logistic regression of species colonisation success on the Galápagos archipelago

Parameter	Coefficient	<i>z</i> value	95% CI	<i>P</i> values	AIC
Model: P/A ~ ND					929.165
ND	-3.508	-13.247	(-3.922 to -3.069)	< 0.001	
Model: P/A ~ ND + LDD					930.823
ND	-3.069	-11.464	(-3.644 to -2.611)	< 0.001	
LDD	0.596	1.589	(-0.140 to 1.381)	0.112	
Model: P/A ~ NO					983.761
NO	0.553	11.719	(0.398 to 0.640)	< 0.001	
Model: P/A ~ NO + LDD					985.910
NO	0.552	11.783	(0.297 to 0.640)	< 0.001	
LDD	-0.037	-0.126	(-0.704 to 0.460)	0.900	
Model: P/A ~ LDD					1145.028
LDD	-0.772	-3.312	(-1.172 to -0.371)	< 0.001	

The response variable was the presence/absence of species in the archipelago (P/A, 0 = absence, 1 = present). Species dispersal strategy was coded as a binary variable representing species' long-distance dispersal strategy (LDD, 0 = absent, 1 = present). For species climatic suitability, we used two variables (see methods): niche dissimilarity (ND, lower values indicate higher similarity) and niche overlap (NO, higher values indicate greater overlap). 100 bootstrap replicates were used to estimate confidence intervals (CI).

Ecuador, Perú and Colombia being the likely source for most colonising species. Contrary to standard expectations for oceanic islands, our results indicate that the Galápagos flora was shaped mainly by habitat filtering rather than dispersal limitation. First, the match between a species' continental climate niche and the Galápagos climate was the single best predictor of colonisation success. Second, plant phylogenetic structure on individual islands within the archipelago was better explained by island area and climate than by island isolation. Third, islands with plant communities that were phylogenetically similar shared similar climate conditions but were not close geographically. *In situ* speciation also shapes the phylogenetic structure of the archipelago by increasing clustering with respect to the continental pool, but it has the opposite effect on individual islands.

Archipelago assembly from continental floras

We might expect species assemblages on islands to show, at a regional scale, strong phylogenetic clustering (Emerson & Gillespie 2008), and clustered patterns have been reported for angiosperm island assemblages with respect to the total pool of insular species (Weigelt *et al.* 2015). We find that this pattern also holds true for the Galápagos flora relative to the continental source pool. Our results indicate that the immediately adjacent landmass of western South America was most likely the main source pool of colonisers for the Galápagos, matching previous work by Porter (1984). The relative contribution of the different continental floras might differ somewhat if we also consider the Galápagos endemic species, although it is more challenging to accurately infer the geographical histories of such species, and continental South America remains their most likely area of origin (Andrus *et al.* 2009; Tye & Francisco-Ortega 2011).

Phylogenetic clustering of species assemblages and a phylogenetic signal in colonisation together suggest that assembly

processes determining the composition of the Galápagos flora are influenced by species' traits that co-vary with phylogeny. This covariance could be driven by either dispersal or habitat filtering. If dispersal was more important, the presence of species on the archipelago should be best explained by their ability to disperse across long distances. If environmental filtering was more important, the presence of species should be best explained by climatic suitability. We found evidence for a role of both processes, but environmental filtering based on climate suitability was most important. Our results might seem unexpected for an oceanic archipelago 1000 km from the source pool, which should impose a strong dispersal filter (Nip-Van Der Voort *et al.* 1979; Kadmon & Pulliam 1993; Whittaker *et al.* 1997). However, we suggest that given sufficient time, such as the approximately 14 million years in the case of the Galápagos archipelago (Werner *et al.* 1999), even poor dispersers could have an opportunity for colonisation, but the lack of suitable habitats could be an insurmountable barrier to establishment. Indeed, the severe conditions for plant growth of the arid Galápagos environments likely prevented the establishment of immigrant species from adjacent continental habitats (Hamann 1981).

It remains possible that co-variation between dispersal strategy and climatic suitability reduced our ability to differentiate between these potential influences – and we do not dispute that overrepresentation of some species groups on islands is influenced by dispersal ability (see e.g. Heleno & Vargas 2015). However, our inference that high dispersal ability is not *essential* is consistent with observations that a substantial proportion of the Galápagos flora, and that of other oceanic islands, has no obvious mechanism for long-distance dispersal (Carlquist 1966a; Porter 1983; Vargas *et al.* 2012; Heleno & Vargas 2015). This pattern was previously ascribed, at least in part, to the loss of dispersal ability on islands (Carlquist 1966b,c, 1974; but see Patiño *et al.* 2015), yet some continental ancestors of island species also lack such mechanisms (Vargas *et al.* 2014). For these species, colonisation seems to be achieved by chance association with dispersal vectors, such as the muddy feet of wading birds (Darwin 1859). Indeed, a new consensus is growing that long-distance dispersal events are often associated with non-standard dispersal mechanisms (Higgins *et al.* 2003; Nathan 2006), and that such mechanisms might be relatively common. Hence, dispersal might be less limiting than often assumed, at least over long time periods, whereas the importance of environmental matching between source pools and colonisation sites may have been underestimated.

Island assembly within the archipelago

Individual island assemblages also showed a general tendency for phylogenetic clustering consistent with predictions of strong filtering. However, this pattern was not universal, with some islands (e.g. Santa Cruz) instead showing evidence for overdispersion. The relative importance of different processes shaping species composition thus seems to vary among islands. In particular, phylogenetic clustering could be driven by island isolation, speciation and/or strong environmental filtering by a habitat type on phylogenetically conserved traits

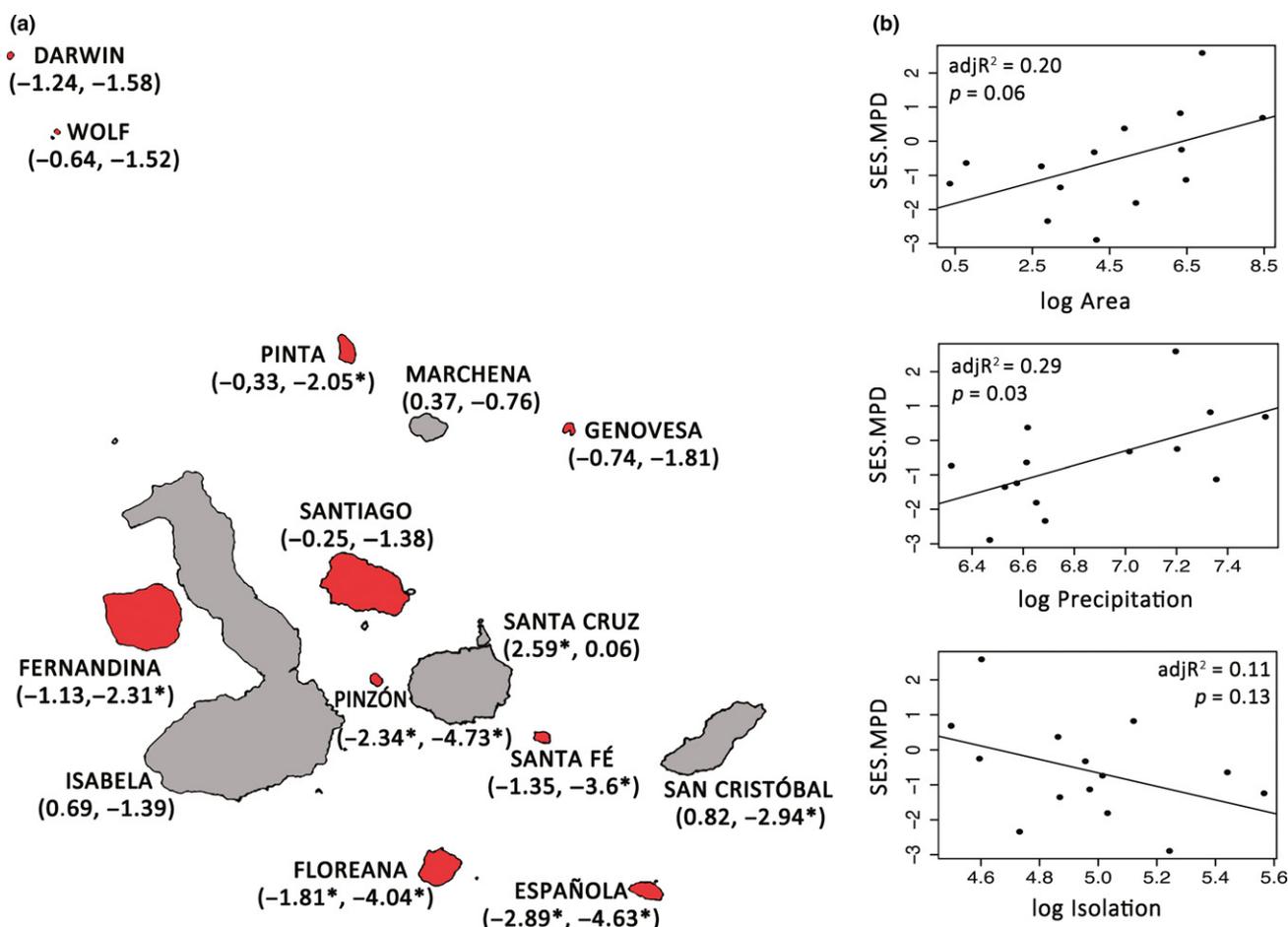


Figure 3 Island phylogenetic structure. (a) Map of the 14 main Galápagos islands coloured by their phylogenetic structure. Red indicates phylogenetic clustering and grey indicates phylogenetic overdispersion with respect to the species pool for the archipelago. In parentheses, standard effect sizes of mean pairwise distances (SES.MPD) for species on each island, with and without including endemic species respectively. Positive values correspond to overdispersed assemblages, whereas negative values correspond to clustered assemblages, significant SES.MPD values indicated by an asterisk (*). (b) Biplots showing the single effect of island area [km²], annual precipitation [mm], and isolation [km] on SES.MPD. However, multivariate linear models showed significant and independent effects of area ($z = 0.583$; $P = 0.022$), and annual precipitation ($z = 0.569$; $P = 0.030$), but not isolation ($z = -0.464$; $P = 0.094$).

(Webb *et al.* 2002; Emerson & Gillespie 2008); whereas phylogenetic overdispersion could result from competitive exclusion of closely related species, filtering across multiple habitats on an island, and/or environmental filtering for a single habitat

Table 3 Multiple linear regression evaluating drivers of island phylogenetic structure (SES.MPD)

Predictor variable	Coefficient (z)	Adjusted Standard error	95% CI	P values
Area	0.583	0.254	(0.086 to 1.080)	0.022
Temperature	0.522	0.273	(-0.013 to 1.057)	0.056
Precipitation	0.569	0.263	(0.055 to 1.084)	0.030
Isolation	-0.464	0.277	(-1.008 to 0.080)	0.094
Endemism	-0.409	0.337	(-1.069 to 0.250)	0.224

Standardised coefficients were estimated by averaging the parameters from the top AIC_C models ($\Delta \text{AIC}_C < 4$). Predictor variables included area (km²), annual mean temperature (°C) and annual precipitation (mm), island isolation (km) and endemism (calculated as the proportion of endemic species present on each island). Variables were log transformed and standardised to a mean of 0 and standard deviation of 1 prior to analysis. Confidence intervals are shown in parentheses (CI).

type when key traits are convergent in the phylogeny (Webb *et al.* 2002; Cavender-Bares *et al.* 2004).

We found that phylogenetic overdispersion was more common on islands that were larger, warmer and wetter. We suggest that this pattern is unlikely to arise via competitive interactions, which should be stronger on *smaller* islands with less habitat heterogeneity (Cardillo *et al.* 2008; Emerson & Gillespie 2008). Instead, we suggest that larger islands show phylogenetic overdispersion as a result of environmental filtering, because larger islands harbour multiple habitats (Van Der Werff 1983; Kohn & Walsh 1994; Parent & Crespi 2006) that should favour the establishment of different clades with different niche requirements. In contrast, if dispersal were the primary process shaping island phylogenetic structure, we would expect more isolated islands to show greater phylogenetic clustering (assuming phylogenetic conservatism of dispersal traits). However, we found no association between phylogenetic structure and island isolation. In addition, phylogenetic turnover among islands was correlated with climate differences rather than geographical distances, providing further support that habitat filtering is more important than dispersal in structuring species assemblages.

Speciation and phylogenetic structure

Oceanic archipelagoes provide many classic examples of rapid evolution and adaptive radiation, such as silverswords in Hawaii, Darwin's finches in Galápagos and anoles in the Greater Antilles. We expected that such speciation for plants in Galápagos would increase phylogenetic clustering (Vamosi *et al.* 2009). As predicted, the inclusion of endemics, some of which form *in situ* radiations, elevated clustering across the archipelago. However, the inclusion of endemics tended to reduce rather than enhance clustering on individual islands. We suggest this trend may reflect the restricted distributions of endemic species across the archipelago (Vargas *et al.* 2014) and speciation via anagenesis (Stuessy *et al.* 2006). A high frequency of speciation by anagenesis, as may be indicated by the low proportion of congeneric endemic species on individual islands (about ~30% of endemics in our analysis are found as single members of their genus), might simultaneously drive phylogenetic clustering of the archipelago flora and phylogenetic overdispersion within individual islands because sister taxa may rarely co-occur on the same island.

Concluding remarks

The patterns we report were robust across our sensitivity analyses; however, we acknowledge several limitations that could be improved in future work. For example, it is likely that we did not sample the complete continental species pool, and our phylogenetic tree lacked resolution at the species level; although this is not expected to impact our conclusions (Swenson 2009), it limits our ability to detect processes acting at finer spatial and temporal scales. In addition, the WorldClim data used for our habitat analysis can be less precise in regions with few climatic stations, such as tropical mountainous regions (Soria-Auza *et al.* 2010). However, our ability to detect a climate signal despite these limitations suggests that environmental filtering is likely strong. Finally, the Galápagos flora has likely been influenced by multiple processes that we did not consider, including volcanic activity, changes in sea levels, and island subsidence (Ali & Aitchison 2014; Geist *et al.* 2014; Triantis *et al.* 2016). We explored island ontogeny, which might capture some of this complex history. Although this factor was additionally significant, it did not change our conclusions regarding the effect of dispersal and habitat filtering.

In conclusion, we show that the native Galápagos flora is a phylogenetically clustered subset of species from the adjacent mainland, with Ecuador, Perú and Colombia being the most important species sources. Contrary to expectations, we found that habitat filtering rather than dispersal limitation was likely the predominant process structuring plant species composition. We suggest that the importance of filtering by environment may have been underestimated in previous studies of species assembly on oceanic islands, where dispersal filtering is traditionally assumed to be the dominant driver. In particular, while dispersal limitation might be most important in early stages of colonisation, other processes (e.g. habitat filtering, speciation, competition) should later dominate as more species arrive from the regional pool and habitats become occupied (Silvertown

et al. 2005; Emerson & Gillespie 2008). We note that our results might help explain why adaptive radiation is common on oceanic archipelagos as they indicate that some colonising species are not necessarily good dispersers but might have specific niche requirements, facilitating reproductive isolation.

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AUTHORSHIP

All authors designed the study; SCE and JD performed data analyses and wrote the first draft of the manuscript; JD, AH and NE reviewed the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.43b1t>.

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SUPPORTING INFORMATION

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