



Stochastic versus deterministic assembly of oceanic island biota: leaf-dwelling lichens on the Galápagos and on Cocos Island

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Abstract

We used a simulation approach to test whether species composition on oceanic islands follows deterministic assembly rules based on probabilities of successful dispersal and establishment. The study was performed with two island biota in the eastern Pacific: the Galápagos, dominated by dry vegetation and montane humid forest, and Cocos Island, covered by wet tropical forest. We used leaf-dwelling (foliicolous) lichens as the study group and compiled occurrence data from previous studies on both island biota and new collections from the Galápagos. Species composition was simulated using randomization from a continental species pool, without and with filtering through ecogeographic parameters. Parameters for filtering were continental distribution range, commonness, and microsite exposure for successful dispersal, and preferences regarding vegetation type, seasonality, elevation, and microhabitat for successful establishment. Whereas neutral random selection predicted insular species composition imprecisely, ecogeographic parameter filtering resulted in rather accurate prediction. Commonness was the parameter that most contributed to the determination of species assembly. Empirical comparison with sites in continental Ecuador and Costa Rica suggests a closer affinity of the Galápagos with Ecuador, indicating that distance plays some role in species assembly as well. Based on our results we conclude that insular species assembly in this group of organisms is largely deterministic, rejecting a purely neutral approach.

Highlights

- Composition of randomized assemblies from a known species pool occurring on the American continent supports the hypothesis that island colonization largely follows deterministic assembly rules.
- Stochastic components included a small number of unpredictable species and missing species as a result of disharmonic assembly.
- Commonness was the most important parameter in shaping assembly.
- Empirical comparison with sites in continental Ecuador and Costa Rica suggests a closer affinity of the Galápagos with Ecuador.
- This study appears to be the first to test species assembly in island biota through simulation based on predictions from continental source metacommunities.

Keywords

Cocos Island, foliicolous lichens, Galápagos Islands, Guajalito, Jatun Sacha, Las Cruces, La Selva, lichens, ordination, species assembly

Introduction

Island biota are ideal to study the effects of geographic isolation on community assembly (MacArthur and Wilson 1967; Gillespie 2007; Whittaker and Fernández-Palacios 2007; Losos and Ricklefs 2009; Brown et al. 2013; Whittaker et al. 2023). The biota of islands that originated as fragments of larger continental land masses, such as Madagascar, are in large part the result of independent evolution of preexisting biota, intermixed with de-novo colonization through long distance dispersal (Wright et al. 1997; Wilmé et al. 2006; Yoder et al. 2006; Vences et al. 2009; Ali and Hedges 2022). Oceanic islands without any past connection to the continent, such as the Hawaiian archipelago or the Galápagos Islands, instead developed their biota literally from scratch, combining colonization through long distance dispersal and subsequent evolution in isolation (Wagner et al. 1999; Wagner and Herbst 2002; Carlquist et al. 2003; Parent et al. 2008; Givnish et al. 2009).

The neutral or equilibrium theory of island biogeography postulates that the assembly of island biota is independent of species-specific niche relationships and competitive effects, an assumption that was subsequently expanded to community ecology (Hubbell 2001; Rosindell et al. 2011). Based on this theory, island species assembly is determined by dispersal, immigration, and extinction rates as a function of time, size, and distance from a source (MacArthur and Wilson 1967), where each species of a given source community has the same chance to colonize an island. Yet, the probability of successful dispersal and establishment also depends on species-specific traits (Alzate and Onstein 2022), following the concept of assembly and response rules (Diamond 1975; Connor and Simberloff 1979; Drake 1990; Keddy 1992; Weiher and Keddy 1995; Moyle and Light 1996; Azeria and Kolasa 2008; Esselstyn et al. 2012; Whittaker et al. 2023). The complexity of dispersal and other traits of species-rich communities (Ozinga et al. 2004) may, however, mask species-specific traits to the extent that overall community assembly appears approximately neutral (Connor and Simberloff 1979). Addressing these questions requires an approach capable of discerning deterministic and stochastic effects on species composition.

The neutral theory in island biogeography has received support through analyses of species richness. However, richness is not necessarily correlated with composition, and it does not allow to discern trait-based effects (Kadmon and Pulliam 1993; Cassey et al. 2006; Gillespie 2007). Modeling composition is less straightforward than modeling richness, as simulations require more complex parametrization (Cassey et al. 2006; Gilbert and Bennett 2010; Laughlin and Laughlin 2013; Götzenberger et al. 2016; Barbier et al. 2018; Munoz et al. 2018; Spruch et al. 2019; Tatsumi et al. 2019; Shinohara et al. 2023). Also, community modeling through simulation usually operates at the level of individuals and with species abundances, as do other quantitative approaches to community assembly, such as CATS (Community Assembly by Trait Selection; Shipley et al. 2006; Warton et al. 2015; Strahan et al. 2018; Keddy and Laughlin 2021).

To our knowledge, no study has attempted to predict insular species assembly through simulation based on a source region, although quantitative empirical studies show some predictive patterns (Diamond 1975; Power 1975; Kadmon and Pulliam 1993; Kadmon 1995; Khedr and Lovett-Doust 2000; Azeria and Kolasa 2008; Burns et al. 2010). Molecular phylogenetic analyses that have enabled identification of sources of evolutionary radiations in island biota (e.g., Parent and Crespi 2006; Parent et al. 2008; Carvajal-Endara et al. 2017) reveal individual evolutionary histories rather than general predictive patterns.

Here we employ a simulation approach to address species assembly of leaf-dwelling (foliicolous) lichens on the Galápagos and on Cocos Island, the only tropical oceanic archipelagos in the eastern Pacific. Cocos Island is a single island dominated by wet tropical vegetation, about 550 km southeast of Costa Rica and approximately 1.9–2.4 million years old (Castillo et al. 1988; Trusty et al. 2006; Montoya 2007). In contrast, the Galápagos are an archipelago consisting of 14 major and numerous minor islands (Snell and Stone 1985) about 925 km west of the coast of Ecuador. The extant islands are between 0.7 and 4.2 million years old (Bailey 1976; Geist 1996; Geist et al. 2004; O'Connor et al. 2007) and are dominated by dry vegetation, with wet forest only developed on some of the higher mountains on, e.g., Santa Cruz Island and San Cristóbal Island (Wiggins and Porter 1971; White et al. 1993; McMullen 1999; Tye et al. 2011).

Assuming that the eastern Pacific Galápagos Islands and Cocos Island have been colonized principally from the American continent, we use leaf-dwelling (foliicolous) lichens as a case study to ask how the observed species composition can be predicted from metacommunities in the source region and potentially by species-specific traits that facilitate dispersal. Foliicolous lichens colonize living leaves of vascular plants, most typically in tropical rain and cloud forests (Lücking 2008). We hypothesize that successful dispersal and establishment are dependent on ecological and ecogeographical parameters as proxies of species-specific traits.

Methods

Inventories of the target island biotas

A list of leaf-dwelling lichens was compiled for the Galápagos (Fig. 1) based on collections made between February 1964 and April 2014 on eight islands (Española, Floreana, Isabela, Pinta, Pinzón, San Cristobal, Santa Cruz, Santiago). The collections are chiefly housed in the herbarium of the Charles Darwin Research Station in Puerto Ayora, Santa Cruz (CDS), as well as in other herbaria, including the University of Colorado Museum in Boulder (COLO). A total of 113 species were identified (Suppl. material 1: appendix S1), among them 23 presumed endemic to the archipelago (including 14 new to science to be described elsewhere), with 90 species shared with continental America based on published inventories (Lücking 2008). For Cocos Island (Fig. 1), we used the data from an earlier study made by Lücking and Lücking (1995);



Figure 1. Map of the geographic location of the sample sites illustrating geographic distance and physical distribution barriers (mountains, oceans).

the collections, housed at The Field Museum in Chicago (F), with duplicates at Herbarium Berolinense (B), were revised using modern taxonomic concepts (Lücking 2008; Jiang et al. 2020), distinguishing 100 species (Suppl. material 1: appendix S1), five endemic and 95 shared with the continent. A total of 38 species were shared between both island biota, all also found on the continent (Suppl. material 1: appendix S1).

Predictive modeling of island biota species assemblies through simulation

To perform predictive modeling of island community assembly for the Galápagos and for Cocos Island, we defined the entire continental area from the southeastern United States to Chile and Argentina as the potential source region, as the occurrence of genuine foliicolous lichen communities in the Americas is restricted to this area (Lücking 2008). Based on published inventories (Lücking 2008; Flakus and Lücking 2008; Flakus 2013; Santos et al. 2020; Martínez-Colín et al. 2021), we assembled a list of 632 species for the above defined source area. The 28 species only known from either the Galápagos or Cocos Island were excluded. The 632 species were divided into three groups: (A_1) present in the Galápagos and on the continent (90 species); (A_2) present on Cocos Island and on the continent (95); and (B) not known from either the Galápagos or Cocos Island (447).

We considered using the R package *ecolottery* (Munoz et al. 2018) to analyze species assembly; however, the underlying algorithms are generally based on individuals and species abundances and hence too complex for our question, which focuses on presence/absence data. We therefore employed a simplified simulation approach using non-metric multidimensional scaling (NMS), a standard method in community ecology (McCune and Grace 2002), to generate simulated presence/absence communities, without and with parameterized filters.

For each species, we determined scores for six environmental parameters considered important for dispersal and colonization success (Suppl. material 1: appendix S2): preferred vegetation type, seasonality, microsite (habitat exposure or light regime), elevation, distribution range, and commonness. Where available, we used previously published scores (Lücking 1997; Herrera-Campos et al. 2004; Martínez-Colín et al. 2021). For the remaining taxa, we derived new scores using data on ecology and distribution (Lücking 2008). We also modified some previously published scores based on additional data (Suppl. material 1: appendix S3).

Each parameter was scored in a way that the highest score corresponded to the highest probability of successful dispersal and colonization (see below). The scores were then multiplied for all six parameters for each species, divided by the theoretical maximum, and adjusted by the power of $1/6$, to obtain a combined environmental E

score for each species that ranged between 0 and 1 (Suppl. material 1: appendix S2):

$$E = [V \times S \times M \times A \times D \times F / (V_{\max} \times S_{\max} \times M_{\max} \times A_{\max} \times D_{\max} \times F_{\max})]^{1/6}$$

where V = preferred vegetation type, S = preferred seasonality, M = preferred microsite, A = preferred elevation, D = distribution range, and F = frequency. We employed a randomized assembly simulation to compare observed versus expected species composition for the island biota, first under the null hypothesis that species composition was neutral, then under the alternative hypothesis that composition was influenced by ecological and ecogeographical parameters expressed by the E score. For the latter, we made the following assumptions:

- The probability of successful dispersal is a function of continental species abundance, distribution range, and microsite exposure (besides being a function of distance and time); abundant species with wide distribution and found in more exposed microsites have a higher probability of being dispersed to an oceanic island than rare species with narrow distribution preferring sheltered and shaded microsites.
- The probability of successful establishment and colonization is a function of how well a species ecologically fits into the environment in the target area. For that, we took into consideration suitable vegetation types in the Galápagos and on Cocos Island, with Cocos Island featuring lowland rain and montane cloud forest and the Galápagos montane cloud forest only. The latter are further characterized by dry thornbush and exposed rock areas, which are not suitable for foliicolous lichens.

The combined E score was considered a proxy for the probability of a species of being present in a given island biota, based on predicted habitat match and likelihood of dispersal. Using the E score as weight, we simulated subsets of species from groups A₂ + B (for the Galápagos) and A₁ + B (for Cocos Island). For this purpose, we assigned a random number R between 0 and 1 to each species, multiplied with the combined E score, and pooled all species with a R × E > L_{RE}, with L_{RE} set to a value resulting in an average number of 90 (for the Galápagos Islands; L_{RE} = 0.400) or 95 species (for Cocos Island; L_{RE} = 0.392). This was repeated 100 times for each island biota.

The expected assemblies under a null model of zero influence of environmental parameters were simulated using the same approach but excluding the E scores, with R > L_R, L_R resulting in an average number of 90 (for the Galápagos Islands; L_R = 0.859) or 95 species (for Cocos Island; L_R = 0.851). All simulations and the actually observed species compositions for both island biota were ordinated using non-metric multidimensional scaling (NMS), to visualize the placement of the observed biota compared to a cloud of simulated species assemblies vs. simulated spe-

cies assemblies filtered by E score. To support the graphic visualization, we compared the distance values between the island biota and each of the simulated subsets using a non-parametric Mann-Whitney U test.

To filter out species from the overall continental species pool expected in the island biota based on their ecogeographical parameters (i.e., reflecting potentially favorable traits for successful dispersal onto one or both of the archipelagos), we computed the difference D between their frequencies in the simulated random repeats with and without implementing the E score. We then performed linear regression between D and the E score for each species, to determine at which value of E the regression line intersected D = 0 (i.e., an E score that made no difference whether a species was more or less frequently present in the simulated repeats). That value was used as the cut-off to calculate the amount of species with a higher E score, i.e., those more likely to appear in the individual island biota.

In order to test whether the Galápagos biota has a higher affinity to Central or to South America, we repeated the procedure under two scenarios: only including species present in South America or only those present in Central America. For each scenario we generated 100 random repeats and calculated the distance values between the observed composition and each of the random samples, comparing the two scenarios using a non-parametric Mann-Whitney U test. This approach was only done for Galápagos, as for Cocos Island we found that assembly was not predicted by the E score alone.

In addition to the simulation approach, we also used an empirical approach to assess the composition of the island biota compared to that of the continent. With the 632 species divided into the three groups outline above, (A₁), (A₂), (B), we compared the distribution of scores for the six parameters between group A₁ and groups A₂ + B and group A₂ and groups A₁ + B using a non-parametric Mann-Whitney U test.

We also compared overall species composition (including the putatively endemic additional 28 species) between the Galápagos, Cocos Island, and four selected lowland and montane sites (Fig. 1) in continental Ecuador and Costa Rica (Lücking 1999a, b): Jatun Sacha Biological Reserve (Napó, Ecuador, lowland at 450 m elevation), Guajalito Reserve (Pichincha, Ecuador, montane at 1800 m elevation), La Selva Biological Station (Alajuela, Costa Rica, lowland at 50 m elevation), and Las Cruces Biological Station (Puntarenas, Costa Rica, montane at 1200 m elevation). To that end, we employed NMS and cluster analysis. The four sites were selected due to their geographic situation (two in Central and two in South America), representing the two ecosystems prevailing in the two archipelagos (lowland and montane rainforest), with all four sites being of comparable extension regarding the inventoried area (about 10 ha each) and each having been inventoried using the same approach (Lücking 1999a, 1999b).

Statistical tests were performed in STATISTICA 6.0™. Multivariate analyses were performed in PC-Ord 6.0 (McCune and Mefford 1999; McCune and Grace 2002), with

the following parameters: as distance measure for both NMS and clustering we used the Sørensen (Bray-Curtis) index; NMS was run with 100 repeats for real data and with randomization using 250 repeats, with three axes as final solution, step length = 0.20, stability criterion = 0.000010, and maximum of 250 iterations. The algorithm used for clustering was flexible beta, set to -0.25.

Results

All environmental parameters resulted in significant differences between lichens found in the Galápagos compared to those not known from there (Fig. 2, Table 1). The strongest effect was found for frequency, followed by vegetation, elevation, distribution, microsite, and seasonality. For Cocos Island, five of the six parameters showed significant effects: frequency, followed by distribution, vegetation, seasonality, and elevation. No significant effect was found for microsite. Thus, for Cocos Island the strongest effects were found for parameters presumably influencing the probability of successful dispersal, whereas for the Galápagos, the strongest effects involved parameters related to both successful dispersal and establishment.

Ordination of the two island biota with the continental sites (Fig. 3) suggested a closer relationship of the Galápagos with the montane site from continental Ecuador (Guajalito), followed by the Costa Rican montane site (Las Cruces), suggesting that habitat ecology was more important for biotic similarities than geography. However, for ecologically equivalent continental sites (montane: Guajalito and Las Cruces; lowland: Jatun Sacha and La Selva), distance did affect biotic similarity at least for the Galápagos. No discernable effect was found for Cocos Island, which was equidistant in species space to the continental sites in Central and South America.

Cluster analysis suggested close similarity in species composition between the two continental lowland sites (Jatun Sacha, La Selva), with the Costa Rican montane site (Las Cruces) as sister to this group (Fig. 3). Cocos Island clustered with this group at a low similarity level, whereas the Galápagos and the Ecuadorian montane site (Guajalito) clustered separately.

The simulation approach showed the Galápagos foliicolous lichen biota to fall near the center of a tight cluster formed by the randomized subsets filtered by E score (Fig. 4). The 3-dimensional ordination was significant at $p = 0.0040$. The outcome for Cocos Island also showed a relationship of the observed composition with that predicted by E score, but the observed composition fell slightly outside the tight cluster (Fig. 4). Also here, the 3-dimensional ordination was significant at $p = 0.0040$.

The E score corresponding to a difference $D = 0$ in the frequency between simulated species assemblies with or without ecogeographical indices was 0.454, thus species with an E score of 0.454 had equal probability to appear in a simulated repeat with or without considering the E score. A total of 260 out of 632 species exhibited

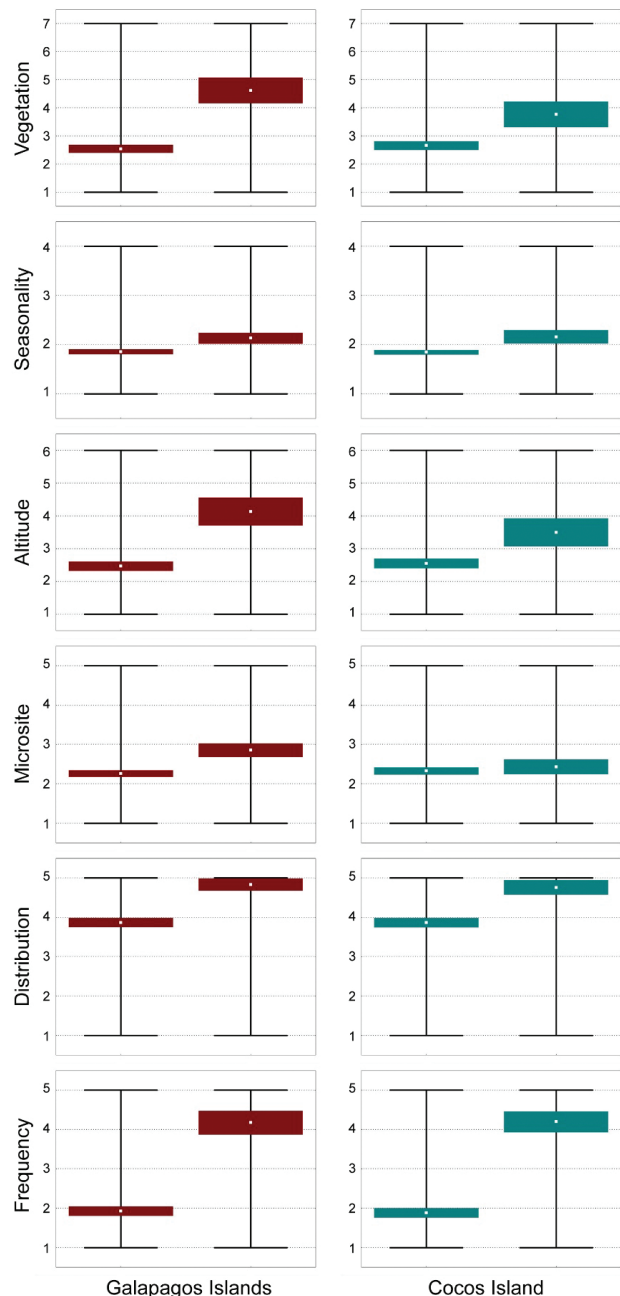
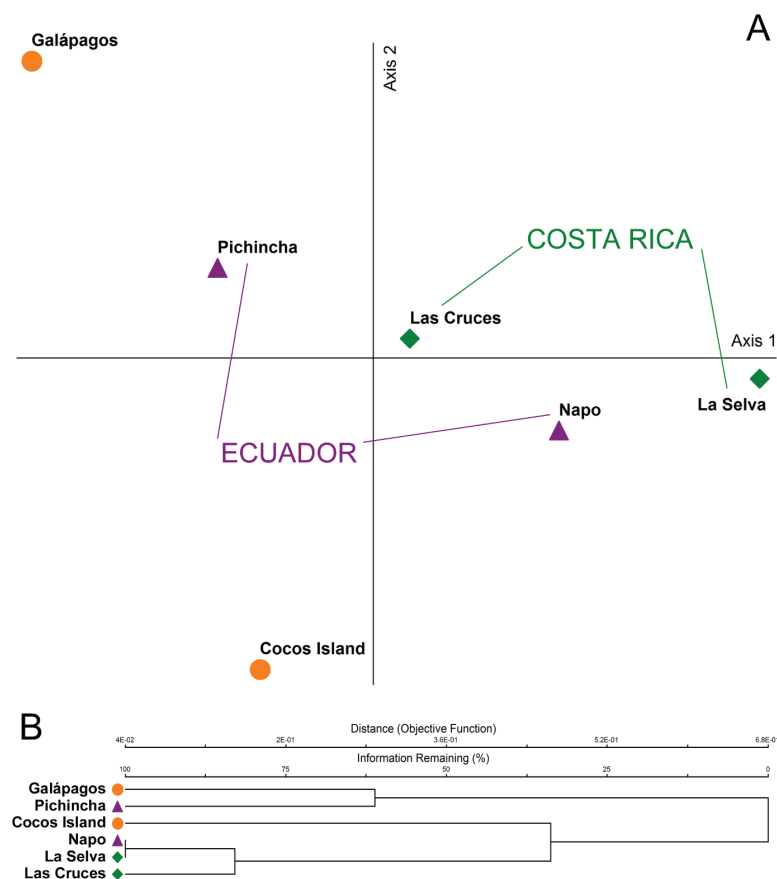


Figure 2. Ecological parameters scores for lichens present in the island biota (left columns) and those known only from the continent (right columns), calculated using a Mann-Whitney U test. The y-axis indicates the range of scores for each parameter (see Suppl. material 1: appendix S2 for exact definition of each score for each parameter). The further apart the two scores are, the more important is the ecological parameter for the observed differences. Diagrams on the left show scores for the Galápagos Islands, those on the right the ones for Cocos Island.

an E score higher than 0.454, up to a maximum of 0.963 (Suppl. material 1: appendix S3). Of these, 78 species (out of 90) occur in the Galápagos Islands and 73 (out of 95) on Cocos Island. A total of 61 species had an E score higher than 0.708, halfway between the minimum (0.454) and maximum (0.963). Of these, 44 species occur in the Galápagos and 29 on Cocos Island. Thus, the

Table 1. Results of the comparison of environmental parameter scores between lichens present in the island biota and those known only from the continent, using a Mann-Whitney U test.

Parameter	Galápagos Islands		Cocos Island	
	Z adjusted	p-level	Z adjusted	p-level
Vegetation	-8.68	0.0000	-4.72	0.0000
Seasonality	-4.33	0.0000	-4.48	0.0000
Microsite (habitat exposure)	-6.46	0.0000	-1.39	0.1638
Elevational range	-7.47	0.0000	-4.28	0.0000
Distribution Range	-6.59	0.0000	-6.52	0.0000
Commonness	-11.42	0.0000	-12.52	0.0000

**Figure 3.** NMS ordination (above) and cluster analysis (below) of the Galápagos and Cocos Island compared to four continental sites, based on reported species compositions of foliicolous lichens for each site.

higher the E score, the higher the proportion of species observed in the island biota, i.e., the higher the likelihood for a given species to be present in either archipelago, with the Galápagos consistently showing a higher percentage than Cocos Island.

Of the 50 species with the highest E scores, 43 were found in the Galápagos and/or Cocos Island. The seven missing taxa included six Gomphillaceae (*Asterothyrium argenteum*, *A. leptosporum*, *A. leucophthalmum*, *A. microsporium*, *Calenia monospora*, *Psorotheciopsis patellarioides*) and one Strigulaceae (*Strigula nemathora* f. *hypothelia*). The 50 species with the next highest E scores had 22 missing in both the Galápagos and Cocos Island, among these 14 Gomphillaceae, including four additional species of *Asterothyrium* and one of *Psorotheciopsis*. Thus, there appears to be a disproportional absence of

Gomphillaceae and particularly of the two closely related genera *Asterothyrium* and *Psorotheciopsis*.

Among the 260 species with an E score higher than 0.454, nine families were represented by five or more species (Table 2). Among these, Gomphillaceae, with 100 species, Byssolomataceae (formerly known as Pilocarpaceae; 55), and Porinaceae (34), were the most representative. Among the 78 species of these observed in the Galápagos, Byssolomataceae (28 species), Gomphillaceae (23), and Coccocarpiaceae (6) were most speciose, with only Byssolomataceae (36% versus 21%), Coccocarpiaceae (7.7% versus 3.5%) and Coenogoniaceae (6.4% versus 3.5%) showing an increased proportion compared to the 260 species overall. Slightly different figures apply to Cocos Island, with Byssolomataceae (21 species), Gomphillaceae (19), and Strigulaceae (10) being most speciose and Byssolomataceae (29% versus 21%),

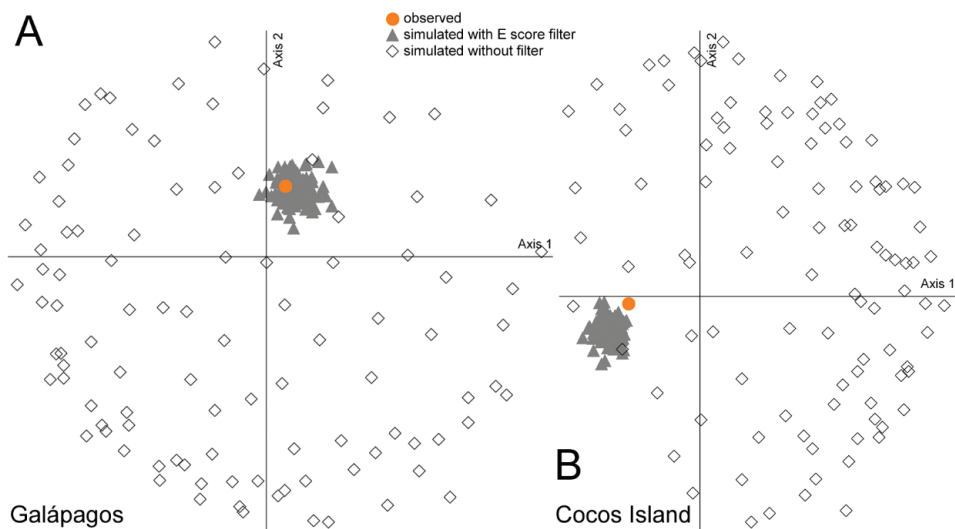


Figure 4. NMS ordination of species composition in the Galápagos (left; Group 0) and Cocos Island (right; Group 0) in comparison with randomized subsets obtained by using environmental parameters (Group 1) and with entirely stochastic subsets disregarding environmental parameters (Group 2). Galápagos lies at the center of the random subsets generated by using environmental parameters, whereas Cocos Island lies close to the corresponding subset.

Table 2. Families with five or more species among the 260 species with an E score of higher than 0.454, and their relative proportion of species present in the two island biota.

Family	Species	Out of	Percentage	Galápagos	Out of	Percentage	Cocos	Out of	Percentage
Graphidaceae	100	260	38.5%	23	78	29.5%	19	73	26.0%
Byssolomataceae	55	260	21.2%	28	78	35.9%	21	73	28.8%
Porinaceae	34	260	13.1%	5	78	6.4%	9	73	12.3%
Strigulaceae	18	260	6.9%	5	78	6.4%	10	73	13.7%
Coenogoniaceae	9	260	3.5%	6	78	7.7%	2	73	2.7%
Coccocarpiaceae	9	260	3.5%	5	78	6.4%	0	73	0.0%
Roccellaceae	7	260	2.7%	0	78	0.0%	3	73	4.1%
Arthoniaceae	6	260	2.3%	1	78	1.3%	2	73	2.7%
Malmideaceae	5	260	1.9%	0	78	0.0%	0	73	0.0%

Strigulaceae (13.7% versus 6.9%), and Roccellaceae (4.7% versus 2.9%) those with an increased percentage compared to the 260 species. Thus, in both island biota, Byssolomataceae was consistently over-represented.

When comparing the observed species composition in the Galápagos with the simulated subsets generated focusing on species present in South America vs. those present in Central America, the average Sørensen distance was not significantly different (adjusted $Z = 1.41$, $p = 0.1586$; South America: 0.63 ± 0.041 ; Central America: 0.64 ± 0.040). There was a slight tendency for the Galápagos to fall within the portion of the diagram that had a higher proportion of simulated subsets generated from the pool of species present in South America (Suppl. material 1: appendix S4).

Discussion

Approach and study group

To our knowledge, this is the first study that explores deterministic vs. stochastic components of species assembly on remote oceanic islands using a simulation approach for

a large community of species from a continental source metapopulation. Island species composition has usually been addressed using quantitative empirical approaches (Ward and Thornton 2001), explicitly so when examining species composition on relatively small river islands in the southern United States (Kadmon and Pulliam 1993), or islands close to the Canadian sea shore (Burns 2007), both focusing on plants. Determinism vs. stochasticity has also been addressed in evolutionary radiations (e.g. Whittaker and Fernández-Palacios 2007; Losos 2010) or for habitat filtering correlated with phylogenetic relationships among plants (Carvajal-Endara et al. 2017). In most studies, assembly rules were analysed with a focus on competitive effects, often using bird guilds as model groups (Diamond 1975; Sanderson et al. 2009). In the latter study (Sanderson et al. 2009), also used a simulation approach to generate a null model, but this was restricted to the pairwise occurrence of bird species present on the analysed island biota and did not attempt to draw simulated communities from a continental source. The study by Cavajal-Endara et al. (2017), focusing on Galápagos plant communities, comes closest to our approach in comparing the Galápagos biota to a large continental reference pool, taking into account environmen-

tal parameters and species-specific dispersal capacities. However, these authors did not simulate communities but instead placed them into a phylogenetic framework.

Here we used leaf-dwelling lichens as a case study, since the simulation approach requires a large proportion of ‘matrix-derived’ species (Watson 2002), i.e., taxa shared between islands and continental source biota. In land plants, endemism in oceanic islands, such as the Hawaiian archipelago or the Galápagos, reaches 40–90%, in terrestrial vertebrates and arthropods 50–98% (Loope et al. 1988; Wagner et al. 1999; Wagner and Herbst 2002; Parent et al. 2008; Tye et al. 2011; Jaramillo et al. 2014; Jiménez-Uzcátegui et al. 2006; Roque-Álbelo and Landry 2018; Buchholz et al. 2020; Whittaker et al. 2023), rendering a simulation approach less effective, as many or most of the taxa present in an island biota cannot be predicted through simulation from a source region but are the result of complex evolutionary histories. In foliicolous lichens, the degree of endemism is considered low, currently estimated at 20% for the Galápagos and 5% for Cocos Island, leaving 80–95% ‘matrix-derived’ species that are shared with the continent. One may argue that these figures are based on phenotype-derived taxonomic concepts, which have been challenged for island lichen biota in some studies (Moncada et al. 2014, 2020; Dal Forno et al. 2017; Lücking et al. 2017; Simon et al. 2018). Unfortunately, few molecular phylogenetic studies are as yet available for foliicolous lichens, and we cannot currently place the Galápagos foliicolous lichen biota into a phylogenetic context. The available studies focused on other regions, such as China, New Zealand, and Brazil (Ford et al. 2019; Woo et al. 2020; Jiang et al. 2021; Xavier-Leite et al. 2022). Cryptic diversification in foliicolous lichen has usually been detected within complexes corresponding to previously recognized morpho-taxa, i.e. the cryptic species are closely related to each other and share the same ecology, such as in the genera *Gyalectidium* and *Tricharia* (Xavier-Leite et al. 2022). Thus, even if some cryptic speciation may have occurred in the Galápagos foliicolous lichen biota, these species can still be treated as “matrix-derived” with regard to the underlying species complex. Sanderson et al. (2009) applied similar considerations when referring to bird taxa in island biota as superspecies, i.e. evolutionary units of closely related species.

Deterministic vs. stochastic components of island species assembly

Our results demonstrate that, while the exact species composition cannot be predicted from the continental source metacommunity, a close enough prediction is possible. The foliicolous lichen biota in the Galápagos and on Cocos Island are a subset of taxa that have comparatively high E scores, thus a higher probability to be successfully dispersed and established on oceanic islands. The composition of foliicolous lichen island biota is therefore largely deterministic in terms of the parameters that predict the assembly pool, but to some extent remains stochastic with regard to the subset of species actually

observed out of that pool that made it to the islands, since less than 80 out of the 260 species of the potential assembly pool are observed in each of the archipelagos (71 out of the 100 with the highest E scores). Whether this is an effect of time (more species may arrive successively) or competition (each archipelago has a maximum carrying capacity), or whether there are additional filter effects in place, is unknown. Competition is rather unlikely, given the ephemeral nature of the leaf substrate and the notion that epiphyll cover is mostly below 10% (Lücking 1998a). The over-representation of certain taxa, such as Byssolomataceae, and the absence of others that would have been predicted based on the environmental parameters, such as certain Gomphillaceae and particularly species of the genus *Asterothyrium*, underlines the disharmonic nature of the Galápagos foliicolous lichen biota, a known phenomenon in island biota (Williamson 1981; König et al. 2021). In the present case, the exact reason for this disharmony is not known, but one factor not taken into account is phorophyte composition and particularly leaf longevity as a phorophyte-specific trait, as certain lichen taxa appear in early successional stages whereas others depend on longer leaf time spans (Lücking 1998b; Martínez-Colín et al. 2021). Another factor is of course the notion that sampling rare species itself is stochastic, i.e. the lack of rare species in a sample is not proof of their absence.

Our predictive model allows us to evaluate key environmental parameters for long distance dispersal and colonization success of leaf-dwelling lichens. It comes as no surprise that commonness is of primary importance for the composition of island biota. The probability of successful dispersal to an oceanic island through vectors such as air currents directly relates to the commonness of a species in the source area, also because the latter is an indication of the effectiveness of species-specific dispersal mechanisms. Rare species are less likely dispersed across large distances and rarity in itself may be a result of inefficient dispersal. Common species typically also have broader ecological amplitudes and are better equipped to successfully colonize a new area that might not exactly match conditions of the source area (Andow 2003). The distribution range of an organism also influences its potential dispersal to remote oceanic islands, not only because it may shorten the distance between source and destination, but a broader range also increases the probability of random dispersal through a variety of vectors. Commonness might thus be a better predictor of dispersal capabilities than actual dispersal traits. In their study on the Galápagos flora, Carvajal-Endara et al. (2017) found a stronger effect of environmental filters than dispersal traits shaping species composition, but they did not include commonness as a parameter. In foliicolous lichens, environmental parameters were more predictive for the Galápagos than for Cocos Island. In the natural vegetation of the Galápagos, leaf-dwelling lichens are largely restricted to mountain and cloud forests of the humid highlands, whereas the dry lowland vegetation represents a barrier to successful colonization. Thus, even though the Galápagos offer much broader

habitat diversity than Cocos Island, this does not translate into greater opportunity for foliicolous lichens, since in the Galápagos, only species adapted to mountain forests can successfully establish. Although much smaller and less diverse ecologically, Cocos Island encompasses a wider range of habitats suitable for foliicolous lichens, including lowland and montane forests, therefore habitat preferences are not as critical for successful colonization of that island.

Tolerance of species towards seasonality appears to be equally important for Cocos Island and the Galápagos. This comes as a surprise, because the rain forests in Cocos Island do not exhibit substantial seasonality. Lichens restricted to permanently wet rain forest should thus find suitable conditions on Cocos Island. This contrasts with species adapted to at least some seasonality, such as in the Galápagos, where rainfall markedly varies throughout the year (Colinvaux 1972, 1984; Trueman and d'Ozouville 2010). Thus, slightly different suites of species are better adapted to colonize either Cocos Island or the Galápagos, and seasonality acts differently as a limiting factor.

A dominant parameter providing a filter for successful dispersal and establishment is the elevational range where foliicolous lichen species occur, particularly in the Galápagos. Notably, the affinity of the Galápagos foliicolous lichen biota is closer to continental montane cloud forest than to lowland rain forest, even if absolute elevations would suggest otherwise. On Santa Cruz, where most of the data about the foliicolous lichen biota originate, the *Scalesia* forests and *Miconia* scrub of the humid zone occur between 300 and 700 m elevation. In Ecuador, the most similar location in terms of the foliicolous lichen biota is Guajalito, at 1800 m elevation, and not Jatun Satcha, which at 400–500 m elevation lies within the range of the Galápagos foliicolous lichen biota of Santa Cruz, yet displays a different species composition (Lücking 1999a). The compression of elevational belts in island biota might be explained by a lower mass elevation effect (MEE), augmented by the effects of oceanic currents (Troll 1973; Van der Werff 1978; Zhao et al. 2015; Irl et al. 2016; Kienle et al. 2023). Unfortunately much of the original vegetation of the Galápagos highlands has been agriculturally modified and affected by invasive species in the past century, but this should not have affected the occurrence of potentially natural vegetation corresponding to montane forest within the same elevational zonation observed today (Restrepo et al. 2012; Trueman et al. 2013; Rivas-Torres et al. 2018). This means that the current *Scalesia*-forests and *Miconia*-scrubland can be used as proxies for the natural humid zone present prior to human interventions, supporting the interpretation of the observed zonal compression as a result of a lower MEE.

An additional factor may be geographic barriers between potential source area and islands. Whereas variation in the geographic distance of the four continental sites from Galápagos is negligible, the location of the sites in relation to geographic barriers is notable: for species to reach the Galápagos from the Amazon, they have to cross the Andes, whereas those occurring on the western slopes of the Andes (Chocó) do not face such a barrier. Since the mountain

forest at Guajalito (Chocó) differs in ecology from the lowland forest at Jatun Sacha (Amazon), the factors of elevation and geographical barrier cannot be readily separated; to test the barrier hypothesis, a comparison of lowland locations west and east of the Andes would be needed. The only existing inventory of foliicolous lichens thus far at a lowland site in the Chocó is that of Tutunendo, listing 113 species (Mateus et al. 2012). This site has not been included in the analysis as the sampling procedure differed from the other four sites and the sampling is likely very incomplete. Fifty-nine species occurring in the Galápagos are also present at Tutunendo and/or Jatun Sacha; of these, 21 are shared between Tutunendo and Jatun Sacha, whereas five were found only at Tutunendo and 33 only at Jatun Sacha. Thus, the proportion of species shared between the Amazon site and the Galápagos, but not present at the Chocó site, is substantially higher (56%) than the proportion shared between the Galápagos and the Chocó site, but not present at the Amazon site (8.5%). This does not support the hypothesis of the Andes acting as a geographic barrier.

Dispersal and establishment

An aspect not addressed in this study is how dispersal efficiency and colonization success affect endemism on oceanic islands. Leaf-dwelling lichens thrive in wet tropical forests. The higher degree of inferred endemism in the Galápagos versus Cocos Island, with 20% versus 5%, is thus remarkable. Endemism is an indirect measure of isolation, both spatially and temporally. A reason for the difference could be the higher geological age of the Galápagos, with over four million years for the oldest extant island and an estimate of over 14 million years for now submerged islands (Rassmann 1997; Werner et al. 1999; Christie et al. 1992; Werner et al. 1999; Harpp et al. 2005). Ecological factors may also explain the higher degree of endemism of leaf-dwelling lichens in the Galápagos. While Cocos Island is dominated by contiguous rain forest, in the Galápagos the humid cloud forest occurs in isolated patches across the various islands, with few potential phorophytes providing long-lived leaves. Leaf-dwelling lichens are mostly found on shrubs, such as the endemic *Miconia robinsoniana*, or fern fronds (*Pteridium*, *Polypodium*, *Tecaria*), including the endemic tree-fern *Cyathea weatherbyana*, and are otherwise common on introduced plants (especially *Citrus* and *Coffea*). Given these constraints, the natural vegetation available for colonization by these lichens in the Galápagos was likely highly fragmented and may have contributed to a higher degree of endemism.

Our approach relied on ecogeographical parameters as proxies for species traits, in particular those that would facilitate successful dispersal and establishment, e.g., fitting habitat preferences, commonness, and exposure to dispersal agents. We did not take into account the actual dispersal traits, such as the species-specific nature of propagules. In plants, species with wind-dispersed seeds appear to be more efficiently dispersed than those with heavy fruits (Barrett 1998). Porter (1976) demonstrated

for the Galápagos that most plant species reached the archipelago by birds, favoring seeds that stick to surfaces or those from bird-adapted fruits, although this finding was challenged by Vargas et al. (2012).

In lichens, little is known about dispersal mechanisms and efficiency of propagules. Two traits must nevertheless be considered relevant: diaspore characteristics and photobiont availability. Microscopic diaspores (soredia, isidia, spores) are an important component of the “air spora”, the most minute viable parts of “aerial plankton”. The minute dispersal agents of lichens are subject to the same aerodynamics as any other, wind-distributed fungal spores and pollen (Gregory 1973; Lacey and West 2006). Nevertheless, for how long lichen propagules remain viable in the air and how efficiently they are carried along remains largely unknown. Functional traits of these propagules could act as filters, increasing or decreasing the probability for successful long distance dispersal for particular species (Burns 2005). Sedimentation rates, terminal velocity and thus the suspension in air are directly linked to size, density and shape of a particle (McCartney and Fitt 1985; Gregory 1973; Lacey and West 2006). Long distance dispersal through the atmosphere further depends on propagule viability; diaspores suspended in air are subjected to desiccation, high radiation and other extreme environmental stresses (Gregory 1973; Lacey and West 2006). Smith (1995) reported an increased proportion of species with pigmented and/or large ascospores among Hawaiian lichens, suggesting these two traits might act as dispersal filters. However, ascospore traits are also correlated with other ecological characteristics such as habitat preference and commonness (Cáceres et al. 2008).

The second important trait is photobionts, especially since most leaf-dwelling lichens disperse by ascospores and rely on encountering an appropriate photobiont (Lücking 2008). A close correlation has been reported between habitat preferences and association with particular photobionts (Lücking 1999c; Yahr et al. 2004), to the extent that parameters such as microsite preference may be a proxy for photobiont associations. Belinchón et al. (2015) suggest that the relationship of mycobionts with photobionts correlates with distribution patterns along climate gradients. Svensson et al. (2016) observed that photobiont availability may limit colonization success for a particular mycobiont, even if other lichen species that share the same photobiont are already present in the immediate vicinity.

Two further aspects are disturbance and introduced species, both going hand in hand (Pyle 1995; Cronk and Fuller 1995; Myers and Bazely 2003; Von Holle 2005; McDougal and Turkington 2005; Theoharides and Dukes 2007; Price et al. 2011; Quiroz et al. 2011). Disturbance primarily affects species that occur in native habitats and especially those in sheltered microsites, so that in disturbed biota the proportion of rare and/or endemic taxa might be reduced. One would therefore expect the stochastic element of disturbed island communities to be reduced, leading to overestimation of deterministic components. Species introduced by humans will increase this effect, since intentional and acciden-

tal introductions favor abundant taxa with wide distribution ranges (Sakai et al. 2001). For our study group we expect these effects to be present but minor. Leaf-dwelling lichens are less affected by disturbance because they survive in small forest fragments, and accidental introductions will likely not add species that are not already present; yet, disturbance effects may have eliminated very rare species.

Oceanic vs. continental islands

The approach presented here applies to oceanic islands (“immigration experiments”). Continental islands or fragments (“landbridge archipelagos”) do not develop their biota from scratch, but start with an already present species composition that subsequently changes through a combination of evolutionary processes, extinction and de-novo colonization. Apart from evolutionary divergence and de-novo colonization, i.e. only considering matrix-derived species, relaxation through extinction may result in a nested pattern of species composition compared to the once connected continental landmass (Wright et al. 1997). If a continental island starts with a “complete” biota, comparable to the continental species pool, whereas an oceanic island starts from zero, to what extent would extinction on one hand and de-novo assembly on the other result in potentially similar, nested species composition? The probability of extinction from a pre-existing pool vs. the probability of successful dispersal and establishment into an “empty” environment from a source pool should be linked: common versus rare species are less versus more likely to become extinct from a pre-existing pool and, given our data, are also more versus less efficient in reaching and colonizing remote islands. Unfortunately, at least the Neotropics do not seem to offer a natural constellation to test this hypothesis in situ for foliicolous lichen biota.

Conclusions

Our analysis of foliicolous lichens in the Galápagos and on Cocos Island strongly suggests that these species reached the islands not purely by chance. Instead, the biota of leaf-dwelling lichens in both areas represent a nested subset of species determined by habitat filtering and dispersal efficiency as expressed by commonness. Therefore, even though the exact species composition of island biota cannot be predicted, the pool of species from which these biota are assembled is not random and can be determined with a certain accuracy.

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Author Contributions

RL and FB conceived this study. All authors collected the material and worked on taxonomic identifications. RL and BM assembled the final classification of the species. RL and FB analysed the data and wrote the draft manuscript. All authors revised the manuscript.

Data Accessibility

All data analyzed in this study are available through the supplementary material, specifically Suppl. material 1: appendices S1–S4.

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Supplementary materials

Supplementary material 1

appendices S1–S4 (.pdf)

Link: <https://doi.org/10.21425/fob.17.133819.suppl1>