

Phylofloristics: an example from the Lesser Antilles

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Abstract

Aims

The last decade has seen many plant ecologists integrating phylogenetic analysis into ecology to explain patterns of species co-occurrence and compositional similarity across assemblages. Despite the advances in this area, there are still some challenges that need to be addressed. One challenge is that most of the phylogenetic studies of plant assemblages have focused only on a small proportion of all of the vascular plants that co-occur (e.g. woody plants), while much of the remaining co-occurring flora has been ignored.

Methods

Here we introduce an analytical approach that we term phylofloristics that analyzes the compositional similarity of floras in relation to spatial and environmental gradients to understand their assembly. As an illustration, we assembled a large phylogenetic tree for the flora of the Lesser Antilles and evaluated the patterns of floristic and phylofloristic similarity among the island-specific floras. We analyzed

the relationship of these similarities with spatial and environmental distance and compared the results for non-endemic and endemic lineages.

Important Findings

The results show a major influence of environmental heterogeneity on the assembly of island floras and far less evidence for the importance of dispersal limitation of lineages and species. This study highlights the importance of incorporating broader taxonomic sampling to improve our understanding of assembly processes in ecology. We expect future phylofloristic studies will improve the approach we have taken by generating more refined phylogenetic trees and by incorporating phylogeographic information.

Keywords: biogeography, Caribbean, flora, phylogeny, plant geography

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INTRODUCTION

The composition of plant assemblages can in large part be explained by a long history of biogeographic and evolutionary events that are often not the focus of ecologists (Webb *et al.* 2002). Analyses of the composition, assembly and turnover of plant assemblages that only focus on present day and local-scale ecological interactions are therefore incomplete and will not be able to successfully explain the primary reasons why plant species composition varies across regions (Swenson 2011a, 2013). While the injection of phylogenetic information into ecology has often been aimed at answering questions regarding the relationship between similarity and co-occurrence of species on local-scales (e.g. Swenson *et al.* 2006, 2012a; Webb 2000), one of the great promises of integrating phylogenetic information into ecology is that it will help unveil the biogeographic and evolutionary processes that explain the majority of the variation in species composition

and diversity among floras (Swenson 2013). In other words, phylogenies have been commonly, and controversially, used as proxies for ecological similarity in ecology, but they may also be used as backbone pieces of information from which inferences regarding the assembly of regional species pools can be derived.

We argue that in order to continue the successful integration of phylogenetics and ecology, future investigations likely will have to scale out spatially. This scaling out will capture the regional species pool and thus result in the taxonomic sampling of the ‘community phylogeny’ to become less sparse, allowing for stronger inferences about relatedness and co-occurrence. For example, plotting spatial distributions or traits on a community phylogeny of 300 species in a rain forest entails analyzing one to a few species in a genus that may contain hundreds of species that are not sampled. Thus, the inferences one can make about the imprint of evolution on co-occurrence are limited (Swenson 2013). Expanding the

spatial scale of the study increases the sampling within lineages and will likely increase our ability to make useful inferences regarding the evolutionary and biogeographic imprint on present day co-occurrence. In so doing, this also moves the field away from basing research on an assumed relationship between ecological similarity and relatedness and towards using the phylogeny as a piece of baseline information on which traits and distributions can be draped.

One approach to making stronger inferences in ecology using densely sampled phylogenies is to focus on one or a few lineages. This approach is attractive as it allows for detailed insights regarding the evolutionary history underlying present day distributions and co-occurrence. That said, this approach is generally only useful if the lineage or lineages studied are dominant (e.g. Cavender-Bares *et al.* 2004) or form their own trophic level (e.g. Gillespie 2004; Losos *et al.* 1998). In most other cases, the lineage being studied does not dominate the flora or fauna being analyzed and does not form its own trophic level. Thus, many interactions are not considered. We cannot fault such studies as it is difficult to conduct a phylogenetic analysis of an entire flora although in the not too distant future we foresee that advances in informatics and sequencing technology will permit phylogenetic analysis of entire floras (Smith *et al.* 2009). In particular, advances in our mapping of the spatial distributions of plant species and our ability to infer large phylogenetic trees will pave the way for truly large-scale analyses of the assembly of floras (Swenson 2011a, 2013).

In this paper, we introduce the term ‘phylofloristics’ to define a phylogenetically enabled analysis of the species composition between entire floras that are spatially well-defined regional species pools. The aim of this analysis is to uncover the evolutionary and biogeographic history that potentially explains the assembly processes shaping regional species pools. As it is currently not possible to generate a molecular phylogenetic tree for an entire flora down to the species level, due to a lack of sequence for all species, we illustrate our phylofloristic approach with a phylogenetic tree resolved to the genus level for angiosperms of the Lesser Antilles. Therefore, evolutionary and biogeographic relationships between congeners will not be detected.

We focus on the Lesser Antilles (Fig. 1) in this article for several reasons. First, islands are spatially well defined, thereby permitting concrete analyses of phylofloristic similarity and eliminating the need to arbitrarily define the spatial boundaries of the regional species pools being compared. Second, the Caribbean as a tropical region is a biodiversity hot spot and thus allows the assembly of large regional species pools. Lastly, the flora in the Lesser Antilles is well documented compared with that in most other tropical regions, surpassed in detail by perhaps only the Hawaiian archipelago. Recent floristic work of the entire West Indies provides the taxonomic standardization necessary to apply phylofloristic analyses (e.g. Acevedo-Rodriguez and Strong 2008; Howard 1974, 1977, 1979, 1988, 1989a, 1989b; Santiago-Valentin and Olmstead 2004). This work has also provided baseline

information regarding the floristic similarity between islands in the region and between the species pools of islands and the mainland, which can be compared to phylogenetic similarity measures between the same species pools.

Here we ask the same fundamental questions that are addressed in floristic analyses and community assembly analyses, but the analytical approach incorporates phylogenetic information. Specifically, we ask the following: (i) What is the degree of the floristic and phylofloristic similarity between islands? (ii) Does the spatial or environmental distance between islands best predict their similarity? We expect dispersal limitation to increase the variance explained by space and habitat filtering to increase the variance explained by the environment. (iii) Is the similarity of the non-endemic component of island floras better explained by spatial or environmental distance and how does that compare to the endemic component? We expect that non-endemic species are better dispersers and therefore are less likely to have their compositional similarity dictated by spatial distance. (iv) What additional biogeographic and evolutionary information can be distilled through the use of phylogenetic information that cannot be detected by analyzing the floristic similarity of islands? It is expected that islands that are closer together may share congeners due to dispersal limitation and *in situ* speciation and this evolutionary similarity may not be detected using species-level metrics without additional genus- or family-level metrics. The analytical approach borrows conceptual and analytical tools from studies that have sought to quantify phylogenetic beta diversity of assemblages (e.g. Bryant *et al.* 2008; Swenson 2011b; Swenson *et al.* 2012a, 2012b; Qian *et al.* in press; Zhang *et al.* 2013) with the primary difference

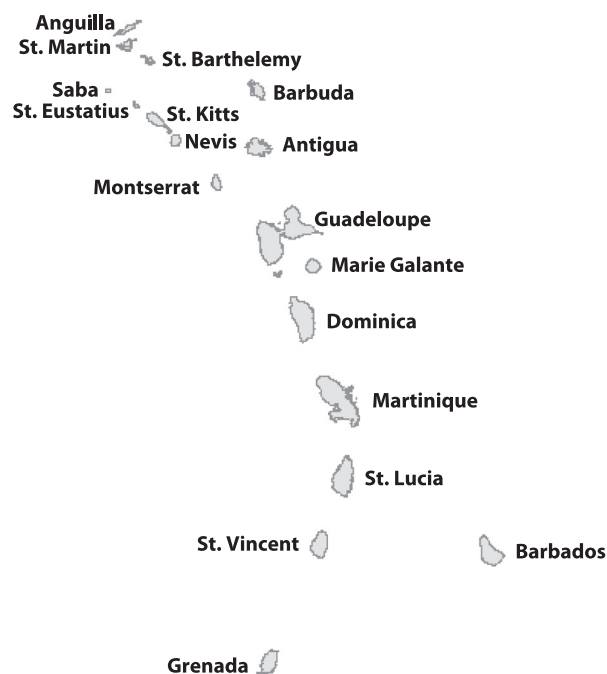


Figure 1: a map of the Lesser Antilles.

being that our study focuses on the entire flora of angiosperms and entire large-scale and spatially well-defined regional species pools.

METHODS

Floristic data and construction of the phylogenetic tree

The present analyses utilized the *Flora of the Lesser Antilles: Leeward and Windward Islands* published in six volumes by Howard (1974, 1977, 1979, 1988, 1989a, 1989b; Table 1). The flora presents a comprehensive synonymized inventory of the vascular plants on each of islands in the Lesser Antilles. Only native species were utilized for the analyses. All sub-species and varieties were not recognized in the analyses. Thus, island specific varieties were considered the same species and represented as a single tip in the phylogeny.

A phylogenetic hypothesis was constructed for all of the species in the flora using the software Phylomatic (Webb and Donoghue 2005; Fig. 1, online supplementary material). Phylomatic utilizes the angiosperm phylogeny group III phylogeny as a reference tree to which the species could be appended *via* taxonomy basally and terminally of this backbone. The majority of congeneric relationships were not resolved in the phylogeny. In order to assess the sensitivity of the results to tree topology, the phylogeny was randomly resolved 100 times using the software Mesquite. The original phylomatic tree and the 100 resolved phylogenies were used in the following analyses, but we report only the mean statistical result from the 100 trees.

Analyses

The floristic similarity of the Lesser Antilles islands was initially quantified using a Jaccard's Index in the R package 'vegan'. This provided a metric of the species similarity between islands. Next, the phylogenetic similarity between islands was quantified using two different metrics. The first metric, D_{pw} , is a pairwise phylogenetic dissimilarity between two communities, k_1 and k_2 , which serves as an overall, or 'basal', indicator of phylofloristic dissimilarity. It is defined as the following:

$$D_{pw} = \frac{\sum_{i=1}^{n_{k_1}} f_i \overline{\delta_{ik_2}} + \sum_{j=1}^{n_{k_2}} f_j \overline{\delta_{jk_1}}}{2}$$

where n_{k_1} is the number of species in community k_1 , f_i is the relative abundance of species i in community k_1 (here scored as presence or absence), and $\overline{\delta_{ik_2}}$ is the mean pairwise phylogenetic distance between species i in community k_1 and all species in community k_2 excluding conspecific species. Thus D_{pw} serves as a metric of the overall phylogenetic dissimilarity between the two communities.

The second metric, D_{nn} , is a nearest neighbor phylogenetic dissimilarity that serves as a 'terminal' indicator of phylofloristic similarity. It is defined as the following:

$$D_{nn} = \frac{\sum_{i=1}^{n_{k_1}} f_i \min \delta_{ik_2} + \sum_{j=1}^{n_{k_2}} f_j \min \delta_{jk_1}}{2}$$

where n_{k_1} is the number of species in community k_1 , f_i is the relative abundance of species i in community k_1 , and $\min \delta_{ik_2}$ is the phylogenetic branch lengths between species i in community k_1 and its nearest phylogenetic neighbor in community k_2 that is not the same species. Previous work has demonstrated that D_{nn} is very strongly correlated with other metrics such as PhyloSor and UniFrac and generally uncorrelated with D_{pw} (Swenson 2011b). Thus, utilizing D_{nn} and D_{pw} allows us to analyze both major classes, terminal and basal, of phylogenetic beta diversity metrics (Swenson 2011b).

As the two metrics of phylogenetic dissimilarity are likely to be related to the species richness of individual islands and the underlying species beta diversity, a null model analysis was conducted. In particular, a null distribution was generated for each island comparison by randomizing the names of the taxa on the phylogeny 9999 times. During each iteration, the D_{pw} and D_{nn} were calculated for each island comparison. These null distributions were used to calculate standardized effect sizes (Gotelli and Graves 1996), where the mean of the null distribution was subtracted from the observed mean dissimilarity, D_{pw} or D_{nn} , and divided by the standard deviation of the null distribution. It is important to note that the randomization procedure maintained the community presence-absence matrix. In other words, the observed island species richness values, species occupancy rates and therefore patterns of potential dispersal limitation were fixed.

In order to visualize which islands grouped together floristically and phylofloristically hierarchical clustering was performed on the raw Jaccard's Index, D_{pw} and D_{nn} results. The present work was also interested in determining whether patterns of floristic and phylofloristic dissimilarity are dependent upon whether the taxa being analyzed are endemic to the West Indies or not. Thus, the data set was split into non-endemic and endemic species based on the six volumes by Howard (1974, 1977, 1979, 1988, 1989a, 1989b). Lastly, all phylofloristic and floristic similarities between islands were compared with spatial and environmental distance and area differences between islands using partial Mantel tests. The environmental distance was calculated in two ways. First, we compared the maximum elevation of islands. Second, we compared the habitat diversity on islands using the habitat diversity metric from the study done by Ricklefs and Lovette (1999).

Table 1: the area, maximum elevation and habitat diversity of the Lesser Antillean islands analyzed in this study

Island	Latitude	Longitude	Area (km ²)	Maximum elevation (m)	Habitat diversity	# Native species	# Endemic species
Anguilla	18.22	63.07	90	300	1.00	184	23
Antigua	17.05	61.80	280	400	1.14	543	78
Barbados	13.16	59.53	460	340	1.22	407	33
Barbuda	17.05	61.80	160	300	1.00	162	31
Dominica	15.41	61.36	751	1450	2.79	775	191
Grenada	12.28	61.72	310	840	3.26	240	24
Guadeloupe	16.25	61.58	1510	1500	3.73	1016	234
Marie Galante	15.90	61.22	160	300	1.12	226	32
Martinique	14.67	61.00	1100	1340	3.08	954	220
Montserrat	16.75	62.20	100	910	2.61	442	92
Nevis	17.28	62.72	130	1100	2.70	128	37
Saba	17.63	63.23	13	860	1.80	282	42
St Barthelemy	17.90	62.83	22	300	1.00	247	31
St Eustatius	17.50	62.97	20	600	1.22	249	45
St Kitts	17.28	62.72	170	1140	2.90	363	75
St Lucia	13.90	60.97	616	960	3.08	796	158
St Martin	18.07	63.05	85	410	1.22	294	41
St Vincent	13.20	61.21	350	1240	3.27	694	130

Habitat diversity values were taken from [Ricklefs and Lovette \(1999\)](#).

RESULTS

Floristic similarity

A Jaccard's Index was used to quantify species compositional similarity. The phylogenetic compositional similarity was calculated using a pairwise distance metric, D_{pw} , and a nearest neighbor distance metric, D_{nn} . In general, there was very little difference in the clustering of island floras when comparing all native species with non-endemic native species using the Jaccard's or phylogenetic metrics ([Fig. 2](#); [Table 2](#)). The clustering results for the endemic floras were generally inconsistent with the clustering results from the all native species and the non-endemic native species analyses ([Fig. 2](#); [Table 2](#)).

Null model results

The two phylogenetic compositional similarity metrics utilized in this study are likely influenced by the species compositional similarity and diversity of island pairs. This is illustrated by the general congruence between the Jaccard's Index and D_{nn} results ([Fig. 2](#); [Table 2](#)). In order to determine where the phylogenetic compositional similarity of island pairs was higher or lower than that expected, given the underlying species compositional similarity, a null modeling analysis was performed. The null model results produced cluster dendrograms that were incongruent across metrics (i.e. D_{pw} and D_{nn}) and across groupings (i.e. all native species, non-endemic native species and endemic native species; [Fig. 3](#); [Table 3](#)).

Floristic similarity, distance, area and island similarity

Island similarity was calculated as the difference in island maximum elevations and the difference in island habitat diversity ([Ricklefs and Lovette 1999](#)). Geographic distance was a poor predictor of species and phylogenetic compositional similarity when analyzing all native species or all non-endemic native species ([Table 4](#)). These results were consistent when using raw measures of phylogenetic similarity or the standardized effect size results from the null model. Geographic distance was positively correlated with the floristic and phylofloristic similarity of the endemic floras of islands, but the null model results for the D_{nn} metric were negatively correlated with geographic distance ([Table 4](#)). In other words, upon correcting for the underlying species compositional similarity influencing the raw D_{nn} metric, distant islands tended to have higher than expected phylofloristic similarities. The similarity in island area was positively correlated with D_{pw} , whereas the correlation with D_{nn} was weakly negative or not significant across natives, endemics and non-endemics ([Table 4](#)). The Jaccard results were not correlated with the similarity in island area.

The difference in island maximum elevation and island habitat diversity was positively correlated with the dissimilarity in island species and phylogenetic compositions. This was consistent when analyzing all native species, non-endemic native species and endemic species and when examining the raw results and the null model results. The main exceptions to this general finding were the standardized effect sizes for D_{pw} that showed no relationship ([Table 4](#)). Thus, similarity in



Figure 2: a cluster dendrogram representing (a) the species floristic similarity, (b) the pairwise phylofloristic similarity, D_{pw} , between the islands of the Lesser Antilles or (c) the nearest neighbor phylofloristic similarity, D_{nn} , between the islands of the Lesser Antilles. The numbers in bold next to dendrogram nodes indicate the number of times (out of 100) that the phylofloristic analysis of the randomly resolved trees supported the topology generated from the original phylomatic tree.

the maximum height and habitat diversity on Lesser Antilles islands was a better predictor of the species and phylogenetic compositional similarity of the islands than geographic distance.

DISCUSSION

In this work we have sought to extend traditional species-based floristic analyses to incorporate phylogenetic

Table 2: a correlation matrix of the Jaccard's Index, D_{pw} and D_{nn} results

		Native			Non-endemic			Endemic		
		Jaccard	D_{pw}	D_{nn}	Jaccard	D_{pw}	D_{nn}	Jaccard	D_{pw}	D_{nn}
Native	Jaccard	—								
	D_{pw}	0.099	—							
	D_{nn}	0.902	−0.039	—						
Non-endemic	Jaccard	0.992	0.113	0.908	—					
	D_{pw}	0.076	0.991	−0.064	0.086	—				
	D_{nn}	0.900	−0.016	0.990	0.914	−0.046	—			
Endemic	Jaccard	0.804	−0.110	0.693	0.727	−0.105	0.634	—		
	D_{pw}	0.092	0.821	−0.017	0.099	0.749	0.010	−0.092	—	
	D_{nn}	0.733	−0.337	0.838	0.691	−0.338	0.781	0.828	−0.279	—

The correlations were calculated using Mantel Tests on the dissimilarity matrices used to make the cluster dendrograms. Values in boldface indicate $P < 0.05$.

information. This phylofloristic approach seeks to uncover the phylogenetic similarity of entire floras through the use of conceptual and analytical advances made by those quantifying phylogenetic beta diversity (e.g. Bryant *et al.* 2008; Swenson 2011b; Swenson *et al.* 2012a). We have tested this approach using the flora for the islands in the Lesser Antilles. The species-level compositional similarity of all islands was calculated using a Jaccard's dissimilarity for all native species. We then repeated the analysis using only non-endemic native species and only endemic species. Mantel tests were then used to quantify the degree to which spatial distance, difference in island maximum elevation and difference in island habitat diversities predicted species compositional dissimilarity. Interestingly, spatial distance was a non-significant predictor of species compositional dissimilarity between islands for all native species and for non-endemic native species. Thus, the compositional similarity of islands and the assembly of the species composition in the Lesser Antilles is not well explained by historical dispersal limitation. Rather, other processes are likely more important for determining the distribution of species in the Lesser Antilles. This is supported by the demonstration that species compositional dissimilarity increased with the dissimilarity in the maximum elevation of islands and the dissimilarity in habitat diversity. In other words, the compositional similarity of islands was more related to the overall similarity in the environmental complexity of islands rather than the spatial distance *per se*. The one principle exception to this result is that the compositional dissimilarity of endemic species between islands was correlated with spatial distance. Thus, dispersal limitation after presumably *in situ* speciation plays a significant role in dictating the compositional similarity of island endemics, but this pattern is generally masked when examining the entire flora containing a very large number of non-endemic species that appear to have no strong evidence of dispersal limitation.

The phylofloristic similarity analyses generally reflected those uncovered using the species-level Jaccard index. Specifically, in all but one case the spatial distance between

islands was not a significant predictor of the phylofloristic dissimilarity and the similarity of island complexity, similarity in maximum elevation and habitat diversity were generally significant predictors of phylofloristic similarity. The two main exceptions of this were the pairwise phylofloristic similarity of all native species or all non-endemic native species between islands where only similarity in maximum elevation was a significant predictor and similarity in habitat diversity was not. Thus, similar to the species-based analyses, the phylofloristic analyses found little support for the importance of dispersal limitation of species or lineages during the assembly of the entire Lesser Antilles flora with the one principle exception being the importance of dispersal limitation for endemic species distributions among islands. Rather, similarity in the complexity of the topography or habitats between islands is a better predictor of species or phylofloristic similarity indicating the general importance of habitat filtering of species and lineages during the assembly of the island floras.

One key limitation of the analysis of the raw species similarity or raw phylogenetic similarity of the island floras is that the islands themselves are not of equal area, area of the islands correlates roughly with their maximum elevation and habitat diversity and area of the islands is not spatially auto-correlated across the system. Thus, sampling effects alone based on area could account for the lack of support for spatial distance predicting compositional similarity and the general support for habitat and topographical similarity. In other words, big islands are simply more prone to be more similar because each has a higher species diversity on average. To explore this possibility, we conducted a null model analysis where we controlled the observed spatial distributions of individual species, the species richness on each island and their species compositional similarity while only varying the relatedness of species. From such an analysis, we can address whether the phylofloristic similarity of island floras is greater or less than expected, given the observed differences in area and species richness and how this deviation from expected relates to spatial and environmental distance

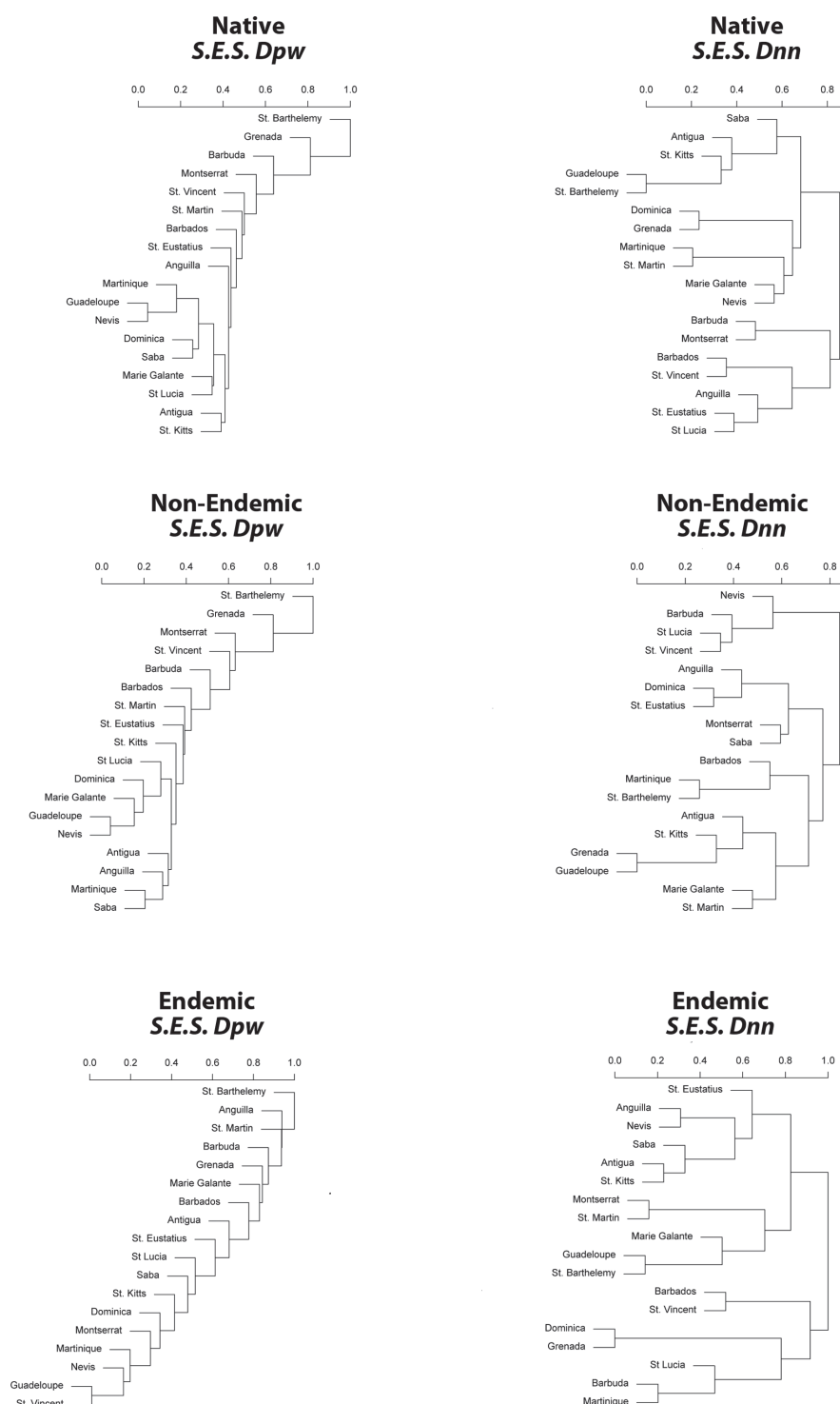


Figure 3: a cluster dendrogram representing the standardized effect size results for the phylofloristic analyses between the islands of the Lesser Antilles. The numbers in bold next to dendrogram nodes indicate the number of times (out of 100) that the phylofloristic analysis of the randomly resolved trees supported the topology generated from the original phylomatic tree.

between islands. The standardized effect size results from the null model analysis of the pairwise phylogenetic similarity between islands ($S.E.S. D_{pw}$) removed all relationships between compositional similarity, spatial distance and environmental distance. Specifically, after controlling for

everything except for relatedness, we found that the pairwise phylogenetic compositional similarity of islands could not be predicted by spatial or environmental gradients. Further, the D_{pw} values, which account for 'basal' similarity, were generally undistinguishable from random. This result is likely due

Table 3: a correlation matrix of the S.E.S D_{pw} and S.E.S. D_{nn} results

		Native		Non-endemic		Endemic	
		S.E.S. D_{pw}	S.E.S. D_{nn}	S.E.S. D_{pw}	S.E.S. D_{nn}	S.E.S. D_{pw}	S.E.S. D_{nn}
Native	S.E.S. D_{pw}	—					
	S.E.S. D_{nn}	0.275	—				
Non-endemic	S.E.S. D_{pw}	0.988	0.295	—			
	S.E.S. D_{nn}	0.224	0.875	0.235	—		
Endemic	S.E.S. D_{pw}	0.826	0.269	0.747	0.307	—	
	S.E.S. D_{nn}	−0.094	0.569	−0.084	0.341	−0.036	—

The correlations were calculated using Mantel Tests on the dissimilarity matrices used to make the cluster dendrograms. Values in boldface indicate $P < 0.05$.

Table 4: results of Mantel Tests between the metrics of island floristic similarity, distance between islands, the difference in the maximum elevations of islands and the difference in island habitat diversities

	Metric	Distance (km)	Area (km ²)	Difference in island maximum elevation (m)	Difference in island habitat diversity
Native	Jaccard	0.1635	0.0627	0.3559	0.3192
	D_{pw}	−0.1883	0.4083	0.2197	0.05137
	D_{nn}	0.06156	−0.2371	0.2543	0.2301
	S.E.S. D_{pw}	−0.2604	−0.4895	0.117	−0.01645
	S.E.S. D_{nn}	−0.03507	−0.5421	0.6358	0.4497
Non-endemic	Jaccard	0.1154	0.0167	0.2834	0.2547
	D_{pw}	−0.1862	0.4276	0.2258	0.04415
	D_{nn}	0.04588	−0.2464	0.1833	0.1713
	S.E.S. D_{pw}	−0.2696	−0.5086	0.1253	−0.01729
	S.E.S. D_{nn}	0.1104	−0.5380	0.3924	0.2729
Endemic	Jaccard	0.4384	0.1418	0.5012	0.4941
	D_{pw}	−0.1126	0.3589	0.2552	0.1581
	D_{nn}	0.273	−0.2634	0.296	0.3158
	S.E.S. D_{pw}	−0.1849	−0.4099	0.05495	−0.004581
	S.E.S. D_{nn}	−0.2523	−0.0649	0.5242	0.3714

Island habitat diversity values were gleaned from [Ricklefs and Lovette \(1999\)](#). Values in boldface indicate $P < 0.05$.

to the masking of important phylogenetically ‘terminal’ patterns through the comparison of many very distantly related lineages (e.g. pteridophytes and asters). To explore this, we turn to the standardized effect size results for the nearest phylogenetic neighbor similarity between islands (S.E.S. D_{nn}). These results show a strong and consistent relationship between the topographic or habitat diversity dissimilarity between two islands and their nearest phylogenetic neighbor dissimilarity even when controlling for every observed pattern aside from relatedness. In other words, even when controlling for differences in species alpha diversity within each island, species beta diversity between islands and the spatial distributions of individual species, the similarity in the environment between two islands is a better predictor of their phylofloristic similarity than spatial distance. This is further underscored by the fact that the S.E.S. D_{nn} results are negatively correlated with spatial distance for endemic species. In other words, islands that are close together tend to have a

significant dissimilarity in their phylogenetic composition if they have dissimilar environments.

From the null modeling results, we can make a few important statements. First, dispersal limitation appears to have played a very minor role in structuring the floras of individual islands in the Lesser Antilles whether viewed from a species- or clade-based perspective. Second, environmental selection by species or clades has played a key role during the assembly of the Lesser Antillean flora. Specifically, the colonization and persistence of species or clades on an island in this archipelago is based more on the environmental context rather than whether or not they could disperse to that island. Third, pairwise phylogenetic metrics may be suboptimal for phylofloristic analyses, given their calculation of similarity between extremely distant relatives that likely have no clear biogeographic or evolutionary basis for comparison. Lastly, there is a non-random phylofloristic structure among islands even after removing the effect of the underlying species similarity

and this non-random structure is strongly associated with environmental similarity of islands. Thus, even if two islands share few or no species, the phylogenetic similarity can still be predicted based on the environmental similarity because species from the same clade co-occur on different islands likely in the same environments but do not occur on both islands. This additional level of information and detail cannot be obtained from a traditional species-based floristic analysis and demonstrates one fundamental advantage of the phylofloristic approach.

Caveats and conclusions

The analyses presented show strong support for environmental selection of clades during the assembly of island floras in the Lesser Antilles. Although these results are clear, we would like to emphasize there are some limitations to this study and areas where future phylofloristic analyses could be improved. First, the phylogenetic tree was largely unresolved within genera and this limits more detailed investigations into the biogeography and evolutionary history of assembly in this system. It is likely that this additional information may, e.g. increase the relationship between phylogenetic dissimilarity and spatial distance for endemic species if species have colonized and speciated *in situ* in a stepping-stone fashion as is commonly seen in the Hawaiian flora. Thus, we may expect stronger spatial relationships for endemic species, but we suspect this additional phylogenetic detail would not greatly alter the non-endemic results and therefore not the results for the entire native flora (Santiago-Valentin and Olmstead 2004). Second, there is no temporal component to the geographic analyses. For example, long-term changes in island area and topographic complexity were not considered and this ignorance likely weakens our ability to adequately understand why some islands have high or low compositional similarity with respect to their spatial and environmental similarity. Finally, related to the lack of temporal information regarding island geography and physiography, the analyses lack information about intraspecific phylogeography, extinction and island-specific extirpation. Previous research has nicely linked these pieces of information for avian lineages in the region (Ricklefs and Bermingham 2001) and the lack of this information in this study likely masks many important evolutionary and biogeographic processes underlying the assembly of floras on these islands. These omissions and obstacles will likely lurk for most future phylofloristic studies although the first obstacle of generating large and well-resolved phylogenetic trees for entire floras or the majority of floras may likely be greatly eroded in the coming years (Smith *et al.* 2009). The removal of this obstacle will greatly help refine analyses and promote more focused investigations into the evolutionary and biogeographic imprint on community assembly and species co-occurrence that cannot be detected by analyzing species compositions alone.

SUPPLEMENTARY MATERIAL

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