Species assemblages of insular Caribbean *Sticta* (lichenized Ascomycota: Peltigerales) over ecological and evolutionary time scales

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ABSTRACT

Phylogenetic approaches to macroevolution have provided unique insight into evolutionary relationships, ancestral ranges, and diversification patterns for many taxa. Similar frameworks have also been developed to assess how environmental and/or spatial variables shape species diversity and distribution patterns at different spatial/temporal scales, but studies implementing these are still scarce for many groups, including lichens. Here, we combine phylogeny-based ancestral range reconstruction and diversification analysis with community phylogenetics to reconstruct evolutionary origins and assess patterns of taxonomic and phylogenetic relatedness between island communities of the lichenized fungal genus *Sticta* in the Caribbean. Sampling was carried out in the Greater Antilles (Cuba, Jamaica, Dominican Republic, and Puerto Rico) and Lesser Antilles (Dominica, Guadeloupe, and Martinique). Data for six molecular loci were obtained for 64 candidate Caribbean species and used to perform both macroevolutionary phylogenetics, which also included worldwide taxa, and phylobetadiversity analyses, which emphasized island-level communities. Our work uncovered high levels of island endemism (~59%) in Caribbean *Sticta*. We estimate initial colonization of the region occurred about 19 Mya from a South American ancestor. Reverse migration events by Caribbean lineages to South America were also inferred. We found no evidence for increased diversification rates associated with range expansion into the Caribbean. Taxonomic and phylogenetic turnover between island-level communities was most strongly correlated with environmental variation rather than with geographic distance. We observed less dissimilarity among communities from the Dominican Republic and Jamaica than between these islands and the Lesser Antilles/Puerto Rico. High levels of hidden diversity and endemism in Caribbean *Sticta* reaffirm that islands are crucial for the maintenance of global biodiversity of lichenized fungi. Altogether, our findings suggest that strong evolutionary links exist between Caribbean and South American biotas but at regional scales, species assemblages exhibit complex taxonomic and phylogenetic relationships that are determined by local environments and shared evolutionary histories.

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1. Introduction

The Caribbean islands, comprised by the low-lying Bahamas Archipelago, the geologically diverse Greater Antilles and volcanic-arc islands of the Lesser Antilles, stand out in terms of spatial extent, species richness and levels of endemism when compared to other insular systems of the Neotropics. Nearly 8,000 endemic vascular plants and about 900 endemic vertebrate species are known for these islands (Hedges 2001; Acevedo-Rodríguez and Strong, 2008). Multiple biotic and abiotic factors can be invoked to explain such patterns, yet stronger influence in this respect could be attributed to this region's high number of islands (i.e. greater than 800), close proximity to continental areas and presence of broad environmental and elevational gradients (−39 m to + 3098 m).

Studies on Caribbean Island biotas have had a profound impact on our understanding of the evolution and diversification of a variety of lineages. This archipelago has been pivotal for exploring many biogeographical processes such as colonization and extinction dynamics in island systems (Ricklefs, 2009), and demonstrated the importance of repeated evolution of similar phenotypes in insular adaptive radiations (Losos et al., 1998). As such, the Caribbean represents a vital biogeographic region for evaluating how ecological and evolutionary processes interact to shape biodiversity patterns in natural systems (Ricklefs and Bermingham, 2008).

Like other insular regions, our understanding of the ecology and evolution of Caribbean biotas has been mostly shaped by observations on animals, particularly vertebrates (Rodríguez-Silva and Schlupp, 2021). For the Caribbean islands, the most notable example is that of *Anolis* lizards which underwent an impressive adaptive radiation (Losos et al., 1998). Work on many other groups, including plants (Aguirre-Santoro et. al., 2020; Cervantes et al., 2016; Hidalgo et al., 2020) and birds (Bellemain et al., 2008; Ricklefs and Lovette, 1999) have also been instrumental. What remains a major challenge is determining if ecological and evolutionary processes that have been characterized using these organisms operate analogously in other groups. Of relevance in this context are fungi as they parallel vertebrates and invertebrates in terms of their estimated contribution to global biodiversity (Larsen et al., 2017), but have comparatively fewer studies focusing on different aspects of their ecology and evolution.

Advances in molecular phylogenetic approaches have been critical for shedding light on biogeographic patterns and evolutionary processes in fungi and other highly diverse taxa. A notable case within this group are lichenized fungi (i.e. lichens), fungi that associate with a photosynthetic partner (green algae and/or cyanobacterium), and specific components of the microbiome contained in the lichen thallus, including bacteria and cortical fungi (Hawksworth and Grube, 2020; but see Lücking et al., 2021). It was generally believed that, at the species level, lichens have wider distributions than vascular plants and animals (Feuerer and Hawksworth, 2007; Galloway, 1979; Lücking, 2003; Smith, 1993); however, molecular data have shown that diverse lineages, often with a distinct geographic structure and sometimes without discernable phenotypic differentiation, are frequently found within nominal species previously considered to be widespread (Crespo and Lumbsch, 2010; Dal Forno et al., 2017; Leavitt et al., 2016; Onuţ-Brännström et al., 2017; Singh et al., 2015; Widhelm et al., 2021). These discoveries had a major impact on studies focusing on island lichens as they soon revealed that insular biotas were much more than subsets of continental lineages, but diverse species assemblages with truly unique evolutionary histories (Dal Forno et al., 2017; Mercado-Díaz et al., 2014; Moncada et al., 2014; Sérusiaux et al., 2011; Simon et al., 2018).

The currently available information about species richness and the underlying evolutionary mechanisms and biogeographical histories that led to extant diversity patterns is relatively sparse for lichens in the Caribbean islands. Only a few phylogenetic studies focused on taxonomic revisions of genera have included material from this region. Notably, many have uncovered previously unrecognized, endemic

species- and even genus-level lineages (Lücking et al., 2020, 2017a; Mercado-Díaz et al., 2020, 2014), suggesting that species richness and the phylogenetic diversity represented in these island communities are likely underestimated. Furthermore, along with species' biogeographic histories, evolving environmental preferences are known to similarly influence diversity and distribution patterns (Ackerly, 2003; Ndiribe et al., 2013; Wiens, 2004). Numerous tools have been developed to better dissect the influence of these processes, including the analysis of Taxonomic Beta Diversity (TBD) and Phylogenetic Beta Diversity (PBD) (i.e. "phylobetadiversity", or "phylogenetic turnover") (Graham and Fine, 2008; Swenson, 2011). When analyzed in tandem with environmental (e.g. elevation, climate) and spatial (geographic distance) variables, TBD and PBD analyses allow us to jointly evaluate how local (e.g. environmental filtering) and regional (e.g. speciation, dispersal) processes influence community assembly at both ecological and evolutionary time scales (Graham and Fine, 2008; Leprieur et al., 2012). Unfortunately, efforts integrating such approaches for better understanding the evolution of lichen communities are still wanting.

Sticta (Schreb.) Ach. is a genus of lichenized fungi recognizable by their large foliose thalli, the presence of conspicuous, well-defined lower surface pores (i.e. cyphellae), and the ability to form associations with both cyanobacteria and green algae, sometimes by the same fungus and even the same individual. Like with other genera, the evolutionary history of *Sticta* in the Caribbean is poorly understood, but recent work by Mercado-Díaz et al. (2020) on Puerto Rican assemblages provide some context. This study revealed that present-day communities were constituted by several widespread species, but also by presumed endemics that evolved from lineages apparently derived from South American ancestors. The authors noted, however, that suggested geographic affinities and potential evolutionary micro-radiations proposed for some clades represented tentative hypotheses in need of further studies, preferably utilizing ancestral range reconstruction and diversification analysis. The recent circumscription of *S. damicornis* as a presumably restricted Greater Antillean endemic (Moncada et al., 2018) further attest to potentially complex distribution patterns for the genus in this region.

In this study, we co-analyzed genetic sequences resulting from comprehensive sampling efforts in the Caribbean islands and remotely sensed environmental datasets to reconstruct the eco-evolutionary history of *Sticta* in this region. Phylogenetic reconstructions were used to assess evolutionary relationships, determining the degree of regional endemism and infer the timing of colonization events. Ancestral range reconstruction analysis was used to test presumed South American affinities hypothesized by Mercado-Díaz et al. (2020). Moreover, we carried out diversification analysis to evaluate if colonizing the Caribbean increased diversification rates. Similar to Mercado-Díaz et al. (2020), we anticipate levels of endemism to be underestimated. We also expect to detect evidence of an evolutionary radiation resulting from increases in diversification after range expansion, mostly from South America.

Lastly, we implemented TBD and PBD approaches to both assess the relatedness of island-level communities within the insular Caribbean and to tease apart the role of geographic distance versus environmental preferences in explaining regional-scale patterns of species richness and distribution. Given the high dispersal ability inferred for this genus (Widhelm et al., 2018) and the relatively small inter-island distances, we expect patterns of taxonomic and phylogenetic turnover to be more strongly correlated to environmental variables than with geographic distance. *Sticta* is most diverse in wet montane forests and alpine grasslands (páramos in the Neotropics) (Moncada, 2012; Moncada et al., 2020), therefore high elevation communities (e.g. Dominican Republic and Jamaica) are expected to be more diverse and less dissimilar (both taxonomically and phylogenetically) among each other than they are to communities in lower elevations (e.g. Lesser Antilles).

2. Methods

2.1. Sampling and DNA sequencing

Sampling for this study encompasses more than 100 collecting sites scattered throughout the Greater- (Cuba, Dominican Republic, Jamaica, Puerto Rico) and the Lesser Antilles (Dominica, Martinique, Guadeloupe). These sites were clustered around 19 sampling areas (Fig. 1, described in Table S1). Details of sampling in Puerto Rico (treated as a single sampling area) is described elsewhere (Mercado-Díaz et al., 2020). Collecting efforts were carried out in well preserved, low- (ca. 90 m) to high-elevation (ca. 2,130 m) forests. Sampling localities occur in vegetation types broadly classified as Tropical and Subtropical Moist Broadleaf Forests and Coniferous Forests. These areas contain preferred habitat types for *Sticta*, including Upper Montane and Cloud Forests. Sampling efforts in the region started in 2015 and have yielded a total of 595 specimens to date (deposited at: Field Museum [F], Herbario del Jardín Botánico de la Universidad de Puerto Rico, Río Piedras [UPR], Universidad Distrital Francisco José de Caldas [UDBC], and Botanischer Garten und Botanisches Museum Berlin [B]). Part of this material was used to generate our molecular data.

Sequences from six gene regions were generated and used for phylogenetic analysis of the fungal symbionts. The loci include the internal transcribed spacer (ITS ~ 600 bp), which is the universal barcode for fungi (Schoch et al., 2012), the mitochondrial small subunit (mtSSU ~ 800 bp), the nuclear large subunit (nuLSU ~ 550 bp), the DNA replication licensing factor (MCM7 ~ 600 bp), the RNA polymerase II largest subunit (RPB1 ~ 900 bp), and the RNA polymerase II second largest subunit (RPB2 ~ 700), the latter three being low-copy nuclear protein-coding genes. DNA extraction and amplification procedures are further described in Appendix A.

2.2. Filtering and candidate species delimitation

Newly generated Caribbean sequences were assembled in Geneious 8.1.7 (https://www.geneious.com) and queried in the BLASTn suite in GenBank (Benson et al., 2018) for initial assessment. After confirming correspondence to the genus *Sticta*, single-locus alignments of these new sequences were assembled using the "auto" mode threshold and default settings for MAFFT 7.017 (Katoh and Standley, 2013) plugin in Geneious. We generated a first set of Maximum Likelihood (ML) trees based on RAxML (see section 2.4 for procedures) to assess congruence between these datasets. The program *compat*, which detects topological conflict between supported clades in phylogenetic trees (Kauff and Lutzoni, 2002), was further used to assess conflicting placement of individuals in single-gene topologies. This analysis was based on a 70% bootstrap threshold and allowed us to identify potentially problematic sequences.

Taxonomical knowledge on Caribbean *Sticta* is rudimentary with most known names corresponding to widespread taxa and/or species with ranges that so far exclude the Caribbean region (e.g. *Sticta filix* [Ranft et al., 2018], *Sticta fuliginosa* and *Sticta sylvatica* [Magain and Sérusiaux, 2015]). To circumvent poor knowledge about taxa represented in our material, candidate species were obtained by using an integrative taxonomic approach. We refrain here from providing extensive details about methods and resulting species delimitations as this will be part of subsequent work aimed at clarifying taxonomic issues of Caribbean *Sticta*. Nonetheless, our approach broadly followed phylogenetic analysis described below and methods outlined in Mercado-Díaz et al. (2020). We first compiled an ITS alignment with data for 448 Caribbean samples and sequences from 2,130 tentatively identified samples from an ongoing global study (Moncada et al. in prep.). To help us determine conspecificity with delimited worldwide taxa, a RAxML tree (not shown) was generated to assess nestedness of our samples
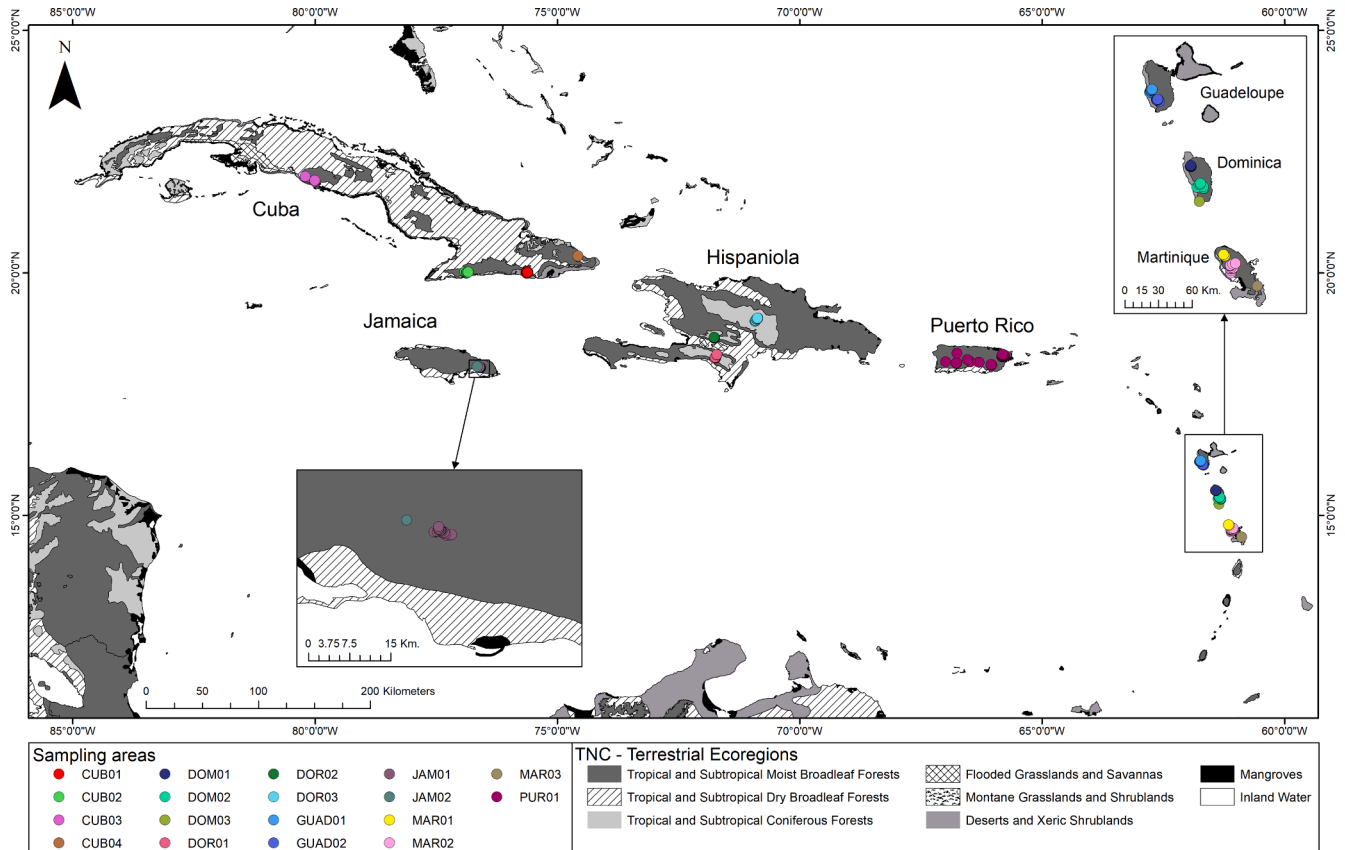

Fig. 1. Map of sampling areas (colored dots) of *Sticta* in the Caribbean. Terrestrial ecoregions from The Nature Conservancy (TNC) are used as a base layer. Refer to Table S1 for additional information on sampling areas.

within strongly supported clades. Species delimitation with PTP and GMYC (Fujisawa & Barraclough, 2013; Zhang et al., 2013) was also carried out. We performed Maximum Likelihood delimitation with PTP assuming a single coalescent rate averaged over all species (Kapli et al., 2017). For GMYC, a time-calibrated tree was first generated with BEAST (not shown). This analysis was carried out with method = "simple" and implemented in R using the package SPLITS (Ezard et al., 2009). Candidate species-level lineages were further validated by assessing morphological characters in representative specimens. For each candidate species, we identified the samples for which we obtained the highest amount of sequence data (ITS + additional loci) and used these for subsequent analyses.

2.3. Alignment assembly, partitioning schemes, and substitution models

Single-gene alignments for a broader taxon sampling were generated once candidate Caribbean species were obtained. These alignments included representative sequences for each candidate Caribbean species, sequences representing Widhelm et al. (2018) global taxonomic sampling, and sequences for three outgroup species (*Lobaria pulmonaria, Pseudocyphellaria crocata, Ricasolia amplissima*). We generated a second set of ML trees (RAxML) based on these alignments to corroborate congruence between single gene topologies. Since no major conflicts were detected between single-locus trees, concatenated alignments were assembled. Species with at least two of the six targeted loci were considered for concatenation and only one individual per taxon was included in alignments. Despite having limited data for *Sticta* aff. *laciniosa*-2 (ITS only), this species was included in concatenated datasets as it represented one of the less common *Sticta* species with a green-algal photobiont.

The best partitioning scheme and optimal molecular substitution models for concatenated alignments were determined using partition models in IQ-TREE 2.0.5 (Chernomor et al., 2016; Minh et al., 2020) and IQ-TREE implementation of PartitionFinder v1.1.1 (Lanfear et al., 2012) and ModelFinder (Kalyaanamoorthy et al., 2017) (Table S2). This analysis was run using the *-spp* option which allows each partition to have its own evolutionary rate, and the *-m TESTMERGEONLY* option which implements the greedy algorithm of PartitionFinder. Seventeen pre-delimited character sets were analyzed in IQ-TREE. These included the intragenic regions within ITS (i.e. 18S, ITS1, 5.8S, ITS2 and 28S), codon positions in protein coding genes (i.e. MCM7, RPB1, RPB2), an intron within RPB1, and the genes mtSSU and nuLSU. Separate model selection for MrBayes (see below) was performed using the *-mset mrbayes* option due to lower number of substitution models available for this program.

2.4. Phylogenetic analysis

Phylogenetic analysis proceeded with RAxML and the program MrBayes v3.2.6 (Ronquist et al., 2012). For RAxML, we performed *a posteriori* bootstrapping analysis with the bootstrap convergence test using the extended majority-rule consensus tree criterion (autoMRE). Our concatenated dataset was subjected to partitioned analysis (*-q* option) which allowed for estimation and optimization of individual alpha-shape parameters, GTR rates, and empirical base frequencies. MrBayes analysis was performed using two parallel Markov Chain Monte Carlo (MCMC) runs with four chains each. The number of generations was set at 30 million using a sampling frequency of 1,000. A 25% burn-in was used to summarize sampled trees and parameter values. Post-burnin trees were pooled to calculate the 50% majority-rule consensus tree. Convergence of chains was assessed in Tracer v.1.5 (Rambaut and Drummond, 2009). Clades were considered supported if bootstrap values were equal or above 70% or if posterior probabilities were equal or above 0.95. Trees were visualized using FigTree v.1.4.2 (Rambaut, 2012). Major clades identified by Widhelm et al. (2018) (Clade I-V) were also added to these to facilitate interpretation. Congruence between

RAxML and MrBayes trees was assessed with *ivy* (https://github.com/rhr/ivy [Last accessed: 5/17/2022]).

The Gblocks web server (https://molevol.cmima.csic.es/castresana/Gblocks_server.html [Last accessed: 9/25/2020]) was used to evaluate if a low degree of sequence conservation in ITS affected phylogenetic reconstructions described so far. This tool allows to identify and remove gaps and non-conserved sites in alignments (Castresana, 2000). Since no major differences were found between filtered and unfiltered datasets, and to reduce chances of eliminating potentially informative sites (Tan et al., 2015), phylogenetic analyses were based on unfiltered datasets.

2.5. Divergence dating

Divergence times were estimated in BEAST v2.6.1 (Bouckaert et al., 2014) using input files prepared in BEAUTi (Bouckaert et al., 2014). We carried out concatenation analyses allowing clock and tree models to be linked and sites models to be unlinked. Transition rates and base frequencies from the model selection results were fixed and branch rates were estimated using relaxed lognormal molecular clocks.

A Calibrated Yule Model was used for divergence time estimation. The birth rate was assigned an exponential distribution with mean = 0.1. Default gamma distribution was used for ucldStdev whereas an exponential distribution (mean = 1) was applied to ucldMean. Node ages from a fossil-calibrated phylogeny that was inferred using target captured nuclear protein coding loci (Widhelm et al., 2019) were used to date our tree. One calibration point constrained the age of the MRCA for the crown of this genus to 25 ± 8 MY and was assigned a log-normal distribution with M = 3.2 and S = 0.2. The second node calibration was also assigned a log-normal distribution with M = 4.17 and S = 0.1 and constrained the age for the MRCA between *Sticta* and *Pseudocyphellaria* to 65 ± 10 MY. Following previous studies (Mercado-Díaz et al., 2020; Widhelm et al., 2018, 2019), both node calibrations were forced to be monophyletic.

Two independent BEAST analyses using the RAxML topology as the starting tree and a chain length of 5.0×10^7 generations were run. Tree and log files had a sampling frequency of 5,000. Convergence and mixing of parameters were evaluated in Tracer v.1.6 (Rambaut and Drummond, 2009) and effective sample sizes (ESS) were confirmed to be greater than 200. Trees from independent runs were combined in LogCombiner v.1.8.0 (Rambaut and Drummond, 2013a) after excluding the first 10% of sampled trees in each run as burn-in. A maximum clade credibility (MCC) tree was generated in TreeAnnotator v.1.8.2 (Rambaut and Drummond, 2013b) from the combined posterior distribution of trees (18,000) using a 0.5 posterior probability cutoff and node heights set at "common ancestors".

It is worth noting that we consistently confronted convergence issues with several parameters when analysis with BEAST was carried out using a partitioning-by-gene scheme. This was seen under different parameter configurations and when using both a full dataset (6-loci) and a reduced 4-loci dataset that excluded both RPB1 and RPB2, which had data for only 25% and 39% of the species, respectively. Many factors might underlie this type of issue, such as overparameterization (Zheng and Wiens, 2015) and problematic accessions. In our case, proper mixing and convergence were achieved when a 4-loci (i.e. ITS, MCM7, mtSSU, nuLSU) dataset with a partitioning scheme based on the greedy algorithm of PartitionFinder was used for analyses. Divergence dating results are therefore based on this latter alignment.

2.6. Geographic range evolution

To reconstruct the geographic origins of *Sticta* in the Caribbean, species were coded with respect to their occurrence in nine broad biogeographic regions: Afrotropical (AF), Australasia (AU), Caribbean (CA), Central America (CAM), Hawaii (HA), North America (NA), Oriental (OR), Palearctic (PA), and South America (SA). This geographic

coding broadly follow biogeographic realms from Wallace (1876), except that we treat Central America, the Caribbean and the Hawaiian region as distinct biogeographic areas.. Species distributions for extra-Caribbean species mostly followed (Widhelm et al., 2018) with updates in the distribution of several species obtained from Moncada et al. (2020).

We used the RASP platform (Yu et al., 2015) to reconstruct ancestral ranges based on the Dispersal–Extinction–Cladogenesis (DEC) model from Ree and Smith (2008). The analysis was carried out using our MCC tree and considered branch support for the interpretation of results. Considering that the maximum number of biogeographic regions that a species within our sampling occurs is six, the analysis was set to reconstruct a maximum of six ranges at ancestral nodes. Range reconstruction was modelled without disallowing ranges which is in line with presumed high dispersal capabilities of *Sticta* and lichens in general (Werth, 2011; Widhelm et al., 2018). Analyses were carried both with and without dispersal constraints. Additional details about these analyses and the dispersal constraints matrix can be found in Appendix B and Table S3.

2.7. Diversification analyses

Trait-dependent diversification analysis was performed using the Geographic State-Dependent Speciation and Extinction (GeoSSE) model (Goldberg et al., 2011) as implemented in the R package *diversitree* (Fitzjohn, 2012). GeoSSE is unique among other models within the SSE framework as it allows testing hypotheses related to the link between macroevolutionary rates and the geographic distribution of lineages (Goldberg et al., 2011). Species assigned to three geographic character states (i.e. endemic to the Continental Neotropics "A" or the Caribbean "B", and present in both regions "AB") were analyzed. This process entailed evaluating ten macroevolutionary scenarios which allowed us to evaluate if colonization of the Caribbean triggered changes speciation and/or extinction rates and assess potential dispersal asymmetries. To do this, we constructed a full, unconstrained model in which speciation (sA, sB, sAB), extinction (xA, xB), and dispersal (dA, dB) could vary between areas, and then fitted nine different constraints. Additional details are provided in Appendix C.

Model inadequacy (i.e. potential for inflated Type I error rates) has been raised as an issue likely affecting SSE models (Rabosky and Goldberg, 2015; but see Caetano et al., 2018). In GeoSSE models, inadequacies seem to be most closely linked to assigning species membership to particular geographic regions and/or to uncertainties related to tree topology (e.g. polytomies) (Alves et al., 2017). To assess the potential influence of these factors, we adjusted simulation analyses from Alves et al. (2017) to test for model inadequacy in our GeoSSE inference. Additional methodological details about these simulations are provided in Appendix D.

As an update to previous analyses (Widhelm et al., 2018), we also investigated heterogeneity in rates of speciation and extinction in our multilocus time-calibrated tree using the Bayesian Analysis of Macroevolutionary Mixtures program, BAMM (Rabosky, 2014). Specifications about methodology used in this analysis are provided in Appendix E.

2.8. Taxonomic and phylogenetic turnover of Caribbean Sticta communities

2.8.1. Taxonomic and phylogenetic beta diversity matrices

Taxonomic and phylogenetic turnover in island-level communities of *Sticta* in the Caribbean was assessed using Taxonomic Beta Diversity and Phylogenetic Beta Diversity. The former (i.e. TBD), provides useful means to estimate the amount of overlap in species composition between areas (Baselga, 2010; Koleff et al., 2003). PBD adds a temporal dimension to beta diversity and is better defined as the phylogenetic distance (branch lengths) between samples of individual organisms between any two sites (Graham and Fine, 2008).

As a first step for these analyses, we generated a community data matrix of species present in islands within this region. Thus, communities analyzed are defined by island membership (island-level communities) and the totality of species in the dataset represents our regional species pool. Since we lacked abundance estimates, this community matrix was based on presence/absence data. We quantified TBD, which was regarded as species composition dissimilarity between island communities, using the *Jaccard* index. Calculation of this index was accomplished using the "vegdist" function in *vegan* R package (Oksanen et al., 2019).

To estimate PBD, we followed methods documented above for phylogenetic reconstructions with BEAST and generated a time-calibrated tree that only included Caribbean species. A RAxML tree was also produced and used as the starting topology for this analysis. Since convergence/mixing issues were not confronted during preliminary analysis, this tree was based on a 6-gene dataset. We used our BEAST tree and our community data matrix to calculate two PBD dissimilarity metrics. These are categorized as "terminal" (tPBD), which are sensitive to turnover near the tip of trees (*Unifrac*) and "basal" (bPBD), which are sensitive to turnover deeper in the phylogeny ($D_{Rao's}$ or "Rao's D") (Swenson, 2011). The R package *picante* (Kembel et al., 2010) was used for these calculations, specifically the functions "unifrac" (*Unifrac*) and "raoD" ($D_{Rao's}$). To better understand how communities differ in terms of their composition and evolutionary history, we decomposed TBD and PBD indices into components accounting for "true" turnover and "nestedness" (or "phylogenetic diversity gradients" if using a PBD metric) (Baselga, 2010; Leprieur et al., 2012). "True" turnover implies replacement of some species by others whereas "nestedness" of species assemblages occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites (Baselga, 2010). Decomposition was accomplished with the functions "phylo.beta.pair" and "beta.pair" from the R package *betapart* (Baselga et al., 2013). Since tools for decomposing beta diversity have only been developed for *Jaccard* and *Unifrac*, decomposition was exclusive to these two indices.

We carried out preliminary analysis to assess correspondence of *Unifrac* and $D_{Rao's}$ to other tPBD (e.g. 1 - *Phylosor*, D_{nn}) and bPBD (e.g. D_{pw}, $H_{Rao's}$) metrics that have been developed and found that these yielded analogous patterns (not shown). Similarly, previous work has demonstrated that 1 - *PhyloSor* and D_{pw} are largely redundant with *Unifrac* and $D_{Rao's}$, respectively (Jin et al., 2015; Swenson, 2011). In line with these results and observations, taxonomic and phylogenetic beta diversity analyses presented here focused exclusively on *Jaccard*, *Unifrac* and $D_{Rao's}$.

Taxonomic richness and phylogenetic diversity are often correlated, therefore to make better inferences about observed patterns, we calculated phylogenetic diversity ("PD") for each island using the "pd.calc" function of the R package *caper* (Orme et al., 2014). Obtained values were plotted against "species richness" and "maximum elevation" per island to facilitate interpretation of results.

2.8.2. Environmental and geographic distances

We used data on elevation, precipitation, maximum and minimum temperatures, evapotranspiration, the Normalized Difference Vegetation Index (NDVI, Huete et al., 1985), the Enhanced Vegetation Index (EVI, Liu and Huete, 1995), and the Terrain Ruggedness Index (TRI, Riley et al., 1999) to generate an environmental distance matrix for island-level communities. These parameters influence or have the potential of influencing species diversity patterns of lichens at both local and regional scales (Armstrong, 2015; Nupoor et al., 2015). We used specimen locality data to estimate mean, median, and maximum elevation values for each island-level community. Strong covariation between these parameters was found during preliminary analysis; thus, only maximum elevation was kept for downstream analysis. Likewise, positive correlations between other environmental variables could potentially inflate differences between islands in terms of their

environmental distances. To account for this, a principal component analysis (PCA) was carried out on our environmental matrix and the first two PCA axes were extracted to create an Euclidean distance matrix which was used for subsequent analysis.

Cloud computing for visualization of remotely sensed data was used to obtain data for environmental parameters. Inter-island geographic distances were obtained by combining geographic information systems and R. Procedures to obtain these estimates are further described in Appendix F.

2.8.3. Influence of environmental and geographic distances on TBD and PBD

We plotted geographical and environmental distances against TBD and PBD metrics to visualize associations between them. Mantel tests were used to assess the significance of the correlation between these measures. Because low statistical power and/or spatial autocorrelation biases might affect assessments with Mantel tests, we used the Procrustes superimposition method (Peres-Neto and Jackson, 2001) to corroborate correlations that yielded statistically significant associations. TBD and PBD metrics were subjected to ordination analysis with Principal Coordinate Analysis (PCoA) and resulting axes were used for Procrustean analysis. Functions "mantel" and "protest" from the R package *vegan* (Oksanen et al., 2019) were used to perform these tests.

2.8.4. Null modeling of Sticta communities

We used a null modelling approach to ask if taxonomic and phylogenetic relatedness between *Sticta* communities in the Caribbean differed from random expectation. To do this, we first used the "randomizeMatrix" function in *picante* to execute 100 randomizations of our community data matrix. As we were only interested in evaluating turnover deviations from null expectation, the argument null.model() from "randomizeMatrix" was set to "richness". Using the functions described above, we calculated TBD and PBD metrics for each of these 100 null communities. Following from previous work (Graham et al., 2009; Leprieur et al., 2012), we used a standardized effect sizes (SES) approach to evaluate if observed values for our TBD and PBD metrics differed significantly from values estimated for null communities. SES values greater than 1.96 were considered indicative of higher-than-expected turnover (more dissimilarity between communities) whereas SES values below −1.96 were indicative of lower-than-expected turnover (less dissimilarity between communities).

3. Results

3.1. Molecular data and phylogenetic analysis

A total of 637 sequences, including 189 newly generated sequences (ITS: 41, MCM7: 28, mtSSU: 24, nuLSU: 38, RPB1: 6, RPB2: 52) were used for analyses presented in this work (Table S4). Analysis with RAxML and MrBayes using 4- and 6-loci yielded similar results, therefore results are based on the six-locus dataset and are presented using the MrBayes tree (Fig. 2). The likelihood value for the two cold chains in our Bayesian trees was −37,725.67 and −37,736.21 whereas the final optimization likelihood for the ML tree was −38,090.91. Final alignments used for all analyses are available on Mendeley Data (Mercado-Díaz, 2023).

We found sixty-four candidate species of *Sticta* in the Caribbean. Two of these species had insufficient sequence data, therefore only 62 are included in our multilocus phylogeny (Fig. 2). Of these species, 38 (59%) are only known from this region, whereas 26 (41%) are also recorded from elsewhere.

Phylogenetically, *Sticta* was recovered as a monophyletic group sister to the genus *Pseudocyphellaria* (Fig. 2). We recovered the five major ingroup clades reported by Widhelm et al. (2018), although only Clades II, IV, and V were strongly supported by both RAxML and MrBayes. Caribbean species were found to be associated with Clades I-III

exclusively. Clade I, which contains the smallest number of species occurring in the Caribbean (6), was only strongly supported in MrBayes. Eighteen Caribbean species were found within Clade II. Seven species, including two from the Caribbean (i.e. *Sticta* sp-2, *Sticta* sp-9, *S. neopulmonarioides, S.* aff. *zahlbruckneri, S. latior, S. inversa,* and *S. macrothallina*) formed a paraphyletic grade associated with Clade II. These were not included in Clade II since several of these were nested in other clades in Widhelm et al. (2018). Clade III, on the other hand, includes the highest number of species with Caribbean affinities (38) but methods did not yield strong support for its monophyly. Altogether, Clades I, II, III and the seven species forming the paraphyletic grade associated with Clade II formed a strongly supported clade according to RAxML and MrBayes, but relationships among them remain unresolved. While Clade IV's status as the earliest diverging group was strongly supported, the relationship of Clade V to the rest of the clades in the tree remained unresolved.

3.2. Divergence dating and biogeographic analysis

According to our BEAST analysis (Fig. S1), the divergence of *Sticta* from *Pseudocyphellaria* occurred about 63.3 Mya (95% Highest Posterior Density (HPD): 51.3–75 Mya). The origins of *Sticta*, on the other hand, date back to the late Oligocene, about 26.2 Mya (HPD: 17.9–34.5 Mya).

The DEC model without dispersal constraints yielded a higher likelihood (lnL = -455.8) compared to the model with dispersal constraints (lnL = -459.8) and is therefore used to highlight results. According to this analysis, biogeographical patterns are mostly being driven by dispersal events (Global cost: 121). Instances of vicariant speciation and extinction events were less influential (Global cost: 23, Global cost: 0, respectively). Moreover, dispersal events from the Continental Neotropics (i.e. SA + CAM) to the Caribbean were estimated at 16.5 whereas 18 were inferred to have happened in the reverse direction.

Ancestral ranges are plotted only for strongly supported clades (Fig. 3). Multiple areas (i.e. SA, AF, HA, AU) yielded the highest probability for the ancestral range of the crown node for *Sticta* (~67%, not shown). The earliest diverging clades had the most probable geographic origins in the Afrotropics (Clade V) and the Australasian region (Clade IV). Clades I, II, and III, which include all Neotropical species in our tree, share a common ancestor with an ancestral range traced back to South America (Fig. 3, node "A"). The earliest putative arrival of *Sticta* to the Caribbean is linked to the common ancestor of all species within Clade III (node "C"). This species likely colonized the Caribbean from South America during the early Miocene about 19 Mya (HPD: 12.6–26.3 Mya). Within this Clade, the Caribbean was inferred to be the most probable ancestral range for two nodes ("E" and "F") that diversified into species with both Caribbean and extra-Caribbean distributions. Taxa that originated from node "E" (~11 Mya, HPD: 5.6–16.4 Mya) are mostly Caribbean endemics, except for *Sticta riparia* which dispersed to South America from the Caribbean and *Sticta* aff. *laciniosa* which only occurs in that continent. Most species that originated from node "F" (~14 Mya, HPD: 9.2–19.7 Mya) have at present a strictly Caribbean distribution. Some species including *Sticta laselvae, S. andreana,* and *S. pseudobeauvoisii*, however, seem to have ancestors in this region but now are found only in South America. Besides their presence in South and/or Central America, the geographic span of other species that originated from node "F" extends, in some cases, to the Afrotropics (i.e. *S. weigelii, S.* aff. *weigelii-3)* and Hawaii (*S. scabrosa*). Species within both Clades I and II, on the other hand, were inferred to have originated from South American ancestors (nodes "B" and "D", respectively). Except for *Sticta* sp. 3 which derived from a South/Central American ancestor, the rest of the species with Caribbean distribution within Clade I have an inferred South American origin. All Caribbean taxa in Clade II originated from South American ancestors that spread to the Caribbean and remained widely distributed (e.g. *S.* aff. *ciliata-4, S.* aff. *ciliata-2, S. dilatata, S. pseudodilatata*) or diverged to become Caribbean endemics (e.g. *S. parvilobata, S.* aff. *ciliata-5*, all species within the "*harrisii/*aff.
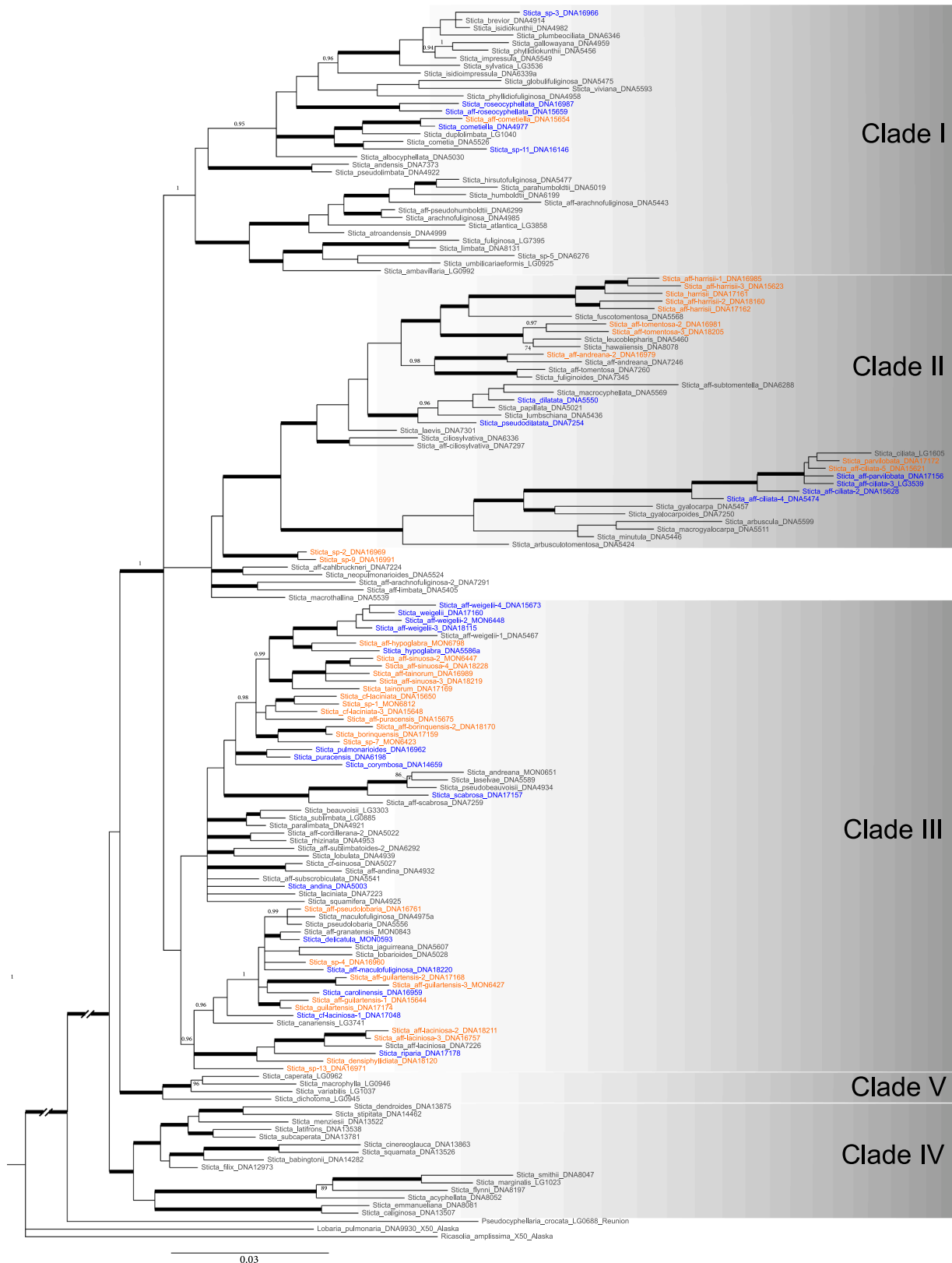
Fig. 2. 50% majority rule consensus tree obtained from MrBayes based on six nuclear and mitochondrial loci (ITS, MCM7, nuLSU, RPB1, RPB2, mtSSU). Species thus far endemic to the Caribbean are colored in orange, whereas species occurring in the Caribbean but also known from other regions are shown in blue. Species so far not known from this region are identified in gray.
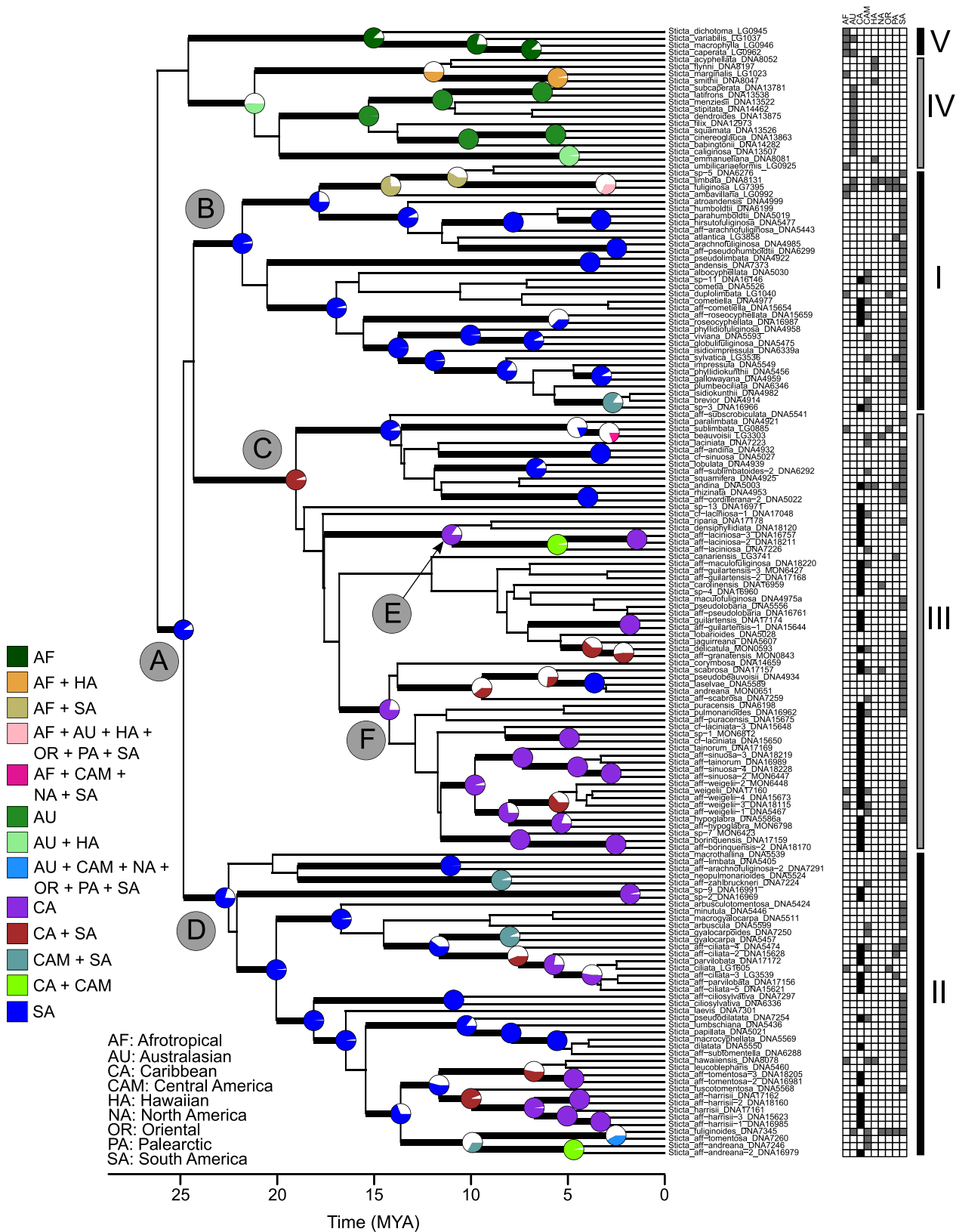
Fig. 3. Ancestral range reconstruction analysis without dispersal constraints based on our 4-loci MCC tree (outgroups removed). Matrix to the right indicates the presence of species in the Caribbean (black) and the other biogeographic regions analyzed (gray). Major clades are identified with black and gray bars to the far right. Labeled nodes indicate the common ancestors for Clades I, II, and III ("A"), Clade I ("B"), Clade II ("D"), Clade III ("C"), and the earliest ancestors of potential Caribbean origin (Nodes "E" and "F"). Ancestral ranges reconstructed are only shown for strongly supported clades. Horizontal scale: Millions of years ago (MYA).

harrisii" group).

Ancestral ranges reconstructed with dispersal constraints were in broad agreement with those without restrictions (Fig. S2). Differences concerning strongly supported nodes containing Caribbean taxa are described in detail in Table S5. In general, probabilities for the most likely ancestral ranges were lower using dispersal constraints. South America was more frequently recovered as the single ancestral range of many nodes that were otherwise inferred to be Caribbean or both South American and Caribbean. This was notable in Clade III. Additionally, Central America was more frequently included in ancestral areas reconstructed for several nodes in Clade II. Ancestral ranges inferred for all major nodes highlighted in Fig. 3 were identical between these analyses, except for node "D" which was recovered as both South American and Caribbean, and node "E" which had Central American and Caribbean origins.

3.3. Diversification analyses

The distribution of geographic character states in the 119-tip MCC tree used for GeoSSE analysis is shown in Fig. S3. Model selection results as well as parameter estimates for full and constrained GeoSSE models analyzed are provided in Table S6. Models without between-region speciation (sAB ~ 0) and without dependence of dispersal rates (dA ~ dB), as well as those assuming no dispersal from the Caribbean (dB ~ 0) and no dispersal from the Continental Neotropics (dA ~ 0) were statistically supported. This result was the same both when the root was unfixed and when the root was fixed for the Continental Neotropics. Only the model with no dispersal from the Caribbean (dB ~ 0) was supported when the root was fixed to the Caribbean.

For the most part, speciation and extinction rates for the Continental Neotropics and the Caribbean converged to similar values (Fig. 4A, 4B). In contrast, between-region speciation rates were slightly lower than rates in individual areas (Fig. 4A) and dispersal rates from the Caribbean were slightly higher than rates from the Continental Neotropics (Fig. 4C). The magnitude of differences was more pronounced for dispersal rates, whereas speciation and extinction rates showed similar rate differences (Fig. 4D).

Model inadequacy tests of our GeoSSE analysis show that for all transition rates evaluated and for both neutral and random traits simulated on our MCC tree, there is a high chance of incorrectly
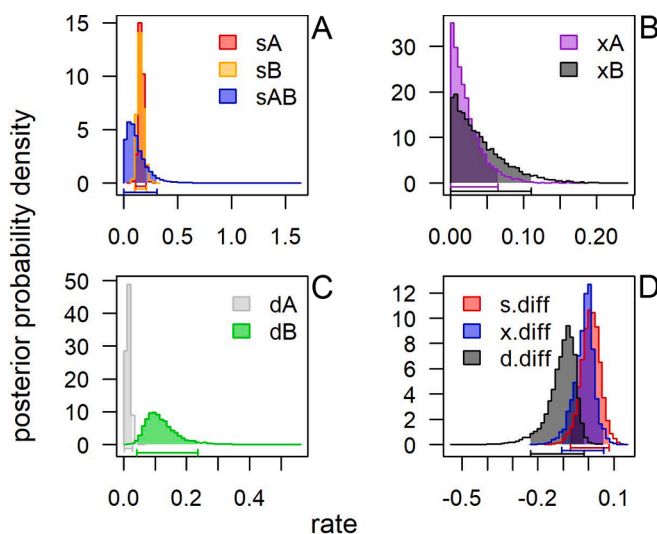
rejecting the null hypotheses of no between-region speciation (Fig. S4) and no dependence on dispersal rates (Fig. S5). The only noteworthy deviation from this generalization was observed when testing for no between-region speciation, specifically the simulation of neutral traits with a 0.05 transition rate. In this simulation, the proportion in which the null would be correctly rejected was 55%.

The frequency for zero number of regime shifts in the posterior distribution of samples in our BAMM analysis was 0.92 which suggests that distinct rate shifts are likely absent in our multilocus MCC tree. As hinted in the net diversification through time plot, decreases in diversification rate in the mean phylorate plot are at first slightly pronounced but decelerate over time (Fig. S6). Accordingly, a steady increase in the number of lineages is also observed.

3.4. Taxonomic and phylogenetic turnover of Caribbean Sticta communities

3.4.1. Effects of environmental and geographic distance on TBD and PBD
Data for environmental parameters generated for each island-level community is shown in Table S7. PCA axis 1 (Variance explained = 71%) was most strongly correlated with maximum elevation and max/min temperature whereas PCA axis 2 (Variance explained = 17%) was most strongly correlated with precipitation and TRI (ruggedness) (Table S8).

Correlation analysis with Mantel tests shows a significant association between all TBD and PBD metrics and environmental distances (Fig. 5). These relationships were further supported in our Procrustes analysis (Fig. S7). In contrast, association of these indices with geographic distance was not statistically significant. (Fig. S8).

A strong positive correlation between PD and species richness per island was also observed. These variables were positively correlated with maximum elevation (Fig. 6). Partitioning of *Jaccard* and *Unifrac* indices into "true" turnover and "nestedness" (*Jaccard*) or "phylogenetic diversity gradients" (*Unifrac*) components showed that taxonomic and phylogenetic dissimilarities are mostly driven by "true" turnover (Fig. S9).

3.4.2. Between-island taxonomic and phylogenetic dissimilarities
Analysis of dissimilarities estimated with TBD and PBD metrics show that the Lesser Antilles (Dominica, Guadeloupe, Martinique) and Puerto Rico are taxonomically similar (white to light blue [*Jaccard*]), and as a group, they are most dissimilar to Jamaica and Dominican Republic (dark blue) (Fig. 7A). Cuba, on the other hand, does not reflect strong patterns of dissimilarity with any of the other islands, although tends to be slightly less dissimilar to Dominica. Phylogenetic dissimilarity as evaluated with *Unifrac* mirror patterns observed with the *Jaccard* index, whereas analysis with the D_{Rao} metric reflects less dissimilarity between Cuba and Dominica and high dissimilarity between Dominican Republic vs. Martinique, Jamaica, and Guadeloupe.

With few exceptions, results from our null modeling/SES analysis broadly validate the aforementioned patterns (Fig. 7B). Taxonomic dissimilarity seems to be greatest between the Lesser Antilles (excluding Dominica) vs. Dominican Republic + Jamaica. The Lesser Antilles as a whole, and Puerto Rico, are strongly similar and some islands show strong affinities with Cuba (i.e. Puerto Rico, Martinique, Dominica). Puerto Rico is strongly dissimilar to Jamaica. Patterns observed with SES – *Unifrac* resemble those with SES – *Jaccard* but are less pronounced. Strong phylogenetic dissimilarity was only observed between Dominican Republic vs. Guadeloupe + Martinique, and Puerto Rico vs. Jamaica. Cuba remained similar only to Dominica. Significantly less dissimilarity between Cuba and Dominica + Puerto Rico was the only major pattern that emerged from SES – D_{Rao}.
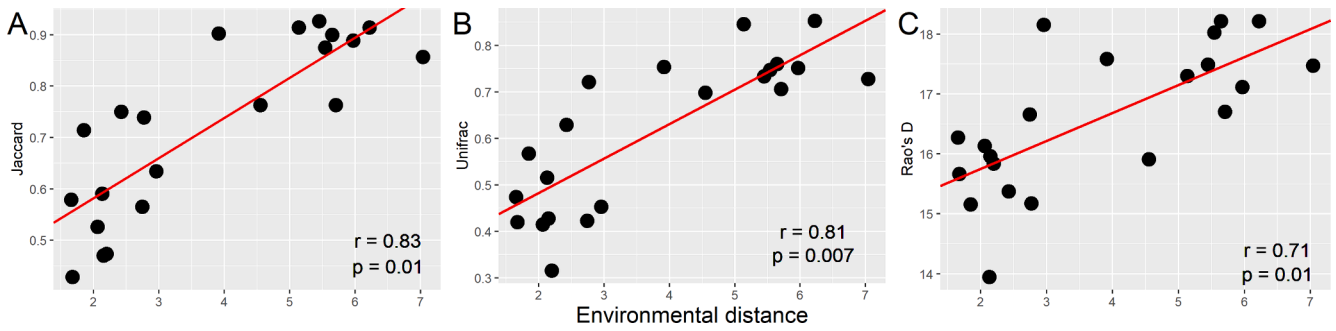

Fig. 4. Posterior probability distributions for speciation (A), extinction (B) and dispersal (C) rates, and rate differences (D) for our full, unfixed root GeoSSE model. Region "A" represents the Continental Neotropics and Region "B" corresponds to the Caribbean region. Both geographical regions are denoted as "AB".

Fig. 5. Relationship between Taxonomic Beta Diversity (TBD), terminal Phylo Beta Diversity (tPBD) and basal Phylo Beta Diversity (bPBD) metrics with environmental distance. A) Jaccard, B) UniFrac, C) Rao's D. All associations were statistically significant according to Mantel tests.
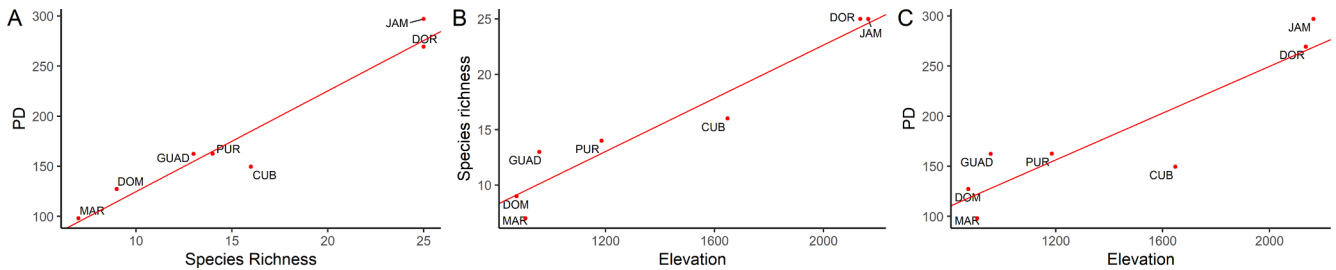

Fig. 6. Relationships between A) species richness vs. phylogenetic diversity, B) species richness vs. elevation, C) phylogenetic diversity vs. elevation, in *Sticta* communities from islands in the Caribbean. CUB: Cuba, DOM: Dominica, DOR: Dominican Republic, GUAD: Guadeloupe, JAM: Jamaica, MAR: Martinique, PUR: Puerto Rico.
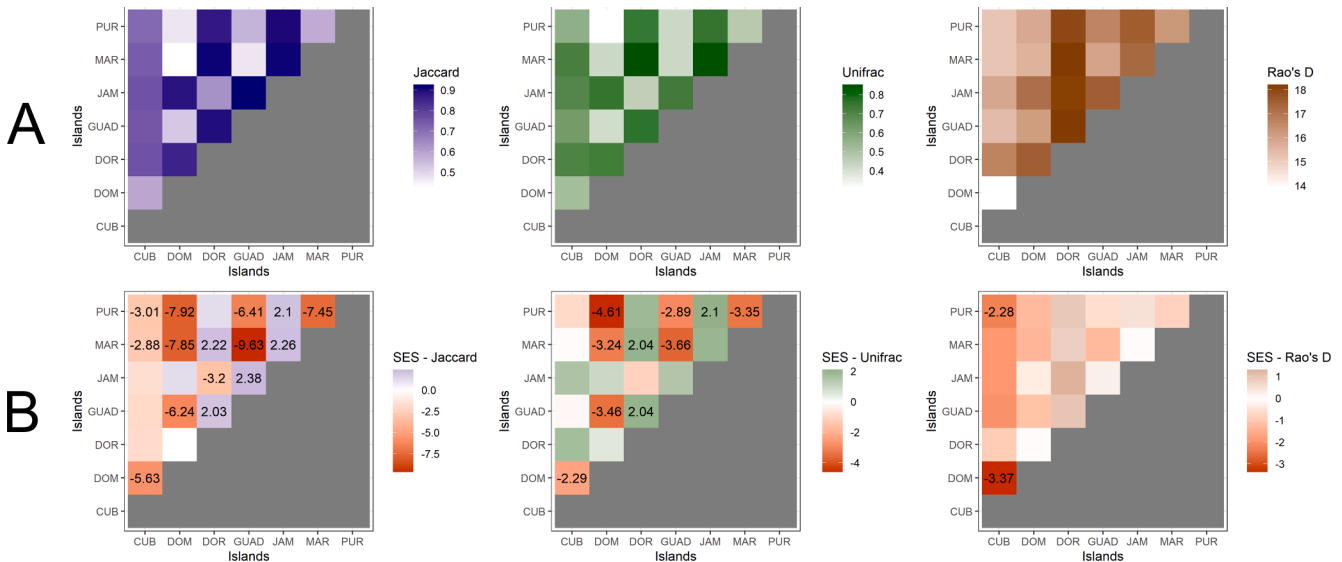

Fig. 7. Heatmaps illustrating taxonomic and phylogenetic dissimilarities between Caribbean islands. Dissimilarities were estimated from TBD and PBD indices calculated for A) empirical, and B)100 null (simulated) communities. Standardized Effect Sizes (SES) values are shown in grid cells of B) whenever these were lower or higher than |1.96|. Darker colors in A) indicate higher dissimilarities and darker brick red colors in B indicate high similarities. CUB: Cuba, DOM: Dominica, DOR: Dominican Republic, GUAD: Guadeloupe, JAM: Jamaica, MAR: Martinique, PUR: Puerto Rico.

4. Discussion

4.1. Diversity, endemism, and phylogenetic patterns

High diversity and degrees of endemism are distinctive features of insular Caribbean biotas. In this study, we found that at least 64 species of *Sticta* occur in the Caribbean islands, 38 of these (~60%) being potentially endemic to this region. These values are comparable (or higher) to estimates from other insular systems (see below) suggesting

that high biodiversity is also a salient attribute for Caribbean *Sticta*. Not long ago, high levels of diversity and endemism were unexpected for insular lichens. However, an increasing number of phylogenetic studies continue to demonstrate that high endemism in lichen fungi is a common phenomenon in these settings. Within the Caribbean, Puerto Rican *Sticta* endemism may be as high as 69% (Mercado-Díaz et al., 2020) which is about the same degree of endemism attributed to this group in the relatively young Hawaiian archipelago (Moncada et al., 2020). About 89% of the *Sticta* species in Madagascar and Indian Ocean Islands

(Simon et al., 2018) are also believed to be endemics. Studies in groups within the same family (e.g. *Lobariella*, *Pseudocyphellaria* [Moncada et al., 2014; Lücking et al., 2017b]) and distantly related genera (e.g. *Dictyonema*, *Nephroma*, [Dal Forno et al., 2017; Sérusiaux et al., 2011]) are consistent with this view, with inferred rates of insular endemism between 69% and 100%.

Topological discrepancies between the different phylogenies inferred for this study highlight limitations for correctly interpreting the evolutionary history of this group. Of these limitations, differences in gene sampling deserve mention. For instance, similar to results presented by Widhelm et al. (2018), our BEAST analysis yielded strong support for the five major clades presented in that work. This was somewhat expected since the main phylogeny in Widhelm et al. (2018) was inferred in the same program using a similar gene dataset. However, statistical evidence in favor of the monophyly of Clades I and III was lacking when other phylogenetic methods (e.g. RaxML/MrBayes) and additional gene data (RPB1 and RPB2) were used. The paraphyletic grade associated with Clade II further attest to these issues as alternate patterns of clade association were noted for the same species in Widhelm et al. (2018). Further extending gene sampling will certainly help overcome this type of incongruencies. In addition, parameter variation in reconstruction methods, such as slight differences in models and priors or different strategies for operators, likely underlie some of the inconsistencies observed. Along with improving taxon coverage, adequately addressing this type of methodological limitations will be crucial for properly reconstructing elusive events in the evolution of this group.

4.2. Timing and geographic range evolution

The estimated crown age for *Sticta* (~26.2 Mya) is highly similar to the one obtained in Widhelm et al. (2019) (~25.2 Mya) and reaffirm that the group likely emerged during the Late Oligocene. As indicated, the earliest colonization event of *Sticta* in the Caribbean presumably occurred about 19 Mya (node "C", Fig. 3) which imply that the islands must have had suitable habitat for colonization during this period. Plant fossils from different islands in this region provide support for this scenario. For instance, fragmentary megafossils and fossil pollen/spores from the Oligocene have been recovered from Puerto Rico (Graham, 2003; Graham and Jarzen, 1969), including a fossil fruit endocarp from the early Oligocene (Herrera et al. 2014). Microfossil floras the mid-Eocene are also known from Cuba (Graham et al. 2000) further evidencing that upland vegetation existed during *Sticta* colonization of the Caribbean.

Ancestral range reconstruction based on nine biogeographic regions provided further resolution into the evolution of ranges within this group. For instance, the early diverging Clade IV was found to be more narrowly restricted to the Afrotropics. The common ancestor to Clades I, II, and III, which gave rise to all Caribbean species around the early Miocene, was also inferred to have originated in South America. South American affinities have been suggested for many Caribbean lineages, including *Sticta* in Puerto Rico (Mercado-Díaz et al., 2020). Other notable examples include non-volant terrestrial vertebrates (Hedges, 2006; Marivaux et al., 2020), spiders (McHugh et al., 2014), fishes (Weaver et al., 2016), and several groups of plants (Aguirre-Santoro et al., 2020; Filipowicz and Renner, 2012; Regalado et al., 2018; Santiago-Valentín and Olmstead, 2003). Furthermore, several Central American species for which we had limited sequence data emerged as sister to Caribbean lineages during preliminary analysis suggesting that some lineages may have derived from Central American ancestors. This agrees with previous work on various plant groups (e.g. *Coccoloba* and members within the subfamily Acalyphoideae) that have demonstrated affinities of Caribbean taxa to Central American floras (Cervantes et al., 2016; Koenemann and Burke, 2020). Additional investigation into these affinities, which should include increased taxon representation from this region, might reveal that directions and frequency of colonization events

between both regions are, in fact, underestimated.

We want to note that while speciation via "jump dispersal" or "founder event" likely influenced range evolution patterns in our study system, we opted not to consider range reconstruction models that account for this speciation mode (e.g. DEC + J model (Matzke, 2014)). This decision was based on (Ree and Sanmartín, 2018) whom indicate that the DEC model without additional parameterization (e.g. "+j" parameter) is likely a defensible choice in scenarios where the central goal is inferring ancestral ranges and not testing hypotheses related to processes of range evolution.

4.3. Reverse colonization

Our work suggests that after diverging from the ancestor to Clade III, two lineages inferred to be Caribbean endemics (i.e. nodes "E" and "F", Clade III) gave rise to species that eventually re-colonized South America and other regions. Re-colonization of continents by island lineages is highly debated as theory assumes unidirectional movements of species from continents to islands (MacArthur and Wilson, 1967). Underlying this prediction are "island syndromes" which involve the loss of dispersal power and defensive traits in island clades (Whittaker and Fernández-Palacios, 2001). Reverse colonization of continents by island species has been amply documented in animals and plants (Bellemain and Ricklefs, 2008; Carine et al., 2004; Herrando-Moraira et al., 2019). While for the Caribbean islands evidence is more limited, several studies have supported scenarios of reverse colonization, particularly in plant lineages (Cano et al., 2018; Nieto-Blázquez et al., 2020). We thus suspect reverse colonization events have had an important role in the biogeographic history of *Sticta* in this region. This is further supported by our GeoSSE analysis (see below) as dispersal rates "out of the Caribbean" (dB) were slightly higher than those from the continental Neotropics (dA).

Several bryophyte studies (Hutsemékers et al., 2011; Laenen et al., 2011; Patiño and Vanderpoorten, 2015) and one study on lichens (Sérusiaux et al., 2011) evidence that organisms that produce spores and/or other small asexual diaspores, such as lichens, should display increased capacity for reverse colonization from islands to continents. Such ability rests on the presumed ease with which these propagules are spread, either via abiotic (e.g. wind) and/or biotic (e.g. birds) vectors (Johansson et al., 2021; Muñoz et al., 2004; Ronnås et al., 2017). However, conditions favoring reverse colonization transcend those associated with organismal properties. Although work on lichens is still wanting, the availability of vacant niches in continental areas might be important. This was demonstrated by Hutsemékers et al. (2011) who showed that a severe bottleneck in continental populations of the moss *Rynchostegium riparioides* during the last glacial maximum likely facilitated colonization of this species from Macaronesia to Europe. Wind currents with a predominant island-to-mainland direction might also be critical since establishment is ultimately a function of propagule pressure (Gillespie et al., 2012). Tradeoffs between the proximity of archipelagos to continents and the age of the lineages should also be major reverse colonization determinants. For example, for Hawaiian endemics, which are relatively young (<6 My, Moncada et al., 2020), short time scales coupled with the remoteness of the islands might have precluded range expansion to continental areas. Conditions for Caribbean endemics that were identified in this study and gave rise to reverse colonizing species were certainly more favorable since these species were older and inhabited an archipelago that, by the time they evolved, was already close to South and Central America. Madagascar, on the other hand, have attributes amenable for reverse colonization (e.g. the island is geologically old [~ 88 My] and moderately close to the African continent [< 430 Km.]), but *Sticta* endemics from this island are also of young age (<11 Mya [Simon et al., 2018]) which has likely limited this type of events. More studies characterizing the ideal conditions promoting reverse colonization will be central for reaching a holistic understanding of processes underlying distributional patterns in these

poorly studied groups.

4.4. Diversification in the Caribbean

Evidence presented here align with findings from Mercado-Díaz et al. (2020) suggesting that *Sticta* communities in the insular Caribbean resulted from multiple colonization events and in-situ evolution as opposed to a single colonization event followed by species radiation, as has been observed in communities from Madagascar and the Indian Ocean Islands (Simon et al., 2018). This agrees with the lack of significant rate shifts inferred in BAMM and results from our GeoSSE analysis which showed that the colonization of the Caribbean islands did not trigger changes in diversification rates.

Some studies on plants suggest that species radiations occur in the insular Caribbean (Aguirre-Santoro et. al., 2020; Cervantes et al., 2016; Filipowicz and Renner, 2012; Hidalgo et al., 2020). However, except for Aguirre-Santoro et al. (2020) notable work on the genus *Wittmackia*, the few studies that have explicitly tested for diversification rate shifts have not found evidence for increases in diversification triggered by island colonization (Cano et al., 2018; Nieto-Blázquez et al., 2020). It is therefore possible that lichen radiations are rare, at least at the level of the Caribbean archipelago, although confounding factors would need to be further investigated. For instance, it is likely that our relatively small dataset might have introduced sampling artifacts (Davis et al., 2013). Uncertainties in reconstructions and the influence of extinction imply that rate changes may remain undetected. Other issues that would need addressing are inaccurate rate estimates due to lack of fossil data (Didier et al., 2017) and the possibility of life-history traits (e.g. high dispersal capacity) influencing the detection of bursts of lineage-splitting events (Claramunt et al., 2012). Yet, failing to uncover evidence of regional-level diversification does not rule out diversification at island-level scales. Supporting this scenario are the smaller "micro-radiations" that have been suggested for some clades of *Sticta* in Puerto Rico and those detected for *Sticta* and *Lobariella* in Hawaii (Lücking et al., 2017b; Moncada et al., 2020). Detailed within-island studies are needed to further explore such scenarios, although this will require overcoming methodological limitations associated with analyzing datasets with smaller sample sizes.

Support for a model favoring the influence of between-region speciation (sAB) suggests that allopatric speciation of widespread species may have had a heightened role in Caribbean *Sticta* diversification. Range-splitting speciation in this context might have been favored by the effectiveness of oceans for limiting long-distance dispersal, as has been recently suggested for Anoles (Landis et al., 2022). Yet, caution should be exercised when interpreting these results since similar to what has been predicted and tested in the past (Alves et al., 2017; Rabosky and Goldberg, 2015), our simulations suggested the presence of model inadequacy issues. Topological uncertainty associated with poorly supported clades further exacerbate these conclusions.

4.5. Taxonomic and phylogenetic turnover of Caribbean Sticta communities

4.5.1. Environmental structuring of taxonomic and phylogenetic beta diversity

A significant positive correlation between taxonomic beta diversity and environmental gradients suggests that at ecological scales, environmental filtering plays a pivotal role for Caribbean *Sticta* community assembly. Most of the variance in our environmental PCA (71%) was explained by axis 1, thus we attribute observed variation to changes in elevation and concomitant fluctuations in temperature. Although alpha-diversity along elevational gradients have been well characterized for lichens in continental ecosystems (Wolf, 1993; Baniya et al., 2010; Bässler et al., 2016; Soto-Medina et al., 2019), taxonomic turnover as a function of variation along environmental axes (particularly elevation), especially in the tropics, is less understood. Our work documented

increases in species richness with elevation, however, partitioning of beta diversity components showed that patterns were being driven by 'true' turnover. This agrees with studies evidencing strong variation in macro- and micro-lichen species composition along altitudinal gradients in mountainous neotropical areas (Soto-Medina et al., 2019; Wolf, 1993) and attests to the compositional "uniqueness" that characterize communities at each elevational strata.

Correlations of environmental PCA axes with PBD metrics mirror those with TBD and further indicate that irrespective of geographic distance between islands, *Sticta* species within the same elevational/temperature community tend to be more closely related to each other than they are to species in other elevational zones in the same island. Communities at opposite extremes along elevational gradients are therefore phylogenetically most distant within this region. These findings reiterate the importance of environmental filtering as a major factor regulating species composition in these island-level communities, but most importantly, they suggest that these communities are apparently tracking key environmental attributes of their habitats over evolutionary time. Phylogenetic niche conservatism might therefore represent a salient feature of assembly processes in these metacommunities. Niche conservatism associated with environmental conditions is a predominant pattern in most empirical studies on phylobetadiversity, but studies on groups other than plants and animals are scarce. One example is the study by Wang et al. (2013) which showed that phylogenetic dissimilarity was strongest among habitat types in bacterial communities of subsurface lake environments distributed throughout China. Peixoto et al. (2014) work on bats uncovered strong spatial distance effects on global-scale patterns of phylobetadiversity, however, they noted that strong environmental gradients may influence assemblages occurring in adjacent biogeographic regions. This reaffirms the influence of environmental gradients on phylogenetic turnover, although it also suggests that spatial scale ultimately determines the degree to which their effects are detectable.

Determining the importance of phylogenetic niche conservatism vs. evolutionary lability in Caribbean lichen metacommunities will certainly require additional efforts, particularly testing for phylogenetic signal at the metacommunity level (Pillar and Duarte, 2010). Results from other efforts evaluating phylogenetic structure of lichen communities would also be ideal for comparative purposes, but studies are still scarce. Lucking et al. (2016) showed that *Parmeliaceae* communities in major biomes of Mexico exhibit different degrees of phylogenetic clustering. More recently, Nascimento et al. (2021) suggested that underlying differences in climatic and edaphic conditions that are seen between major vegetation types from Brazil are indirectly linked to contrasting patterns of phylogenetic overdispersion and clustering of lichen metacommunities. Additional work using phylogenetic frameworks to disentangle the links between environmental variation and species distributions can also be informative. Moncada et al. (2021) is notable in this respect as they showed that divergent genetic structuring in geographically overlapping populations of *S. scabrosa* (tropical lowland species with a "weedy" character) and *S. andina* (upper montane, cloud forest/paramo specialist) were likely driven by autecological preferences. Yet, population-level studies in lichens often uncover cases of cryptic speciation in putatively widespread lineages (Alors et al., 2016; Fernández-Mendoza and Printzen, 2013; Otálora et al., 2010). This stresses the need for additional assessment of geographic distance as a potential driver of phylogenetic structuring in many of these communities.

4.5.2. Relatedness of Sticta communities among Caribbean islands

Understanding patterns of relatedness among island-level communities in the Caribbean is challenging as few studies exist and most address these issues outside phylogenetic frameworks. Our study showed significantly low taxonomic and phylogenetic dissimilarity between *Sticta* from the Lesser Antilles and Puerto Rico suggesting that both areas have similar species composition and high degree of shared

evolutionary history. This agrees with studies suggesting strong affinities between Puerto Rico and the Lesser Antilles in several groups of plants (Dewalt et al., 2016; Nieto-Blázquez et al., 2020). However, further efforts to assess the pervasiveness of such pattern are needed as links of Puerto Rican species to Greater Antillean communities have also been proposed (Acevedo-Rodríguez and Strong, 2008). A thorough evaluation of the mechanistic factors potentially driving these patterns could be informative in this respect. For instance, vicariant events cannot be invoked as land bridges that presumably connected these areas in the past (Iturralde-Vinent and MacPhee, 1999; Philippon et al., 2020) predate the origin of the genus (this study, Widhelm et al., 2018). Long-distance dispersal through hurricanes have stronger explanatory power (Gillespie et al., 2012). In fact, prevailing tracks seem to connect more often the Lesser Antilles to Puerto Rico (https://www.nhc.noaa.gov/climo/ [Last accessed: 2/1/2021]) which would effectively increase between-islands interconnectivity. Separately, it was also notable that despite species composition between them being significantly similar, the degree of shared phylogenetic history between Jamaican and Dominican Republic communities was not statistically different to what would be expected from comparisons to a randomly assembled community. Sampling artifacts could certainly underlie this lack of statistical signal. Alternatively, community phylogenetic structure might be more strongly driven by ecological time-scale factors (e.g. competition, predation, etc.) which were not considered in our study.

Highest taxonomic and phylogenetic diversities associated with island-level communities from Dominican Republic and Jamaica (see Fig. 6) likely underlie statistically significant taxonomic and phylogenetic dissimilarities observed between Dominican Republic and some of the Lesser Antilles, and between Jamaica and Puerto Rico. Likewise, most variation in both taxonomic and phylogenetic beta diversity was attributed to 'true' turnover (see Fig. S9) which further attest to compositional and evolutionary distinctiveness of these communities. Similar to other groups of plants and birds (Hughes and Atchison, 2015; Madriñán et al., 2013; Ryan et al., 2007), some *Sticta* lineages (Moncada et al., 2021) have evolved affinities to cold, high elevation environments. Observed dissimilarities between these sets of islands are therefore likely attributed to the presence of small ranged species potentially restricted to high elevation environments in Dominican Republic and Jamaica. According to community phylogenetics theory, these are likely paleoendemics that have a low degree of shared evolutionary history with species from communities at lower elevations (see Table 1 in Graham and Fine, 2008). Conversely, significantly low phylogenetic dissimilarity observed between Cuba and the islands of Puerto Rico and Dominica in terms of the basal metric D_{Rao} deserves further investigation. These findings suggest that shared environmental tolerances between these communities evolved during the early diversification of *Sticta* in this region.

Due to limited time, communities from several islands which are known to harbor or that theoretically have suitable habitat for *Sticta* (e. g. Trinidad and Tobago, St. Lucia, etc.) could not be surveyed for this study. We do not expect patterns uncovered by our taxonomic and phylogenetic beta diversity analyses to have been significantly affected by this sampling limitation. For instance, Trinidad and Tobago certainly harbor habitats amenable for this group, yet these continental islands were only recently separated from South America (~15,000 year ago) and thus they are expected to have closer affinities to the biotas of that continent. Data for islands like St. Lucia and St. Vincent are scarce, but many specimens (see https://herbarium.natsci.msu.edu/research/checklists/aribbean-islands/) are representative of the *Sticta weigelii* morphodeme which is also the case for surveyed islands nearby (e.g. Martinique). Given that these islands also share a similar geological history and that communities from the Lesser Antilles in our study form a cohesive taxonomic and phylogenetic unit, we expect our sampling to have indirectly accounted for these unsampled communities.

5. Conclusions

Our study revealed that *Sticta* is represented by at least 64 species in the Caribbean, 38 of these potentially endemic to this region. This fraction of endemics is comparable to what has been found in recent studies of lichenized fungi in other archipelagos emphasizing the importance of island systems for the maintenance of biodiversity in this group. Although further work will be needed to better characterize geographic affinities with Central America, we showed that Caribbean *Sticta* diversity has a marked South American ancestry. In addition, after diverging from broadly distributed species, several putative Caribbean lineages expanded their range back to South America, thus exemplifying potential cases of reverse colonization. We have not found any evidence that range expansion to the Caribbean triggered increases in diversification.

To our knowledge, this is the first study to implement a phylobetadiversity approach to explore patterns of taxonomic and phylogenetic relatedness in insular lichen communities. In line with known habitat preferences for *Sticta*, we confirmed that niche differences linked to environmental variation along elevational gradients are major drivers of taxonomic and phylogenetic turnover in island-level communities from the Caribbean. Less dissimilarity was seen between high elevation communities of Dominican Republic and Jamaica and between low elevation assemblages in the Lesser Antilles and Puerto Rico. Taxonomic and phylogenetic diversity was positively correlated with elevation. This suggests that small ranged endemic species abundant in high elevation environments and species with wider distributions in the Lesser Antilles and Puerto Rico drive most of the taxonomic and phylogenetic turnover observed. These findings provide a broad picture of community assembly in Caribbean *Sticta* over evolutionary time but also highlight the notable contribution of Hispaniolan and Jamaican communities to *Sticta* diversity in this region. Additional work at smaller spatial scales would still be needed to further disentangle patterns of relatedness, particularly between communities within each island.

Our study demonstrates the important contribution that Caribbean lichens make to global biodiversity. It also adds to the growing body of work demonstrating that unique evolutionary patterns that characterize island lineages are not exclusive to plants or metazoan assemblages, but are also evident in speciose, understudied groups such as lichens.

CRediT authorship contribution statement

Joel A. Mercado-Díaz: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Robert Lücking:** Conceptualization, Resources, Data curation, Writing – review & editing. **Bibiana Moncada:** Resources, Data curation, Writing – review & editing. **Keron C. St. E. Campbell:** Resources, Writing – review & editing. **Cesar Delnatte:** Resources, Writing – review & editing. **Lemuel Familia:** Resources, Writing – review & editing. **Banessa Falcón-Hidalgo:** . **Angel Motito-Marín:** Resources, Writing – review & editing. **Yoira Rivera-Queralta:** Resources, Writing – review & editing. **Todd J. Widhelm:** Resources, Writing – review & editing. **H. Thorsten Lumbsch:** Conceptualization, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2023.107830.

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