

Biotic homogeneity of putative biogeographic units in the Neotropics: A test with Sapotaceae

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Abstract

Aim: To evaluate Morrone's (2001, *Biogeografía de America Latina y el Caribe*. Zaragoza, Spain: CYTED, ORCYT-UNESCO, Sociedad Entomológica Aragonesa (SEA)) Neotropical regionalization by testing the prediction that biotas are more homogeneous within than among biogeographic units.

Location: Neotropics.

Methods: We conducted pairwise comparisons of beta diversity of Sapotaceae species within and between biogeographic units in the hierarchical regionalization proposed by Morrone (2001, *Biogeografía de America Latina y el Caribe*. Zaragoza, Spain: CYTED, ORCYT-UNESCO, Sociedad Entomológica Aragonesa (SEA)), at a spatial resolution of 1-degree cells. We used a null model to control differences in sampling effort across 1-degree cells and performed beta-diversity comparisons conditional on geographic distance to control for distance decay of biotic similarity.

Results: None of the biogeographic units proposed by Morrone (2001, *Biogeografía de America Latina y el Caribe*. Zaragoza, Spain: CYTED, ORCYT-UNESCO, Sociedad Entomológica Aragonesa (SEA)) was biotically homogeneous with respect to all other units at the same hierarchical level. This was the case even for units commonly reported to be isolated and to host distinctive taxa like "Choco." However, five of 45 biogeographic units were biotically homogenous relative to several other units. These units were "Cuba," "Chaco," "Varzea," "Cauca" and "Costa Pacifica Mexicana." Also, beta diversity within units was often lower than beta diversity between units at relatively short geographic distances.

Main conclusions: The distribution of Sapotaceae species showed generally low biotic homogeneity within Morrone's (2001, *Biogeografía de America Latina y el Caribe*. Zaragoza, Spain: CYTED, ORCYT-UNESCO, Sociedad Entomológica Aragonesa (SEA)) biogeographic units and did not support his biogeographic regionalization. This result suggests a strong role for dispersal and biotic interchange among biogeographic units and across barriers like the Andes. It also casts doubt on the usefulness of Morrone's (2001, *Biogeografía de America Latina y el Caribe*. Zaragoza, Spain: CYTED, ORCYT-UNESCO, Sociedad Entomológica Aragonesa (SEA)) biogeographic units as tools for the identification of priority areas for the conservation of biodiversity. However, relatively high biotic homogeneity within some biogeographic units suggests that they capture significant spatial patterns. In particular, noteworthy

biotic homogeneity within “Cuba,” “Cauca” and “Costa Pacifica Mexicana” could be explained by isolation. Also, in “Costa Pacifica Mexicana,” patterns of biotic homogeneity could reflect closer affinities to humid lowland montane forest in Central America than to lowland rain forest in South America. Finally, substantial biotic homogeneity within “Varzea” could result from common adaptation to edaphic environments near the Amazon River.

KEYWORDS

beta diversity, biogeographic regionalization, Neotropics, provincialism, Sapotaceae

1 | INTRODUCTION

A central tenet of biogeography is that organisms are distributed across geographic space in a non-random fashion, forming spatial aggregations of endemic taxa with overlapping distributions, a phenomenon known as provincialism (Lomolino, Riddle, Whittaker, & Brown, 2010). At least since the 19th century provincialism has been described by drawing divisions on Earth that reflect patterns of biotic similarity (e.g. De Candolle, 1820; Sclater, 1858; Wallace, 1876), thus delimiting areas heralded as “biogeographic units.” These units are often regarded as parts of hierarchical systems of nested areas (e.g. McLaughlin, 1992; Cracraft, 1994; Morrone, 2001; Kreft & Jetz, 2010; Holt et al., 2013; but see Stoddart, 1992) known as “biogeographical regionalization.” Realms or regions are the largest areas in these systems, frequently delimited according to the distribution of higher taxa, such as families and orders. Lower in the biogeographic hierarchy are increasingly smaller areas, for instance subregions and provinces, delimited according to the distribution of taxa at increasingly lower taxonomic ranks, including genera and species. In this way, subregions are nested within realms and provinces within subregions (see Morrone, 2009). These proposed biogeographic units, as well as their relationships in terms of biotic similarity, play significant roles in attempts to uncover the history and current spatial structure of life on earth (Lomolino et al., 2010), and in plans for the conservation and management of biological diversity (Ladle & Whittaker, 2011; Whittaker et al., 2005).

Despite its significance for basic science and biodiversity conservation, delineation of biogeographic units in tropical regions of Earth remains uncertain (Escalante, 2009; Kreft & Jetz, 2010; Mackey, Berry, & Brown, 2008). In no small part, this uncertainty stems from the fact that many extant species have not been described (the Linnaean shortfall, Essl, Rabitsch, Dullinger, Moser, & Milasowszky, 2013) and that the geographic distribution of described species is poorly known (the Wallacean shortfall, Sheth, Consiglio, Lohmann, & Jiménez, 2012). The Linnaean and Wallacean shortfalls are particularly important impediments for the accurate delineation of units at the lower ranks of the hierarchies proposed by biogeographic regionalization. These units cover relatively small areas and are based on the geographic distribution of taxa at low taxonomic ranks, often species. Therefore, their delimitation requires data with high spatial

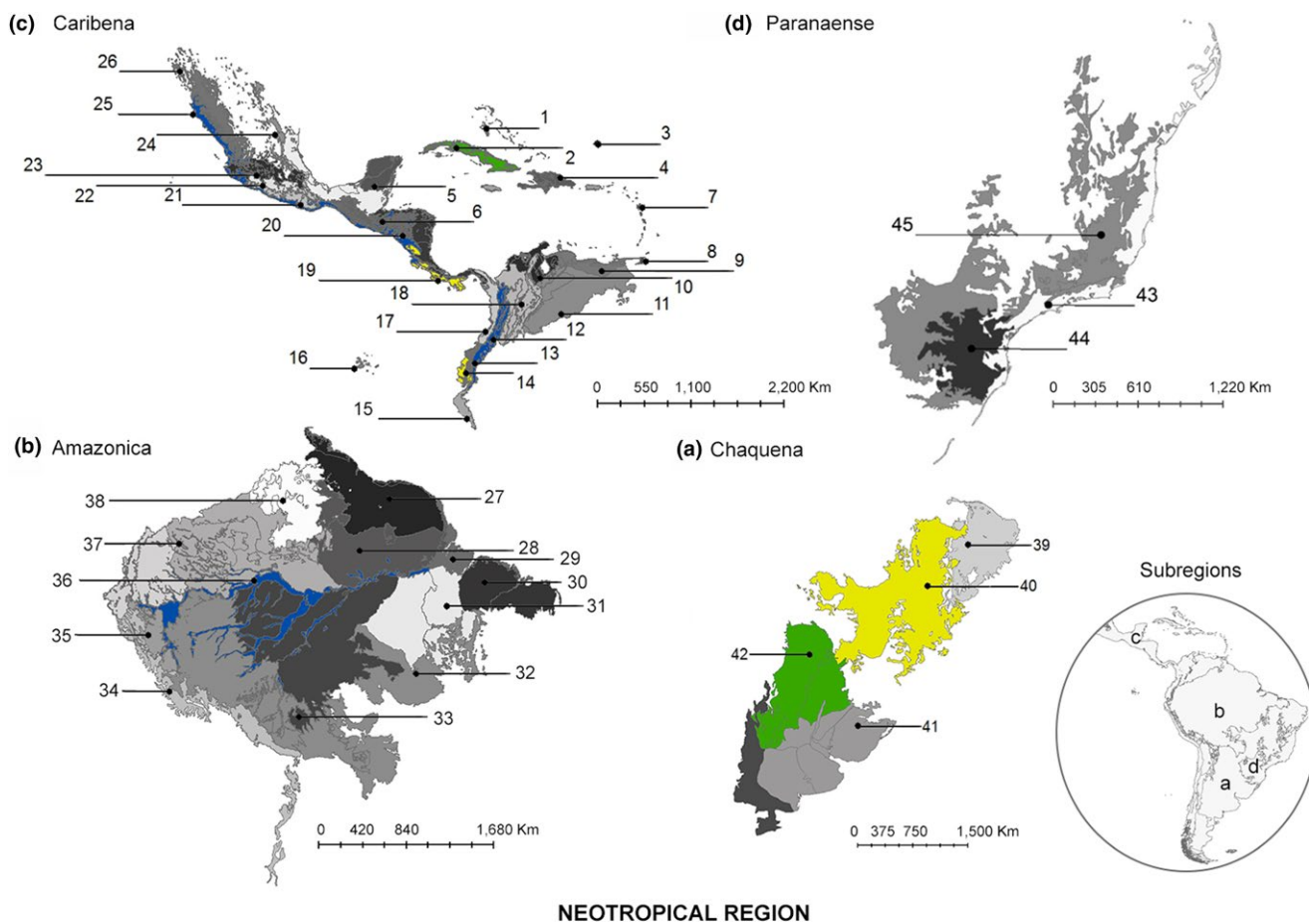
and taxonomic resolution. Because availability of these data may often be limited, proposed biogeographic regionalization may best be regarded as working hypotheses that yield testable predictions (Mackey et al., 2008; Whittaker et al., 2005). As data with high spatial and taxonomic resolution become increasingly available, further progress can be made by testing these predictions, thus determining the extent to which putative biogeographic units constitute accurate portrayals of provincialism.

A key prediction implicit in proposed biogeographic regionalization is the biotic homogeneity of putative biogeographic units. In particular, whether putative biogeographic units accurately describe the spatial aggregation of endemic taxa (i.e. provincialism), then biotas should be more homogeneous within than among units (Stoddart, 1992; Lomolino, Riddle, & Brown, 2006, page 342; Kreft & Jetz, 2010). In other words, change in taxon composition between sites within a given biogeographic unit should occur at lower rates than change in taxon composition between sites located in different biogeographic units. Several methods are commonly used to propose biogeographic units at any level in the hierarchy (e.g. subregions or provinces), are designed to identify areas that contain distinctive endemic taxa (e.g. Morrone, 2014a; Szumik & Goloboff, 2004), but any given area (even a randomly selected area) may contain distinctive endemic taxa and, nonetheless, lack spatially homogeneous biota relative to other areas (Lomolino et al., 2006, page 342). Other proposals of biogeographic units are based on analyses that cluster sites according to their biotic similarity (e.g. Holt et al., 2013; Kreft & Jetz, 2010; Moullot et al., 2013; Oliveira, Márquez, & Real, 2013; Vilhena & Antonelli, 2015). However, biotic similarity among sites can be largely driven by geographic distance (Soininen, McDonald, & Hillebrand, 2007), and thus, putative biogeographic units identified using this kind of criterion may not reflect true discontinuities but arbitrary division of a gentle gradient of taxon turnover across geographic space (Magnusson, 2004; Fortin & Dale, 2005, page 180). Therefore, empirical tests of the spatial discontinuities in taxon turnover predicted by proposed biogeographic units should ideally control for distance decay of biotic similarity (Soininen et al., 2007). Such tests seem scarce (Lomolino et al., 2006; but see Stuart, Losos, & Algar, 2012), and yet they are required to examine the merit of putative biogeographic units, again even when such units are known to host distinctive endemic taxa.

Here, we view the Neotropical biogeographic units proposed by Morrone (2001), and further described by Morrone (2006, 2009), as working hypotheses. We focus on testing whether they are homogeneous in terms of one component of the biota: plant species in the family Sapotaceae. These biogeographic units, delineated according to the geographic distribution of vascular plants, insects and birds, hierarchically divide the Neotropical region into provinces nested within subregions (Figure 1). This is the most comprehensive biogeographic regionalization currently available for the Neotropics. It is based on various kinds of analysis, including parsimony analysis of endemism, and approaches in cladistic biogeography and panbiogeography. The biogeographic regionalization of Morrone

(2001) figures prominently in discussions of Neotropical provincialism (e.g. Daza, Castoe, & Parkinson, 2010; Espinosa, Llorente, & Morrone, 2006; Fiaschi & Pirani, 2009; Luebert & Weigend, 2014) and has been used in studies focused on biodiversity conservation (Calderón-Patrón et al., 2016; Contreras-Medina & Luna-Vega, 2007; González-Oreja, 2011; Torres-Miranda, Luna-Vega, & Oyama, 2011).

Despite their prominence, we are unaware of any test of the biotic homogeneity of any of the biogeographic units proposed by Morrone (2001). A few studies have evaluated the regionalization originally proposed by Morrone (2001) using independent data sets and cladistic biogeographical analyses known as parsimony analysis of endemism (Echeverry & Morrone, 2010; Morrone, 2014b), but



Caribena subregion

1. Bahamas
2. Cuba
3. Puerto Rico
4. Espanola
5. Peninsula de Yucatan
6. Chiapas
7. Antillas Menores
8. Trinidad Tobago
9. Costa Venezolana
10. Maracaibo
11. Llanos Venezolanos
12. Cauca
13. Occidente de Ecuador
14. Ecuador Arido
15. Tumbes Piura
16. Islas Galapagos
17. Choco
18. Magdalena
19. Occidente del Istmo de Panama
20. Oriente de America Central
21. Sierra Madre del Sur
22. Depresion de Balsas

NEOTROPICAL REGION

23. Eje Volcanico Transmexicano
24. Sierra Madre oriental
25. Costa Pacifica Mexicana
26. Sierra Madre occidental
27. Guyana Humeda
28. Roraima
29. Amapa
30. Para
31. Tapajos Xingu
32. Pantanal
33. Madeira
34. Yungas
35. Napo
36. Varzea
37. Imeri
38. Guyana

Amazonica subregion

39. Caatinga
40. Cerrado

Chaquena subregion

39. Caatinga
40. Cerrado

Paranaense subregion

43. Bosque Atlantico Brasileno
44. Bosque Araucaria Angustifolia
45. Bosque Paranaense

FIGURE 1 Neotropical biogeographic units proposed by Morrone (2001), defined using a variety of methods including panbiogeography, cladistic biogeography and areas of endemism analyses. The proposed biogeographic units form a hierarchy in which regions are divided into subregions and subregions into provinces (from 1 to 45 in the legend). Biotic differences were found in >80% of the total pairwise comparisons performed in the provinces Cuba (2) and Chaco (42; green), in 70%–80% in Varzea (36), Cauca (12) and Costa Pacifica Mexicana (25; blue); in 60%–70% in Ecuador Arido (14), Occidente del Istmo de Panama (19) and Cerrado (40; yellow)

these analyses are not designed to examine the biotic homogeneity of biogeographic units. As already mentioned, the fact that a given area contains endemic taxa does not add evidence about biotic homogeneity across that area. Particular biogeographic units proposed by Morrone (2001) have also been evaluated in terms of coverage of species thought to be endemic to those units (Särkinen, Iganci, Linares-Palomino, Simon, & Prado, 2011). While useful, this kind of evaluation does not address the extent to which biogeographic units are biotically homogeneous. Here, we address this gap using a recently assembled data set with relatively high spatial and taxonomic resolution on the distribution of Sapotaceae species, an important component of the Neotropical regional flora in terms of diversity and abundance (Bartish, Richardson, & Swenson, 2011; Burnham & Johnson, 2004; Pennington, 1990, 2007). Specifically, we tested if variation in species composition (beta diversity) within biogeographic units was lower than across biogeographic units, while controlling for potential confounding effects of geographic distance and heterogeneous botanical sampling effort.

2 | METHODS

2.1 | Study group

Sapotaceae, comprising 53 genera and more than 1,100 species (Govaerts, Frodin, & Pennington, 2001; Pennington, 1991, 2007), is a group of trees and a few shrubs predominantly distributed in the tropics, and particularly diverse in Africa, Asia and the Neotropics in lowland and lower montane rain forest (Pennington, 1990, 1991; Swenson & Anderberg, 2005; Swenson, Richardson, & Bartish, 2008).

The distributional range of the family in the American continent extends from the Southern United States to Northern Chile (Pennington, 1990, 2007). About 450 species of Sapotaceae are found within the Neotropics. They predominantly occur in forests below 1,000 m elevation, reaching heights of 40–45 m as canopy trees. A few species occur at higher altitude, including *Chrysophyllum lanatum* and *Pouteria lucuma*, both known from localities at 3,000 m elevation. Indeed, Sapotaceae is an important component of Neotropical lowland rainforests in terms of numbers of species and individuals (Bartish et al., 2011; Burnham & Johnson, 2004; Pennington, 1990, 2007). Therefore, they are a useful model system for biogeographic studies in the Neotropics.

2.2 | Species occurrence data

Occurrence records of Neotropical Sapotaceae species were compiled from the Herbario Nacional, Herbario Forestal, Herbario Amazónico Colombiano, Herbario de la Universidad del Valle, Herbario “Choco” in Colombia, and the PADME, GBIF and TROPICOS databases. Duplicate records and records with ambiguous or tentative species level determination were excluded from the data set. Specimen records missing geographic coordinates for the collection locality were georeferenced, whenever enough information was

available. The final data set comprised 28,276 records (40 of those records represented introduced Sapotaceae species; see Table S1) representing 460 species of Sapotaceae occurring in the Neotropics. We used this data set to estimate the occurrence of Sapotaceae species in sampling units defined as 1-degree cells overlaid on the Neotropics (Figure 2).

2.3 | Boundaries of putative biogeographic units

We divided the Neotropics into biogeographic subregions and provinces sensu Morrone (2001). To represent biogeographic divisions in a spatially consistent fashion, we aggregated polygons of the shapefile of world terrestrial ecoregions (Morrone, 2001; Olson & Dinerstein, 2002; Olson et al., 2001) into areas corresponding to Morrone's subregions and provinces using explicit synonymy between ecoregions and biogeographic units, and then assigning sampling units defined as 1-degree cells to the latter (Figure 1).

2.4 | Testing for biotic homogeneity while controlling for geographic distance and sampling effort

If putative biogeographic units are biotically homogeneous, then variation in species composition (i.e. beta diversity, Anderson et al., 2011) between sites within a biogeographic unit should be lower than that between sites located in different biogeographic units. We tested this prediction by comparing beta diversity of Sapotaceae species between 1-degree cells located within a biogeographic unit to that between 1-degree cells located in different biogeographic units. We performed these comparisons conditional on geographic distance, to control for distance decay of biotic similarity (Soininen et al., 2007). In particular, we controlled for “great circle distance,” which is the shortest distance between 1-degree cells calculated over a WGS84 ellipsoidal model of Earth's surface (Hijmans, Williams, & Vennes, 2014). In this way, we tested whether beta diversity of Sapotaceae species within biogeographic units was lower than beta diversity of Sapotaceae species across biogeographic units, after correcting for the effect of geographic distance on species turnover. The biogeographic units proposed by Morrone (2001) are arranged in a hierarchy in which provinces are nested within subregions and subregions are nested within the Neotropical region (Figure 1). Accordingly, we conducted nested comparisons of beta diversity. In other words, for each pair of provinces within each subregion, we tested whether beta diversity was lower within than across the provinces, and for each pair of subregions within the Neotropical region, we tested whether beta diversity was lower within than between subregions.

We measured beta diversity of Sapotaceae species between sampling units (i.e. 1-degree cells) as the number of shared species. This measure is influenced by differences in the number of observed species between 1-degree cells, which may stem from differences in botanical collecting effort. We therefore used a null model that controls for differences in the number of species

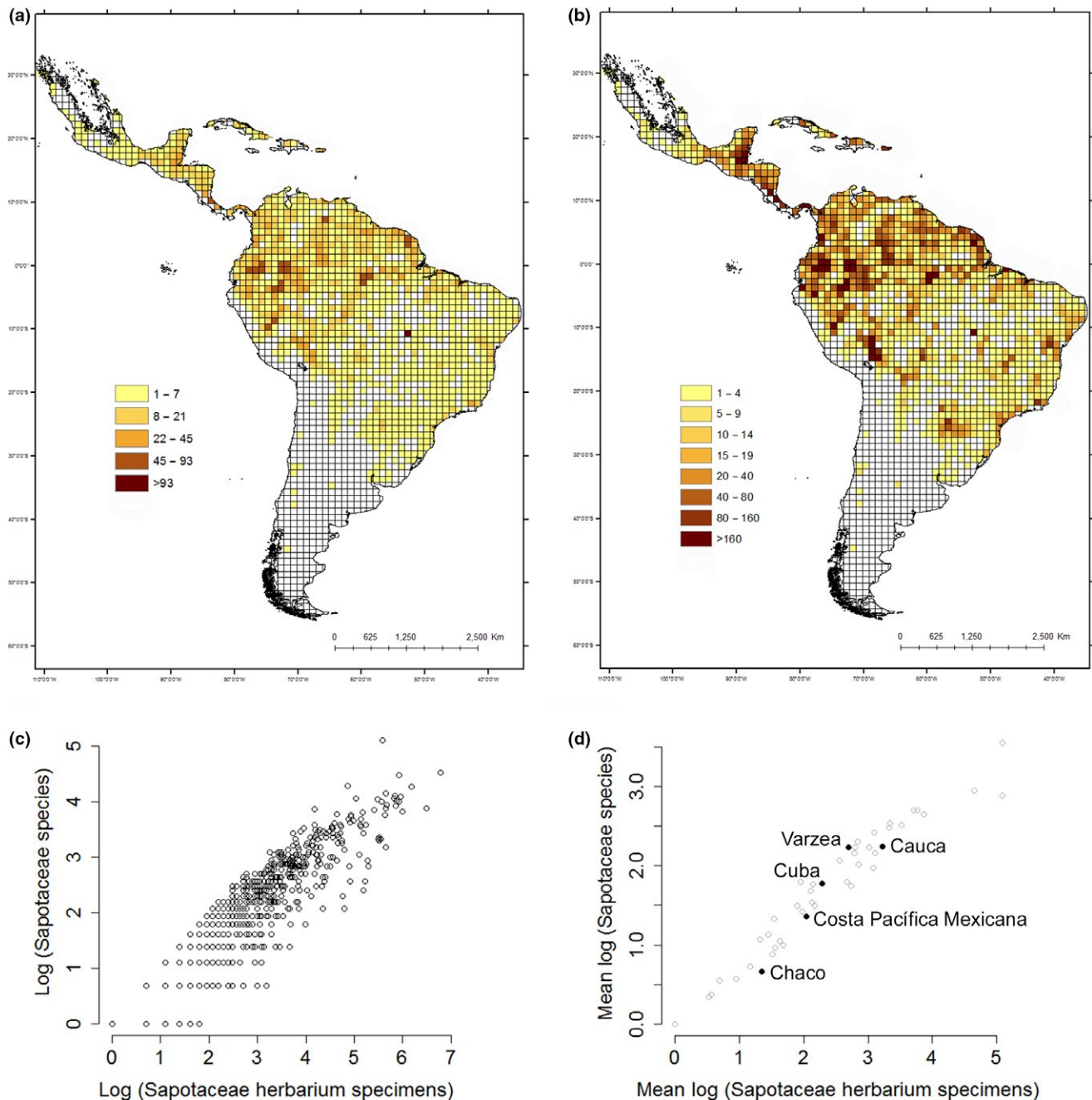


FIGURE 2 Geographic distribution of Sapotaceae collection records (a) and Sapotaceae species (b). Collecting effort has been concentrated in the northern Amazon in Ecuador, Peru, Colombia and Brazil and does not equally represent other areas in the known distributional range of Sapotaceae (a). According to our data set, the highest number of Sapotaceae species occurs at the transitional areas between Cerrado and the Amazon, and in northern Amazon in Ecuador, Peru, Colombia and Brazil (b). Units in dark shades represent the highest values in collection density/species richness; units in light shades represent the lowest values in collection density/species richness, and units in white represent areas where no occurrences/species were registered. An Albers conic equal-area projection was used. (c) Relationship between number of Sapotaceae herbarium specimens and number of Sapotaceae species across 1-degree sampling units in a logarithmic scale. (d) Relation between mean number of Sapotaceae herbarium specimens and mean number of Sapotaceae species across provinces as defined by Morrone (2001). Note that provinces that were biotically homogeneous relative to several other provinces (labelled, filled symbols) were not better sampled than other provinces (open symbols)

between sampling units (Chase & Mayers, 2011; Raup & Crick, 1979). This null model created 1,000 null species assemblages for every 1-degree cell in the analysis, by randomly sampling a “regional” species pool until the observed number of species in the

1-degree cell was matched. The “regional” species pool was defined according to the hierarchical structure of the biogeographic units proposed by Morrone (2001). Thus, when comparing beta diversity within and across a pair of subregions belonging to the

Neotropical region, the “regional” species pool was defined as the set of species known from the Neotropical region. Likewise, when comparing beta diversity within and across a pair of provinces belonging to a particular subregion, the “regional” species pool was defined as the set of species known from the subregion containing the pair of provinces. For all species in the “regional” species pool, the probability of being part of a null species assemblage in any given 1-degree cell was proportional to the occupancy of that species in the “regional” species pool. In the case of comparing beta diversity within and across a pair of subregions belonging to the Neotropical region, occupancy was the proportion of 1-degree cells occupied by the species across the Neotropical region. Likewise, when comparing beta diversity within and across a pair of provinces belonging to a particular subregion, occupancy was the proportion of 1-degree cells occupied by the species across the subregion. Because the species composition of null assemblages for any given 1-degree cell reflected overall occurrence across a larger region, it could differ substantially from the observed assemblage in that 1-degree cell. However, all 1,000 null assemblages for any given 1-degree cell had a number of species equal to the number of species known to occur in that 1-degree cell.

For a given pair of 1-degree cells i and j , we randomly paired their respective 1,000 null assemblages and calculated the number of shared species between null assemblages. Thus, for a given pair of 1-degree cells i and j , we obtained a null distribution of the number of shared species, $SS_{null,ij}$. This null distribution, composed of 1,000 values, portrays the number of species shared between 1-degree cells i and j that one would expect if biogeographic regions were not biotically homogeneous. Crucially, this expectation is conditional on the number of species known to occur in each 1-degree cell (i and j) because, as stated above, null assemblages for any given 1-degree cell had a number of species equal to the number of species known to occur in that 1-degree cell. Therefore, observed values of the number of species shared between 1-degree cells that substantially deviate upwards (downwards) from $SS_{null,ij}$ indicate that a pair of 1-degree cells shares more (less) species than one would expect if biogeographic regions were not biotically homogeneous. We measured the extent of these deviations using a standardized effect size:

$$SES_{ij} = \frac{SS_{obs,ij} - SS_{null,mean,ij}}{SS_{null,sd,ij}}, \quad (1)$$

where, SES_{ij} is standardized effect size of the shared number of species between 1-degree cells i and j , $SS_{obs,ij}$ is the observed number of shared species between 1-degree cells i and j , $SS_{null,mean,ij}$ is the mean value of $SS_{null,ij}$, and $SS_{null,sd,ij}$ is the standard deviation of $SS_{null,ij}$. Note that the standardized effect size, SES_{ij} , is inversely related to beta diversity.

To test the prediction that, after correcting for geographic distance, beta diversity within a biogeographic unit was lower than beta diversity between biogeographic units, we used the following model

of distance matrix regression (Legendre & Legendre, 1998) for every pair of provinces within each subregion, and for every pair of subregions within the Neotropical region:

$$SES_{ij} = a_0 + a_1 \cdot Z1_{ij} + a_2 \cdot Z2_{ij} + a_3 \cdot D_{ij} + a_4 \cdot D_{ij} \cdot Z1_{ij} + a_5 \cdot D_{ij} \cdot Z2_{ij} + \epsilon_{ij} \quad (2)$$

where the response variable SES_{ij} is the standardized effect size (Equation 1) for pairs of degree cells (i and j), $Z1_{ij}$ is a dummy variable with a value of 1 if both degree cells (i and j) are in biogeographic unit 1 (a province or subregion) and zero otherwise, $Z2_{ij}$ is a dummy variable with a value of 1 if both degree cells (i and j) are in biogeographic unit 2 and zero otherwise, D_{ij} is geographic distance between degree cells i and j (measured as great circle distance), and ϵ_{ij} is the error term. Finally, terms a_0 through a_5 in the right hand side of Equation 2 are regression coefficients. Empirical support for the prediction (that beta diversity within a biogeographic unit is lower than beta diversity between biogeographic units) requires a_1 and a_2 to be statistically significant and positive, so that the regression lines for pairs of degree cells within biogeographic units would have a higher intercept than pairs of degree cells located in different biogeographic units. It also requires that these differences in intercepts do not fade away with distance. That is, the regression lines for pairs of degree cells within biogeographic units should be higher across the entire range of geographic distance (Figure 3).

To test the statistical significance of the regression coefficients in Equation 2, we created null distributions for each coefficient by permuting at random the rows of the response matrix and the corresponding columns, following the procedure described in Legendre and Legendre (1988). For every pair of provinces within each subregion, and for every pair of subregions within the Neotropical region, we simplified the regression model (Equation 2) by excluding regression coefficients that were not statistically significant, following model simplification procedures in Crawley (2002). We examined regression coefficients and respective regression lines to determine whether there was empirical support for the prediction that variation in species composition between sites within a biogeographic unit should be lower than that between sites located in different biogeographic units. In particular, for every pair of biogeographic units (provinces within each subregion or subregions within the Neotropical region), we determined if the mean number of shared species (measured as standardized effect size) for any given geographic distance was higher between 1-degree cells located in the same biogeographic unit than between 1-degree cells located in different biogeographic units (Figure 3).

2.5 | Feasible pairwise comparisons of putative biogeographic units

Ideally, the biotic homogeneity of each putative biogeographic unit would be examined with respect to all other units at the same hierarchical level and within the same upper-level unit. This was feasible for all subregions within the Neotropical region. However, not

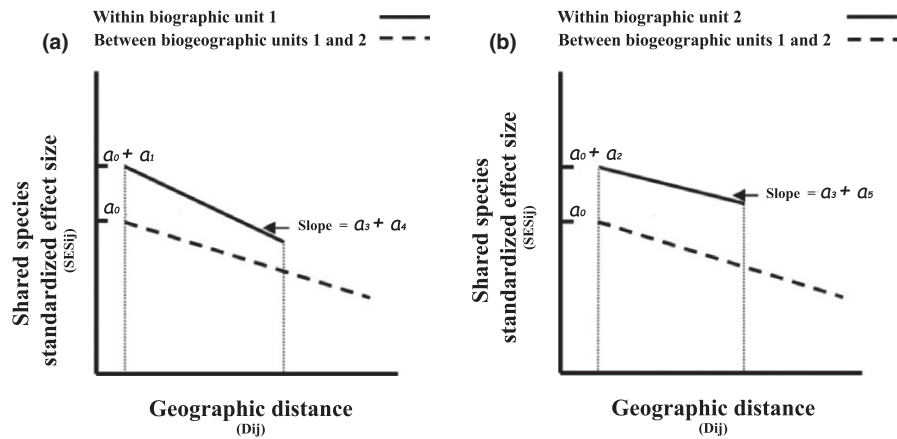


FIGURE 3 Predicted matrix regression results if putative biogeographic units accurately describe provincialism. The mean number of shared species for any given geographic distance is described by regression lines according to Equation 2 and should be higher for pairs of 1-degree cells located in the same biogeographic unit than for pairs of 1-degree cells located in different biogeographic units. Comparison of shared number of species was performed conditional on geographic distance, and thus only within the range of geographic distance shown by the vertical dotted lines in panels (a) and (b). If coefficient a_1 in Equation 2 is statistically significant and positive, then the regression line for pairs of degree cells within biogeographic unit 1 would have a higher intercept than pairs of degree cells located in different biogeographic units (a). Likewise, if coefficient a_2 in Equation 2 is statistically significant and positive, then the regression line for pairs of degree cells within biogeographic unit 2 would have a higher intercept than pairs of degree cells located in different biogeographic units (b). Note that, potentially, results can differ between panels (a) and (b): the number of shared species may be higher between 1-degree cells located in biogeographic region 1 than between 1-degree cells located in different biogeographic regions, even if the number of shared species is not higher between 1-degree cells located in biogeographic region 2 than between 1-degree cells located in different biogeographic regions

all pairwise comparisons between provinces within subregions were possible because there were no data for some provinces. Moreover, the geographic distances separating 1-degree cells located in the same province did not always overlap the geographic distances separating 1-degree cells located in different provinces (Figures 4 and 5), thus preventing comparison of beta-diversity conditional on geographic distance (Figure 3). For the Caribeña subregion, we were able to test the biotic homogeneity of 27 of 28 provinces with respect to nine or more provinces (mean number of pairwise comparisons = 9.37, $SD = 5.77$, minimum = 9, maximum = 26). In the case of subregion Amazonica, we tested the biotic homogeneity of all 13 provinces with respect to at least five other provinces within the subregion (mean number of pairwise comparisons = 8.92, $SD = 2.87$, minimum = 5, maximum = 12). Finally, for subregions Chaqueña and Paranaense, we were able to test the biotic homogeneity of all provinces with respect to at least one other province within the respective subregion (Chaqueña: mean number of pairwise comparisons = 2, $SD = 0.82$, minimum = 1, maximum = 3; Paranaense: mean number of pairwise comparisons = 2, $SD = 0$, minimum = 2, maximum = 2).

3 | RESULTS

Beta diversity between 1-degree cells (sampling units) located in the same subregion was not generally lower than beta diversity between 1-degree cells located in different subregions (Figure S1). Thus, the analysis did not support the idea that the four

Neotropical subregions proposed by Morrone (2001) are biotically homogeneous with respect to each other in terms of Sapotaceae species. Data were assessed from a total of 1,442 1-degree cells sampling units.

According to Morrone (2001), each of the four subregions in the Neotropical region is divided into provinces. The northernmost of these subregions, the Caribeña subregion, is divided into 29 provinces (Figure 1). Tests of biotic homogeneity for 28 of these provinces showed that none was biotically homogeneous with respect to all other provinces (Figure 4). However, Cuba was homogeneous in 84% of the pairwise comparisons performed, Cauca in 75% and Costa Pacifica Mexicana in 73% (Figures 4–6).

At the centre of the Neotropical region is the subregion Amazonica, divided into 13 provinces (Figure 1). None of these provinces was biotically homogeneous with respect to all other provinces (Figure 5). However, the Varzea province was homogeneous in 75% of all possible pairwise comparisons (Figure 5).

The two remaining Neotropical subregions are Chaqueña and Paranaense, divided into four and three provinces, respectively (Figure 1). Within the Chaqueña, Chaco showed support in 100%, Cerrado in 67% and Pampa in 50% of all possible pairwise comparisons (Figure S1). In case of the Paranaense subregion, Bosque Araucaria Angustifolia and Bosque Paranaense were biotically homogeneous relative to Bosque Atlantico Brasileiro (50% of the two possible pairwise comparisons). Bosque Atlantico Brasileiro was not biotically homogeneous compared with any other province (Figure S1).

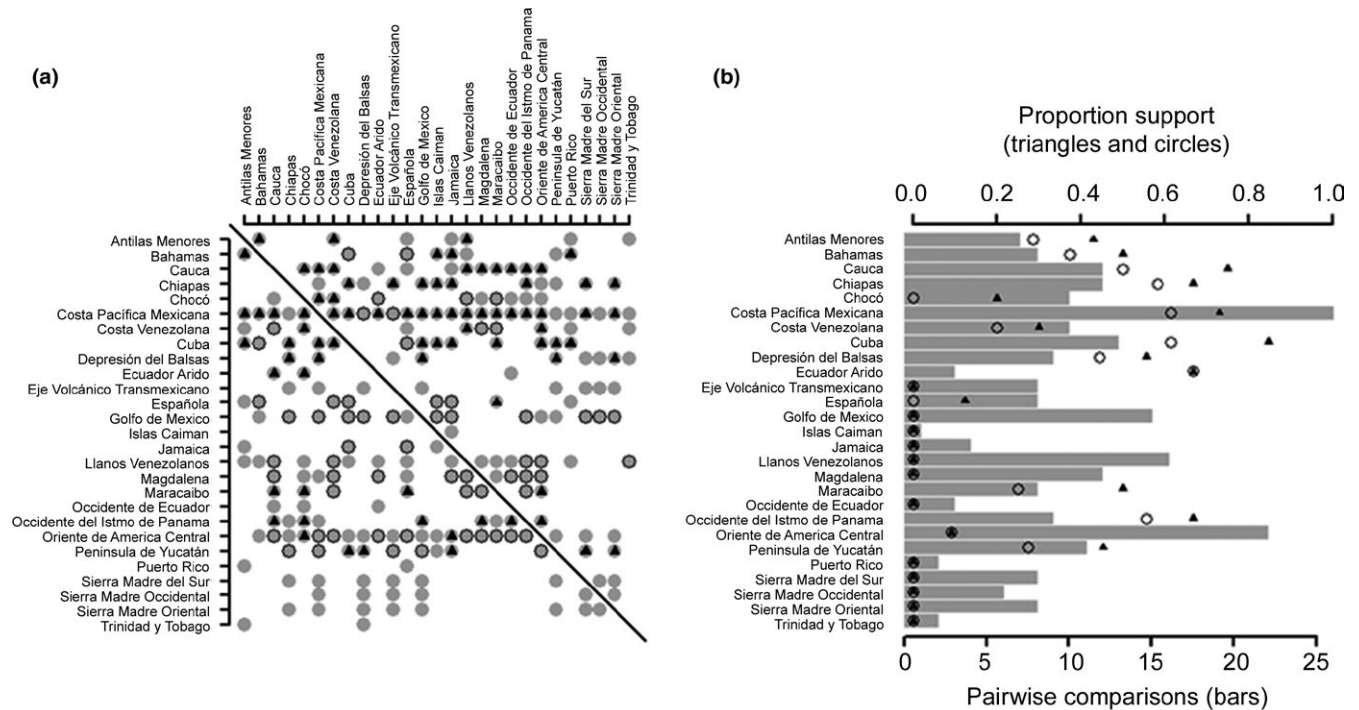


FIGURE 4 Summary of results from the test of biotic homogeneity for provinces in the subregion Caribeña. (a) Results for pairs of provinces in the subregion Caribeña. Each row shows the results of tests of biotic homogeneity of a particular province (i.e. the province after which the row is labelled) relative to each of the provinces in the columns. Gray dots indicate that there was overlap between the geographic distances separating 1-degree cells located within the (row) province and the geographic distances separating 1-degree cells located in different provinces. Thus gray dots show the pairs of provinces for which the test of biotic homogeneity could be (and was) performed. Triangles indicate that beta diversity within the (row) province was lower than beta diversity between the pair of provinces, thus empirically supporting the prediction of biotic homogeneity. Black circles indicate that beta diversity within the (row) unit is lower than beta diversity between the pair of units at short geographic distances only, thus failing to support the prediction of biotic homogeneity. (b) Summary of results for each province, showing the number of pairwise comparisons for which the test of biotic homogeneity could be (and was) performed (gray bars, lower axis) and the proportion of pairwise comparisons for which the prediction of biotic homogeneity was supported (triangles and circles, upper axis)

In 136 of 395 total pairwise comparisons performed, including subregions and provinces, beta diversity between 1-degree cells (sampling units) located in the same biogeographic unit was lower than beta diversity between 1-degree cells located in different biogeographic units at relatively short geographic distances. However, these differences did not hold at larger geographic distances (e.g. Figure 7).

Specifically, in seven of 12 pairwise comparisons within the Neotropical Region, beta diversity was lower within the same subregion than beta diversity between subregions only at relatively short distances (Figure S2). This pattern was more frequent in the Caribeña and Paranaense units. In Caribeña, three of three and in Paranaense two–three total pairwise comparisons showed biotic homogeneity at short geographic distances (Figure S2).

As for the Caribeña subregion, in 62,253 pairwise comparisons, beta diversity was lower within the same province than beta diversity between provinces only at short geographic distances (Figure S2). For instance, beta diversity between the Golfo de México province and each of 11 other provinces was higher than beta diversity within Golfo de México at short geographic distances (e.g. Figure 7). Likewise, beta diversity between Oriente de América Central and

each of 10 other provinces was higher than beta diversity within Oriente de América Central at short geographic distances.

The same pattern was found in the Amazonica subregion for 64 of 116 pairwise comparisons between provinces (e.g. Figure 5). For example, in the case of the Imeri and Yungas provinces, nine of 12 pairwise comparisons showed lower beta diversity within units than between units only at relatively short geographic distances (e.g. Figures 5–7). Finally, two of eight pairwise comparisons of provinces within the subregion Chaquena, and one of six within the subregion Paraense, displayed lower beta diversity within than between provinces only at short geographic distances (Figure S2).

4 | DISCUSSION

Overall, our study did not empirically support the prediction of biotic homogeneity for the biogeographic units proposed by Morrone (2001). After accounting for the effect of distance and unequal botanical sampling, species beta diversity between biogeographic units was higher than species beta diversity within biogeographic units in only 113 of 395 pairwise comparisons. The

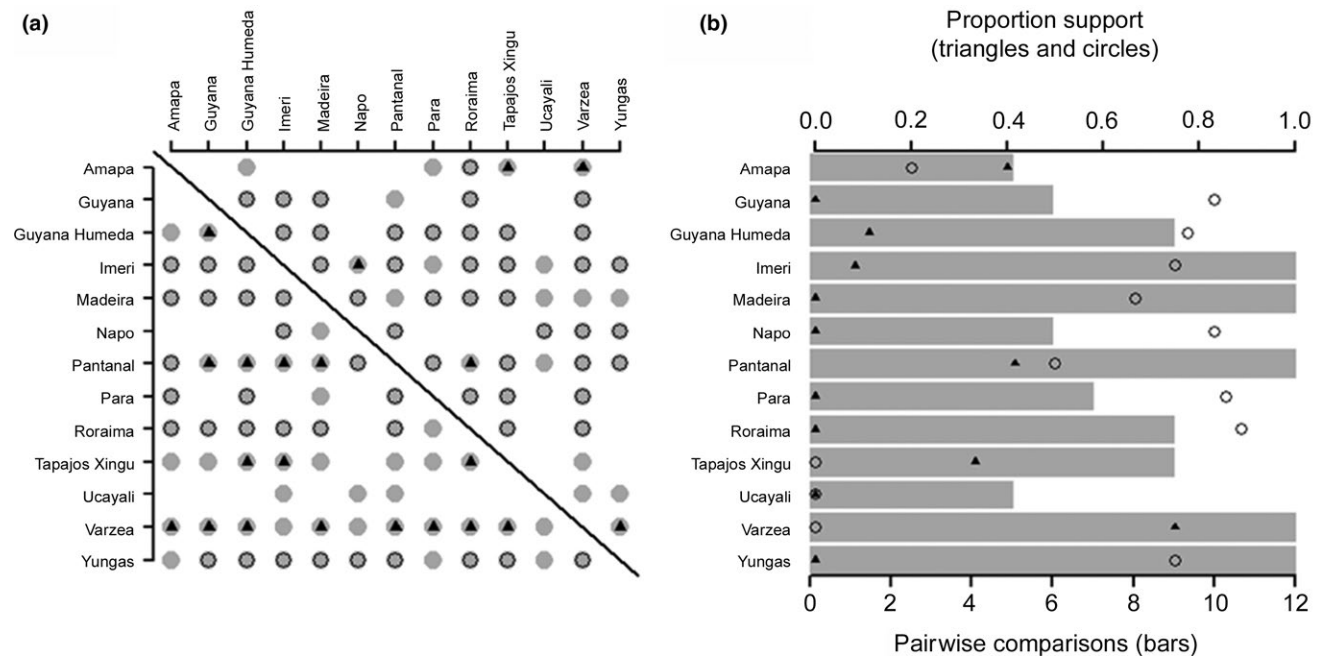


FIGURE 5 Summary of results from the test of biotic homogeneity for provinces in the subregion Amazonica. (a) Results for pairs of provinces in the subregion Amazonica. Each row shows the results of tests of biotic homogeneity of a particular province (i.e. the province after which the row is labelled) relative to each of the provinces in the columns. Gray dots indicate that there was overlap between the geographic distances separating 1-degree cells located within the (row) province and the geographic distances separating 1-degree cells located in different provinces. Thus gray dots show the pairs of provinces for which the test of biotic homogeneity could be (and was) performed. Triangles indicate that beta diversity within the (row) province was lower than beta diversity between the pair of provinces, thus empirically supporting the prediction of biotic homogeneity. Black empty circles indicate that beta diversity within the (row) unit is lower than beta diversity between the pair of units at short geographic distances only, thus failing to support the prediction of biotic homogeneity. (b) Summary of results for each province, showing the number of pairwise comparisons for which the test of biotic homogeneity could be (and was) performed (gray bars, lower axis) and the proportion of pairwise comparisons for which the prediction of biotic homogeneity was supported (triangles and circles, upper axis)

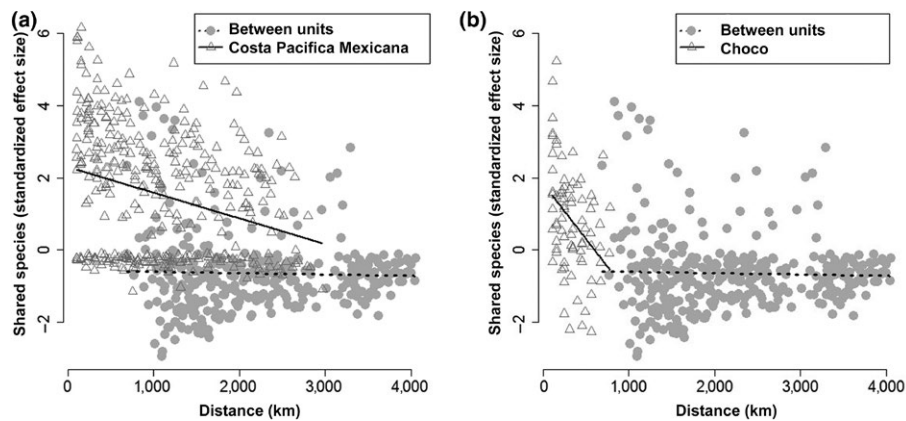


FIGURE 6 Comparison of beta diversity within and between two provinces of subregion Caribeña: Costa Pacifica Mexicana and Choco. Beta diversity within each of these provinces was lower than beta diversity between them, thus empirically supporting the prediction of biotic homogeneity. (a) Comparison of beta diversity within province Costa Pacifica Mexicana to beta diversity between provinces Costa Pacifica Mexicana and Choco. (b) Comparison of beta diversity within province Choco to beta diversity between provinces Choco and Costa Pacifica Mexicana. Symbols represent pairs of 1-degree cells, and lines are matrix regression lines. Note that the regression lines for within province beta diversity are higher than that for between province beta diversity, thus supporting the prediction that variation in species composition between sites within a biogeographic unit should be lower than that between sites located in different biogeographic units

lack of biotic homogeneity within most of Morrone's units could be explained by dispersal events that have driven distributional patterns in Sapotaceae (Armstrong et al., 2014; Bartish et al.,

2011; Richardson et al., 2014). If the distribution of Sapotaceae has been largely affected by dispersal then a regionalization like that of Morrone (2001) based on cladistics and parsimony

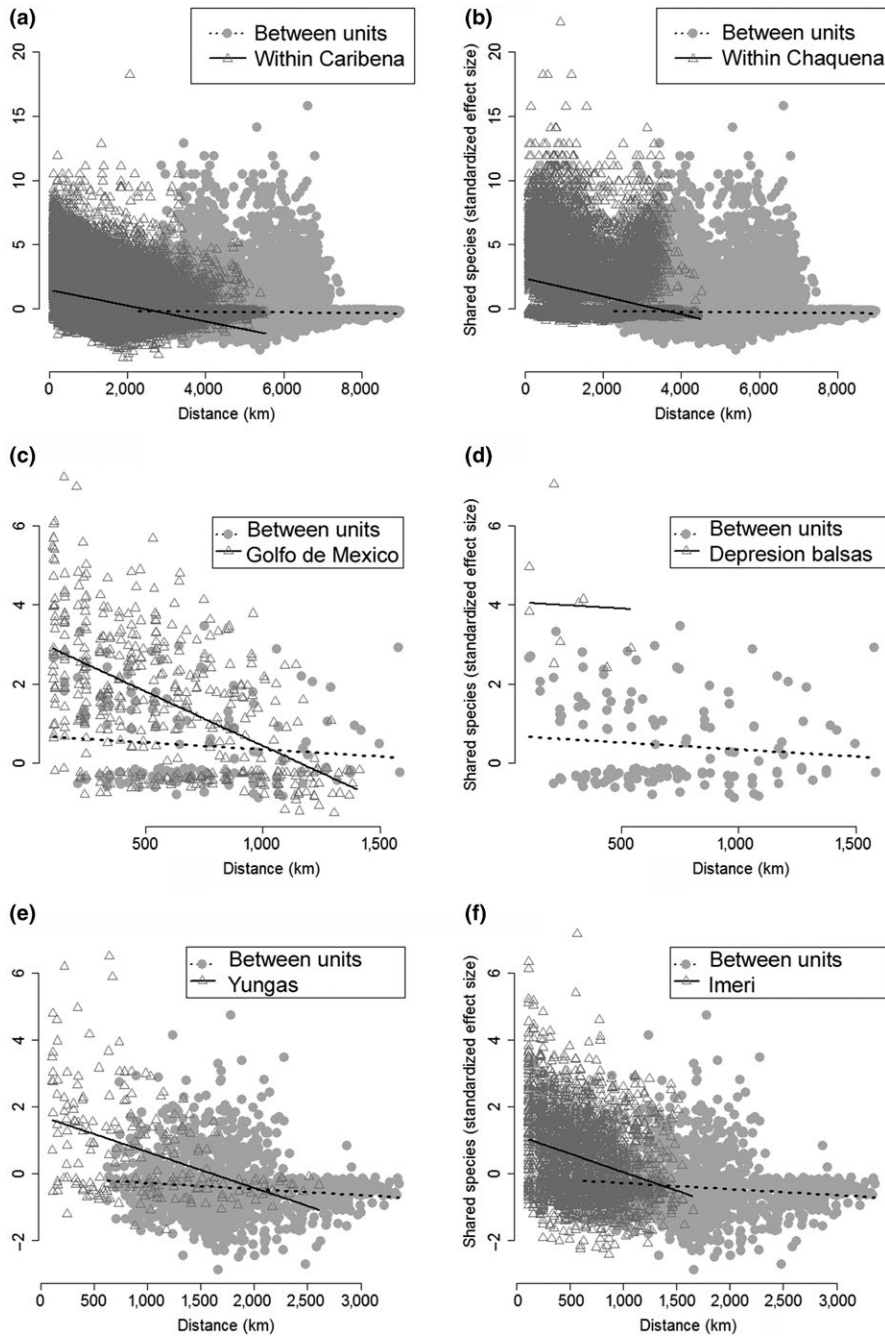


FIGURE 7 Comparison of beta diversity within and between units in the Neotropical Region. (a,b,c,e,f) At short geographic distances, beta diversity between units (Caribeña vs. Chaquena, Golfo de Mexico vs. Depresion Balsas and Yungas vs. Imeri) was higher than beta diversity within the same biogeographic unit, but the pattern disappeared at larger geographic distances thus failing to support the prediction of biotic homogeneity: that variation in species composition between sites within a biogeographic unit should be lower than that between sites located in different biogeographic units. (d) For all distances considered, beta diversity between Depresion de Balsas and Golfo de Mexico was higher than beta diversity within Depresion de Balsas. Thus, in contrast with the results shown in panels (a,b,c,e,f), the results in panel (d) support the prediction of biotic homogeneity. Symbols represent pairs of 1-degree cells, and lines are matrix regression lines

methods (Morrone, 2001, 2014a,b), which assumes vicariance as the main mechanism driving patterns in the assembly of communities (Brown & Lomolino, 1998; Crisp, 2006; Lomolino et al., 2010; Morrone, 2001, 2014a,b; Nelson & Platnick, 1981), may not coincide with Sapotaceae's distributional patterns. However, as discussed in the next section, five of 45 biogeographic units evaluated were biotically homogenous relative to several other units ("Cuba," "Chaco," "Varzea," "Cauca" and "Costa Pacifica Mexicana"), suggesting that the biogeographic units proposed by Morrone (2001) capture at least some aspects of provincialism resulting from shared history, whereby dispersal is limited either by barriers or species have locally diversified lacking enough time to colonize proximal areas.

4.1 | Provincialism in Neotropical Sapotaceae

The distinctive aggregation of Sapotaceae species in the Cauca province (Figures 1 and 4) could be explained by isolation (Alvarez & Kattan, 1995; Banda et al., 2016; Kroonenberg, Bakker, & Van der Wiel, 1990). Dispersal between Cauca (mainly covered by dry tropical forests) and other units in the Caribeña subregion could have been prevented in the South by Andean ranges, in the West by the Western Cordillera, in the East by the Central cordillera, and by wet forests in the North.

A similar case was found in Costa Pacifica Mexicana (Figures 1 and 4), where relatively high biotic homogeneity could also have been caused by isolation due to mountain barriers. This province

shares a border in the West with the Pacific Ocean and in the East with mountain ranges running along Central and North America, for example the Sierra Madre mountain range in Mexico and Guatemala (Morrone, 2001). These mountain barriers could affect community assembly in Costa Pacifica Mexicana by separating taxa on either side of their slopes. Communities in the lowland rain forest of these areas, as opposed to those in South America, are thought to have closer affinities to humid lowland montane forest in Central America than to other lowland rainforests in the Neotropics (Gentry, 1982b; Magallon et al., 2014; Wendt, 1993). This could mean that families like Sapotaceae that occur in higher numbers below 1,000 m of elevation and are species rich in lowland rainforests in other areas, are under-represented in units like the Costa Pacifica Mexicana (Magallon et al., 2014).

Mountain barriers alone do not explain patterns of aggregation for Sapotaceae species in the Caribeña subregion, however. We may have expected the Choco province (Figure 1), also apparently isolated in this case by the Andean mountains, to show relatively high biotic homogeneity (Pirie, Chatrou, Mols, Erkens, & Oosterhof, 2006; Winterton et al., 2014), but this was not the case, suggesting that dispersal has prevented provincialism. Taxa in the Choco province would have been connected to the Central American flora by the closure of the Isthmus of Panama, and dispersal events between Choco and other provinces in inter-Andean valleys or on the eastern side of the Andes in the Caribeña subregion could have taken place across areas where the mountains are lower (e.g. Fine et al., 2014; Dexter et al., 2017). In fact, the Choco and inter-Andean valleys of areas like Magdalena and Cauca are linked by lowland regions in the northern Caribbean region of Colombia and lowland passes adjacent to La Macarena and Norte de Santander (Gentry, 1982a,b). These areas of lowland are, however, occupied by or are adjacent to areas of dry forest or desert in the Caribbean and Magdalena valley (Banda et al., 2016), respectively. The climates in these areas may have acted as barriers to overland dispersal of predominantly wet forest restricted Sapotaceae, but they may be recently developed and not had time to have an effect on the distribution patterns in the family (Pennington et al., 2004).

In the Cuba province on the other hand, biotic distinction (Figure 4) could be explained by long periods of isolation, which may have allowed enough time for speciation since the island emerged in the middle Eocene (Graham, 2003; Iturralde-Vinent, 1981; Iturralde-Vinent & MacPhee, 1999). Cuba is the most plant species (ca. 6,850 vascular plants) and endemic rich (ca. 3,178 vascular plants) within the Greater Antilles. For instance, *Pouteria moaensis*, *P. cubensis*, *P. micrantha*, *P. aristata*, *Sideroxylon acunae*, *S. ekmanianum* and *Micropholis polita* are Sapotaceae species endemic to this island (Figueredo, 2008; Martínez-Quezada, 2009; Pennington, 1990). Endemic flora in Cuba also includes taxa reported to have diversified at ca. 45 million years (Graham, 2003). This is particularly important especially when compared with other units like Jamaica or Haiti/Dominican Republic, which are of relatively similar size and also isolated, but are of younger origin.

Significant patterns of biotic homogeneity in terms of Sapotaceae species were also detected in the Amazonia subregion. Several pairwise comparisons showed lower beta diversity within Varzea than between Varzea and other provinces (Figures 1 and 5), even though homogeneity was not evident across all geographic distances or across all pairwise comparisons. Relatively high biotic homogeneity of Varzea could be explained by abrupt edaphic changes between areas flooded by the Amazon River and terra firme away from the river that could act as an adaptive barrier delimiting floral communities. This would not be the case in other provinces within Amazonica where edaphic changes may be more localized (García-Villacorta, Dexter, & Pennington, 2016) and not detectable using broad divisions like those of Morrone (2001).

Our analyses also detected significant patterns and high values of biotic homogeneity in areas where Sapotaceae occurs but is not dominant, particularly in the Chaco province. The high relative values of biotic homogeneity found in Chaco could in part, be a consequence of the widespread occurrence of *Pouteria gardneriana* within this province. This species was reported by Morrone (2001) as a characteristic taxon for the Chaquena subregion, and in our data set, it was found as abundant in the Chaco province.

In addition to biotic distinction of the Cauca, Costa Pacifica Mexicana, Cuba, Varzea and Chaco provinces, in several comparisons among subregions and in 129 of 383 pairwise comparison among provinces, beta diversity was higher between units than within units at short geographic distances only (e.g. Figures 4, 5, 7 and S2). This pattern suggests that the limits of some subregions and provinces sensu Morrone (2001) correspond to true biogeographic borders in terms of the distribution of Sapotaceae, but that there may be additional discontinuities within these biogeographic units that have not been identified.

An alternative explanation focuses on distance decay of biotic similarity (Soininen et al., 2007). In particular, the biogeographic units proposed by Morrone (2001) could have reasonably sharp spatial limits defined by high turnover in species composition over short geographic distances. At the same time, these units would be characterized by relatively smooth inner gradients in species composition. Given enough geographic distance, these inner spatial gradients would result in high species turnover, compared to that between sampling units belonging to different biogeographic units. If this were the case, some of the biogeographic units proposed by Morrone (2001) could be regarded as “bona fide” or real-world structures in the sense that they would be delimited by relatively sharp spatial boundaries. In other words, they would not be “fiat” spatial units defined by arbitrary boundaries such as some political and administrative boundaries (Smith, 1995; Smith & Varzi, 2000). Despite their “bona fide” status, the biogeographic units in question would not be biotically homogeneous, due to internal distance decay of species similarity (continuous regression lines in Figures 5, 7 and S2). There seem to be few, if any, discussions explicitly distinguishing the spatial boundaries of putative biogeographic units from the biotic homogeneity of these units. Yet, distinguishing these two properties of putative biogeographic units seems fundamental to provincialism

and, more generally, to our understanding of the geographic structure of biotas and its implications for biodiversity conservation (see below).

4.2 | Methodological considerations

The lack of support for biotic homogeneity of units in Morrone (2001) regionalization could be primarily the result of dispersal events having an important effect on the distribution of Sapotaceae, but it is also likely influenced by our limited understanding about the world's biodiversity and its geographic characteristics, that is the Wallacean and Linnaean shortfalls (see Introduction and Hopkins, 2007). In the present work, we attempted to control the effects of these variables by implementing a null model that accounts for differences in collection effort across 1-degree grid cells (see Guisan & Zimmermann, 2000; Ferrier, Manion, Elith, & Richardson, 2007 and Elith et al., 2011 for alternative methods to account for differences in collection effort). Specifically, our null model aimed to account for the concentration of collection effort in areas like northern Amazonia and northern Peru/southern Colombia, and relatively low collection effort in areas possibly rich in Sapotaceae species, like the Choco biodiversity hotspot (Figure 2). We believe few studies have accounted for geographic heterogeneity of collection effort in the past (but see Raup & Crick, 1979), and think that our main results reflect at least in part the actual distributions of Sapotaceae species. It is worth noting that the biogeographic units that were biotically homogeneous relative to several other units (Chaco, Cuba, Varzea, Cauca and Costa Pacifica Mexicana) were not exceptional in terms of sampling effort (Figure 2d). Thus, the absence of support for biotic homogeneity in many other biogeographic units seems difficult to explain as an artefact of poor sampling. However, we also recognize that Sapotaceae species are likely to be discovered in the future and that depiction of distributional ranges of species already known to science is bound to change as botanists explore undercollected Neotropical regions.

The recognition of patterns in the distribution of taxa is also strongly influenced by the choice of metrics to assess biotic similarity. Metrics for biotic similarity have been commonly developed combining variables to measure patterns of nestedness and species turnover. This approach has proven useful in popular indices like Jaccard and Sorensen. Nonetheless, nestedness and species turnover are the result of different processes that may not be clearly assessed if they are interpreted simultaneously (Mouillot et al., 2013). The aim of our analyses was to test whether the limits of the biogeographic units proposed in Morrone's biogeographic regionalization correspond to spatial changes in the occurrence of Sapotaceae species beyond what one may expect from distance decay of biotic similarity. It is beyond the scope of this study to assess the degree to which biogeographic units based on metrics that consider the degree to which species assemblages in sampling units (1-degree cells) constitute nested subsets (Baselga, 2012; Almeida-Neto, Frensel, & Ulrich, 2012; Ulrich & Almeida-Neto, 2012; Mouillot et al., 2013).

4.3 | Sapotaceae as a study group

Biogeographic regionalization, like that of Morrone (2001), have often been proposed using information on a few selected taxa (Brown & Lomolino, 1998), but ideally their predictions should be tested using data on additional groups of organisms (Magnusson, 2004; Whittaker et al., 2005). Although the biogeographic regionalization proposed by Morrone (2001) was partly based on information on the distribution of vascular plants, Sapotaceae do not figure prominently among the taxa used to characterize different biogeographic units, as opposed to plant families such as Burseraceae, Gunneraceae, Onagraceae, Passifloraceae and Podocarpaceae. In particular, Morrone (2001) included Sapotaceae as a characteristic taxon in only one biogeographic unit: *P. gardneriana* in the Chaqueña subregion. Moreover, the Sapotaceae data set used in this study (comprising 28,276 records representing 460 species) was recently compiled and curated to achieve relatively high spatial and taxonomic resolution and thus was not available for the delineation of biogeographic units by Morrone (2001).

The test of biotic homogeneity presented here, based on data on the distribution of Sapotaceae species, is largely independent from the original data used by Morrone (2001). However, it seems reasonable to use Sapotaceae species as exemplar taxa because they are important representatives of tropical lowland rain forest, which cover extensive areas within the Neotropics. Additionally, according to our results, Sapotaceae also seem to be an appropriate group for recognizing patterns in habitats considered marginal for its distribution. For instance, patterns of biotic distinction were found in units dominated by grasslands and savannahs, like Chaco, Ecuador Arido, Occidente del Istmo de Panama and Cerrado. It is certainly possible that future tests performed with data on other taxa will support the biogeographic regionalization proposed by Morrone (2001), and that Sapotaceae prove to be an exception. Different taxa may have distinct evolutionary histories that determine distinct current distribution patterns (Proches, 2006).

4.4 | Implications for biodiversity conservation

The identification of priority areas for biodiversity conservation is ideally based on complete information about the geographic distribution of species (Rodrigues & Brooks, 2007). Yet, with the exception of a few well-known groups of organisms, the geographic distribution of many Neotropical species is poorly known (the Wallacean shortfall, Sheth et al., 2012). Therefore, the identification of priority areas for the conservation of biodiversity is often based on spatial units that attempt to represent the overall geographic structure of biotas, such as biogeographic regions, biomes or "vegetation types" (Ladle & Whitaker, 2011; Margules & Sarkar, 2007; Whittaker et al., 2005), but such prioritization would be meaningless if the spatial units in question (biogeographic regions, biomes or "vegetation types") are not biotically homogeneous. In that case, conservation areas located in different biogeographic regions would not necessarily be more biotically distinct than conservation areas located within

a biogeographic region. The lack of biotic distinction would prevent efficient conservation planning that can only be achieved if the new establishment of areas for conservation adds unrepresented elements within a network of Protected Areas (i.e. complementary sensu Margules & Sarkar, 2007), and if the maximum number of species is preserved in the minimum possible extension (i.e. minimum set criterion see Pawar et al., 2007). Our results indicate that the biogeographic units proposed by Morrone (2001) are not biotically homogeneous in terms of Sapotaceae species composition, casting doubt about the usefulness of these units in conservation prioritization. Further studies of biotic homogeneity focused on various taxa are needed to determine the generality of these results and, more broadly, to improve our understanding of provincialism across the Neotropics.

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BIOSKETCH

Julieth Serrano is a researcher in tropical plant biology with a special interest in biogeography, ecology and conservation. The ultimate aim of her research is to apply this knowledge in applied conservation in some of the most biodiverse places on earth.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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