BIOGEOGRAPHICAL HISTORY OF THE YUCATAN PENINSULA ENDEMIC FLORA (SPERMATOPHYTA) FROM A PHYLOGENETIC PERSPECTIVE[1]

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Abstract. The increased availability of phylogenetic, morphological, and geographic information from different biological groups has allowed for the testing of several scenarios on the origin and assembly of the biota around the world. The biogeographical approaches used to understand the origin of the Yucatan Peninsula Biotic Province (YPBP) flora were previously based on floristic comparisons and do not consider the phylogenetic relationships among taxa, complicating the understanding of their biogeographical history. In order to improve the understanding of biogeographical and evolutionary processes implied in the occurrence of the endemic flora of the YPBP, we constructed a geobiotic scenario, which integrates lineage divergence events obtained from previous phylogenetic and biogeographical studies, along with geological/tectonic and climatic events occurring in the area. To strengthen the biogeographical hypotheses, we constructed a phylogenetic tree as a framework for an approximation of the periods of history with the greatest influence on the evolution of the flora. Additionally, we searched for morphological traits of relevance for dispersal, establishment, and adaptation to the current environmental conditions of the YPBP. The evidence gathered in the present work strongly suggests that the origin of the endemic flora of the YPBP has been driven by various factors and processes that occurred at different times in the history of the Earth (mainly in the Pliocene and early Pleistocene). These include hybridization, isolation after long-distance dispersal from the Antilles, as well as the influence of environmental changes during the Pleistocene. Those climatic fluctuations reduced the geographic range of some ancestral lineages, leading to geographic isolation of populations in the northern part of the YPBP, where the climate has been more stable over time.

Keywords: Dispersal syndromes, divergence times, extinction, geographic isolation, Pleistocene, phylogenetic relationships, speciation

Endemic species are species distributed exclusively in a natural, predefined area and are considered unique results of evolution (Hobohm, 2014), highlighting the importance of "endemism" for biogeography. Specific locations across the Earth with high levels of endemism are often associated with climatic stability, serving as refugia for paleoendemic lineages that had broader distributions in the past (Anderson, 1994). Additionally, endemism is associated with sites of rugged relief, high levels of environmental heterogeneity (Noroozi et al., 2018), and geographical isolation, such as on oceanic islands or mountain peaks, which promote genetic differentiation and subsequent allopatric differentiation (Kier et al., 2009; Losos and Ricklefs, 2009). In contrast, sites with a history of high climatic instability tend to host fewer endemic species, often of recent local divergences known as neoendemic lineages (Merckx et al., 2015; Noguera-Urbano, 2016). Endemic species are useful for establishing the boundaries of biogeographical areas (Crother and Murray, 2011; Morrone, 2014) and are essential criteria for the conservation of biological diversity at local, regional, and global scales (Fattorini, 2017).

Phylogenetic hypotheses provide direction for the reconstruction of geographic distributions and for the elucidation of the processes of diversification, dispersal, extinction, and vicariance (Santiago-Valentín and Olmstead, 2004; Kadereit, 2017; Morrone, 2022). The study of the geographic distribution of phylogenetically related endemic species can improve the understanding of the biogeographical processes which shaped the biota of a given area. For example, areas with geographically restricted sister species suggest in situ diversification processes, where the time elapsed has been insufficient for the expansion of their distribution range (Kadereit, 2017), and/or where there are geographic or ecological barriers preventing the sister species from achieving more extensive distributions (Merckx et al., 2015). Moreover, allopatric speciation resulting from vicariant divergence can be inferred from geographically isolated sister species (Morrone, 2004; Luebert and Weigend, 2014; Chiapella and Demaio, 2015; Kadereit, 2017). The increased availability of phylogenetic, morphological, and geographic information from different biological groups has allowed for the testing of several scenarios on the origin and assembly of the biota around the world (e.g., Chiapella and Demaio, 2015; Kadereit, 2017; Zizka, 2019). Additionally, knowledge of the divergence times of closely related species, evaluated in the context of tectonic or paleoclimatic events, helps to elucidate speciation events by isolation after long-distance dispersal (Grandcolas et al., 2008; Andrus et al., 2009; Luebert and Weigend, 2014). Furthermore, the analysis of functional traits of relevance for their distribution and establishment, such as growth form and dispersal syndrome, may strengthen the biogeographical hypotheses of interest (Wen et al., 2014).

[1] Supplementary material available here.

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The Yucatan Peninsula Biotic Province (YPBP) is considered a biogeographical unit based on its biotic, physiographic, morphotectonic, and environmental attributes (Barrera, 1962; Morrone, 2019). It is located in the Neotropics (Fig. 1) on the karst platform impacted by the meteorite that triggered the fifth mass extinction on Earth, approximately 65 Mya (Renne et al., 2013). The southern YPBP re-emerged from the seabed during the Oligocene (~32 Mya) and continued to be exposed in staggered episodes up to the Holocene (<0.01 Mya) on the northern coast (Bryant et al., 1991; Lugo-Hubp et al., 1992). This geological phenomenon suggests a recent establishment and evolution of the flora in this region, particularly in coastal zones (Miranda, 1958). Today, this area (ca. 300, 000 km^2) harbors a floristic diversity of ca. 2, 860 taxa of vascular plants (modified from Carnevali et al., 2010b), of which around 6% are endemic (180 spp.) and quasi-endemic species (8 spp.) (Carnevali et al., 2021b). Quasi-endemics are limited to the area of endemism but also reach the border or transition zones with adjacent biogeographical provinces or are represented by a few isolated populations beyond the boundaries and into neighboring provinces. This percentage is relevant considering the relatively short time that has elapsed since the re-emergence of the YPBP, its low relief complexity, and its relatively close connection with the rest of Mexico and Central America (Ramos, 1975; Lugo-Hupb et al., 1992; Morrone, 2019).

It has been hypothesized that the origin of endemism in the northern YPBP was strongly influenced by Pleistocene climatic fluctuations that resulted in the fragmentation of tropical dry forests (TDF), leading to the isolation and differentiation of many plant groups (Carnevali et al., 2003; Espadas-Manrique et al., 2003; Espadas-Manrique, 2004). Miranda (1958) suggested that the origin of these endemic species may be explained by edaphic conditions in the area and the establishment of lineages from southern Mexico and northern Central America in these new environmental conditions. However, the biogeographical approaches used to understand the origin of the YPBP flora have been based on floristic comparisons (Estrada-Loera, 1991; Ibarra-Manríquez et al., 2002; Espadas-Manrique et al., 2003; Ramírez-Barahona et al., 2009) and do not consider phylogenetic relationships. Studying the phylogenetic relationships of the endemic flora of the YPBP is necessary for understanding past scenarios of the origin of the biota (Morrone, 2022) and a first step to estimating possible responses to anthropogenic disturbances and future environmental changes (e.g., Edwards and Still, 2008).

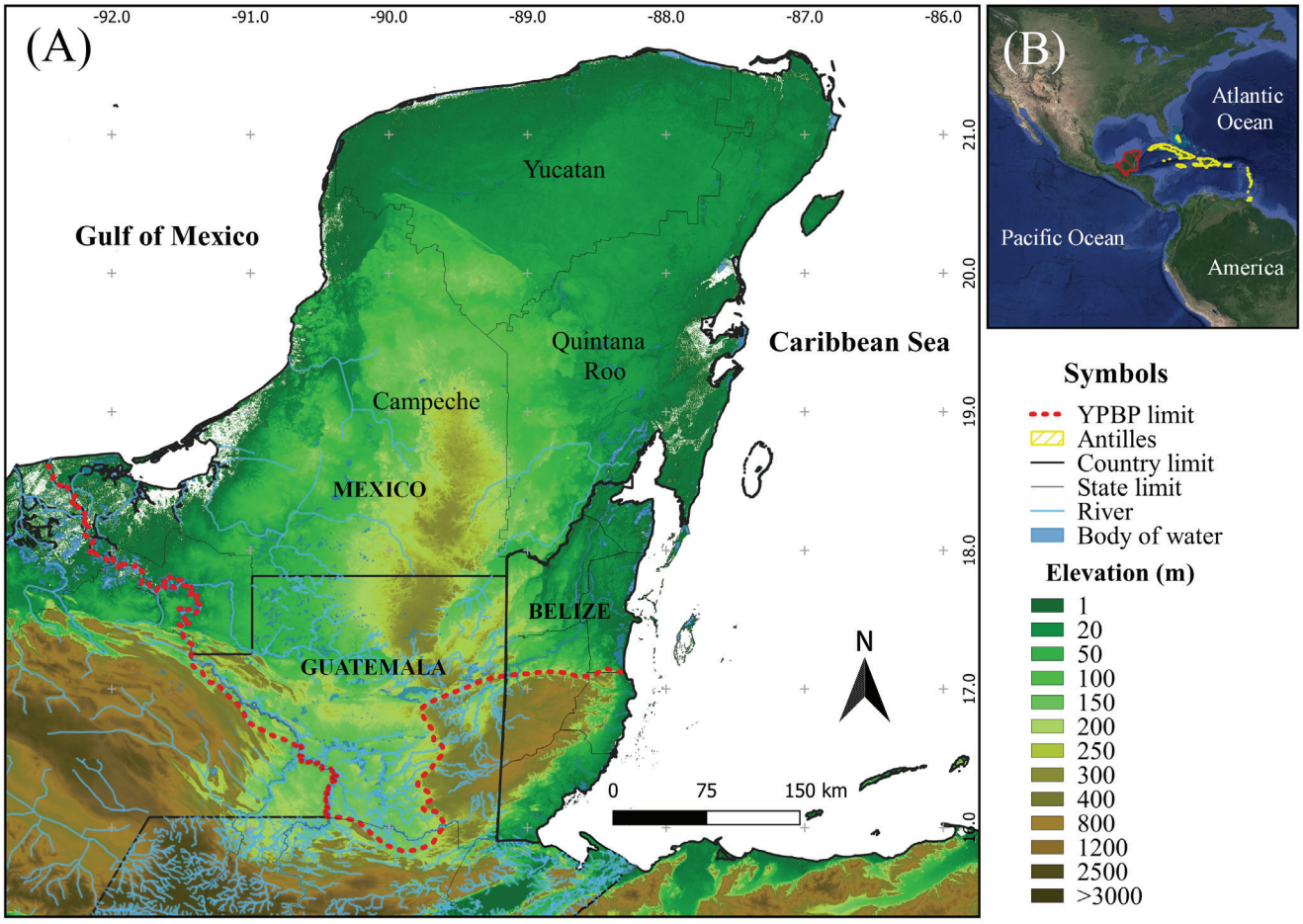

FIGURE 1. Study area. **A**, Elevations of the YPBP karst platform and the occurrence of surface rivers, concentrated mainly in the south; **B**, Geographic location of the Yucatan Peninsula Biotic Province (YPBP) in the Neotropics, note the proximity to the Antilles (highlighted in yellow).

Here, we review the documentation of geological/tectonic and climatic events that have occurred in the area, as well as lineage divergence events obtained from previous phylogenetic and biogeographical studies, in order to improve the understanding of the biogeographical and evolutionary processes implied in the occurrence of the endemic flora of YPBP. We constructed a phylogenetic tree as a framework for an approximation of the periods of history with the greatest influence on the evolution of the flora. To strengthen the biogeographical hypotheses, we searched for morphological traits of relevance for dispersal, establishment, and adaptation to the current environmental conditions of the YPBP.

We hypothesized that the origin of the endemic flora was mostly influenced by climatic changes that occurred during the Pleistocene, reflected in the current geographical distribution of allopatric sister species with high niche conservatism in seasonally dry habitats and in recent divergence times. This geographic isolation should be independent of the ability of the lineages to disperse long distances. However, the environmental characteristics of the YPBP, insularity (at least of the northern dry ecosystems), and climatic gradient, could have promoted another evolutionary process that contributed to the diversity of the endemic flora, such as isolation after a long-dispersal event (either from the West Indies and from other parts of America) or ecological divergence (with respect to adjacent areas or inside the environmental gradient).

Methods

For the compilation of phylogenetic and biogeographical hypotheses, we performed a metasearch of evolutionary and biogeographical scientific publications based on molecular phylogenetic and/or morphological evidence of endemic and quasi-endemic taxa of the YPBP. First, we used the Datataxa script (Ruiz-Sánchez et al., 2019) to extract meta-information on articles from the Genbank database (Benson et al., 2018). The search categories were Phylogenetic studies (including the terms phylogen*, monop*, systemat*, sistemat*, relationsh*, relacio*), Phylogeographic studies (phylogeog*, filogeog*), Phylogenomic analysis (phylogenom*, genome-scale, "plastid genome"), Diversity studies (diver*, geneti*, pop*, pobl*) and Biogeography (biogeog*). The endemic species list of Carnevali et al. (2021b) was updated with the addition of taxa recently recognized as endemic (e.g., *Echites yucatanensis* Millsp. ex Standl.; Carnevali et al., 2021a) and recently described species (e.g., *Matelea falcata* Juárez-Jaimes, G.M. Hernández-Barón & W.D. Stevens; *Gonolobus caamali* Carnevali & R. Duno) (Apocynaceae). Additionally, other taxa were included that were not considered endemic by those authors (e.g., *Harpalyce torresii São-Mateus & M. Sousa*, *H. yucatanense* Miranda ex São-Mateus & M. Sousa, *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J. Ortiz), sometimes because they were found at the southernmost boundary of the YPBP (e.g., *Miconia hondurensis* Donn. Sm., (Melastomataceae), *Rhynchospora pusilla* Chapm. ex M.A. Curtis (Cyperaceae)).

Second, a search for biogeographical and systematic studies based on morphological data was conducted for each taxon endemic to the YPBP from the academic search engine Google Scholar (https://scholar.google.com/), with the name of the taxon in question as a keyword (e.g., *Justicia_dendropila*).

The nomenclature used follows the Angiosperm Phylogenetic Group IV classification system (APG, 2016). Information on phylogenetic relationships and divergence dates was extracted based on bootstrap, Neighbor-joining (NJ), Maximum Parsimony (MP) or Maximum Likelihood (MV) methods. Only those phylogenetic relationships whose statistical support was above 60% and whose analyses included a sampling of more than 50% of the species of the genus present in the study area were considered. Where possible, divergence dates were extracted both for cladogenetic events at the species level and for the most recent clade in which the endemic species was included, if the phylogenetic resolution did not reach the specific level.

In order to have an approximation of the age of origin of the endemic taxa, two data sources were used. In one approach, divergence dates, and their confidence intervals, were extracted from previously published chronograms (e.g., Cuenca et al., 2007; Cuevas-Chapa, 2016; Lavor et al., 2018). This information was contextualized within the framework of paleoclimatic and geological events that have occurred since the exposure of the YPBP seafloor 32 Mya (Szabo et al., 1978; Lugo-Hubp et al., 1992; Aragón-Moreno et al., 2012). Additionally, a phylogenetic reconstruction was performed with V.Phylomaker (Jin and Qian, 2019), a package implemented in the open source software R (Core Team, 2021. This software generates dated phylogenies (timelines) from a list of species and compared them with a mega phylogenetic tree of vascular plants (GBOTB.extended.tre) that includes 74, 533 species and all 479 families known to date. For this purpose, a list of vascular plant species obtained from the YPBP Digital Flora (Duno et al., 2019) and updated with the aforementioned endemic species list was used. Because V.Phylomaker uses the list of species accepted by The Plant List (TPL; http://www.theplantlist.org/) as a reference, in order for the program to identify the correct branch insertion position, new names were updated using the r.bind function. Since the phylogeny obtained is not resolved at the species level, the values for divergence times are probably overestimated for some plant lineages, especially those with few representatives in the YPBP. FIGTREE package (Rambaut, 2009) was used for phylogeny visualization.

To document the general distribution patterns of the endemic flora, as well as its related taxa, a search of herbarium records in national (CICY, MEXU) and foreign (MO, SELBY) institutions was performed, and records with supporting collections were obtained from the GBIF online database (www.gbif.org). This information was compared and supplemented with information obtained from other online databases (e.g., SEINet, Jstor, Tropicos), protologues, and regional floras, such as Flora of Guatemala (Gentry and Standley, 1974), Flora Mesoamericana (e.g., Davidse

et al., 1994), Digital Flora of the Yucatan Peninsula (Duno et al., 2019), Flora of the Valley of Mexico (Rzedowski & Rzedowski, 2001), and Flora Novogaliciana (McVaugh, 1987; 1995). A database containing information on habit, habitat, phenology, pollination and dispersal syndromes, reproductive aspects of the species, as well as morphological characters of possible adaptive relevance, was compiled from the review of these data sources. Biogeographical provinces follow Morrone (2019), except in the case of the southern limits of the YPBP, which follow Lundell (1934) and Carnevali et al. (2010b). Those authors have a broader geographic delimitation of the area based on topography and hydrology, characteristics which could help explain the role of the southern transitional zone.

Results

Phylogenetic hypothesis

A total of 184 endemic and quasi-endemic species were included in the search. According to Datataxa, only 63 YPBP endemic taxa have been included in studies with genetic data recorded in GenBank, either phylogenetic (49), biogeographical (9), phylogeographic (2) or population genetic diversity (1) (some of these studies include more than one taxon, i.e., González Martínez, 2019 and Majure et al., 2012). However, phylogenetic hypotheses based on molecular information with high support and resolution were only found for 34 endemic species, representing 18 vascular plant families, and 18.4% of the endemic flora diversity (Appendix 1). Most of the hypothetical relationships were found at the species level, with five species belonging to unsolved clades consisting of two or three taxa.

Divergence times

We found 12 divergence times based on dated phylogenies, eight of them (66%) corresponding to the Pleistocene (Appendix 1; Fig. 2A). Regarding the phylogenetic tree constructed with V.Phylomaker (Fig. 2B), the greatest peak of evolutionary divergence (32 divergence nodes; 17% of endemic species) occurred 4–2 Mya, corresponding to the late Pliocene and early Pleistocene.

Distribution patterns

Most of the hypothesized sister species of the endemic taxa compiled in this work have an allopatric distribution and are absent in the YPBP (17 spp.). Of these, three are in the Antilles region, 11 taxa have their distribution limits in adjacent biogeographical provinces to the YPBP, and three are in provinces farther away from continental America, mainly in the Chiapas Highlands, the Mexican Plateau, and Pacific Lowlands provinces. Three pairs of taxa are allopatric within the limits of the YPBP, and are distributed along the north-south humidity and temperature gradients of the YPBP. Sympatric distributions were found in eight pairs of phylogenetical related taxa, which have the following distribution: three of them are fully restricted to the YPBP, four have a broader distribution along YPBP and the neotropics, and two are widely distributed in Central America but are limited to the southern part of the YPBP (Appendix 2).

Morphological characteristics

There is a great diversity of growth forms in the YPBP endemic taxa, including parasitic herbs, climbing shrubs, and epiphytes, but the most common are trees (47), shrubs (38), and terrestrial herbs (29). Most of the endemic species have dispersal mechanisms that can reach long distances, such as animal-dispersed berries (84) and those with adaptations for wind (67) or water dispersal (12). Another less diverse group of species have mechanisms for medium- to short-distance dispersal, such as explosive (36) or gravity dispersal (4).

Discussion

Influence of the Pleistocene on the origin of the YPBP endemic flora

During the Miocene (23–5.3 Mya), xeric, savannah, and tropical dry forest (TDF) communities dominated the YPBP and many other Neotropical areas (Becerra, 2005; De-Nova et al., 2011; Leyden, 1984; Pennington et al. 2000, 2009, 2018; Islebe and Leyden, 2006). The climatic instability that characterized the Pleistocene (2.6–0.01 Mya) led to local and mass extinctions that affected lineages in different areas of the YPBP. On one hand, the biotic dispersal of plant communities of boreal affinity led to the replacement of whole biomes in the Neotropics, particularly in the southern part of the YPBP (Gutiérrez-Ayala et al., 2012; Islebe and Leyden, 2006). Expansions and contractions of the distribution ranges of these plant communities resulted in the fragmentation of the TDF and increased its isolation by restricting it to the northern part of the YPBP. This could have promoted allopatric speciation processes in lineages with high niche conservatism, as has occurred in many Neotropical lineages (Becerra, 2005; De-Nova et al., 2011; Montaño-Arias et al., 2018; Pennington et al., 2000, 2009; Rivera-Martínez et al., 2022). Therefore, the origin and current distribution of these species are the result of contraction in the geographic range of the ancestral species, which inherently led to local extinction processes (Habel et al., 2010).

The northern part of the YPBP has experienced greater climatic stability over time, with generally warm and dry environments (Torrescano-Valle and Islebe, 2015), so it likely functioned as a refuge for lineages adapted to these environments, such as some groups of plants and reptiles (Rzedowski, 1991; Espadas-Manrique et al., 2003; Lee, 2010). This area coincides with the tropical deciduous forest with columnar cacti (TDFCC), a variant of the TDF endemic to parts of Yucatan associated with limestone outcrops and consistent flooding during the rainy season (Perry et al., 1989; Beach, 1998; Espadas-Manrique et al., 2003; Batllori-Sanpedro et al., 2006). It is also home to a great diversity of endemic plant species (91 spp.), which represent about 54% of the total endemic spermatophyta flora, mainly in the Apocynaceae, Cactaceae, and Euphorbiaceae families (Carnevali et al., 2021). Although

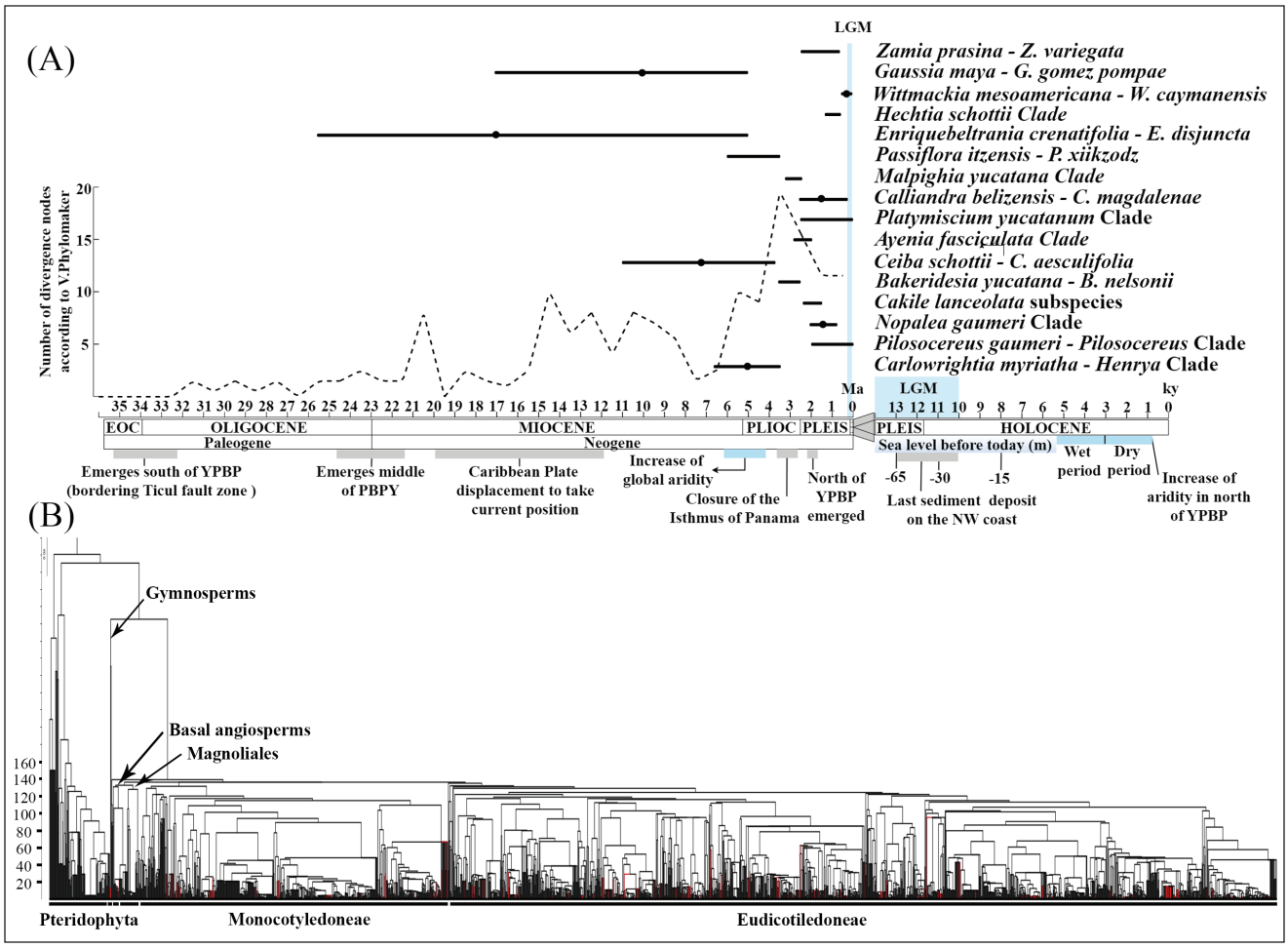

FIGURE 2 (above). Geobiotic scenario of the Yucatan Peninsula Biotic Province (YPBP). Constructed from divergence dates of endemic vascular plants of the YPBP published in previous works (black circles), and their confidence intervals (black lines), and complemented with the number of cladogenetic events (dashed line) according to a phylogenetic tree (below) generated from V.Phylomaker (2, 824 native taxa = black branches; 184 endemic taxa = red branches) in relation to the geological and climatic events that have occurred since their resurgence from the seafloor. Geological data based on Ramos (1975) and climatic data taken from Orellana et al. (1999).

many of these species inhabit diverse environments in the northern part of the YPBP (Carnevali et al., 2021), others are restricted to a single vegetation association, such as *Zephyranthes orellanae* Carnevali, Duno & J.L. Tapia in the TDFCC, or to a few localities, such as *Ruehssia calichicola* (Carnevali & Juárez-Jaimes) L.O. Alvarado (Carnevali et al. 2010a, 2016). These restrictions could be related to the micro-scale environmental heterogeneity of the area (see *In situ speciation* section).

It is well known that climate variations in the Pleistocene (2.6–0.01 Mya) played a central role in the recent biogeographical distribution of many vascular plant species (Gentry, 1982; Ramírez-Barahona and Eguiarte, 2013; Tribsch and Schönswetter, 2003). The influence of the Pleistocene on the YPBP biota has been reported for various biological groups, including endemic plants and several vertebrate groups (Lee, 2010; Espadas-Manrique, 2004; Stinnesbeck et al., 2021). Geographic isolation between species endemic to the YPBP and their phylogenetically related congeneric species, especially those restricted to TDF habitats and that diverged after the late Pliocene (<3.5 Mya), supports this hypothesis (Fig. 2; Appendix 1).

We found evidence of vicariance processes in the continental Neotropics such as in geographically isolated TDF sister species. For example, *Myrmecophila christinae* Carnevali & Gómez-Juárez (Orchidaceae) is geographically separated by the Isthmus of Tehuantepec from *M. grandiflora* (Lindl.) Carnevali, Tapia-Muñoz & I. Ramírez, which is distributed on the Mexican portion of the Pacific Lowlands and Veracruz provinces (Carnevali et al., 2003) (Fig. 3A). The vicariant distribution patterns observed for several groups of *Myrmecophila* Rolfe sister species, all native to the TDF, suggest that this genus previously had a much wider distribution (Carnevali et al., 2003). Also, *Bakeridesia yucatana* (Standl.) D.M. Bates (Malvaceae), currently restricted to the eastern part of the YPBP, diverged from *B. nelsonii* (Rose) D.M. Bates during the last quarter of the Pleistocene (Donnell, 2012; Hoorn et al., 2019). The latter species thrives in dry forests from southeastern Mexico to northern Nicaragua. *Platymiscium yucatanum* Standl.

(Fabaceae) diverged during the Quaternary period and has a wide distribution in the YPBP, but it is geographically isolated from all of its congeners (Saslis-Lagoudakis et al., 2008). We found 18 similar evolutionary hypotheses proposed in taxonomic studies based on morphological similarity and species sharing the same distribution pattern (Appendix 1).

Other studies on lineages distributed in the YPBP which did not include endemic species have also demonstrated the influence of the Pleistocene on the current flora. For instance, the genus *Neomillspaughia* S.F. Blake (Polygonaceae) is composed of three species restricted to fragments of TDF in Central America (Ortiz-Díaz et al., 2013). However, only *N. emarginata* (H. Gross) S.F. Blake is found in the YPBP, while the other two species grow within a minimum distance of 300 km between southern Guatemala and northern Nicaragua (Ortiz-Díaz et al., 2013). Also, the phylogenetic and geographic structure among some Capparaceae groups reflects the isolation of ancestral populations that were previously connected (Mercado and Escalante, 2019). The evolution of many lineages within families such as Malpighiaceae and Fabaceae is closely linked to the history of the TDF (da Silva et al., 2012; Willis et al., 2014a). Given the geographic distance between the remaining TDF fragments, and the role of humid tropical forests of the mountains of southern Mexico and Guatemala as environmental barriers for TDF communities, vicariance is the likely factor which restricted these taxa to the YPBP.

The multiple evolutionary divergence events of endemic species between the late Pliocene (<5.3 Mya) and the early Pleistocene (Fig. 2) support the notion that climatic changes during this period influenced the divergence of species. However, it is important to consider that the lack of phylogenetic resolution of the outermost nodes (species level) may lead to overestimating the age of the divergence of some groups, such as several groups with few representatives in the YPBP [e.g., *Loeselia campechiana* C. Gut. Báez & Duno] or others with unresolved relationships (e.g., *Justicia* L.). Therefore, it is estimated that a larger number of more recent divergence events may have occurred. Despite this, the calibrated phylogenetic framework (e.g., V.Phylomaker trees) has contributed to several biogeographical and ecological studies (Capichoni and Gerdhold, 2020), and they provide approximations of the time of divergence at the level of genera or clades within genera.

Although most cases correspond to lineages restricted to TDF habitats, the Pleistocene also influenced the evolution of lineages typical of colder and humid environments. The southern portion of the YPBP was arid during glacial peaks alternating with humid interglacial periods (Leyden, 1984; Islebe and Leyden, 2006; Metcalfe et al., 2009; Gutiérrez-Ayala et al., 2012). This climatic change possibly caused the extinction of entire communities of boreal species, leaving only a few relict communities of endemic species or 'paleoendemic' species, respectively. A phylogeographic study of *Zamia prasina* W. Bull (Zamiaceae) shows that its populations remained restricted to the southeastern YPBP during the Last Glacial Maximum (Pleistocene-Holocene) (Montalvo-Fernández et al., 2019). Paleoclimatic reconstruction models employed in that work indicate very few or no environments available for successful establishment of populations in the YPBP at that time, which suggests scenarios of local extinction followed by the re-expansion of the distribution range throughout the warmer Mid-Holocene periods. This pattern is consistent with the glacial refuge hypothesis (Ramírez-Barahona and Eguiarte, 2013). Additionally, the genetic structure of *Pinus caribaea* var. *hondurensis* (Sénécl.) W.H. Barret & Golfari (Pinaceae) indicates a demographic history associated with expansion and contraction events (Rebolledo et al., 2018). Populations of this species in northern Belize are more closely related to populations in Honduras than to populations closer to southern Belize.

Enriquebeltrania Rzed. (Euphorbiaceae) is a genus endemic to Mexico with just two known species: *E. crenatifolia* (Miranda) Rzed., and *E. disjuncta* De-Nova & Sosa. Separated by more than 2,000 km and by the Mexican Highlands, both taxa grow in similar coastal environments (De-Nova et al., 2006) (Fig. 3B). It has been hypothesized that this geographic separation occurred as a result of the displacement of the Chortis Block in a west-to-east direction along the Mexican Pacific coast approximately 45–38 Mya (Cuevas-Chapa, 2016). However, there is still uncertainty about the validity of this displacement model due to the complex tectonic history of the Caribbean (Moreno and Manea, 2021). An alternative hypothesis, proposed here, is that during the Oligocene-Miocene, this group was more diverse and widespread along coastal areas, but the marine fluctuations during the Pleistocene and Holocene led to extinctions that resulted in the geographic separation of these species. No fossils belonging to this genus have been found; therefore, we can only speculate that both species come from a common ancestral species whose intermediate populations went extinct in other coastal regions due to changes in sea level or climatic shifts. The surviving populations had to be highly resilient and moved to the newly emerged coastal environments. Moreover, the myrmechocorous dispersal syndrome of the genus may have contributed to its geographic restriction.

While geographic isolation may shed light on the processes involved in the generation of endemism, dispersal may obscure interpretations. We found ten cases where the most likely phylogenetically related species to an endemic taxon is present in the YPBP but has a broad distribution in Mexico, Central America, and the Antilles (Appendix 1). Some of these species pairs are sympatric in the YPBP, such as *Bonellia flammea* (Millsp. ex Mez) B. Ståhl & Källersjö and *B. macrocarpa* (Cav.) B. Ståhl & Källersjö (Primulaceae); *Ceiba schottii* Britten & Baker f. and *C. aesculifolia* (Kunth) Britten & Baker f. (Malvaceae); *Coccoloba spicata* Lundell and *C. diversifolia* Jacq. (Polygonaceae); *Gliricidia maculata* (Kunth) Kunth ex Walp. and *G. sepium* (Jacq.) Kunth ex Walp. (Fabaceae); *Metastelma yucatanense* W.D. Stevens and *M. schlechtendalii* Decne. (Apocynaceae); *Tillandsia dasyliriifolia* Baker and *T. limbata* Schltdl. (Bromeliaceae). Distinguishing between different allopatric

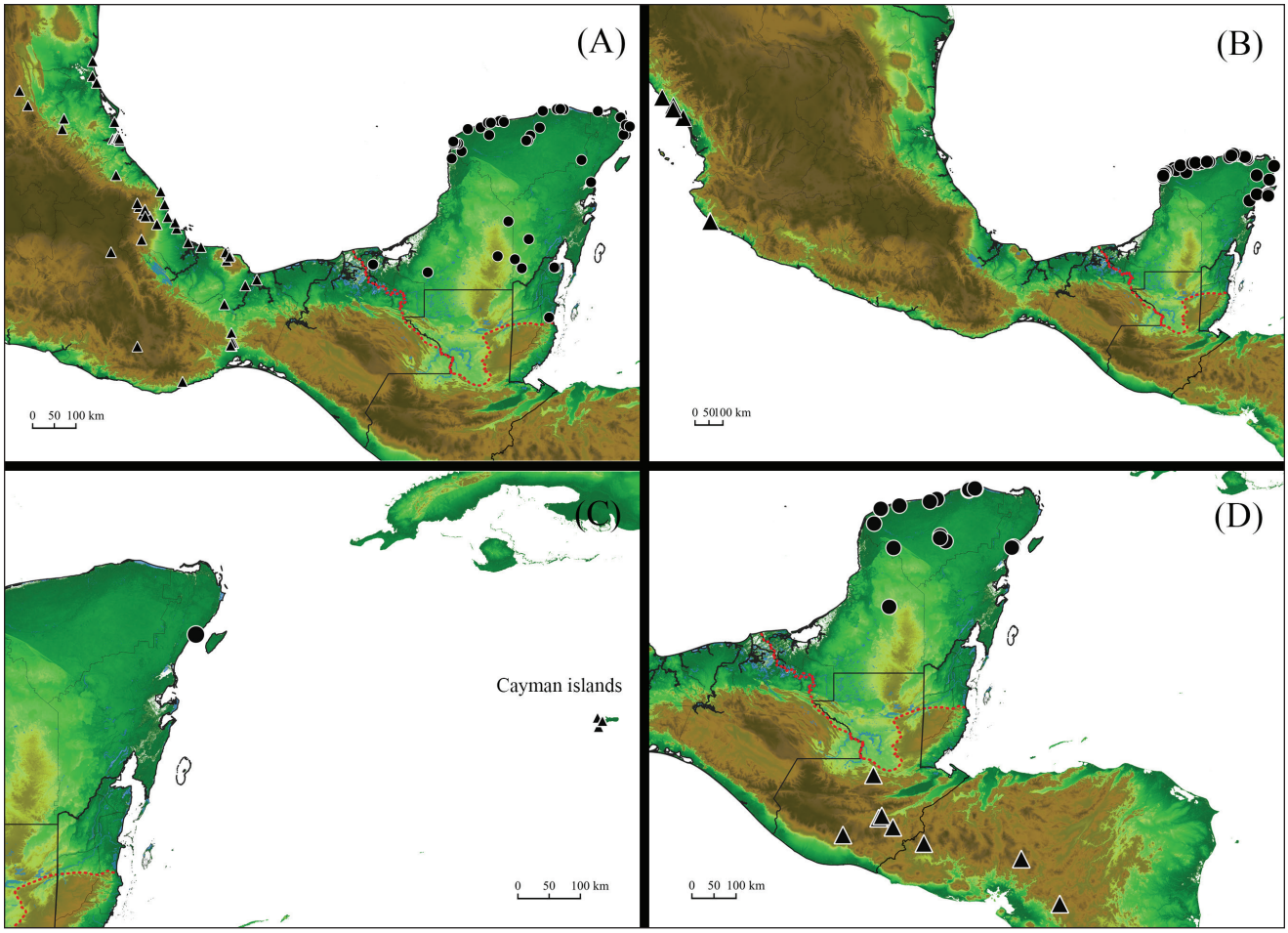

FIGURE 3. Geographic distribution of endemic taxa and their phylogenetically most closely related relatives, representing some of the potential biogeographical settings that gave rise to the endemic flora of the YPBP. **A**, *Myrmecophila christinae* (●) and *M. grandiflora* (▲); **B**, *Enriquebeltrania crenatifolia* (●) and *E. disjuncta* (▲); **C**, *Wittmackia mesoamericana* (●) and *W. caymanesis* (▲); **D**, *Beaucarnea pliabilis* (●) and *B. guatemalensis* (▲).

mechanisms (vicariance or establishment after dispersal) is one of the main challenges in biogeography (Runemark et al., 2012). However, these patterns may suggest dispersal processes that took place after divergence by isolation of these species in the past. This scenario is supported by the relative accessibility to the YPBP territory for several groups of plants.

Other endemic TDF species may have experienced incipient divergence processes given the geographical separation of their populations during the Pleistocene. Today, isolated populations in the Central Depression of Chiapas (Mexico) and Central America of near endemic species of the YPBP, such as *Bakeridesia gaumeri* (Standl.) D.M. Bates (Malvaceae), *Chiococca motleyana* Borhidi (Rubiaceae), *Mammillaria columbiana* subsp. *yucatanensis* (Britton & Rose) D.R. Hunt (Cactaceae), and *Stenocereus laevigatus* (Salm-Dyck) Buxb. (Cactaceae), might well be in the process of genetic and morphologic differentiation. These taxa have not been recognized as separate species, likely due to the lack of thorough systematic studies.

Long-Distance Dispersal Followed by Geographic Isolation

Floristic affinities of the YPBP and the Antilles have been reported for some groups within Apocynaceae, Arecaceae, Icacinaceae, Orchidaceae, Rubiaceae and Salicaceae, among others (Miranda, 1958; Rzedowski, 1978; Estrada-Loera, 1991; Chiappy-Jhones et al., 2001; Trejo-Torres and Ackerman, 2001; Ibarra-Manríquez et al., 2002). However, the main affinity between these two regions is for widely distributed taxa, especially those from coastal environments, suggesting recent dispersal and establishment (Espejel, 1987; Estrada-Loera, 1991).

The endemic flora of the YPBP originating from the Caribbean may have arisen as a result of long-distance dispersal followed by geographic isolation, along with the processes of gene drift and adaptation to new local conditions (Lomolino, 2016). Long-distance dispersal is a relatively rare phenomenon in nature, where migrating populations would have to circumvent the effects of bottleneck phenomena, such as inbreeding depression (Levin et al., 2003). This could explain why there are

only three cases of endemic taxa with sister species from the Caribbean. Additionally, the geographic proximity between the YPBP and the Antilles has probably allowed continued gene flow between populations of species with long-distance dispersal capabilities (anemochory, hydrochory, or zoochory). For example, a great diversity of birds, such as *Vireo olivaceus* L. (Vireonidae), disperse the fruits of species such as *Erythroxylum havanense* Jacq. (Erythroxylaceae) (Islam, 2011). A high dispersal capacity of fruits and seeds limits speciation as it increases gene flow, while limited dispersal promotes rapid genetic differentiation and speciation (Givnish, 2010; Levin et al., 2003).

The best documented case of this speciation mechanism is that of *Wittmackia mesoamericana* (I. Ramírez, Carnevali & Cetzal) Aguirre-Santoro (Bromeliaceae), the only member of the genus in continental Central America. The other species of the genus are concentrated in the Antilles (Aguirre-Santoro, 2018) (Fig. 3C). This species diverged from *W. caymanensis* (Britton ex L.B. Sm.) Aguirre-Santoro about 0.1 Mya (Aguirre-Santoro et al., 2015; Aguirre-Santoro et al., 2016), and its fleshy berries are likely dispersed by birds. The fruits of most members of the subfamily Bromelioideae (Smith and Downs, 1979) have similar dispersal scenarios. However, only a single wild population of this species is known to exist on the east coast of the YPBP (Quintana Roo, Mexico). This is most likely due to the low success of the expansion of its range, coupled with local extinction events that are associated with land use changes in that area of the YPBP (Ellis et al., 2017). Two similar cases occur within the Eudicotyledoneae, although these endemic species have a wider geographical distribution in the YPBP, suggesting an older origin and a better adaptation to the local conditions: e.g., *Thouinia paucidentata* Radlk. (Sapindaceae), whose sister species, *T. portoricensis* Radlk., is endemic to Puerto Rico (Acevedo-Rodríguez et al., 2017). Members of this genus that display anemochory are distributed in the Caribbean, and they diversified mainly in limestone soils (González-Gutiérrez et al., 2016). Finally, *Randia truncata* Greenm. & C.H. Thomps. (Rubiaceae), restricted to the northern YPBP, appears to be closely related to *R. ciliolata* C. Wright (Appendix 1), a species restricted to Jamaica and western Cuba (Gustafsson and Persson, 2002).

The biotic exchange between these land masses has occurred in both directions and has had different implications for the evolution of the flora. In the west-to-east direction, the YPBP has served as a bridge for the dispersal of the biota from Mexico and Central America to the Antilles, where some groups of plants have experienced adaptive radiation by occupying the multiple available niches in these islands. For example, in *Encyclia* Hook. (Orchidaceae), at least three lineages have dispersed to the Antilles, and one of them subsequently, and rapidly, diversified there (Carnevali et al., 2022). In the east-to-west direction, there are diverse Antillean lineages with few representatives in the YPBP, such as *Casearia yucatanensis* (Standl.) T. Samar. & M.H. Alford (Salicaceae) and *Coccothrinax readii* H.J. Quero (Arecaceae) (Jestrow et al., 2017). This distribution pattern suggests sporadic dispersal events with little or no subsequent diversification.

Although the YPBP has not been an area of great plant diversification, the conditions there have facilitated the passage of lineages from the Antilles and northern South America to other parts of Mexico, where groups such as *Diospyros* L. (Ebenaceae) and *Pilosocereus* Byles & G.D. Rowley (Cactaceae) have diversified (García-Díaz et al., 2015; Lavor et al., 2018, 2020). Additional geographic disjunctions with the Caribbean have been reported for genera of Arecaceae, such as *Sabal* Adans. (Zona, 1990; Heyduk et al., 2016) and *Pseudophoenix* H. Wendl. ex Sarg. (Zona, 2002); however, neither phylogenetic nor biogeographical studies have addressed this.

In situ speciation

The present review found phylogenetic evidence of four clades completely restricted to the YPBP in the genera *Dictyanthus* Decne. (Fig. 4A), *Matelea* Aubl. (Apocynaceae), *Nopalea* Salm-Dyck (Cactaceae, often included in *Opuntia* Mill.) (Fig. 4B), and *Passiflora* L. (Passifloraceae), each including two species. The low species diversity found in these clades may indicate two important aspects of the history of the region. First, this pattern may suggest that cladogenetic events occurred very recently: i.e., these are neoendemic lineages that have been unable to expand their distribution range or diversify further (Bruchmann and Hobohm, 2014). The times of divergence between *Nopalea inaperta* Schott ex Griffiths and *N. gaumeri* Britton & Rose (~2 Mya) (Majure et al., 2012) support this hypothesis (Fig. 2). Also, *Passiflora itzensis* (J.M. MacDougal) Port.-Utl. and *P. xiikzodz* J.M. MacDougal diverged 6–4 Mya but have not spread to other areas of the Neotropics (Porter-Utley, 2014). Second, the relative orographic and environmental homogeneity in the YPBP does not provide a broad variety of niches where lineages can undergo adaptive radiation, as has occurred on many islands worldwide (Kier et al., 2009; Givnish et al., 2014). Nonetheless, the YPBP has an environmental gradient and a microenvironmental heterogeneity that have favored in situ evolutionary divergence processes at different geographic scales, as detailed below.

On a microenvironmental scale, selective local adaptation processes also seem to have led to the divergence of some lineages in the YPBP. For example, morphological differences in androgynophore length and the position of floral nectaries between the sister species *Passiflora itzensis* and *P. xiikzodz* (Porter-Utley, 2014) may have led to selective pressures and, ultimately, sympatric speciation among them. The biogeographical evidence indicates that this genus underwent rapid diversification spreading to Central America from North America (Muschner et al., 2012) involving large floral variation among its species (Acha et al., 2021). In the Apocynaceae, *Dictyanthus aeneus* Woodson and *D. yucatanensis* Standl. are sister species (González-Martínez, 2019) that coexist in TDFs in the northern part of the YPBP, although in different microenvironments (Fig. 4A). *Dictyanthus aeneus* grows in the shady understory, while *D. yucatanensis* thrives in open environments, such as forest margins and along road edges (Carnevali, 2021b). However, the infrequent occurrence of natural hybrids between the two species (Carnevali, 2011) suggests that barriers to gene flow between them are still not well-established.

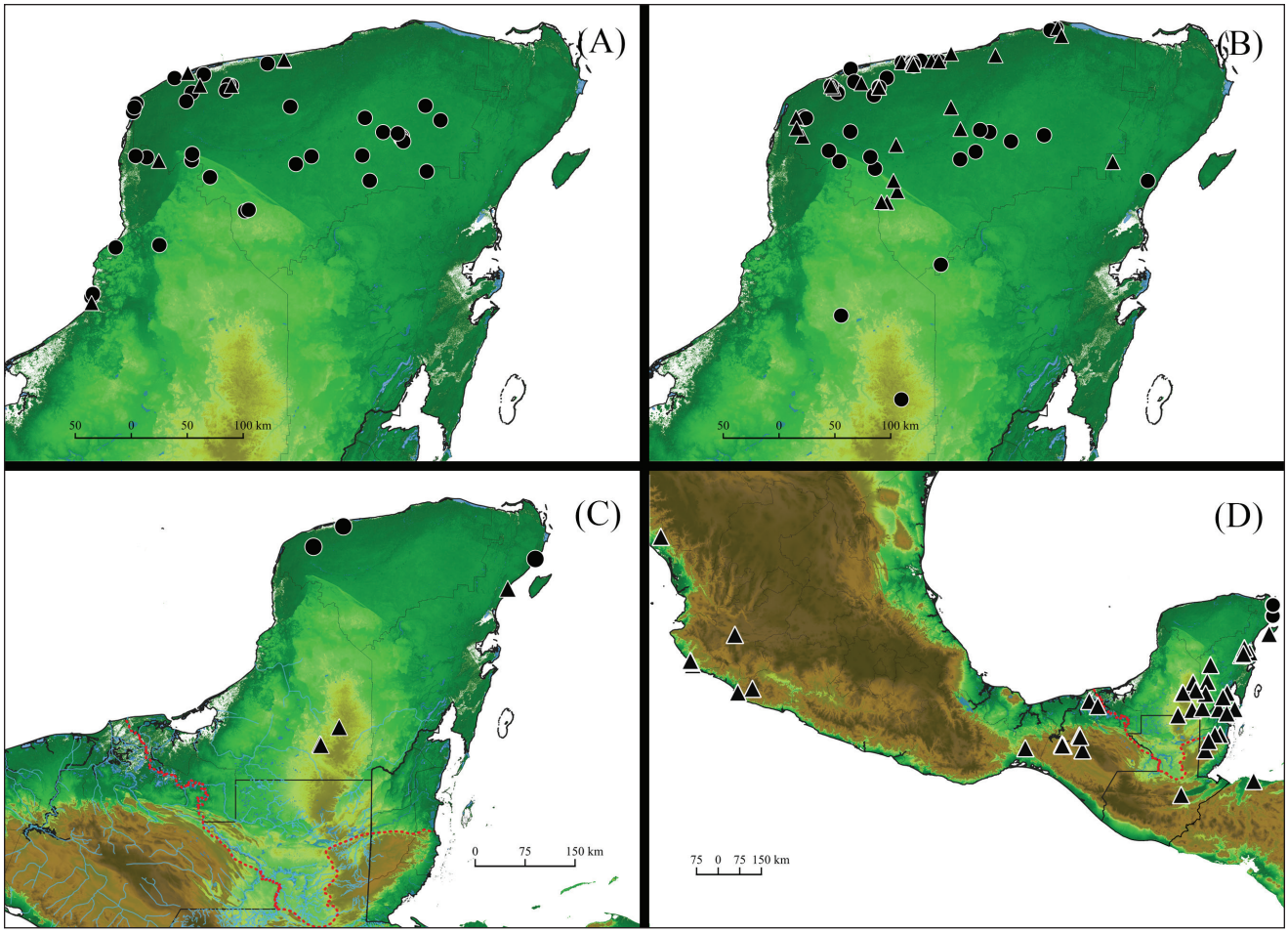

FIGURE 4. Geographic distribution of endemic taxa and their phylogenetically most closely related relatives, representing some of the potential biogeographical scenarios that gave rise to the endemic flora of the YPBP. **A**, *Dictyanthus aeneus* (▲) and *D. yucatanensis* (●); **B**, *Nopalea gaumeri* (●) and *N. inaperta* (▲); **C**, *Wimmeria lundelliana* (▲) and *W. obtusifolia* (●); **D**, *Citharexylum calvum* (●) and *C. hirtellum* (▲).

The relatively more complex orographic conditions in the southern portion of the YPBP (Duch, 1991), combined with higher moisture and nutrient levels in the soil (Bautista et al., 2011; 2015), led to a greater number of available niches than in the northern part of the YPBP. These conditions possibly favored sympatric diversification processes in these rainforests, which gave rise to neoendemic species; however, these divergences are likely very recent due to the climatic instability during the Pleistocene. The availability of humid niches in the southern YPBP may be a plausible explanation for the endemism of *Syngonanthus* Ruhland (Eriocaulaceae) (3 endemic spp.) rather than a limitation in their dispersal capacity (anemochory or hydrochory), as observed in the large number of microendemics within the genus (Echternacht, 2012). Also, although the phylogenetic relationships of many *Justicia* species inhabiting the YPBP are unknown, at least five are microendemic taxa, restricted to humid sites in the central and southern areas of the YPBP.

On a regional scale, climatic and edaphic gradients in the YPBP may have favored adaptive processes, resulting in differentiated populations over time. According to some studies on the biogeography of the flora of the YPBP (Espadas-Manrique et al., 2003; Ibarra-Manríquez et al., 2002), there is a marked separation in the biotic components between the north and south of the YPBP, where the climatic conditions are markedly different (Orellana et al., 1999). This environmental divergence seems to have shaped the speciation between sister species that inhabit different geographic areas within it, such as *Harpalyce torresii* São-Mateus & M. Sousa and *H. yucatanense* São-Mateus & M. Sousa (Fabaceae) (São-Mateus, 2018), and, based on morphological similarity, between *Wimmeria lundelliana* Carnevali, R. Duno, J.L. Tapia & I. Ramírez and *W. obtusifolia* Standl. (Celastraceae) (Carnevali et al., 2009) (Fig. 4C). Also, *Citharexylum calvum* Moldenke (Verbenaceae) has a few populations inhabiting the driest tropical forests of the northeast YPBP, and its most likely related species, *C. hirtellum* Standl., has a wider distribution in the wetter forests in the southern YPBP, Mexico, and Central America (Frost et al., 2017; 2020) (Fig. 4D). This genus originated in the mesic environments of central-northern Mexico, with at least three transitions to arid environments (Frost et al., 2017). Additionally, the pattern of geographic divergence between the legumes *Mariosousa dolichostachya* (S.F. Blake) Seigler & Ebinger, endemic to the central and northern areas of the YPBP, and *M. usumacintensis* (Lundell) Seigler & Ebinger, distributed in Mexico, Central America, and the south of the YPBP,

coincides with the environmental gradient of this province (Miller et al., 2017).

In the YPBP, many endemic species are not restricted to a single vegetation type but are widely distributed throughout the territory (Carnevali et al., 2021b). This suggests that environmental barriers have not been strong enough to promote diversification processes within the YPBP. The lack of important geographic barriers, coupled with dispersal capabilities observed in many endemic species, probably favored broad distribution within the YPBP. Nonetheless, some cases suggesting divergence processes at the subspecies level within the YPBP have been documented from phylogeographic and population structure studies. *Cakile lanceolata* subsp. *alacranensis* (Millsp.) Rodman (Brassicaceae) is a taxon restricted to the driest areas of the coastal dune vegetation in the Alacrán reef, an ecologically restrictive area in terms of humidity and temperature. In fact, the subspecific taxa of *C. lanceolata* (Millsp.) O.E. Schulz diverged less than 2 Mya (Willis et al., 2014b). A study on *Metastelma schlechtendalii* Decne. (Apocynaceae) also reported genetic differentiation between populations in the southern and northern areas of the YPBP (Liede-Schumman et al., 2014).

Evolutionary Divergence in Areas Adjacent to the YPBP from Adaptation to Local Conditions

Some authors have highlighted the strong floristic affinity of the YPBP with Central America and Mexico (Miranda, 1958; Estrada-Loera, 1991; Ibarra-Manríquez et al., 2002; Duno de Stefano et al., 2012). However, this region has significantly different environmental restrictions compared to contiguous geographic areas, including complex microtopology and northwest-to-southeast edaphic and climate gradients (Vargas et al., 2014). The combination of the climatic, orographic, and edaphic characteristics of the YPBP has likely acted as an ecological filter for several plant lineages. Despite the lack of obvious geographic barriers, some families which are widely distributed in the Neotropics, such as Crassulaceae and Ericaceae, are completely absent in this area. Other families, such as Marcgraviaceae, Melastomataceae, Polemoniaceae, and Pinaceae, barely reach the southern, more humid, limits of this province. This pattern is interesting because the absence of orographic barriers that could prevent the arrival of lineages from the southern part of the YPBP indicates the likelihood that ecological factors restrict the establishment of many biological groups in this area.

The environmental conditions of the YPBP possibly promoted evolutionary divergence between populations in this area and neighboring areas of southern Mexico and Central America. This phenomenon has already been evidenced in biogeographical works indicating a marked pattern of biotic separation between these areas (e.g., Poaceae, Dávila-Aranda et al., 2004; amphibians and reptiles, Barrera, 1962). This same pattern of geographic divergence was found in 13 taxa endemic to the YPBP; the phylogenetically closest relatives of these taxa have a relatively broad distribution and long-distance dispersal characteristics, but do not penetrate the YPBP territory (Appendix 2). Taxonomic studies of selected groups based on morphological similarity indicate that at least 18 other pairs of hypothetically related species show the same distribution pattern. Since most of these species have long-distance dispersal mechanisms, this low diversity cannot be attributed to a limited dispersal capability. Also, it is important to note that quasi-endemic species, such as *Acalypha gentlei* Atha (Euphorbiaceae), *Eugenia winzerlingii* Standl. (Myrtaceae) or *Haematoxylum campechianum* L. (Fabaceae), which also appear in the Gulf of Mexico province, could reflect the transitional zone characteristic of the southern portion of the YPBP, and explain the historical challenge of its southern delimitation (Morrone, 2019). These species grow in the more atypical humid conditions of the YPBP, which is mainly dry.

Some taxa endemic to the YPBP have morphological characteristics that are particularly distinctive from the rest of the species in the same genus. These adaptive morphological characters may be of evolutionary importance for the taxa. For example, *Beaucarnea pliabilis* (Baker) Rose (Nolinaceae) has a larger number of foliar papillae that protect stomata in contrast to its sister species *B. guatemalensis* Rose, which grows in humid tropical forests from central Guatemala to northern Nicaragua (Rojas-Piña et al., 2014) (Fig. 3D). As observed in other species of Asparagaceae (Solano et al., 2017), these differential adaptations between lineages suggest that their evolutionary divergence may be associated with the colonization of drier environments and provide indications of the selective pressures that shaped their diversification. *Pilostyles maya* P. Ortega, Gonz.-Martínez & S. Vázquez is the only species in the genus that has hermaphroditic flowers, a condition considered ancestral and rare in Apodanthaceae, where most species are dioecious or monoecious (Azevedo, 2010; Schaefer and Renner, 2011). Additionally, *P. maya* presents cleistogamous flowers, an autapomorphic character in the genus (Ortega-González et al., 2020). Both characters require low energy expenditure and are deemed reproductive strategies that increase the likelihood of self-pollination (Bawa and Beach, 1981; Cardoso et al., 2018). This may be advantageous in the absence of pollinators or in the variable seasonal conditions of the YPBP.

In some cases, the occurrence of species with highly atypical morphological traits within their group has caused them to be considered separate, monotypic genera. This may be evidence of the ecological divergence mentioned above. For example, *Plagiolophus* Greenm. (Asteraceae) is the only member of the tribe *Ecliptinae* that has a projection on the apex of the cypsela (or apical rostrum) (Azevedo-Bringel, 2014). This structure facilitates its attachment to mammalian hair or to the feathers of birds, thus promoting long-distance dispersal (Sorensen, 1986). However, this genus is restricted to the Yucatan peninsula and is phylogenetically related to the genus *Jefea* Strother, which is absent from the YPBP. *Attilaea abalak* E. Martínez & Ramos (Anacardiaceae) has characteristics similar to species of *Spondias* L., but it is distinguished by having a climbing (vs. arborescent) habit, and a bicarpellary (vs. unicarpellary) gynoecium (Martínez and Ramos, 2007; Mitchell and Daly, 2015). Both characters can be ecologically favorable for faster establishment when invading new areas and for increasing the possibility of seed dispersal relative to members of *Spondias* (Howe and Smallwood, 1982).

Finally, the only two species of *Manfreda* Salibs. (Asparagaceae) present in the YPBP, *M. paniculata* L. Hern., R.A. Orellana & Carnevali and *M. petskinil* R.A. Orellana, L. Hern. & Carnevali, have different characteristics than the rest of the genus: perennial (vs. deciduous) leaves, paniculate (vs. racemose) inflorescences, and flowers subtended by a single bracteole (vs. two bracteoles) (Hernández-Sandoval et al., 2008). These authors suggest that geographic isolation may have promoted its evolutionary and morphological divergence. However, an intergeneric hybrid origin between *Manfreda* and *Agave* L. has also been proposed for *M. paniculata* L. Hern., R.A. Orellana & Carnevali (Carnevali, 2013). The uniqueness or peculiarity of the morphological characters in these species may be the result of the extinction of morphologically similar lineages or ancestral lineages, or of morphological divergences arising from selective pressures related to the YPBP environment.

Hybridization

In vascular plants, hybridization is a process that regulates and catalyzes biological diversity, being more common in some groups than in others (Rieseberg et al., 2007; Schley et al., 2022). Natural hybrids have been documented within families, such as Orchidaceae [*Maxillariella* × *yucatanensis* (Carnevali & R. Jiménez) M.A. Blanco & Carnevali, and *Myrmecophila* × *laguna-guerrerae* Carnevali, Ibarra-González & J.L. Tapia] and Fabaceae [*Vachellia* × *cedilloi* (L. Rico) Seigler & Ebinger]. Also, in *Tillandsia* L. (Bromeliaceae), *T. maya* I. Ramírez & Carnevali has intermediate morphology between *T. brachycaulos* Schltdl. and *T. balbisiana* Schult. f., suggesting a hybrid origin (Ramírez et al., 2000). However, we only found phylogenetic evidence for the hybrid origin of *Stylosanthes quintanarooensis* Gama & Dávila (Fabaceae), a tetraploid species which likely arose from a single clone locally adapted to humid conditions in southeastern YPBP (Stappen et al., 2002).

Another work suggests hybrid origin in Anthericaceae. The genus *Echeandia* Ortega has a large variation in the number of chromosomes between species, suggesting that hybridization has been a key driver of diversification (Cruden, 1999; Rodríguez and Castro-Castro, 2005). In fact, *E. luteola* Cruden, endemic to the YPBP, is pentaploid (n = 40), which supports the hypothesis of a hybrid origin (Cruden, 1994). The populations mentioned above thrive mainly in flooded plant communities, particularly in the southern YPBP, where communities of seasonal and perennial environments converge. These hybrid zones are usually common in overlapping areas of different environments, also known as ecotones (Schley et al., 2022). However, only a few isolated individuals (in some cases, only a single individual) have been found in these areas. Thus, whether hybridization processes lead to successful hybrid speciation events is still an unanswered question (Mallet, 2007).

It is worth noting that the study of natural populations in the YPBP is biased by the lack of specialists for multiple taxonomic groups in the region; therefore, hybrid speciation events are probably more common than reported, since that adaptive introgression is especially common in novel or disturbed environments (Rieseberg et al., 2007).

Anthropogenic influence

Anthropogenic activities have impacted the flora of the YPBP since the establishment of the Mayan civilization about 10, 000 years ago (Binford, 1983; Rico-Gray and García-Franco, 1991). The plant communities inhabiting the YPBP have been modified throughout its long anthropogenic history (Rico-Gray and García-Franco, 1991; Chiappy et al., 2000; Fedick and Morrison, 2004; Dupuy et al., 2015). At the peak of the Mayan civilization, some 3,000–4,000 years ago, the high population density caused a profound impact on the vegetation, climate, and soil in the region (Binford, 1983; Islebe et al., 1996). However, the forests are highly resilient and have recovered, even after the sisal industry significantly impacted the landscape (Ceccon et al., 2002; González-Iturbe et al., 2002). These forests currently account for the second largest patch of continuous vegetation in America, but the region has the highest deforestation rates in the Neotropics (Ellis et al., 2017).

The flora of the YPBP currently faces serious anthropogenic threats from changes in land use due to urban and agricultural expansion, as well as from energy and tourism projects (Sánchez-Sánchez et al., 2015; Reyes-García et al., 2019). Approximately 51% of the endemic taxa are listed in a risk category, of which some 44% are listed as threatened or critically threatened (Carnevali et al., 2021b).

Conclusions

The evidence gathered in the present review strongly suggests that the origin of the endemic vascular flora of the YPBP has been driven by various factors and processes that occurred at different times in the history of the Earth. However, the biogeographical and phylogenetic patterns of most of the species studied show the influence of Pleistocene climatic fluctuations on the processes of speciation. Such environmental changes may have had different consequences for the flora and resulted in different distribution patterns, depending on the dispersal and adaptive capabilities of the lineages. Additionally, although less frequently, other processes such as hybridization, local adaptation, and geographic isolation after long-distance dispersal, must also have contributed to the creation and diversification of the endemic flora of this region.

Greater climatic stability in the northern region of the YPBP allowed for the isolation of lineages associated with drier and more seasonal environments compared to the southern region. The environmental conditions of the YPBP promoted ecological divergence within this area, while the regional environmental conditions led to processes of large-scale divergence. However, the probability of dispersal between the YPBP and the Antilles, given their geographic proximity and the various dispersal capabilities of species, has prevented differentiation by isolation in the lineages that have arrived in the YPBP.

Added at proof stage

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Literature Cited

Acevedo-Rodríguez, P., K. J. Wurdack, M. S. Ferrucci, G. Johnson, P. Días, R. G. Coelho, G. V. Sommer, V. W. Steinmann, E. A. Zimmer, and M. T. Strong. 2017. Generic relationships and classification of tribe Paullinieae (Sapindaceae) with a new concept of supertribe Paulliniodae. Syst. Bot. 42(1): 96–114.

Acha, S., A. Linan, J. MacDougal, and C. Edwards. 2021. The evolutionary history of vines in a Neotropical biodiversity hotspot: Phylogenomics and biogeography of a large passion flower clade (*Passiflora* section *Decaloba*). Mol. Phyl. & Evol. 164: 107260.

Aguirre-Santoro, J. 2018. Taxonomic revision of the Caribbean-endemic species of *Wittmackia* (Bromeliaceae). Phytotaxa 336(2): 101–147.

Aguirre-Santoro, J., F. A. Michelangeli, and D. W. Stevenson. 2016. Molecular phylogenetics of the *Ronnbergia* Alliance (Bromeliaceae, Bromelioideae) and insights into their morphological evolution. Molec. Phylogen. Evol. 100: 1–20.

Aguirre-Santoro, J., J. Betancur, G. K. Brown, T. M. Evans, F. Salgueiro, M. Alves-Ferreira, and T. Wendt. 2015. Is *Ronnbergia* (Bromeliaceae, Bromelioideae) a geographically disjunct genus? Evidence from morphology and chloroplast DNA sequence data. Phytotaxa 219(3): 261–275.

Anderson, S. 1994. Area and endemism. Quart. Rev. Biol. 69(4): 451–471.

Andrus, N., A. Tye, G. Nesom, D. Bogler, C. Lewis, R. Noyes, P. Jaramillo, and J. Francisco-Ortega. 2009. Phylogenetics of *Darwiniothamnus* (Asteraceae: Astereae)—molecular evidence for multiple origins in the endemic flora of the Galápagos Islands. J. Biogeogr. 36(6): 1055–1069.

Apg (angiosperm Phylogeny Group). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181(1): 1–20.

Aragón-Moreno, A. A., G. A. Islebe, and N. Torrescano-Valle. 2012. A ~3800-yr, high-resolution record of vegetation and climate change on the north coast of the Yucatan Peninsula. Rev. Palaeobot. Palynol. 178: 35–42.

Azevedo, B. B. 2010. Ciclo de vida, fenologia e anatomia floral de *Pilostyles* (Apodanthaceae-Rafflesiaceae sl): subsídios para um posicionamento filogenético da familia Apodanthaceae. M Sc. thesis, Department of Botany, University of São Paulo, São Paulo.

Azevedo-Bringel, J. B. 2014. Contribuicao ao studio de Heliantheaea (Asteraceae): revisao taxonomica e filogenia de *Reincourtia* Cass. Ph.D. dissertation, Department of Botany, University of Brasilia, Brazil.

Barrera, A. 1962. La Península de Yucatán como Provincia Biótica. Revista Soc. Mex. Hist. Nat. 23: 71–105.

Batllori-Sampedro E., J. I. González-Piedra, J. Díaz-Sosa, and J. L. Febles-Patrón. 2006. Caracterización hidrológica de la región costera noroccidental del estado de Yucatán, México. Bol. Inst. Geogr. 59: 74–92.

Bautista, F., G. Palacio-Aponte, P. Quintana, and J. A. Zinck. 2011. Spatial distribution and development of soils in tropical karst areas from the Peninsula of Yucatan, Mexico. Geomorphology 135(3–4): 308–321.

Bautista, F., O. Frausto, T. Ihl, and Y. Aguilar. 2015. An update soil map of The Yucatan State, Mexico: Geomorphological approach and WRB. Ecosis. Recur. Agropec. 2(6): 303–315.

Bawa, K. S., and J. H. Beach. 1981. Evolution of sexual systems in flowering plants. Ann. Missouri Bot. Gard. 68: 254–274.

Beach, T. 1998. Soil constraints on northwest Yucatán, Mexico: Pedoarchaeology and Maya subsistence at Chunchucmil. Geoarchaeology 13(8): 759–791.

Becerra, J. X. 2005. Timing the origin and expansion of the Mexican tropical dry forest. PNAS 102(31): 10919–10923.

Benson, D. A., M. Cavanaugh, K. Clark, I. Karsch-Mizrachi, J. Ostell, K. D. Pruitt, and E. W. Sayers. 2018. GenBank. Nucleic Acids Res. 46(D1): D41–D47.

Binford, M. W. 1983. Paleolimnology of the Peten Lake District, Guatemala I. Erosion and deposition of inorganic sediment as inferred from granulometry. Hydrobiologia 103(1): 199–203.

Borges, R. L., S. G. Razafimandimbison, N. Roque, and C. Rydin. 2021. Phylogeny of the Neotropical element of the *Randia* clade (Gardenieae, Rubiaceae, Gentianales). Plant Ecol. Evol. 154(3): 458–469.

Bruchmann, I., and C. Hobohm. 2014. Factors that create and increase endemism. Pages 51–68 in C. Hobohm, ed., Endemism in vascular plants. Springer Netherlands, Dordrecht.

Bryant, W. R., J. Lugo., and C. Córdova. 1991. Physiography and bathymetry. Pages 13–28 in A. Salvador, ed., The Gulf of Mexico Basin. The Geological Society of America, Colorado.

Burke, J. M., A. Sánchez, K. Kron, and M. Luckow. 2010. Placing the woody tropical genera of Polygonaceae: a hypothesis of character evolution and phylogeny. Amer. J. Bot. 97: 1377–1390.

Capichoni M., J., and P. Gerhold. 2020. Environment and evolutionary history depict phylogenetic alpha and beta diversity in the Atlantic coastal White-sand woodlands. J. Veg. Sci. 31(4): 643–645.

Cardoso F., J. C., M. L. Viana, R. Matias, M. T. Furtado, A. P. de Souza Caetano, H. Consolaro, and V. L. Garcia De Brito. 2018. Towards a unified terminology for angiosperm reproductive systems. Acta Bot. Brasil. 32: 329–348.

Carnevali, G. 2011. *Dictyanthus* (Apocynaceae: Asclepiadoideae) en Yucatán: hermanas, "juntas pero no revueltas". Desde el Herbario CICY 3: 10–11.

Carnevali, G. 2013. *Agave, Manfreda* o ambos: *Manfreda paniculata*. Desde el Herbario CICY 5: 66–68.

Carnevali Fernández-Concha, G., I. Ramírez-Morillo, J. E. Pérez-Sarabia, J. L. Tapia-Muñoz, H. E. Medina, W. Cetzal-Ix, S. Hernández-Aguilar, L. L. Can Itzá, N. E. Raigoza Flores, R. Duno de Stefano, and G. A. Romero-González. 2021b. Assessing the risk of extinction of vascular plants endemic to the Yucatán Peninsula Biotic Province by means of distributional data. Ann. Missouri Bot. Gard. 106(1): 424–457.

Carnevali, G., I. Tamayo-Cen, C. E. Méndez-Luna, I. M. RamírezMorillo, J. L. Tapia-Muñoz, W. Cetzal-Ix, and G. A. Romero-González. 2022. Phylogenetics and historical biogeography of *Encyclia* (Laeliinae: Orchidaceae) with an emphasis on the *E. adenocarpos* complex, a new species, and a preliminary species list for the genus. Org. Divers. & Evol. 1–35.

Carnevali Fernández-Concha, G., J. C. Trejo Torres, V. Juárez-Jaimes, R. Duno S., J. L. Tapia-Muñoz, I. M. Ramírez-Morillo, and W. R. Cetzal-Ix. 2016. *Marsdenia calichicola* (Apocynaceae), a narrow endemic, endangered new species from the Mexican Yucatan Peninsula. Phytotaxa 270(2): 46–154.

Carnevali, G., J. L. Tapia, N. H. Williams, and W. M. Whitten. 2003. Sistemática, filogenia y biogeografía de *Myrmecophila*. Lankesteriana 7: 29–32.

Carnevali F. C., G., J. L. Tapia-Muñoz, R. Duno de Stefano, and I. Ramírez-Morillo. 2010b. Flora Ilustrada de la Península de Yucatán: Listado Florístico. Centro de Investigación Científica de Yucatán, A.C., Mexico.

Carnevali Fernández-Concha, G., R. Duno de Stefano y J. L. Tapia Muñoz. 2021a. Una breve pesquisa sobre *Echites yucatanensis* (Apocynaceae). Desde el Herbario CICY 13: 96–101.

Carnevali F. C., G., R. Duno de Stefano, J. L. Tapia-Muñoz, and I. Ramírez-Morillo. 2010a. Reassessment of *Zephyranthes* (Amaryllidaceae) in the Yucatán Peninsula including a new species, *Z. orellanae*. J. Torrey Bot. Soc. 137(1): 39–48.

Carnevali Fernández-Concha, G., R. Duno de Stefano, J. L. Tapia Muñoz, and I. M. Ramírez Morillo. 2009. Notes on the Flora of the Yucatan Peninsula IX: A reappraisal of the genus *Wimmeria* (Celastraceae), including the new species *W. lundelliana*. Novon 19(2): 150–155.

Ceccon, E., I. Olmsted, C. Vázquez-Yanes, and J. Campo-Alves. 2002. Vegetation and soil properties in two tropical dry forest of differing regeneration status in Yucatan. Agrociencia 36(5): 621–631.

Chiapella, J. O., and P. H. Demaio. 2015. Plant endemism in the Sierras of Córdoba and San Luis (Argentina): understanding links between phylogeny and regional biogeographical patterns. PhytoKeys 47: 59–96.

Chiappy Jhones, C., L. Gama, L. Giddings, V. Rico-Gray, and A. Velázquez. 2000. caracterización de los paisajes terrestres actuales de la península de Yucatán. Investig. Geogr. 42: 28–39.

Chiappy-Jhones, C., V. Rico-Gray, L. Gama, and L. Giddings. 2001. Floristic affinities between the Yucatan Peninsula and some karstic areas of Cuba. J. Biogeogr. 28(4): 535–542.

Crother, B. I., and C. M. Murray. 2011. Ontology of areas of endemism. J. Biogeogr. 38(6): 1009–1015.

Cruden, R. W. 1994. *Echeandia* Ortega. In G. Davidse, M. S. Sousa, A. O. Charter, eds., *Alismatácea a Ciperácea. Fl. Mesoamericana*. 6:27–30. Instituto de Biología, UNAM, Mexico.

Cruden, R. W. 1999. A new subgenus and fifteen new species of *Echeandia* (Anthericaceae) from Mexico and the United States. Novon 9(3): 325–338.

Cuenca, A., and C. B. Asmussen-Lange. 2007. Phylogeny of the Palm tribe Chamaedoreeae (Arecaceae) based on plastid DNA sequences. Syst. Bot. 32(2): 250–263.

Cuenca, A., C. B. Asmussen-Lange, and F. Borchsenius. 2007. A dated phylogeny of the palm tribe Chamadoreeae supports Eocene dispersal between Africa, North and South America. Molec. Phylogen. Evol. 46: 760–775.

Cuevas-Chapa, R. 2016. Filogenia, biogeografía y tiempos de divergencia en *Enriquebeltrania* (Euphorbiaceae). B. Sc. thesis, Centro Universitario de Ciencias Biológicas y Agropecuarias, University of Guadalajara, Jalisco.

da Silva, M. J., L. P. de Queiroz, A. M. de Azevedo T, G. P. Lewis, and A. P. de Sousa. 2012. Phylogeny and biogeography of *Lonchocarpus* sensu lato and its allies in the tribe Millettieae (Leguminosae, Papillionideae). Taxon 61(1): 93–108.

Daniel, T. F., L. A. McDade, M. Manktelow, and C. A. Kiel. 2008. The "*Tetramerium* lineage" (Acanthaceae: Acanthoideae: Justicieae): delimitation and intra-lineage relationships based on cp and nrITS sequence data. Syst. Bot. 33(2): 416–436.

Davidse, G., M. S. Sánchez, and A. O. Chater. 1994. *Alismataceae a Cyperaceae*, Vol. 6 of *Flora Mesoamericana*. Universidad Nacional Autónoma de México, Mexico City.

Dávila-Aranda, P., R. Lira-Saade, and J. Valdés-Reyna. 2004. Endemic species of grasses in Mexico: a phytogeographic approach. Biodivers. & Conserv. 13(6): 1101–1121.

Davis, C. C., and W. R. Anderson. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. Amer. J. Bot. 97(12): 2031–2048.

De-Nova, J. A., R. Medina, J. C. Montero, A. Weeks, J. A. Rosell, M. E. Olson, L. E. Eguiarte, and S. Magallón. 2011. Insights into the historical construction of species-rich Mesoamerican seasonally dry tropical forest: the diversification of *Bursera* (Burseraceae, Sapindales). New Phytol. 193(1): 276–287.

De-Nova, J. A., V. Sosa, and K. J. Wurdack. 2006. Phylogenetic relationships and the description of a new species of *Enriquebeltrania* (Euphorbiaceae *s.s.*): An enigmatic genus endemic to Mexico. Syst. Bot. 31(3): 533–546.

Donnell, A. A. 2012. A systematic revision of *Bakeridesia* Hochr. (Malvaceae). Ph.D. dissertation, College of Arts and Sciences, Ohio University, Ohio.

Donnell, A. A., H. E. Ballard Jr., and P. D. Cantino. 2012. *Callianthe* (Malvaceae): A new genus of Neotropical Malveae. Syst. Bot. 37(3): 712–722.

Duch G., J. 1991. Fisiografía del Estado de Yucatán: su relación con la agricultura. Centro Regional de la Península de Yucatán. División de Ciencias Forestales. Universidad Autónoma de Chapingo, México.

Duno de Stefano, R., G. Carnevali Fernández-Concha, I. M. Ramírez Morillo, J. L. Tapia Muñoz, L. L. Can Itzá, S. Hernández-Aguilar, and T. Embrey. 2019. Flora de la Península de Yucatán. Centro de Investigación Científica de Yucatán, A.C., https://cicy.mx/sitios/flora%20digital/

Duno-de Stefano, R., L. L. Can-Itzá, A. Rivera-Ruiz, and L. M. Calvo-Irabién. 2012. Regionalización y relaciones biogeográficas de la Península de Yucatán con base en los patrones de distribución de la familia Leguminosae. Rev. Mex. Biodivers. 83(4): 1053–1072.

Dupuy J. M., R. Durán García, G. García Contreras, J. Arellano Morin, E. Acosta Lugo, M. E. Méndez González, and M. Andrade Hernández. 2015. Conservation and use. Pages 169–193 in G. A. Islebe, B. Schmook, S. Calmé, J. L. León-Cortés, eds., Biodiversity and conservation of the Yucatán Peninsula. Sprinter, Switzerland.

Echternacht, A. L. 2012. Sistemática de *Comanthera* e de *Syngonanthus* (Eriocaulcaceae). Ph.D. dissertation, University of San Paulo, Sao Paulo.

Edwards, E. J., and C. J. Still. 2008. Climate, phylogeny and the ecological distribution of C4 grasses. Ecol. Lett. 11(3): 266–276.

Ellis, E. A., U. H. Gómez, and J. A. Romero-Montero. 2017. Los procesos y causas del cambio en la cobertura forestal de la Península Yucatán, México. Ecosistemas 26(1): 101–111.

Espadas-Manrique, C. M. 2004. Estudio fitogeográfico de las especies endémicas de la península de Yucatán. Ph.D. dissertation, Unidad de Recursos Naturales, Centro de Investigación Científica de Yucatán, CICY, Yucatán.

Espadas-Manrique, C., R. Durán, and J. Argaez. 2003. Phytogeographic analysis of taxa endemic to the Yucatán Peninsula using geographic information systems, the domain heuristic method and parsimony analysis of endemicity. Divers. & Distrib. 9(4): 313–330.

Espejel, I. 1987. A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula. J. Biogeogr. 14(6): 499–519.

Estrada-Loera, E. 1991. Phytogeographic relationships of the Yucatán Peninsula. J. Biogeogr. 18(6): 687–697.

Fattorini, S. 2017. Endemism in historical Biogeography and conservation biology: concepts and implications. Biogeographia 32(1): 47–75.

Fedick, S. L., and B. A. Morrison. 2004. Ancient use and manipulation of landscape in the Yalahau region of the northern Maya lowlands. Agric. Human Values 21: 207–219.

Frost, L. A., S. A. Tyson, P. Lu-Irving, N. O´Leary, and R. G. Olmstead. 2017. Origins of North American arid-land Verbenaceae: more than one way to skin a cat. Amer J. Bot. 104(11): 1708–1716.

Frost, L. A., N. O´Leary, L. P. Lagomarsino, D. C. Tank, and R. G. Olmstead. 2020. Phylogeny, classification, and character evolution of tribe *Citharexylum* (Verbenaceae). Amer. J. Bot. 108(10): 1982–2001.

García Díaz, R., J. A. Cuevas Sánchez, S. Segura Ledesma, and F. Basurto Peña. 2015. Panbiogoegraphic analysis of *Diospyros* spp. (Ebenaceae) in México. Rev. Mexicana Cienc. Agríc. 6(1): 187–200.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69(3): 557–593.

Gentry, J. L., and P. C. Standley. 1974. Solanaceae. In J. L. Gentry and P. C. Standley, eds., Flora of Guatemala, Volume 24, Part X. Chicago: Field Museum of Natural History.

Givnish, T. J. 2010. Ecology of plant speciation. Taxon 59(5): 1326–1366.

Givnish, T. J., M. H. Barfuss, B. Van Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, R. S. Jabaily, D. M. Crayn, J. A. C. Smith, K. Winter, G. K. Brown, T. M. Evans, B. K. Holst, H. Luther, W. Till, G. Zizka, P. E. Berry, and K. J. Sytsma. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. Mol. Phyl. & Evol. 71: 55–78.

González-Gutiérrez, P. A., J. L. Gómez-Hechavarría, and O. Leyva Bermúdez. 2016. A new species of *Thouinia* (Sapindaceae) from northeastern Cuba. Revista Jard. Bot. Nac. Univ. Habana 37: 85–91.

González-Iturbe, J. A., I. Olmsted, and F. Tun-Dzul. 2002. Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. Forest Ecol. Managem. 167(1–3): 67–82.

González-Martínez, C. A. 2019. *Dictyanthus* Decne. (Apocynaceae: Asclepiadoideae: Gonolobinae) un género casi endémico de México e ignorado en las filogenias. Master thesis, Universidad Nacional Autónoma de México, Ciudad de México, Mexico.

Granados, M., C., X. Granados-Aguilar, S. Donadío, G. A. Salazar, M. Flores-Cruz, E. Hágsater, J. R. Starr, G. Ibarra-Manríquez, I. Fragoso-Martínez, and S. Magallón. 2017. Geographic structure in two highly diverse lineages of *Tillandsia* (Bromeliaceae). Botany 95: 641–651.

Grandcolas, P., J. Murienne, T. Robillard, L. Desutter-Grandcolas, H. Jourdan, E. Guilbert, and L. Deharveng. 2008. New Caledonia: a very old darwinian island? Phil. Trans. Soc. 363(1508): 3309–3317.

Gustafsson, C., and C. Persson. 2002. Phylogenetic relationships among species of the neotropical genus *Randia* (Rubiaceae, Gardenieae) inferred from molecular and morphological data. Taxon 51(4): 661–674.

Gutiérrez-Ayala, L.V., N. Torrescano-Valle, and G. A. Islebe. 2012. Reconstrucción paleoambiental del Holoceno tardío de la reserva Los Petenes, Península de Yucatán, México. Rev. Mexicana Cienc. Geol. 29(3): 749–763.

Habel, J. C., T. Assmann, T. Schmitt, and J. C. Avise. 2010. Relict species: from past to future. Pages 1–5 in J. C. Habel and T. Assmann, eds., Relict Species. Springer, Berlin, Heidelberg.

Hernández-Hernández, T., J. W. Brown, B. O. Schlumpberger, L. E. Eguiarte, and S. Magallón. 2014. Beyond aridification: multiple explanations for the elevated diversification of cacti in the New World succulent biome. New Phytol. 202: 1382–1397.

Hernández-Sandoval, L., R. Orellana, and G. Carnevali. 2008. Two new species of *Manfreda* Salisb. (Agavaceae) from the Yucatán Península, Mexico. J. Torrey Bot. Soc. 135(2): 168–177.

Heyduk, K., D. W. Trapnell, C. F. Barrett, J. Leebens-Mack. 2016. Phylogenomic analyses of species relationships in the genus *Sabal* (Arecaceae) using targeted sequence capture. Biol. J. Linn. Soc. 117: 106–120.

Hobohm, C. 2014. *Endemism in vascular plants*. Springer Dordrecht Heidelberg New York London.

Hoorn, C., R. van der Ham, F. de la Parra, S. Salamanca, H. T. Steege, H. Banks, W. Star, B. J. van Heuven, F. A. Carvalho, G. Rodríguez-Forero, and L. P. Lagomarsino. 2019. Going north and south: The biogeographic history of two Malvaceae in the wake Neogene Andean uplift and connectivity between the Americas. Rev. Paleobot. Palynol. 264: 90–109.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Rev. Ecol. Syst. 13: 201–228.

Ibarra-Manríquez, G., J. L. Villaseñor, R. Durán, and J. Meave. 2002. Biogeographical analysis of the tree flora of the Yucatan Peninsula. J. Biogeogr. 29(1):17–29.

Islam, M. 2011. Tracing the evolutionary history of Coca (*Eryhtroxylum*). Ph.D. dissertation, Department of Ecology and Evolutionary Biology, University of Colorado, Colorado.

Islebe, G. A., H. Hooghiemstra, M. Brenner, J. H. Curtis, and D. A. Hodell. 1996. A Holocene vegetation history from lowland Guatemala. Holocene 6(3): 265–271.

Islebe, G. A., and Leyden, B. 2006. La vegetación de Guatemala durante el Pleistoceno Terminal y Holoceno. Pages 15–23 in Cano, E.B., and J. C. Schuter, eds., Biodiversidad de Guatemala. Universidad del Valle de Guatemala, Guatemala.

Jestrow, B., B. Peguero, F. Jiménez, R. Verdecia, L. González-Oliva, C. E. Moya, W. Cinea, M. P. Griffith, A. W. Meerow, M. Maunder, and J. Francisco-Ortega. 2017. A conservation framework for the Critically Endangered endemic species of the Caribbean palm *Coccothrinax*. Oryx 52(3): 452–463.

Jin, Y., and H. Qian. 2019. V.Phylomaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42(8): 1353–1359.

JSTOR Global Plants. Accessed 2021–2022. https://www.plants.jstor.org

Kadereit, J. W. 2017. The role of *in situ* species diversification for the evolution of high vascular plant species diversity in the European Alps—a review and interpretation of phylogenetic studies of the endemic flora of the Alps. Perspect. Pl. Ecol., Evol. Syst. 26: 28–38.

Källersjö, M., and B. Stahl. 2003. Phylogeny of Theophrastaceae (Ericales s. lat.). Int. J. Plant Soc. 164(4): 579–591.

Kiel, C. A., T. F. Daniel, and L. A. McDade. 2018. Phylogenetics of New World "justicioids" (Justicieae: Acanthaceae): major lineages morphological patterns, and widespread incongruence with classification. Syst. Bot. 43(2): 459–284.

Kier, G., H. Kreft, T. M. Lee, W. Jetz, P. L. Ibisch, C. Nowicki, J. Mutke, and W. Barthlott. 2009. A global assessment of endemism and species richness across island and mainland regions. Proc. Natl. Acad. Sci. 106(23): 9322–9327.

Lavin, M., M. F. Wojcciechowski, A. Richman, J. Rotella, M. J. Sanderson, and A. B. Matos. 2001. Identifying Tertiary radiations of Fabaceae in the Greater Antilles: alternatives to cladistic vicariance analysis. Int. J. Plant Sci. 162(S6): S53–S76.

Lavin, M., M. F. Wojcciechowski, P. Gasson, C. Hughes, and E. Wheeler. 2003. Phylogeny of robinioid legumes (Fabaceae) revisited: *Coursetia* and *Gliricidia* recircumscribed, and a biogeographical appraisal of the Caribbean endemics. Syst. Bot. 28(2): 387–409.

Lavor, P., A. Calvente, L. M. Versieux, and I. Sanmartin. 2018. Bayesian spatio-temporal reconstruction reveals rapid diversification and Pleistocene range expansion in the widespread columnar cactus *Pilosocereus*. J. Biogeogr. 46(1): 238–250.

Lavor, P., L. M. Versieux, and A. Calvente. 2020. Phylogenetic relationships of *Pilosocereus* (Cactaceae) and taxonomic implications. PlantNow 1(2): 52–70.

Lee, J. C. 2010. From Bloomington, Indiana to Balankanché, Yucatán: Reflections of a naturalist in tropical America. Herpetology 66(2): 113–123.

Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Ann. Rev. Ecol. Evol. Syst. 34(1): 575–604.

Leyden, B. W. 1984. Guatemala forest synthesis after Pleistocene aridity. Proc. Nat. Acad. Sci. 81: 4856–4859.

Liede-Schumann, S., M. Nikolas, U. C. Soares e Silva, A. Rapini, R. D. Mangelsdorff, and U. Meve. 2014. Phylogenetics and biogeography of the genus *Metastelma* (Apocynaceae-Asclepiadoideae, Asclepiadeae: Metastelmatinae). Syst. Bot. 39(2): 594–612.

Lomolino, M. V. 2016. The unifying, fundamental principles of biogeography: understanding Island Life. Front. Biogeogr. 8(2): e29920.

Losos, J. B., and R. E. Ricklefs. 2009. Adaptation and diversification on islands. Nature 457(7231): 830–836.

Luebert, F., and M. Weigend. 2014. Phylogenetic insights into Andean plant diversification. Front. Ecol. Evol. 2(27): 1–17.

Lugo-Hubp, J., J. F. Aceves-Quesada, and R. Espinasa-Pereño. 1992. Rasgos geomorfológicos mayores de la Península de Yucatán. Rev. Mexicana Cienc. Geol. 10(2): 143–150.

Lundell, C. L. 1934. Preliminary sketch of the phytogeography of the Yucatan Peninsula 12 [of Contributions to American Archaeology]. Carnegie Institution of Washington, Washington, D.C.

Majure, L. C., R. Puente, M. P. Griffith, W. S. Judd, P. S. Soltis, and D. E. Soltis. 2012. Phylogeny of *Opuntia* s.s. (Cactaceae): Clade delineation, geographic origins, and reticulate evolution. Amer. J. Bot. 99(5): 847–864.

Mallet, J. 2007. Hybrid speciation. Nat. Rev. 446(7133): 279–283.

Martínez, E., and C. H. Ramos Álvarez. 2007. Un nuevo género de Anacardiaceae de la Península de Yucatán. Acta Bot. Hung. 49(3–4): 35–358.

McDade, L. A., T. F. Daniel, and C. A. Kiel. 2018. The *Tetramerium* lineage (Acanthaceae, Justicieae) revisited: Phylogenetic relationships reveal polyphyly of many New World genera accompanied by rampant evolution of floral morphology. Syst. Bot. 43(1): 97–116.

McDonnell, A., M. Parks, and M. Fishbein. 2018. Multilocus phylogenetics of New World milkweed vines (Apocynaceae, Asclepiadoideae, Gonolobinae). Syst. Bot. 43(1): 77–96.

McVaugh, R. 1987. Flora Novo-Galiciana (Leguminosae) V. University of Michigan Press, Ann Arbor.

McVaugh, R. 1995. Euphorbiacearum sertum Novo-Galicianarum Revisarum. Contr. Univ. Michigan Herb. 20: 173–215.

Mercado Gómez, J. D., and T. Escalante. 2019. Areas of endemism of the Neotropical species of Capparaceae. Biol. J. Linn. Soc. 126(3): 507–520.

Merckx, V. S., K. P. Hendriks, K. K. Beentjes, C. B. Mennes, L. E. Becking, K. T. Peijnenburg, A. Afendy, et al. 2015. Evolution of endemism on a young tropical mountain. Nature 524(7565): 347–350.

Metcalfe, S., A. Breen, M. Murray, P. Furley, A. Fallick, and A. McKenzie. 2009. Environmental change in northern Belize since the latest Pleistocene. J. Quat. Sci. 24 (6): 627–41.

Miller, J. T., V. Terra, C. Riggins, J. E. Ebinger, and D. Seigler. 2017. Molecular phylogenetics of *Parasenegalia* and *Pseudosenegalia* (Fabaceae: Mimosoideae). Syst. Bot. 42(3): 465–469.

Miranda, F. 1958. Estudios acerca de la vegetación. Pages 215–271 in E. Beltrán, ed., Los recursos naturales del Sureste y su Aprovechamiento. Ediciones del Instituto Mexicano de Recursos Naturales Renovables, AC.

Mitchell, D. J., and D. C. Daly. 2015. A revision of *Spondias* L. (Anacardiaceae) in the Neotropics. PhytoKeys 55: 1–92.

Montalvo-Fernández, G., L. F. Sánchez-Teyer, G. Carnevali, A. P. Vovides, R. Gaytán-Legaria, M. M. Ortiz-García, J. A. Muñoz-López, and J. Martínez-Castillo. 2019. Impact of late Pleistocene-Holocene climatic fluctuations on the phylogeographic structure and historical demography of *Zamia prasina* (Cycadales: Zamiaceae). Bot. Sci. 97(4): 588–608.

Montaño-Arias, G., I. Luna-Vega, J. J. Morrone, and D. Espinosa. 2018. Biogeographical identity of the Mesoamerican dominion with emphasis on seasonally dry tropical forests. Phytotaxa 376(6): 277–290.

Moreno, E. J., and M. Manea. 2021. Geodynamic evaluation of the pacific tectonic model for Chortis block evolution using 3D numerical models of subduction. J. S. Am. Earth Sci. 112: 103604.

Morrone, J. J. 2004. *Homología biogeográfica. Las coordenadas espaciales de la vida*. Universidad Nacional Autónoma de México, Mexico.

Morrone, J. J. 2014. Biogeographical regionalisation of the Neotropical region. Zootaxa 3782 (1): 1–110.

Morrone, J. J. 2019. Regionalización biogeográfica y evolución biótica de México: encrucijada de la biodiversidad del Nuevo Mundo. Rev. Mex. Biodivers. 90: e902980.

Morrone, J. J. 2022. When phylogenetics met biogeography: Willi Henning, Lars Brundin and the roots of phylogenetic and cladistic biogeography. Cladistics 39(1): 58–69.

Muschner, V. C., P. M. Zamberlan, S. L. Bonatto, and L. B. Freitas. 2012. Phylogeny, biogeography and divergence times in *Passiflora* (Passifloraceae). Genet. Molec. Biol. 35(4): 1036–1043.

Noguera-Urbano, E. A. 2016. Areas of endemism: travelling through space and the unexplored dimension. System. Biodivers. 14(2): 131–139.

Noroozi, J., A. Talebi, M. Doostmohammadi, S. B. Rumpf, H. P. Linder, and G. M. Schneeweiss. 2018. Hotspots within a global biodiversity hotspot-areas of endemism are associated with high mountain ranges. Sci. Rep. 8(1): 1–10.

Orellana L., R., M. Balam Ku, I. Bañuelos R., E. García de miranda, J. A. González-Iturbe, F. Herrera C., and J. Vidal L. 1999. Atlas de Proceso territoriales de Yucatán. Universidad Autónoma de Yucatán, Yucatán.

Ortega-González, P. F., S. Ríos-Carrasco, C. A. González, N. Bonilla-Cruz, and S. Vázquez-Santana. 2020. *Pilostyles maya*, a novel species from Mexico and the first cleistogamous species in Apodanthaceae (Cucurbitales). Phytotaxa 440(4): 255–267.

Ortiz-Díaz, J. J., I. Arnelas, J. Tun, and J. S. Flores. 2013. *Neomillspaughia emarginata* (Polygonaceae), a new species from Central America. Phytotaxa 144(1): 56–60.

Pennington, R. T., C. E. R. Lehmann, and L. M. Rowland. 2018. Tropical savannas and dry forests. Curr. Biol. 28(9): 527–548.

Pennington, R. T., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forest and Quaternary vegetation changes. J. Biogeogr. 27(2): 261–273.

Pennington, R. T., M. Lavin, and A. Oliveira-Filho. 2009. Woody plant diversity, evolution and ecology in the Tropics: perspectives from seasonally dry tropical forest. Annual Rev. Ecol. 40(19): 437–457.

Perry, E., J. Swift, J. Gamboa, A. Reeve, R. Sanborn, L. Marin, and M. Villasuso. 1989. Geologic and environmental aspects of surface cementation, north coast, Yucatan, Mexico. Geology 17(9): 818–821.

Pezzini, F. F., K. G. Dexter, J. G. de Carvalho-Sobrinho, C. A. Kidner, J. A. Nicholls, L. P. de Queiroz, and R. T. Pennington. 2021. Phylogeny and biogeography of *Ceiba* Mill. (Malvaceae, Bombacoideae). Front. Biogeogr. 13.2, e49226.

Pinzón, J. P., I. Ramírez-Morillo, G. Carnevali, M. H. Barfuss, W. Till, J. Tun, and J. J. Ortíz-Díaz. 2016. Phylogenetics and evolution of the *Tillandsia utriculata* complex (Bromeliaceae, Tillandsioideae) inferred from three plastid DNA markers and the ETS of the nuclear ribosomal DNA. Bot. J. Linn. Soc. 181(3): 362–390.

Porter-Utley, K. 2014. A revision of *Passiflora* L. subgenus *Decaloba* (DC.) Rchb. supersection *Cieca* (Medik.) J.M. MacDougal & Feuillet (Passifloraceae). Phytokeys 43: 1–224.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rambaut, A. 2009. FigTree. Tree figure drawing tool. http://tree.bio.ed.ac.uk/software/figtree/

Ramírez-Barahona, S., A. Torres-Miranda, M. Palacios-Ríos, and I. Luna-Vega. 2009. Historical biogeography of the Yucatan Peninsula, Mexico: a perspective from ferns (Monilophyta) and lycopods (Lycophyta). Biol. J. Linn. Soc. 98(4): 775–786.

Ramírez-Barahona, S., and L. E. Eguiarte. 2013. The role of glacial cycles in promoting genetic diversity in the Neotropics: the case of cloud forest during the Last Glacial Maximum. Ecol. & Evol. 3(3): 725–738.

Ramírez M., I. M., G. Carnevali F. C., and M. F. Chi. 2000. Portraits of Bromeliaceae from the Mexican Yucatan Peninsula-II: A new species of *Tillandsia*. J. Brom. Soc. 50: 62–67.

Ramírez-Morillo, I. M, G. Carnevali, J. P. Pinzón, K. Romero-Soler, N. Raigoza, C. Hornung-Leoni, R. Duno, J. L. Tapia-Muñoz, and I. Echevarría. 2018. Phylogenetic relationships of *Hechtia* (Hechtioideae; Bromeliaceae). Phytotaxa 376(6): 227–253.

Ramos, E. L. 1975. Geological summary of the Yucatan Peninsula. Pages 1056–1095 in A. E. Nairn, and F. G. Stehli, eds., The Gulf of Mexico and the Caribbean. Springer, Boston, Massachusetts.

Rebolledo Camacho, V., L. Jardón Borbolla, I. Ramírez Morillo, A. Vázquez-Lobo, D. Piñero, and P. Delgado. 2018. Genetic variation and dispersal patterns in three varieties of *Pinus caribaea* (Pinaceae) in the Caribbean Basin. Plant Ecol. Evol. 151(1): 61–76.

Renne, P. R., A. L. Deino, F. J. Hilgen, K. F. Kuiper, D. F. Mark, W. S. Mitchell III, L. E. Morgan, R. Mundil, and J. Smit. 2013. Time scales of critical events around the Cretaceous-Paleogene boundary. Science 339(6120): 684–687.

Reyes-García, C., C. Espadas-Manrique, A. García Quintanilla, and M. Tamayo-Chim. 2019. El tren maya ¿Por qué están tan preocupados los biólogos?. Desde el Herbario CICY 11: 119–125.

Rico-Gray, V., and J. G. García-Franco. 1991. The Maya and the vegetation of the Yucatan Peninsula. J. Ethnobiol. 11(1): 135–142.

Rieseberg, L. H., S. C. Kim, R. A. Randell, K. D. Whitney, B. L. Gross, C. Lexer, and K. Clay. 2007. Hybridization and the colonization of novel habitats by annual sunflowers. Genetica 129(2): 149–165.

Rivera-Martínez, R., I. Ramírez-Morillo, J. A. De-Nova, G. Carnevali, J. P. Pinzón, K. J. Romero-Soler, and N. Raigoza. 2022. Spatial phylogenetics in Hechtioideae (Bromeliaceae) reveals recent diversification and dispersal. Bot. Sci. 100(3): 692–709.

Rodríguez, A., and A. Castro-Castro. 2005. Notas sobre *Echeandia pihuamensis*, *E. robusta* y *E. sinaloensis* y estado de conservación de las especies mexicanas. Ibugana 13(1): 3–9.

Rojas-Piña, V., M. E. Olson, L. O. Alvarado-Cárdenas, and L. E. Eguiarte. 2014. Molecular phylogenetics and morphology of *Beaucarnea* (Ruscaceae) as distinct from *Nolina*, and the submersion of *Calibanus* into *Beaucarnea*. Taxon 63(6):1193–1211.

Ruiz-Sánchez, E., C. A. Maya-Lastra, V. W. Steinmann, S. Zamudio, E. Carranza, R. M. Murillo, and J. Rzedowski. 2019. Datataxa: a new script to extract metadata sequence information from Genbank, the Flora of Bajío as case study. Bot. Sci. 97: 754–760.

Runemark, A., J. Hey, B. Hansson, E. I. Svensson. 2012 Vicariance divergence and gene flow among islet populations of an endemic lizard. Mol. Ecol. 21(1):117–129.

Rzedowski, G. C. de, and J. Rzedowski. 2001. Flora fanerogámica del Valle de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico.

Rzedowski, J. 1978. Vegetación de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Limusa, Mexico.

Rzedowski, J. 1991. Diversidad y orígenes de la flora fanerogámica de México. Acta Bot. Mexicana 14: 3–21.

Sánchez-Sánchez, O., G. A. Islebe, P. J. Ramírez-Barajas, and N. Torrescano-Valle. 2015. Conservation and use. Pages 153–167 in G. A. Islebe, B. Schmook, S. Calmé, and J. J. León-Cortés, eds., Biodiversity and conservation of the Yucatán Peninsula. Springer Cham, Heidelberg, New York, Dordrecht, London.

Santiago-Valentin, E., and R. G. Olmstead. 2004. Historical biogeography of Caribbean plants: introduction to current knowledge and possibilities from a phylogenetic perspective. Taxon 53(2): 299–319.

São-Mateus B., W. M. 2018. Filogenia molecular e tempo de divergência em *Harpalyce* (Leguminosae, Papilionoideae) e sinopse taxonômica da sect. Brasilianae. Ph.D. dissertation, Universidad Federal do Rio Grande do Norte, Natal, Brazil.

Saslis-Lagoudakis, C., M. W. Chase, D. N. Robinson, S. J. Russell, and B. B. Klitgaard. 2008. Phylogenetics of neotropical *Platymiscium* (Leguminosae: Dalbergieae): systematics, divergence times, and biogeography inferred from nuclear ribosomal and plastid DNA sequence data. Amer. J. Bot. 95(10): 1270–1286.

Schaefer, H., and S. S. Renner. 2011. Phylogenetic relationships in the order Cucurbitales and a new classification of the gourd family (Cucurbitaceae). Taxon 60(1): 122–138.

Schley, R. J., A. D. Twyford, and R. T. Pennington. 2022. Hybridization: a "double-edged sword" for Neotropical plant diversity. Bot. J. Linn. Soc. 199(1): 331–356.

Seigler, D. S., J. E. Ebinger, and J. T. Miller. 2006. *Mariosousa*, a new segregate genus from *Acacia* s.l. (Fabaceae, Mimosoideae) from central and North America. Novon 16(3): 413–420.

SEINet Portal Network. Accessed 2022. http//:swbiodiversity.org/seinet/index.php

Sharber, W. V. 2018. Systematics, evolution, and biogeography of *Ayenia* (Malvaceae subfamily Byttnerioideae). Ph.D. dissertation, University of Miami, Florida.

Smith, L. B., and R. J. Downs. 1979. Bromelioideae (Bromeliaceae). In T. Zanoni, T. ed., Flora Neotropica. The New York Botanical Garden, New York.

Solano, E., T. Terrazas, J. Reyes-Rivera, and H. Serrano-Casas. 2017. Anatomía comparativa de raíz, tallo, hoja y base del pedúnculo de *Manfreda* (Asparagaceae: Agavoideae). Rev. Mex. Biodivers. 88: 899–911.

Sorensen, A. E. 1986. Seed dispersal by adhesion. Annual Rev. Ecol. Syst. 17: 443–463.

Souza, E. R., G. P. Lewis, F. Forest, A. S. Schnadelbach, C. van den Berg, and L. P. Quieroz. 2013. Phylogeny of *Calliandra* (Leguminosae: Mimosoideae) based on nuclear and plastid molecular markers. Taxon 62(6): 1200–1219.

Sousa, M., S. Sotuyo, and E. Pedraza-Ortega. 2014. Sistemática de *Lonchocarpus* sección *Punctati* (Fabaceae: Millettieae), basada en datos morfológicos y moleculares, con la descripción de nueve especies nuevas. Acta Bot. Mex. 109: 79–131.

Stappen J. V., U. Gama López, P. Dávila, G. Volckaert. 2002. Molecular evidence for the hybrid origin of a new endemic species of *Stylosanthes* Sw. (Fabaceae) from the Mexican Yucatán Peninsula. Bot. J. Linnean Soc. 140(1): 1–13.

Stinnesbeck, S. R., W. Stinnesbeck, E. Frey, J. Aviles Olguin, and A. G. González. 2021. *Xibalbaonyx exinferis* n. sp. (Megalonychidae), a new Pleistocene ground sloth from the Yucatán Peninsula, Mexico. Hist. Biol. 33(10): 1952–1963.

Szabo, B. J., W. C. Ward, A. E. Weidie, and M. J. Brady. 1978. Age and magnitude of the late Pleistocene sea-level rise on the eastern Yucatan Peninsula. Geology 6(12): 713–715.

Torrescano-Valle, N., and G. A. Islebe. 2015. Holocene paleoecology, climate history and human influence in the southwestern Yucatan Peninsula. Rev. Palaeobot. Palynol. 217: 1–8.

Trejo-Torres, J. C., and J. D. Ackerman. 2001. Biogeography of the Antilles based on a parsimony analysis of orchid distributions. J. Biogeogr. 28(6): 775–794.

Tribsch, A., and P. Schönswetter. 2003. Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. Taxon 52(3): 477–497.

Tropicos.org. Missouri Botanical Garden. Accessed 2021–2022. https://tropicos.org

Vargas, R., C. Gardi, M. Angelini, S. Barceló, J. Comerma, C. Cruz Gaistardo, A. Encina Rojas, A. Jones, P. Krasilnikov, M. L. Mendonça Santos Brefin, L. Montanarella, O. Muñiz Ugarte, P. Schad, M. I. Vara Rodríguez, and R. Vargas, eds. 2014. Atlas de suelos de América Latina y el Caribe. Comisión Europea-Oficina de Publicaciones de la Unión Europea.

Wen, J., J. Q. Zhang, Z. L. Nie, Y. Zhong, and H. Sun. 2014. Evolutionary diversifications of plants on the Qinghai-Tibetan Plateau. Front. Genet. 5(4): 1–16.

Willis, C. G., B. F. Franzone, Z. Xi, and C. C. Davis. 2014a. The establishment of Central American migratory corridors and the biogeographic origins of seasonally dry tropical forest in Mexico. Front. Genet. 5(433): 1–14.

Willis, C. G., J. C. Hall, R. Rubio de Casas, T. Y. Wang, and K. Donohue. 2014b. Diversification and the evolution of dispersal ability in the tribe Brassiceae (Brassicaceae). Ann. Bot. 114(8): 1675–1686.

Zizka, A. 2019. Big data suggest migration and bioregion connectivity as crucial for the evolution of Neotropical biodiversity. Front. Biogeogr. 11.2, e.40617.

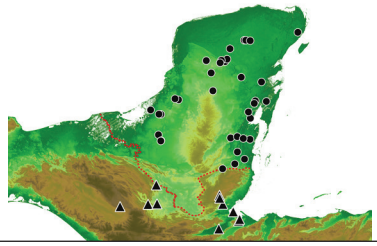
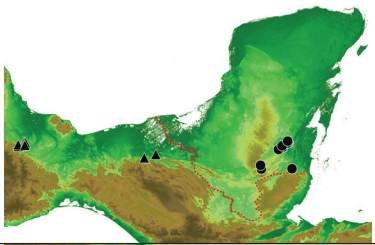
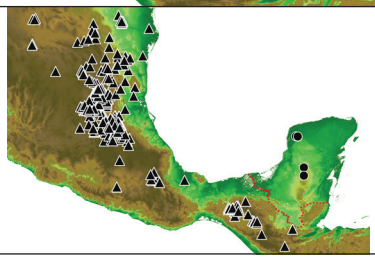
Zona, S. 1990. A monograph of *Sabal* (Arecaceae: Coryphoideae). Aliso 12(4): 583–666.

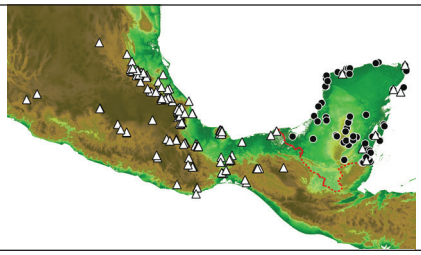
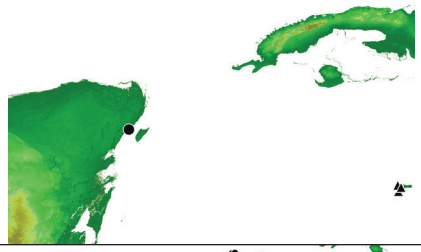
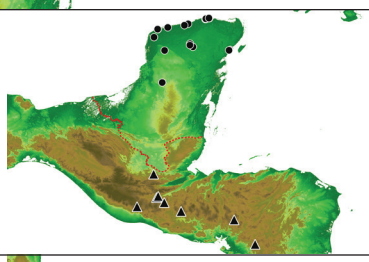
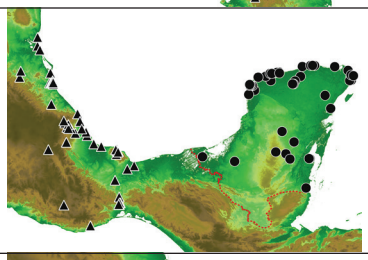
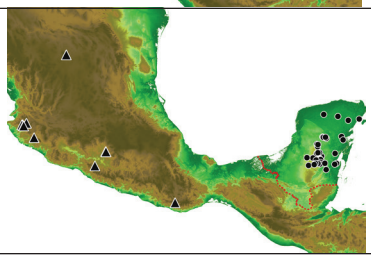
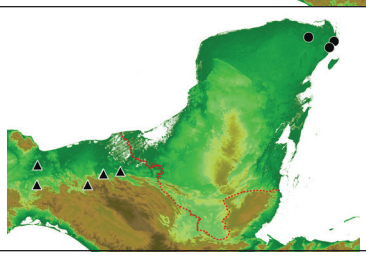
Zona, S. 2002. A revision of *Pseudophoenix*. Palms 46(1): 19–38.

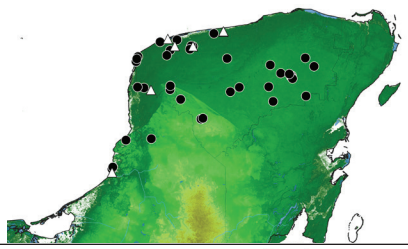
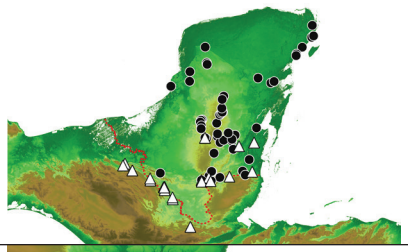
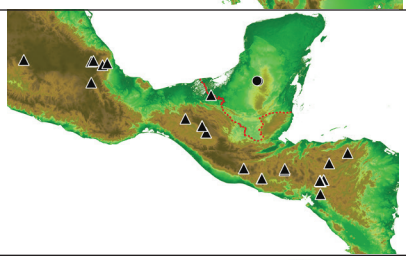
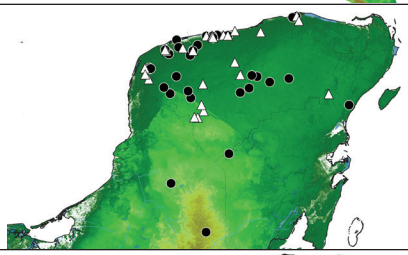
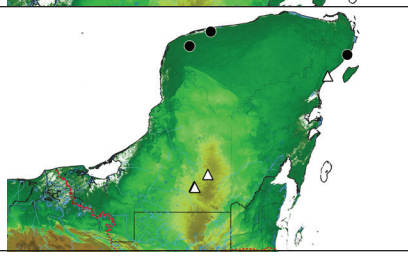
Appendix 1

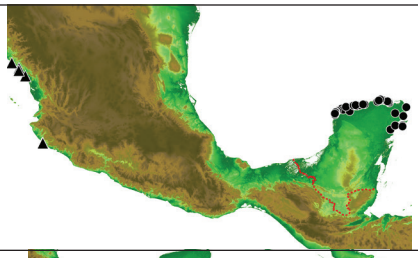
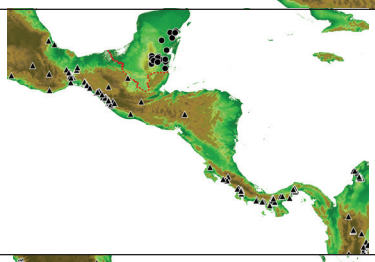
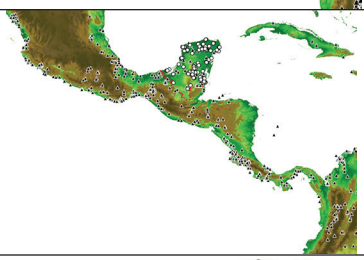
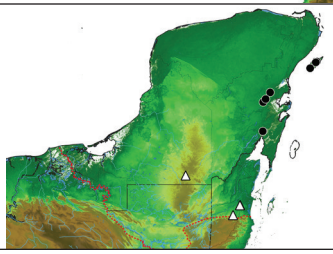
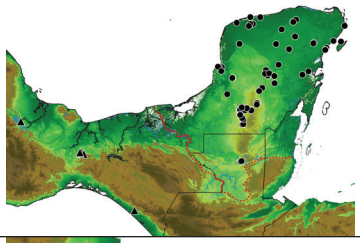
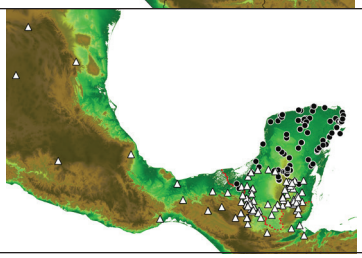
Possible biogeographic hypothesis about origin of YPBP endemic species, according to their phylogenetic relationships and estimated divergences times taken from previous work (values in parenthesis), and according to a phylogenetic reconstruction with the V.Phylomaker package [values in brackets], as well as biological attributes of biogeographical relevance. YPBP endemic or quasiendemic taxa (●) and their sister taxon or taxa (▲), unless otherwise noted when both of them are endemic.

Abbreviations. **Growth forms, (Categories)** ARB = Arborescent, EPI = Epiphyte, HER = Herbaceous, LIA = Liane, SHR = Shrubby, SUC = Succulent; (Subcategories) Cli = Climbing, Palm = Palm, Par = Parasitic, Ros = Rosseted, Shr = Shrubb, Shr-l = Shrubb-like, Suf = Suffrutex, Tree = Tree, Tree-l = Tree-like. **Dispersal syndromes**, ANE = Anemochory, BAL = Balochory, BAR = Barochory, HYD = Hydrochory, ZOO = Zoochory; (Subcategories) Chi = Chiropterophily, Epi = Epizoochory, Mast = Mastocory, My = Myrmecochory, Orn = Ornithophily. **Phylogenetic evidence**, N= Nuclear, C= Chloroplast, BS = Bootstrap, CF= Concordance factors, ML = Maximum Likelihood, MP =Maximum Parsimony, JN = Jacknife, PP = Posterior Probability.

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Zamiaceae *Zamia* ~60 (2/2)	*Zamia prasina* / *Z. variegata* **1.7** (0.74–2.28) **[12.9]**		**SHR** **Shr-l**	**ZOO** **Mast**	Molecular (N+C) Montalvo-Fernández et al., 2019
Arecaceae *Gaussia* 5 (1/1)	*Gaussia maya* / *G. gomez-pompae* **10** (5–17) **[12.97]**		**ARB** **Palm**	**ZOO** **Orn, Chi**	Molecular (N+C) 100 BS / 0.95 PP Cuenca et al., 2007; Cuenca and Asmussen-Lange, 2007
Bromeliaceae *Hechtia* > 90 (1/1)	*Hechtia schottii* / Clade (*H. lepidophylla*, *H. glomerata*, *H. ghiesbreghtii*) ~1 **[24.2]**		**SUC** **Ros**	**BAR**	Molecular (N+C) & Morphology 0.56 PP Ramírez-Morillo et al., 2018; Rivera-Martínez et al., 2022

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Bromeliaceae *Tillandsia* > 650 (21/6)	*Tillandsia dasyliriifolia* / *T. limbata* **[0.02]**		**EPI**	**ANE**	Molecular (N+C) & Morphology >0.85 PP Pinzón et al., 2016; Granados et al., 2017
Bromeliaceae *Wittmackia* 44 (1/1)	*Wittmackia mesoamericana* / *W. caymanensis* **(<0.3)** **[8.26]**		**EPI (Facul)**	**ZOO (Orn)**	Molecular (N+C) & Morphology 43 ML / 0.49 CF Aguirre-Santoro, 2015; Aguirre-Santoro et al., 2016
Nolinaceae *Beaucarnea* ~12 (1/1)	*Beaucarnea pliabilis* / *B. guatemalensis* **[25.7]**		**ARB** **Tree-l**	**ANE**	Molecular © 99 BS / 0.99 PP + (N) 88 BS /1.0 PP Rojas-Piña et al., 2014
Orchidaceae *Myrmecophila* 8 (4/1)	*Myrmecophila christinae* / *M. grandiflora* **[0.91]**		**EPI**	**ANE**	Molecular & Morphology (N) 79 MP Carnevali et al., 2003
Acanthaceae *Carlowrightia* 28 (2/2)	1. *Carlowrightia myriantha* / *Chalarothyrsus amplexicaulis* 2. *Henrya* Clade **5** (3.5–6.8) **[2.54]**		**SHR** **Suf**	**BAL**	1. Molecular 0.95 PP / 89 ML McDade et al., 2018 2. Molecular 100 BS / 89 MP Daniel et al., 2008
Acanthaceae *Justicia* > 700 (22/7)	*Justicia dendropila* / *J. valvata* **[14.3]**		**SHR** **Shr**	**BAL**	Molecular (N+C) (0.98 PP / 51 BS) Kiel et al., 2018

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Apocynaceae *Dictyanthus* 17 (4/2)	*Dictyanthus aeneus* (▲) / *D. yucatanensis* (●) **[15.4]**		**HER** **Cli**	**ANE**	Molecular (N+C) + Morphology 0.99 PP González-Martínez, 2019
Apocynaceae *Matelea* ~100–200 (8/4)	*Matelea gentlei* / *M. micrantha* **[3.32]**		**HER** **Cli**	**ANE**	Molecular (C) 98 ML McDonnell et al., 2018
Apocynaceae *Metastelma* > 70 (4/1)	*Metastelma yucatanense* / *M. schlechtendalii* **[0.19]**		**HER** **Cli**	**ANE**	Molecular (C) Ev_supp Liede-Schumann et al. 2014
Apodanthaceae *Pilostyles* 11 (1/1)	*Pilostyles maya* / *P. mexicana* **[15.08]**		**HER** **Par**	**ND**	Molecular (C) 0.67 PP / 61 BS Ortega-González et al., 2020
Cactaceae *Nopalea* 10 (2/2)	*Nopalea inaperta* (▲) / *N. gaumeri* (●) **1.5** (1–2) **[2.56]**		**SUC** **Shr**	**ZOO**	Molecular (C+N) 0.55 PP / 60 BS Majure et al., 2012; Hernández-Hernández et al., 2014
Celastraceae *Wimmeria* ~15 (4/2)	*Wimmeria lundelliana* (▲) / *W. obtusifolia* (●) **[5.49]**		**ARB** **Tree**	**ANE**	Morphological similarity Carnevali et al., 2009

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Euphorbiaceae *Enriquebeltrania* 2 (1/1)	*Enriquebeltrania crenatifolia* / *E. disjuncta* **17.6** (6.21–32.2) **[22.03]**		**SRH** **Shr**	**ZOO (Myr)**	Molecular (C+N) (100 BS / >0.98 PP) De Nova et al., 2006; Cuevas-Chapa, 2016
Fabaceae *Calliandra* ~135 (6/2)	*Calliandra belizensis* / *C. magdalenae* <2.6 **[20.8]**		**SHR** **Shr**	**BAL**	Molecular (N+C) (0.98 PP / 0.94 BS) Souza et al., 2013
Fabaceae *Gliricidia* 3 (2/1)	*Gliricidia maculata* / *G. sepium* **[0.85]**		**ARB** **Tree**	**BAR**	Molecular (N+C) (99 BS) Lavin et al., 2001, 2003
Fabaceae *Harpalyce* 34 (4/2)	*Harpalyce torresii* (▲) / *H. yucatanense* (●) **[9.78]**		**ARB** **Tree**	**BAL**	Molecular (N) 99 BS / 100 ML São Mateus, 2018
Fabaceae *Lonchocarpus* ~180 (12/3)	*Lonchocarpus yucatanensis* / *L. wendtii* **[6.6]**		**ARB** **Tree**	**ANE**	Molecular (N) (100 PP) Sousa et al., 2014
Fabaceae *Mariosousa* 13 (1/1)	*Mariosousa dolichostachya* / *M. usumacintensis* **[25.1]**		**ARB** **Tree**	**BAR**	Molecular (N+C) (100 BS / 1 PP) Seigler et al., 2006; Miller et al., 2017

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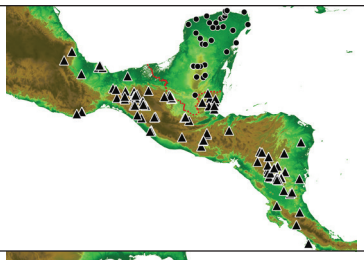
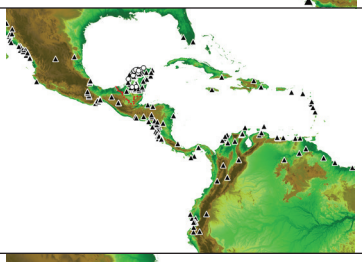
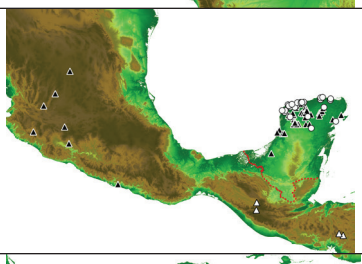
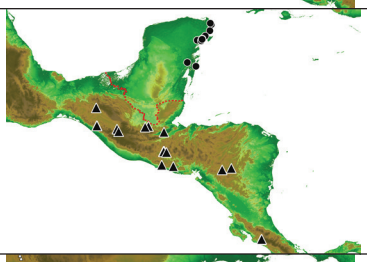
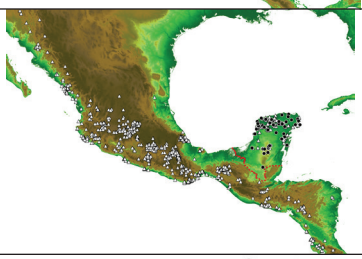
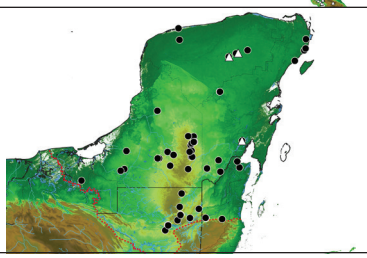
Fabaceae *Platymiscium* ~20 (1/1)	*Platymiscium yucatanum* / *P. dimorphandrum* + *P. jejunum* **<2.5** **[62.36]**		**TREE** **Tree**	**ANE**	Molecular (N+C) + Morphology 96 BS / 1 PP Saslis-Lagoudakis et al., 2008
Malpighiaceae *Malpighia* >50 (8/2)	*Malpighia souzae* / *M. emarginata* + *M. stevensii* **[2.14]**		**SHR** **Shr**	**ZOO**	Molecular (N+C) + Morphology (54 BS) Davis and Anderson, 2010
Malvaceae *Ayenia* ~70 (3/1)	*Ayenia fasciculata* / *A. simulatrix* + *A. abutilifolia* **~2.6** **[9.8]**		**SHR** **Shr**	**BAL / ZOO (EPI)**	Molecular (C) 59 BS Sharber, 2018
Malvaceae *Bakeridesia* ~30 (4/1)	*Bakeridesia yucatana* / *B. nelsonii* **~3** **[6.63]**		**SHR** **Shr**	**ZOO (Epi)**	Molecular (N+C) Donnell et al., 2012; Donnell, 2012; Hoorn et al., 2019
Malvaceae *Ceiba* 18 (2/1)	*Ceiba schottii* / *C. aesculifolia* + one accession of *C. samauma* **7.3** (3.7–11) [3.05]		**TREE** **Tree**	**ANE**	Molecular (N+C) Pezzini et al., 2021
Passifloraceae *Passiflora* ~500 (21/6)	*Passiflora itzensis* (▲) / *P. xiikzodz* (●) **[13.7–6.2*]**		**HER** **Cli**	**ZOO**	Molecular (N) & Morphology Porter-Utley, 2014

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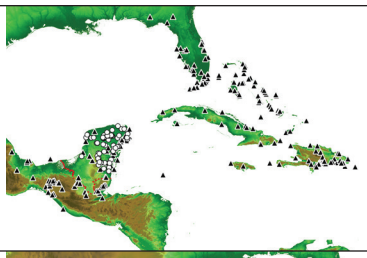
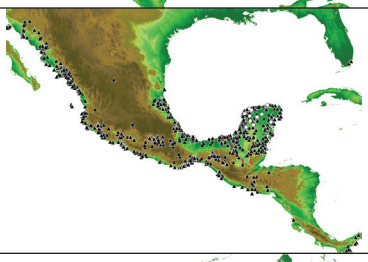
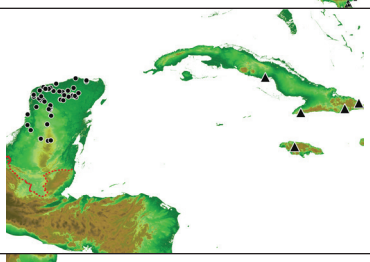
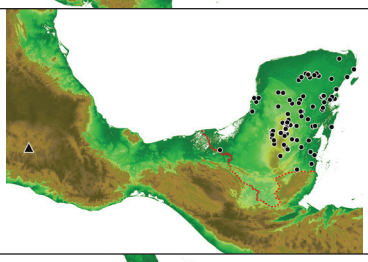
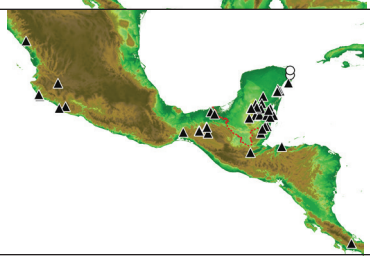
Polygonaceae *Coccoloba* ~150 (14/5)	*Coccoloba spicata* / *C. diversifolia* **[4.5]**		**TREE** **Tree**	**ZOO**	Molecular (N+C) 26 MP / 70 ML Burke et al., 2010
Primulaceae *Bonellia* ~22 (5/3)	*Bonellia flammea* / *B. macrocarpa* **[5.7]**		**SHR** **Shr**	**ZOO**	Molecular (C) & Morphology 91 JN Källersjö and Stahl, 2003
Rubiaceae *Randia* >110 (5/3)	*Randia truncata* / *R. ciliolata* [+ *R. mitis* in Borges et al., 2021] **[1.6]**		**TREE** **Tree**	**ZOO**	Molecular (N+C) 0.99 PP / 98 BS Gustafsson and Persson, 2002; Borges et al., 2021
Sapindaceae *Serjania* ~230 (14/2)	*Serjania yucatanensis* / *Balsas guerrirensis* **[4.3]**		**LIA**	**ANE**	Molecular (N+C) 0.93 PP / 81 BS Acevedo-Rodríguez et al., 2017
Sapindaceae *Thouinia* ~30 (3/1)	*Thouinia paucidentata* / *T. portoricensis* **[12.5]**		**LIA**	**ANE**	Molecular (N+C) 82 BS Acevedo-Rodríguez et al., 2017
Verbenaceae *Citharexylum* ~130 (7/1)	*Citharexylum calvum* / *C. hirtellum* **[2]**		**SHR** **Shr**	**ZOO**	Molecular (N+C) 60 ML / 100 PP Frost et al., 2017; 2020