Title: Evolutionary origins of the Mesoamerican-eastern United States floristic disjunction: current status and future prospects

Gregory W. Stull[1]

[1]Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013, USA,

Email: stullg@si.edu.

Abstract: Biogeographic disjunction patterns, where multiple taxonomic groups are shared between isolated geographic areas, represent excellent systems for investigating the historical assembly of modern biotas as well as fundamental biological processes such as speciation, diversification, niche evolution, and evolutionary responses to climate change. Studies on plant genera disjunct across the Northern Hemisphere (NH), particularly between eastern North America (ENA) and eastern Asia (EAS), have yielded tremendous insight on the geologic history and evolutionary assembly of rich temperate floras. However, one of the most prevalent disjunction patterns involving ENA forests has been largely overlooked: that of taxa disjunct between the eastern US (EUS) and cloud forests of Mesoamerica (MAM), with examples including sugar maple (*Acer saccharum*), dogwood (*Cornus florida*), sweetgum (*Liquidambar styraciflua*), redbud (*Cercis Canadensis*), hop hornbeam (*Ostrya virginiana*), and beechdrops (*Epifagus virginiana*). Despite the remarkable nature of this disjunction pattern, which has been recognized for over 70 years, there have been surprisingly few recent efforts to empirically examine its evolutionary and ecological origins. Here I synthesize previous systematic, paleobotanical, and phylogenetic and phylogeographic studies to establish what is known, and unknown, about this disjunction pattern to provide a roadmap for future research. I argue that this disjunction pattern, and the evolutionary history and fossil record of the Mexican flora more broadly, represents a key missing piece in the broader puzzle of Northern Hemisphere biogeography. I also suggest that the EUS-MAM disjunction pattern represents an excellent system for examining fundamental questions about how plant traits and life history strategies mediate plant evolutionary responses to climate change, and for predicting how broadleaf temperate forests will respond to the ongoing climatic pressures of the Anthropocene.

Keywords: biogeography, cloud forests, eastern United States, geographic disjuncts, Mexico, Northern Hemisphere, phylogeography, temperate forests.

Nearly all plant species show disjunctions in their geographic range, but typically at a relatively small spatial scale that reflects local or regional discontinuities in suitable habitat (Heywood, 1991). When populations, sister species, or clades show disjunctions at a broader geographic scale, this raises important questions about the underlying evolutionary history, especially when particular disjunctions are repeated across numerous taxa (Wood, 1972). Such shared disjunctions offer an unparalleled opportunity to reconstruct how geologic history has shaped the assembly of modern plant communities. More broadly, they also represent excellent systems for studying myriad fundamental processes in ecology and evolution, including speciation and diversification (Xiang et al., 2004; Yang et al., 2018), niche evolution (Wasof et al., 2015; Melton et al., 2022), biotic interactions (Quiroga et al., 2020), community assembly (Donoghue and Smith, 2004; Donoghue, 2008; Manos and Meireles, 2015; Dick and Pennington, 2019; Jiang et al., 2019), and evolutionary responses to climate change over both small and larger time scales (Qian & Ricklefs, 2004; Hamilton and Eckert, 2007; Kuhn et al., 2016).

One of the earliest-recognized and best-studied disjunction patterns concerns temperate plant genera disjunct across continents of the Northern Hemisphere (Boufford and Spongberg, 1983), and particular attention has been paid to disjuncts between the rich temperate forests of eastern North America (ENA) and eastern Asia (EAS; Wen, 1999). However, one of the most prevalent disjunction patterns involving ENA forests has been largely overlooked: that of populations and sister lineages disjunct between the eastern US (EUS) and cloud forests of Mesoamerica (MAM, ranging approximately from central Mexico to northern Costa Rica; Fig 1). This disjunction pattern has been recognized for over 70 years (e.g., Miranda and Sharp, 1950; Braun, 1955), with botanists noting the remarkable presence of numerous mesic temperate taxa of the EUS (e.g., *Carpinus caroliniana*, *Fagus grandifolia*, *Liquidambar styraciflua*) in isolated cloud forests of MAM (Hernández et al., 1951). Despite the remarkable nature of this disjunction, there have been surprisingly few recent efforts to empirically examine its evolutionary and ecological origins. A handful of previous studies provide valuable preliminary insight on the geologic time frame in which the disjunction was formed (e.g., Graham, 1999; Manos and Meireles, 2015), and phylogeographic patterns have been documented for a few taxa (Morris et al., 2008; Ruiz-Sanchez and Ornelas, 2014; Vargas-Rodriguez et al., 2015), but otherwise the evolutionary history of this disjunction pattern remains largely obscure.

On the one hand, the taxonomic extent of this disjunction has not been fully enumerated; most studies on this disjunction note around 10 to 30 examples (e.g., Dressler, 1954; Martin and Harrell, 1957). Furthermore, the vast majority of these disjuncts have not been subjected to close systematic study. Many disjunct populations currently treated as a single species should perhaps be considered separate species; this would have profound conservation implications given the vulnerability of Mesoamerican cloud forests and various EUS plant communities to climate change and human disturbance (Ponce-Reyes et al., 2012; Hamilton et al., 2021). Beyond determining the number of lineages showing this disjunction and clarifying their taxonomic status, we have a poor understanding of precisely when these disjunctions were formed and whether they show concordant temporal/spatial patterns representing shared evolutionary history in response to particular geologic events (e.g., Miocene-Pliocene aridification or Pleistocene glaciation). The extent to which various biological attributes and interactions (e.g., growth form, dispersal mode, pollination mode) have mediated speciation or connectivity between EUS and MAM populations remains essentially unknown. Therefore, collectively, we currently know surprisingly little about the evolutionary history of one of the most prevalent disjunction patterns involving North American forests.

In this review, I provide an overview of this important but understudied disjunction pattern, including a preliminary assessment of the total number of plant taxa showing EUS-MAM disjunctions. I then synthesize insights from relevant systematic, paleobotanical, and molecular studies to establish what is known and unknown about the evolutionary history of EUS-MAM disjuncts, and to suggest critical directions for future work. I argue that this disjunction pattern, and the evolutionary history of the Mexican flora more broadly, represents a key missing piece in the broader puzzle of Northern Hemisphere biogeography, and that the EUS-MAM disjunction pattern in particular represents an excellent system for examining fundamental questions about how plant traits and life history strategies mediate plant evolutionary responses to climate change.

BACKGROUND

Miranda and Sharp (1950) were among the first to fully recognize the remarkable floristic similarities between cloud forests of MAM and the mesic temperate forests of the EUS. They highlighted 50 species shared between these regions representing various life histories and lineages (Appendix 1). Mesic temperate forests of the EUS are relatively broad in extent, in contrast to the cloud forests of MAM, which occur in isolated "islands" throughout the highlands of Mexico and Central America, typically above 1000 meters, where precipitation levels are suitable. Most of these MAM cloud forests rich in EUS temperate elements occur along the Sierra Madre Orientale (SMOr), but they also occur in isolated fragments in the Sierra Madre Occidental (SMOc), Trans-Mexican Volcanic Belt (TMVB), the Sierra Madres del Sur and de Chiapas (SMdS, SMdC), and the Central American Highlands (CAH) (Fig. 2). MAM cloud forests and EUS broadleaf forests are separated by a large arid expanse of grassland and desert ranging across the central and southwestern US and northern Mexico. Since the landmark paper by Miranda and Sharp (1950), there has been considerable interest in this biogeographic pattern, and many have speculated about the evolutionary and geologic history underlying its formation (e.g., Carlson, 1954; Dressler, 1954; Braun, 1955; Martin and Harrell, 1957; Graham, 1973, 1999; Lorenzo et al., 1983; Greller, 1990), but there have been surprisingly few recent empirical studies to explore the evolutionary history of EUS-MAM disjuncts.

TAXONOMIC EXTENT OF THE EUS-MAM DISJUNCTION

To my knowledge, there has been no published attempt to comprehensively review all plant taxa with EUS-MAM disjunctions. Miranda & Sharp (1950) presented 50 spp. of vascular plants present in both regions; however, some of the included species (e.g., *Chimaphila umbellata*, *Equisetum laevigatum*) are broadly distributed, with ranges extending beyond these two defined regions. Most other studies on this disjunction list the same major tree taxa (e.g., *Acer saccharum*, *Carpinus caroliniana*, *Fagus grandifolia*, *Liquidambar styraciflua*). To fill this gap, I generated a near-comprehensive database of flowering plants showing this disjunction (Appendix 1). While the present list is limited to angiosperms, this disjunction has been recognized in other groups of organisms (e.g., monilophytes, lycophytes, bryophytes, fungi, vertebrates; Sharp 1941, 1948; Miranda and Sharp 1950; Martin and Harrell 1957), and hopefully this work will inspire biologists to further examine this disjunction in other major lineages across the tree of life. Among angiosperms, I have identified 97 examples of this disjunction, including 73 species and 24 sister-lineages (either sister species or sister clades), representing 45 families and all major growth forms (Appendix S1). Future work will undoubtedly reveal additional examples.

SYSTEMATICS OF DISJUNCT SPECIES COMPLEXES

Although the majority (~75%) of EUS-MAM disjuncts represent populations currently treated as a single species (see Appendix 1), very few of these disjunct species have been subjected to close systematic and phylogeographic study across their geographic range—exceptions include *Acer saccharum* s.l. (Vargas-Rodriguez et al. 2015), *Liquidambar styraciflua* (Morris et al. 2008; Ruiz-Sanchez & Ornelas 2014), and *Tilia americana* s.l. (McCarthy & Mason-Gamer 2020). Furthermore, the Flora of North America series does not include Mexico, and therefore disjunct populations in MAM cloud forests were generally not factored into considerations of species boundaries of EUS taxa. While some of these disjunct populations do indeed seem morphologically identical (e.g., *Schisandra glabra*; Panero & Aranda 1998), others show considerable, yet often complex, patterns of phenotypic variation across their geographic range—e.g., *Carya spp*. (Manning 1949, 1962; Stone 1962), *Hamamelis spp.* (Bradford and Marsh 1977; Leonard 2006), *Tilia americana s.l*. (McCarthy and Mason-Gamer 2020). Many of the disjunct populations in MAM have also been treated in conflicting ways by different botanists (e.g., Martínez 1940; Bailey et al. 1970; Furlow 1987), as distinct species, subspecies, or varieties (e.g., *Acer skutchii* vs. *Acer saccharum* subsp. *skutchii*), and few of these have been rigorously examined using extensive genomic data, currently available computational tools, and more clearly defined species concepts.

EVOLUTIONARY ORIGINS OF THE EUS-MAM DISJUNCTION

Geologic context and evolutionary scenarios

After the Mid-Miocene Climatic Optimum (~15 Ma), there were significant global and regional changes in temperature and precipitation, with general trends toward cooling and aridification, that clearly had a large impact on the evolution and distribution of plants in the Americas (Strömberg 2005; Graham 2010; Strömberg & McInerney 2011). Cooling temperatures after the Miocene may have prompted southward migration of many warm temperate elements. With the further expansion of arid habitats in the late Miocene (~5.3 mya) and at the end of the Pliocene (~2.6 mya), migratory corridors between temperate broadleaf forests of EUS and MAM may have been disrupted, with broadleaf temperate populations in MAM then being generally confined to upland habitats with sufficient precipitation and cooler temperatures. Climatic fluctuations during Pleistocene glacial cycles, which are known to have broadly impacted species ranges (Davis 1983; Soltis et al. 2006), may also have created opportunities for many mesic temperate lineages to establish in lowland areas of MAM during glacial episodes (Fig. 3), followed by restriction to higher elevation MAM cloud forests during warmer interglacial phases (Martin & Harrell 1957; Vargas-Rodrigez et al. 2015). At present, however, it is largely unclear how different phases and aspects of climate change over the past 15 Ma shaped the formation of EUS-MAM disjunctions. As noted above, Pleistocene glaciation might have also resulted in the reconnection of previously disjunct EUS-MAM populations or the formation of complex patterns of gene flow among intermittently connected MAM populations, or both (Fig. 3). Furthermore, cloud forests of the TMVB or SMdS, for example, might show distinct genetic patterns given their isolation from the SMOr and EUS. While much about EUS-MAM disjuncts remain unknown, the fossil record and previous phylogeographic and phylogenetic studies provide important insights, which I outline below.

The fossil record

The prevailing evidence from the fossil record (e.g., Graham 1999, 2010; Ramírez-Arriaga et al. 2014a, 2014b, 2017) suggests that this disjunction pattern formed after the mid-Miocene, with northern temperate elements (with Paleogene fossil records in the EUS) appearing in MAM palynofloras particularly after the mid-Pliocene. Graham (2010) generally favors a gradual introduction (from north to south) of the temperate elements after the mid-Miocene, and downplays the importance of Pleistocene glaciation in shaping this disjunction given the earlier appearance of genera such as *Alnus*, *Fagus*, *Liquidambar*, and *Ulmus* in the MAM highlands. This fossil evidence is critically important but also, by itself, insufficient for understanding the history of this disjunction in greater detail. Notably, the pre-Pleistocene presence of temperate genera in MAM does not mean that Pleistocene glaciation has not been important for this disjunction pattern: recent range fluctuations in response to glaciation might have resulted in intermittent gene flow between disjunct EUS and MAM populations (Fig. 3), resulting in complex geographic patterns of generic variation across (Vargas-Rodriguez et al. 2015; Ruiz-Sanchez & Ornelas 2014). Most of the relevant paleobotanical studies are also based on fossil pollen, which is advantageous in that captures a regional view of standing vegetation, but disadvantageous in that trees with wind-pollination tend to be over-represented and that pollen often has relatively limited systematic resolution (although this latter issue is somewhat methodologically dependent; Mander and Punyasena, 2014).

Only a small proportion of EUS-MAM disjuncts have useful fossil records and, as noted above, the life history bias of the fossil record prevents us from using the fossil record alone to understand how life history differences might manifest distinct patterns within the broader context of EUS-MAM disjunctions. We might expect species with different life histories or traits (e.g., woody vs. herbaceous, wind vs. animal pollination or dispersal) to show distinct patterns in terms of their dispersibility, rates of phenotypic and niche evolution, and propensity for speciation vs. population connectivity (e.g., Smith and Beaulieu 2009; Vasconcelos, et al. 2021). Furthermore, sampling biases in the fossil record could further mislead inferences of evolutionary history. The USA (as well as Europe and Asia) are better studied from a paleobotanical perspective than Mexico and many other parts of the Neotropics (Xing et al. 2016). As a consequence, the oldest records of various lineages are perhaps more likely to be known from the USA, and younger records from MAM might then be interpreted as evidence for a north-to-south migration pattern. While it does indeed seem likely that north-to-south is the prevailing directionality of migration in this biogeographic pattern, it is important to consider the alternative and, if migration was bidirectional, whether northward vs. southward migrations happened at different times. Also, as appears to be the case with *Liquidambar* (Ruiz-Sanchez & Ornelas 2014), initial migrations from north to south might have been followed by more recent migrations in the opposite direction as populations expanded out of glacial refugia.

It is also important to consider that the EUS-MAM disjunction pattern is part of the broader, and more complex, history of Northern Hemisphere biogeography. Some species or lineages disjunct between EUS-MAM also have sister species in East Asia or WNA (e.g., Cartrema americana, *Hamamelis* spp.). Some Mesoamerican endemics (e.g., *Ticodendron*) have fossil records from the Cenozoic of WNA, Europe, or Asia (Manchester, 2011), and there are multiple lineages currently disjunct between Mesoamerica (or the Neotropics more broadly) and temperate-tropical Asia with rich fossil records in the Northern Hemisphere (e.g., *Engelhardioideae*, *Symplocos*, *Turpinia*; Herrera et al. 2014; Tiffney, 1979; Tiffney et al., 2018;

Huegele and Manchester, 2019). This highlights that Mesoamerica (somewhat like temperate-tropical Asia) represents an important refuge for thermophilic elements of the Cenozoic Boreotropical flora. More broadly, it is clear that the floras of North America and Mesoamerica have been broadly shaped by the dynamic history of floristic exchange across the Northern Hemisphere, as well as within North America and between North America and other parts of the Neotropics (Manos and Meireles, 2015). The EUS-MAM disjunction therefore represents one important, and understudied, component of this broader, complex history of Northern Hemisphere biogeography.

Molecular data

Plant molecular studies relevant to the EUS-MAM geographic disjunction include a comparative study on divergence times of Northern Hemisphere disjuncts (Manos and Meireles 2015) as well as a few of phylogeographic studies of iconic examples of this disjunction pattern: *Acer saccharum* (Vargas-Rodriguez et al., 2015), *Fagus grandifolia* (Morris et al. 2010), *Liquidambar styraciflua* (Morris et al. 2008; Ruiz-Sanchez and Ornelas, 2014). The study by Manos and Meireles (2015) included nine EUS-MAM disjuncts and showed disjunct divergence ranging from 9 to 3 mya, a timeframe generally consistent with the fossil record, supporting the notion that this disjunction pattern was largely formed after the mid-Miocene. It is difficult to draw broad phylogeographic generalizations from the limited number of completed studies, but available data suggests the presence of gene flow among at least some MAM and EUS populations during the Pleistocene, as well as some degree of genetic isolation among different mountainous regions of Mexico (SMOr vs. SMOcc vs. SMdS), consistent with a comparative phylogeographic study on both plant and animal species distributed across MAM cloud forests (Ornelas et al. 2013), which identified phylogeographic breaks also at the Isthmus of Tehuantepec and the Chiapas Central Depression (Fig. 2). Perhaps the most critical take-away from these studies is that many of these disjuncts will likely not show neat geographic patterns in genetic diversity, or at least not strictly at the level of the EUS vs. MAM, and that dense, comprehensive geographic sampling (across both EUS and MAM) is essential for better understanding the dynamic history of plant migration and gene flow across these areas over the past 15 Ma. While this might mean that the EUS-MAM disjunction is not as tidy as, say, the ENA-EAS disjunction in terms of showing discrete geographic divergences, I argue this complexity makes for a richer system to explore the dynamics of plant speciation and migration in response to finer-scale changes in regional and global climate.

CONSERVATION OF NORTH AMERICAN FORESTS

The EUS-MAM disjunction pattern encompasses two biodiversity hotspots, Mesoamerica (Myers et al. 2000) and the North American Coastal Plain (Noss 2015), both of which face serious threats from both habitat loss and climate change (Ramírez-Marcial et al. 2000; Ponce-Reyes et al. 2012; Hamilton et al. 2021). Research on the EUS-MAM disjunction pattern therefore represents a critical framework for understanding the evolutionary history of these biodiverse regions and informing conservation efforts. A better understand the species limits and geographic patterns of genetic diversity of EUS-MAM disjuncts represents one important lens for guiding conservation, which would be complemented by further investigations of spatial phylogenetic patterns across North America (Sosa et al. 2018; Mishler et al. 2020). Despite sharing many species in common, mesic forests of EUS and cloud forests of MAM likely show distinct patterns of phylogenetic diversity and endemism given their differing regional species pools (Dick & Pennington 2019).Yet understanding how biodiversity shared between these regions contributes to their overall spatial phylogenetic patterns will greatly inform our understanding of how these communities were historically assembled and help identify priority regions for conservation (Thornhill et al. 2016; Spalink et al. 2018).

FUTURE DIRECTIONS

Improved phylogeographic and phylogenomic sampling of EUS-MAM disjuncts, across their geographic breadth, will allow for the documentation of previously unrecognized biodiversity and the temporal reconstruction of geographic divergences, aided by improved approaches for divergence dating in phylogeographic and shallow phylogenomic contexts (e.g., Ogilvie et al. 2017; Oaks 2019). Paired with examinations of niche evolution and species distribution models, such datasets will provide excellent insight on the evolutionary history of this disjunction pattern in terms of when it was formed and in response to what climatic pressures. However, there are also exciting opportunities for using EUS-MAM disjuncts as a comparative framework for studying how different traits and life history attributes influence a lineage's ability to disperse and evolve in response to climate change, given than EUS-MAM disjuncts represent a plethora of taxonomic groups, growth forms, and life history strategies (Appendix 1). Another intriguing aspect of this disjunction pattern is that it mirrors some distribution patterns in East and Southeast Asia (Ohsawa, 1993; Osawa and Nitta, 2002), where a temperate flora shifts from the lowlands at higher latitudes to the mountains at lower latitudes. This raises a number of interesting questions: what eco-evolutionary processes and climatic pressures are driving this parallel distribution pattern? Is it generally easier for temperate lineages to move than evolve during episodes of climate change (Donoghue 2008)? Do these temperate lineages lack the traits necessary to survive, or remain competitive, in lowland tropical forests? What biological or ecological contexts have facilitated cases of greater *in situ* evolutionary shifts, or instances of parallel phenotypic evolution in cases where lineages are able to independently shift between climatic zones (Donoghue et al., 2022)?

It is also important to consider how EUS-MAM disjuncts fit into the broader picture of Northern Hemisphere biogeography, given that this distribution pattern is nested within, or intermingled with, other well-established NH disjunction patterns (e.g., ENA-EAS, ENA-WNA). Broader analytical frameworks, including fossil data, will be important for reconstructing unique histories and identifying universal themes concerning the biogeographic history of the NH and beyond. While the fossil Cenozoic fossil records of the USA, Europe, and Asia are relatively well-documented, the fossil record of Mexico and Central America (M/CAM) remains greatly understudied in comparison, although the many completed studies on Mexican paleobotany provide an excellent foundation to build upon (e.g., Cevallos-Ferriz et al., 2012). Further research on the M/CAM fossil record should greatly improve our understanding of the evolution of the remarkably diverse Mesoamerican flora as well as the role of M/CAM as a biogeographic conduit between North and South America during the Cenozoic, which will contribute greatly toward our broader understanding of Northern Hemisphere biogeography.

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attention to the presence of similar distribution patterns of temperate taxa in East and Southeast Asia.

DATA AVAILABILITY STATEMENT

The occurrence data used for Figure 1, obtained from iDigBio (https://idigbio.org), is available here (fill in upon acceptance). The compiled list of EUS-MAM disjuncts is presented in Appendix S1.

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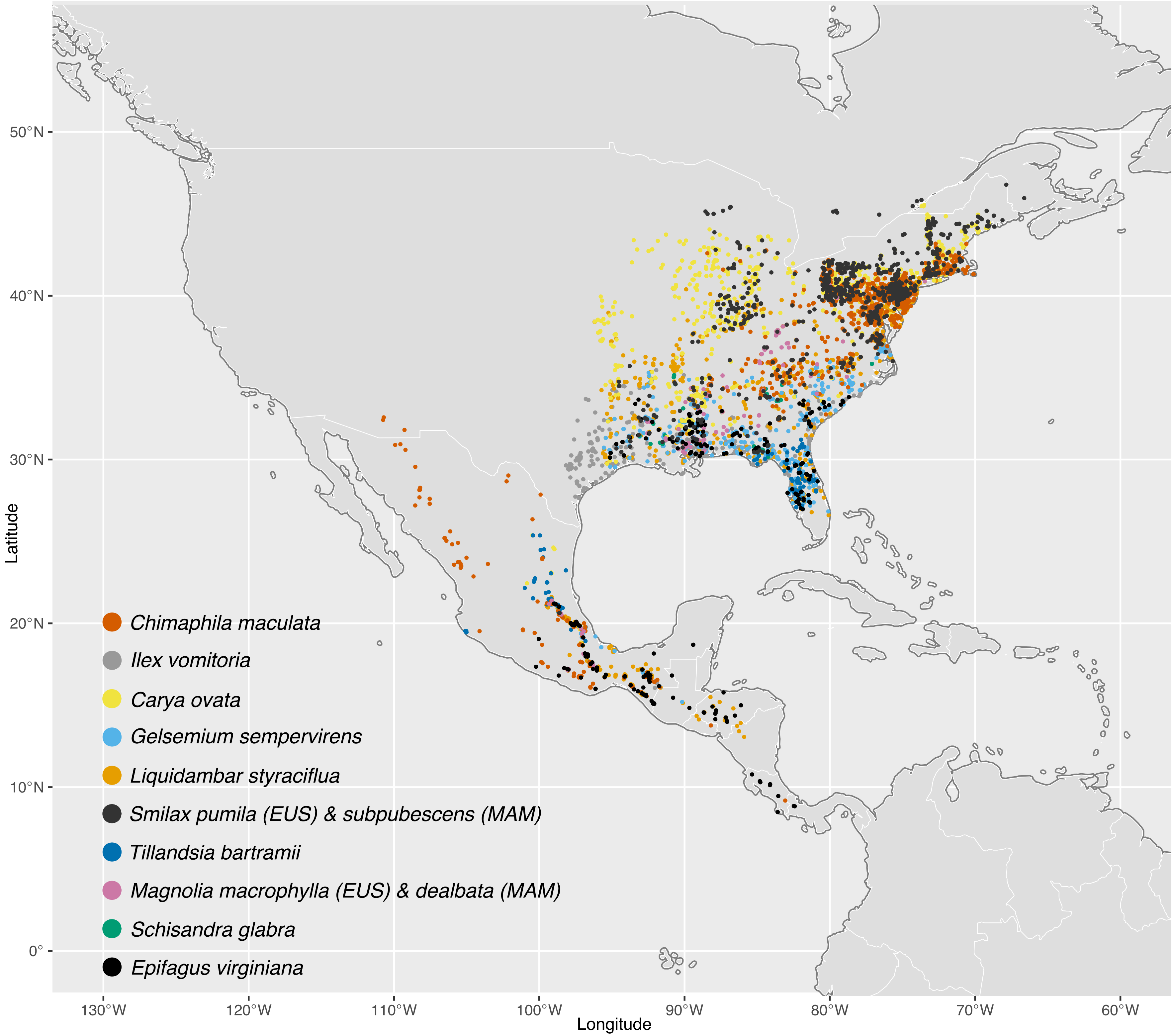
APPENDIX S1. List of lineages showing disjunctions between the eastern USA (in some cases including Canada) and the Mesoamerican highlands. Species included in Miranda and Sharp (1950) are highlighted with an asterisk. This compilation was generated by (1) examining lists from papers on this disjunct pattern as well as general floristic lists from the relevant regions, and (2) by surveying the distributions and sister-species relationships of the species comprising the floras of Appalachia and southeastern North America.

FIGURE CAPTIONS

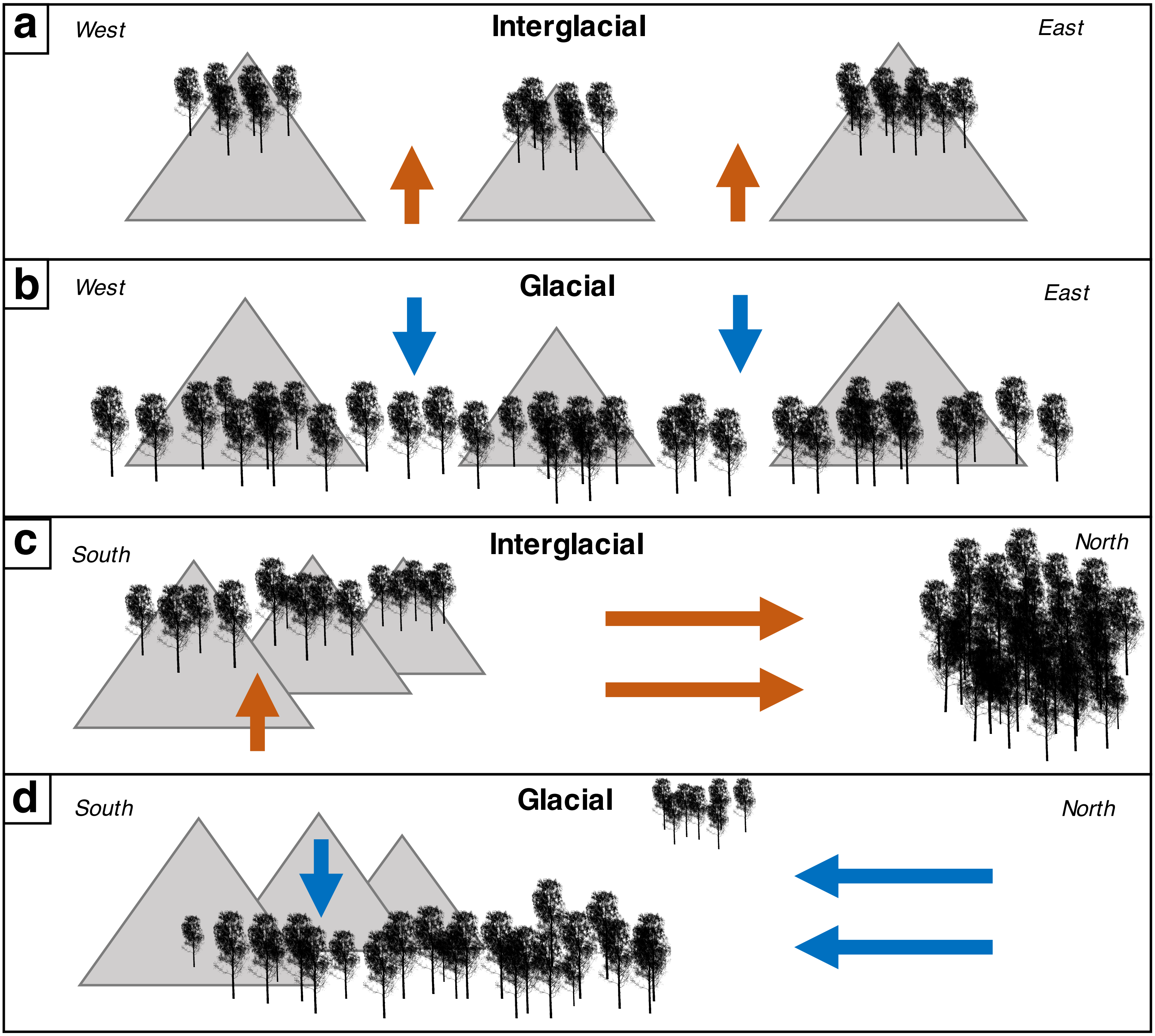
Figure 1. Selected examples of species and sister species with disjunct distributions between the eastern US (extending in Canada in a few cases) and Mesoamerica. Occurrence data was obtained from iDigBio (https://www.idigbio.org) and errant occurrences (determine via comparisons with published distribution maps) were manually removed. Maps were made using ggplot2 (Wickham, 2016) in R version 3.6.1 (R Core Team 2021).

Figure 2. Physical map of North America and Mesoamerica with major mountain ranges and topographic features highlighted. SMOcc = Sierra Madre Occidental; SMOr = Sierra Madre Oriental; TMVB = Trans-Mexican Volcanic Belt; SMdS = Sierra Madre del Sur; SMdC = Sierra Madre de Chiapas; CAH = Central American Highlands.

Figure 3. Schematic of elevational (a, b, c, d) and latitudinal (c, d) distribution shifts of mesic temperate forests during interglacial and glacial phases. Orange and blue arrows show the direction of forest migration during interglacial (upslope) and glacial (downslope) phases, respectively. See Ramírez-Barahona and Eguiarte (2013) and Mastretta-Yanes et al. (2015) for similar conceptual models.


50°N
40°N
30°N
20°N
10°N
0°
Latitude
130°W
120°W
110°W
100°W
90°W
80°W
70°W
60°W
Longitude
Chimaphila maculata
Ilex vomitoria
Carya ovata
Gelsemium sempervirens
Liquidambar styraciflua
Smilax pumila (EUS) & subpubescens (MAM)
Tillandsia bartramii
Magnolia macrophylla (EUS) & dealbata (MAM)
Schisandra glabra
Epifagus virginiana


Chihuahuan Desert
SMOcc
SMOr
Isthmus of Tehuantepec
TMVB
SMdC
SMdS
Chiapas Central Depression
CAH


a
West
Interglacial
East
b
West
Glacial
East
c
South
Interglacial
North
d
South
Glacial
North