



# Biogeography of Neotropical Meliaceae: geological connections, fossil and molecular evidence revisited

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## Abstract

We here provide, first, a general introduction into the woody angiosperm family Meliaceae, including updated numbers of the genera and species found in different parts of the globe, paying attention to geographic centres of diversity and patterns of endemism. Second, and more specifically, we review the latest literature concerning land connections (i) between Eurasia and North America, (ii) between North America and South America, as well as (iii) dispersal paths between Africa and South America that have existed since the proposed evolutionary origin of modern Meliaceae, i.e. from the Upper Cretaceous onwards (ca. 100 Million years ago). Comparing geological evidence with the fossil record as well as biogeographic studies, there is indication that the nowadays pantropically distributed family has made use of all these three routes. Five out of the eight modern Neotropical genera have a fossil record, namely *Carapa* Aubl., *Cedrela* P. Browne, *Guarea* F. Allam., *Swietenia* Jacq., and *Trichilia* P. Browne. *Carapa* and *Trichilia* have a modern transatlantic disjunction (distribution in Africa, Central and South America), and a fossil record in Africa and North/Central America (*Trichilia*), or Africa and Eurasia (*Carapoxylon*). *Cedrela* has a rich fossil record in Eurasia and the Americas. The global decrease in temperatures and a lack of *Cedrela* fossils in North America from the Late Miocene onwards suggest the genus had gone extinct there by that time, leading to its modern distribution in Central and South America. Oligocene to Pliocene fossils of *Guarea*, *Swietenia* and *Trichilia* in Central American key regions support biotic interchange between North and South America at various times.

**Keywords** Angiosperms · Boreotropics · *Cedrela* · Dispersal · Land bridge · South America

## 1 Introduction

The mahogany family, Meliaceae, comprises woody plants widely distributed throughout the tropics and subtropics, occurring occasionally in temperate zones. With ca. 740 species in 58 genera (Table 1 and references therein), Meliaceae is a medium-sized family in Sapindales. The Indo-Malesian region is the geographic centre of diversity,

harbouring ca. 220–223 species in 28 genera (Table 1). Africa-Madagascar is almost as diverse as Indo-Malesia with ca. 205 species in 26 genera, followed by Australasia (ca. 151–152 spp in 22 genera). Interestingly, only eight genera are present in the Neotropics, but they are as diverse as the Africa-Malagasy region as for the number of species (202). The two species-rich Neotropical genera *Trichilia* P. Browne and *Guarea* F. Allam. constitute two recent radiations that have been identified in Meliaceae (Koenen et al. 2015). Concerning endemic genera, six are present in the Neotropics: *Cabrarea* A. Juss., *Cedrela* P. Browne, *Guarea* F. Allam., *Ruagea* H. Karst., *Schmaradua* H. Karst., and *Swietenia* Jacq. Africa-Madagascar harbours the highest number of endemics (20 out of 26 genera; Table 1). In addition, 13 out of these 20 genera are small, having four species or less, such as *Ekebergia* Sparrm. and *Lepidotrichilia* (Harms) T.D. Penn. & Styles, with a few of them being even monospecific (e.g. *Neoguarea* (Harms) E.J.M. Koenen & J.J.de Wilde, *Nymania* Lindb., *Quivisianthe* Baill.). In some cases, such as

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**Table 1** Genera of Meliaceae occurring in each biogeographic region, with indication of the number of species per genus and region

Region	Genera	No spp per genus	No spp per region	References
Neotropics	<i>Cabralea</i> A. Juss	1	1	Pennington et al. (1981)
	<i>Carapa</i> Aubl	29	12	Kenfack et al. (2011), Palacios (2012)
	<i>Cedrela</i> P. Browne	19	19	Muellner et al. (2009a, b), Pennington and Muellner (2010), Köcke et al. (2015), Palacios et al. (2019)
	<i>Guarea</i> F. Allam	70	70	Pennington and Clarkson (2013), Palacios (2016)
	<i>Ruagea</i> H. Karst	15	15	Pennington et al. (2021)
	<i>Schmardaëa</i> H. Karst	1	1	Pennington et al. (1981)
	<i>Swietenia</i> Jacq	3	3	Pennington et al. (1981), Mabberley (2011)
	<i>Trichilia</i> P. Browne	103	81	Pennington (2016)
Total Neotropics	8		202	
Africa-Madagascar	<i>Astrotrichilia</i> <sup>a</sup> (Harms) T. D. Penn. & Styles	13	13	Madagascar Catalogue (2021)
	<i>Calodectarya</i> <sup>a</sup> Leroy	2	2	Madagascar Catalogue (2021)
	<i>Capuronianthus</i> <sup>a</sup> J.-F. Leroy	2	2	Madagascar Catalogue (2021)
	<i>Carapa</i> Aubl	29	17	Kenfack et al. (2011), Fischer et al. (2021)
	<i>Ekebergia</i> <sup>b</sup> Sparrm	4	4	Mabberley (2011, 2017)
	<i>Entandrophragma</i> <sup>b</sup> C. DC	11	11	Mabberley (2011, 2017)
	<i>Heckeldora</i> <sup>2</sup> Pierre	7	7	de Wilde (2007), Koenen and de Wilde (2012)
	<i>Humbertioturraea</i> <sup>a</sup> J.-F. Leroy	7	7	Madagascar Catalogue (2021)
	<i>Khaya</i> A. Juss	5	5	Mabberley (2011, 2017)
	<i>Lepidotrichilia</i> (Harms) T. D. Penn. & Styles	4	4	Mabberley (2011, 2017)
	<i>Leplaea</i> <sup>b</sup> Vermeesen	7	7	Koenen and de Wilde (2012)
	<i>Lovoa</i> <sup>b</sup> Harms	2	2	Mabberley (2011, 2017)
	<i>Malleastrum</i> <sup>a</sup> (Baill.) J.-F. Leroy	24	24	Madagascar Catalogue (2021)
	<i>Melia</i> L	3	1	Mabberley (2017), Sivaraj et al. (2018)
	<i>Naregamia</i> Wight & Arn	2	1	Mabberley (2011, 2017)
	<i>Neobeguea</i> <sup>a</sup> J.-F. Leroy	3	3	Madagascar Catalogue (2021)
	<i>Neoguarea</i> <sup>b</sup> (Harms) E. J. M. Koenen & J. J. de Wilde	1	1	Koenen and de Wilde (2012)
	<i>Nymania</i> <sup>b</sup> Lindb	1	1	Mabberley (2011, 2017)
	<i>Pseudobersama</i> <sup>b</sup> Verdc	1	1	Mabberley (2011), Pennington and Styles (1975)
	<i>Pseudocedrela</i> <sup>b</sup> Harms	1	1	Mabberley (2011, 2017)
	<i>Pterorhachis</i> <sup>b</sup> Harms	2	2	Mabberley (2011, 2017)
	<i>Quivisanthe</i> <sup>a</sup> Baill	1	1	Madagascar Catalogue (2021)
	<i>Trichilia</i> P. Browne	103	22	Pennington (2016)
	<i>Turraea</i> L	ca. 60	ca. 60	Mabberley (2011, 2017)
	<i>Turraeanthus</i> <sup>b</sup> Baill	3	3	Mabberley (2011, 2017)
	<i>Xylocarpus</i> J. Koenig	3	3	Mabberley et al. (1995), Mabberley (2017)
Total Africa-Madagascar	26		ca. 205	

**Table 1** (continued)

Region	Genera	No spp per genus	No spp per region	References
Indo-Malesia	<i>Aglaia</i> Lour	ca. 120	ca. 75	Pannell (1992, 1997, 2004, 2005, 2020), Mabberley et al. (1995), Takeuchi (2000, 2009), POWO (2019), Pannell et al. (2020)
	<i>Anthocarapa</i> Pierre	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Aphanamixis</i> Blume	3	3	Mabberley et al. (1995), Mabberley (2017)
	<i>Azadirachta</i> A. Juss	2	2	Mabberley et al. (1995), Mabberley (2017)
	<i>Chisocheton</i> Blume	ca. 50–53	ca. 38–40	Mabberley (1979, 2003), Mabberley et al. (1995), Wongprasert et al. (2011)
	<i>Chukrasia</i> A. Juss	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Cipadessa</i> Blume	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Didymocheton</i> Blume	43	8	Holzmeyer et al. (2021)
	<i>Dysoxylum</i> Blume ex Raspail	28	22	Holzmeyer et al. (2021)
	<i>Epicharis</i> Blume	7	4	Holzmeyer et al. (2021)
	<i>Goniocheton</i> Blume	4	3	Holzmeyer et al. (2021)
	<i>Heynea</i> Roxb	2	2	Mabberley et al. (1995), Mabberley (2017)
	<i>Lansium</i> Corrêa	3	3	Mabberley et al. (1995), Mabberley (2017)
	<i>Melia</i> L	3	2	Mabberley (2017), Sivaraj et al. (2018)
	<i>Munronia</i> Wight	ca. 5–6	ca. 5–6	Mabberley et al. (1995), Zhang et al. (2009), Cuong et al. (2014)
	<i>Naregamia</i> Wight & Arn	2	1	Mabberley (2011)
	<i>Prasoxylon</i> M. Roem	7	5	Holzmeyer et al. (2021)
	<i>Pseudocarapa</i> Hemsl	5	3	Holzmeyer et al. (2021)
	<i>Pseudoclausena</i> T. Clark	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Reinwardtiodendron</i> Koord	ca. 6–7	6	Mabberley et al. (1995), Mabberley (2017)
	<i>Sandoricum</i> Cav	5	5	Mabberley et al. (1995), Mabberley (2017)
	<i>Sphaerosacme</i> Wall. ex M. Roem	1	1	Pennington and Styles (1975), Mabberley (2011)
	<i>Soymida</i> A. Juss	1	1	Mabberley (2011), Mabberley 2017
	<i>Toona</i> M. Roem	6	6	Mabberley (2011), Rueangruca et al. (2015)
	<i>Turraea</i> L	ca. 60	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Vavaea</i> Benth	4	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Walsura</i> Roxb	16	16	Mabberley et al. (1995), Mabberley (2017)
	<i>Xylocarpus</i> J. Koenig	3	3	Mabberley et al. (1995), Mabberley (2017)
Total Indo-Malesia	28		ca. 220–223	

**Table 1** (continued)

Region	Genera	No spp per genus	No spp per region	References
Australasia	<i>Aglaia</i> Lour	ca. 120	ca. 52	Pannell (1992, 1997, 2004, 2005, 2020), Mabberley et al. (1995), Takeuchi (2000, 2009), POWO (2019), Pannell et al. (2020)
	<i>Anthocarapa</i> Pierre	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Aphanamixis</i> Blume	3	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Azadirachta</i> A. Juss	2	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Chisocheton</i> Blume	ca. 50–53	ca. 15–16	Mabberley (1979), Mabberley et al. (1995)
	<i>Didymocheton</i> Blume	43	39	Holzmeyer et al. (2021)
	<i>Dysoxylum</i> Blume ex Raspail	28	8	Holzmeyer et al. (2021)
	<i>Epicharis</i> Blume	7	4	Holzmeyer et al. (2021)
	<i>Goniocheton</i> Blume	4	2	Holzmeyer et al. (2021)
	<i>Melia</i> L	3	1	Mabberley (2017), Sivaraj et al. (2018)
	<b><i>Owenia</i></b> F.Muell	5	5	Mabberley (2011, 2017)
	<i>Prasoxylon</i> M. Roem	7	4	Holzmeyer et al. (2021)
	<i>Pseudocarapa</i> Hemsl	5	2	Holzmeyer et al. (2021)
	<i>Pseudoclausena</i> T. Clark	1	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Reinwardtiidendron</i> Koord	ca. 6–7	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Sandoricum</i> Cav	5	1	Mabberley et al. (1995), Mabberley (2017)
	<b><i>Synoum</i></b> A. Juss	1	1	Mabberley (2011)
	<i>Toona</i> M. Roem	6	3	Mabberley (2011), Rueangrua et al. (2015)
	<i>Turraea</i> L	ca. 60	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Vavaea</i> Benth	4	4	Mabberley et al. (1995), Mabberley (2017)
	<i>Walsura</i> Roxb	16	1	Mabberley et al. (1995), Mabberley (2017)
	<i>Xylocarpus</i>	3	3	Mabberley et al. (1995), Mabberley (2017)
Total Australasia	22		ca. 151–152	

Genera endemic to one biogeographic region are highlighted in bold

<sup>a</sup>Genera endemic only to Madagascar

<sup>b</sup>Genera endemic only to Africa

for *Ekebergia*, *Neobeguea*, *Nymanina* and *Quivisianthe*, the low number of species might indicate substantial extinction, as they are relatively old genera (older than 30 Million years of age, Myr; Koenen et al. 2015). Indo-Malesia harbours seven endemic genera (*Chukrasia* A. Juss., *Cipadessa* Blume, *Heynea* Roxb., *Lansium* Corrêa, *Munronia* Wight, *Sphaerosacme* Wall. ex M.Roem., and *Soymida* A.Juss.), and Australasia has the lowest number with only two genera being endemic (*Owenia* F. Muell. and *Synoum* A. Juss.).

During the last two decades, enormous progress has been achieved towards resolving the phylogenetic relationships of Meliaceae and several genera within it. The first molecular phylogenetic study of the family (Muellner et al. 2003)

provided support for the recognition of only two subfamilies (Melioidae and Cedreloideae; the latter previously known by the invalid name Swietenioideae (see Thorne 2007)), instead of four, as formerly recognized by Pennington and Styles (1975). Monophyly of the tribes Aglaieae, Sandoricaceae and Melieae, as circumscribed by Pennington and Styles (1975), was demonstrated by Muellner et al. (2008a, b). At the same time, Guareeae was found to be paraphyletic and a complex evolutionary history of Turraeeae, Trichilieae and Vavaeeae was revealed by incongruencies found between plastid and nuclear DNA datasets (Muellner et al. 2008a, b), which was in accordance with their problematic circumscription based on morphology (Pennington and Styles 1975). Koenen et al. (2015) investigated the evolution of

rainforest hyperdiversity using Meliaceae as a case study and provided the latest and most comprehensive phylogenetic analysis of Meliaceae to date, mainly based on datasets of phylogenetic studies by Muellner et al. (2003, 2005, 2006, 2008a, b, 2009a, b, 2010, 2011), Köcke et al. (2013), and Grudinski et al. (2014a, b), but also adding new data. Apart from these, further studies have contributed to disentangle the phylogenetic relationships within several genera of Meliaceae, such as *Aglaiia* (Muellner et al. 2005; Grudinski et al. 2014a, b; Pannell et al. 2020), *Dysoxylum* (Holzmeyer et al. 2021), *Guarea* (Pennington and Clarkson 2013), *Ruagea* (Rojas-Andrés et al. in prep), *Trichilia* (Clarkson et al. 2016), *Cedrela* (Muellner et al. 2009a, b), *Carapa* (Kenfack 2011; Duminil et al. 2012), and *Toona* (Lin et al. 2018), among others.

Ecologically, the species of Meliaceae, being trees and shrubs characterized by their compound leaves (simple in a few genera), grow in a wide variety of habitats, from rain forests to semi-deserts and mangrove swamps. In the Neotropics, most of the species are evergreen (ca. 80%), while others are deciduous, and occur from the sea level up to 3400–3500 m. They are common in lowland rain forests (e.g. *Cabranea*, *Carapa*, *Guarea*, *Trichilia*), as well as in montane rainforests (e.g. *Cabranea*, *Carapa*, *Cedrela*, *Ruagea*), cloud forests of the Andes (e.g. *Ruagea*, *Schmardaea*), and tropical deciduous forests (*Cedrela*, *Swietenia*, *Trichilia*). Species of some genera also occur in gallery forests (*Cabranea*, *Carapa*, *Swietenia*), riparian woodlands (*Carapa*), open dry pastures (*Schmardaea*) and rough scrub or rocky hillsides (*Swietenia*) (Pennington et al. 1981, 2021; Pennington and Muellner-Riehl 2010; Kenfack 2011; Pennington and Clarkson 2013; Pennington 2016).

Dispersal is a crucial ecological process that allows species to expand their range. In Meliaceae, dispersal is achieved by several mechanisms, and all of these are present in the Neotropical Meliaceae. The winged seeds of Cedreloideae are wind-dispersed, while the unwinged seeds of *Carapa* with corky testa are capable of hydrochory and zoochory (Mabberley 2011). In the remaining genera, the arilate or fleshy seeds (e.g. *Guarea*, *Ruagea*, *Trichilia*) are dispersed by birds or mammals (Pennington and Styles 1975).

With the aim of shedding light on the current knowledge about the biogeography of Neotropical Meliaceae, in the following, we first review the latest knowledge concerning land connections and thus potential dispersal paths that existed since the origin of Meliaceae in the Upper Cretaceous (ca. 100 Million years ago, Ma). Then, we review the rich fossil record of those genera nowadays occurring in the Neotropics, as well as the evolutionary and biogeographic studies that have been performed on Meliaceae during the last ca. 20 years. Based on all these

lines of evidence, we shed light on how modern Neotropical taxa may have reached South America from other parts of the world.

## 2 Land connections and dispersal paths

The Neotropical flora is composed of indigenous and immigrant lineages. The first ones were already present in South America when it started separating from Africa about 135–130 Ma (McLoughlin 2001). The immigrant species reached South America from other continents by two main ways: (1) via long-distance dispersal by means of migratory birds, wind, or in natural rafts of soil and vegetation (Renner 2004; Van Duzer and Munz 2004), and (2) through dispersal paths (compare Graham 2018) in the form of continuous land bridges or stepping-stone island chains, such as those that allowed the expansion of the boreotropical flora during the Upper Cretaceous and early Paleogene (Morley 2003; Pennington and Dick 2004). In the following, we will provide an updated review of the literature concerning the geological connections between South America and adjacent regions that have existed since the Upper Cretaceous and that might have been relevant as dispersal paths for megathermal angiosperms to reach South America (Fig. 1).

**Connections between Eurasia and North America** – During the Upper Cretaceous (100–66 Ma), the Northern Hemisphere was divided into two floristic provinces according to pollen types. The Normapolles province in eastern North America and Europe, and the Aquilapollenites province in western North America and Asia (Wolfe 1975). Both provinces were isolated by epicontinental seaways; the Turgai Strait, in the area currently occupied by the Ural Mountains, separated Europe and Siberia; the Mid-Continental seaway, where the High Plains of North America are nowadays, separated western and eastern North America (Tiffney 1985). Towards the latest Cretaceous—early Paleocene, the epicontinental seaways separating the Normapolles and Aquilapollenites provinces started to retreat (Sanmartín et al. 2001; Brikiatis 2014). This, together with the existence of land connections between North America and Eurasia allowed the spread of taxa throughout the Northern Hemisphere giving rise to the “boreotropical flora” (Wolfe 1975; Tiffney 1985; Brikiatis 2014).

*The Beringia dispersal route.* Beringia, defined as the region extending from the Lena River in Russia to the Mackenzie River in Canada, has long been recognized by biogeographers as an important route for biotic exchange (e.g. Hultén 1937; Hopkins 1967; Szalay and McKenna 1971; Sanmartín et al. 2001). Connecting North East Asia and

northwestern North America (Fig. 1), the Bering area served as a dispersal path since its formation in the Upper Cretaceous (ca. 100 Ma), with periods of complete land exposure alternating with those of marine connection between the Arctic and Pacific oceans (Sanmartín et al. 2001; Brikiatis 2014). Thus, plant dispersal was possible until the late Pliocene (3.5 Ma) through a continuous or a discontinuous land bridge (Sanmartín et al. 2001). The Bering route was mostly used by deciduous and temperate plants, while dispersal of megathermal elements of the boreotropical flora was probably more restricted. Winter light was probably a primary limitation for evergreen angiosperms in this area, which was located further north (ca. 75° N) during the K/Pg boundary than it is at present (Tiffney 1985; Morley 2003; Manchester et al. 2009; Brikiatis 2014). On the other hand, the terranes currently forming the southern edge of Alaska have arrived at their current position at different times, with two major events of collision taking place during the Mesozoic (Wrangellia composite terrane) and the Cenozoic (Yakutat terrane) (Trop and Ridgway 2007; Enkelmann et al. 2017). Before accreting, these terranes might have formed a stepping-stone island chain connecting North America with Asia through island chains associated with the Aleutian arc, thus acting as a southern dispersal route for megathermal plants in the Beringian area (Tiffney 1985). Post-Eocene climatic cooling finally restricted the passage of broadleaved evergreen taxa across the Bering land bridge (Tiffney 2000).

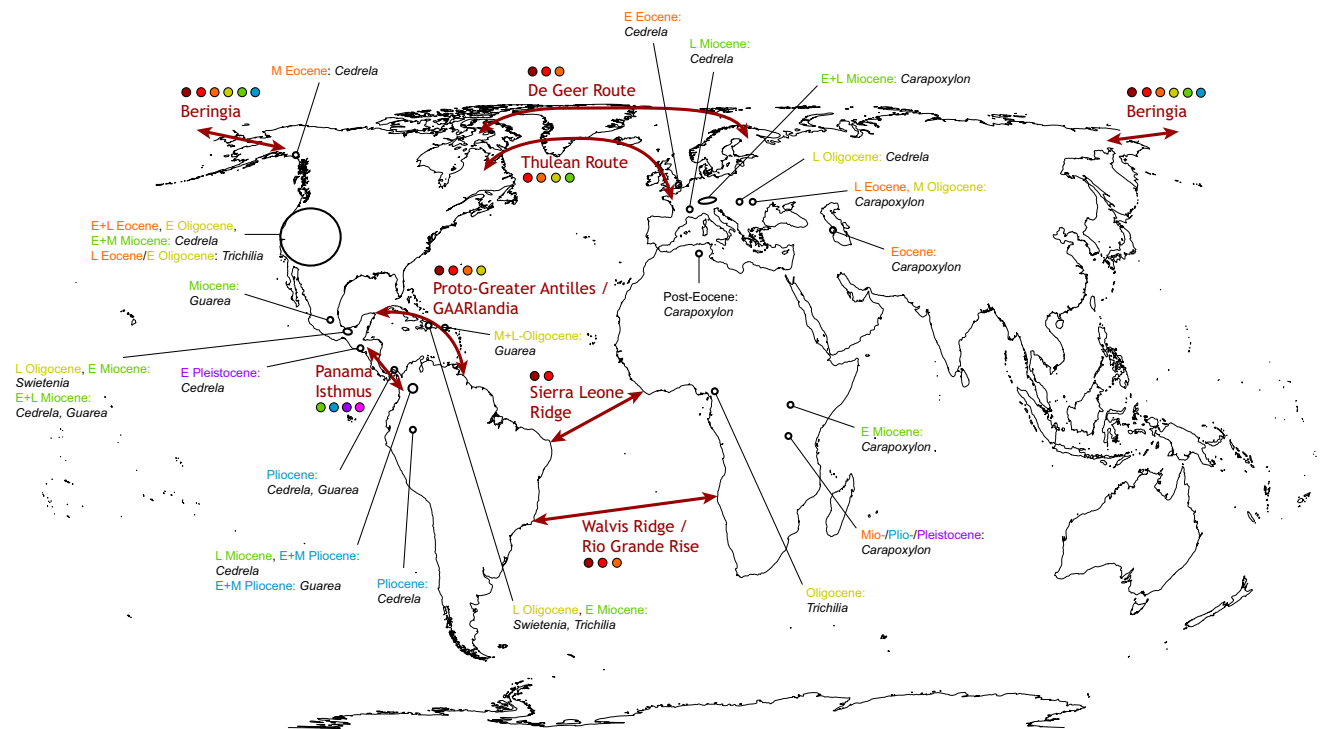
*The North Atlantic land bridges: the De Geer and the Thulean routes.* The De Geer and the Thulean routes constituted two different temporal and geographic land bridges connecting eastern North America and Europe via Greenland (Brikiatis 2014; Fig. 1). The De Geer route was a northerly path joining Northern Scandinavia to North America via a subaerial Barents Shelf, northern Greenland and Queen Elisabeth Islands (Tiffney 1985; Brikiatis 2014). It was terrestrially exposed from the late Maastrichtian to the early Palaeocene (around 71–63 Ma; Brikiatis 2014) and during the Eocene (56–34 Ma), until the areas involved rifted apart in the late Eocene—early Oligocene (Tiffney 1985; Sanmartín et al. 2001). The Thulean route offered a southerly connection to North America from France and the British Isles via the Faroes, Iceland, southern Greenland and Baffin Island (Tiffney 1985; Brikiatis 2014). This area formed a continuous land bridge during two time frames in the late Paleocene (ca. 57 Ma and ca. 56 Ma; Brikiatis 2014) until it was broken in the early Eocene (Tiffney and Manchester 2001). While a continuous land connection between North America and Europe was interrupted in the late Eocene at the latest, some degree of connectivity, probably through island chains, might have allowed floristic exchange of temperate taxa during the Oligocene and Miocene (Tiffney and Manchester 2001). The De Geer route was probably less relevant than the Thulean route for evergreen taxa of the boreotropical flora,

in part because of winter light limitation. This assumption is supported by the presence of only deciduous plants in the early Eocene flora of Ellesmere Island (Tiffney 1985). In addition, the Danish-Polish Through isolated Fennoscandia from the rest of Europe from the early Albian (ca. 113 Ma) to the early Oligocene (ca. 34 Ma) (Rögl 1998; Lehmann et al. 2013). The southern position of the Thulean route and its temporal coincidence with the late Paleocene/early Eocene Thermal Maximum clearly allowed the dispersal of megathermal plant taxa through this route (Morley 2003).

**Connections between North America and South America** – North and South America started to diverge from each other in the Upper Triassic-Lower Jurassic when Gondwana and Laurasia started to rift apart (Pitman et al. 1993). Effective joining of both continents through a continuous land bridge was not complete until the closure of the Isthmus of Panama, at around 3 Ma (O’Dea et al. 2016). However, impermanent connections occurred at different times since the Upper Cretaceous, allowing floristic interchange (Wolfe 1975; Pennington and Dick 2004).

*Proto-Greater Antilles route.* During the late Cretaceous (Campanian; ca. 80 Ma) the leading edge of the Caribbean Plate, which corresponds to the present Greater Antilles and Aves Ridge, formed an island arc connecting Yucatan with South America (Fig. 1). This route, which was at a convergent margin, was subjected to tectonic stress, motion and sea level fluctuations, probably changing from a corridor to a filter to an impasse (Pitman et al. 1993). Vertebrate and pollen fossils provide evidence for the existence of a connection during the late Cretaceous and Paleocene (Morley 2003). This route was interrupted around the middle Eocene (49–39 Ma) when the Caribbean Plate further drifted eastwards (Morley 2003).

*GAARlandia.* Near the Eocene–Oligocene boundary (ca. 33–35 Ma) the leading edge of the Caribbean plate would have formed a large peninsula extending from South America until central Cuba (Iturralde-Vinent and MacPhee 1999). This landspan, called GAARlandia (Greater Antilles + Aves Ridge; Fig. 1), would have been continuous or discontinuous, with some narrow water gaps between islands. On its western edge, it would have been separated from Central America only by two narrow straits, the Havana-Matanzas and the Yucatan channels. The GAARlandia hypothesis has been used to explain the dispersal of plants such as *Styrax* (Styracaceae; Fritsch 2003), *Croton* (Euphorbiaceae; van Ee et al. 2008), and *Ficus* (Moraceae; Pederneiras et al. 2018); and animals such as sloths (MacPhee et al. 2000; Dávalos 2004), rodents (MacPhee et al. 2003; Dávalos 2004), toads (Alonso et al. 2012), and frogs (Moen and Wiens 2009). While the role of GAARlandia in explaining Caribbean



**Fig. 1** World map showing the land connections and dispersal paths that Meliaceae may have used since the Upper Cretaceous, as well as the fossil findings of those Meliaceae genera which have a modern distribution in the Neotropics (see Tables 2, 3, 4, 5, 6 and 7 for details). E, Early; M, Middle; L, Late. Coloured circles above or below the route names indicate the epochs when the routes were available. For details see main text. Dark red: Upper Cretaceous; red: Paleocene; orange: Eocene; dark yellow: Oligocene; green: Miocene; blue: Pliocene; purple: Pleistocene, pink: Holocene. The map uses Equal Earth projection. It was created with R packages ‘rnatualearth’ v. 0.1.0 (South 2017) and ‘sp’ v.1.4–5 (Pebesma and Bivand 2005; Bivand et al. 2013), and modified manually

biogeography of non-flying terrestrial animals remains controversial (Ali 2012), this landspan might have well functioned as a filter connection through an island chain allowing plant dispersal in a stepping-stone manner (Pennington and Dick 2004).

**Panama land bridge.** The most important interchange between the Americas occurred at ca. 3 Ma resulting in an increased dispersal of terrestrial mammals in both directions. This wave of migration, known as the Great American Biotic Interchange (GABI; Simpson 1980; Webb 2006), followed the formation of the Isthmus of Panama (Fig. 1). However, the timing of formation of the Panama Isthmus has been the subject of recent debate (e.g. Stone 2013; Erkens 2015; O’Dea et al. 2016; Jaramillo et al. 2017; Molnar 2017). The classic scenario consists of a relatively rapid rise of the isthmus with a final closure at 4–3 Ma (Coates and Stallard 2013; O’Dea et al. 2016), while other studies found evidence for an earlier formation at around 15–13 Ma or even 25 Ma (e.g. Farris et al. 2011; Montes et al. 2012, 2015; Bacon et al. 2015). According to the model of Montes et al. (2015), marine connections probably occurred through shallow and transient channels, west of where the Panama Canal is nowadays, which would have allowed some degree

of biotic interchange. A recent study provides a revised kinematic reconstruction of the Central American Seaway (CAS) region, reconciling alternative models about the time of the CAS closure (McGirr et al. 2021). According to it, the Isthmus of Panama would have suffered fluctuations in dynamic uplift or subsidence and intermittent shallow-water connections would have existed until the CAS was completely closed at ca. 3 Ma. This is consistent with an earlier availability of the Panama land-bridge for many terrestrial organisms, including plants, for which it has been shown that many lineages already dispersed across the Isthmus of Panama prior to the entire closure of the CAS (Cody et al. 2010).

**Connections between Africa and South America** – Separation of Africa and South America began at about 135–130 Ma with sea-floor spreading in the South Atlantic. At lower latitudes, both continents remained connected along the area of the Benue Trough (in west equatorial Africa) and the North Brazilian Coast until 119–105 Ma (McLoughlin 2001). In spite of an opening Atlantic, numerous plant dispersals between Africa and South America have been documented until the Maastrichtian (ca. 72 Ma) based on

the simultaneous appearance of novel pollen types in both continents (Morley 2003). The frequency of plant dispersals decreased gradually after this time, enhancing provincialism, with crossings taking place even until the Miocene (Morley 2003). Studies on Annonaceae and Asteraceae have invoked this dispersal route to explain current distribution patterns of these plant families (Richardson et al. 2004; Katinas et al. 2013). While the latest dispersal events might have been achieved via sweepstake dispersal, the high frequency of crossings during the Upper Cretaceous and Paleogene suggests the existence of a dispersal route involving the area of the Walvis Ridge/Rio Grande Rise and Sierra Leone Ridges (Fig. 1). According to paleogeographic reconstructions, the currently submerged Walvis Ridge and Rio Grande Rise (between 20° and 30° S) constituted a series of islands and shallow waters in the South Atlantic until the Eocene (40–50 Ma), after continuous land connection had been severed in the early-mid Cretaceous (Parrish 1987; Lawver and Gahagan 2003; Markwick and Valdes 2004; de Oliveira et al. 2009). This route would have allowed plant dispersal in an island-hopping mode.

### 3 Fossil record of Meliaceae in Europe, the Americas, and Africa

Apart from the geological conditions, outlined in detail above, which can potentially favour the arrival of megathermal angiosperms, such as Meliaceae, in the Neotropics, the fossil record provides valuable evidence for actual presence in key regions. First, fossils found in those areas that may have acted as dispersal corridors, such as (former) land connections, provide evidence that a specific route was used at a certain time. Second, gradients of fossil age found e.g. at different latitudes can provide information about dispersal directions (shifts in distribution due to climate change). Third, fossils found in Central and South America provide information when certain taxa were already present in the Neotropics themselves. For Meliaceae with their relatively rich fossil record, there is evidence for all three examples, further detailed in the following.

Out of the eight genera occurring in the Neotropics nowadays (Table 1), five have a known fossil record, namely (in alphabetical order) *Carapa*, *Cedrela*, *Guarea*, *Swietenia*, and *Trichilia* (Tables 2, 3, 4, 5, 6, and 7; due to the large number of fossil findings in Meliaceae, these lists cannot possibly claim to be complete). Out of these genera, hydro- and zoochorous *Carapa* and zoochorous *Trichilia* have a transatlantic disjunction, with a modern distribution in both Africa and South America. Each of them could therefore potentially be used to test biogeographic explanations for this transatlantic disjunction. For both genera, phylogeny-based

biogeographic studies are currently underway (*Trichilia*: Kannan et al. in preparation; *Carapa*: Kenfack et al. in preparation).

Although fossils that exhibit only characteristics of *Carapa* have not been identified to date, wood fossils exhibiting characters shared among several genera of extant Meliaceae, including *Carapa*, have been found in several sites in Eurasia and Africa (*Carapoxylon*, Table 2). The oldest fossil record of *Carapa*'s presumable ancestor, *Carapoxylon*, exhibiting characters shared among modern *Carapa*, *Xylocarpus* and *Entandrophragma*, dates back to the Eocene, Oligocene and Miocene of Africa and Europe (Mädel 1960; Lakhanpal and Prakash 1970; Prakash 1976; Selmeier 1989), pointing towards an Old World origin of the genus.

Extensive paratropical evergreen *Carapoxylon* forests are known from the mid Miocene of Germany (Böhme et al. 2007). The earliest African records of *Carapoxylon* date back to the Oligocene of Algeria (Louvet 1963; Prakash 1976) and to the Miocene of the Congo and Burundi (Lakhanpal and Prakash 1970; Fairon-Demaret et al. 1981; Dupéron-Laudoueneix and Dupéron 1995). Based on the fossil record of *Carapa*'s ancestral lineage, which is confined to the Old World, one may assume that it is more likely that modern Neotropical *Carapa* is derived from an old world stock. Since no fossils of *Carapoxylon* have been found in North America, there is no supporting evidence for the use of Beringia or the De Geer and the Thulean routes (see Sect. 2.1), and thus the use of a boreotropical route to finally arrive in the Neotropics. Long-distance dispersal may thus be viewed as a viable explanation for *Carapa*'s transatlantic disjunction and modern distribution on both continents, Africa, and South America. This is supported by yet unpublished phylogenetic work on the genus (Kenfack et al. in preparation). Until new data are available, it remains speculative whether lineages would have been old enough to also make use of the Walvis Ridge/Rio Grande Rise and Sierra Leone Ridges which would have allowed plant dispersal in an island-hopping mode until the Eocene (see Sect. 2.3).

For the second genus having a transatlantic disjunction, *Trichilia*, the putatively oldest fossil record is from the Eocene–Oligocene boundary of Florissant, Colorado (MacGinitie 1953; Table 7). Interestingly, these fossil leaflets match those of the living *Trichilia havanensis* Jacquin (“the correspondences are exact and leave no doubt as to the correct assignment of the fossil”, MacGinitie 1953, p. 132), a species which in the genus has an isolated phylogenetic position outside the core clade(s) of *Trichilia* (Clarkson et al. 2016, supported by Kannan et al. in preparation) and thus—also based on independent genetic evidence—may be postulated to constitute an early representative of this evolutionary lineage (“living fossil”). Pollen fossils (with putative association to *Trichilia*) are known from



the Oligocene of Cameroon (Salard-Cheboldaeff 1978). Several fossil flowers were found in Dominican amber deposits, the latter being of controversial age (Chambers et al. 2011; Chambers and Poinar 2012a, b). The youngest proposed age is 20–15 Ma (Miocene), based on foraminifera (Iturralde-Vinent and MacPhee 1996), while the oldest proposed age is 45–30 Ma (Eocene–Oligocene), based on coccoliths (Cêpek in Schlee 1990). There is no fossil evidence supporting a boreotropical route through Eurasia. Phylogenetic work currently underway (Kannan et al. in preparation) will provide important clues for putting the fossil record into a bigger biogeographic picture. For example, as for *Carapa*, long-distance dispersal may be invoked as a viable explanation for *Trichilia*'s transatlantic disjunction and modern distribution in both Africa and South America. The fossil record from the Eocene in North America and the Oligocene–Miocene in key regions of Central America further suggests that the genus made use of geological connections provided by GAARlandia, existing near the Eocene–Oligocene boundary (ca. 33–35 Ma; Sect. 2.2), probably in a stepping-stone manner.

A different case is presented by the example of *Cedrela*, for which ample evidence supports the use of a Northern Hemisphere, boreotropical dispersal route (Tables 3 and 4). The genus has a modern distribution in both Central and South America and has been subject to detailed biogeographic reconstruction and investigation of its ecological niche evolution, drawing together independent evidence from both extant species and the fossil record (Muellner et al. 2010; Koecke et al. 2013). These investigations have been facilitated by the fact that—compared to the other genera in Meliaceae—*Cedrela* has an exceptionally rich fossil record, including findings in biogeographic key regions (Tables 3 and 4). The latter include: Eocene fossil findings in Alaska, supporting a potential use of the Bering land bridge; Eocene, Oligocene, and Miocene findings both in different European countries (incl. the British isles) and North America, in line with a potential use of both North Atlantic land bridges (the De Geer and the Thulean routes; see Sect. 2.1); and Miocene, Pliocene and Pleistocene fossil findings across Central America (Mexico, El Salvador, Panama), providing evidence for using the Panama land bridge as dispersal route between North and South America (see Sect. 2.2). The global decrease in temperatures and a lack of *Cedrela* fossils in North America (north of Mexico) from the late Miocene onwards suggests the genus had gone extinct there by that time. The fossil record of *Cedrela* suggests a major biome shift from paratropical conditions into warm-temperate seasonal climates in the early Oligocene of western North America (Koecke et al. 2013). Besides Northern Hemisphere extinctions, the fossil record indicates niche tracking into more southern areas, finally leading to its present distribution restricted to Central and South America. For example,

*Cedrela* species were present in La Quinta (southeastern Mexico, Table 3) and Gatún (Panamanian isthmus, Table 3) by the Miocene and Pliocene, respectively. These Central American fossils occurred in subtropical habitats of wet and seasonal conditions, respectively. The ancestral niche reconstructions and comparison with the fossil record by Koecke et al. (2013) revealed that climatic tolerances of species are less conserved in one clade than in the other. The increase in climatic disparity within one clade follows the major Andean uplift and the Miocene cooling 10–7 Ma (Hoorn et al. 2010). Fossil evidence shows that *Cedrela* was present in South America in the Miocene (fossil from Salto de Tequendama in Colombia, Hooghiemstra et al. 2006), which is in agreement with molecular dating analysis (Koecke et al. 2013; see Sect. 3). The initial Andean uplift (23–10 Ma; Hoorn et al. 2010) provided habitats comparable to those north of the Panamanian isthmus. Furthermore, as outlined further above (Sect. 2.2), the Panamanian isthmus may have already closed much earlier (early Miocene; Farris et al. 2011; Montes et al. 2012) than previously suggested (late Pliocene to early Pleistocene; Bartoli et al. 2005), providing opportunities for the wind-dispersed *Cedrela* to disperse into South America (Koecke et al. 2013).

Evidence of the importance of both, the Proto-Greater Antilles/GAARlandia as well as Panamanian isthmus routes, for biotic interchange between North and South America at various times, is further provided by Oligocene to Pliocene fossils of *Guarea*, *Swietenia* and *Trichilia* in Central American key regions (Tables 5, 6 and 7). Flower fossils of *Trichilia* and *Swietenia* are known from the late Oligocene or early Miocene tropical forests of Hispaniola (Chambers et al. 2011, Chamber and Poinar 2012b; Tables 6 and 7). *Guarea* is known from several fossil sites, ranging from the mid Oligocene of northern Puerto Rico, to the early to late Miocene fossils of Mexico, as well as Pliocene fossils from Panama and Colombia (Table 5).

#### 4 Biogeographic studies on modern Meliaceae

The first global biogeographic study of Meliaceae, based on a generic-level phylogenetic framework and using information from fossils and extant distribution of diversity/endemism, was performed by Muellner et al. (2006). This study indicated that Meliaceae likely were of Gondwanan origin, that dispersal played an important role for Meliaceae to achieve their modern distribution, that the direction of dispersal might have been an “out-of-Africa” scenario with important dispersal routes across Eurasia and between Eurasia and North America provided by Beringia and the North Atlantic land bridge(s), and North America and South America via island chains and/or direct land connections.

**Table 2** Fossil record of the potential early ancestor (*Carapoxylon*) of *Carapa* from Europe and Africa

Stratum, Ma	Location/formation	Literature
Eocene	Peninsula Abşeron, Perekeschkul near Baku, Azerbaijan	Mädel (1960)
Late Eocene	Cluj Limestone formation, Romană Quarry, Mănăştur-Cluj-Napoca locality, Romania	Petrescu (1987)
Middle Oligocene	Zimbor beds, Mesteacănu village, Sălaj County, Romania	Petrescu (1978)
Post-Eocene, probably Oligocene	Tinrhert, Algeria (“Algeria, in the South-Constantinois, 4 h by truck to the east of the Ferkanne oasis, i.e. to the south of Khenchela and to the north of Negrine. The deposit is therefore situated approximately at the southern limit of the Nemen[t]cha mountains”, Louvet, 1963)	Prakash (1976; new combination of former <i>Entandrophramoxylon boureaui</i> by Louvet 1963)
Early Miocene, Late Oligocene (middle Burdigalian), ca. 17.5–17.3	Ortenburg xyloflora, Germany	Böhme et al. (2007), and references therein
Early Miocene, Oligocene, Burdigalian, ca. 18.5	Ortenburg, Ottnang, Germany	Selmeier (1989)
Late early Miocene, Late Karpatian, ca. 17.0–16.3	Southern Franconian Alb xyloflora, Germany	Böhme et al. (2007), and references therein
Late Miocene, Late Karpatian, 17.0 to ~16.3	Randecker Maar, Germany	Mädel (1960)
Early Miocene, probably Burdigalian	Karugamania beds, outcrop at the foot of Bogoro scarp, Lake Albert, Congo	Lakhanpal and Prakash (1970; follow the generic concept of <i>Carapoxylon</i> by Mädel 1960, but fossil may be closer to <i>Entandrophragma</i> than to <i>Carapa</i> )
Miocene, Pliocene, Pleistocene	Cibitoke, Upper Rusizi Valley, Burundi	Fairon-Demaret et al. (1981), Dupéron-Laudoueneix and Dupéron (1995)

As the fossil genus *Carapoxylon* comprises taxa with varying affinities to several extant genera (e.g. *Carapa*, *Xylocarpus*, *Entandrophragma*), only those fossils are given in the list below which show resemblance to *Carapa*. Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. In case fossil age can reliably be attributed to a certain, shorter time frame, age is given in Million years ago (Ma)

Although at that time still based on a limited consideration of the fossil record, Muellner et al. (2006) suggested that populations in North America, Europe, and East Asia were presumably eliminated as tropical climates disappeared from these areas during the Miocene, and were forced to move southwards into more favourable climates, which later was corroborated by more in-depth studies on single genera with a particularly good fossil record, even allowing for the investigation of fossil niche evolution through time, such as *Cedrela* (Muellner et al. 2010; Koecke et al. 2013; see also previous section). The work by Muellner et al. (2006) thus supported the idea that the entry of megathermal (frost-intolerant) angiosperms into southern continents from Oligocene to Pliocene must be considered as an important means of establishing modern pantropical distribution patterns. It is worth to note here that indeed the currently oldest known fossil of Meliaceae is an exceptionally well-preserved fruit from the Upper Cretaceous (79–72 Ma, Campanian) of North America (Atkinson 2020). A family-scale macroevolutionary study by Koenen et al. (2015), focusing on temporal dynamics of evolution of rainforest clades within Meliaceae, suggested that these rainforest clades diversified from the Late Oligocene or Early Miocene onwards, and that

most species-level diversity of Meliaceae in rainforests was rather recent.

Building upon the insights of the family-level study by Muellner et al. (2006), which had hinted at a particularly rich fossil record spanning three continents for *Cedrela*, Muellner et al. (2010) and Koecke et al. (2013) investigated the biogeographic history and evolution of Cedreleae in more detail. Based on molecular clock dating, crown group diversification in *Cedrela* started in the Oligocene/Early Miocene and intensified in the late Miocene and early Pliocene. Interestingly, modern Central American *Cedrela* species do not form a clade, implying re-entry from South America into Central America after the closure of the Panamanian isthmus (Muellner et al. 2010), which is in agreement with the fossil evidence (see Sect. 3). Muellner et al. (2010) mentioned that, while modern *Cedrela* was distributed in both dry and humid habitats, morphological features might suggest an origin in dry forest under seasonal climates, fitting with Miocene and Pliocene *Cedrela* fossils from deciduous forests. This topic was picked up again by Koecke et al. (2013), who investigated also the pre-Miocene fossil record in more detail (see also previous Sect. 3), while at the same time employing an independent niche modelling approach based

**Table 3** Fossil record of *Cedrela* from North and Central America

Stratum, Ma	Formation/location	Literature
Early Eocene, 51–50	Wind River Formation of Northwestern Wyoming, USA	Hickey and Hodges (1975)
Early Eocene, 52–49	Chalk Bluffs, Sierra Nevada, USA	MacGinitie (1941)
Late Middle Eocene, 40.4–37.2	Samovar Hills, Kulthieth Formation, Gulf of Alaska, USA	Wolfe (1977)
Late Eocene, 36.21 ± 0.26	John Day, near Post, Oregon, USA	Manchester and McIntosh (2007)
Eocene–Oligocene boundary, 34	Florissant, Central Rocky Mountain region, Colorado, USA	Brown (1937), MacGinitie (1953), Graham (1993), Manchester (2001)
Early Oligocene, 33.6	John Day, Oregon/Iron Mountain, USA	Meyer and Manchester (1997)
Early Oligocene, 33.6–32.1	John Day, Oregon/Cove Creek, USA	Meyer and Manchester (1997)
Early Oligocene, 32.5	John Day, Oregon/Fossil, USA	Meyer and Manchester (1997)
Early Oligocene, 32.1	John Day, Oregon/Crooked River and Lost Creek, USA	Meyer and Manchester (1997)
Early Miocene, 23–16	La Quinta, near Simojovel, Chiapas, Mexico	Graham (1999)
Early Miocene, 18	Buffalo Canyon, W Nevada, USA	Axelrod (1991)
Early Miocene, 18.5	Middlegate Basin West, Central Nevada, USA	Axelrod (1985)
Early Miocene, 17	Carmel Valley, California, USA	Axelrod (2000)
Late early Miocene, 16	Mascall and Latah, John Day basin, USA	Bestland et al. (2008)
Middle Miocene, 15	Temblor, California, USA	Axelrod (1995, 2000)
Late Miocene	Paraje Solo, Veracruz near San José del Carmen, southeast of Coatzacoalcos, Mexico	Graham (1976)
Middle late Miocene	Salto de Tequendama, Colombia	Hooghiemstra et al. (2006)
Early Pliocene	Subachoque Valley, Cordillera Oriental, Colombia	Hooghiemstra et al. (2006)
Middle Pliocene	Facatativá, Cundinamarca Department, Colombia	Hooghiemstra et al. (2006)
Pliocene	Iquitos region, Peru	Pons and Franceschi (2007)
Pliocene	Gatún, Panama	Graham (1991a)
Early Pleistocene, 2–3	Cuscatlán, Sisimico Valley, El Salvador	Lötschert and Mädler (1975)

Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. In case fossil age can reliably be attributed to a certain, shorter time frame, age is given in Million years ago (Ma)

**Table 4** Fossil record of *Cedrela* from Europe

Stratum, Ma	Formation/location	Literature
Early Eocene	London Tard Clay, UK	Reid and Chandler (1933), Chandler (1964)
Late Oligocene, 28–24	Eger Wind, Vértesszölös and Kesztlölc, Hungary	Hably (2006), Erdei et al. (2007)
Late Miocene	Murat, Cantal, France	Roiron (1991), Legrand (2003)

Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. In case fossil age can reliably be attributed to a certain, shorter time frame, age is given in Million years ago (Ma)

**Table 5** Fossil record of *Guarea* from Central and South America

Stratum, Ma	Formation/location	Literature
Middle to late Oligocene	San Sebastian Formation, northern Puerto Rico	Graham and Jarzen (1969)
Early Miocene	La Quinta Formation in Simojovel, Chiapas, Mexico	Graham (1999)
Late Miocene	Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico	Graham (1976)
Miocene	“Bloque Tlaxcala”, San Esteban Tizatlán, Tlaxcala State, central Mexico	Zayas-Ocelotl et al. (2014)
Pliocene	Gatun Formation, Panama	Graham (1991a, b)
Early Pliocene	Subachoque Valley, Cordillera Oriental, Colombia	Hooghiemstra et al. (2006)
Middle Pliocene	Facatativá, Cundinamarca Department, Colombia	Hooghiemstra et al. (2006)

Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. Age is given in Million years ago (Ma)

**Table 6** Fossil record of *Swietenia* from Central America

Stratum, Ma	Formation/Location	Literature
Late Oligocene-early Miocene	Simojovel de Allende, Chiapas, Mexico	Castaneda-Posadas and Cevallos-Ferriz (2007)
Late Oligocene-early Miocene tropical forests of Hispaniola; controversial dating between 45–30 and 20–15	Mines in the Cordillera Septentrional, between the cities of Puerto Plata and Santiago, Hispaniola, Dominican Republic	Chambers and Poinar (2012a)

Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. Age is given in Million years ago (Ma)

**Table 7** Fossil record of *Trichilia* from Africa and Central America

Stratum, Ma	Formation/Location	Literature
Eocene–Oligocene boundary, 34	Florissant, Central Rocky Mountain region, Colorado, USA	MacGinitie (1953)
Oligocene	Kwa-Kwa drilling site, Cameroon	Salard-Cheboldaëff (1978; “ <i>Ils pourraient représenter le genre Trichilia...</i> ”)
Late Oligocene-early Miocene tropical forests of Hispaniola; controversial dating between 45–30 and 20–15	Mines in the Cordillera Septentrional, between the cities of Puerto Plata and Santiago, Hispaniola, Dominican Republic	Chambers et al. (2011), Chambers and Poinar (2012b)

Fossils with ambiguous taxonomic affiliation to modern taxa were not included in this list. In case fossil age can reliably be attributed to a certain, shorter time frame, age is given in Million years ago (Ma)

on data from extant species of *Cedrela*. In brief, Koecke et al. (2013) found that *Cedrela* experienced a major biome shift from paratropical conditions into warm-temperate seasonal climates already in the early Oligocene of western North America (see Sect. 3). By the Miocene, *Cedrela* extended from North America to northern South America (Fig. 1, Table 3). Diversification in the early evolutionary history was mainly driven by changes in precipitation. Temperature had an increasing impact on ecological diversification of *Cedrela* from the Miocene onwards. Sister-species comparisons revealed that recent speciation events may be related to divergence of climatic tolerances. Koecke et al. (2013) concluded that these results highlight the complexity of climatic niche dynamics, and show how ecological niche conservatism and evolution have acted on different temporal scales and climatic parameters in *Cedrela*.

Apart from the larger-scale geographic analyses mentioned above, several studies on selected modern Neotropical Meliaceae species, or their complexes, have been conducted in the past two decades. Among these are the works by Cavers et al. (2003, 2013) on *Cedrela odorata* L., by Mangaravite et al. (2019) on *C. fissilis* Vell., and by Scotti-Saintagne et al. (2013) on a species complex in *Carapa*. Cavers et al. (2003) studied populations of *Cedrela odorata* in Central America, phylogenetically grouped into three lineages (northern, central and southern), and spatial analysis confirming a deviation from a pattern of isolation by distance. The authors attributed this finding to a likely repeated colonization of Central America from South American source populations. Repeated colonization

of Central America, both from the North and South, is in line with the fossil record as well as the phylogeny of the genus (see further above; Muellner et al. 2010; Koecke et al. 2013; Table 3). What was unknown at the time of publication of the work by Cavers et al. (2003), however, was that “*Cedrela odorata*”, until then believed to be one of the two widespread species in the genus (apart from *C. fissilis*), has multiple independent origins, with at least three species hiding under its name (Muellner et al. 2009a, b, 2010; Pennington and Muellner 2010), rendering the “species” polyphyletic, as delimited back then. This calls for caution when conducting population genetic, phylogeographic work, on extremely widespread tropical species, as they might, in fact, constitute different evolutionary lineages, hard to differentiate morphologically (“cryptic species”). The type of *C. odorata* is from Jamaica, and a specimen from the West Indies fell in a clade with the sequences from El Salvador and Belize, indicating that the Central American accessions represented *C. odorata* in the strict sense (Muellner et al. 2010). Cavers et al. (2013) found evidence of four morphologically cryptic species within *C. odorata*, based on an expanded dataset. These new data supported diversification of *Cedrela* in South America with subsequent recolonization into Central America prior to the formation of the Isthmus of Panama. Cavers et al. (2013) also found within-species phylogeographical divergence across the Andes and within Central America, the latter suggestive of Pleistocene climatic influence. The impact of Quaternary climatic fluctuations on *Cedrela* populations was investigated in more detail by Mangaravite et al. (2019), who combined analyses of

genetic diversity, phylogeographic patterns, and past geographic distributions with a particular focus on highland populations of *C. fissilis*. Different phylogeographic scenarios have been proposed for plants in Neotropical cloud forests during the Last Glacial Maximum based on paleoecological data: the dry refugia hypothesis and the moist forest hypothesis (Ramírez-Barahona and Eguiarte 2013). The habitat suitability projections over the past 140,000 years by Mangaravite et al. (2019) showed less fragmentation relative to the present, indicating a higher connectivity and gene flow. Overall, the results provided support for both the moist forest as well as the dry refugia hypothesis, suggesting a mixture of these processes has acted through space and time. In their work on Neotropical representatives of *Carapa*, Scotti-Saintagne et al. (2013) suggested an Amazonian centre of origin and diversification, with subsequent migration to the Pacific coast of South America and Central America. Their results pointed towards gene flow occurring among species, with introgression supported by the absence of complete lineage sorting between nuclear and chloroplast genomes. Scotti-Saintagne et al. (2013) argued that the lack of phylogeographical structure may be a result of the ineffectiveness of geographical barriers among populations and of reproductive isolation mechanisms among incipient and cryptic species.

## 5 Future perspectives

A careful revision of the entire fossil record of Meliaceae will be an important step into a more comprehensive understanding of the biogeographic history of this nowadays pantropically distributed family, which may serve as a prime example for understanding the evolution of rainforest (and related) taxa on a global scale. Another aim will be to arrive at a complete sampling of the ca. 740 modern species currently recognized in the family for phylogenetic investigations, accompanied by molecular clock dating making use of the rich fossil record. This needs to be complemented by biogeographic reconstructions making use of both, the distribution of modern taxa, as well as the fossil record. Detailed niche reconstructions using the fossil record, so far only accomplished for *Cedrela* (Köcke et al. 2013), need to be expanded to other genera, to understand the relative importance of both, niche conservatism, and niche evolution, for diversification in the family through time until the present, with possible general implications for the future fate of woody tropical lineages. All this will likely only be achievable by a scientific community effort, bringing together researchers from different disciplines, who have a keen interest in Meliaceae evolution. The vision of this longer-term research agenda would be to establish this—also

economically very important—family as a model group for a better understanding of angiosperm evolution.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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