

Chapter 2

Historical Biogeography of the Meliponini (Hymenoptera, Apidae, Apinae) of the Neotropical Region

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The Meliponini have a pantropical distribution (Indo-Australia, the Neotropics and Africa-Madagascar) which includes continental disjunctions unique among the Apidae, revealing a complex history of vicariance events of great antiquity. The trait of disjunction by vicariance permits the inference that Meliponini possibly had their origin on the ancient Gondwanan continent and possess a minimum age near 100 million years (Camargo and Pedro 1992). The oldest known fossil of Meliponini is *Cretotrigona prisca*, from upper Cretaceous New Jersey—USA, c.a. 65–96 Ma (Michener and Grimaldi 1988a, b; Engel 2000).

From a few species (possibly only one that left descendants) which remained isolated in South America, after fragmentation of Gondwana, and final separation of that continent from Africa, came all existing diversity of the Neotropical region,

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Table 2.1 Genera and number of Meliponini species from the Neotropical region (in alphabetical order)

Genus	Number of species
<i>Aparatrigona</i> Moure, 1951	2
<i>Camargoia</i> Moure, 1989	3
<i>Celetrigona</i> Moure, 1950	1
<i>Cephalotrigona</i> Schwarz, 1940	5
<i>Dolichotrigona</i> Moure, 1950	10
<i>Duckeola</i> Moure, 1944	2
<i>Friesella</i> Moure, 1946	1
<i>Frieseomelitta</i> Ihering, 1912	16
<i>Geotrigona</i> Moure, 1943	20
<i>Lestrimelitta</i> Friese, 1903	19
<i>Leurotrigona</i> Moure, 1950	2
<i>Melipona</i> Illiger, 1806	69(+10 ssp.)
<i>Meliwillea</i> Roubik, Lobo and Camargo, 1997	1
<i>Mourella</i> Schwarz, 1946	1
<i>Nannotrigona</i> Cockerell, 1922	10
<i>Nogueirapis</i> Moure, 1953	3
<i>Oxytrigona</i> Cockerell, 1917	8
<i>Parapartamona</i> Schwarz, 1948	7
<i>Paratrigona</i> Schwarz, 1938	29
<i>Paratrigonoides</i> Camargo and Roubik, 2005	1
<i>Partamona</i> Schwarz, 1939	32
<i>Plebeia</i> Schwarz, 1938	38
<i>Proplebeia</i> Michener, 1982 [†]	4
<i>Ptilotrigona</i> Moure, 1951	3
<i>Scaptotrigona</i> Moure, 1942	21
<i>Scaura</i> Schwarz, 1938	5
<i>Schwarziana</i> Moure, 1943	2
<i>Schwarzula</i> Moure, 1946	2
<i>Tetragona</i> Lepeletier and Serville, 1828	13
<i>Tetragonisca</i> Moure, 1946	4
<i>Trichotrigona</i> Camargo and Moure, 1983	1
<i>Trigona</i> Jurine, 1807	32
<i>Trigonisca</i> Moure, 1950	25

[†] extinct genus

which comprises 33 genera, including one that is extinct, *Proplebeia* (Table 2.1), and 391 nominate taxa at the species-group level, following the recent catalog by Camargo and Pedro (2007b).¹

Evolution of Neotropical Meliponini, in isolation since the upper Cretaceous, resulted not only in the abovementioned large taxonomic diversity, but also in a great variety in life histories, for example: species with obligate necrophagic habits, species

¹ The online version <http://moure.cria.org.br/catalogue?id=27560>, updated on 07 February 2012 by SRM Pedro, includes now 412 species (SRMP, personal note)



Fig. 2.1 *Trigona hypogea*, collecting meat at a dead lizard. Photo: provided by D. Wittmann

that cultivate yeast associated with pollen, species having mutualistic relationships with scale insects, etc., in addition to a wide variety of methods used in nest construction.

The obligate necrophagy habit (Fig. 2.1) is known in three species—*Trigona necrophaga*, *T. hypogea*, and *T. crassipes* (Roubik 1982; Camargo and Roubik 1991), the only bees which do not collect pollen (the corbicula is rudimentary in all of them) nor floral nectar; flesh of dead animals is their only protein source (and supply of lipids, carbohydrates and salts); sugars are obtained from ripe or rotting fruit on the ground, extrafloral nectaries, fallen flowers on the ground, etc. (and, possibly, the glycogen obtained from carcasses serves as a glucose source). Collected carrion is transported in the stomach, and regurgitated in storage pots, in the form of a yellowish or greenish jelly which is broken down (probably under the action of digestive enzymes) and mixed with “honey.”

In the storage pots (Fig. 2.2), the proteinaceous paste mixed with honey undergoes the action of the bacteria. In the larval food of *T. necrophaga*, Gilliam et al. (1985) found five species of *Bacillus* with reducing enzymatic activity related to protein and lipid metabolism and hydrolysis of carbohydrates, likely involved in digestion of the animal remains, in addition to production of amino acids and antibiotics. In *T. hypogea*, the pots, after being filled with a proteinaceous substance, mixed with “honey,” are sealed and chemical reactions proceed inside them for 12–16 days (Noll et al. 1996). At the end of this maturation period, “honey” is obtained, free of reduced sugars, almost transparent, good tasting, and rich in free amino acids.

The storage of pollen associated with yeast—*Candida* sp.—is only known in species of the genus *Ptilotrigona*, as reviewed by Camargo et al. (1982, *sic* = 1992)² and Camargo and Pedro (2004). Three species comprise the genus: *Ptilotrigona lurida*,

² SRMP note.



Fig. 2.2 Necrophagous bee nest, *Trigona hypogea* (Itaituba, PA, Brazil); *left*, the storage pots with products derived from meat mixed with “honey”. Photo: J.M.F. Camargo

of wide range in Amazonia, *P. pereneae*, endemic to western Amazonia, and *P. occidentalis*, which occurs from northwestern Ecuador to Darién and an isolated population in the area of the Osa Peninsula in Costa Rica (Camargo and Pedro 2004). The studies were made with *P. lurida*, for which dozens of nests were observed (Fig. 2.3).

Pots containing “honey” or sweet liquids are rare or even absent in the nests, while pollen pots, associated with yeast (Fig. 2.4) are found in great number (in one of the three nests studied there was about 3.0 kg of pollen). The activity of yeast promotes the desiccation and stored life of the pollen; it makes pollen dry enough that it can produce a wrinkling and deformation of the pots.

Another interesting aspect, still lacking complementary studies, is that utilization of resins (principally floral resins of the genus *Clusia*), collected by these bees and added to cerumen used for construction of storage pots and brood cells, is that it has bactericidal activity, but no fungicidal effect. The action of such resins can promote the growth of yeast free of bacteria (Lokvam and Braddock 1999; Camargo and Pedro 2004). It is only suggested but not proven, even now, that a part of the sugars, used by bees, may be derived from the metabolic activity of the yeast.

Associations between certain species of Meliponini and free-living phytophagous hemipterans, which make sugar secretions (honeydew), are well known, but their mutualistic associations with sedentary hemipterans, coccids, are known only among species of the genus *Schwarzula* (Camargo and Pedro 2002). Silvestri (1902)

³*sic*, = *Schwarzula timida*. *Scaura timida* was entered by error in the original text (Pedro SRM, personal communication).



Fig. 2.3 Nest of *Ptilotrigona lurida* (Camanaus, AM, Brazil); in the lower portion a large mass of pots can be seen, where the pollen associated with yeast is stored. Photo: J.M.F. Camargo

was the first to suspect mutualism between *Scaura timida*³ and scale insects, but detailed observations only were made by Camargo and Pedro (2002), who observed dozens of nests of *Schwarzula coccidophila*, residing in galleries excavated by the larva of the moth *Cossula* sp. (Cossidae) in the branches of *Campsiandra angustifolia* (Caesalpinaceae), on the banks of the Rio Negro, Amazonas state, Brazil. The scale insects (*Cryptostigma* sp.) are found attached to the gallery walls, in the nest interior, where they receive protection and care from the bees (Fig. 2.5), and, in exchange, offer sweet secretions and additional wax the bees use in nest construc-

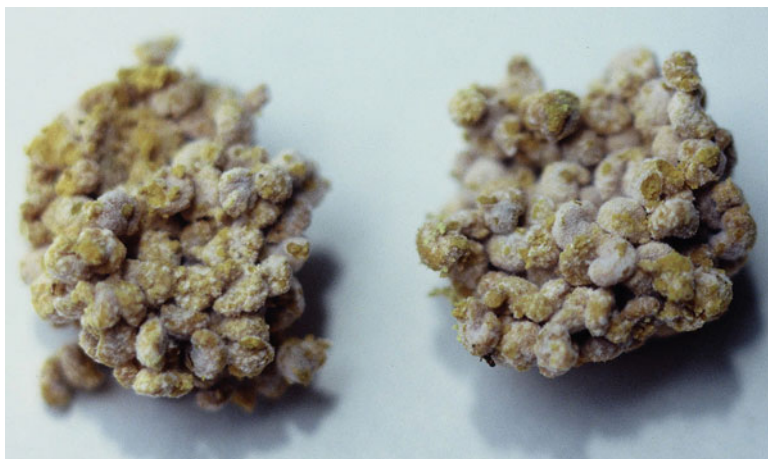


Fig. 2.4 *Ptilotrigona lurida*, closeup of pollen covered with yeast. Photo: J.M.F. Camargo



Fig. 2.5 *Schwarzula coccidophila*, closeup of the scale insects—*Cryptostigma* sp.—in the nest interior, being attended by a bee (Tapurucuara-Mirim, AM, Brazil). Photo: J.M.F. Camargo

tion. The secretions are a subproduct of sap from the plant, on which the scale insects feed. When stimulated by attending bees, the scale insects liberate, through the anus, a small droplet of the sugary liquid, which is ingested by the attendant. These bees are the only known species which have, within their own nest, a permanent source of carbohydrates, in addition to additional wax for building. Only pollen is collected at flowers (Camargo and Pedro 2002).

Another extraordinary behavior is found in *Trichotrigona extranea* (Fig. 2.6), a monotypic genus and until now only known from a single locality, in the middle



Fig. 2.6 Nest of *Trichotrigona extranea*, a bee that does not build storage pots and does not store any kind of food; closeup of brood cells (Samaúma, AM, Brazil). Photo: J.M.F. Camargo

Rio Negro region of Amazonas, Brazil. The colonies are very small, with less than 200 adults, located in small cavities in dead branches (of *Buchenavia suaveolens*); they construct no storage pots and do not store food of any kind. It is likely these bees are cleptobiotic, but not in the manner of *Lestrimelitta*, which robs, during mass raids, the food stores of a host and transfers them to the storage pots of its own nest. Supposedly, the workers (and also possibly the males) of *T. extranea*, individually use and have free access to the food stores of the host species (perhaps of *Frieseomelitta*, very common in the region and sharing nest habits similar to those of *Trichotrigona*; Camargo and Pedro 2007a).

There exists, also, a great diversity in nest architecture, ranging from subterranean, with complex structures for the control of humidity and air circulation, to



Fig. 2.7 Nest aggregation of *Partamona batesi*, in active termite nest (*Nasutitermes acangussu*); endemic in the Tefé region, central Amazonia, Brazil. Photo: J.M.F. Camargo

nests in tree cavities, within the nests of other social insects, such as termites and ants, to exposed arboreal nests. Among these, species of the genus *Partamona* are noteworthy, which are among the most formidable nest builders known, primarily considering the nest entrance structures (Figs. 2.7 and 2.8), conspicuous and richly ornamented, which “facilitate” recognition of the nest and function as true flight targets (several of these species—like *P. batesi*, Figs. 2.7 and 2.8a—construct nests in large aggregations, with the nest entrances very close to each other).

The nest of *P. vicina*, of Amazonas state, is one of the most sophisticated known (Fig. 2.9); the nest entrance structure (Fig. 2.9a) opens upon a wide chamber or vestibule, filled with a structure similar to intertwined roots, constructed with earth and resin (Fig. 2.9b), forming a large labyrinth, where workers stay and constitute

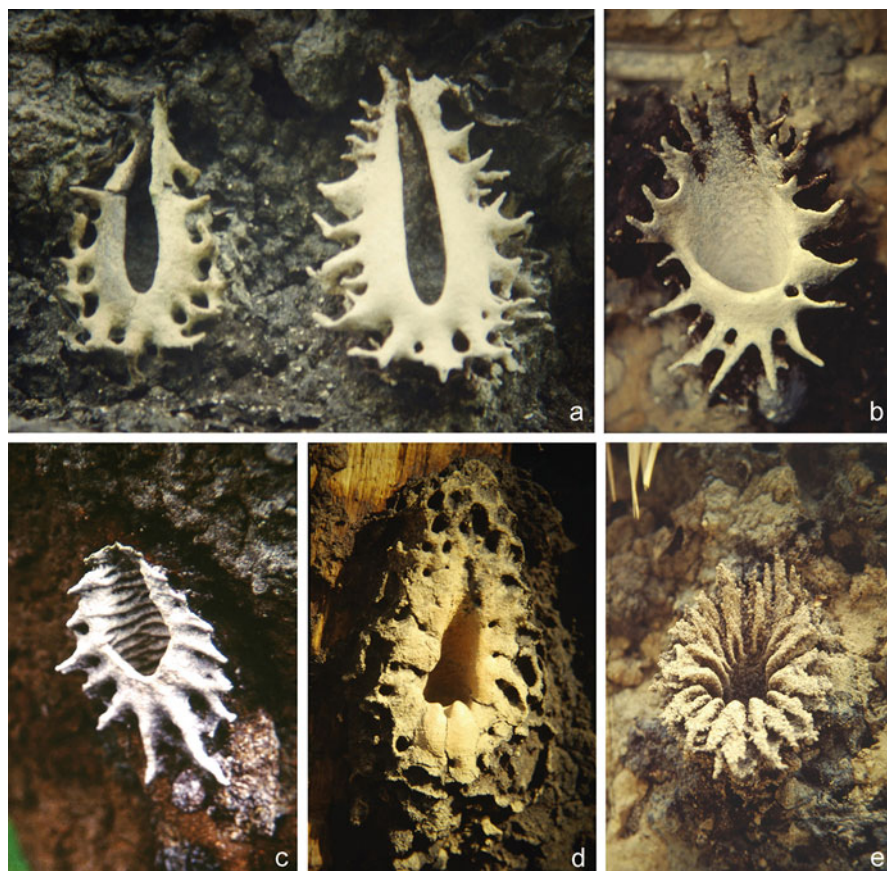


Fig. 2.8 Nest entrances of *Partamona*; (a) *P. batesi* (endemic in the Tefé region); (b) *P. gregaria* (endemic in the region of lower Tapajós); (c) *P. pearsoni* (endemic to north of the Amazon/Negro rivers); (d) *P. chapadicola* (endemic to Maranhão—eastern Pará); (e) *P. vicina* (of wide Amazonian distribution). Photo: J.M.F. Camargo

the first force of nest defense; the vestibule is connected, through a small tunnel, to a second cavity or atrium (Fig. 2.9c), filled with waxy lamellae, cells and small pots, generally containing an acidic liquid, constituting a typical “false nest.” From this “false nest,” there is a small tunnel leading to the true nest, where the brood and food are located (Fig. 2.9d), and their various satellite chambers—containing honey pots. The entire assemblage of structures and chambers is important in nest defense, against invasions of other insects, primarily cleptobiotic social insects, such as *Lestrimelitta* spp., for example (cf. Camargo and Pedro 2003).

There exists, also, a great diversity in form and size, from the robust *Melipona fuliginosa*, ca. 11.0–13.0 mm in length, to the minuscule *Leurotrigona pusilla*, ca. 2.0 mm in length (Fig. 2.10).

Some species of Meliponini are exploited, economically, since pre-Colombian times. Some native peoples of South America, such as the Kayapós, from southern



Fig. 2.9 Nest of *Partamona vicina*, in active termite nest (*Amitermes excellens*); (a) entrance; (b) vestibule/labyrinth, where the defense force is located; (c) atrium/false nest; (d) true nest, with brood cells, food storage pots, etc. (Muçum, Tapajós, PA, Brazil). Photo: J.M.F. Camargo

Pará, Brazil (Fig. 2.11), make varied use of the products from these bees, in food, medicine, ritual, tool making, etc., and also as a model for social organization for their own communities (cf. Posey and Camargo 1985; Camargo and Posey 1990).

The causes of this diversification, especially taxonomic, in the Neotropical region, have been the subject of many speculations. Through the decades of 1960–1970 the postulate of ecological “refuges” emerged. This postulate attempted to associate the known pattern of endemism and speciation in Amazonia with climatic cycles (glacial and interglacial) in the recent quaternary. Although this attempt, a priori, can explain some of the current distribution patterns, it barely touches the problem of the history of the taxa; it only deals with regional fragments of recent history.



Fig. 2.10 Nest of *Leurotrigona pusilla* (Curicuriari, AM, Brazil), in a gallery made by a beetle. This is the smallest known meliponine (body length ca. 2.0 mm). The nest is of ca. 4 cm in length. Photo: J.M.F. Camargo



Fig. 2.11 Kayapó Indians (Gorotire, PA, Brazil), on a trip to collect meliponine nests. These Indians are bee experts. Photo: J.M.F. Camargo

Only recently, some work based on the methods conceived in phylogenetic systematics and vicariance biogeography, involving monophyletic taxa, with large ranges in the Neotropical region, permit access to some periods of evolutionary history/

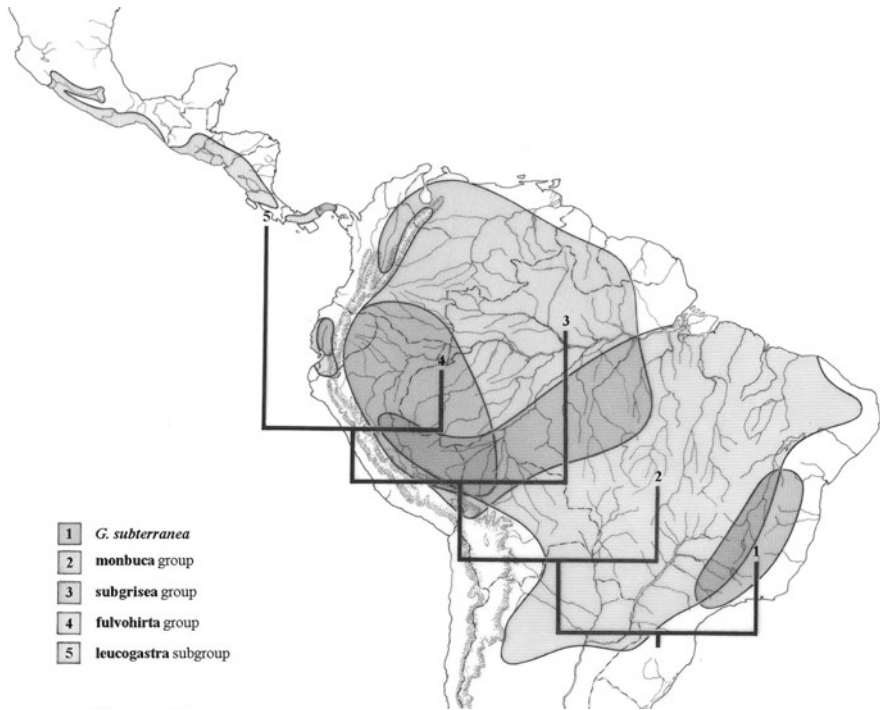


Fig. 2.12 Area and biological cladograms for the subgroups of *Geotrigona* (this is the first area cladogram proposed for Neotropical Meliponini), from Camargo and Moure (1996)

biogeography with great significance in the Neotropical area, permitting, for the first time, integration of space, time and form. The first works on evolutionary biogeography of Meliponini through the viewpoint and protocol of vicariance biogeography were of Camargo and Moure (1996), Camargo (1996) and Camargo and Pedro (2003). The first biological and area cladograms were for the species of the genera *Paratrigona* and *Geotrigona* (Fig. 2.12), and more recently *Partamona* (Fig. 2.13). The results reveal that the species subgroups within each of these genera are notably congruent in terms of biogeographic compartmentalization, that is, when the taxa are placed on the biological cladograms by their respective areas of endemism, the results obtained for the subgroups of the first two genera are the same (particularly in relation to the species of *Partamona*), indicating the same relationships between areas or biogeographic compartments. These results, obviously, suggest a general pattern of biogeographic coevolution in the Neotropical region.

The sequence of events in vicariance/cladogenesis provides, therefore, a definition of a hierarchy in the formation of biogeographic boundaries or geological compartmentalization and barriers, as in Figs. 2.14 and 2.15.

The first great barrier is formed along the alignment of the Madeira/Amazonas Rivers (possibly epicontinental seas related to the Tapajonic transgressions, in the



Fig. 2.13 Areas of endemism and biogeographical components, inferred from the species of *Partamona*; Chocó-CA (from northwestern Peru to Mexico); SWAm (a component delimited, on the north, by the alignment of the Uaupés/Negro rivers, on the south, by the Madeira/Mamoré rivers, and on the west, by the Andean mountain range); NAm (north of the Negro/Amazonas rivers); SEAm (area to the south of the Madeira/Amazonas rivers to northwestern Argentina); Atl (Atlantic area, from Bahia to Paraná). See Fig. 1.15a (taken from Camargo and Pedro 2003)

lower Miocene), dividing the Neotropical region into two large compartments: NW–SE (Fig. 2.14a). In the NW compartment a further break occurred (approximately along the line of the Caqueta/Japura rivers, possibly related to the transgression of the Maracaibo seas in the mid Miocene; Fig. 2.14b), separating North Amazonia (NAm) from all of southwestern Amazonia (SWAm) and the north Andean, Central American—Mexico block (Choco-AC). And, finally, a break separating SWAm from the Choco-AC component (Fig. 2.14c), related, possibly, with orogeny of the equatorial Andes, which attained heights greater than 3,000–4,000 m in the Plio-Pleistocene. In the SE component, there is a separation between the southeastern Atlantic region (Atl) and southeast Amazonia (SEAm). The breaks, giving rise to the crown (present) species, may be related to the climatic events of the Pleistocene, as postulated by the proponents of ecological “refuges.”

The first image that arises from this biogeographic and geological compartmentalization of the Neotropical region is that Amazonia (Fig. 2.16) is not a single historical unit, and rather, it is composed of three great biogeographic compartments with distinct temporal and phylogenetic relationships (Fig. 2.14, area cladogram).

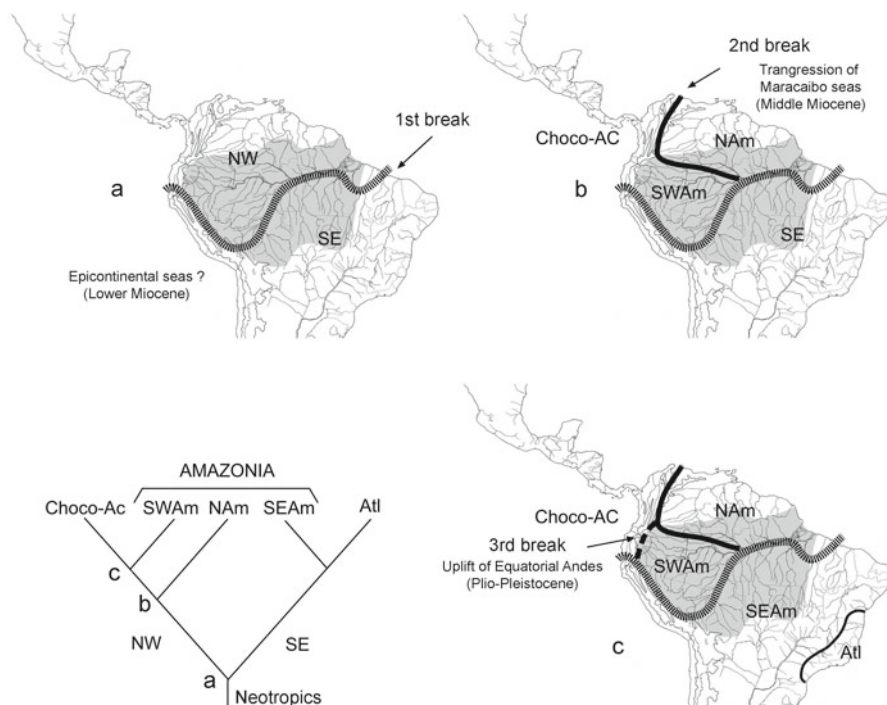


Fig. 2.14 Sequence of events of separation and vicariance in the Neotropical region. The *shaded area* is Amazonia, which, from the biogeographic perspective of vicariance, is not an historical unit, taken from Camargo (2006)

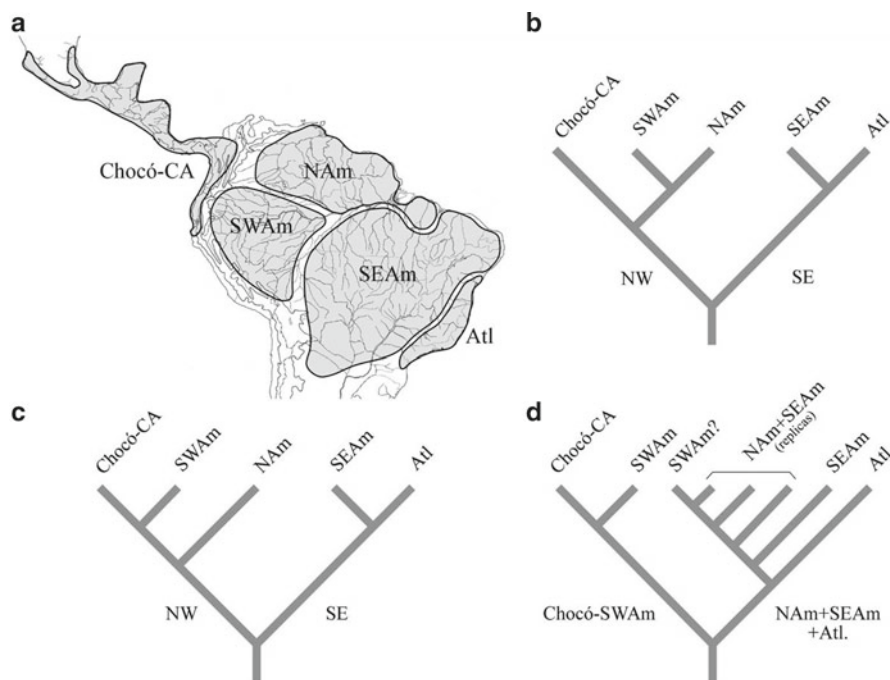


Fig. 2.15 Principal biogeographic elements which unify the Neotropical region ; (a) the diverse area cladograms obtained; (b) those proposed by Amorim and Pires (1996); (c) those proposed by Camargo (1996) and Camargo and Moure (1996); (d) those proposed by Camargo and Pedro (2003) (taken from Camargo and Pedro 2003). See legend in Fig. 1.13



Fig. 2.16 The magnificent Amazonian forest (upper Rio Negro region), produced by millions of years of evolution, habitat of many Meliponini and a megadiverse biota, today at the mercy of an irresponsible and uncontrolled devastation. Photo: J.M.F. Camargo

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Pot-Honey

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