

# Chapter 2

## Mangrove Floristics and Biogeography Revisited: Further Deductions from Biodiversity Hot Spots, Ancestral Discontinuities, and Common Evolutionary Processes

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### 2.1 Introduction

Mangroves are dominant coastal shoreline habitats of tropical and subtropical regions of the world (Tomlinson 2016; Spalding et al. 2010). They comprise chiefly flowering trees and shrubs uniquely adapted to tidal conditions and a special combination of factors that influence coastal and estuarine shorelines, like seawater, periodic inundation and exposure, waves and wind, strong currents and runoff, and fine sediments (Duke et al. 1998). In such settings, mangroves take the form of distinctly vegetated and often densely structured habitats of verdant closed canopies that clad coastal margins and estuaries of the tropics and subtropics.

In tropical waters, mangrove stands are often positioned between two of the world's iconic ecosystems—coral reefs and tropical rainforests. These are each, biota-structured ecosystems of tropical shorelines, intimately linked by integrated roles in coastal and estuarine ecosystem processes. However, such links are threatened by human development and habitats like mangroves are in serious decline worldwide (Duke et al. 2007). These habitats are also further dependent on mobile biota uniquely adapted to the habitats' unusual and often dramatic physicochemical gradients. Developed over millennia, these linked and mutual relationships have become vital to the survival of each species (e.g., Mumby et al. 2004).

Mangroves are recognized further for their unique morphological and physiological adaptations for coping with salt, exposed conditions, saturated soils, and regular tidal inundation along this unique estuarine and coastal marine habitat. Some of these distinctive attributes include: exposed breathing roots above ground; extra stem support structures; salt-excreting leaves; low water potentials and high intracellular salt concentrations for maintaining favorable water relations in saline environments; and

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their unusual viviparous, water-dispersed propagules. Such a unique combination of attributes has enabled mangroves to dominate tropical shorelines worldwide. In this chapter, the floristics and biogeography of these amazing plants and habitat has been re-evaluated; this includes taking a fresh look at some of the key factors responsible for their unusual diversity and distribution worldwide.

## 2.2 Factors Influencing Mangrove Distributions

The genetic composition of today's mangrove flora, while clearly subject to present-day climatic and geographical conditions (Duke 1995; Duke et al. 1998; Triest 2008), appears to be largely relict. Species are where they are today because of past events and circumstances. As such, today's distributional patterns cannot always be explained by current-day deterministic factors alone. Moreover, each mangrove plant type is influenced by a combination of attributes including: individual physiologies, ecology, dispersal ability, propagule buoyancy and longevity, geological circumstances, evolutionary rates, and the genesis of each taxon.

The key criteria are summarized in the following ten generalized factors (ordered in 3 groupings) as the ones mostly influencing the biogeography and evolution of mangroves. These criteria are based on the observations of a number of authors, including Tomlinson (2016), Duke et al. (1998), and Triest (2008), and modified further here.

### 2.2.1 Floristics and Biogeography

1. *Diversity of Plant Types Makeup Mangrove Habitat.* The species numbers of 80 taxa are not necessarily high, but mangrove taxa are present in a broad cross-section of plant family lineages (Tomlinson 2016). They chiefly comprise a small but diverse selection of shrub and tree species from 18 plant families with around 69 species and 11 hybrid intermediates (Table 2.1). There are 32 genera represented with all but one being a flowering plant (Table 2.2).
2. *Variable Ranges for Different Species.* The distributional ranges of mangrove species vary considerably (Spalding et al. 2010; Duke 2011, 2013, 2014a). While some extant mangrove taxa occur worldwide, others have more local distributional ranges. The overall high concentration of mangrove species in the Indo-Malesian area today defines the chief diversity hot spot for mangroves, comparable with other shallow water, tropical marine habitats, like seagrass and reefal coral species (Hoeksema 2007). And likewise, a further secondary hot spot for mangroves occurs in the Caribbean Central American area. A general feature of mangrove taxa is their high incidence of hybrid species (as mostly infertile, intermediate forms), along with sibling species (species that are unusually similar in morphology and genetic makeup).

**Table 2.1** Mangrove species of the world: Families and genera shaded are exclusively mangrove; Genera marked with an asterisk have been classified comprising their own family, named, Diospyraceae, Barringtoniaceae, Aegicerataceae, Nypaceae, Aegialitidaceae, and Pellicieraceae, respectively; Species underlined refer those of the Atlantic East Pacific region. Species in bold occur naturally in both regions; Reported hybrid taxa are shown with an “X” before the species name

Families with Mangroves	Family Relatives of Mangrove Taxa	Family Genera	Mangrove Genera	Non-Mangrove	Mangrove Spp.	Species of Mangroves
Acanthaceae	Black-eyed Susan, Shrimp Plants	250-300	<i>Acanthus</i>	30	2	<i>Acanthus ebracteatus</i> <i>Acanthus ilicifolius</i>
(ex Verbenaceae; or Avicenniaceae)	Grey Mangroves	1	<b><i>Avicennia</i>*</b>	0	8	<i>Avicennia alba</i> <i>Avicennia bicolor</i> <i>Avicennia germinans</i> <i>Avicennia integra</i> <i>Avicennia marina</i> <i>Avicennia officinalis</i> <i>Avicennia rumphiana</i> <i>Avicennia schaueriana</i>
Arecaceae	Palms	200	<i>Nypa</i> *	0	1	<i>Nypa fruticans</i>
Bignoniaceae	Trumpet, Tulip Tree, Jacarandas	120	<i>Dolichandrone</i>	9	1	<i>Dolichandrone spathacea</i>
Fabaceae	Baobab, Balsa, Kapok, Durian	31	<i>Tabebuia</i> <i>Camptostemon</i>	<u>245</u> 0	<u>1</u> 2	<i>Tabebuia palustris</i> <i>Camptostemon philippinense</i> <i>Camptostemon schultzei</i>
(or Bombaceae)	Cassia, Tamarind, Legumes	150	<i>Cynometra</i>	70	1	<i>Cynometra iripa</i>
(or Caesalpiniaceae)			<i>Mora</i> <i>Muelleria</i>	<u>19</u> <u>3</u>	<u>1</u> <u>1</u>	<i>Mora oleifera</i> <i>Muelleria moniliformis</i>
Combretaceae	Combretum, Quiqualis	20	<i>Lumnitzera</i>	0	3	<i>Lumnitzera littorea</i> <i>Lumnitzera racemosa</i> <i>Lumnitzera X rosea</i>
			<i>Laquncularia</i> <i>Conocarpus</i>	<u>0</u> <u>0</u>	<u>1</u> <u>1</u>	<i>Laquncularia racemosa</i> <i>Conocarpus erectus</i>
Ebenaceae	Ebony, Persimmons	3	<i>Diospyros</i> *	400	1	<i>Diospyros littorea</i>
Euphorbiaceae	Castor Oil, Spurges	300	<i>Excoecaria</i>	35-40	1	<i>Excoecaria agallocha</i>
Lecythidaceae	Brazil Nuts	15	<i>Barringtonia</i> *	40	1	<i>Barringtonia racemosa</i>
Lythraceae	Crepe Myrtle, Henna, Cuphea	25	<i>Crenea</i>	<u>30</u>	<u>1</u>	<i>Crenea patentinervis</i>
(or Sonneratiaceae)	<i>Duabanga</i>	2	<i>Pemphis</i> <i>Sonneratia</i> *	1 0	1 9	<i>Pemphis acidula</i> <i>Sonneratia alba</i> <i>Sonneratia apetala</i> <i>Sonneratia caseolaris</i> <i>Sonneratia griffithi</i> <i>Sonneratia X gulngai</i> <i>Sonneratia X hainanensis</i> <i>Sonneratia lanceolata</i> <i>Sonneratia ovata</i> <i>Sonneratia X urama</i>
Malvaceae	Silvery leaf trees, Hibiscus, Cocoa, Kola, Bottle Trees	70	<i>Brownlowia</i> <i>Heritiera</i>	<u>2</u> 29	<u>1</u> 2	<i>Brownlowia tersa</i> <i>Heritiera fomes</i> <i>Heritiera littoralis</i>
(or Sterculiaceae)			<i>Pavonia</i>	<u>1</u>	<u>2</u>	<i>Pavonia paludicola</i> <i>Pavonia rhizophorae</i> <i>Xylocarpus granatum</i>
Meliaceae	Mahogany, Rosewood	50	<i>Xylocarpus</i>	1	2	<i>Xylocarpus moluccensis</i> <i>Aegiceras corniculatum</i>
Myrsinaceae	Turnip-wood, Mutton-wood	35	<i>Aegiceras</i> *	0	2	<i>Aegiceras floridum</i> <i>Osbornia octodonta</i>
Myrtaceae	Eucalyptus, Bottlebrush, Guavas	80-150	<i>Osbornia</i>	0	1	

(continued)

**Table 2.1** (continued)

Pellicieraceae	Tea, Camellia, Franklinia	1	<i>Pelliciera</i> *	0	1	<i>Pelliciera rhizophorae</i>
Plumbaginaceae	Sea Lavender, Thrifts	10	<i>Aegialitis</i> *	0	2	<i>Aegialitis annulata</i> <i>Aegialitis rotundifolia</i>
Pteridaceae	Ferns	35	<i>Acrostichum</i>	0	3	<b><i>Acrostichum aureum</i></b> <i>Acrostichum speciosum</i> <i>Acrostichum danaeifolium</i>
Rhizophoraceae	Crossostylis, Cassipourea	16	<i>Bruguiera</i>	0	7	<i>Bruguiera cylindrica</i> <i>Bruguiera exaristata</i> <i>Bruguiera gymnorhiza</i> <i>Bruguiera hainesii</i> <i>Bruguiera parviflora</i> <i>Bruguiera</i> X <i>rhychnopetala</i> <i>Bruguiera sexangula</i>
			<i>Ceriops</i>	0	5	<i>Ceriops australis</i> <i>Ceriops decandra</i> <i>Ceriops pseudodecandra</i> <i>Ceriops tagal</i> <i>Ceriops zippeliana</i>
			<i>Kandelia</i>	0	2	<i>Kandelia candel</i> <i>Kandelia obovata</i>
			<b><i>Rhizophora</i></b>	0	12	<i>Rhizophora</i> X <i>annamalayana</i> <i>Rhizophora apiculata</i> <i>Rhizophora X brevistyla</i> <i>Rhizophora X harrisonii</i> <i>Rhizophora X lamarckii</i> <i>Rhizophora mangle</i> <i>Rhizophora mucronata</i> <i>Rhizophora racemosa</i> <b><i>Rhizophora samoensis</i></b> <i>Rhizophora X selala</i> <i>Rhizophora stylosa</i> <i>Rhizophora X tomlinsonii</i>
Rubiaceae	Coffee, Gardenia, Quinine	500	<i>Scyphiphora</i>	0	1	<i>Scyphiphora hydrophylacea</i>

**Table 2.2** Distribution of family, genera, and species in the two subregion hot spots of the world as the Indo West Pacific (IWP) and the Atlantic East Pacific (AEP); Summarized counts from Table 2.1

	IWP	AEP	Worldwide
Families	17	9	18
Genera	24	11	32
Species + hybrids	63	19	80
Hybrids	9	2	11
Species – Hybrids	54	17	69
Subspecific taxa	4	1	5

3. *Phylogenetic Relationships within Key Mangrove Genera.* It is important to have detailed information about the relationships amongst species of polyspecific mangrove genera (like *Avicennia*, *Bruguiera*, *Rhizophora*, *Sonneratia*). This is essential for identifying and understanding the genetic lineages and relationships amongst closely related taxa (Duke 1992, 1995, 2010; Duke et al. 2002; Duke

and Ge 2011; Lo et al. 2014). Such knowledge is further useful when ranking species by ancestral age, and in constructing phylogenies. There is also the idea, pursued in this treatment, of possible common patterns existing between genera where each entity may have evolved, diversified, and speciated in response to common overwhelming geophysical circumstances and drivers.

### 2.2.2 Extant Influencing Factors

4. *Dispersal by Sea*. Mangroves have mostly, *water-buoyant propagules* dispersed by water currents across seas and between estuaries, driven by wind, waves, tides, and ocean circulation (Rabinowitz 1978; Lo et al. 2014). Over half the mangrove species have unusually, well-developed viviparous propagules instead of seeds. By contrast, vivipary is rare in other plant ecotypes. But, one unanswered question remains: how does vivipary influence dispersal? It is clear that long distance dispersal (compare with Nathan et al. 2008) in mangroves is fundamentally important and well utilized, but there appear to be finite limits to both seed and viviparous propagule viability and longevity in transit (e.g., Drexler 2001). This is most evident however in the absence of native mangrove species in key locations, like the central Pacific Hawaiian Islands, prior to their introduction by people (Allen 1998).
5. *Topographic Elevation Range*. Mangroves are naturally restricted to a very *narrow elevation range* between mean sea level and the highest water levels of spring tides (Duke 1992; Duke et al. 1998). At lower limits of the range, they appear constrained by tidal inundation frequencies mostly less than 50% of the time, dependent on possible limitations during submergence with gas exchange of exposed roots. At higher intertidal margins, species appear constrained by desiccation as well as competition for light from supratidal upland specialists. To cope with conditions in the intertidal zone, mangrove plants have well-recognized specialized abilities to deal with salt and saturated airless soils, by their distinctive exposed air breathing root surfaces and lenticels.
6. *Ecological and Climate Conditions*. Mangroves are *constrained worldwide by extant climatic conditions*. Generally, mangroves are confined to sheltered tropical coastlines where mean monthly seawater temperatures drop only to around 20 °C (Duke et al. 1998). Based on observed different latitudinal limits (e.g., Duke 2006), there appear to be species-specific differences in temperature tolerances. However, a recent assessment has challenged this view, reporting no differences between widely distributed genera, *Avicennia* and *Rhizophora* (Quisthoudt et al. 2012). This view is however at odds with present understandings, and it may be limited by not accounting for observed variations in temperature tolerances amongst and between species; as an example, a notable cold-tolerant variant is known for *Avicennia marina*, var. *australasica* in south eastern Australia, and there are a number of other examples (Duke 1992, 1995, 2006). These observations emphasize the great importance of knowing the

ecophysiological tolerances of each genotype, especially those at distributional endpoints. Furthermore, mangrove taxa are often restricted further to areas of higher rainfall, as well as estuaries of larger riverine catchments (Duke et al. 1998). Mangroves can be more abundant and diverse in areas of unconsolidated sediments, like the mouths of larger estuaries, while also growing on hard substrates of rock and coral.

### 2.2.3 *Dispersal Pathways and Evolutionary Processes*

7. *Disjunctions of Distribution.* There are several major genetic *discontinuities amongst present-day mangrove distributions* worldwide (Duke 1995; Triest 2008; Takayama et al., 2013). Such disjunctions are marked by extant genetic anomalies where no current dispersal barriers exist. Disjunctions may be characterized by: the presence or absence of taxa, or the presence of sibling taxa on either side of an anomaly. It is also likely that relationships amongst taxa may be proportional to the magnitude and age of the disjunction, as well as to the specific characters of each plant involved—especially in their dispersal ability, propagule buoyancy, and longevity; also *cs.* Nathan et al. (2008). For these reasons, an ancient primary disjunction is recognized separating the Atlantic East Pacific (AEP) and Indo West Pacific (IWP), with distinct species, common genera, and separate families; while “younger” disjunctions, like that between SE Asia and Australia, is marked by sibling species, separate intra-specific forms, with notable common genera and families.
8. *Distributional Fluctuations.* Where climate conditions and sea levels change, the *distributional extent of individual mangrove species both expand and contract* (Duke 1995; Duke et al. 1998). This indicates that while mangroves are able to disperse and colonize unoccupied shorelines, they also at times have become extinct along other shorelines.
9. *Appreciable Geological Age.* Mangroves are known to exist from ancient *fossil records of macrofossils and pollen* dating back to the mid Cretaceous era, possibly up to around 100 million years ago (Churchill 1973; Plaziat et al. 2001). This is the case in varying degrees for extant common genera today. Where recognizable fossil taxa match existing mangrove plants, this reveals a genetically conservative situation where the presence of persistent genotypes as common species is indicative of relatively slow rates of genetic mutation and diversification over tens of millions of years. As such, species numbers today are indicative of the realised speciation rates for each lineage.
10. *Continental Drift Theory and Mangrove Evolution.* The dispersal and speciation of key mangrove angiosperm lineages took place at the same time as the *breakup of the massive supercontinent of Gondwana* (Duke et al. 2002; Triest 2008). Over the last 55 million years at least, large continental fragments have moved around the globe ferrying plants and animals with them. This explains

why plants with both low and high dispersal abilities may have comparable distributional ranges. Over time, oceans and seaways that once existed have closed, while land barriers have both emerged and disappeared. Understanding the occurrence of these barriers and their effectiveness, helps explain how water-borne mangrove plants might have dispersed to their current day distributional endpoints. Furthermore, in the Indo West Pacific (IWP), former Gondwanan southern land mass fragments, including Africa, India and Australia, have migrated dramatically northward to separately join with Asia. These massive movements must surely have seriously influenced the diversity and distribution of mangroves and other species throughout the region.

The relative importance and influence of each criterion explained here (1–10) is entirely species-dependent. And, for this treatment, criteria 1, 2, and 3 rely on best available *taxonomic discrimination* along with the most up to date records of worldwide *distributions*. Criterion 4 concerns dispersal by propagules, which can be over-rated for long-distance dispersal if data on propagule buoyancy and longevity for individual taxa are unavailable. And, while vivipary in mangroves may enhance *long-distance dispersal*, its key function and value lies in its enhanced *success* for essential local *re-establishment, rejuvenation, and habitat turnover*. In all cases, dispersal ability must always be considered finite and limited. Criteria 4, 5, and 6, describe the predominant and major *physiological constraints* that particularly influence within-site species distributions, based chiefly on temperature, moisture, and tides. Criteria 7, 8, 9, and 10 all relate to biological *evolutionary processes in response to historical changes in geological and climatic conditions*, where these influence changes to genetic makeup with mutations and occasional speciation.

This treatment considers all these relevant, prominent features of each species entity by taking a closer look at individual occurrence records. Summary information is presented for each mangrove genus, listing all species and hybrids (Appendix 1). Detailed descriptions that accompany these observations include diagnostic characters along with current distribution maps of all mangrove taxa, as displayed in the e-book field guide, *World Mangrove ID* (Duke 2013, 2014a). Other extant influencing factors have been explained further and summarized by Duke et al. (1998).

## 2.3 Floristics and Distribution

Mangrove plants collectively form an ecological type rather than a genetic entity with a singular genetic makeup for coping with intertidal life. Amongst the 32 genera with mangrove species, each entity has separately refined its own obligate specialized attributes for the tidal wetland habitat. These features are manifest in entities with often distinctive anatomy, physiology, and functionality. Each genus has varying numbers of representatives for each of the 18 plant families (see Table 2.1; Duke 2011, 2014a). And, all but one are flowering plants; the odd one is

*Acrostichum*, the fern family Pteridaceae. Their collective occupation of the upper tidal zone is considered a relatively recent geological occurrence, mostly post Cretaceous. Otherwise, mangrove habitat is comparable to rainforests, with all families present in mangroves being present also in tropical rainforests.

Of these 32 plant genera, 17 are exclusive to mangrove habitat, including: *Acrostichum*, *Aegialitis*, *Aegiceras*, *Avicennia*, *Bruguiera*, *Camptostemon*, *Ceriops*, *Conocarpus*, *Kandelia*, *Laguncularia*, *Lumnitzera*, *Nypa*, *Osbornia*, *Pelliciera*, *Rhizophora*, *Scyphiphora*, and *Sonneratia*. The other 15 genera are less specialized, with both mangrove and non-mangrove entities present, including, *Acanthus*, *Barringtonia*, *Brownlowia*, *Crenea*, *Cynometra*, *Diospyros*, *Dolichandrone*, *Excoecaria*, *Heritiera*, *Mora*, *Muelleria*, *Pavonia*, *Pemphis*, *Tabebuia*, and *Xylocarpus*.

As an example, *Pemphis* has a widespread IWP species, and a sole upland species located inland as an isolated population on the island of Madagascar (Tomlinson 2016). While others, like *Brownlowia*, *Diospyros*, and *Tabebuia*, have single mangrove species and a greater number of upland species (Duke 1992). In addition, unusually widespread and distinct hybrid intermediates are reported in five genera including, *Bruguiera*, *Lumnitzera*, *Sonneratia*, *Rhizophora*, and *Avicennia* (Huang et al. 2014; note that the recently reported *Avicennia* hybrid lacks morphological description). Overall, the total number of mangrove species in each genus is relatively low, being one or two. For relatively larger genera, the number of mangrove species plus hybrids worldwide does not exceed 12.

These relatively low levels of diversity are believed to be the result of the harsh and saline growth conditions present in intertidal habitats. The extreme conditions favor high levels of optimized efficiency for the survival and evolution of mangrove inhabitants (cs. Provine 2004). Such broadly defined factors support the underlying tenet in this treatment, which states that the resilience and survival of each species is largely dependent on its individual distribution, dispersal capabilities, levels of taxonomic divergence, and phylogeny. In this way, evolving local and regional environmental/ecological factors are expected to have a key role in defining the genetic characteristics that ultimately define all mangrove taxa known today.

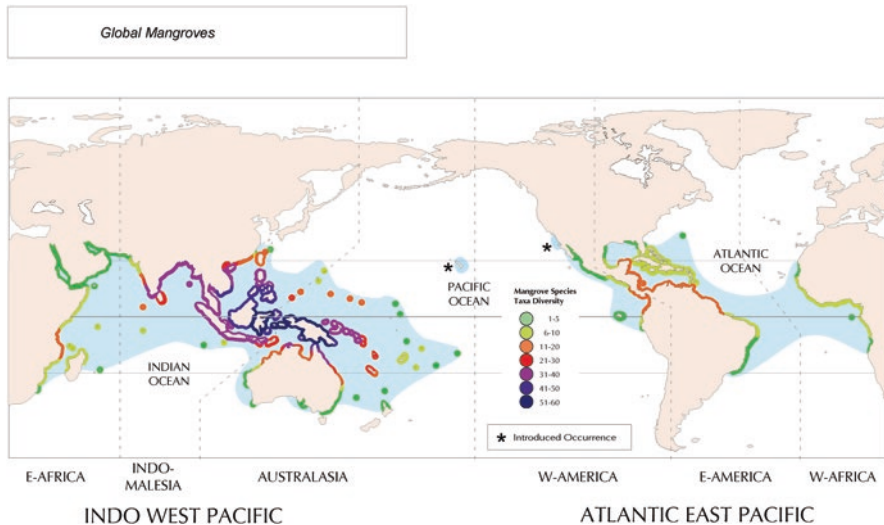
All mangrove species in the world today are considered in this review, along with their current distribution maps, showing records of living, introduced, and fossil records (Duke 2013, 2014a; see Appendix 1). These maps provide the latest information available on the distribution of each entity. But, despite such outcomes, the description and characterization of mangrove plant types remains incomplete. Hence, there is an ongoing need to revise and update each entity, especially since occurrences are likely to change (Duke et al. 2007). There might also be new undescribed taxa. For example, with *Pelliciera*, while currently described as one species (Tomlinson 2016), it appears this taxon has subspecific forms within its limited Central American range (Castillo-Cardenas et al. 2005; plus personal observations). There are also notable taxonomic discrepancies and gaps in established larger genera, like *Rhizophora* in northern South America and West Africa (Ceron-Souza et al. 2010; Triest 2008).



## 2.4 Dispersal Pathways and Evolutionary Processes

Prior assessment of mangrove global biogeography (including, Duke 1992, 2011, 2014b; Tomlinson 2016; Triest 2008) shows a general consensus for two hot spots disproportionately spanning sub-regions of the Indo West Pacific (IWP) and Atlantic East Pacific (AEP). These are shown in Fig. 2.1 along with all distribution information summarized from the 70 species maps (excluding hybrids). While the IWP hot spot, also referred to as the Indo Australian Archipelago biodiversity hot spot (Cowman and Bellwood 2013), is about three times more diverse, there are significant species concentrations in the AEP spanning the Caribbean American Isthmus. Both hot spots form gradients in species richness driven by estuarine diversity along respective tropical shorelines. In this way, estuarine systems influenced by individual catchment runoff (Duke et al. 1998), act as diversity nodes to form species enclaves and gradients connecting intertidal habitats. At its center, the IWP hot spot hosts 54 mangrove species, along with around 500 species of coral and 5000 species of fish (Hoeksema 2007). By contrast, the AEP hot spot has 17 mangrove species and proportionately fewer associated shallow water marine species.

The genesis of mangrove hot spots seems almost certainly due to past changes in continental drift acting in concurrence with speciation and dispersal events driving vicariance and re-association (cs. Duke 1995; Duke et al. 2002). To have such a profound influence, these massive changes in global geography have coincided with



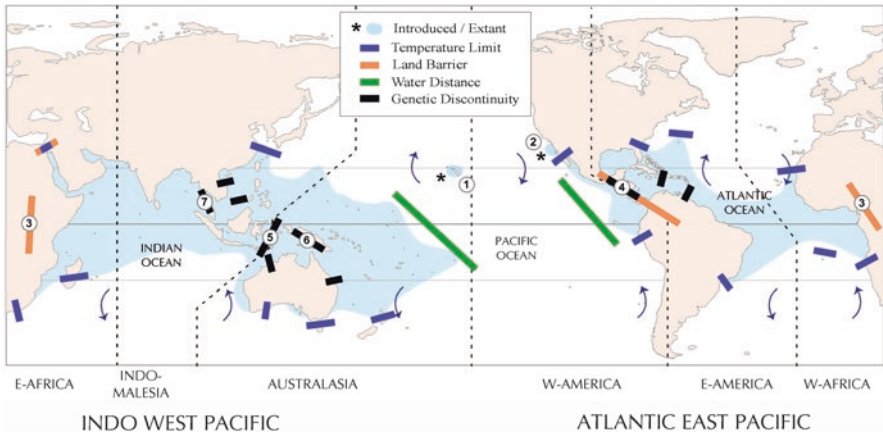
**Fig. 2.1** The current world map of the distribution of mangroves (*blue shading*) showing diversity as numbers of specific taxa (species and nominal hybrids). Also identified are two outlying areas where mangrove taxa have been introduced in recent decades. Overall, there is notable separation in eastern and western global bioregions with two disproportionate diversity hot spots: the dominant Indo Australian Archipelago area north of Australia; and a lesser one, the Caribbean American Isthmus area north-west of South America

the evolution of early angiosperms to derive the dominant mangrove entities known today. Over time, the global displacement of continental fragments has changed dramatically to form today's distribution maps with biota occurring for the most part constrained according to current day circumstances. But, there are notable unexplained patterns sparking debate and speculation about their relevance to the evolution of mangroves.

The approach in this article has been to further review current evidence, identifying each vital clue to understanding how each mangrove entity might have evolved. The evidence (also see Fig. 2.1) includes: (1) areas of species occurrence and richness; (2) hot spots associated with clines in species diversity; and (3) unexplained discontinuities across hot spot gradients in the absence of apparent current-day influences on gene flow.

## 2.5 Dispersal Barriers

Extant mangrove distributions are collectively defined by a number of tangible barriers blocking water-borne gene dispersal (Duke et al. 1998; Duke et al. 2002; Triest 2008), including: (a) cold water (<20 °C in summer) mostly in higher latitudes; (b) land mass, mostly longitudinally applied; and (c) broad water expanses, also mostly longitudinal. The current locations of these three barrier types are displayed in Fig. 2.2. The effectiveness of land barriers and adverse cold temperatures are each



**Fig. 2.2** Dispersal barriers of temperature, land, and water compared with genetic discontinuities restricting gene flow around coastal margins of the Atlantic East Pacific and the Indo West Pacific regions (Adapted from Triest 2008): The extant distributional range of mangroves with areas of outlying introduced populations are shown as blue shaded areas; The circumstances surrounding the four barriers (1–4) and three discontinuities (5–7) marked are discussed in the text

relatively self-evident. Mangroves are restricted to mostly tropical latitudes except in deviations created by respective oceanic circulation patterns affecting ocean shoreline occurrences (arrows show major oceanic current gyres).

Ocean water distances can be barriers to buoyant propagule dispersal where widespread mangrove taxa have viviparous, living propagules with distinctly limited survival times at sea (e.g., see Steinke 1986; Drexler 2001). While it is evident that seed-distributing mangrove types are less widespread (no families in common between IWP and AEP regions), it is also curious why species with greatly different survival abilities have comparable global ranges (both IWP and AEP), like *Rhizophora* and *Avicennia*. Their viviparous propagules can last up to 150 days, or less than 15 days, respectively. In the absence of more information on dispersal abilities for each mangrove entity, it suffices to say that water distance can be a barrier if propagules have limited capacity to stay afloat and remain viable. In support of this contention, there are other important clues displayed in two examples of species introductions, where modern day ranges have been artificially extended to isolated previously unoccupied mangrove-suitable habitat. These are evidence of active natural barriers.

In one case (Fig. 2.2, site 1), *Rhizophora mangle* was artificially established during the 1920s in the northern Pacific Hawaiian islands, accompanied by a second introduced species *Bruguiera sexangula* (Allen 1998). Their establishment and subsequent spread among these islands clearly demonstrated the suitability of previously unoccupied habitat. Hence, the only thing preventing their introduction to these islands before this was the ocean water surrounding them—for at least around 5000 years. This is tangible evidence of an existing water distance barrier for mangroves crossing the Pacific Ocean. Only two mangrove species, *Acrostichum aureum* and *Rhizophora samoensis*, and three genera (*Avicennia*, *Rhizophora*, *Acrostichum*) occur naturally on both sides of the barrier. And, there are significantly greater lower taxonomic level differences within respective subregions (see Table 2.2). The oddity in this, has been the westward dispersal of *R. samoensis*, which appears only possible naturally if facilitated by an ancient chain of volcanic islands (Schlanger et al. 1981; Schlanger and Premoli-Silva 1981). And, this suggestion has some credibility where there are corresponding distributional records of a small number of shallow water reef fishes across the southwestern Pacific (Cowman and Bellwood 2013). In the Atlantic however, water distances appear much less effective as a barrier. While this ocean has large ocean water distances, there appears to be qualified gene flow between eastern and western shorelines (Takayama et al. 2013). In support of this contention, all seven native species on the African west coast occur also in the Americas (Table 2.3). And, while four genera on the American east coast are not recorded on the African west coast, five common genera occur naturally on either side of the ocean. However, the depauperate diversity of mangrove assemblages in West Africa remains a mystery. It is proposed that this low diversity might reflect the relative stability of this area over the last 40–50 my.

In a second example (Fig. 2.2, site 2), a mangrove outlier population on the North American west coast was established with the introduction of *Avicennia*

**Table 2.3** Tentative ranking of mangrove genera (for the relevant species present in mangroves) by age (oldest to youngest, 1–32) based on earliest fossil evidence coupled with distributional extent across global regions and subregions (IWP = Indo West Pacific; AEP = Atlantic East Pacific; E Africa = East Africa; Indo Mal = Indo Malesia; Austral Asia = southern Asia to Australia; W Amer = West America; E Amer = East America; W Africa = West Africa), shown as numbers of species excluding hybrid intermediates. Dated (mya) fossil evidence were described by Plaziat et al. (2001), others (\*) were deduced from Appendix 2

				IWP	IWP	IWP	AEP	AEP	AEP
	Mangrove Genera	Fossil Age (mya)	Spp	E Africa	Indo Mal <sup>1</sup>	Austral Asia <sup>1,2</sup>	W Amer <sup>2,3</sup>	E Amer <sup>3,4</sup>	W Africa <sup>4</sup>
1	<i>Nypa</i>	55	1		1	1	Introd	Introd	Introd
2	<i>Acrostichum</i>	55	3	2	2	2	2	2	2
3	<i>Rhizophora</i>	50	6	1	3	4	2	2	2
4	<i>Avicennia</i>	50	8	1	4	4	2	2	1
5	<i>Pelliciera</i>	50	1				1	1	
6	<i>Sonneratia</i>	50	6	1	6	4			
7	<i>Bruguiera</i>	50	6	1	5	6		Introd	
8	<i>Ceriops</i>	50	5	1	3	3			
9	<i>Heritiera</i>	40	2	1	2	1			
10	<i>Laguncularia</i>	25–40*	1		Introd		1	1	1
11	<i>Conocarpus</i>	25–40*	1			Introd	1	1	1
12	<i>Lumnitzera</i>	40*	2	1	2	2		Introd	
13	<i>Xylocarpus</i>	40*	2	1	2	2			
14	<i>Pemphis</i>	40*	1	1	1	1			
15	<i>Aegiceras</i>	40	2		2	1			
16	<i>Pavonia</i>	25–40*	2				2	1	
17	<i>Aegialitis</i>	25–40*	2		1	1			
18	<i>Acanthus</i>	25–40*	2		2	2			
19	<i>Muellera</i>	25–40*	1				1	1	
20	<i>Camptostemon</i>	10–25*	2		1	1			
21	<i>Barringtonia</i>	10–25*	1		1	1			
22	<i>Scyphiphora</i>	25–40*	1		1	1			
23	<i>Osbornia</i>	10–25*	1		1	1			
24	<i>Cynometra</i>	25–40*	1		1	1			
25	<i>Dolichandrone</i>	25–40*	1		1	1			
26	<i>Excoecaria</i>	25–40*	1		1	1			
27	<i>Crenea</i>	25–40*	1					1	
28	<i>Diospyros</i>	5–10*	1			1			
29	<i>Mora</i>	3–4*	1				1		
30	<i>Kandelia</i>	25–40*	2		2				
31	<i>Brownlowia</i>	25–40*	1		1				
32	<i>Tabebuia</i>	3–4*	1				1		

Notes: Comparison between major regional discontinuities defined in part by: 1. Malay Peninsula & Wallace's Line; 2. Pacific Ocean; 3. Central American Isthmus; 4. Atlantic Ocean. The barriers dividing these area groupings have different causal factors; see Fig. 2.2; mya = millions of years ago

*marina* to Mission Bay, around 30–50 years ago (Kay 2007). There were no mangroves extant in this area beforehand. The local native mangrove populations of *Avicennia germinans* are currently limited to a few 100 km further south in northern Mexico, presumably constrained by the temperature limited growth of that species. Of course, this needs to be assessed further, but the south east Australian source stock of introduced *A. marina* has greater cold tolerance than the local *Avicennia* species; this concurs with the unusual natural occurrence of *A. marina* at exceptionally high latitude sites in Australia. This shows notable limitations with the conclusion by Quisthoudt et al. (2012) that high latitude limits might be usefully re-evaluated considering temperature tolerances of individual species and their local genotypes. In any case, as shown for Hawaii, in Mission Bay, artificial and recent occupation of vacant habitat has proven to be suitable for mangroves, previously not occupied by natural means. Could this be evidence of different temperature tolerances of different genotypes, and the current effectiveness of a temperature barrier on native mangrove species along the American Northwest coast?

The effectiveness of land barriers is aptly demonstrated in one prime example (Fig. 2.2, site 3; Table 2.3)—the African land mass. This long-established land barrier works together with the Pacific Ocean water barrier to effectively divide the AEP and IWP global regions. For the African land barrier, only one species, *Acrostichum aureum*, occurs in common between east and west coasts. And, at the genus level, while there are three in common, two other Atlantic genera are unknown in the Indian Ocean, and seven Indian Ocean genera are unknown in the Atlantic.

In another example of a land barrier (Fig. 2.2, site 4), the Central American Isthmus (CAI) has been much less effective in blocking gene flow. While eight genera are shared, there are just two genera not shared across the CAI. The diminished effectiveness of this barrier however corresponds with its recent age, with closure of the isthmus land bridge between the Pacific and Atlantic Oceans, 3–4 mya (Coates et al. 1992; Schmidt 2007). This clearly demonstrates why extant barriers must be assessed in their historical context when evaluating their longer-term effectiveness.

In summary, the map in Fig. 2.2, shows the locations of key extant barriers along with those examples of introduced taxa mentioned earlier. The figure also shows the location of a number of potentially ancient barriers (black bars). These appear no longer to function as currently situated, but each is recognized for its otherwise odd and localized genetic discontinuity at differing taxonomic levels.

## 2.6 Discontinuities and Deductions Surrounding Relict Barriers

There are notable genetic discontinuities within and amongst present-day barriers (Fig. 2.2, sites 4–7 for example). Our knowledge of these instances is based on prior biogeographical accounts (e.g., Tomlinson 2016; Triest 2008; Spalding et al. 2010) along with other detailed assessments of gene flow amongst specific taxa in

particular areas (Duke et al. 2002; Takayama et al. 2013; Lo et al. 2014). Such discontinuities are manifest as unexplained distributional patterns where the range of a taxon might end abruptly, or where sibling (closely related) genotypes exist either in separation or coexisting in overlapping distributional ranges. These instances stand out because they are largely unexplained in the context of the present-day barriers described previously. But, where discontinuities might be artifacts of past geological events over 10 mya, these are better considered as valuable evidence from which we might identify taxa at particular dates and circumstances.

One significant discontinuity exists between Indo-Malesian and Australasian subregions (Fig. 2.2, site 5). The boundary of contact is well-recognized as Wallace's Line, marking the collision juncture of Australian and Asian biotas around 20 mya (e.g., Duke et al. 2002). For mangrove plants, this is marked by 21 genera in common, while 2 are restricted to Asia, and one to the south. But, while 35 species (Appendix 1) are shared between subregions, 7 species are partially or wholly restricted to the south including *Aegialitis annulata*, *Avicennia integra*, *Bruguiera exaristata*, *Camptostemon schultzei*, *Ceriops australis*, *Ceriops pseudodecandra*, and *Diospyros littorea*. And, 11 others are restricted to the north, *Aegialitis rotundifolia*, *Aegiceras floridum*, *Brownlowia tersa*, *Camptostemon philippinense*, *Ceriops decandra*, *Ceriops zippeliana*, *Heritiera fomes*, *Kandelia candel*, *Kandelia obovata*, *Sonneratia apetala*, and *Sonneratia griffithii*.

Another recognized discontinuity is that between north and south coasts of New Guinea (Fig. 2.2, site 6). This is part of the same collision event that formed Wallace's Line (Duke 1995). While this discontinuity is much "weaker" (=lower taxonomic level differences), it is marked by sibling taxa replacing each other on either coast like *Avicennia alba* and *A. marina*, *Rhizophora apiculata* (Asian form) and *R. apiculata* (Australian form), and *Sonneratia caseolaris* and *S. lanceolata*.

In recent years, a discontinuity between east and west coasts of the Malay Peninsula (Fig. 2.2, site 7) has been identified in a number of detailed genetic studies (Triest 2008; Guo et al. 2016), but its effectiveness depends on the relevant mangrove's dispersal abilities. For dispersal specialists, like *Rhizophora*, local gene exchanges are governed predominantly by current flows (Lo et al. 2014; Wee et al. 2014), while for species with more limited dispersal abilities, like *Ceriops* and *Lumnitzera* there is a notable ancient land barrier effect (Tan et al. 2004; Liao et al. 2007; Su et al. 2006). The circumstances are explained by the partial submergence of an ancient much larger Sund Peninsula whose remnant outcrops now form the Indonesian Archipelago. The submergence event was the result of the massive collision between Australian and Asian land masses as these continental fragments continue to relocate and adjust. The separation of biotas in the Indian Ocean and the South China Sea therefore appear to have much greater isolation than expected. At least nine species (Appendix 1) affected include: *Aegialitis rotundifolia*, *Ceriops decandra*, *Ceriops zippeliana*, *Ceriops tagal*, *Heritiera fomes*, *Kandelia candel*, *Kandelia obovata*, *Sonneratia apetala*, and *Sonneratia griffithii*. Much of the genetic differences concern variations within individual species.

## 2.7 Localized Extinction Events and Recovery

Mangrove distributions have varied considerably over more than 50 million years with both notable range extensions and instances of localized extinction (Duke 1995; Plaziat et al. 2001; Triest 2008). Events most likely to have caused such extreme outcomes have almost certainly been associated with changes in climate, reduced rainfall, and cooling temperatures. A key driver for these events could be associated with shifts in continental fragments as they drifted from one climate zone to another. Or, it could be changes to climate zones from altered oceanic circulation patterns and/or atmospheric conditions.

For north–south orientated sections of coastline in particular, temperature increases have driven poleward shifts, while temperature decreases have driven retreat and extinction from higher latitudes. This is shown in global fossil records (Plaziat et al. 2001) with species also becoming extinct from entire regions of warmer temperatures when rainfall decreased dramatically, like the Middle East and the Caribbean–northern South America areas 20–30 mya. The following case studies illustrate some key processes at play.

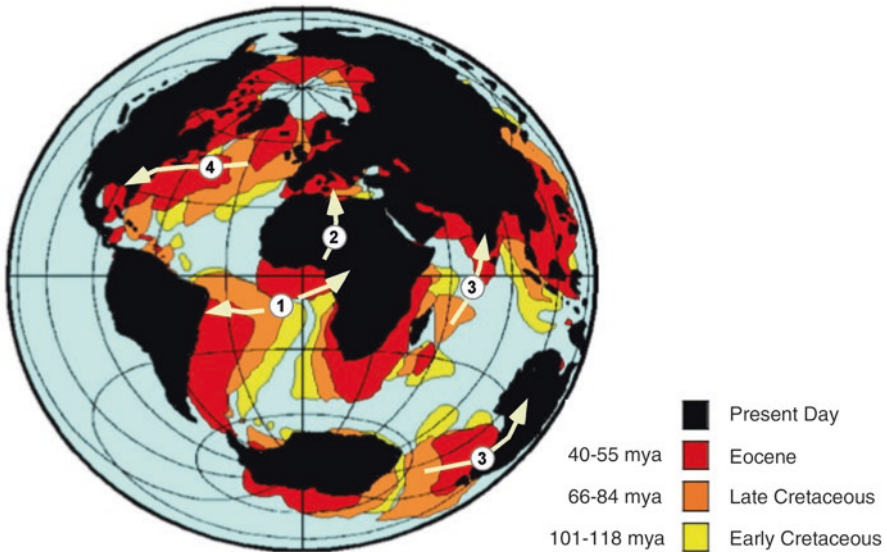
Consider the widespread IWP taxon, the mangrove palm, *Nypa fruticans* (Appendix 1). It is restricted naturally today to wet, warm areas within the IWP region. However, fossil evidence shows its past distribution included not only both IWP and AEP regions, but that it also sometimes was in sites of notably higher latitude  $>40^\circ$  north and south around 50–55 mya. It is significant that in recent times, the species has been reintroduced into the AEP on multiple occasions (Duke 2013, 2014a), demonstrating the current suitability of such locations and massive changes in local climates. Today, the nearest comparable restrictive climate conditions would be those currently present in the Middle East, west of India. In these locations, *Nypa* is excluded despite its proximity to viable, abundant populations further east. And, the dispersal capacity of *Nypa* is apparently reasonably effective with notable scattered populations spread across islands of the North-West Pacific, and further afield.

A number of mangrove species and genera have shown latitudinal range contractions from past fossil distributions (Appendix 1), including, *Acrostichum*, *Aegiceras*, *Avicennia*, *Bruguiera*, *Ceriops*, *Heritiera*, *Pelliciera*, and *Rhizophora*. However, only *Pelliciera* has shown partly comparable reductions in longitudinal range. Curiously, this relates to similar areas of the AEP in each case. Unlike *Nypa*, *Pelliciera* was not quite extinguished in the AEP, but its broad ancestral range was notably reduced to its western limit (Plaziat et al. 2001). Since then, there has been limited recovery east. As noted for *Nypa*, there are few current-day restrictions in climate, so such climate factors apparently appear not to be limiting the species today. However, *Pelliciera* does seem to have serious limitations for long-distance dispersal because of its poorly buoyant propagules. Furthermore, these are heavily consumed by small crabs (Dangremond 2015). These observations demonstrate the diverse factors to be considered along with the species-specific eco-physiological attributes of each species entity.

## 2.8 Time Line of Geological Events, Dispersal, and Speciation

Instances of speciation, extinction, and dispersal are driven by internal and external factors where a concurrence of events offers preliminary evidence. As such, ages estimated by carbon dating or genetic dating from rates of mutation and divergence might correspond with dates from fossil records and relevant geological events. In this way, three key instances of diversification seem relevant to the dominant genera of mangrove plants namely *Rhizophora* and *Avicennia*: (1) the diversification and dispersal to both AEP and IWP regions from a more or less common point of origin; (2) secondary diversification separately of each lineage in AEP and IWP occurrences; and (3) subsequent further secondary diversification.

The key global geological changes of continental drift that took place during the last 118 million years are shown in Fig. 2.3. Over this period, there were a series of dramatic and progressive global events with each having profound influences on the plants and animals living during these times. The four most significant circumstances (Fig. 2.3) include, Event 1: the separation of Africa and South America (~100 mya) and progressive opening of the South Atlantic Ocean; Event 2: the closure of the Tethys Sea between Africa and Eurasia 25–35 mya; Event 3: the separation of India (70–75 mya) and Australia (~50 mya) with their subsequent collisions



**Fig. 2.3** Maps of continental drift in four stages between 118 mya and the present day. Notable events shown with arrows, include: (1) widening of the Southern Atlantic; (2) closure of the Tethys Sea (between Africa and Eurasia); (3) narrowing of the Pacific with northern drifts of India and Australia across the Indian Ocean; and (4) opening of the North Atlantic Ocean



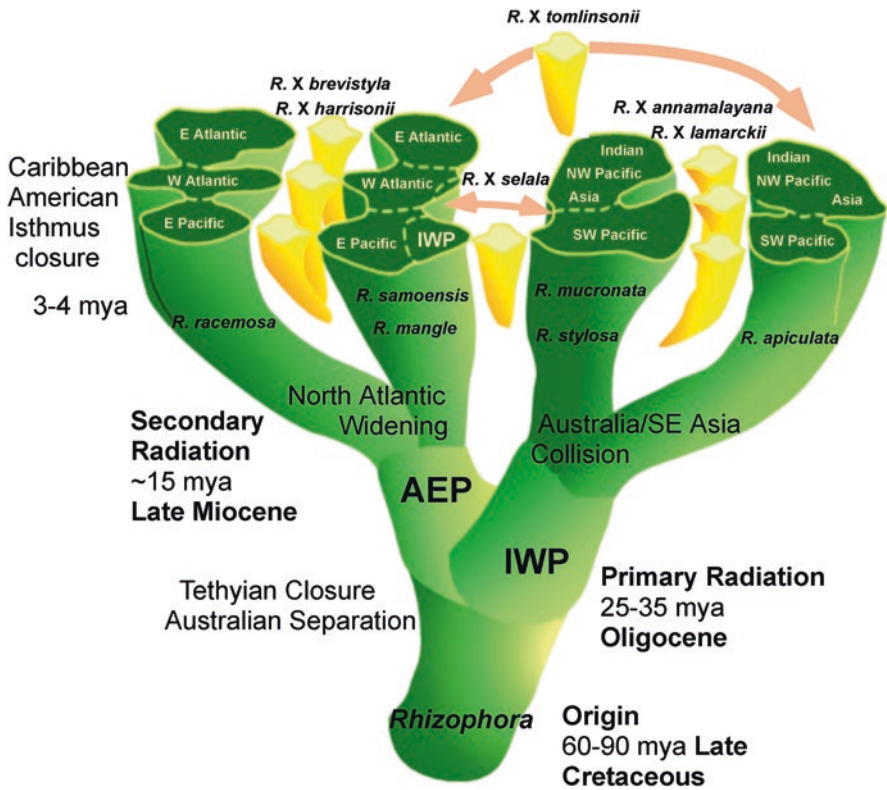
with Asia (~40 mya and ~15 mya, respectively); and Event 4: the opening of the North Atlantic (from ~60 mya onwards).

Fossil evidence (Table 2.3) links mangrove plants with at least the last three circumstances from 55 mya onwards. However, for the first point, it is reasonable to speculate that precursor mangrove flowering plants would almost certainly have benefitted from the creation and progressive widening of the South Atlantic Ocean. The first angiosperm flowering plants appeared nearby around this time. Prior to the Tethys closure, around 40–55 mya, recognized mangrove genera, *Nypa*, *Acrostichum*, *Rhizophora*, *Avicennia*, *Pelliciera*, *Sonneratia*, *Bruguiera*, *Ceriops*, *Heritiera*, and *Aegiceras* were present around its shoreline, as well as further afield. It seems likely that these populations were for the most part contiguous. Species like *Nypa* were notably widespread, suggestive of widespread, moist, warm climatic conditions. Then with the closure of the Tethys, widely spread taxa would have been divided as precursors of AEP and IWP regional differences. This was likely to be compounded by populations separated along the northern and southern shorelines of the ancient Tethys Ocean. The subsequent diversification of species was largely dependent on individual circumstances as each genus further diversified and dispersed.

Based on extant and fossil records of *Rhizophora*, a schematic for the phylogeny of genotypes of this genus (Fig. 2.4; Duke et al. 2002) shows likely speciation pathways portrayed as coincident with the geological circumstances described earlier (Fig. 2.3). In consideration of such matters in concordance with known physiological constraints (cs. Figure 2.2), the dispersal and distribution of evolving taxa are described in the following scenario. While AEP and IWP taxa were being separated by the Tethys closure, each was becoming more influenced by region specific events. To better understand these events and circumstances, it is useful to follow likely dispersal paths with known positions of land masses and oceans during periods identified by available fossil evidence (Fig. 2.5; e.g., Plaziat et al. 2001).

In the AEP, *Rhizophora* populations with blunt obtuse leaf tips would have spread along shorelines of the newly forming Atlantic oceans. One group (Fig. 2.5, path #2), as proposed *R. racemosa* progenitors, progressed south from Africa to South America. While the other (Fig. 2.5, path #4), as possible *R. mangle* progenitors may have spread west along the North American coastline before migrating south as conditions progressively cooled during the Eocene. The early progenitor lineages had separated and developed over millions of years, remaining isolated until they were reunited as different species when North and South American land masses merged and formed (Fig. 2.5, point C). The further separation of *R. mangle* and its sibling, *R. samoensis*, is likely to have arisen during this time as populations became isolated on opposing sides of North America which was finally completely isolated after closure of the Caribbean American Isthmus (Fig. 2.5, path #3). During this time, *R. mangle* and *R. racemosa* more or less matched ranges on both sides of the Atlantic.

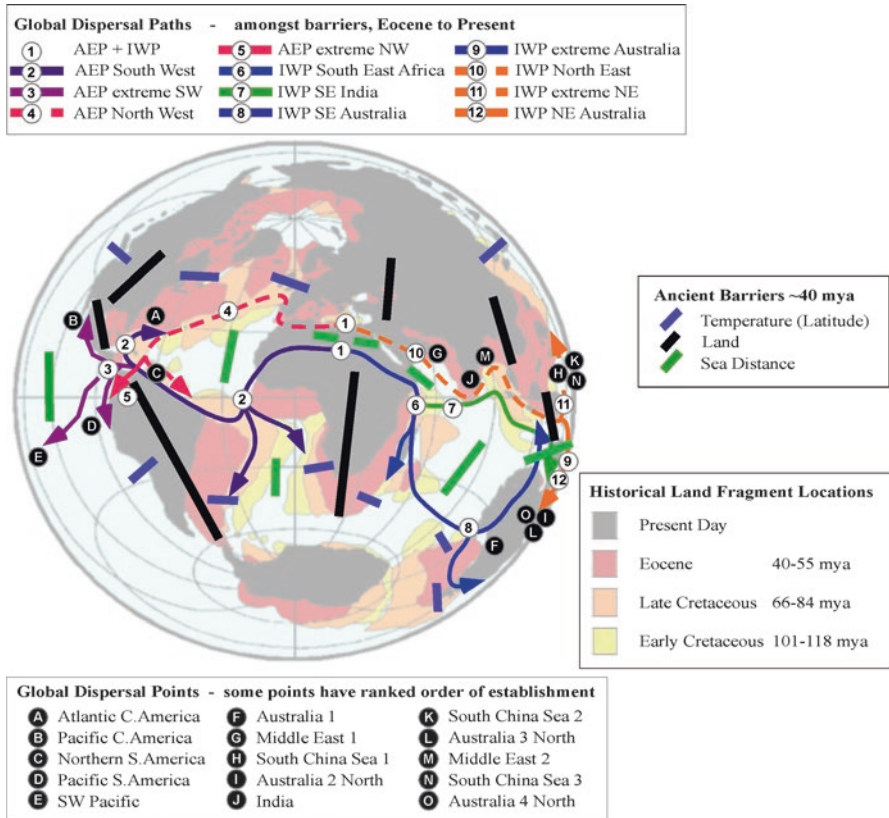
In the IWP, *Rhizophora* populations with spiked mucronate leaf tips would have spread east along shorelines of the ancestral Indian Ocean as the far western shores of a vast Pacific Ocean. One group (Fig. 2.5, path #10), as proposed *R. apiculata* progenitors, may have progressed eastward to Southeast Asia where founding popu-



**Fig. 2.4** A proposed phylogeny for *Rhizophora* taxa between present day and 118 mya, assuming a single ancestral progenitor possibly created with the emerging Atlantic Oceans (Duke et al. 2002): Seen as a “slice in time,” two major radiations with subsequent divergences in extant vicariant populations from global subregions (AEP and IWP) to ocean areas (green lineages). Hybrid intermediates (yellow lineages) are known to species at each instance of co-existence

lations possibly became isolated on either side of the Sund Peninsula. Meanwhile, the other group (Fig. 2.5, path #6), as *R. mucronata* progenitors, spread south along the East African shoreline where some plants spread to the island of India as it drifted north. The Indian land mass carried populations of *R. mucronata* north to join the Asian shoreline (Fig. 2.5, path #7). Other plants would have spread to the Australian shoreline, and changed slightly to become the *R. mucronata* sibling, *R. stylosa* (Fig. 2.5, path #8). Then, after Australia collided with the Sund Peninsula and Southeast Asia, all diverging IWP species would have been united into the overlapping distributions seen today (Fig. 2.5, point H & I). It is of some interest, that the dispersal and speciation processes were somewhat similar in respective hemispheres where divergent populations appear to be reunited (equalized) after long periods of separation and divergence.

It is of additional great significance, that two distinct and different genera, *Rhizophora* and *Avicennia*, in particular, have comparable global distributions;



**Fig. 2.5** Proposed dispersal pathways taking account of all mangrove species with the help of fossil records; continental locations; land, sea, and temperature barriers; and, overall species affinities

despite acknowledged differences in key functional characteristics, including dispersal ability (cs. Steinke 1986; Drexler 2001). This firmly suggests there might be common overall circumstances influencing dispersal and distribution beyond individual plant differences. So, why do these different genera have similar global distributions? It has been explained earlier that this is despite dispersal being limited by extant land and sea distance barriers. Could it be that the influence of continental drift dominates the evolution of mangrove plants rather than their functional differences? The answer may be explored further by investigating whether common patterns exist in *Avicennia* and other genera, when substituting each genus in the previous scenario for *Rhizophora*. In doing so, some consideration can be made for local influences, particularly, any reported differences in dispersal ability, along with respective levels of taxonomic differentiation.

In the scenario for *Avicennia*, the corresponding AEP species might be as follows: *A. germinans* for *R. racemosa*; *A. schaueriana* for *R. mangle*; and *A. bicolor*

for *R. samoensis*. And, matching IWP species would be: *A. marina* for *R. stylosa*; *A. officinalis* for *R. apiculata*; *A. alba* for *R. mucronata*; and two other—*A. integra* appears to a sibling derivative of *A. officinalis* while *A. rumphiana* is a sibling derivative of *A. marina*.

Then, while *Sonneratia* is only recorded in the IWP, the corresponding species for that comparison include *S. alba* for *R. stylosa*; *S. apetala* for *R. apiculata*; *S. caseolaris* for *R. mucronata*; and three others—*S. lanceolata* is a sibling derivative of *S. caseolaris*; but *S. ovata* and *S. griffithii* appear to be outlier derivatives of *S. alba*.

For *Bruguiera* in the IWP only, the corresponding species for that comparison include *B. exaristata* for *R. stylosa*; *B. parviflora* for *R. apiculata*; *B. gymnorhiza* for *R. mucronata*; while *B. sexangula* is a derivative of *B. gymnorhiza*; but *B. cylindrica* and *B. hainesii* are outlier derivatives of *B. parviflora*.

For *Ceriops* in the IWP only, the corresponding species for that comparison include *C. australis* for *R. stylosa*; *C. decandra* for *R. apiculata*; *C. tagal* for *R. mucronata*; while *C. zippeliana* and *C. pseudodecandra* are outlier derivatives of *C. decandra*.

While these comparable groupings and patterns require further validation, they do match the hypothesis of common overall dominance of geophysical influences over individual differences in affected taxa. In making this case, it is not suggested that mangrove taxa have common rates of evolution or common taxonomic diversification, nor that we should underestimate the importance of individual functional differences, like dispersal capabilities, propagule longevity, and phenologies. In fact, it is more likely that with greater awareness of such shared influences, this will allow greater understanding of the deterministic role of individual attributes in the evolution of each taxon.

## 2.9 Shared Evolutionary Processes and Dispersal Pathways

The first step is to review the initial patterns in distributional occurrences with the known dispersal endpoints for each taxa. All mangrove species (excluding recognized hybrid intermediates) have been assigned to 15 spatiotemporal endpoint groupings, summarized in Table 2.4. Five groups occur in the AEP with two on northern coastlines and three on southern coastlines, notably within its ancient Tethyan context. Similarly, 10 groups occur in the IWP with three on northern coastlines and seven on southern coastlines. Groups with repeated names and number, represent likely overlapping dispersal routes associated with similar extant locations.

To better understand these groupings, each has been located on an Eocene map (Fig. 2.5, starting from red-shaded continents). On this map, ancient dispersal barriers and pathways of the day (~40 mya) have also been tentatively defined (cp. Fig. 2.2). Dominant barriers include temperature (active across latitudes), sea distances (defined by the dispersal and establishment capability of each species), and

**Table 2.4** Assignment of 70 extant mangrove taxa (species, subspecies, varieties) to 18 dispersal endpoints grouped west (A–E) and east (F–O) of the ancient Tethys Ocean 40–55 mya (see Figs. 2.5 and 2.6). Each is then further assigned to northern or southern hemispheres, as separating increasingly isolated shorelines. These groups correspond with 12 dispersal pathways, discussed later (see Table 2.5). See Appendix 2 for specific group attributions and estimates of taxa numbers and approximate age (mya)

Site #	Dispersal Endpoints	Description	Taxa	Age mya
A	<b>Atlantic Central America</b>	Northern Tethys West	7	25-40
B	<b>Pacific Central America</b>	Northern Tethys West	8	3-4
C	<b>Northern South America</b>	Southern Tethys West	5	25-40
D	<b>Pacific South America</b>	Southern Tethys West	5	3-4
E	<b>South West Pacific</b>	Southern Tethys West	1	2
F	<b>Australia 1</b>	Southern Tethys East	11	10-25
G	<b>Middle East 1</b>	Southern Tethys East	10	25-40
H	<b>South China Sea 1</b>	Southern Tethys East	10	25
I	<b>Australia North 2</b>	Southern Tethys East	10	5-10
J	<b>India</b>	Southern Tethys East	10	40
K	<b>South China Sea 2</b>	Southern Tethys East	10	25
L	<b>Australia North 3</b>	Southern Tethys East	10	5-10
M	<b>Middle East 2</b>	Northern Tethys East	18	25-40
N	<b>South China Sea 3</b>	Northern Tethys East	20	10-25
O	<b>Australia North 4</b>	Northern Tethys East	19	5-10

land barriers (where they prevent water-borne dispersal). Fossil evidence has helped define the effectiveness and presence of these ancient barriers (cs. Plaziat et al. 2001).

As proposed for the evolution of *Rhizophora* taxa (Fig. 2.4; Duke et al. 2002), these were widely distributed before closure of the Tethys Sea during the latter Eocene, around 45 mya. Using the Eocene map in Fig. 2.5, there were a number of mangrove genera present along the northern and southern shorelines of the Tethys, of Laurasia, and Gondwana, respectively. With the northward movement of Africa, the Tethys closed cutting off western and eastern distributions. The effect would have been to isolate northern and southern populations that separated over time, becoming more isolated entities in AEP and IWP regions. All these observations, and those that follow, are based on known extant and fossil records, in full consideration of individual attributes of each relevant species entity.

Those in the AEP are likely to have dispersed westward in two more or less separate pathways: a southern path along the coasts of West Africa and South America; and, a northern path along the North American east coast, forced south as conditions cooled, and the Atlantic widened.

For the IWP, dispersal eastward had also started out following two isolated pathways: a northern path along the coast to the Middle East and Southeast Asia; and, a southern path along the coasts of East Africa, India, and Australia. To complicate the dispersal outcomes, the latter two land masses with mangrove inhabitants moved rapidly north at different times to collide with the Middle East and Southeast Asia (respectively) during this period.

In both AEP and IWP, there were, at first, partly isolated pathways that independently later reunited toward their respective dispersal extremes. This has led to the consequential genesis of greater diversity and further radiation that now characterizes each region – and, it has led to the creation of the respective hot spots of extant diversity. The greater complexity of geomorphic changes in the IWP is presumed to be the reason for the greater genetic diversity in that region.

Combining these observations, the proposed common dispersal pathways are depicted in 12 key locations of likely isolation (Table 2.5), leading to genetic differentiation and speciation for respective mangrove genera (Figs. 2.5 and 2.6, Appendix 2). These relate also to the 15 extant location endpoints (Table 2.4). The broad assessment of evidence considered for these depictions include, location and age of fossil records; period maps of continental drift; distribution maps of each species; phylogenetic relationships between and among taxa; extant discontinuities; and key barriers of land, water, and climate.

The decision for grouping species in this treatment is based on the idea that instances of genetic divergence and speciation could only have taken place when circumstances resulted in prolonged isolation or during founder events where dispersal from established populations might have reached unoccupied niches suitable for mangrove establishment and diversification. And, that these circumstances would be utilized by all genetic entities present at the time.

## 2.10 Common Drivers of Diversification and Speciation

While it appears less likely that mutations amongst mangroves taxa have led to genetic differentiation in a process of sympatric speciation (Maynard-Smith 1966), there are other features of these taxa indicative of other recognizable processes of speciation. One is the number of closely related, sibling taxa. While it is notable that some sibling taxa have slightly different ecological preferences, the ranges of these entities often overlap. This implies that the reason for their isolation is no longer applicable, with once separate populations being reunited.

Considering all relevant evidence, it seems the diversification of mangrove plants has largely been driven by three key processes of speciation:

- (a) *Allopatric speciation* (Mayr 1970): incidents of isolation by land, sea, or temperature barriers blocking gene flow
- (b) *Peripatric speciation* (Provine 2004): founder populations (with their smaller subset of genes) multiplying rapidly into more or less vacant habitat
- (c) *Parapatric speciation* (Doebeli and Dieckmann 2003): the reunification of extreme ends of wide, linearly distributed species (as with the broad global shoreline surrounding the Tethys Sea) having notable diversification and genetic drift along its length

The number and diversity of families and genera with representatives specialized for mangrove habitat clearly show that the evolution and speciation of mangrove

**Table 2.5** Proposed common dispersal pathways are depicted in 12 key locations of likely isolation, leading to genetic differentiation and speciation for the respective mangrove genera (Figs. 2.5 and 2.6, Appendix 2). These relate to 15 extant location endpoints (Table 2.4). The broad assessment of evidence considered for these depictions include the following: location and age of fossil records; period maps of continental drift; distribution maps of each species; phylogenetic relationships between and among taxa; extant discontinuities; and key barriers of land, water, and climate

Path #	Dispersal pathway	Description	Age mya
1	AEP + IWP	Division of the AEP and IWP with the closure of the Tethys Sea, isolated by the landmass of Africa and Laurasia	40–55
2	AEP South West	AEP South Western pathway from West Africa and across the widening Atlantic to eastern South America; later more or less isolated by the Atlantic but reunited with the North-Western taxa	25–40
3	AEP extreme South West	AEP across northern South America to the western coast, later isolated by the Caribbean American Isthmus	3–4
4	AEP North West	AEP North Western pathway from western Laurasia (Europe) and across the widening North Atlantic to eastern North America; soon isolated by the Atlantic but later reunited with the South-Western taxa	25–40
5	AEP extreme North West	AEP across southern North America to the western coast, later isolated by the Caribbean American Isthmus	3–4
6	IWP South East Africa	IWP South Eastern pathway from northern Africa to eastern Africa into the Indian Ocean; later reunited with Middle Eastern taxa	25–40
7	IWP South East India	IWP from East Africa northward across the Indian Ocean on the Indian landmass to collide with the Middle East; reuniting respective taxa	40
8	IWP South East Australia	IWP from East Africa south and eastward across the Indian Ocean to Australia when breaking away from Gondwana to travel north towards South East Asia to reunite respective taxa	10–25
9	IWP extreme Australia	IWP around Australia from the north coast to isolated founding populations in South East Asia, as Australia collided with the Austral Malesian Archipelago	5–10
10	IWP North East	IWP north eastern pathway from the Middle East to South East Asia	24–40
11	IWP extreme North East	IWP from South East Asia to the South China Sea, to be first isolated by the earlier barrier of the Sund Peninsula (submerged as the Austral Malesian Archipelago), and then later reunited with its submergence	10–25
12	IWP North East Australia	IWP from the Austral Malesian Archipelago to northern Australia, as Australia collided with the Austral Malesian Archipelago	5–10

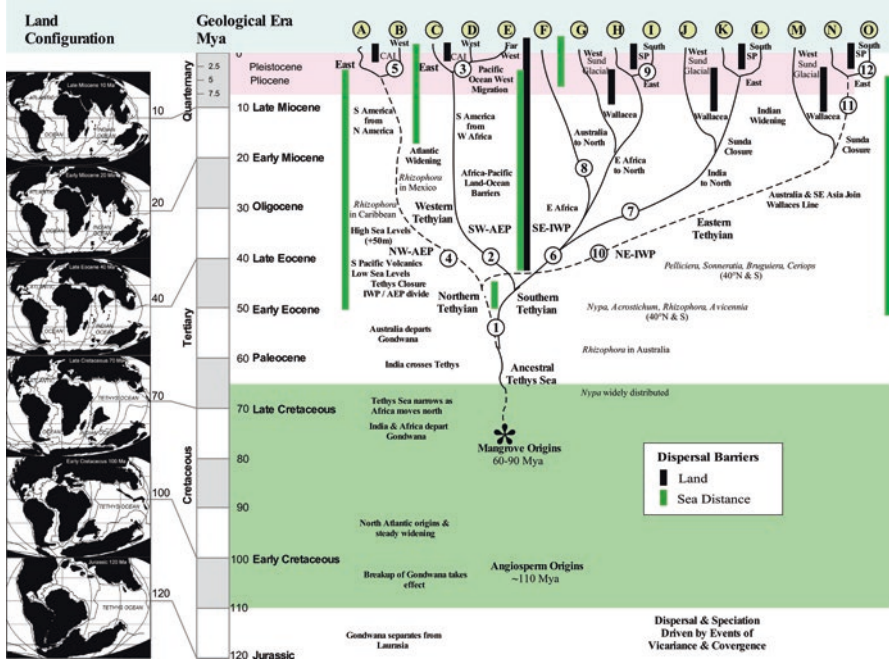


Fig. 2.6 Proposed timeline of common phylogenies of all mangrove species noting global dispersal points (A–O) and dispersal pathways (1–12). Also see Fig. 2.5

plants has taken place on multiple occasions, and independently within various families and genera. As the drivers of diversification and speciation appear strongly influenced by major geological and climatic events, it seems reasonable to conclude that respective phylogenetic pathways of each genetic entity might follow a common structure. The premise is that all taxa have been mostly subjected to the same guiding dominant influences with the same notable events of speciation.

In Fig. 2.6, a common, encompassing phylogenetic tree structure is proposed for the derivation of every mangrove plant taxa. The pathway describes how a small number of progenitors of key plant genera might have diversified from their respective origins during the last 60–90 my. During this time, mangrove taxa appear to have first dispersed east and west, then along northern and southern shores of a diminishing Tethys Sea. The dominant genera had reportedly distributed globally long before closure of the ancient Tethys Sea during the mid-Eocene period, around 45 mya (Plaziat et al. 2001). This is consistent with the presence of dominant mangrove genera in both AEP and IWP regions today. It is notable that similar patterns occur in seagrass and corals (Hoeksema 2007).

Dominant and widespread mangrove genera include *Nypa*, *Rhizophora*, *Avicennia*. While *Nypa* has no reported diversification more than its apparently sole species entity, the other two have clear diversification with speciation for common



specialized ecological niches, as well as comparable distinct regional forms. This implies these taxa were influenced by a common driver, where the physical environment might have strongly guided and helped form the necessary mangrove traits and features that individually characterize each taxon. While the precise origin of these primary mangrove taxa remains unknown, the separation of South America from Africa would have provided the necessary physical circumstances consistent with the creation of mangrove traits. These circumstances include a slow and progressive increase in salinities as two massive, complex estuarine margins spread apart before becoming the southern Atlantic Ocean. And, this all would have taken place in the formative early years of flowering plants, around 90–110 mya.

It is also curious why so many groups of plants of such antiquity have so few species today, and why these plants have mostly remained unchanged throughout their long fossil record, up to 55 my. A key deduction is that events causing speciation have been rare. And, this concept is consistent with the current proposition of a common phylogenetic structure for the evolution of extant mangrove plants. This is especially the case since each instance of speciation must have been marked by notable and very unusual circumstances. While these events appear to have determined the common phylogenetic tree structure, this does in no way imply that all mangroves originated from the same place, or at the same time. But, it does however provide a means to narrow down the options for determining the individual features of each species and genotype.

For limited range species, like *Mora oleifera* (Duke 2013, 2014a; see Appendix 2), there are a number of important knowledge gaps. This species, restricted to the Pacific coast of Central America, appears to have originated quite recently as there are few if any fossil records. Of course, this observation would be amended if there were fossil evidence, and/or, if this species were found to have unusual dispersal limitations. While there may be other questions about its nearest relatives (nearby, there are 7–9 upland species of *Mora*), it is of some interest that this species has exceptionally large propagules—the largest embryo of any plant. But, it is not really known how buoyant they are, or whether they might be predated upon by small crabs, like those consuming *Pelliciera* propagules (Dangremond 2015). Its limited distributional range however is consistent with either poor dispersal, or that it is newly evolved, or both.

Such questions concern most, if not all, mangrove taxa. So, in the absence of further evidence, it may be concluded that species with limited distributions, might also have recent origins. For example, it was deduced for *Mora oleifera* therefore, that this species was likely to have arisen after closure of the Central American Isthmus, less than 3–4 mya.

Another taxon, the genus *Camptostemon*, appears to have been around only after 10–25 mya, and diversified as two species around 5–10 mya.

Taxa like the genus *Lumnitzera*, are more difficult to place. While the genus is restricted to the IWP, this does imply its post-Tethyan origins, since 40 mya. However, its subsequent diversification and its occurrence in East Africa, does suggest its presence along the Southern Tethys Eastern pathway rather than in the north. There does not appear to be any relevant major dispersal events from north to south.

As such, the two species appear to have diverged with the passage of India north, leaving the other entity to possibly migrate eastward unchanged to Australia.

A summary of estimated ages for mangrove-related representatives from all 32 genera is shown in Table 2.3. While the deductions may be altered and amended in the future as new information comes to hand, the proposed common phylogenetic tree structure does offer a practical working understanding of how and where each mangrove species evolved and dispersed to locations where they exist today.

## 2.11 Summary and Conclusions

In summary, there are six key deductions and findings raised in this treatment:

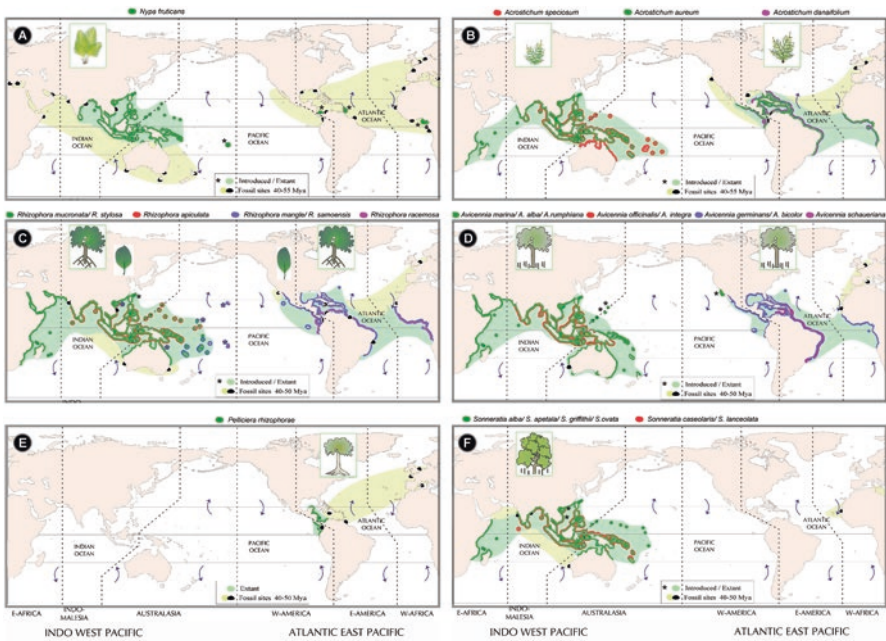
1. The mangrove niche is inhabited by around 80 tree and shrub species (including 11 hybrid intermediates) of 32 genera from 17 families worldwide. These mangrove species are widely distributed, but constrained by natural barriers of temperature, water distance, and land masses. For the most part, the effectiveness of each barrier is self-evident, marked by genetic differences or endpoints, as genetic discontinuities.
2. The natural distribution of individual species and genotypes are mostly distinct with few occupying the same range. Taxa are individually constrained by their respective tolerances for key functional factors like temperature, precipitation and evaporation, salinity, soil type, inundation frequency and tidal regimes, as well as individual adaptations in anatomy, physiology, phenology, propagule buoyancy and dispersal longevity, and establishment ability.
3. There are significant instances where extant dispersal barriers have been fully effective in recent times, leaving suitable habitat niches vacant. Because mangrove plants all have buoyant, water-dispersed propagules, the effectiveness of land mass barriers are self-evident. This is complicated for barriers of climate (temperature, rainfall) and water distance because these are dependent on individual capabilities and tolerances of each plant type. But, in all cases, when people intervene by introducing a plant type to habitat previously unoccupied by that genotype, this proves two things: a) that suitable habitat was available; and b) that the introduced entity was unable to disperse and arrive there naturally.
4. There are a number of genetic discontinuities that lack obvious current-day barriers. These can only be explained by past geological circumstances where previous barriers are no longer effective, like Wallace's line in the IWP. The presence of these occurrences implies there can be appreciable lags in genetic mixing and natural dispersal amongst previously established populations. The relevance and role of each discontinuity is determined by its location; its geological age; and, the level of taxonomic differences in responsible biota.
5. Species distributions worldwide are divided naturally into two global regions of the Indo West Pacific (IWP) and Atlantic East Pacific (AEP), distinguished by relatively high level taxonomic differences in families and genera. Genetic hot

spots are present in each region, but that in the IWP is well recognized for its concurrent and comparable concentrations of mangroves, corals, sea grasses, reef fishes; collectively and individually known for its globally high diversity as the hot spot triangle. These common diversity patterns across different plant and animal taxa demonstrate the overwhelming dominance of geo-physical circumstances over individual functional differences in biota. In this way, plant and animal life appears more to have been shaped and driven by their individual responses to the changing geophysical environment, rather than the other way around.

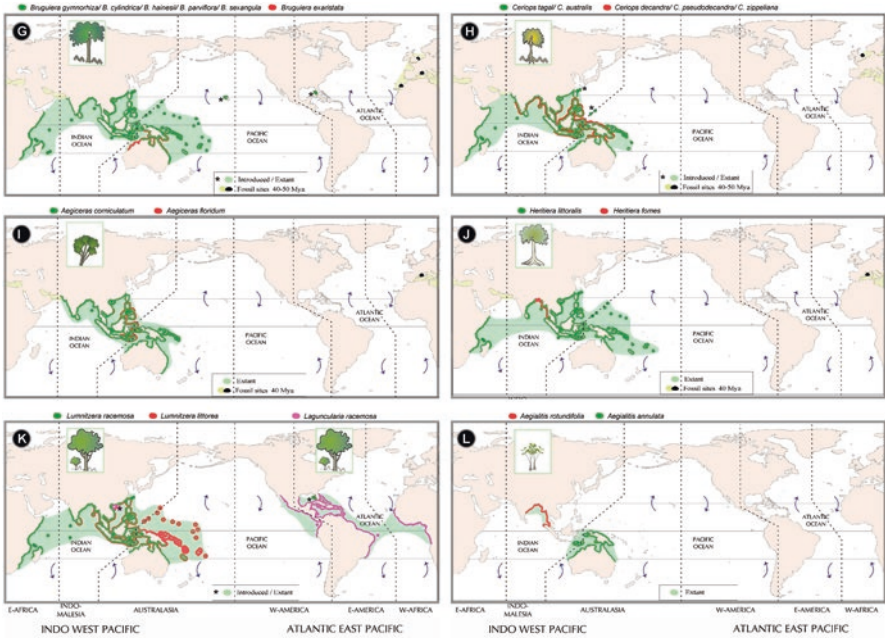
6. In conclusion, this treatment offers the novel hypothesis that all mangrove species have dispersed, diversified, and evolved following more or less, common, overall phylogenetic pathways formed by the overwhelming geophysical occurrences over the last 100 my. And, it is within these constraints that each taxon displays its individual differences depending on their own circumstances in genesis location and date, as well as their biological capabilities and tolerances in growth and mutation, including their notable attributes of propagule buoyancy, longevity, and establishment success.

## Appendix 1

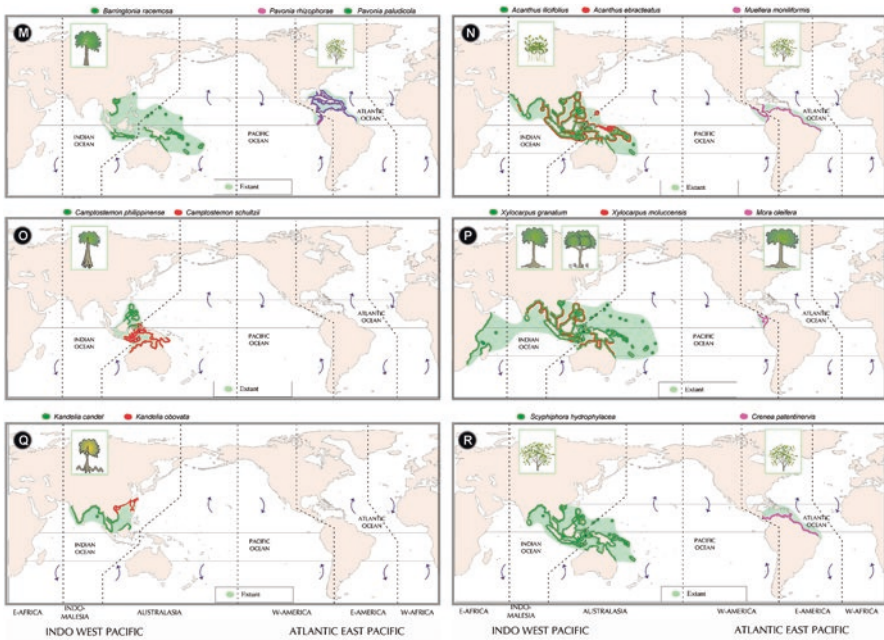
*Distribution Maps.* Listed are 24 distribution maps (A–X) showing 32 genera with 70 species of mangrove plants. Hybrid species are not included because their ranges for the most part match the overlapping distributions of parental taxa. For more references, specific descriptions, images, and distributional maps of each species, refer to the *World Mangrove* e-book app (Duke 2013, 2014a).



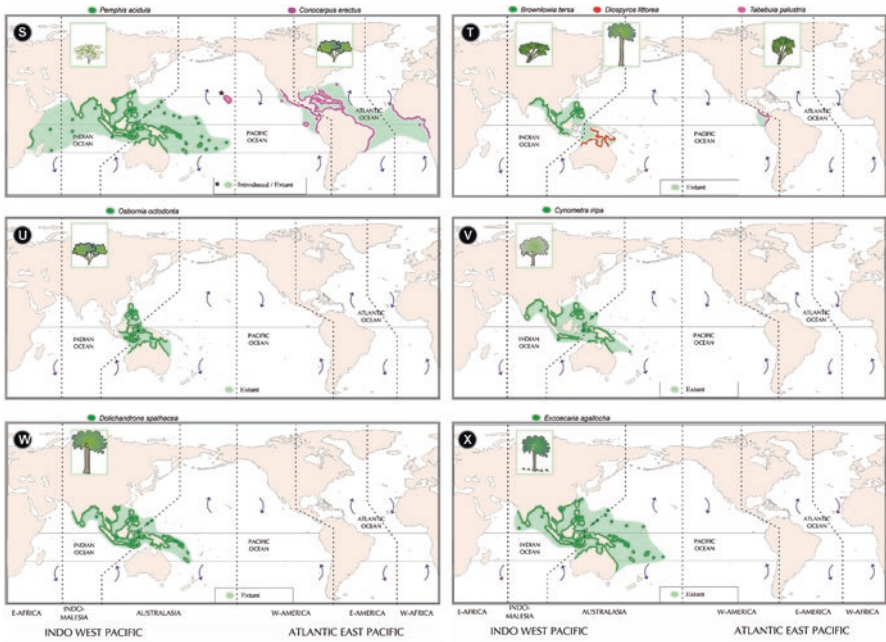
**Fig. 2.7** (A) Distribution of mangrove species of the genus *Nypa*, showing extant, introduced, and fossil occurrences. Species: *N. fruticans* van Wurm 1781. (B) Distribution of mangrove species of the genus *Acrostichum*, showing extant, introduced, and fossil occurrences. Species: *A. aureum* L. 1753, *A. danaeifolium* Langsdorff and Fischer 1810, *A. speciosum* Willd. 1810. (C) Distribution of mangrove species of the genus *Rhizophora*, showing extant, introduced, and fossil occurrences. Species: *R. mucronata* Lam. 1804, *R. stylosa* Griff. 1854, *R. apiculata* Blume 1827, *R. mangle* L. 1753, *R. samoensis* (Hochr.) Salvoza 1936, *R. racemosa* Meyer 1818. (D) Distribution of mangrove species of the genus *Avicennia*, showing extant, introduced, and macro fossil occurrences. Species: *A. marina* (Forssk.) Vierh. 1907, *A. alba* Blume 1826, *A. rumphiana* Hallier f. 1918, *A. officinalis* L. 1753, *A. integr*a N.C. Duke 1988, *A. germinans* (L.) Stearn 1958, *A. bicolor* Standley 1923, *A. schaueriana* Stapf and Leechman ex Moldenke 1939. (E) Distribution of mangrove species of the genus *Pelliciera*, showing extant and fossil occurrences. Species: *P. rhizophorae* Planchon & Triana 1862. (F) Distribution of mangrove species of the genus *Sonneratia*, showing extant, introduced, and fossil occurrences. Species: *S. alba* J.Sm. in A.Rees 1816, *S. apetala* Buch.-Ham. 1800, *S. griffithii* Kurz 1871, *S. ovata* Backer 1929, *S. caseolaris* (L.) Engl. 1897, *S. lanceolata* Blume 1851



**Fig. 2.8** (G) Distribution of mangrove species of the genus *Bruguiera*, showing extant, introduced, and fossil occurrences. Species: *B. gymnorhiza* (L.) Savigny ex Lam. & Poirlet 1798, *B. cylindrica* (L.) Blume 1828, *B. hainesii* C.G. Rogers 1919, *B. parviflora* (Roxb.) Griff. 1836, *B. sexangula* (Lour.) Poir. 1816, *B. exaristata* Ding Hou 1956. (H) Distribution of mangrove species of the genus *Ceriops*, showing extant, introduced, and fossil occurrences. Species: *C. tagal* (Perr.) C.B. Robinson 1908, *C. australis* (C.T.White) Ballment, T.J. Sm. & J.A. Stoddart 1988, *C. decandra* (Griff.) Ding Hou 1958, *C. pseudodecandra* Sheue, Liu, Tsai and Yang 2010, *C. zippeliana* Blume 1849. (I) Distribution of mangrove species of the genus *Aegiceras*, showing extant and fossil occurrences. Species: *A. corniculatum* (L.) Blanco 1837, *A. floridum* Roemer & Schultes 1819. (J) Distribution of mangrove species of the genus *Heritiera*, showing extant and fossil occurrences. Species: *H. littoralis* Aiton 1789, *H. fomes* Buch.-Ham. 1800. (K) Distribution of mangrove species of the genus *Laguncularia* and *Lumnitzera*, showing native and introduced occurrences. Species: *Laguncularia racemosa* (L.) Gaertn. f. 1805; *Lumnitzera racemosa* Willd. 1803, *Lumnitzera littorea* (Jack) Voigt 1845. (L) Distribution of mangrove species of the genus *Aegialitis*. Species: *A. annulata* R.Br. 1810, *A. rotundifolia* Roxburgh 1824



**Fig. 2.9** (M) Distribution of mangrove species of the genus *Barringtonia* and *Pavonia*. Species: *B. racemosa* (L.) Spreng. 1826; *P. paludicola* Nicolson ex Fryxell 1989, *P. rhizophorae* Killip. ex Kearney 1954. (N) Distribution of mangrove species of *Acanthus* and *Muellera* genera. Species: *A. ebracteatus* Vahl 1791, *A. ilicifolius* L. 1753; *M. moniliformis* L.f. 1781. (O) Distribution of mangrove species of the genus *Camptostemon*. Species: *C. philippinense* (Vidal) Becc. 1898, *C. schultzii* Mast. 1872. (P) Distribution of mangrove species of the genus *Mora* and *Xylocarpus*. Species: *M. oleifera* (Triana) Ducke 1925; *X. granatum* J.König 1784, *X. moluccensis* (Lam.) M. Roemer 1846. (Q) Distribution of mangrove species of the genus *Kandelia*. Species: *K. candel* (L.) Druce 1914, *K. obovata* C.R. Sheue, H.Y. Liu & W.H. Yong 2003. (R) Distribution of mangrove species of the genus *Crenea* and *Scyphiphora*. Species: *C. patentinervis* (Koehne) Standl. 1947; *S. hydrophylacea* C.F. Gaertn. 1791



**Fig. 2.10** (S) Distribution of mangrove species of the genus *Conocarpus* and *Pemphis*, showing native and introduced occurrences. Species: *C. erectus* L. 1753; *P. acidula* J.R. Forst. & G. Forst. 1775. (T) Distribution of mangrove species of the genus *Brownlowia*, *Diospyros*, and *Tabebuia*. Species: *B. tersa* (L.) Kosterm. 1959; *D. littoralis* (R.Br.) Kosterm. 1977; *T. palustris* Hemsl. 1882. (U) Distribution of mangrove species of the genus *Osbornia*. Species: *O. octodonta* F.Muell. 1863. (V) Distribution of mangrove species of the genus *Cynometra*. Species: *C. iripa* Kostel. 1835. (W) Distribution of mangrove species of the genus *Dolichandrone*. Species: *D. spathacea* (L.f.) K. Schum. 1889. (X) Distribution of mangrove species of the genus *Excoecaria*. Species: *E. agallocha* L. 1759

## Appendix 2

*Table of Species Groupings.* Presented are tables showing proposed phylogenetic groupings of 32 mangrove genera (A: with 8 genera, B: with 11 genera, and C: with 13 genera) with selections of key species in each of the 15 global spatiotemporal groupings discussed in the chapter.

**Table 6a** Proposed phylo-genetic groupings of 8 of 32 mangrove genera and all respective species in 15 spatio-temporal groups

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Northern Ailur_Galmer	Tethys West Pacif_Salmer	Southern Nor_Salmer	Tethys West Pacif_Salmer	SW_Pacific	Southern Austral 1	Tethys East Mid_East 1	S_China_S 1	N_Austral 2	India	S_China_S 2	N_Austral 3	Mid_East 2	S_China_S 3	N_Austral 4
25-40 mya >	3-4 mya >	25-40 mya >	3-4 mya >	2 mya >	< 10-25 mya >	< 25-40 mya >	25 mya	< 5-10 mya >	< 40 mya >	25 mya	< 5-10 mya >	< 25-40 mya >	< 10-25 mya >	< 5-10 mya >
<Extinct/ Reintrod>	<Extinct/ Reintrod>	<Extinct/ Reintrod>	<Extinct>		Nypa fruticans?	<Extinct>						Nypa fruticans	Nypa fruticans	Nypa fruticans
Acrostichum daneifolium	Acrostichum daneifolium	Acrostichum aureum	Acrostichum aureum		Acrostichum aureum	Acrostichum aureum	Acrostichum aureum	Acrostichum m aureum	Acrostichum aureum	Acrostichum aureum	Acrostichum aureum	Acrostichum speciosum	Acrostichum speciosum	Acrostichum speciosum
Rhizophora racemosa	Rhizophora racemosa	Rhizophora margin	Rhizophora samoensis	Rhizophora samoensis	Rhizophora stylosa	Rhizophora micronata	Rhizophora micronata	Rhizophora micronata	Rhizophora micronata	Rhizophora micronata	Rhizophora micronata	Rhizophora apiculata	Rhizophora apiculata	Rhizophora apiculata southern
Avicennia germinans	Avicennia germinans	Avicennia schaueriana	Avicennia bicolor		Avicennia marina varieties	Avicennia marina varieties	Avicennia rumphiana	Avicennia rumphiana	Avicennia alba varieties	Avicennia alba varieties	Avicennia alba varieties	Avicennia officialis	Avicennia officialis	Avicennia integra
Pelticera rhizophorae red	Pelticera rhizophorae red				Pelticera rhizophorae									
		<Extinct>			Sonneratia alba	Sonneratia alba	Sonneratia griffithii	Sonneratia ovata	Sonneratia caecolaris	Sonneratia lanceolata	Sonneratia lanceolata	Sonneratia apetala		
		<Extinct>			Bruguiera exaristata	Bruguiera gymnorhiza	Bruguiera gymnorhiza	Bruguiera gymnorhiza	Bruguiera seangula	Bruguiera seangula	Bruguiera seangula	Bruguiera parviflora	Bruguiera cylindrica	Bruguiera cylindrica
					Ceriops australis	Ceriops tagal	Ceriops tagal	Ceriops tagal	Ceriops tagal	Ceriops tagal	Ceriops tagal	Ceriops decandra	Ceriops zippelliana	Ceriops pseudodecandra



**Table 6b** Further proposed phylogenetic groupings of 11 of 32 mangrove genera and all respective species in 15 spatiotemporal groups

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Northern	Tethys West	Southern	Tethys West	← Tethys →	Southern	Tethys East						Northern Tethys East		
Atlan_CAmer	Pacif_CAmer	Nor_SAmer	Pacif_SAmer	SW_Pacific	Austral 1	Mid_East1	S_China_S1	N_Austral2	India	S_China_S2	N_Austral3	Mid_East 2	S_China_S3	N_Austral 4
25-40 mya >	3-4 mya >	25-40 mya >	3-4 mya >	2 mya >	< 10-25 mya	< 25-40 mya	25 mya	< 5-10 mya	< 40 mya	25 mya	< 5-10 mya	< 25-40 mya	< 10-25 mya	< 5-10 mya
					Heritiera littoralis	Heritiera littoralis	Heritiera littoralis	Heritiera littoralis	Heritiera littoralis	Heritiera littoralis	Heritiera littoralis	Heritiera fomes	Heritiera globosa	
					Lumnitzera racemosa	Lumnitzera racemosa	Lumnitzera racemosa	Lumnitzera racemosa	Lumnitzera littorea	Lumnitzera littorea	Lumnitzera littorea			
					Pemphis acidula	Pemphis acidula	Pemphis acidula	Pemphis acidula	Pemphis acidula	Pemphis acidula	Pemphis acidula			
					Xylocarpus granatum	Xylocarpus granatum	Xylocarpus granatum	Xylocarpus granatum	Xylocarpus rumphii	Xylocarpus rumphii	Xylocarpus rumphii	Xylocarpus moluccensis	Xylocarpus moluccensis	Xylocarpus moluccensis
												Agliceras floridum	Agliceras coniculatum	Agliceras coniculatum
		Conocarpus erectus	Conocarpus erectus	×								Brownlowia tersa	Brownlowia tersa	Brownlowia argentata
		Laguncularia racemosa	Laguncularia racemosa	×								Dolichandrone spathacea	Dolichandrone spathacea	Dolichandrone spathacea
Crenoa patentervis				×								Kandelia candel	Kandelia obovata	Kandelia obovata

**Table 6c** Further proposed phylo-genetic groupings of 13 of 32 mangrove genera and all respective species in 15 spatio-temporal groups

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Northern	Tethys West	Southern	Tethys West	← Tethys →	Southern	Tethys East						Northern Tethys East		
Atlas_C_Amer	Pacif_C_Amer	Nor_S_Amer	Pacif_S_Amer	← AEP-IMP →	Austral 1	Mid_East 1	S_China_S 1	N_Austral 2	India	S_China_S 2	N_Austral 3	Mid_East 2	S_China_S 3	N_Austral 4
25-40 mya >	3-4 mya >	25-40 mya >	3-4 mya >	< 40-55 mya >	< 10-25 mya	< 25-40 mya	25 mya	< 5-10 mya	< 40 mya	25 mya	< 5-10 mya	< 25-40 mya	< 10-25 mya	< 5-10 mya
Pavonia paludicola	Pavonia rhizophoreae			X								Aegialitis retundifolia	Aegialitis annulata	Aegialitis annulata
Muellera moniliformis	Muellera moniliformis			X								Acanthus ilicifolius	Acanthus ebracteatus	Acanthus ebracteatus ebarbatus
	Morza obliifera			X								Cynometra iripa	Cynometra iripa	Cynometra iripa
	Tabebuia palustris			X								Scyphiphora hydrophyllacea	Scyphiphora hydrophyllacea	Scyphiphora hydrophyllacea
												Excoecaria agallocha	Excoecaria agallocha	Excoecaria agallocha ovalis
													Campylodemon philippense	Campylodemon philippense
													Barringtonia racemosa	Barringtonia racemosa
													Osbornia octodonta	Osbornia octodonta
														Disopyros fitorea

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