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Mangroves: Unusual Forests at the Seas Edge

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Abstract

Mangroves form distinct sea-edge forested habitat of dense, undulating canopies in both wet and arid tropic regions of the world. These highly adapted, forest wetland ecosystems have many remarkable features, making them a constant source of wonder and inquiry. This chapter introduces mangrove forests, the factors that influence them, and some of their key benefits and functions. This knowledge is considered essential for those who propose to manage them sustainably. We describe key and currently recommended strategies in an accompanying article on mangrove forest management (Schmitt and Duke 2015).

Keywords

Mangroves; Tidal wetlands; Tidal forests; Biodiversity; Structure; Biomass; Ecology; Forest growth and development; Recruitment; Influencing factors; Human pressures; Replacement and damage

Mangroves: Forested Tidal Wetlands

Introduction

Mangroves are trees and shrubs, uniquely adapted for tidal sea verges of mostly warmer latitudes of the world (Tomlinson 1994). Of primary significance, the tidal wetland forests they form thrive in saline and saturated soils, a domain where few other plants survive (Fig. 1). Mangrove species have been independently derived from a diverse assemblage of higher taxa. The habitat and structure created by these species are correspondingly complex, and their features vary from place to place. For instance, in temperate areas of southern Australia, forests of *Avicennia* mangrove species often form accessible parkland stands, notable for their openness under closed canopies (Duke 2006). By contrast, along tropical equatorial coastlines, and most everywhere else in the world, *Rhizophora* species ubiquitously dominate as more or less impenetrable thickets and forests of arching stilt roots (Fig. 2).

A well-recognized benefit of mangrove forests is their fundamental role in coastal erosion, flooding and storm protection, and fisheries where the habitat they form, uniquely provides shelter and food for marine bait species, as well as the nurturing of juvenile commercial species of fish, crustaceans, and mollusks (e.g., Meynecke et al. 2008). The forested stands are known also for their traditional forest products, including timber for construction and local energy demands (e.g., Walters 2005). Despite these uses, and others, these wetland forests have only in a few instances been managed sustainably. This is largely because of the different ways these places respond to extreme pressures experienced by shoreline tidal

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Fig. 1 Typical *Rhizophora*-dominated mangrove forest of tropical latitudes with tall stems based in a tangle of stilt roots. Tree heights can be 50 metre tall forests, or 1–2 metre impenetrable thickets (Boigu, Torres Strait, Australia; Photo N.C. Duke 2010)

Fig. 2 The complex stilt and aerial roots of *Rhizophora* mangroves (left, Ounjou, New Caledonia; Photo S. Virly 2013) contrast with *Avicennia* breathing roots, or pneumatophores, that often dominate mangroves of temperate regions, like southern Australia (right, Bunbury, Western Australia; Photo N.C. Duke 2013)

habitats. Furthermore, only a relatively few healthy functioning estuarine systems survive, mostly due to their isolation among an ever-diminishing number of protected coastal locations in the world.

The majority of mangrove habitats are under serious threat from direct human pressures and removal, coupled with increasing threats from sea level rise. Because mangroves are so intimately constrained to the tidal zone, all the inhabitants must regenerate elsewhere so the ecosystem can relocate upland and survive. While there is little doubt some human communities care for these habitats, there is an urgent need for all responsible, to better appreciate how these forests fundamentally differ from terrestrial forests. Armed with a greater understanding of their unique attributes, more appropriate management strategies can be applied to protect and manage them more effectively. But, where we are unable to apply such targeted forest management strategies, then the future of mangroves, as functional and beneficial habitat, is at best uncertain.

In general, healthy stands appear stable and long-lived, but appearances can be deceptive. Regrettably, these habitats are highly vulnerable. And, they are becoming increasingly more damaged and disturbed each year as the pressures mount (Duke et al. 2007). It seems the various benefits are not valued where it matters. A key aim with this chapter is to help improve our understanding of these ecosystems. The unique and extraordinary features of mangrove forests are described briefly. We point out the factors influencing them, along with their key benefits. In a companion chapter on mangrove management (Schmitt and Duke 2015), we describe how people are making a difference by adopting assessment, monitoring, and mitigation measures that will help enhance natural processes unique to this forested wetland habitat.

Why Are Mangroves So Important?

The short answer is “mangroves provide a wide range of ecosystem services” or in other words benefits people obtain from ecosystems. These include provisioning services (food, fiber, timber, fuel), regulating services (erosion protection, flood control, storm protection, climate regulation, biological regulation, pollution control, and detoxification), supporting services (biodiversity, soil formation, nutrient cycling), and cultural services (spiritual and inspirational, recreational, aesthetic, educational) (Millennium Ecosystem Assessment 2005).

Mangroves play an important role in coastal protection because they reduce wave energy (Mazda et al. 1997; Horstman et al. 2014) and by doing so reduce coastal erosion, erosion of sea dikes, and flooding. Figure 3 shows an example where the height of incoming waves is reduced from 1.0 m to 5 cm by a 1.5 km wide belt of 6-year-old mangroves; in areas without mangroves, the waves are reduced to 75 cm in height. Horstman et al. (2014) recorded a maximum wave energy reduction of 79 % over a 141 m transect of mangrove forest. In a review report, McIvor et al. (2012a) conclude that all evidence suggests that mangroves can reduce the height of wind and swell waves with a wave height of less than 70 cm between 13 % and 66 % over a stretch of 100 m of mangroves. In addition, storm surge water level reductions through mangroves from 5 to 50 cm per kilometer of mangrove forest width have been measured. One kilometer of mangrove forest is expected to reduce surface wind waves by more than 75 % (McIvor et al. 2012b). This has also clear financial benefits as has been shown for northern Vietnam. Here, US$ 1.1 million invested in mangrove rehabilitation saved dike maintenance costs of US$ 7.3 annually (Brown et al. 2006).

In addition to storm, flood, and erosion protection, mangroves provide food, shelter, and nursery ground for aquatic species. Many papers have been published about the benefits of mangroves for fisheries production. Some of them include compelling figures for the value of mangroves such as Schatz (1991) who estimated that 1 ha of healthy mangroves produces about 1.08 t of fish per year in the Philippines or Aburto-Oropeza et al. (2008) who calculated that 1 ha of mangroves contributes about US$ 37,500 per year to fisheries in the Gulf of California (Mexico).

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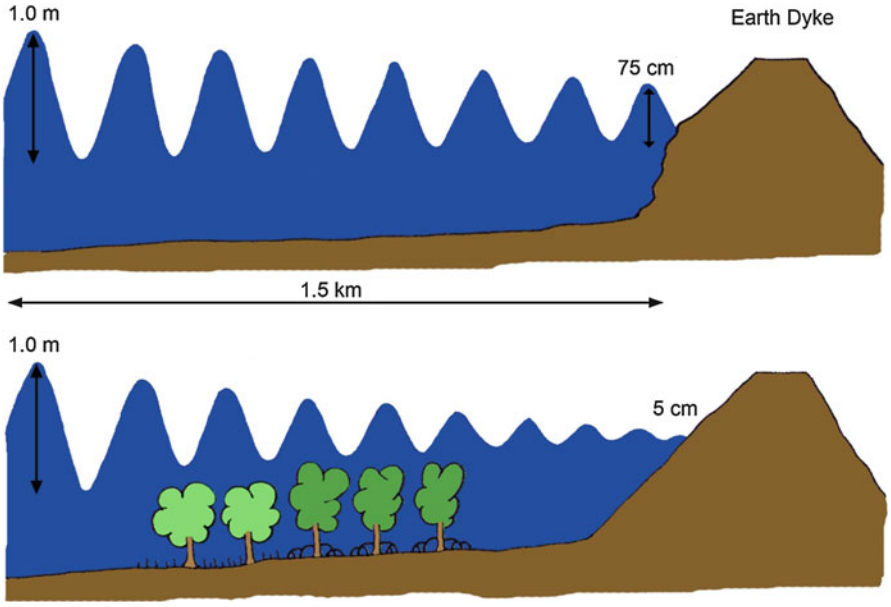

Fig. 3 Attenuation of wave height by a 1.5 km wide belt of 6 year old mangroves compared with an area of the same width without mangroves (modified from Mazda et al. 1997)

More recently Lee et al. (2014) provided a review of the roles of mangroves for (1) carbon dynamics – export or sink – (2) nursery role, (3) shoreline protection, and (4) land-building capacity. Literature about the land-building capacity of mangroves has also been reviewed by McIvor et al. (2013) and revealed rates of surface elevation increase between 1 mm/year and 10 mm/year. Therefore, in certain sites with sufficient sediment supply and without alteration in hydrological conditions, mangroves may be able to keep pace with sea level rise.

The important role of mangroves for carbon storage and thus for climate change mitigation has been discussed widely since the paper by Donato et al. (2011) which stated that mangroves are among the most carbon-rich forests in the tropics, containing on average 1,023 Mg carbon per hectare. The organic rich soils of mangrove forests in the Indo-Pacific region account for 49–98 % of the carbon storage of the mangrove forest area. "Combining our data with other published information, we estimate that mangrove deforestation generates emissions of 0.02–0.12 Pg carbon per year – as much as around 10 % of emissions from deforestation globally, despite accounting for just 0.7 % of tropical forest area" (Donato et al. 2011, p. 1).

Unusual Forest Type

Mangroves are one of the world's dominant coastal ecosystems comprised chiefly of trees and shrubs uniquely adapted to marine and estuarine tidal conditions (Tomlinson 1994). These tidal forests occupy an unusual and variable biome interfaced between land and sea, specifically between mean sea level and highest tide levels. They form distinctly vegetated and densely structured habitat with verdant closed canopies cloaking coastal margins and estuaries of equatorial, tropical, and subtropical regions around the world (Duke 2011). In wetter places, mangrove forests dominate intertidal margins of unconsolidated fine sediments. In more arid settings, mangroves share their tidal niche with diminutive cousins, a shrubby vegetation type called tidal salt marsh, plus salt pan expanses with a remarkable microalgal surface layer (Hyndes et al. 2014). With each annual wet season, these parched flats of dry dormant tiny plants burst into life to feed a host of waiting fish, crustaceans, and other dependent marine-estuarine life.

This zone around the world is the favoured niche of a small number of highly specialized plant species. Eighty or so overall form this unique habitat that is both complex and biomass rich. However, while the

Table 1 Mangrove species of the world (see Duke 2013; revised, updated ex Duke 1992; Duke et al. 1998). Families and genera shaded are exclusively mangrove. Genera marked with an asterisk have been classified previously as comprising their own family, namely, Aegialitidaceae, Aegicerataceae, Avicenniaceae, Barringtoniaceae, Diospyraceae, Nypaceae, and Sonneratiaceae, respectively. Species underlined refer to those of the Atlantic-East Pacific region. Species in bold occur naturally in both regions

Families with Mangroves	Family Relatives of Mangrove Taxa	Family Genera	Mangrove Genera	Non-Mangrove	Mangrove Spp.	Species (plus some varieties) of Mangroves
Acanthaceae	Black-eyed Susan, Shrimp plants	250–300	*Acanthus*	30	2	*Acanthus ebracteatus* subsp. *ebracteatus* *Acanthus ebracteatus* subsp. *ebarbatus* *Acanthus ilicifolius*
(Ex Verbenaceae)	Grey mangroves	1	*Avicennia**	0	8	*Avicennia alba* *Avicennia bicolor* *Avicennia germinans* *Avicennia integra* *Avicennia marina var. marina* *Avicennia marina var. australasica* *Avicennia marina var. eucalyptifolia* *Avicennia officinalis* *Avicennia rumphiana* *Avicennia schaueriana*
Arecaceae	Palms	200	*Nypa**	0	1	*Nypa fruticans*
Bignoniaceae	Tulip tree, jacarandas	120	*Dolichandrone*	9	1	*Dolichandrone spathacea*
			Tabebuia	245	1	*Tabebuia palustris*
Combretaceae	Combretum, Quiqualis	20	*Lumnitzera*	0	3	*Lumnitzera littorea* *Lumnitzera racemosa* *Lumnitzera* X *rosea*
			Laguncularia	0	1	*Laguncularia racemosa*
			Conocarpus	0	1	*Conocarpus erectus*
Ebenaceae	Ebony, persimmons	3	*Diospyros**	400	1	*Diospyros littorea*
Euphorbiaceae	Castor oil, spurges	300	*Excoecaria*	35–40	1	*Excoecaria agallocha* var. *agallocha* *Excoecaria agallocha* var. *ovalis*
Fabaceae (Ex Caesalpiniaceae)	Cassia, tamarind, legume	150	*Cynometra*	70	1	*Cynometra iripa*
			Muellera	3	1	*Muellera moniliformis*
			Mora	19	1	*Mora oleifera*
Lecythidaceae	Brazil nuts	15	*Barringtonia**	40	1	*Barringtonia racemosa*
Lythraceae	Crepe myrtle, henna, Cuphea	25	*Pemphis*	1	1	*Pemphis acidula*
			Crenea	50	1	*Crenea patentinervis*
	Duabanga	2	*Sonneratia* *	0	9	*Sonneratia alba* *Sonneratia apetala* *Sonneratia caseolaris* *Sonneratia griffithi* *Sonneratia* X *gulngai* *Sonneratia* X *hainanensis* *Sonneratia lanceolata* *Sonneratia ovata* *Sonneratia* X *urama*

(*continued*)

Table 1 (continued)

Malvaceae	Native hibiscus		*Brownlowia*	100	1	*Brownlowia tersa*
			Pavonia	3	2	*Pavonia paludicola* *Pavonia rhizophorae*
(Ex Bombaceae, or Fabaceae)	Baobab, balsa, kapok, durian	31	*Camptostemon*	0	2	*Camptostemon philippinense* *Camptostemon schultzii*
(Ex Sterculiaceae)	Cocoa, kola, bottle trees	70	*Heritiera*	29	2	*Heritiera fomes* *Heritiera littoralis*
Meliaceae	Mahogany, rosewood	50	*Xylocarpus*	1	2	*Xylocarpus granatum* *Xylocarpus moluccensis*
Myrtaceae	Eucalyptus, guavas	80–150	*Osbornia*	0	1	*Osbornia octodonta*
Pellicieraceae	Tea, Camellia, Franklinia	1	*Pelliciera**	0	1	*Pelliciera rhizophorae*
Plumbaginaceae	Sea lavender, thrifts	10	*Aegialitis**	0	2	*Aegialitis annulata* *Aegialitis rotundifolia*
Primulaceae (Ex Myrsinaceae)	Turnip-wood, mutton-wood	35	*Aegiceras**	0	2	*Aegiceras corniculatum* *Aegiceras floridum*
Pteridaceae	Ferns	35	*Acrostichum*	**0**	**3**	***Acrostichum aureum*** *Acrostichum speciosum* *Acrostichum danaeifolium*
Rhizophoraceae	Crossostylis, Cassipourea	16	*Bruguiera*	0	7	*Bruguiera cylindrica* *Bruguiera exaristata* *Bruguiera gymnorhiza* *Bruguiera hainesii* *Bruguiera parviflora* *Bruguiera* X *rhynchopetala* *Bruguiera sexangula*
			Ceriops	0	5	*Ceriops australis* *Ceriops decandra* *Ceriops pseudodecandra* *Ceriops tagal* *Ceriops zippeliana*
			Kandelia	0	2	*Kandelia candel* *Kandelia obovata*
			Rhizophora	0	12	*Rhizophora* X *annamalayana* *Rhizophora apiculata* *Rhizophora brevistyla* *Rhizophora* X *harrisonii* *Rhizophora* X *lamarckii* *Rhizophora mangle* *Rhizophora mucronata* *Rhizophora racemosa* ***Rhizophora samoensis*** *Rhizophora* X *selala* *Rhizophora stylosa* *Rhizophora* X *tomlinsonii*
Rubiaceae	Coffee, Gardinia, Quinine	500	*Scyphiphora*	0	1	*Scyphiphora hydrophylacea*

habitat has a relatively low number of taxa, the diversity of botanical lineages is high, shown by the 18 plant families represented (see Table 1). For the plants, their overall importance greatly exceeds their physical presence and stature. The diversity, extent, and intensity of influential factors have shaped this coastal habitat to reflect the highly dynamic forces acting at all temporal scales.

Mangroves are a unique ecological assemblage, remarkable for their relatively small number of widely distributed flowering plant types, evolved mostly post-Cretaceous over the last 60–100 million years (Tomlinson 1994; Duke 1995). The relatively recent evolution of these plants may explain their seemingly low diversity, but this feature has arguably also to do with the harsh environmental conditions defining the niche. Today's mangrove flora includes representatives of 18 plant families, as testament to the adaptive success of the various phylogenetic plant lineages venturing into the intertidal zone from mostly upland rain forest ancestors. This small group of highly specialized plants taps rich estuarine nutrients with characteristically shallow arrays of belowground roots with distinctively vascular, air-breathing anatomy. Specialized aboveground roots and buttresses further provide exposed air-breathing surfaces and physical support, as well as significant habitat among their overall structure, a feature shared notably with adjacent upland forests and reef-building corals.

While some phyletic origins remain uncertain (Lo et al. 2014), ancestral mangrove plant taxa are generally known to have reinvaded marine environments in multiple episodes from diverse angiosperm lineages, culminating in today's mangrove flora (Duke 2011). Their appearance and evolution appear constrained by key functional attributes essential to their survival in saline, inundated settings where isotonic extremes, desiccation, and hydrologic exposure combine as uniquely harsh constraints on organisms living in tidal zones and in estuaries. To achieve success in these conditions, mangroves share a number of ecophysiological traits with highly evolved mechanisms to cope with life at the land-sea interface. Key adaptations include salt tolerance, translocation of gases to aerate roots, and elaborate reproductive strategies.

The land-sea interface is a dynamic environment, where subtle natural changes in climate, sea level, sediment, and nutrient inputs have dramatic consequences for the distribution and health of mangroves (e.g., Gedan et al. 2011). Local human disturbance of mangroves includes eutrophication, dredging, landfill, overfishing, and sedimentation. The combined pressures of human disturbances (e.g., Duke et al. 2007) and global climate change have led to mangroves becoming "endangered communities" in numerous areas. Small-scale rehabilitation projects have demonstrated the great difficulty in scaling up to effective, large-scale restoration. Urgent specialized protective measures need to be implemented to avoid loss of mangroves and the resulting environmental degradation of coastal ecosystems, especially in the face of anticipated, rapid rises in sea level.

Mangroves Defined

Mangroves, also known as **mangrove forests**, are vegetated tidal habitat comprised of saltwater-tolerant trees and shrubs, forming a unique assemblage of plant types, sometimes called tidal forests or mangrove forests to distinguish them from the individual plants (Duke 1992). Mangrove plants are trees, shrubs, palms, or ground ferns, generally exceeding one half meter in height, that normally grow above mean sea level and below the highest tidal levels in soft sediments along the upper intertidal zone of less exposed marine coastal environments and estuarine margins.

Genetically Diverse Ecological Entity

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the upper half of the intertidal zone of coastal areas worldwide. They are well known for their morphological and physiological adaptations for life coping with salt, saturated soils, and regular tidal inundation (Tomlinson 1994; Duke 2006), notably with specialized attributes like exposed breathing roots above ground, extra stem support structures, salt-excreting leaves, low water potentials, and high intracellular salt concentrations to maintain favorable water relations in saline environments and viviparous water-dispersed propagules.

Among the 32 plant genera known to have mangrove representatives, there is specialization for the tidal wetland habitat in a relatively large number of 18 plant families (see Table 1; also see Duke (2013)). All but one in each case are angiosperms, flowering plants: this is *Acrostichum*, ground ferns, of the family Pteridaceae (Fig. 4). As such, mangrove habitat is a recent-era, ecological entity rather than a genetically uniform group. This compares with rain forests, from which mangroves might be considered a specialized subgroup. Furthermore, 17 genera are exclusively found in mangrove habitat (*Acrostichum*, *Aegialitis*,

Fig. 4 The growth form of mangrove plants vary from the ground fern, *Acrostichum* (left: Diahot River, New Caledonia; Photo N.C. Duke 2006) to tall trees with buttressed trunks like *Heritiera littoralis* (right: Choiseul, Solomon Islands; Photo N.C. Duke 2010), as well as the tangled roots of Rhizophoras (Figures 1 & 2).

Aegiceras, *Avicennia*, *Bruguiera*, *Camptostemon*, *Ceriops*, *Conocarpus*, *Kandelia*, *Laguncularia*, *Lumnitzera*, *Nypa*, *Osbornia*, *Pelliciera*, *Rhizophora*, *Scyphiphora*, *Sonneratia*), while 15 others include non-mangrove species as well. This latter group includes *Acanthus*, *Barringtonia*, *Brownlowia*, *Crenea*, *Cynometra*, *Diospyros*, *Dolichandrone*, *Excoecaria*, *Heritiera*, *Mora*, *Muellera*, *Pavonia*, *Pemphis*, *Tabebuia*, and *Xylocarpus*. In one case, *Pemphis* has a single upland species located inland as an isolated population on the island of Madagascar. In others, like *Brownlowia*, *Diospyros*, and *Tabebuia*, while there is just one mangrove species, the number of upland species is much higher. In addition, unusually widespread and distinct hybrid forms are reported also in four genera including *Bruguiera*, *Lumnitzera*, *Sonneratia*, and *Rhizophora*. Overall, the total number of mangrove species in these genera is relatively low, being one or two. For the relatively larger genera, the number of mangrove species plus hybrids does not exceed 12. These measures of relatively low diversity are believed to be the result of harsh growth conditions present in intertidal habitats. In general, the physical conditions that mangroves cope with provide a rigorous survival constraint in evolution, requiring a high level of optimized efficiency for survival of each genetic variant and mutation. The survival limits of each species are reflected partly in their individual distribution patterns. In this way, local and regional environmental factors are believed to play a key role in defining the ecological entities that ultimately define each mangrove taxon.

Mangroves at the Terrestrial-Marine Interface: A Conjoint Niche

Mangrove forests are home to two uniquely distinct subcommunities, one being intertidal marine habitat, while the other being a terrestrial forest canopy. Therefore, mangrove forests are in one way like coral reefs in providing essential structure and habitat for a host of marine and intertidal species with residents among their dense and complex roots, as well as having regular visitors with each flooding tide. But, unlike coral reefs, mangroves also have another specialized niche adjacent in their canopies, above the tidal limit. As noted, mangrove plants are genetically close to tropical rain forest plants, and mangrove forest stands retain a comparable habitat niche in their canopies that are not marine. This canopy habitat supports a host of birds, reptiles, mammals, and insects, some of which are specialists for this further uniquely placed niche of mangrove habitat.

As noted, mangrove plants are not a single genetic entity because the plant types represented in the tidal zone are not all closely related (see Table 1). So, while they sometimes look alike, and have similar adaptations, this tells us more about the constraints of the environment they live in, rather than their family relationships. The plants growing in the tidal zone require serious physiological and anatomical adaptations to survive and flourish in this habitat. However, this does not preclude other plants from occasionally being found within the tidal zone. These are considered "associates" since they occasionally occur in intertidal sediments, but most of the time, they are found elsewhere in upland, nontidal settings (also see Tomlinson 1994). Others do reside mostly in the tidal niche, notably salt marsh plants, but these are smaller in stature than mangrove plants, often less than 1 m in height. A number of others, the epiphytes and parasites, perch in the branches and stems of mangroves. All these plants shape and define mangrove habitat, just as those abiotic conditions of saline, saturated soils have defined them.

Ecological Features of Mangroves

Living in Saline Saturated Soils

Mangroves collectively possess a unique combination of morphological and physiological attributes for living in the tidal environment (Tomlinson 1994). Mangrove soils are regularly waterlogged and loaded with salt. High tides bring marine aquatic and estuarine conditions, while low tides expose mud and roots to aridity, heat, and desiccation. Few other natural habitats are subject to such regular, dramatic changes in abiotic variables, particularly, as regards the combined influences of tides, rainfall, runoff, waves, currents, climate, and sea level change. All these factors have notable and profound influences on the distribution and characteristics of mangroves. Adaptations required for survival in this environment are shared, in part, by plants from at least three other habitat types, namely, deserts, rain forests, and freshwater swamps.

Mangroves have shallow root penetration and breathing roots because their soils are usually saturated and airless (Alongi 2009). Most mangrove roots below ground occur within the top meter of soil, with greater root volumes in shallower depths. Mangroves also have broad support structures above ground, such as buttresses and sturdy prop roots, because the soils are often soft and unconsolidated. The features of shallow depth and support structures are common also in tropical rain forests. Like freshwater swamp trees, mangroves cope with water-saturated soils that limit gaseous exchange by using special breathing roots. Some have shallow, subsurface cable roots with many vertical, fingerlike breathing roots above ground, called "pneumatophores." Other mangrove plant groups have less obvious physical adaptations apart from the ubiquitous, numerous small air-breathing lenticels on lower stem surfaces.

Growth Habit: Tidal Forests and Shrubbery

Growth form varies considerably between species (Tomlinson 1994), with mangrove plants characteristically ranging from trees (like species of *Avicennia, Bruguiera, Rhizophora, Sonneratia*), to shrubs (like *Aegiceras, Osbornia*), to the trunkless palm (*Nypa fruticans*), to ground ferns (*Acrostichum* spp.). Trees and shrubs vary further where they might be columnar and erect (like *Bruguiera parviflora*), spreading and sprawling (like *Acanthus* spp., *Scyphiphora hydrophylacea*), and multiple-stemmed (like *Ceriops decandra* or *C. pseudodecandra*). Growth form might also vary within the same species (like *Lumnitzera littorea* and *Rhizophora* spp.), having both an erect tree form and a tangled thicket form. In general, plants on the edges of stands (both waterward and landward) have more lower limbs and foliage, and their stems are typically sprawling and sinuous, rather than erect and straight. Some species typically form closed canopies with various combinations of species (*Avicennia marina*, *Rhizophora apiculata*, *Bruguiera parviflora*, *Bruguiera gymnorhiza, Camptostemon*, and *Xylocarpus*), while others are commonly found as undercanopy plants beneath the closed canopy (*Aegiceras corniculatum*, *Cynometra iripa*, *Acanthus* spp., *Acrostichum speciosum*, *Brownlowia tersa*, *Ceriops decandra*).

Zonation of Mangrove Vegetation Types

Mangrove species assemblages are characteristically ordered across the tidal profile and upstream in distinct zones. As such, key zones are readily observed with specific combinations found at the waters' edge, landward margin, and intermediate areas (Duke et al. 1998). The selection of species in these assemblages depends also on the position upstream along an estuarine gradient from the sea mouth to the upper tidal reaches, as with the geographic availability of propagules of each species. Downstream specialists include at the seaward lower zone *Sonneratia alba* and *Avicennia* species, at the intermediate zone *Bruguiera gymnorrhiza* and *Ceriops* species, and at the landward zone *Heritiera littoralis*, *Xylocarpus granatum*, *Excoecaria agallocha*, and *Conocarpus erectus*.

Emergent Canopies, Resident Fauna, and Low Tide Visitors

Leaves vary between species (see Tomlinson 1994; Duke 2006) with mangroves having leaves that are simple (like species of *Avicennia*, *Bruguiera*, *Ceriops*, *Kandelia*, *Rhizophora*, *Sonneratia*), compound (like *Cynometra*, *Dolichandrone*, *Xylocarpus*), or pinnate (*Acrostichum*, *Nypa*) (Fig. 5). Shape varies within these basic leaf types, ranging from apiculate (like *Rhizophora* spp.), ovate (like *Sonneratia alba*), lanceolate (like *Sonneratia lanceolata*), to spathulate (like *Lumnitzera*). Other characteristics of leaves also vary including the leaf apex and tip from pointed (like *Avicennia marina*), rounded (like *Avicennia officinalis*, *Camptostemon schultzii*), emarginate (like *Lumnitzera* spp., *Osbornia octodonta*), to mucronate (like *Rhizophora* spp.); the leaf margin from entire (like *Rhizophora* spp.) to serrate (like *Excoecaria agallocha*) or spiny (like *Acanthus ilicifolius*); the surface from smooth and glabrous (like *Bruguiera* spp.,

Fig. 5 Leaf shape of mangroves range from simple leaves like those of *Heritiera littoralis* (left: Daintree River, Australia; Photo N.C. Duke 2006) to compound leaves and pinnate fronds of *Nypa fruticans* (right: Kien Giang, Vietnam; Photo N.C. Duke 2009)

Rhizophora spp., *Ceriops* spp.) to pubescent (like *Heritiera*, *Camptostemon*) or with salt-excreting glands (like *Aegiceras*, *Aegialitis*); containing milky sap (*Excoecaria agallocha*) or not; being large (like *Heritiera littoralis*) or small (like *Pemphis acidula*); and having distinctive petioles with pulvini (like *Heritiera littoralis*) or fully enclosing the stem (*Aegialitis annulata*). Leaves are used by a range of fauna (Saenger 1994) including crabs (notably sesarmids that remove fallen leaves from the ground); moth caterpillars (notably removing standing green leaf surfaces); various leaf miners, thrips, and crickets (causing various leaf damage); and grazing animals like horses, cattle, deer, and goats (causing significant canopy damage).

Mangroves provide key habitat for a diverse range of animals living in forest canopies (Saenger 1994). For instance, these canopies are home to pythons, tree snakes, lizards, spiders, innumerable insects, many species of ants, bird species, native rats, insectivorous bats, fruit bats, monkeys, and the occasional large marsupial and mammal, like tigers in India. New species and expanded distributional ranges are being found all the time. Some birds depend entirely on mangrove habitat for shelter, food, nesting, and rearing their young. Many of the animals make significant contributions to mangrove forest structure and function. For instance, as noted above, animal pollinators like bats, birds, and insects provide the essential service of germination and successful regeneration of existing and new mangrove stands. Other fauna like insect larvae, or caterpillars, consume leaf material and contribute to litter decomposition and recycling. Fruits are also infested and damaged by crabs, insects, and rats, further affecting forest regenerative processes and aiding species selection, forest composition, and structure.

Exposed Roots and Stems, plus High Tide Visitors

Adaptations concerning aboveground breathing roots of many mangrove plants are useful for gas exchange in saturated, nonporous soils depleted of oxygen. Another attribute helping survival in water-saturated environments is structures to support the aboveground mass of the tree. Since roots are unable to penetrate more than a meter or so below ground because of the anaerobic conditions, then lateral support structures provide important stabilization. Roots above ground come in various forms including pneumatophores as pencillike (like *Avicennia* spp.), stiff conical (like *Xylocarpus moluccensis*), flexible conical (like *Sonneratia alba*), and elongate conical (like *Sonneratia caseolaris*, *Sonneratia lanceolata*); knee roots as thick and knobbly (like *Bruguiera* spp.) and thin and wiry (like *Lumnitzera*, *Laguncularia*); stilt roots (like *Rhizophora* spp.); and buttresses (Fig. 4) as sinuous planks (like *Mora*, *Xylocarpus granatum*, *Heritiera littoralis*, *Ceriops*, *Pelliciera*) and erect “fin” buttresses (like *Bruguiera rhynchopetala*, *Xylocarpus moluccensis*). Roots are used by various fauna, but the most notable are burrowing teredo shipworms, plus termites and crabs. The bark is used by a range of fauna including insects such as termites, ants, boring beetle larvae, crickets, and roaches, plus small reptiles like geckos and skinks.

Mangroves provide habitat for a wide variety of animals including those living in muddy sediments (e.g., Salmo-III and Duke 2010). A multitude of animals depend on tidal wetland vegetation for shelter, food, breeding, and nursery needs. Some notable fauna include saltwater crocodiles, mollusks, burrowing worms, polychaete mud worms, fish, various crustaceans, and crabs. Other animals are less obvious and there is much to learn still about the diversity of fauna in mangrove ecosystems. For example, sesarmid crabs have a keystone role in forest growth and development (Smith et al. 1991) where they remove a large number of leaves below ground, aiding retention and recycling of nutrients within mangrove forests. These leaves would otherwise have been flushed away and lost from the habitat with the tide. Some marine fauna are well known, like the larger fishes, barramundi and mangrove jack, which use mangroves during flooding tides. One less known faunal associate of mangroves is green turtles, *Chelona mydas* (Arthur et al. 2009). In Australia, these sea turtles have been observed eating mature fruits of *Avicennia*

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marina cropped from the trees at high tide. Our knowledge of this important but novel activity is limited, but it seems these turtles may contribute also to mangrove ecosystem processes.

Dependent Biota

The plants and animals living in the tidal zone above mean sea level do so because mangroves are there, either for shelter or the structure created and/or because of the food produced from vegetation and associated fauna. There are a number of different types including epiphytes, parasitic plants, and fungi. The presence of such canopy plants in mangroves is often neglected with only a few studies describing the presence of these important components of mangrove forests (e.g., Stevens 1981; Rodriguez and Stoner 1990; Hong and San 1993).

In wet tropic mangroves, epiphytes are plentiful in mangrove trees. The number of epiphytes greatly increases in wet tropical areas. Common epiphytes in mangroves include orchids, ferns, lichens, mosses, and ant plants. Assemblages of epiphytes are many and varied. For example, there are at least two common types of ant plant, including *Myrmecodia beccarii* (the spiny ant plant) and *Hydnophytum formicarum* (the smooth ant plant). These further have a mutualistic or symbiotic relationship with fauna. The relationship between epiphyte and animal possibly evolved in response to poor nutrient conditions. Ant plants have swollen, bulbous stems laced with tiny tunnels and galleries in which small ants live in symbiosis. As such, while the ants get shelter, the plants in return receive nutrients and protection.

As another example, mistletoes parasitize the foliage of specific mangrove plants (e.g., Orozco et al. 1990). They often mimic the leaves of their host. In contrast, flowers of the mistletoe are often unusually spectacular and showy in some cases. Mistletoe flowers also attract mistletoe birds that service flowers and disperse pollen. These specialist birds also eat the fleshy fruit and disperse the seeds. In fact, the sticky mistletoe seeds are difficult for the bird to defecate, so they are forced to remove them by wiping seeds off against a branch, the best place for a new mistletoe to germinate and grow.

Salt Marsh Coinhabitants

Several salt marsh species occur within the mangrove niche, notably in cooler latitudes, as well as in drier places generally (Saenger 1994). As such, mangroves share their tidal niche between mean sea level and the highest tides with this group of distinct plants – the tidal salt marsh. Tidal salt marsh plants are largely distinguished from mangroves by their smaller height. They are usually described as a separate habitat type with plants mostly less than one half meter tall. This definition of tidal salt marsh differs from the definition of mangroves only by the size and character of the vegetation, where tidal salt marsh plants form shrubby, diminutive ground cover. Salt marsh plants dominate where mangrove plants are excluded by either low-temperature or low-moisture conditions, a feature that reflects their hardier nature. Salt marsh species typically proliferate in cooler areas subject to occasional frosts, but they also dominate in hotter arid conditions where annual rainfall is less than 1,500 mm. There is evidence of a landscape-scale dynamic equilibrium between these two plant types where one will replace the other in alternate moisture conditions (Duke et al. 2003). Some of the more common tidal salt marsh species include *Halosarcia* species (samphires), *Sarcocornia quinqueflora* (beaded samphire), *Sclerostegia arbuscula* (shrubby glasswort), *Sesuvium portulacastrum* (sea purslane), *Sporobolus virginicus* (marine couch), and *Suaeda arbusculoides* (jelly bean plant).

Associates Among Mangroves

The occurrence of mangrove and upland plants growing on either side of the high water mark is not always distinct. Mangroves sometimes include additional plant species that are not generally considered mangroves (Tomlinson 1994). However, some authors argue for the inclusion of some, or all, of these species to be called mangroves. The view taken in this chapter is that mangroves are those plants that grow virtually exclusively in tidal habitat. Associate species include *Acanthus volubilis*, *Aglaia cucullata*, *Amphitecna latifolia*, *Annona glabra*, *Brownlowia argentata*, *Cerbera manghas*, *Clerodendrum inerme*, *Dillenia alata*, *Excoecaria indica*, *Heritiera globosa*, *Hippomane mancinella*, *Inocarpus fagifer*, *Melaleuca* sp., *Phoenix paludosa*, *Pongamia pinnata*, *Pterocarpus officinalis*, *Randia fitzalanii*, *Talipariti tiliaceum* (*Hibiscus tiliaceus*), *Thespesia populnea*, *Xylocarpus rumphii*, and *Zamia roezlii*, plus creepers like *Derris trifoliata*. Furthermore, there is often overlap with the closely associated inhabitant of the beach zone where other species of *Calophyllum*, *Casuarina*, *Morinda*, and *Scaevola* are commonly found.

Factors Influencing Mangrove Distribution, Dispersal, and Origins

Global Distribution and Continental Barriers

Present-day global dispersal patterns are dependent on the specialized water-buoyant propagules of most mangroves (e.g., Lo et al. 2014). Their dispersal is constrained by wide bodies of water and land masses that block equatorial circulation. There are four major barriers around the globe today that generally restrict the dispersal of warm coastal marine organisms, including the continents of Africa and Euro-Asia, North and South American continents, the oceans of the North and South Atlantic, and the eastern Pacific Ocean (Duke et al. 2002). The relative effectiveness of each of these barriers differs, depending on geological history, dispersal/establishment ability, and the timing of evolutionary development of respective species. There are two barriers that appear to have been effective during recent geological time, namely, the African and Euro-Asian continents and the Pacific Ocean. Accordingly, mangrove species, along with other tropical shallow marine coastal inhabitants, are divided into two global hemispheres, namely, the Atlantic-East Pacific (AEP) and the Indo-West Pacific (IWP). These global regions span more or less equal portions of the earth, and each has equivalent areas of mangrove (Fig. 6). They further each represent centers of secondary radiation and they share some mangrove genera, like the *Rhizophora*, *Avicennia*, and *Acrostichum*. The AEP has fewer species, and fewer additional genera, although these span two existing barriers. The most diverse mangrove flora occurs in the IWP, and this is constrained between two existing barriers. Based on species presence, each of these regions is divided into three subregions making a total of six in the world, including Western America, Eastern America, Western Africa, Eastern Africa, Indo-Malesia, and Australasia.

Global Influences: Temperature

Mangrove habitats of saline, saturated soils are found throughout tropical regions of the world. Distributions into higher latitudes are generally constrained by the 20 °C winter isotherm in each hemisphere (see Fig. 6; Duke et al. 1998). Deviations from this pattern correspond mostly with the path of oceanic circulation currents where mangrove distributions are often broader on eastern continental margins and more constrained in the west. For instance, in the North and South Atlantic Oceans, cooler currents (each moving toward the equator from the north and south, respectively) reduce the lineal extent of warmer coastline for West Africa. Conversely, on the east coasts of North and South America, the warmer poleward-moving currents extend the warmer coastline. And, since mangroves match these warmer coastlines closely, it demonstrates how these occurrences are profoundly limited by low temperature. However, there are at least three important deviations from this overall global pattern, and these all occur in the Southern Hemisphere. There are three notable instances, occurring along the coastlines of eastern

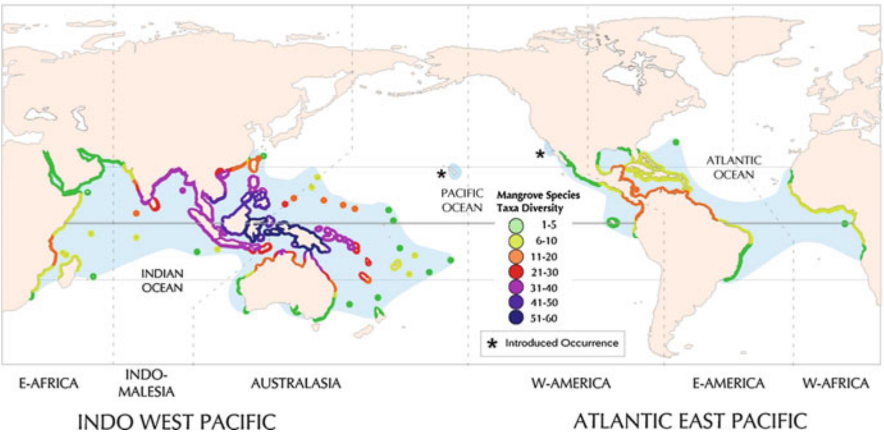

Fig. 6 World distribution of mangrove habitat with numbers of species present along coastlines of 6 sub regions and two global regions (updated from Duke et al. 1998)

South America, across the North Island of New Zealand, and around southern Australia. This could be the result of specific, small-scale extensions of warmer currents, but it appears more likely these cold-adapted populations are relictual, representing refuges of more poleward distributions in the past.

Regional Influences: Tidal and Estuarine Effects

Within any global region, mangrove species are further constrained by localized factors, influenced by geography, hydrology, and climate (Duke et al. 1998). Individual mangrove species rarely occupy entire estuaries from sea mouth to the tidal limit upstream. Each species has a preferred upriver estuarine location based on its range of salinity tolerance. *Estuarine location* is characterized by salinity gradients that are conveniently considered in three sections, including "downstream" as the lower third of the estuary and offshore islands where salinities are close to seawater, "upstream" as the upper third where salinities are influenced either by freshwater or hypersaline runoff, or "intermediate" as the middle third. Particular mangrove species will occupy one or all of these estuarine locations, depending on its salinity tolerance in combination with the local climate and catchment conditions. For instance, species like *Avicennia marina*, *Rhizophora stylosa*, and *Sonneratia alba* commonly occur in downstream locations. By comparison, *Rhizophora mucronata*, *Sonneratia caseolaris*, *Bruguiera sexangula*, and *Barringtonia racemosa* are found upstream in freshwater-influenced estuaries. Some species, like *Avicennia integra*, are notably located in intermediate estuarine locations (Duke 1992).

Individual mangrove species rarely occupy the entire tidal profile from mean sea level to the highest tide levels (Duke et al. 1998). Each species occupies a distinct part, defining its characteristic tidal position. Mangrove species have a special relationship with tidal inundation plus the frequency of wetting and soil type. These influences commonly result in distinct bands of species ecotones that follow tidal contours, referred to as zonation. *Tidal position* of mangroves can be conveniently considered in three parts, influenced by different degrees of tidal inundation, including "low" representing areas inundated by medium high tides and flooded >45 times a month, "mid" representing areas inundated by normal high tides and flooded from 20 to 45 times a month, and "high" representing areas inundated <20 times a month. For example, species like *Avicennia integra* and *Sonneratia alba* commonly occupy low intertidal positions. By comparison, *Heritiera littoralis*, *Xylocarpus granatum*, and *Lumnitzera racemosa* are found in high intertidal positions. Other species, like *Avicennia marina*, *Acanthus ilicifolius*, and *Aegiceras* *corniculatum* are observed at high and low intertidal positions. Their bipolar distributions across the tidal profile are apparently the result of competition with other mangroves and predation by fauna such as small crabs.

Origin, Dispersal and Evolution of Mangroves

Mangroves, as we know them, have been around for at least 50 million years and possibly a lot longer (Duke 1995). For instance, the origins of the genus *Avicennia* have been linked to the opening of the Atlantic Ocean extending back almost 100 million years. In any case, species like *Rhizophora* and *Avicennia* were widely distributed 50–55 million years ago. At that time the ancient Tethys Sea, a shallow equatorial sea full of coral reefs and islands, was fast closing as the massive continental fragments continued to shift and jostle across the globe. This process of continental drift appears to have played a pivotal role in determining both the diversity and type of mangroves found today, as well as their current global distributions. Mangroves have not evolved and dispersed uniformly, and there was no common center of origin. However, mangrove plants share common adaptations; individual species have evolved differently and developed at different rates. Today's distributional patterns are useful fingerprints from which we might trace the origin of each species (e.g., Lo et al. 2014). Current distributions of individual taxa show numerous instances of unusual occurrences and absences that demonstrate finite dispersal limitations, especially across open water. Furthermore, there are some genetic discontinuities that occur despite the lack of any current dispersal barriers. In each case, such unusual distribution patterns provide important clues and evidence of past geological and climatic conditions that tell us something about the origin and evolution of mangroves.

Processes and Functioning of Mangroves

Flowers, Fruiting and Vivipary

Flowers facilitate pollination and fertilization (Fig. 7). They do this by either attracting specific pollinators or by providing a strategy for effective transfer of pollen from male to receptive female reproductive parts. Flowers of mangrove plants (Tomlinson 1994; Duke 2006) are spectacularly variable in structure and color with combined-sex flowers (like *Rhizophora*, *Sonneratia*, *Avicennia*), separate-sex flowers (like *Heritiera littoralis*), and separate-sex trees (like *Excoecaria agallocha*); colors as white (like *Sonneratia alba*, *Lumnitzera racemosa*), red (like *Sonneratia caseolaris*, *Lumnitzera littorea*), pink (like *Lumnitzera rosea*), purple (like *Acanthus ebracteatus* subsp. *ebarbatus*), lilac (like *Acanthus ilicifolius*), pale golden yellow (like *Avicennia integra*), and orange-yellow (like *Avicennia marina*); and size as large (like *Dolichandrone spathacea*), medium (like *Bruguiera gymnorhiza*), and small (like *Avicennia marina*, *Osbornia octodonta*). Flowers are used by a range of fauna including birds with honey eaters (triggering an explosive pollen release in *Bruguiera*) and parrots (cropping *Lumnitzera littorea*); insects with large bees (*Acanthus*), hawk moths (*Sonneratia*), honey bees (*Avicennia*), and flies (*Nypa fruticans*); and nectar-feeding bats (*Sonneratia*).

An important attribute of mangroves is the high percentage of viviparous propagules (Duke 1992, 2011). Vivipary is the bearing of live young where seeds germinate on the parent tree and new seedlings remain attached as they grow. Not all mangroves have this character, with lesser degrees of vivipary and a small group with no apparent specialization (Fig. 8). In most cases, all propagules are buoyant for at least a short dispersal phase. The undeniable dispersal specialists are *Rhizophora*. These have highly developed viviparous propagules believed to endure for several months at sea in a semi-dormant state. In general, however, the propagules of different species possess differing dispersal abilities, causing each species to have distributional ranges that differ according to their capacity to travel specific distances at sea. Fruits,

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Fig. 7 Flowers of mangrove plants vary greatly from the red staminal display of *Sonneratia caseolaris* attractive to nectar feeding microbats (left: Tiponite estuary, New Caledonia; Photo N.C. Duke 2006) to the distinctly mauve flowering heads of *Acanthus ilicifolius* pollinated by large solitary bees (right: Dumbea, New Caledonia; Photo N.C. Duke 2006)

Fig. 8 Propagules of mangrove plants are commonly viviparous (as living seedlings) like *Bruguiera gymnorhiza* which occasionally further displays a rare glimpse of a distinctive chlorophyll-lacking, albino mutation in response to water-borne pollutants (left: Prony, New Caledonia; Photo N.C. Duke 2006), compared to the more normal cryptic seed producers like *Heritiera littoralis* (right: Malekula, Vanuatu; Photo N.C. Duke 2012)

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Fig. 9 Mangroves are mostly distinguished by ever-green verdant canopies of Rhizophoras (left: Maramasike Passage, Solomon Islands; Photo N.C. Duke 2012), but some trees are distiinctly deciduous like *Xylocarpus moluccensis* in winter months (right: Boigu, Torres Strait, Australia; Photo N.C. Duke 2013)

including viviparous propagules, have a range of characteristics including seeds (like *Xylocarpus*, *Osbornia octodonta*, *Sonneratia*), cryptovivipary (like *Avicennia*), and vivipary (like *Rhizophora*, *Bruguiera*, *Ceriops*) and structural features as drupes (like *Sonneratia*), capsules (like *Excoecaria agallocha*), hypocotyls (like *Rhizophora*, *Bruguiera*, *Ceriops*), cotyledons (like *Avicennia*, *Lumnitzera*), kapok (with its dry climate benefit, *Camptostemon schultzii*), fleshy (like *Sonneratia caseolaris*), woody (like *Xylocarpus*), persistent style (like *Sonneratia*, *Avicennia*), keeled pod (like *Heritiera littoralis*), and elongate pointed radicles (like *Rhizophora*).

Forest Growth and Turnover

Mangroves, like other forest stands, are complex living systems that are dynamic, ever-growing, and constantly reestablishing and renewing themselves (Duke 2001). Mangroves differ from terrestrial forests chiefly because of their special adaptations for survival in tidal marine locations. Situated at the seawater margin, these stands are subject to both land and river runoff, as well as the direct action of the sea itself. By using their uniquely evolved features, mangrove plants have been able to readily occupy, dominate, and stabilize exposed tidal foreshore and estuarine environments (Fig. 9). In such dynamic conditions, influenced by severe hydrological and physicochemical conditions and faced with pervasive and progressive changes, like human development and sea level rise, it has been essential for these plants to have successful regenerative strategies. Each occurrence of mangrove habitats today demonstrates the success of the regenerative strategies of these species. Mangrove stands are recognized as dynamic ecosystems that are relatively robust and stable while dominated by a small number of specialist species. In addition, certain species (e.g., *Avicennia*, *Sonneratia*) are pioneers which are capable of fast regeneration after periodic disturbance. Disturbance is a natural feature of coasts – dynamic erosion/accretion and typhoons.

A forest turnover model (Fig. 10) maps out the natural processes involved in mangrove forest dynamics by quantifying turnover in terms of gap creation and recovery (Duke 2001). The accumulative influence of gap replacement, as numerous small-scale disturbances on mangrove forests, appears to explain the

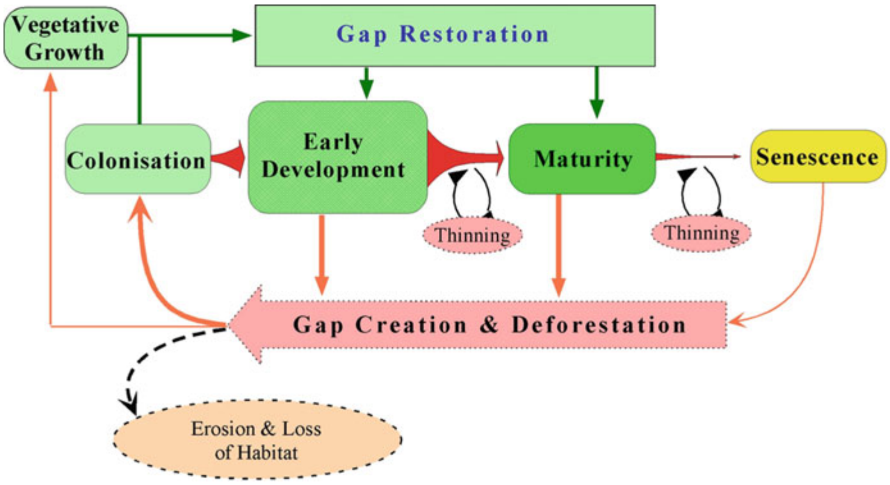

Fig. 10 Combined regeneration and development model for mangrove forest growth (Duke 2001)

peculiar characteristics and presence of mangrove forests. Small gaps are common in terrestrial forests also, but those in mangroves differ because they rarely involve tree falls. In mangroves, the trees usually die standing in small clusters of 10–20 trees. The particular survival advantage of this strategy for mangrove forests is most evident in exposed stands. In these locations, forest structure must be maintained because exposed sediments would rapidly erode and destabilize the forest. Mangrove forests are therefore believed to be at great risk of ecosystem collapse and total loss of habitat. However, their common presence in exposed locations today is testimony to the success of current renewal strategies. But, what about the future? There is growing concern with predictions of future increases in large-scale pollution incidents, more rapid rises in sea level, and increased severity of storms. Each of these factors would seriously challenge the capacity of mangroves to regenerate. The cumulative influence of such factors is therefore expected to seriously threaten the survival of exposed mangrove habitats.

Influential Plant-Animal Relationships

Many mangrove-dependent biota form interlinked community assemblages, with a number of unique and influential plant-animal relationships (Saenger 1994). While mangroves have a relatively low number of species compared with adjacent communities like tropical rain forests and coral reefs, the diversity of organisms that reside in, or utilize, mangroves is surprisingly high. For one thing, they uniquely include both terrestrial and marine biota caught up in the regular ebbs and flows associated with fluctuations of tides as well as river flows. While canopies often remain emergent, lower parts of mangrove forests are regularly inundated and drained in diurnal rhythms. Dependent marine life must either come and go with the tides or be adapted to exposure during low tides and inundation at high tide. During low tides, mangrove marine residents might either seek shelter in burrows of wood or mud or within a shell or other durable cover.

As one example, small mangrove crabs (sesarmids) actively remove and consume leaves and fruits fallen from mangrove forest canopies (Smith et al. 1991). These crabs are considered ecosystem engineers (Lee 1998) because they influence forest growth, diversity, structure, productivity, and function. Instead of leaf biomass being lost from the mangrove system with tidal flushing, it is transferred below ground where it is recycled into surrounding trees and forest structure. And, species of mangrove propagules eaten by crabs are likely to be excluded from future mature forests. It is suggested that this type of faunal activity may help explain the bimodal distribution of *Avicennia marina* across some tidal profiles, along with other unexplained local distributional characteristics (Duke et al. 1998).

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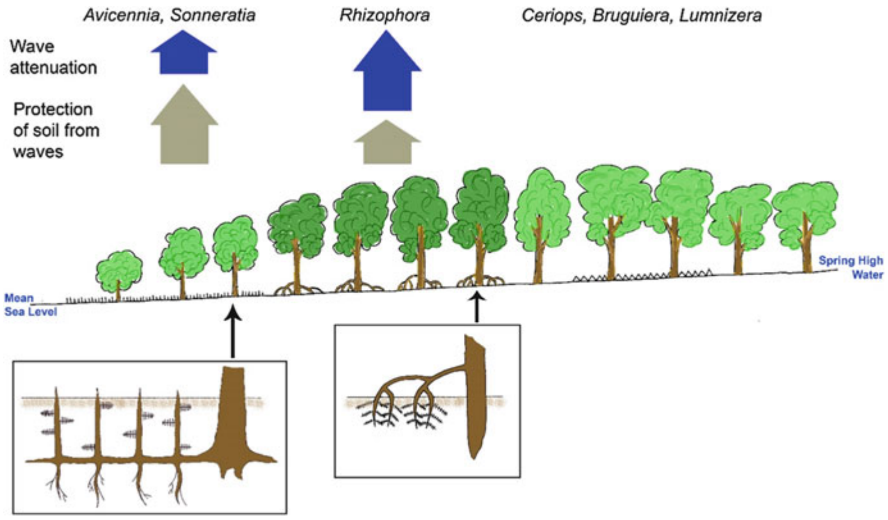

Fig. 11 The zonation system which appears to use different elements of above- and below-ground vegetation densities for optimum soil protection and wave attenuation

Differential Buffering of Shoreline Impacts

Mangrove forests often display a typical band-like zonation which contributes to potentially effective coastal protection where different assemblages have different aboveground root structures (Fig. 11). The aboveground structure and density of mangroves are important for wave attenuation and differ among mangrove species. Horstman et al. (2014) showed that wave attenuation increases significantly with volumetric vegetation densities.

The latter is about 4.4 ‰ in the *Avicennia* zones and 5.8–32 ‰ in the *Rhizophora* zones along the Andaman coast of Trang Province in southern Thailand. This results in reduced wave-influenced erosion, starting with *Avicennia* pioneer species at the seaward edge, backed up by the *Rhizophora* zone.

The differences in belowground root structures also contribute to potentially effective soil stabilization.

Threats and Benefits of Mangroves plus Key Knowledge Gaps

Practical Benefits and Ecosystem Services at Risk

Mangrove forests worldwide are not only being depleted and lost, but they are also being degraded at an alarming rate (Duke et al. 2007). With continued habitat fragmentation, many believe these forests are losing functionality. And, with this, their long-term survival is at risk along with their notable ecosystem services. For example, many fish and shellfish spend all or part of their life cycles in mangroves. Pressures on these biota have important and wide-reaching implications for commercial, recreational, and artisanal fisheries. Depending on location, the importance of mangroves to dependent fisheries fauna ranges from 50 % to 90 % of commercial species having fundamental links with healthy, mangrove-lined estuaries. Other values of mangrove forests include stabilization of coastal and estuarine shorelines, mitigation of flooding and storm impacts, sequestered carbon accumulation in deep peaty sediments, and a supply of low-scale energy needs with timber harvesting.

Mangroves Benefit Corals and Sea Grass

More generally, mangrove habitats are commonly sandwiched between two of the world's iconic tropical ecosystems, coral reefs and tropical rain forests, among which mangroves notably interact and support. In relatively arid places, mangroves cover tidal margins with closed shrubby canopies of greenery that distinctly contrast with parched upland landscapes. Where corals occur in shallow warm seas, mangroves buffer them from the influences of runoff from coastal lands, protecting corals of wet and arid regions from unwanted nutrients and turbid waters. This may be achieved by stabilizing otherwise smothering waterborne sediments and shifting shorelines (Wolanski and Duke 2002). Tidal wetland plant assemblages accordingly provide important ecosystem services that further include structured habitat and nursery sites.

Biota-structured habitats of coral reefs, rain forests, and mangroves play a vital role in coastal ecosystem processes via a combination of well-developed links and interconnectivity, coupled with transient biota uniquely adapted to the unusual and often dramatic physicochemical gradients. Such dependent relationships developed over millennia have become vital to the survival of each habitat. For instance, while sediment-loving mangroves flourish in waters sheltered by coral reef structures, they in turn protect wave-hardy corals from excessive sediments and nutrients in runoff from surrounding catchments. The consequences in upsetting any one of these links will have unexpected but likely far-reaching impacts on such interrelated habitats.

Shoreline Protection

Increased coastal erosion is a serious anticipated consequence of global climate change resulting from rising sea levels coupled with more severe storm waves and winds. Shorelines are protected where mangrove vegetation present acts to reduce and attenuate the eroding forces of coastal waters. The types of mangrove root structures present are thought to help protect vulnerable coastal soils and sediments. Furthermore, Tamooh et al. (2008) showed in a case study in Kenya that the root biomass of species changes according to their position in the zonation. *Sonneratia alba* has a higher root biomass than *Avicennia marina* which again had more root biomass than *Rhizophora mucronata. Sonneratia* which grows at the seaward side is exposed to intensive wave action and thus needs strong root anchorage for support in the unstable substrate. *Sonneratia* and *Avicennia* have more belowground root biomass because of their extensive underground cable root systems, whereas *Rhizophora* species have an extensive aboveground prop root system and a relatively small proportion of belowground biomass (Fig. 11). It is therefore proposed that wave attenuation by root structures along with soil stabilization contributes to coastal protection.

Turbidity and Sedimentation: Coastal Kidneys

Mangroves and tidal wetlands are fundamental to the persistence and survival of highly productive natural coastal environments. Mangroves have many well-acknowledged roles in coastal connectivity supporting enhancements in biodiversity and biomass (Mumby et al. 2004). At another level, commercial advantages note the importance of mangroves, where up to 75 % of the total seafood landed in Queensland comes from mangrove estuarine-related species. These observations indicate that healthy estuarine and near-shore marine ecosystems are biologically and commercially linked. And, these natural systems are intimately related, connected, and dependent. So, where one is impacted, the effect will be felt more widely than might otherwise be expected. This is the case whether these ecosystems are viewed as sources of primary production with complex trophic linkages, as nursery and breeding sites, or as physical shelter and buffers from episodic severe flows and large waves.

Using Mangroves as Indicators of Change

Tidal wetlands and mangroves are ancient ecosystems evolved over the last 100 million years. During this time, the earth, sea level, and climate have changed dramatically. Mangrove habitats of today are composed of plants that are survivors of previous ages. These surviving ecosystems consequently have

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strategies for dealing with change. As tidal wetland ecosystems respond to current changes, they rely on inherent adaptive capacity (Duke et al. 1998). Where changes can be identified, described, measured, and monitored, they form the basis for a more enlightened monitoring and assessment strategy. For example, if a tidal wetland habitat had shifted upland, this might demonstrate and quantify the effects of sea level rise. Two deductions to be made from such observations are that mangroves had responded to sea level rise and that we might evaluate the rate of net change and their success. The value in this approach in combination with direct instrument measures, like sea/tide level elevation stations, is that mangrove plants integrate daily and seasonal fluctuations. These changes, when viewed in aerial images, are amplified depending on lower profile slopes in respective locations. Furthermore, these enhanced shift incidents can be measured retrospectively using interpretations of vegetative condition for specific locations from historical aerial/satellite imagery. These incidents form the basis for questions about the causes of change. In this way, the drivers of change can be both identified and quantified at local and global scales. Some might be delivered directly, others indirectly, while others may be considered natural. In all situations, tidal wetlands respond to changing influences in characteristic ways that are useful indicators of change. With the systematic identification of each type of change in tidal wetlands, then it will be possible to identify each responsible driver and to quantify the importance of each, along with likely, anticipated consequences.

Threats and Pressures

Mangrove ecosystems worldwide, and their associated habitats, are seriously threatened (Duke et al. 2007). For instance, coastal intertidal habitats are seriously threatened by smothering plumes of mud that greatly exceed prior natural levels. This has been exacerbated by large-scale land clearing and conversion of coastal forested wetlands (Fig. 12) into agricultural, port, urban, and industrial developments (Wolanski and Duke 2002). Key coastal rivers in populated areas have become little more than drains transporting eroded mud to settle in downstream estuarine reaches, along nearby shorelines, in shallow embayments, and on inshore reefs. Mangrove-lined estuaries had offered some respite and dampening of this effect, but in recent years these final bastions of natural coastal processes and sediment filterers are succumbing to the increasing and unrelenting pressures of human population expansion into coastal and estuarine regions of tropical shorelines (Duke et al. 2007).

Pollution Impacts: Direct and Indirect

The land-sea interface is a dynamic environment, where subtle natural changes in climate, sea level, sediment, and nutrient inputs have dramatic consequences for the distribution and health of mangroves. Local human disturbance of mangroves includes eutrophication, dredging/filling, overfishing, and sedimentation. The combined pressures of human disturbances (e.g., Duke et al. 2007) and global climate change have led to mangroves becoming “endangered communities” in many places. Small-scale rehabilitation projects have demonstrated the extreme difficulty in scaling up to effective, large-scale restoration. Urgent protective measures need to be implemented to avoid loss of mangroves and the resulting environmental degradation of coastal ecosystems, especially in the face of anticipated climate change.

Knowledge Gaps and Questions for the Future

In conclusion, we identify some key gaps in our understanding of the characteristics of mangrove and tidal wetlands and of how they function. We will cover questions concerning management, rehabilitation, and conservation in the companion chapter (Schmitt and Duke 2015).

Here, we list a number of items needed to address knowledge gaps for a better understanding of mangrove ecosystem habitats and their functionality:

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Fig. 12 Replacement of coastal-fringing mangroves with the development of port and urban areas. (Port Curtis, Queensland; Photo N.C. Duke 1996)

1. Updated accounts on basic descriptive biology of species attributes, their taxonomy, and biogeography of all biota in mangroves and tidal wetlands generally
2. Detailed assessments of features and mechanisms of functionality of mangroves and tidal wetlands, including links between floral and faunal components
3. A classification and evaluation strategy that provides an assessment strategy which is easy to apply, addresses issues of ecosystem condition and health, covers all likely drivers of change, and identifies the highest-quality standards for best practice habitat evaluation and monitoring
4. An environmental habitat monitoring protocol that is applicable across landscape scales, is spatially referenced and based on map imagery, and locates classification parameters of each habitat condition identified (as defined in item 3)
5. Public presentation of evaluation outcomes showing results in relation to each stage of recovery and rehabilitation and its predicted progress along a hypothetical recovery timeline

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