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Cross-references

Climate Change
Coastal Risks: Floods
Coastal Squeeze
Coastal Wetlands
Habitat Loss
Saltmarshes

MANGROVES

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Synonyms

Mangal

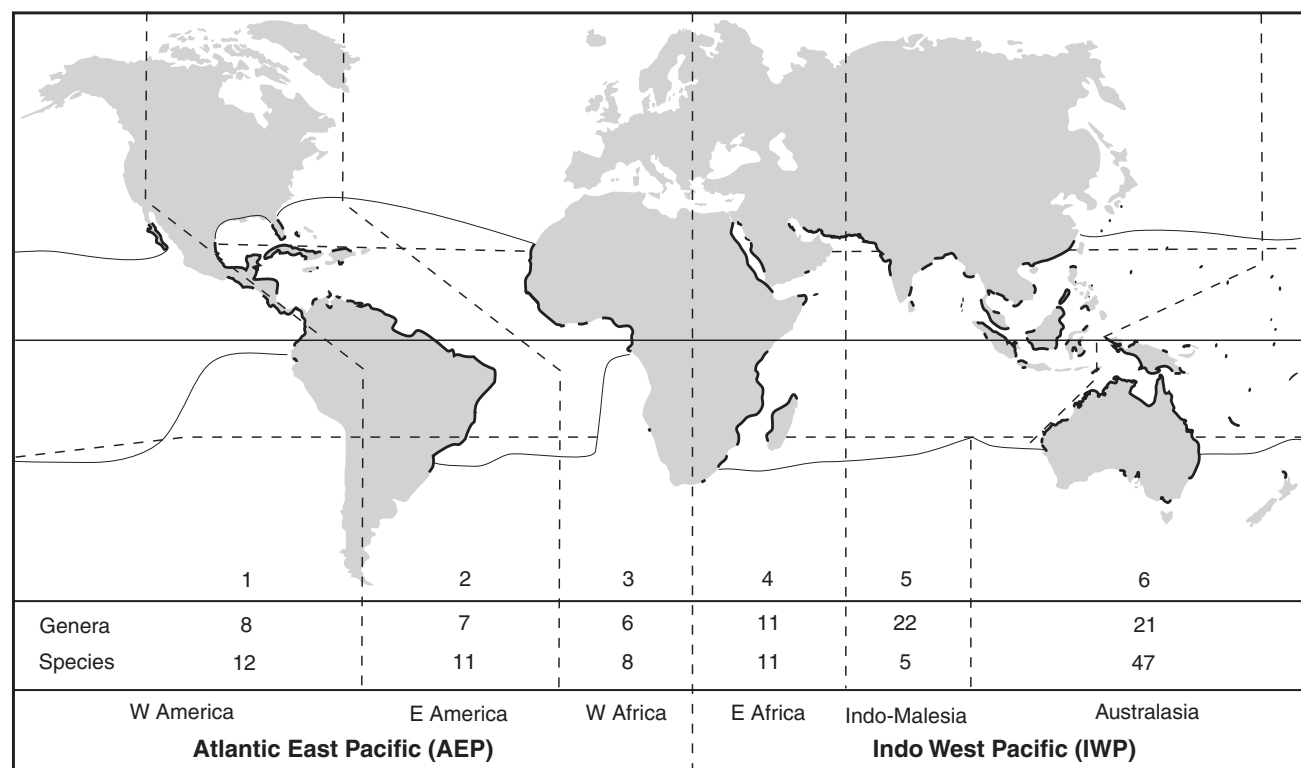
Definition

Mangroves are dicotyledonous woody trees and scrubs that grow above mean sea level to form intertidal forests along subtropical and tropical coasts.

Introduction

Mangroves are forested wetlands living along coasts within low latitudes. These tidal trees and scrubs occur on rocky and sandy shores, but they attain peak size and luxuriance in sheltered muddy areas where quiescent conditions foster establishment and growth of propagules (Lugo and Snedaker, 1974; Chapman, 1976). Forest establishment involves positive feedback in that the saplings and trees trap silt and clay particles brought in by tides and rivers, helping to consolidate the deposits on which they grow. This feedback process continues for the life of the forest until, eventually, the forest floor lies above the reach of tides. Over years and decades, terrestrial plants eventually outcompete and replace the mangroves assuming that geological and ecological processes are in equilibrium. The intertidal zone and its biota are highly dynamic and ever changing, disturbed often enough by weather events, such as storms and cyclones, disease, pests, and anthropogenic intrusions that the progression to terrestrial forest occurs infrequently along most coastlines. Mangroves occupy a harsh environment, subjected daily to tidal and seasonal variations in temperature, salinity, and anoxic soils, and are fairly robust and highly adaptable or tolerant to such changes.

Mangroves occur in a variety of coastal settings dominated by rivers (and the lack thereof), tides, and waves and develop and persist over timescales in which morphological evolution of coastlines occurs; they are pioneers colonizing newly formed mudflats, but they can also shift their intertidal position in the face of environmental change. In relation to changes in sea level, mangrove development can follow one of six patterns: (1) the mangrove surface accretes asymptotically until sediment accumulation raises the forest floor above tidal range – this pattern occurs when sea level is in equilibrium; (2) accretion of sediment keeps pace with a constant rise in sea level; (3) the forest floor accretes at times above tidal range when sea-level rise is irregular; (4) with episodic subsidence but with a stable sea level, the forest floor accretes back to the tidal range; (5) mangrove accretion continues at an irregular pace under conditions of episodic



Mangroves, Figure 1 Global distribution of the world's mangrove forests and their biogeographic provinces. The *bolded lines* indicate mangrove coasts. The number of genera and species within each province is noted below the map (Modified from Alongi 2009).

subsidence but rising sea level; and (6) the forest floor is set back when there is no change in sediment volume with a rise in sea level (Woodroffe, 2003). Thus, mangroves are not static ecosystems, but ever changing, like the interface they occupy between land and sea, and have been traditionally classified as forests occupying overwash islands, coastal fringes, riverine areas, and intertidal basins; scrub forests and other unique settings do occur, especially in relation to the dominance of carbonate (Lugo and Snedaker, 1974).

Mangroves are of great importance economically to coastal inhabitants and ecologically as an integral part of the coastal zone throughout low latitudes and are a prime source of wood for fuel and construction; chemicals for traditional medicine; food; breeding grounds and nursery sites for many terrestrial and marine organisms; sites of accumulation of sediments, carbon, nutrients, and contaminants; as well as offering some protection from erosion and from catastrophic events, such as tsunami and cyclones (Alongi, 2008).

Global distribution, biogeography, and losses

Mangrove forests grow throughout the low latitudes with their global distribution best circumscribed by major ocean currents and the 20 °C isotherm of seawater in

winter (Figure 1). Indonesia, Australia, Brazil, and Nigeria accommodate about 43 % of the world's mangroves, which comprise a total global area of about 138,000 km² (Spalding et al., 2010). There are roughly 70 true mangrove species in 40 genera in 25 families (25 species belong to two families, the Avicenniaceae and Rhizophoraceae) that occur only in these tidal forests, plus a loosely defined group of mangrove associates that also occur in lowland rainforests, freshwater swamps, and salt marsh (Tomlinson, 1986). What is meant by the term "mangrove" is botanically ambiguous, as many different families and genera are not closely related phylogenetically. Mangroves thus represent an ecological rather than a taxonomic assemblage of woody plant species having a variety of common morphological, biochemical, physiological, and reproductive attributes that enable them to inhabit saline soils waterlogged by comparatively warm tidal waters.

Mangroves first appeared on the shores of the Tethys Sea, having diverged from terrestrial forbearers during the Late Cretaceous-Early Tertiary (Ricklefs et al., 2006). The number of species is greatest in the Indo-West Pacific, fostering the traditional explanation that mangroves originated in Southeast Asia and expanded eastward across the Pacific to the west coast of the Americas and westward to East Africa and then to the east and west

coasts of the Atlantic. Movements of the Earth's plates were responsible for the separation of what was once a continuous global distribution; as the various plates separated, some species invariably became extinct, while others diversified regionally. Today, there is a clear separation between the Indo-West Pacific (IWP) and the Atlantic-Caribbean-East Pacific (ACEP) biogeographic regions, as cold waters prevent contact and dispersal between the southern Indian and Atlantic Oceans. Thus, there are six subregions (Western Americas, Eastern Americas, Western Africa, Eastern Africa, Indo-Malesia, Australasia) that fall into the distinct IWP and ACEP regions (Figure 1). Constraints on their global distribution include temperature, rainfall, and human impacts (Duke et al., 1998). Although quite variable geographically, both the number of mangrove species and their total area decline with increasing latitude or decreasing rainfall or both. A poleward expansion of mangroves on at least five continents in relation to the poleward extension of temperature thresholds has occurred concurrent with sea-level rise (Saintilan et al., 2014).

Despite their importance along tropical and subtropical coasts, mangroves are disappearing at an alarming rate due to clearing for coastal development, for aquaculture, and for timber and fuel production (Daru et al., 2013; Polidoro et al., 2010). A global loss rate of 1–2 % has been cited (Spalding et al., 2010), but some areas experience little loss, while others are losing a greater percentage of total area. Approximately 15 % of the world's mangrove species are at a high threat of extinction (Polidoro et al., 2010), especially along the Atlantic and Pacific coasts of Central America, where up to 40 % of mangrove species present are currently at risk. The most landward forests are most often the most threatened with clearing.

Adaptations

Mangroves have many morphological, reproductive, and physiological attributes that make them well adapted to salty soils. These specializations include aerial roots, viviparous embryos, and tidal dispersal of propagules. Mangroves exhibit a number of different strategies to deal with salt, such as salt avoidance and regulation coupled with mechanisms of tolerance; resistance strategies include exclusion, extrusion, storage, succulence, compartmentalization, and osmoregulation (Popp, 1995). Salt tolerance varies greatly among species and there are wide species-specific variations in growth responses. Some species such as *Avicennia marina* do not grow in freshwater and may be obligate halophytes, whereas other species grow well in freshwater and do not have an obligatory need for more than trace amounts of salt. The presence of salt can constrain water relations, as a positive water balance and photosynthesis can only be maintained if the potentials in the plant are lower than in the soil; in high-salinity soils, maintaining water balance presents a problem of trying to take up essential inorganic ions to maintain osmotic balance while trying to avoid adverse

effects of high ionic levels in the cytoplasm (Lovelock and Ball, 2002).

Because the metabolic cost of maintaining water balance is high, mangroves display a number of features to minimize water loss, including low transpiration rates and sclerophylly, expressed as mangrove leaves being thick-walled, usually with a multilayered epidermis covered by a thick, waxy, lamellar cuticle that helps to minimize evaporation. On the lower leaf surface, there is usually a dense field of hairs (e.g., *Avicennia*, *Pemphis*) or scales (e.g., *Camptostemon*) that cover salt glands and stomata to reduce water loss from these openings. Sunken stomata, waxy coatings, a thick cuticle, and widespread, cutinized, and sclerenchymatous cells are xenic characteristics for dealing with a physiologically dry environment (Saenger, 2002). Low transpiration rates are imposed by high salt concentrations. When salinity is lower due to high rainfall in the wet season, transpiration rates and stomatal conductance can be high. However, mangroves overall follow a very conservative water-use strategy.

Conserving water reflects a trade-off between the need for the stomata to open to maintain intercellular CO₂ concentrations and the simultaneous loss of water vapor; thus, carbon gain is balanced by some water loss. Low stomatal conductance limits such water loss but also restricts the uptake of CO₂. This dilemma results in low intercellular CO₂ concentrations, low assimilation rates, and high water-use efficiencies – the ratio of carbon assimilated to water used (Saenger, 2002). High water-use efficiency is achieved by adaptive traits such as specialized leaf and stomatal anatomy, high levels of photooxidative protection, hydraulic architecture (small vessels and dense wood), and greater carbon investment in roots than above-ground tree parts (Feller et al., 2010). Physiological stress is minimized and water-use efficiency is maximized by the ability of many species to adjust the angle of their leaves to avoid high temperatures and maximize heat loss; this adaptation also has a metabolic cost as maintaining a favorable leaf angle comes at the expense of light harvesting and assimilative capacity. Various leaf sizes have also evolved to help achieve a balance between maximizing carbon uptake, minimizing leaf temperatures, and minimizing water expenditure.

Morphological and physiological adaptations to maximize root aeration are a key feature of mangroves to deal with the problem of the lack of oxygen and the presence of potentially toxic metabolites in waterlogged saline soils. Morphological adaptations include relatively high root/shoot ratios as well as a range of aboveground root systems, such as pneumatophores (e.g., *Avicennia*, *Sonneratia*) that break the soil surface from the cable roots; stilt roots (e.g., *Rhizophora*) that branch off from the lower trunk and descent into the substrate; knee roots (e.g., *Bruguiera*) that break the surface but curve back down into the soil; buttress roots (*Xylocarpus*, *Heritiera*) that also branch off from the trunk but do so as flattened, triangular structures; and aerial roots that originate from the trunk or lower branches but usually do not reach the



Mangroves, Figure 2 An extensive monospecific stand of *Bruguiera gymnorhiza* in northern Australia. Note the dense canopy and the absence of an understory.

soil (Figure 2). Some species possess one or more of these root types, but a few species commonly found in aerated and/or coarse-grained deposits close to the soil surface (e.g., *Exocoecaria*, *Aegialitis*) do not have such specialized systems (Tomlinson, 1986).

These various root systems provide aeration for subsurface roots and anchorage for the tree. More frequently inundated mangroves possess a greater variety of above-ground root types. Mangrove roots are composed mostly of aerenchymatous tissue, honeycombed with open gas spaces that run down the longitudinal axis (Tomlinson, 1986); the more that roots are waterlogged, the more gas space that is required for internal conduction. The presence of lenticels in most roots provides further evidence of the need for root ventilation. Gas transport by mangrove roots varies in synchrony with the tide. During tidal immersion, oxygen concentrations decline inside the roots with a concomitant reduction in gas pressure. At low tide when the roots are exposed to the atmosphere, the low gas pressure induces the flow of air back into the roots leading to a renewal of oxygen concentration. Transport of oxygen from roots is so efficient that in some genera the rhizome is surrounded by less hypoxic soils.

Waterlogging leads to a number of other physiological and metabolic changes. Soil anoxia induces mangroves to reduce water stress which in the case of shoots may lead to reduced growth rates due to the accumulation of ethylene or imbalance of gibberellin in the plant, as well as depressed stomatal conductance, photosynthesis, and oxygen transport via the roots and increased foliar sodium levels. The presence of anoxic metabolites (e.g., H_2S) can lead to root hypoxia, which can inhibit nutrient

uptake, reduce tolerance to increasing salinity, and lower rates of root respiration. Mangroves demonstrate a variety of metabolic adaptations to the lack of oxygen (Saenger, 2002).

Mangroves also exhibit a range of adaptations to maximize reproductive success in a hostile environment. Pollination occurs either via wind or by animals such as birds, bats, bees, and other insects, but all mangroves disperse their seedlings by tides. All species of the family Rhizophoraceae produce viviparous seeds (propagules), which germinate precociously while still attached to the parent tree; the embryo ruptures the pericarp and can grow to considerable lengths. Some genera (e.g., *Aegialitis*, *Avicennia*, *Aegiceras*, *Lagunularia*, *Nypa*, *Pelliciera*) produce cryptoviviparous seeds in which the developing hypocotyl does not penetrate the pericarp; both vivipary and cryptovivipary incur considerable parental investment. The seeds of the remaining mangrove species do not germinate while still on the parent tree, but do pass through a resting stage before germinating. There may be some advantage of vivipary, including rapid rooting, prolonged nutrient uptake, and development to maximize the chances of reproductive success, and development of buoyancy. There is little evidence of long-distance dispersal of propagules (Hogarth, 2007), but buoyancy, large size, and food storage may confer some local advantage in maximizing survival that is patchy in time and space; large propagules survive longer and grow better as new recruits than small ones.

Most reproductive activity coincides with the wet tropical summer months, a time conducive to rapid growth as well as dispersal immediately after summer

storms and monsoons. Viviparous seeds may possess adequate food reserves due to their extended development while still on the parent tree and are capable of relatively rapid establishment, but there is a trade-off in that such comparatively large seedlings attract a number of predators – to the extent that seed predation can play an important role in determining recruitment success and species composition and community structure of forests.

Forest structure and dynamics

Patterns of recruitment and of the forest structure that eventually develops are the end result of complex interactions among propagule survivability, environmental factors, including climate, and phenology (Feller et al., 2010). The interplay between extreme trait plasticity and specialized adaptations characterizes mangroves and their environment. Mangrove traits are highly plastic in relation to salinity, nutrient availability, and other environmental drivers such as temperature, light, sea-level rise, and the extent of tidal inundation (Krauss et al., 2008). Such plasticity of plant traits can result in forests of variable species composition, age, and community structure.

The apparent zonation of one or a few species across the intertidal seascape has long been regarded as a conspicuous feature of mangroves (Figure 2). Zonation is an oversimplification as any classification is subjective; some forests conform quite well to such categorization, while others defy any classification. Many drivers have been suggested as the causative agent for these tidal gradients, including geomorphological controls; physiological adaptation to physical gradients, especially salinity; tidal sorting of propagules; differential predation on propagules; and interspecific competition (Smith, 1992; Crase et al., 2013). Some or many of these factors can drive intertidal zonation and can vary within a coastal region and even within an estuary. Environmental gradients and species responses are thus very complex. No one factor regulates zonation where it occurs. It has even been suggested that the process is random with the first species and successive ones present eventually determining community composition (Ellison et al., 2000).

The establishment of seedlings through to mature stages is a complex process for forested ecosystems, with terrestrial forests showing peak structural complexity in middle age with a slow decline toward senescence. Disturbance and recovery in terrestrial forests play a key role in maintaining forest diversity and community structure. Present theory indicates that when species die, they are replaced by fast-growing species that are poor competitors, leading over time to eventual replacement of these pioneers by a succession of superior competitors – mostly to monopolize light – until an equilibrium is achieved in climax and postclimax sequences (Odum, 1981). Mangrove forests, in contrast, appear to have species and communities with more pioneer-stage than mature-stage characteristics, including light-demanding seedlings, competition for light, dispersal by tides rather than by

biota, long propagule dormancy and viability, dependence on seed reserves, continuous production of numerous propagules, early reproductive age, uniform crown shape, prolonged flowering period, poor species richness, no or little canopy stratification, few climbers, and few epiphytes (Smith, 1992).

Changes in forest structure and composition occur within a milieu of natural disturbance to equilibrium or steady-state conditions, as all ecosystems are subject to a variety of disturbances that are a driving force in facilitating adaptive change. The timescale in which mangroves recover from disturbance depends in part on the intensity, duration, and scale of the disturbance. Recovery may follow classic large gap-phase dynamics whereby enhanced recruitment rates are matched by greater mortality following gap formation as the forest returns to a closed canopy state; the primary factor limiting recruitment in gaps is light availability.

Trends in recovery are not stochastic, but the early sequences of species replacement are greatly determined by the species present at initial recovery (Souza et al., 2007). With increasing forest age, tree densities decline but individual trees become larger due to self-thinning; with fewer but larger trees, aboveground biomass increases with forest age. Long-term changes in mangrove forest structure have rarely been examined, but a few studies suggest that mangroves are a mosaic of patches of different stand ages if there is a high frequency of gaps (Berger et al., 2006). If gaps are absent or few, there are still transitory variations in what are otherwise zonal or monospecific forests; intermediate disturbances are unlikely to culminate in a classic climax or postclimax community (Lugo, 1980). As stated by Alongi (2008, p. 5), “stand composition and structure in mangrove forests are the new result of a complex interplay of physiological tolerances and competitive interactions leading to a mosaic of interrupted or arrested successional sequences in response to physical/chemical gradients and to changes in geomorphology.” That is, if a forest remains relatively undisturbed for long time periods relative to individual life spans or if a primary forest is being established, mangroves can undergo a series of successional stages similar to those that are undergone in terrestrial forests. However, in most coastal regions, intertidal areas are frequently disturbed by natural (typhoons, seasonal monsoons) or anthropogenic (wood harvesting, pollution) forces, so mangroves are often a patchwork of interrupted successional stages, as are most ecosystems undergoing ecological succession under stress (Odum, 1981).

Mangrove forests, partly for these reasons, have low plant diversity, have a relatively simple architecture, and rarely have a significant understory, but they do have a variety of features that help make them resilient to disturbance. These characteristics include (1) a large reservoir of belowground nutrient pools that serve to replenish nutrient losses; (2) rapid rates of plant-microbial-soil cycling of carbon and nutrients that facilitate retention of these elements; (3) complex and highly efficient biotic controls,

such as high rates of nutrient-use and water-use efficiency; and (4) positive and negative feedbacks that provide malleability to help dampen variations in recovery. Their simple architecture can lead to rapid recovery or rehabilitation post-disturbance, as there is redundancy of keystone species.

Fauna and trophic structure

Trees and bacteria constitute the bulk of forest biomass, but many other organisms originating from adjacent terrestrial and marine environments are found in mangroves (Macnae, 1968). Birds, bats, monkeys, tigers, insects, fish, amphibians, reptiles, and a rich fauna of estuarine and marine plankton and benthic invertebrates spend all or part of their life cycle in the forest canopy, soils, and tidal waterways (Kathiresen and Bingham, 2001; Nagelkerken et al., 2008). These populations and communities overlap, as mangroves are ecotones having a high level of connectivity with both terrestrial and marine ecosystems (Feller et al., 2010).

The most functionally conspicuous organisms in mangroves are sesarmid and grapsid crabs, being keystone engineers in many forests (Cannicci et al., 2008; Nagelkerken et al., 2008). The significance of crabs as biological drivers of forest structure and function was recognized in the late 1970s and early 1980s (Kathiresen and Bingham, 2001). Sesarmid crabs are very important in shaping mangrove structure and functioning, especially in Old World mangroves, while ocypodid crabs play the same role in New World mangroves. Crabs process a large proportion of algal and leaf biomass and are ecosystem engineers in their ability to bioturbate and aerate mangrove deposits and, along with other predators, consume and bury large quantities of propagules (Kristensen, 2008). A number of models have been proposed to explain the mode of crab control via propagule predation on forest structure: (1) the dominance-predation model, which states that there is an inverse relationship between predation rates of different species in relation to its dominance in the forest; (2) the canopy-gap-mediated model, which postulates that predation can be more intense under closed canopies than in relatively large gaps; (3) the flooding regime model, which suggests that the level of propagule predation is inversely related to inundation time (the more time the forest floor is flooded, the less time crabs have to prey on propagules); and (4) the spatio-temporal biocomplexity model, which hypothesizes that while low water or high water conditions are a key driver in initial plant establishment or failure, other factors related to the dry or wet conditions (e.g., salinity, drought, soil texture) come into play, so forest patch structure may be the result of differences in environmental drivers. Regardless of causative mechanism(s), the net result of propagule predation is reduced completion among saplings.

Mangrove structure and function are shaped by a variety of other organisms. Gastropods, for example,

do so by consuming large volumes of mangrove material, such as litter, algae, and wood, and wood-boring isopods help to facilitate fungal decomposition of wood. Similarly, herbivorous insects such as ants, moths, and caterpillars bore into wood as well as consume flowers, fruits, seeds, and leaves. Ant-plant interactions can play a key role in regulating vegetation structure and function (Cannicci et al., 2008).

Above the substratum, mangrove roots are often overgrown by epibionts such as tunicates, sponges, algae, and bivalves, while the forest floor and canopy – visited by birds, insects, bats, rats, and even monkeys – are fauna-rich. Both the canopy and epibiotic communities are very diverse with close associations between tree and animals; some of the interactions are highly complex (Ellison and Farnsworth, 2001). The functional significance of many of the organisms, especially the vertebrates, is largely unknown. Root epibionts are known to be highly diverse and an attractant for a wide assortment of invertebrates, as well as having an important role in nitrogen transformation processes (Ellison et al., 1996).

Mangrove plankton and nekton are, like their benthic and canopy-living counterparts, key players in the flow of materials and energy in mangrove ecosystems. In both soils and tidal waters, a large proportion of organic matter and energy flow is funneled through a highly diverse, actively growing, “microbial loop or hub” consisting of Archaea, bacteria, protists, and viruses and subsequently transferred to higher consumers such as zooplankton and fish; metabolic by-products such as respired CO₂ and wastes are similarly transferred and integrated into various biogeochemical cycles that help to sustain life (Figure 3). Mangrove microbes are highly abundant and productive, fuelled by new and recycled DOM and inorganic nutrients. Indeed, the first link in the “microbial loop or hub” is the uptake of exudates from phytoplankton cells and cell contents released during “sloppy feeding” by microzooplankton, so there is a strong link between microbial and phytoplankton productivity. Trophic relationships within and between microbial assemblages are virtually unknown, but presumably intense, as protists such as amoebae and flagellates are voracious consumers of bacteria and are known to graze heavily on bacterioplankton (Lee and Bong, 2007). In contrast, phytoplankton communities in mangrove waters are thought to be species-poor due to inhibitory effects of high concentrations of soluble tannins and other polyphenolics. Phytoplankton abundance and productivity range widely in mangroves, usually in relation to light availability and flushing rates of waterways; stagnant or polluted waters are common throughout Asia, for example, with high rates of primary production in these virtual nutrient “soups.”

Zooplankton communities are the crucial link between microbes (to which some of the tiniest zooplankters belong), penaeid shrimps, and zooplanktivorous fish. The main factor controlling zooplankton abundance and species composition is the seasonal change in salinity, with the onset of the monsoon season the prime stimulus



Mangroves, Figure 3 An example of *Rhizophora apiculata* with both large stilt roots and extensive roots descending from lower branches; photo taken in a mixed forest in lower Sumatra, Indonesia.

for shifts in composition and abundance. Mangrove zooplankton communities consist of four components: (1) a stenohaline marine group that penetrates into the estuary mouth, (2) a euryhaline group that penetrates further up estuary, (3) a true estuarine component, and (4) a freshwater group in the upper tidal reaches (Kathiresen and Bingham, 2001). The most conspicuous group are members of the cyclopoid copepod family Oithonidae that may have a selective advantage of small size to avoid prey and a number of strategies to maximize growth and reproduction. Larger zooplankters are an important trophic link to fish but play an equally crucial role as structuring agents of microzooplankton, the latter accounting for as much as 75 % of potential phytoplankton production.

Penaeid prawns and fish have received the most attention among mangrove biota due to their role in commercial and recreational fishing. Prawn species of the genera *Penaeus*, *Metapenaeus*, *Parapeneopsis*, and *Macrobrachium* are the primary fishery targets, and great effort has focused on their life history strategies, distribution, abundance, degree of habitat dependence, and catch

per unit effort (Manson et al., 2005). Shrimps function as mid-level and top omnivores, regulating the abundance of smaller plankton and nekton and spending their post-larval and juvenile stages in mangrove estuaries until emigrating offshore where they spawn in the wet season. Annual shrimp production is more a reflection of catch per unit effort than a true reflection of their productivity, but rates ($13\text{--}756\text{ kg ha}^{-1}\text{ year}^{-1}$) are well within the range of values measured in estuaries and nearshore habitats worldwide (Alongi, 2009).

Fish life cycles are similarly well known, with species richness of permanent and temporary residents being a function of salinity, microhabitat diversity, tides, water depth and clarity, coastal water currents, and proximity to seagrass beds and coral reefs (Faunce and Serafy, 2006). The number of species in any given mangrove estuary can range from <10 to nearly 200, with a tendency for more species in larger estuaries; density and biomass estimates are similarly variable, ranging from 1 to 160 fish m^{-2} and $0.4\text{--}29\text{ g m}^{-2}$ and generally greater than in temperate estuaries (Blaber, 2002). Mangrove fish are grouped into five feeding guilds – herbivorous, iliophagus, zooplanktivorous, piscivorous, and benthic invertebrate feeders – but many species shift their dietary preferences as they age. Wild fish production varies greatly ($17\text{--}1,000\text{ kg ha}^{-1}\text{ year}^{-1}$) worldwide (Alongi, 2009), with peak landings during the post-monsoon and summer months.

Are mangroves major nursery grounds for fish and shrimp? This idea was first articulated nearly fifty years ago (Heald, 1969), but the links between mangroves and edible items were obviously known by indigenous communities much farther back in time. Three hypotheses have been offered to explain the connection between coastal fisheries and mangroves: (1) the food hypothesis, which suggests that mangroves offer an abundant variety of foods; (2) the refugia hypothesis, which suggests that mangroves function as a refuge from predation; and (3) the shelter hypothesis, which suggests that mangroves provide shelter from physical disturbances (Manson et al., 2005). None of these hypotheses are mutually exclusive, and perhaps all three factors may be operating at the same time in the same place. Very little direct evidence exists to explain the relationship between fishery catch and mangroves, but evidence exists to support the notion that coral reef fish use mangroves and seagrasses as essential juvenile habitat (Kimirei et al., 2013). The underlying mechanisms or the cause-and-effect relationships of the connection between fishery yields and mangroves, however, remain poorly understood.

Forest production and photosynthetic performance

Mangroves are among the most productive plants in the sea, as revealed by proxy measurements of leaf and wood production (Alongi, 2009). Belowground production of roots has rarely been measured, but

aboveground net primary production (AGNPP) averages $11 \text{ t DW ha}^{-1} \text{ year}^{-1}$ (Alongi, 2009). This AGNPP rate compares favorably with the mean AGNPP rate for tropical terrestrial forests of $12 \text{ t DW ha}^{-1} \text{ year}^{-1}$. Production rates of both mangroves and other tropical forests overlap highlighting the fact that similar ecological and physiological factors limit production of all trees. Some forests of both habitats in the dry tropics are not very productive compared with the most luxuriant forests in wet tropical regions. Mangroves, like other forests, vary in size and age and in the balance between production and respiration. Measurements of belowground primary production are lacking for all tropical forests, as are measurements of dark leaf respiration and respiration of roots and woody parts, so true estimates of total forest net primary production are sparse. Despite these constraints, mangrove AGNPP declines with increasing distance from the equator, mirroring the decline in mangrove biomass (Alongi, 2009).

The light response curves of mangrove leaves are similar to other tropical plants in which saturation is reached at $300\text{--}400 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ after a steep linear increase to this threshold. Maximum CO_2 assimilation rates can often exceed $25 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ although most rates lie between 5 and $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ as saturation is reached at comparatively low light conditions due to low stomatal conductance and intercellular CO_2 concentrations. Rates of leaf photosynthesis decline with increasing salinity and increasing vapor pressure deficit. Despite these limitations, the median rate of mangrove leaf photosynthesis ($12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) is equal to the median rate ($11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for shade-intolerant terrestrial trees.

The rate of dark leaf respiration in mangroves ranges from 0.2 to $1.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with photosynthesis to respiration (P/R) ratios ranging from 2.1 to 11.2 , which is at the upper end of the range of values for tropical terrestrial species. A few root respiration measurements have been made, mainly on *Avicennia marina* pneumatophores, with highly variable rates among all species (*Rhizophora mangle*, $0.5\text{--}6 \text{ nmol CO}_2 \text{ g}^{-1} \text{ root FW s}^{-1}$; *Avicennia marina*, $2\text{--}3 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ root FW h}^{-1}$). These rates are at the lower end of values for other tropical trees.

The uptake and assimilation of micro- and macronutrients play a key role in determining mangrove growth and production, as mangroves are often limited by the availability of nitrogen (N), phosphorus (P), and iron (Fe). These and many other elements are required to synthesize cells and to manufacture structural and reproductive tissue (Reef et al., 2010). The critical need for N and P has been demonstrated for a number of mangroves, with clear interactive effects among different mangrove species, nutrients, and environmental factors such as salinity, temperature, soil type, and frequency of tidal inundation (Feller et al., 2010).

The ordinarily high photosynthetic rates for mangroves drive a high requirement for nutrients; nutrient-use efficiencies and rates of nutrient resorption by leaves are

correspondingly high. Differences among species in nutrient-use and resorption rates can be explained by differences in the way species allocate nutrients as well as species differences in leaf life spans and how energy and nutrients are vested in chemical defenses. With such a high requirement for nutrients, mangroves have evolved a number of conservation mechanisms (in addition to high resorption efficiencies), including large reservoirs of dead roots belowground, tidal export of predominantly refractory matter, and highly efficient nutrient cycles (Reef et al., 2010).

Phytoplankton and algae living on the forest floor and as epiphytes on aboveground tree parts are additional sources of fixed carbon in mangroves. Algal production in mangrove waters and under the canopy is light limited, and while algal productivity can be high, it is usually dwarfed by tree production (Alongi, 2009).

Nutrient cycling and sources for secondary consumers

The cycling of essential elements such as N in mangrove ecosystems is highly complex and internally regulated by the trees and their interrelationships with soil, water, and microbiota – most of whom are responsible for the bulk of nutrient transformations and recycling processes. Concentrations of dissolved and particulate N and P are low in tropical waters and mangrove soils, but cycle quickly, to the extent that residence times for many nutrient pools are on the order of minutes to hours. Nutrients are transformed, taken up, and assimilated by the trees and other biota both rapidly and efficiently, despite the fact that acquiring nutrients is not a straightforward process. In mangrove soils, for instance, Fe oxyhydroxides and metal sulfide complexes readily bind to organic nutrients, thereby limiting the amount available to the plant. Geochemical redox reactions in soils and sediments are complex and involve a wide array of elements and compounds restricting the uptake of dissolved organic and inorganic nutrients.

Conserving nutrients is advantageous, so large belowground reservoirs of dead roots and maximizing nutrient storage in the youngest tree parts are efficient retention mechanisms. Another effective conservation strategy is to increase the efficiency of various metabolic processes and the utilization of nutrient pools. Mangroves invest a large proportion of root metabolism in the uptake and assimilation of soil ammonium, which translates into a comparatively low-energy investment compared with using nitrate or possibly DON.

The soil N cycle in mangroves indicates that ammonium production (ammonification) is the dominant N transformation process, with proportionally little loss to the atmosphere via anammox (anaerobic ammonium oxidation) and denitrification (production of N_2 gas). High rates of ammonification are supported by dissolved organic nitrogen (DON) released by roots. The uptake of ammonium is fast enough compared to its production that

often nearly all ammonium is taken up by tree roots. Nitrogen fixation and denitrification rates, in contrast, are highly variable and, on average, slow processes. The tight coupling between trees, microbes, and soil nutrient pools is partly a function of the interactive effects between forest age and intertidal position. However, the cycling of P and other elements is poorly known in mangroves.

The need for N in mangrove food webs has attracted much debate as early notions of animal nutrition pointed to N in mangrove detritus as the main fuel for food webs (Heald, 1969). The original paradigm was that microbes attached to detritus reduced complex indigestible vascular plant material to simple, more readily digestible forms, with subsequent microbial enrichment providing sufficient N for adequate nutrition (Ellison and Farnsworth, 2001). The current paradigm derived primarily from work using stable isotopes is that most mangrove consumers preferentially assimilate fresh benthic microalgae and macroalgae, phytoplankton, and algal detritus to meet their N requirements. Such material is nitrogen-rich and more readily digestible than mangrove plant detritus. The discovery that sesarmid and grapsid crabs are foundational ecosystem engineers led to a paradigm shift in recognizing the nutritional importance of algal foods. Crabs were once a prime example of the notion that mangrove secondary consumers met their nutritional needs by voraciously eating large amounts of N-poor mangrove litter and assimilating the associated N-rich microbial biomass. This early explanation seemed reasonable because crabs can consume nearly all standing stock of litter in some forests and paste litter fragments onto their burrow walls facilitating fungal and bacterial colonization, making the material more palpable and nutritious over time (Kristensen, 2008). However, mangrove litter is high in tannins and too poor in nitrogen to sustain adequate nutrition. In reality, crabs, like most other secondary consumers, eat a variety of foods to maintain a balanced diet, obtaining sufficient N from supplemental consumption of animal tissue and meiofauna. Sophisticated feeding experiments have found that the crabs *Episesarma* spp. and *Perisesarma* spp., as well as penaeid shrimp larvae, are omnivorous, eating mostly mangrove detritus and lesser amounts of roots, algae, animal tissue, and surface microbial biofilms (Nordhaus et al., 2011; Gatune et al., 2012).

Mangrove-associated fish and zooplankton also have varied diets but with a preference for algal over detrital foods. An individual mangrove forest may thus have multiple food webs partitioned by dietary preferences for algae, detritus, mixed algal/detrital foods, and animal tissues such as carcasses and smaller consumers such as microzooplankton (Giarrizzo et al., 2011). The nutritional situation can be even more complicated if seagrasses and coral reefs are nearby, as fish residents feed mainly on mangrove-associated foods, but transient fishes actively forage on seagrass or reef-associated prey items (Vaslet et al., 2012). The significance of mangrove N (and other nutrients) thus depends on the location and type of habitat,

relative availability of other primary producers, species dietary preferences, and universal need to maintain a balanced diet.

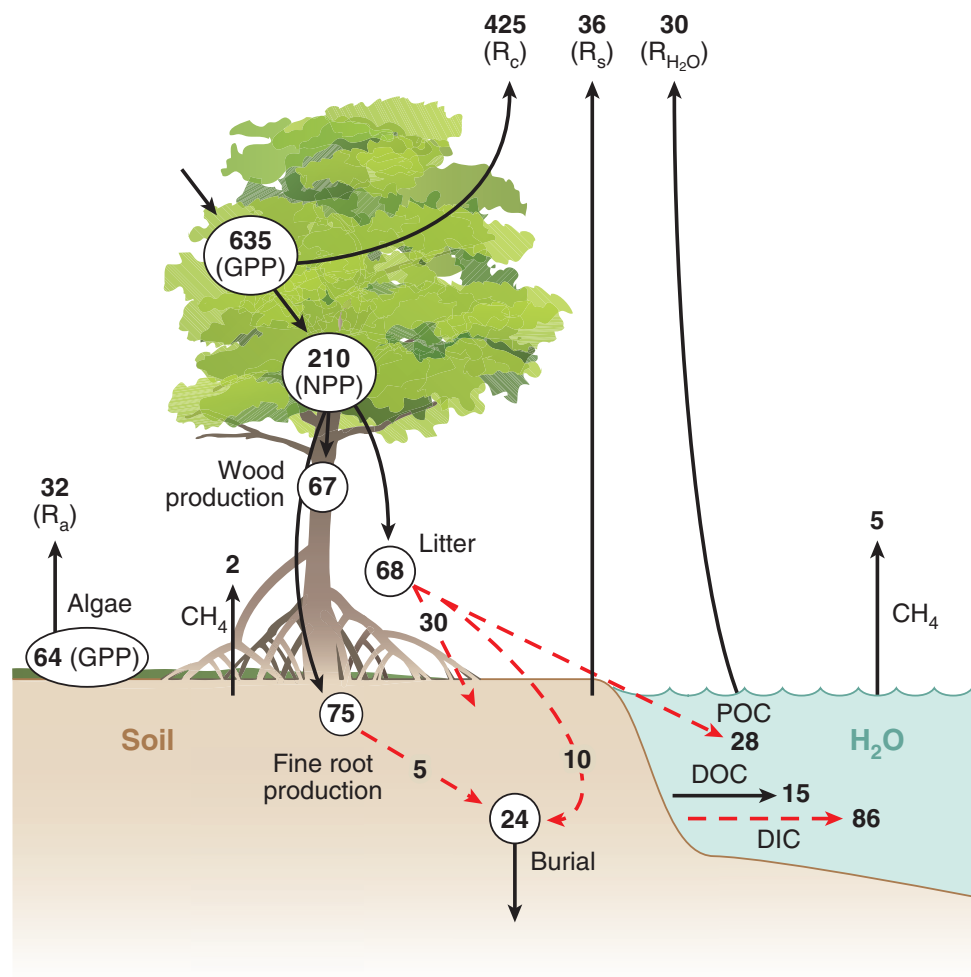
Ecosystem processes: contribution of mangroves in global coastal ocean

Mangrove forests are structurally and functionally interlinked with adjacent terrestrial and marine ecosystems and the atmosphere, exchanging biota, air, water, soils and sediments, nutrients, and other elements, over space and time. Tides represent an energy subsidy, doing work by transporting dissolved and particulate materials, gases, and metabolic by-products between the forest and other ecosystems. The idea that the fertility of coastal wetlands such as mangroves via these exchanges supports primary and secondary production in the adjacent near-shore zone developed in the late 1960s (Heald, 1969), and this “outwelling” hypothesis generated much subsequent research into the role of mangroves in supporting coastal production. After decades of research, it is clear that the amount of material potentially available for export from mangroves is influenced by such factors as forest production, tidal range, the ratio of mangrove to watershed area, local hydrodynamics, amount of rainfall, volume of water exchange, and the extent of activities of crabs and other biota (Alongi, 2009).

Most mangroves export nutrients, but some do not. Globally, mangroves export an average of $28 \text{ T g C year}^{-1}$ of particulate organic carbon (POC), or about 10–11 % of particulate terrestrial carbon export to the global coastal ocean (Alongi, 2014). Mangroves also export large quantities of dissolved organic carbon ($15 \text{ T g C year}^{-1}$) or dissolved inorganic carbon ($86 \text{ T g C year}^{-1}$) to the coastal ocean, with most of the latter originating from subsurface advection of interstitial water within the forest floor. Thus, nearly 75 % of the total C exported from mangroves originates from respiration by microbes and other mangrove biota in soils and tidal waters.

A nitrogen mass balance model of the world's mangroves indicates that (1) $2687 \text{ G g N year}^{-1}$ is required to sustain global mangrove NPP; (2) N burial is about 25 % of total N input into an “average” mangrove forest; (3) about 15 % of total N input to mangrove soils is denitrified; (4) nitrogen fixation accounts for only about 5 % of total N input although nitrogen fixation on above-ground tree parts and in deep root systems has not been adequately measured; (5) production of roots and litter accounts for 40 % and 50 % of mangrove NPP, respectively; (6) tidal losses equate to about 55 % of N input; (7) denitrification and N_2O effluxes account for <10 % of total N losses; and (8) despite proportionally large tidal losses, the global flux of N in mangroves is roughly in balance (Alongi, 2013).

The balance of carbon between photosynthetic gains by autotrophs and respiratory losses from all biota, reflected in the exchange between ecosystems, atmosphere, and adjacent ecosystems, is called the net ecosystem



Alongi DM. 2014.
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Mangroves, Figure 4 Budget of the major pathways of carbon flow ($T\ g\ C\ year^{-1}$) through the world's mangrove forests. *Solid black arrows* represent empirically derived mean values, and *dashed arrows* represent either mean values estimated indirectly (by difference) or pathways suggested from the recent literature. Abbreviations: *DIC* dissolved inorganic carbon, *DOC* dissolved organic carbon, *GPP* gross primary production, *NPP* net primary production, *POC* particulate organic carbon, R_a algal respiration, R_c canopy respiration, R_s soil respiration, R_{H_2O} waterway respiration (From Alongi, 2014). Reprinted with permission from the annual Review of Marine Science, Volume 6 copyright 2014 by Annual Reviews, <http://annualreviews.org>.

production (NEP). NEP varies widely among mangrove ecosystems, but on average, mangroves produce and store more carbon than they lose. A number of carbon mass balance estimates exist for the global expanse of mangroves (Bouillon et al., 2007; Alongi, 2009), with the most recent budget (Figure 4) showing a number of key features of mangrove ecosystems: (1) two-thirds of forest gross primary production is lost as canopy respiration; (2) NPP is nearly evenly allocated to wood, litter, and fine root production; (3) roughly 60 % of carbon buried in soils is likely derived from litter and dead roots with the remainder originating from adjacent upland and marine ecosystems; (4) roughly 50 % of leaf litter is exported by tides with the other half utilized within mangroves; and

(5) nearly all carbon (90 %) lost to adjacent coastal waters and to the atmosphere is derived from respiration. NEP of the world's mangroves equates to $90\ T\ g\ C\ year^{-1}$, a value that compares favorably with NEP for the world's coral reefs ($84\ T\ g\ C\ year^{-1}$), but much less than NEP for salt marshes ($475\ T\ g\ C\ year^{-1}$), seagrasses ($533\ T\ g\ C\ year^{-1}$), and macroalgae ($2,221\ T\ g\ C\ year^{-1}$). Mangrove ecosystems are net autotrophic, with a GPP/R ratio of 1.15, with the remaining fixed mangrove carbon stored in vegetation and soil and, to a much lesser extent, is lost to a variety of human uses. Mangroves occupy 0.5 % of coastal ocean area but account for 8 % of coastal respiration, 7 % of coastal GPP, and 3 % of coastal NEP. Mangroves account for approximately 10–15 % of total

carbon sequestration in the coastal ocean. These budgets show that cycling of carbon and other elements is in rough balance in mangrove ecosystems, despite living in a harsh, tropical environment.

Summary and conclusions

Mangroves occupy only about 0.5 % of the world's coastal area but contribute disproportionately in myriad ways to the ecology and economy of tropical and subtropical coastal zones and their inhabitants. Mangrove forest biomass and production are equivalent to tropical lowland forests. Mangroves have evolved many morphological, reproductive, and physiological traits for life in water-logged saline soils, including aerial roots, viviparous embryos, sclerophylly, low assimilation rates, high root/shoot ratios, and high water- and nutrient-use efficiencies. The forest structure is structurally simple compared with their distant terrestrial relatives, often lacking an understory and having comparatively low tree diversity; species richness is greatest in the Indo-West Pacific supporting the notion that this is also the location of their origin during the Late Cretaceous-Early Tertiary. Tidal gradients in species composition are frequently expressed in relation to combinations of tidal gradients in salinity, frequency of tidal inundation, seed predation, competition, and other drivers, the complex interplay of which leads to forest mosaics of interrupted successional sequences. Trees and bacteria account for most forest biomass, but rich pelagic, arboreal, and benthic food webs consist of both terrestrial and marine flora and fauna. Sesamid and grapsid crabs are foundational ecosystem engineers, although microbes drive carbon and biogeochemical cycles. Mangroves are among the most productive plants in the sea, being highly efficient users of essential micro- and macronutrients.

While statistics for most countries are lacking, many mangrove forests are no longer pristine, even in the most remote locations. In the face of forecasted rises in sea level, the pressures on mangroves worldwide are expected to increase for the foreseeable future.

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Cross-references

Coastal Wetlands
Estuarine Connectivity
Forested Wetland Habitat
Species Zonation
Tidal Flat
Trophic Dynamics

MARINE/FRESHWATER MIXING

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Definition

In an estuarine context, the mixing of marine and freshwater refers to the dynamics of interchange and dilution by freshwater delivered mainly by riverine influx and of marine water delivered by tides, wind-driven currents, and wave action.

The estuarine environment: a zone of mixing between seawater and freshwater

The essence of an estuary is that it is a river-to-marine transitional environment where marine salinity is measurably diluted by (riverine) freshwater in a valley tract, an inlet, a coastal lagoon, or an embayment, producing a salinity gradient from the river to the sea (Cameron and Pritchard, 1963; Pritchard, 1967). As such, the estuarine environment is the zone of mixing between freshwater derived from river sources and marine water from the sea. In terms of hydrochemistry, biota, and processes, there is a riverine component toward the landward part of an estuary and marine component seaward (Day, 1981; Dalrymple et al., 1992; Allen and Posamentier, 1993; Semeniuk et al., 2000; Semeniuk and Wurm, 2000).

Landward parts of estuaries with perennially flowing rivers can remain freshwater throughout the year. Landward parts of estuaries with seasonally flowing rivers fluctuate between freshwater and brackish or between freshwater and marine salinity. At the other extreme, the marine environment generally remains at seawater salinity but, with seasonally strongly flowing rivers, fluctuates between marine and brackish or even freshwater (where freshwater riverine plumes enter the sea). Over the period of a year, a season, or a week, depending on flow rates and volume of delivery of river water and tidal flows, the central estuarine basin can remain perennially brackish or may fluctuate between freshwater and marine with periods of brackish water or fluctuate between brackish and marine. In areas of high evaporation and minimal river influx, the headwaters or even main waters of an estuary may become hypersaline.



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