M

MANGROVES

Norman C. Duke
School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia

Synonyms

Mangrove forest; Mangrove swamp; Mangrove trees; Sea trees; Tidal forest; Tidal swamp; Tidal wetland

Definition

Mangroves. A tidal habitat comprised of salt-tolerant trees and shrubs. Comparable to rainforests, mangroves have a mixture of plant types. Sometimes the habitat is called a tidal forest or a mangrove forest to distinguish it from the trees that are also called mangroves.

Mangrove. A tree, shrub, palm, or ground fern, generally exceeding 0.5 m in height, that normally grows above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal salt marsh. Small shrubs or herbaceous plants, generally less than 0.5 m in height, that normally grow above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal salt pan. Flat areas of fine sediments lacking macrophyte vegetation above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

Tidal wetlands. The combination of mangroves, tidal salt marsh, as salt pan, as habitats distinctly occurring between mean sea level and the highest tides. In arid and cooler settings, mangroves share this tidal niche, or one replaced with diminutive halophyte cousins, the tidal saltmarsh, and flat salt pan expanses with their remarkable microalgal carpet.

Introduction

Mangroves are one of the world's dominant coastal ecosystems comprised chiefly of flowering trees and shrubs uniquely adapted to marine and estuarine tidal conditions (Tomlinson, 1986; Duke, 1992; Hogarth, 1999; Saenger, 2002; FAO, 2007). They form distinctly vegetated and often densely structured habitat of verdant closed canopies (Figure 1) cloaking coastal margins and estuaries of equatorial, tropical, and subtropical regions around the world (Spalding et al., 1997). Mangroves are well known for their morphological and physiological adaptations coping with salt, saturated soils, and regular tidal inundation, notably with specialized attributes like: exposed breathing roots above ground, extra stem support structures (Figure 2), salt-excreting leaves, low water potentials and high intracellular salt concentrations to maintain favorable water relations in saline environments, and viviparous water-dispersed propagules (Figure 3).

Mangroves have acknowledged roles in coastal productivity and connectivity (Mumby et al., 2004), often supporting high biodiversity and biomass not possible otherwise. Mangrove ecosystems are key sources of coastal primary production with complex trophic linkages (Robertson et al., 1992), as nursery and breeding sites of marine and arboreal life (Figure 4), and as physical shelter and a buffer from episodic severe storms, river flows, and large waves.

In tropical waters, mangrove stands are often sandwiched between two of the world's iconic ecosystems of coral reefs and tropical rainforests. Biota-structured ecosystems, like these, play a unique role in coastal ecosystem processes via a combination of well-developed linkages, coupled with transient biota uniquely adapted to unusual and often dramatic physico-chemical gradients. Linked and dependent relationships developed over millennia have become vital to the survival of each biome.

Mangroves, Figure 1 Sinuous channels and tidal wetlands of Missionary Bay, northeastern Australia. Amongst the wide mangrove zones are bare saltpans with saltmarsh patches.

Mangroves, Figure 2 A forest of exposed, above-ground stilt roots of *Rhizophora apiculata*, Daintree River estuary, northeastern Australia.

Mangroves, Figure 3 Mature, viviparous propagules of a *Bruguiera gymnorhiza* tree, near Dumbea, New Caledonia.

Mangroves, Figure 4 A cormorant makes use of an eroding edge tree of *Sonneratia caseolaris*, in the upper Daintree River estuary, northeastern Australia.

Colonial corals flourish in shallow warm seas of coasts where mangroves buffer and protect them from land runoff. Mangroves absorb unwanted nutrients and turbid waters stabilizing otherwise smothering water-borne sediments and depositional shorelines. These specialized plant assemblages provide important ecosystem services along with additional acknowledged roles of highly productive habitat and nursery sites. The consequences in disturbing these habitats is likely to have unexpected and far-reaching impacts on neighboring ecosystems and dependant biota (Duke et al., 2007).

Uniquely mangrove origins and vulnerability

Mangroves are a unique ecological assemblage (Duke et al., 1998), remarkable for their relatively small number of widely distributed flowering plants – evolved mostly post-Cretaceous over the last 60–100 million years. The relatively recent evolution of these plants may explain their comparatively low diversity, but this feature is arguably also related to the harsh environmental conditions defining the niche. Today's mangrove flora includes representatives of at least 21 plant families, testament to the adaptive success of various phylogenetic lineages venturing into the intertidal zone from upland rainforest ancestors. This small group of highly specialized plants tap rich estuarine nutrients with characteristically shallow arrays of below-ground roots bearing distinctively vascular, air-breathing anatomy. Specialized above-ground roots and buttresses further provide exposed air-breathing surfaces and physical support, as well as significant habitat amongst their structure – a characteristic shared with adjacent upland forests and reefal corals.

Ancestral mangrove plants are believed to have reinvaded marine environments in multiple episodes from diverse angiosperm lineages culminating in today's mangrove flora (also Saenger, 2002). Their appearance and evolution appears 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 the tidal zone, and estuaries. The land–sea interface is a dynamic environment, where subtle changes in climate, sea level, sediment, and nutrient inputs have dramatic consequences for the distribution and health of mangroves. Adding to these, direct human disturbance of mangroves include: eutrophication, dredging/filling, overfishing, and sedimentation. The combined pressures, coupled with global climate change and sea level rise, have led to many healthy mangrove areas becoming endangered communities (Duke et al., 2007). Various rehabilitation projects have shown further that it is extremely difficult to achieve effective, large-scale restoration. Urgent protective measures need to be implemented to avoid further mangroves losses and further degradation of coastal ecosystems.

Rich and diverse

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the upper half of the intertidal zone of coastal areas worldwide (Duke, 1992). They are often mistakenly thought of as a single entity. But, like coral reefs, healthy mangroves are functionally diverse and complex. They also provide essential structure and habitat for a host of marine and intertidal species

Mangroves, Figure 5 Terebralia gastropods devouring a fallen mangrove leaf, near Koumac, New Caledonia.

(Figure 5), comprised of both: residents amongst their dense forest of stems and complex roots, and as visitors with each flooding tide. Mangroves are analogous to tropical rainforests also, where they have foliage canopy habitat for birds, mammals, insects, and other invertebrates. Shared ancestral links underlie many similarities between these plant-structured habitats.

Mangroves are not a genetic entity, but an ecological one (Duke et al., 1998). Mangrove vegetation includes a range of functional forms, including trees, shrubs, a palm, and ground fern. The only plant families comprised exclusively of mangrove taxa are Avicenniaceae and Sonneratiaceae, although this continues to be debated. In Table 1, 77 species of mangrove plants are listed for the world. This number however, is not fixed, and varies with different authors since there are a number of subjective and influential factors, including: doubts surrounding the definition of mangroves; whether to include saltmarsh plants; whether to include mangrove associates; and inconclusive taxonomic description of all taxa.

Amongst the 21 flowering plant genera found in mangroves, there is a relatively high degree of specialization for the tidal wetland habitat. Twelve angiosperm genera are exclusively mangrove while ten others include non-mangrove species. This latter group includes: *Aglaia*, *Barringtonia*, *Cynometra*, *Diospyros*, *Dolichandrone*, *Excoecaria*, *Heritiera*, *Mora*, *Pemphis*, *Tabebuia*, and *Xylocarpus*. For *Pemphis*, this genus has only one upland species located inland as an isolated population on the island of Madacascar. Others show different degrees and types of variation. For instance, distinct hybrids are reported in four genera including *Bruguiera*, *Lumnitzera* (Figure 6), *Sonneratia*, and *Rhizophora* (in Table 1, see species prefixed with "X"). Overall, the diversity of species in these genera is often relatively low, being one or two. These relatively low measures of diversity are believed to be the result of harsh growth conditions present in intertidal habitats. Local and regional environmental factors are believed to play a key role in defining the ecological entity that is mangrove habitat. *Rhizophora* species, the most diverse and dominant genus, often occur at the front of mangroves, fronting the sea or channel, and associated with moderate salinities but not extremes. *Avicennia* species, having a wider salinity tolerance, are notably variable occurring in both frontal and upland stands in the Indo-West Pacific.

Structural diversity

Mangrove plants characteristically range from trees (like species of *Avicennia* (Figure 7), *Rhizophora* (Figure 2)), to shrubs (species of *Aegiceras*, *Aegialitis*, *Pemphis*, and *Conocarpus*), to the trunkless palm (*Nypa fruticans* (Figure 8)), and ground fern (*Acrostichum*). Trees and shrubs vary further where they might be columnar and erect (*Pelliciera rhizophorae* (Figure 9), *Bruguiera parviflora*), to spreading, sprawling (*Acanthus* spp., *Scyphiphora hydrophylacea*), and multiple-stemmed (*Ceriops decandra*). Growth form might also vary within the same species (*Lumnitzera littorea* and *Rhizophora*), having both an erect tree form, and low tangled thicket forms. In general, edge plants (both waterfront and landward) have more lower limbs and foliage, and their stems are laterally sprawling and sinuous, rather than erect and straight. Some species typically form combined closed canopies (*Avicennia marina*, *Rhizophora apiculata*, *Bruguiera parviflora*, *Bruguiera gymnorhiza*, *Camptostemon schultzii*, *Xylocarpus* spp.), while others are commonly found as undercanopy plants beneath the closed canopy (like species of *Aegiceras*, *Cynometra*, *Acanthus*, *Acrostichum*, and *Ceriops decandra*).

Mangroves have notable above-ground breathing roots and shallow below-ground anchoring roots, because their soils are usually saturated and airless. The trees have broad support structures, such as buttresses and sturdy prop roots, because soils are often soft and unconsolidated. Root structures above ground include four types: (1) pneumatophores – pencil-like (*Avicennia* (Figure 7)), erect conical (*Xylocarpus moluccensis*), thinly conical (*Sonneratia alba*), and elongate conical (*Sonneratia caseolaris* (Figure 4) and *Sonneratia lanceolata*); (2) knee roots – thick and knobbly (*Bruguiera*) and thin and wiry (*Lumnitzera littorea*); (3) stilt roots (*Rhizophora* (Figure 2)); and (4) buttresses – sinuous planks (*Xylocarpus granatum*, *Heritiera littoralis*, and *Ceriops* spp., *Pelliciera rhizophorae*), and erect "fins" (*Bruguiera* X *rhynchopetala*, *Xylocarpus moluccensis*). Roots are used by various fauna, but most notably by burrowing shipworms, mollusks, termites, and crabs.

Mangroves, Table 1 Mangrove species of the world. Families and genera with zero 'Non-mangrove' are exclusively mangrove (modified from Duke et al., 1998)

Families with mangroves	Family relatives of mangrove taxa	Family genera	Mangrove genera	Non-mangrove	Mangrove spp.	Species of mangroves
Acanthaceae	Black-eyed Susan, Shrimp plants	250–300	*Acanthus*	30	3	*Acanthus ebracteatus* *Acanthus ilicifolius* *Acanthus volubilis*
Arecaceae	Palms	200	*Nypa**	0	1	*Nypa fruticans+*
Avicenniaceae (ex Verbenaceae) (or Acanthaceae)	Grey mangroves	1	*Avicennia*	0	8	*Avicennia alba* *Avicennia integra* *Avicennia marina* *Avicennia officinalis* *Avicennia rumphiana* *Avicennia bicolor* *Avicennia germinans* *Avicennia schaueriana*
Bignoniaceae	Trumpet-tulip tree, Jacarandas	120	*Dolichandrone*	9	1	*Dolichandrone spathacea*
			Tabebuia	245	1	*Tabebuia palustris*
Bombaceae (or Fabaceae)	Baobab, Balsa, Kapok, Durian	31	*Camptostemon*	0	2	*Camptostemon philippinense* *Camptostemon schultzii*
Caesalpiniaceae (or Fabaceae)	Cassia, Tamarind, Legume	150	*Cynometra*	70	1	*Cynometra iripa*
			Mora	19	1	*Mora oleifera*
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	2	*Excoecaria agallocha* *Excoecaria indica*
Lecythidaceae	Brazil nuts	15	*Barringtonia**	40	1	*Barringtonia racemosa*
Lythraceae	Crepe Myrtle, Henna, Cuphea	25	*Pemphis*	1	1	*Pemphis acidula*
Meliaceae	Mahogany, Rosewood	50	*Aglaia*	100	1	*Aglaia cucullata*
			Xylocarpus	1	2	*Xylocarpus granatum* *Xylocarpus moluccensis*
Myrsinaceae	Turnip-wood, Mutton-wood	35	*Aegiceras**	0	2	*Aegiceras corniculatum* *Aegiceras floridum*
Myrtaceae	Eucalyptus, Bottlebrush, 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*
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*

Mangroves, Table 1 (*Continued*)

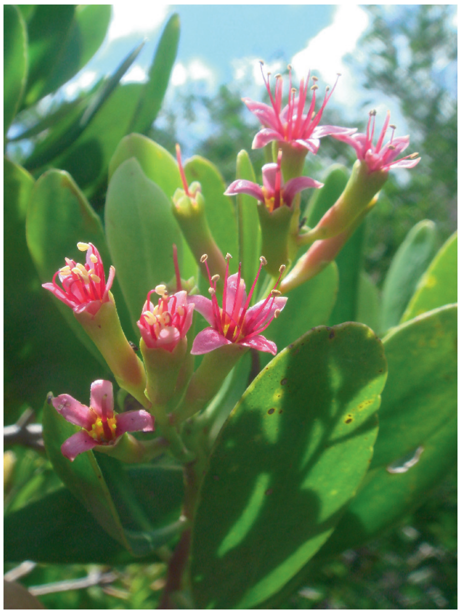
Families with mangroves	Family relatives of mangrove taxa	Family genera	Mangrove genera	Non-mangrove	Mangrove spp.	Species of mangroves
			Ceriops	0	4	*Ceriops australis* *Ceriops decandra* *Ceriops tagal* *Ceriops zippeliana*
			Kandelia	0	2	*Kandelia candel* *Kandelia obovata*
			Rhizophora	0	11	*Rhizophora* X *annamalayana* *Rhizophora apiculata* *Rhizophora* X *lamarckii* *Rhizophora mucronata* ***Rhizophora samoensis*** *Rhizophora* X *selala* *Rhizophora stylosa* *Rhizophora* X *tomlinsonii** *Rhizophora mangle*+ *Rhizophora racemosa* *Rhizophora X harrisonii*
Rubiaceae	Coffee, Gardinia, Quinine	500	*Scyphiphora*	0	1	*Scyphiphora hydrophylacea*
Sonneratiaceae (or Lythraceae)	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*
Sterculiaceae (or Malvaceae)	Cocoa, Kola, Bottle trees	70	*Heritiera*	29	3	*Heritiera fomes* *Heritiera globosa* *Heritiera littoralis*

Genera marked with an asterisk have been classified previously comprising their own family, named: Diospyraceae, Barringtoniaceae, Aegicerataceae, Nypaceae, Aegialitidaceae, and Pellicieraceae, respectively. Species region codes: regular font refers to those from the Indo-West Pacific; underlined names occur in the Atlantic East Pacific; **bold underlined** occur naturally in both; + indicates species introduced to, and established in, the other region
*See Duke (2010)

Factors influencing mangrove distributions

Mangroves have evolved and flourished in their dynamic setting. While mangroves collectively have specialized morphologies and physiologies, these attributes have limits that vary with individual species. The distributional range of each mangrove species reflects its response to the dominant influencing factors at global, regional, and local scales (Duke et al., 1998).

Where mangroves inhabit tropical and subtropical regions of the world, their presence in higher latitudes is generally constrained by the 20°C winter isotherm in the respective hemispheres (Figure 10). Exceptions to this pattern mostly correspond to the paths of oceanic circulation currents where mangrove distributions are broader on eastern continental margins and more constrained on the west. Present day distribution patterns depend on specialized, water-buoyant propagules of mangroves. Their dispersal is constrained by wide bodies of water and continental land masses. Four major barriers restrict dispersal of warm coastal marine organisms (including mangroves) around the world today, namely: the continents of (1) Africa and Euro-Asia; plus (2) North and South American continents; and the oceans of (3) the North and South Atlantic; plus (4) the eastern Pacific. The relative effectiveness of each of these barriers differ, depending on its geological history, dispersal/establishment ability, and the evolutionary appearance of respective species.



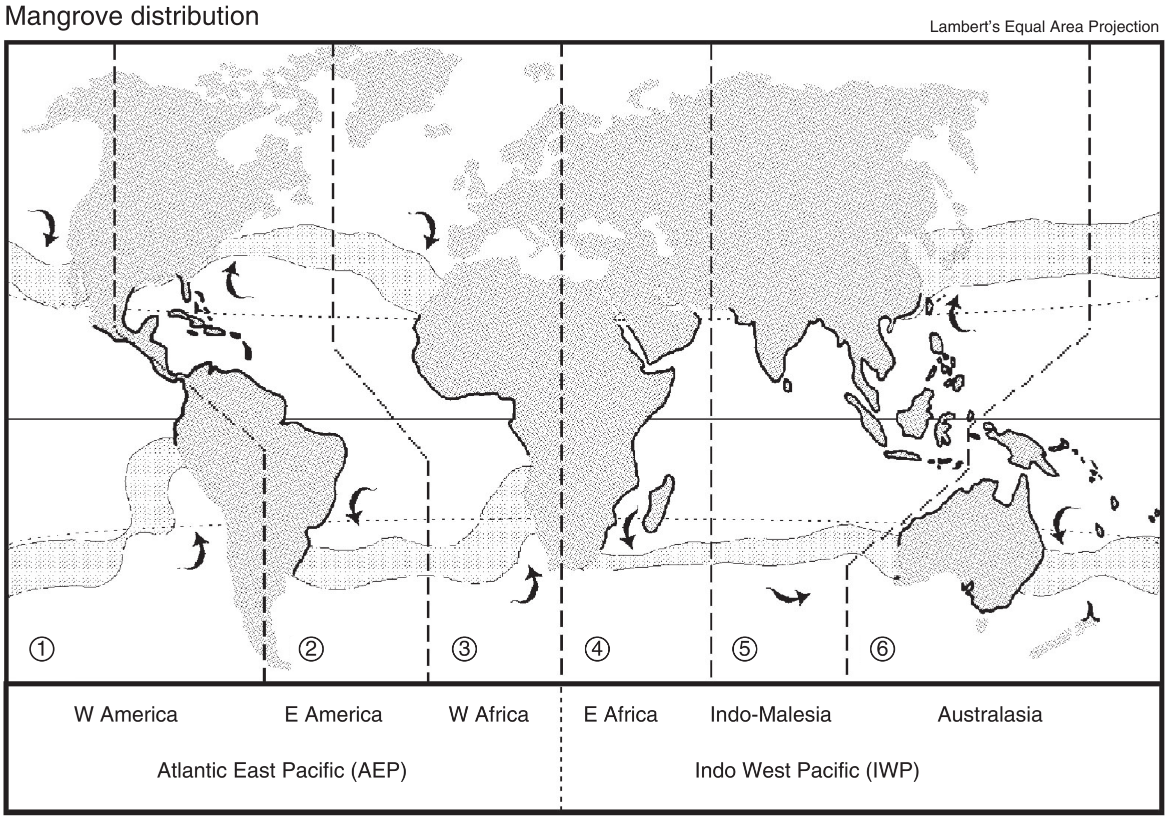
Mangroves, Figure 6 Delicate pink flowers of the rare hybrid shrub, *Lumnitzera rosea*, Le Cap River, New Caledonia.

Mangroves, Figure 7 Sizing up an ancient tree of *Avicennia germinans*, near Braganza, Amazonian Brazil.

Regional distribution patterns of mangroves are further influenced by habitat availability and local environmental factors such as rainfall, estuary size, and tides. In Australia (Duke, 2006), two major environmental factors, temperature and rainfall, largely explain regional distributions where low temperatures limit the latitudinal extent of species – affecting the pool of available species. The relative number of species is also highest in areas of higher rainfall. Species richness declines generally with increasing latitude on north-south coastlines and

Mangroves, Figure 8 Erect fruiting bodies of the striking mangrove palm, *Nypa fruticans*, Kien Giang Province, Vietnam.

Mangroves, Figure 9 Attractive flowers of *Pelliciera rhizophorae* support hummingbirds, near Diablo on the Pacific coast of Panama, Central America.



Mangroves, Figure 10 World distribution of mangroves (*dark line* along coastal margins) showing global regions and subregions with ocean zone limits at the seasonal 20°C isotherm (*source*: Duke et al., 1998).

groupings of islands. In general, species diversity in mangrove stands of equal size is greatest in wet equatorial areas. However, where rainfall is comparable, species diversity is higher in longer estuaries with larger catchments. The influence of rainfall, therefore, not only comes from rain falling directly on mangrove stands, but also as it influences runoff volume from upstream catchments.

At the local scale, individual mangrove species usually occupy only part of an estuary from sea mouth to tidal limit upstream (Duke et al., 1998). Species generally display a preferred estuarine range based on the overall salinity tolerance. For instance, species like *Avicennia marina*, *Rhizophora stylosa*, and *Sonneratia alba* commonly occur in downstream locations. By comparison, *Rhizophora mucronata*, *Sonneratia caseolaris*, and *Bruguiera sexangula* are found upstream in larger, freshwater-dominated estuaries. Furthermore, at this local scale, respective species occupy distinct parts of the tidal profile above mean sea level. Characteristic zonation bands of different mangrove assemblages indicate the pronounced influences of inundation frequency and tidal elevation. 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. Some species, such as *Avicennia marina*, *Acanthus ilicifolius*, and *Aegiceras corniculatum*, are observed at high and low intertidal positions.

Conclusion

Mangroves and tidal wetlands are essential to the sustainability of highly productive natural coastal environments. However, these ecosystems and their dependant biota (Figures 4, 5, and 9) are under serious threat from the escalation this century of large-scale land clearing and conversion of coastal forested wetlands (including mangroves) with the development of coastal lands for agricultural, aquaculture, port, and urban and industrial use (Field, 1995; Duke et al., 2007). In populated areas, key coastal rivers have become little more than drains transporting eroded mud and effluent to settle in downstream estuarine reaches, as well as in shallow embayments and inshore coral reefs. Remaining mangroves have become depauperate, poorly functional vestiges with relatively low resilience. Where healthy, mangrove-lined estuaries had once offered respite and critical dampening of land runoff, in recent years these bastions of coastal buffering and filtering – dubbed "coastal kidneys" – are not responding well to expanding human activities. Efforts to remediate these impacts is being undertaken in many ways with international and regional partnerships, but more is needed as the full impact of global climate change and sea level rise begin to take effect.

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