

Mangrove Forest Functions and Services

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Mangroves stand out as one of the most diverse and biologically significant natural systems in the world. Playing critical roles in maintaining the health and productivity of coastal ecosystems, mangroves provide a range of services and functions, including habitat for local fauna and flora, food and other goods, carbon sequestration, and protection from natural disasters such as storm surges and coastal erosion.

Keywords: carbon sequestration ; climate change ; coastal development ; mangrove biodiversity ; mangrove management ; microbial communities ; mitigation

1. Biotic Communities Associated with Mangroves

1.1. Habitat for Local Communities

Mangrove ecosystems are habitats for local fauna and flora, providing breeding places, shelter, nesting, and nursing areas ^[1] (**Table 1** and **Table 2**). Mangrove canopies are home to several wild animals, such as monkeys, monitor lizards, snakes, and otters ^[2]. The canopy also provides shade and shelter to aquatic-based animals, including amphibians and larger reptiles such as crocodiles ^[3] and dugongs ^[2]. Several birds inhabit mangroves, notably eagles, kingfishers, herons, plovers, terns, cormorants, egrets, and ibises ^[4]. On tree trunks, the residing flora includes orchids, ferns, lilies, and vines ^[5], which are home to invertebrates such as spiders and various insects ^[6]. Other than that, mangrove roots are swarmed by arthropods (crabs, lobsters, and shrimp) ^[7]; Molluscs (barnacles, oysters, mussels, and snails) ^[8]; sponges ^[9]; worms ^[10]; jellyfish ^[2]; and fish such as sea trout, snappers, jacks, tarpon, sea bass, red drums, and snook ^[11]. Moreover, mangroves host diverse epibiont macroalgal communities on their prop roots, trunks, and mud surfaces ^[12]. Mangrove habitats provide shallow water and, in many cases, high turbidity and fine sediment suitable for burrowing animals ^[13]. These factors act to protect animals from their predators by reducing their visibility and lowering their encounter rate with potential predators ^[14]. Mangrove plants, along with kelps, seagrasses, oysters, and corals, are key foundation species of coastal ecosystems ^[15]. Foundation species are crucial for maintaining the structure and resilience of an ecosystem ^[16].

Table 1. List of fauna associated with mangroves.

Group	Common Name	Genus/Species	References
Sponges	Common Mangrove Sponge	<i>Tedania</i> sp.	^[17]
		<i>Mycale</i> sp.	
Worms	Segmented worms	<i>Dysidea</i> sp.	^[18]
		<i>Haliclona</i> sp.	
Insects	Ant	<i>Sabellastarte</i> sp.	^[19]
	Weevils	<i>Polyrachis bicolor</i> sp.	^[19]
	Bettles	<i>Rhynchites</i> sp.	^[20]
	Crabs	<i>Monolepta</i> sp.	^[21]
Crustaceans	Prawns	<i>Ilyogynis microcheirum</i>	^{[22][23]}
		<i>Portunus pelagicus</i>	
		<i>Uca</i> sp.	
		<i>Hippidea</i> sp.	
		<i>Penaeus monodon</i>	
	Barnacles	<i>Exopalaemon styliferus</i>	^{[24][25]}
		<i>Metapenaeus affinis</i>	
		<i>Parapenaeopsis sculptilis</i>	
		<i>Balanus</i> sp.	^{[26][27]}
		<i>Euraphia</i> sp.	
		<i>Tetraclita</i> sp.	

Group	Common Name	Genus/Species	References
Mollusks	Oyster	<i>Crassostrea</i> sp.	[28]
	Clam	<i>Tridacna derasa</i> <i>Tridacna maxima</i> <i>nodontia edentula</i>	[29][30][31]
	Sea slug/sea hares	<i>Dolobella</i> sp.	[32]
	Venus clam	<i>Bursa</i> sp. <i>Paphia amabilis</i> <i>Venus clam Paphia</i> <i>Haliotis asinina</i> <i>Tectus pyramis</i> <i>Echininus cumingii</i> <i>Terebralia sulcata</i> <i>Rhinoclavis sinensis</i> <i>Rhinoclavis vertegus</i> <i>Ficus gracilis</i> <i>Plicacularia pullus</i> <i>Fasciolaria trapezium</i> <i>Oliva reticulata</i> <i>Mitra mitra</i> <i>Trisodos tortuosa</i> <i>Anadara maculosa</i> <i>Chicoreus brunneus</i>	[33][34][35][36][37]
Echinoderms	Sea urchin	<i>Protoreaster</i> sp. <i>Archaster</i> sp. <i>Linckia</i> sp. <i>Clypeaster</i> sp. <i>Cerithium</i> sp. <i>Tripneustes</i> sp. <i>Holothuria</i> sp. <i>Oreaster albeolatus</i> <i>Ophiarachna incrasala</i> <i>Echinocardium cordatum</i> <i>Diadema setosum</i> <i>Laganum laganum</i> <i>Echinometra mathaei</i>	[33][38][39][40]
	Star fish	<i>Astropecten</i> sp. <i>Protoreaster nodosus</i> <i>Linkia laevigata</i>	[40][41]
	Feather star	<i>Comanthina bennetti</i> <i>Comanthina schlegeli</i>	[42]
	Sea star	<i>Luidia</i> sp. <i>Culcita novaeguineae</i>	[43]
	Sea squirt	<i>Didemnum molle</i> <i>Atrium robustum</i> <i>Polycarpa aurata</i> <i>Rhopalea</i> sp.	[44]
Tunicates			
Fishes	Rabbitfish	<i>Siganid</i> sp.	[45]
	Mudskipper	<i>Periophthalmodon</i> <i>Periophthalmus</i>	[45]
	Spot-tail needlefish	<i>Strongylura strongylura</i>	[46]
Amphibians	Mangrove frog	<i>Fejervarya cancrivora</i> <i>Rana cancrivora</i>	[47]
Reptiles	Snake	<i>Cerberus rhybchos</i>	[33]
	Lizard	<i>Tupinambis indicus</i>	[48]
	Crocodiles	<i>Crocodylus porosus</i>	[49]
Birds	Eagles	<i>Haliastur indus</i> <i>Pitta megarhyncha</i>	[50][51]
	Kingfishers	<i>Halcyon senegaloides</i> <i>Todiramphus sordidus</i>	[52]

Group	Common Name	Genus/Species	References
	Herons	<i>Nycticorax nycticorax</i> <i>Egretta gularis</i>	[53][54]
	Plovers	<i>Charadrius</i> sp. <i>Pluvialis</i> sp. <i>Thinornis</i> sp.	[55][56]
	Terns	<i>Sterna paradisaea</i>	[56]
	Crow	<i>Corvus splendens</i>	[57]
	Green pigeon	<i>Treron olax</i>	[57]
	Egrets	<i>Egretta garzetta</i> <i>Egretta immaculata</i> <i>Egretta nigripes</i>	[58][59]
	Bats	<i>Cynopterus brachyotis</i> <i>Acerodon jubatus</i>	[60][61]
	Monkey	<i>Nasalis larvatus</i>	[62]
	Dugong	<i>Dugong dugon</i>	[63]
	Otters	<i>Lutrinae</i> sp.	[64]

Table 2. List of flora associated with mangrove.

Group	Common Name	Genus/Species	References
	Seagrasses	<i>Cymodocea</i> sp. <i>Thalassia</i> sp. <i>Halodule</i> sp. <i>Halophila</i> sp. <i>Enhalus</i> sp.	[65][66]
	Orchids	<i>Acampe</i> sp. <i>Agrostophyllum</i> sp. <i>Apotasi</i> sp. <i>Ascocentrum</i> sp. <i>Bulbophyllum</i> sp. <i>Ceratostylis</i> sp. <i>Cleisostoma</i> sp. <i>Cymbidium</i> sp. <i>Dendrobium</i> sp. <i>Flickingeria</i> sp. <i>Grosourdyia</i> sp. <i>Habenaria</i> sp. <i>Liparis</i> sp. <i>Malaxis</i> sp. <i>Podochilus</i> sp. <i>Pomatocalpa</i> sp. <i>Thelasis</i> sp.	[67][68][69][70][71]
	Lilies	<i>Crinum</i> sp. <i>Hymenocallis</i> sp. <i>Nymphaeaceae</i> sp. <i>Lycoris</i> sp.	[72][73]
	Vines	<i>Cryptostegia grandiflora</i>	[12]
	Ferns	<i>Acrostichum</i> sp. <i>Waterhousea</i> sp.	[74][75]
	Marine algae	<i>Padina</i> sp. <i>Ulva</i> sp. <i>Ventricaria ventricosa</i>	[76][77]

1.2. Mangroves Association with Corals and Seagrass

Mangrove ecosystems are partly linked with and support corals and seagrasses [78]. Mangrove ecosystems have a positive impact on seagrass meadow traits such as shoot length, width, and height, shoot density, root length, number of leaves, leaf biomass, and population dynamics [79]. Mangrove roots trap the fine sediments coming from terrestrial sources and intercept turbid water, preventing it from reaching coral and seagrass systems [80]. On the other hand, coral reefs provide tranquil conditions that increase the deposition of fine sediments in adjusting areas, which supports the growth and development of seagrass beds and mangrove forests [81]. Likewise, corals and seagrasses maintain the balance between organic and inorganic carbon contents in coastal areas, subsequently establishing carbon sinks and sources in the mangrove ecosystem [82]. As mangrove forests, coral reefs, and seagrasses are interdependent ecosystems, to effectively store and export blue carbon in tropical coastal areas, it is essential to maintain the health of each of these coexisting ecosystems [83].

1.3. Reservoir of Microbial Communities

Mangroves are reservoirs of diverse microbial communities that include bacteria and fungi [84]. Organic sediments swept into mangroves by tides are inhabited by bacteria that decompose the organic debris and are primary contributors to carbon cycling [85]. Diverse bacteria in these populations are involved in many other essential ecological functions such as nitrogen fixation [86], photosynthesis [87], phosphate solubilisation [88], enzyme production [89], sulfate reduction [90], antibiotic production [91], anoxygenesis [92], and methanogenesis [93] (**Table 3**). Among fungi, the dominant fungal phyla are *Ascomycetes* and *Basidiomycetes*, which have been reported to be primarily associated with the survival of mangrove plants in waterlogged and nutrient-restricted environments [94] (**Table 3**). The microbial communities of mangroves improve nutrient availability, support the growth of vegetation, and provide protection from pathogenic bacteria, thereby positively impacting species diversity [95].

Table 3. Major microbial groups inhabiting the mangrove forests.

Group	Phyla	Functions	References
Bacteria	<i>Actinobacteria</i>	<ul style="list-style-type: none"> Produce highly bioactive compounds such as antibiotics against pathogenic bacteria, anticancer, and antifungals, and protect mangroves from disease 	[96]
	<i>Chloroflexota</i>	<ul style="list-style-type: none"> Methanogenesis Produce secondary metabolites from root exudates or soil organic matter that can be utilised by other anode-coupling microorganisms Anaerobic degradation of organic compounds, e.g., sulfate reduction Phosphate solubilisation 	[84][95]
	<i>Asgardarchaeota</i>	<ul style="list-style-type: none"> Major contributors to nitrogen cycling in the mangroves, especially involved in nitrification 	[97]
	<i>Bacteroidetes</i>	<ul style="list-style-type: none"> Release a wide range of carbohydrate-active enzymes (CAZymes) that target the different glycans in the soil Phosphorus solubilisation 	[16]
	<i>Thermoproteota</i>	<ul style="list-style-type: none"> Oxidisation of ammonia Sulfate reduction Methanogenesis 	[98]
	<i>Calditrichota</i>	<ul style="list-style-type: none"> Enable mangroves to survive in hot climates 	[99]
	<i>Bacillota</i>	<ul style="list-style-type: none"> Maintains electrolyte balance between mangrove plants and microbial species Oxidation of the precipitated sulfide Participate in the elimination of toxic metals 	[100]
	<i>Thermodesulfobacteriota</i>	<ul style="list-style-type: none"> Regulate the sulfur cycle, oxidise reduced sulfide to sulfate, affecting the sulfur biogeochemistry Converts many metal ions such as Cu, Pb, Cr, Zn, Hg, and As into low-solubility metal sulfides 	[95]

Group	Phyla	Functions	References
	<i>Euryarchaeota</i>	<ul style="list-style-type: none"> Organic matter decomposition Ammonia oxidation 	[84]
	<i>Firmicutes</i>	<ul style="list-style-type: none"> Produce indole-3-acetic acid (IAA) and siderophores Oxidize hydrogen cyanide and thiosulfate Produce ammonia and cellulase Solubilise potassium and zinc 	[101][102]
	<i>Halobacterota</i>	<ul style="list-style-type: none"> Increase salt tolerance and help with sulfate reduction 	[103]
	<i>Nitrososphaerota</i>	<ul style="list-style-type: none"> Ammonia oxidation and nitrification 	[98]
	<i>Nitrospirota</i>	<ul style="list-style-type: none"> Participates in nitrifying process Role in methane metabolism 	[93]
	<i>Planctomycetota</i>	<ul style="list-style-type: none"> Ammonia oxidation in mangroves and the exclusive metabolic capacity to combine ammonium and nitrite or nitrate to form nitrogen gas under anoxic condition 	[104]
	<i>Pseudomonadota</i>	<ul style="list-style-type: none"> Detoxification of pollutants Carbon and nitrogen fixation in mangrove sediments 	[105][106]
	<i>Thaumarchaeota</i>	<ul style="list-style-type: none"> Ammonia oxidation 	[93]
	<i>Zixibacteria</i>	<ul style="list-style-type: none"> Nutrient recycling Key role in carbon and nitrogen fixation Helps in nitrogen fixation 	[107]
	Cyanobacteria <i>Cyanobacteriota</i>	<ul style="list-style-type: none"> Cells provide calcium, magnesium, and phosphorous storage in mangrove ecosystems Develops mycorrhizal associations with roots of mangroves and transports nutrients Helps plants survive in waterlogged conditions 	[108][109]
	Fungi <i>Ascomycota</i>	<ul style="list-style-type: none"> Acts as decomposers Produces a variety of extracellular degradative enzymes, which include cellulase, xylanase, pectinase, and amylase 	[94][110]
	<i>Basidiomycota</i>	<ul style="list-style-type: none"> Involved in detritus processing, phosphate solubilisation, and cellulose degradation 	[111]

2. Mangrove Ecosystem and Economic Functions and Services

There are several functions of mangrove forests other than as habitats for flora and fauna: They act as a carbon sink (blue carbon storage) [112], maintain water quality [113], protect coastal land from natural disasters [114], and support coral and

seagrass ecosystems [115] (Figure 1). In addition, mangroves provide livelihood opportunities for coastal communities through aquaculture, fodder, timber, and ecotourism [116].

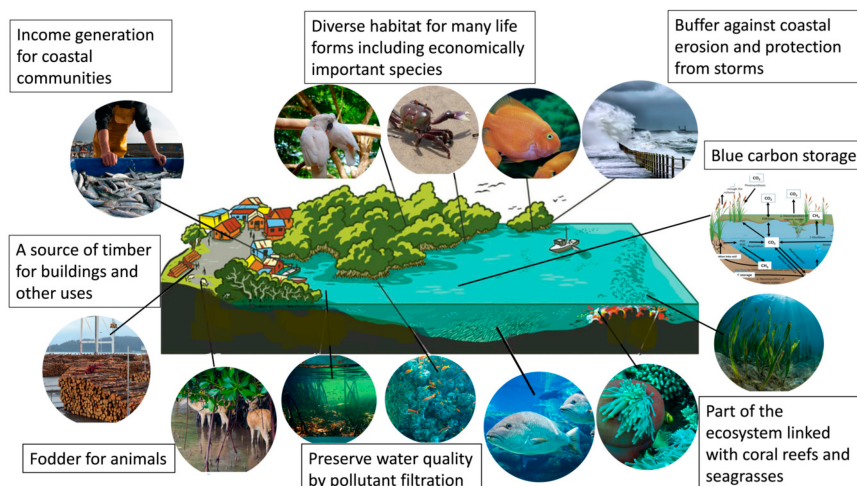


Figure 1. Functions and services of an intact mangrove ecosystem.

2.1. Carbon Sink

Mangroves play an important role in mitigating the effects of greenhouse gases generated by anthropogenic activities such as deforestation, agriculture, and industrial processes. This mitigation involves removing CO₂ from the atmosphere, after which mangrove flora sequester carbon in their above- and below-ground biomass [112]. Mangroves, as a carbon sink, can hold an estimated 1023 Mg/hectare of carbon [117]. Various studies have confirmed that mangroves have a faster carbon sequestering capacity than other ecosystems, such as grasslands or tropical rainforests [118]. According to a report from the Global Mangrove Alliance (GMA) 2022 [119], the total organic carbon stored in mangrove forests at a global level is estimated at around 21,896.56 Mt CO₂e with 2817.23 Mt CO₂e stored in above-ground biomass and 19,079.32 Mt CO₂e stored in the upper 1 m of soil [120]. It can be seen from **Figure 2** that the carbon storage capacity varies quite considerably for different countries, with Indonesia having a relatively strong capacity compared to the other countries. In mangroves, carbon-rich soils extend from 0.5 m to ~3 m in depth and accommodate 49%–98% of the carbon stored by the mangrove ecosystem [121]. **Figure 2** represents the organic carbon storage capacity of mangrove forests in various countries as above-ground biomass (data derived from GMW version 0.3, 2020) [122]. As mangroves store a considerable amount of carbon, the destruction of this habitat disturbs the carbon sink and emits huge amounts of carbon back into the atmosphere, significantly contributing to climate change. Therefore, protecting and restoring mangrove habitats can reduce the impact of climate change [123]. Although it would be great to consider many more countries in this discussion, due to the brevity of the paper, only 12 countries have been included that have the most robust data, as shown in **Figure 2**.



Figure 2. Above-ground carbon storage capacity of mangrove forests in different countries in 2020. Each country has mangrove forests with different carbon storage capacities, which are presented in ranges of carbon storage measured in

metric tons of equivalent carbon (Mt CO₂e) with each range represented by a different colour. The x-axis is a scale bar of the percentages of the total forests in each country that fall into each carbon storage range. (Data sourced from GMW, 2022).

2.2. Natural Water Filters

Mangrove forests act as natural water filters for coastal areas, improving the water quality by trapping sediments and other solid impurities with their roots [113]. This reduces the flow of sediments into offshore waters, thereby reducing erosion [124], maintaining clean habitats for seagrass beds and coral reefs, and contributing to SDG 14, which talks about life below water [125]. Mangroves can grow in saline water and filter 90% of sodium ions (Na⁺) from the surrounding seawater [126]. Their roots comprise a three-layered pore structure in the root epidermis, which facilitates Na⁺ filtration [127]. Additionally, mangrove roots, such as pneumatophores and prop roots, create a low-energy environment, allowing wastewater-containing contaminants to reside for an extended period [128]. Mangrove plants also sequester other metals, including the heavy metals Zn, Mn, and Cu [129]. The study of the mechanisms by which mangrove plants filter water has led to novel water treatment technology: Researchers at Virginia Tech (Virginia Polytechnic Institute and State University, USA) [130] have developed a “synthetic tree” water purifier system inspired by the water filtration technique used in mangrove plants. Specifically, a synthetic tree is composed of a nano-porous “leaf” to produce suction via evaporation, a vertical column of glass tubes similar to the xylem vessels of the tree, and filters attached to the tube inlets, mimicking roots [130]. In another recent study, a group of engineers from Yale University (New Haven, CT, USA) invented a water purification device that mimics the desalinisation ability of mangrove trees based on the principle of cohesion-tension theory in mangroves. In this technique, synthetic leaves can generate highly negative pressures that allow desalination through a reverse osmosis (RO) membrane [131].

2.3. Barriers to Natural Disasters

Mangroves not only prevent soil and coastal erosion by retaining sediments in their aerial roots [124] but also act as barriers against natural disasters. The canopy, trunk, and roots of mangrove plants restrain storm surges [114] and waves [132]. In the aftermath of the Asian tsunami on 26 December 2004 [133], Hurricane Katrina on 23 August 2005, on the US Gulf Coast [134], and the Transoceanic tsunami on 23 January 2022 [135], persuasive evidence emerged from field studies in several countries justifying the role of mangroves as natural barriers protecting coastal habitats and communities. It is quite evident after the tsunami survey that the intact and dense mangroves with higher structural complexity near coastal areas offered fewer fatalities and minimal damage to assets as compared to the areas where mangroves had either been destroyed or transformed to alternate land uses [136][137].

2.4. Livelihood Opportunities for Coastal Communities

About 90% of the global mangrove forests grow in economically less privileged countries [138]. Approximately 100 million people live within a 10 km range of mangrove forests and directly benefit from this ecosystem as a source of livelihood opportunities [139].

2.4.1. Aquaculture

Mangroves are considered hotspot locations for aquaculture [140]. The species commonly reared include various fish, shrimp/prawns, crabs, molluscs, and other invertebrates [141]. Approximately 80 million tonnes of fish were produced globally through aquaculture in 2022 [142]. Extensive mangrove-associated aquaculture has been observed in Indonesia, Malaysia, and the Philippines [143]. Mangrove-associated aquaculture accounts for 21% (1.4 million tons annually) of the coastline fisheries of the ASEAN (Association of South East Asian Nations) region [144]. Of the annual fish and seafood resources, fin fish alone contribute around 1.09 million tons [145], while shrimp/prawn contribute around 0.4 million tons [146]. In addition, fish products from these aquaculture activities are a principal source of food for coastal communities.

Large-scale aquaculture [147], fish farming in cages or in ponds [148], and integrated rice-fish farming [149] have reduced pressure on overexploited fisheries by diversifying fish production other than wild stocks. Small-scale aquaculture, in particular, enables fish farmers to provide food for their families while generating income from the sale of surplus stock [150]. Such activities also create employment opportunities through various enterprises ranging from the processing, distribution, and sale of fish linked to the aquaculture value chain [151]. These livelihood opportunities facilitate the sustainable mangrove ecosystem's ability to successfully contribute to the outcomes of various sustainable development goals set by the United Nations, such as SDG 1, SDG 2, SDG 8, SDG 11, SDG 13, SDG 14, and SDG 15. (The detailed agenda of these SDGs can be seen at <https://www.un.org/development/desa/disabilities/envision2030.html>, accessed on 11 July 2023) [152].

2.4.2. Fodder, Timber and Traditional Medicines

Mangroves also provide fodder, timber, and medicine resources for coastal indigenous communities (**Figure 1**). Cattle, sheep, goats, and buffaloes are domestic animals that are generally fed on mangrove foliage [153]. Mangrove foliage, particularly from *Avicennia marina*, is considered healthy fodder for domestic animals (Mitra, 2020). Mangrove wood, being highly resistant to rot and insects, is frequently utilised as timber as well as for fuel wood [154]. *Rhizophora* spp.,

Xylocarpus sp., *Bruguiera* sp., and *Sonneratia* sp. are significantly important for timber due to the durability of their wood and their large trunk size ^[155]. The timber of these species is used for small watercraft, shipbuilding, and for making utensil handles, furniture, poles, piles, and other building materials ^[156]. Mangrove firewood has been widely used as an energy source by rural communities.

Mangrove services also include the provision of traditional medicine for treating skin ailments and stomach issues ^[157]. Extracts from mangrove-associated species, for example, *Abonnema* and *Nypa fruticans*, have shown antimicrobial activity against some plant and animal pathogens ^[158]. The bioactive compound ecteinascidin, extracted from the mangrove tunicate *Ecteinascidia turbinata*, has been reported to show strong in vivo activity against various cancerous cells ^[159]. Furthermore, the bark of *Ceriops* sp. is a good source of tannin, and its decoction is used in Vedic medicine to stop haemorrhage and in the treatment of malignant ulcers ^[160].

2.4.3. Ecotourism

Ecotourism refers to the form of tourism that focuses on responsible travel that minimises environmental impact and supports local communities ^[161]. Ecotourism in mangrove regions places a strong emphasis on mangrove conservation, education of visitors about the mangrove forest, and providing economic benefit to local communities ^[162]. Ecotourism syndicates three key aspects, viz., (i) ecology, which includes the existence of the elements upon which the mangrove ecosystem depends and also its conservation efforts ^[163], (ii) financial revenue generated as a result of ecotourism activities in sustainable mangroves, a share of which is expended to maintain the ecosystem ^[164], and (iii) empowerment and engagement of the local community in the ecotourism business ^[165]. The species diversity of both fauna and flora and the unique characteristics of mangrove plants have been a great attraction for ecotourism ^[166]. Mangrove areas offer several forms of ecotourism activities, such as sports and recreational activities such as fishing, boating, and camping ^[167]; educational and research tourism in the form of field trips to mangroves to observe and study the mangrove vegetation and life inside the mangroves ^[168]; and health tourism as sites for self-meditation and other therapy ^[169]. Many mangrove forests have been established as tourist attractions by governmental or non-governmental organisations in different regions ^[170]. For example, areas of mangrove forest in Bali, Indonesia, have been established by local communities for the purpose of ecotourism and to maintain the conservation of biodiversity, landscapes, and the ecosystem overall ^[171]. Ecotourism activities carried out by these community groups are supported and fostered by the relevant stakeholders of the region and/or the state government and have been incorporated as a part of their CSR (corporate social responsibility) program ^[172]. The use of mangroves for ecotourism is in accordance with the development directions of the Sustainable Development Goals (SDGs), 12, 13, 14, 15, and 17 ^[173].

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