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Mangrove Ecosystem Ecology and Function

Edited by Sahadev Sharma

MANGROVE ECOSYSTEM ECOLOGY AND FUNCTION

Edited by **Sahadev Sharma**

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Meet the editor

Dr. Sahadev Sharma is a forest ecologist with an international PhD in Plant Ecology and Physiology from the University of the Ryukyus, Okinawa, Japan. He has been conducting research on mangrove forest ecology and physiology from organ to landscape level using a wide spectrum of methods and technologies such as remote sensing and field-based monitoring and sampling, integrating ecological, chemical, and hydrological data. He is associated with the global project SWAMP (Sustainable Wetland Adaptation and Mitigation Program) funded by the United States Agency for International Development. He has working experience in top-class institutes such as the Tokyo Institute of Technology, the University of Hawaii at Manoa, and the Institute of Pacific and Island Forestry. He has been involved in research in different countries (India, Japan, Indonesia, the Philippines, Cambodia, Palau, Hawaii, Mexico, Vietnam and Madagascar). He is the author of about 45 research works published in many peer-reviewed journals and about 60 international conference papers.

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Preface

The suggestion for me to edit this book started with an e-mail from Marina of Intech Publications. Because the book is related to the mangrove ecosystem and because I have been involved in mangrove ecology and physiology for the last 10 years, I therefore agreed. My motivation to edit this book was to share my enthusiasm for the mangrove ecosystem.

Mangroves are a very productive tropical and subtropical ecosystem. They provide many ecosystem services for coastal communities. However, they are the most threatened ecosystem on earth due to anthropogenic influence and climate change. Ongoing coastal development activities and land use changes have led to the decline of mangrove forest areas and a deterioration in the quality of the ecosystem. Therefore, the time is now right to protect mangrove forests through conservation and management, as well as by rehabilitation of degraded and deforested mangrove areas.

The last two decades of mangrove research have been elevated globally to understand rehabilitation, blue carbon dynamics, the impact of sea level rise, and climate change. However, this research has come from only a small number of countries but the need is for a global understanding of mangrove dynamics. Therefore, this book comprises mangrove ecosystem-related research from Central and South America, West Africa, and Asia. It offers an overview of the mangrove ecosystem comprising many interesting chapters focusing on different aspects of ecology, structure, function, and bioprospecting.

We are familiar with the contributions of mangrove forest ecosystem services in terms of meeting global objectives. Mangrove forests can help to achieve sustainable development goals in coastal areas by mitigating climate change by storing and sequestering long-term carbon (SDG 13) and coastal area and ocean shelters related to biological diversity (SDG 14). Mangrove forest can also fit into remaining SDGs.

I would like to thank all the authors for providing important information related to the mangrove ecosystem from their respective countries. Also, I thank them for their cooperation during book editing by submitting chapters and review comments on time.

I would like to thank my family and friends for their support and understanding during the time I was working on this book. I hope it will be valuable for graduate students, mangrove ecologists, and other researchers in the field.

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Introduction

Chapter 1

Introductory Chapter: Mangrove Ecosystem Research Trends - Where has the Focus been So Far

Sahadev Sharma

Additional information is available at the end of the chapter

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Mangroves are trees and shrubs grow in intertidal zone or brackish water of tropical and subtropical coastal areas between 5°N and 5°S latitude spanning over 118 countries. Mangroves grow in harsh environmental conditions such as high saline conditions and are therefore also called halophytes. They can grow in extreme environment due to their morphological and physiological adaptations, including complex root and salt filtration abilities to cope with inundation of salt water and wave action. Mangroves are well adapted to grow in anoxic conditions as they experience regular inundation and saturated soil conditions. There are around 70 known species of mangroves around the globe, out of which 11 are threatened species and are listed in IUCN Red List [1]. Mangrove species have its own ecosystem services; therefore, mangrove loss can impact surrounding coastal ecosystem and associated ecosystems. Mangrove ecosystem has several faunal species because they create characteristics and productive habitat for them. The biodiversity of fauna in mangrove ecosystem is high due to the availability of food resources and their detritus food cycle.

Mangrove forests provide many ecosystem services that include provisioning, regulating, culture, and supporting services. Mangrove forests provide several provisioning services such as food, timber, fuelwood, etc., which provides economic benefits and security to local coastal communities [2]. It was recognized better after 2004 Asian tsunami wave attenuation became one of the regulating services [3]. Mangroves blue carbon storage and sequestration capability are important regulatory services since 2011 because of global climate change mitigation [4]. Mangroves also play an important role in enhancing coastal water quality by stabilizing fine sediment and by absorbing pollutants (like heavy metals) [5]. Mangrove forests also provide a slew of cultural services such as tourism and education as well as cultural heritage and esthetic values to local communities as well as visiting tourists [6, 7].

Though mangroves provide many important ecosystem services, they are one of the most threatened ecosystems in the world [8]. Mangrove forests are being deforested and degraded due to extensive aquaculture pond creation, agriculture, urban development, palm oil

production, and conversions to other land use types [9]. Anthropogenic factors are big threats to mangroves; however, they are also threatened due to climate change impacts such as sea level rise, rising temperature, and increasing storm intensities [10]. These threats are causing variations in river run-off and fresh water inputs which result in species loss and productivity, that eventually will alter aquatic food webs in coastal setting.

Therefore, many researchers, scientists, academicians, stakeholders, and policy makers are involved to maintain the remaining mangrove forest area cover globally. Many government and nongovernment organizations are involved in increasing mangrove area cover such as the IUCN (https://www.iucn.org/news/forests/201707/mangroves-make-great-conservation-allies) and the International Timber Trade Organization (ITTO) (http://www.itto.int/files/user/pdf/E-BROCHURE-Bali%20Call%20to%20Action.pdf) have identified effective mangrove restoration as a key priority.

Past study reassessed ecological role and services of mangrove forest, where authors mainly discussed carbon dynamics, nursery role, shoreline protection, and land building capacity of mangroves [11]. Consequently, this chapter contains information pertaining to mangrove carbon research—how it has evolved over time and also their role in mitigating climate change. In this chapter, important research topics are discussed to enhance our understanding of the global mangrove research covering topics such as climate change, blue carbon, deforestation and degradation, fauna and flora losses, etc. As one might think, all these topics are interrelated and a clear overlap is visible in search engine results. This provides a clear indication of mangrove carbon research trend in the recent years.

1. Methodology

The Web of Science® online database was used to access the mangrove forests research published between years 1980 and 2017. We searched various topics using specific keywords: (1) mangrove, (2) mangrove climate change, (3) mangrove carbon, (4) mangrove blue carbon, (5) mangrove biomass, (6) mangrove litter, (7) mangrove productivity, (8) mangrove deforestation and degradation, (9) mangrove remote sensing, (10) mangrove fauna, (11) mangrove invertebrate, (12) mangrove Polychaeta, (13) mangrove bird, and (14) mangrove mammals.

2. Result and discussions

A total of 14,741 records on keyword "mangrove" were found in the Web of Science. **Figure 1** shows different fields of research within mangrove ecosystem. Approximately, 50% research was done in the field of marine freshwater biology, environmental sciences, and ecology. About 50% of mangrove research fields are broad and comprised many particular research fields such as climate change, productivity, water quality, pollution, physiology, ecology, carbon dynamics, etc.

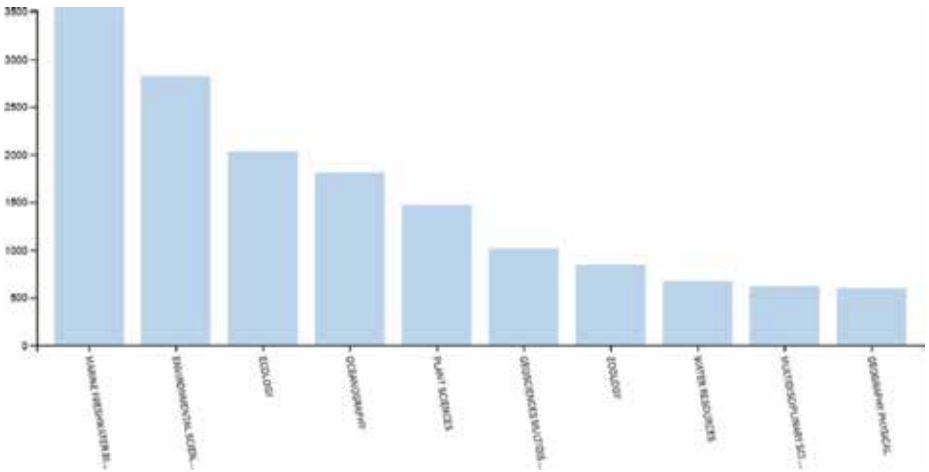

Figure 1. Number of publication belongs to different research field with in mangrove forest.

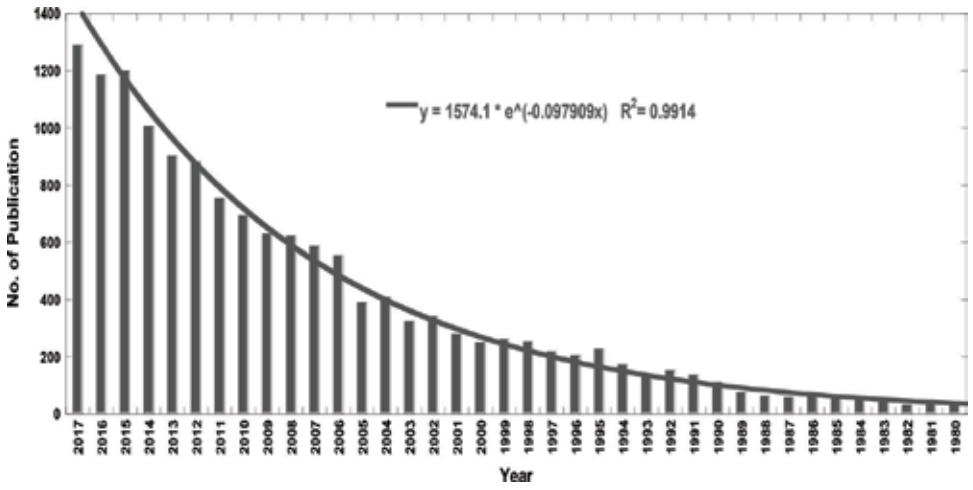

Figure 2. Number of publication records for keyword "mangrove" from 1980 to 2017.

Mangrove research has increased exponentially from 1980 to 2017, although year 2016 and 2017 shows a bit lower publication record as per the curve fitting (**Figure 2**). Year 2015 shows higher publication than year 2016, yet they might not be statistically significantly different.

Mangrove climate change search showed total 1053 publication records. Mangrove climate change research exponentially increased since year 1991 (**Figure 3**). Climate change or global warming is directly related to carbon cycle [12]. Therefore, mangrove carbon keyword was searched and a total of 1927 records were found, which was higher than climate change records. That means researchers were involved in mangrove carbon research than ecological, biological, environmental, and physiological aspects of mangrove research.

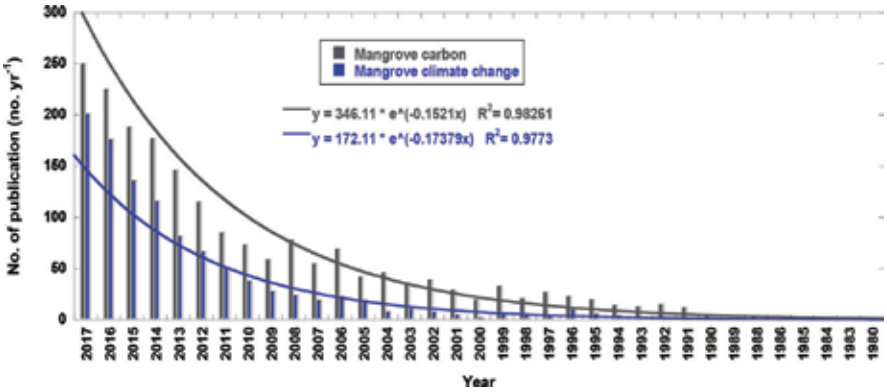

Figure 3. Number of publication records for key words "mangrove climate change" and "mangrove carbon" from 1980 to 2017.

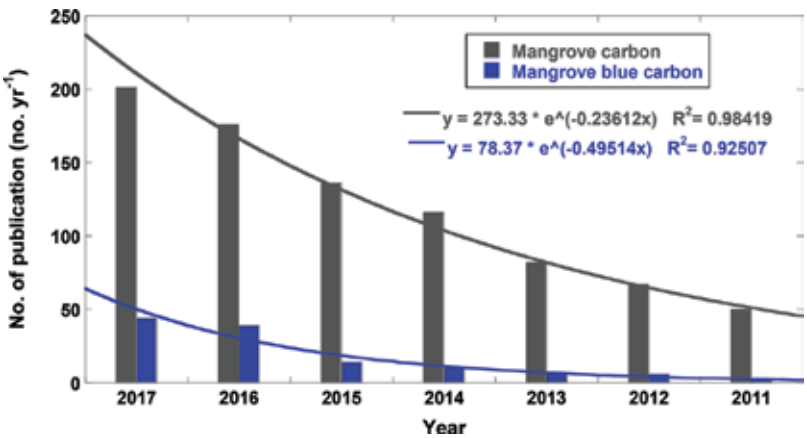

Figure 4. Number of publication records for keywords "mangrove climate change" and "mangrove blue carbon" from 2011 to 2017. Since Nature Geoscience publication [4] and blue carbon term (2009) [13].

Carbon stored in coastal and marine living organism such as mangrove forests, salt marshes, seagrass meadows, and intertidal flats is called "blue carbon," as termed by UNEP in 2009 [13]. The keyword mangrove blue carbon was searched, and a total of 124 records were found on Web of Science. Since 2011, publications on mangrove blue carbon have increased exponentially in terms of mitigating climate change (**Figure 4**). Mangrove climate change research showed very high number of publication after year 2011 (**Figure 3**), while mangrove carbon research showed lower publication as per the exponential graph (**Figure 3**). Mangrove carbon research got a boost since 2011 after a paper was published in the Nature Geoscience Journal [4] and after blue carbon term was coined/introduced [13] (**Figure 4**). **Figure 4** shows exponential increase in publication in the field of mangrove climate change research since year 2011. From **Figure 3**, it is clear that mangrove carbon research was primarily conducted in the field of climate change after year 2011.

Biomass is a measure of carbon stored in mangrove vegetation. Researchers have been measuring mangrove carbon indirectly through biomass [14–18] that is estimated using allometric

models [19–21]. A total of 1180 publications were identified using mangrove biomass keyword. Mangrove biomass research showed an exponential increase in the number of publication (**Figure 5**), although after year 2008, it seems biomass research has decreased. This decrease might be due to that researchers started to convert biomass into carbon for estimating total ecosystem carbon stocks. Measurement of litter fall is an important component of mangrove forest productivity [22–24]. Litter is also an indicator of episodic climate event such as storm [25], phenology [25–28], coastal productivity [29], detritus food cycle [30], etc. Measurement of litter quantity is a traditionally accepted method for measuring mangrove forest productivity. Mangrove litter research publication showed linear increment rather than an exponential increment (**Figure 5**).

Mangrove productivity estimation includes both biomass increment and litter fall production. Mangrove litter and productivity show same exponential rate of publication from year 1981 to 2006 (**Figure 5**), while after year 2006, the number of publications on mangrove productivity still shows an exponential growth (**Figure 5**). These mangrove productivity publications could be from different fields such as marine, phytoplankton, coastal, productivity, etc.

Mangrove deforestation and degradation lead to the loss of carbon that has been stored in the mangrove ecosystems. Keyword mangrove deforestation and degradation show a total of 59 publications from 1996 to 2017. **Figure 6** showed exponential trend but data are fluctuating over years. Earlier studies in the field of deforestation were done to study species loss, area cover loss, loss of ecosystem services, etc., while year 2016 and 2017 showed higher number of publications as compared to earlier years possibly due to climate change research and carbon loss due to deforestation (**Figure 6**).

It is sometimes difficult to work inside mangrove forest due to accessibility, high number of mosquitoes, difficult to walk due to muddy condition, etc. **Figure 5** describes mangrove litter publication that showed weak exponential growth, because for litter studies, researchers need to go every month to field collect litter to understand seasonal trend and production of litter fall [28]. Many researchers started to use technology-based research such as using remote sensing [31], drone [32], camera, and different kind of sensors, eddy covariance system [33],

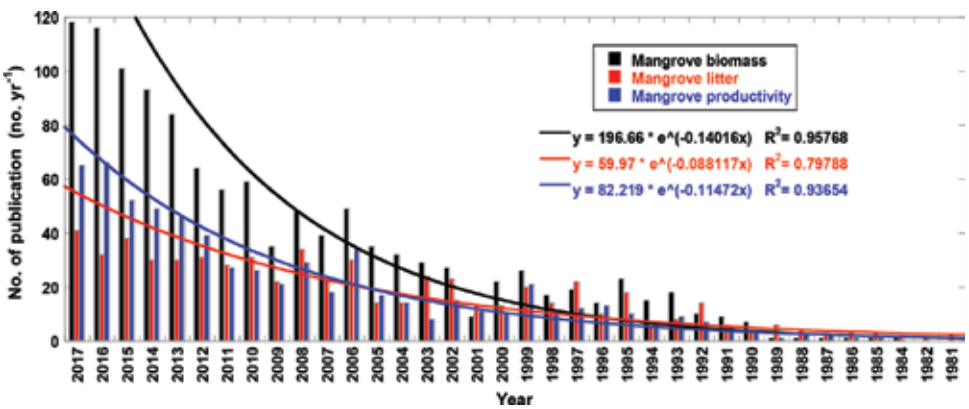

Figure 5. Number of publication records for keywords "mangrove biomass," "mangrove litter," and "mangrove productivity" from 1981 to 2017.

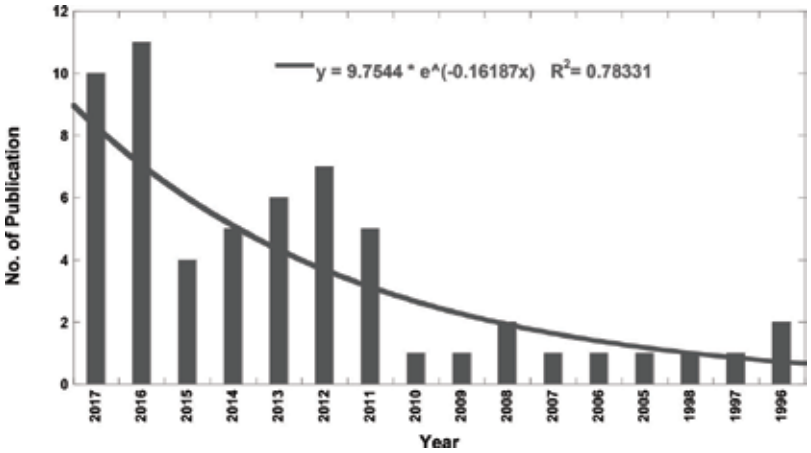

Figure 6. Number of publication records for keywords "mangrove deforestation and degradation" from 1996 to 2017.

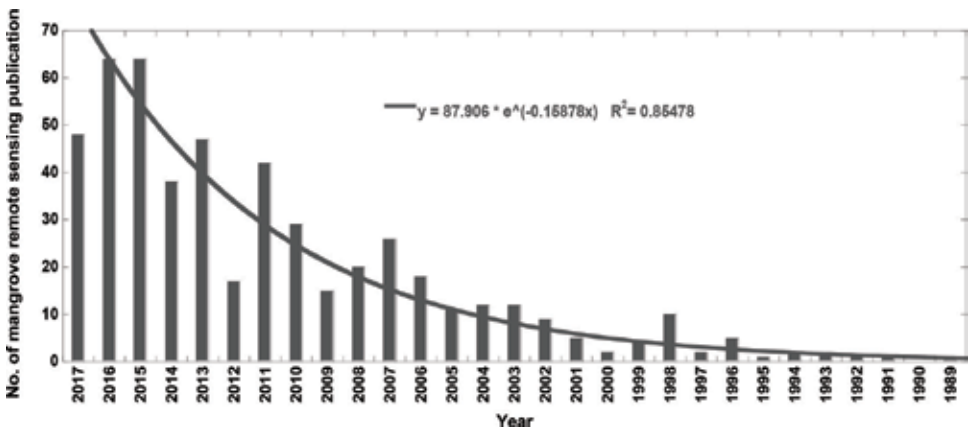

Figure 7. Number of publication records for keyword "mangrove remote sensing" from 1989 to 2017.

etc. Remote sensing is very useful technology to estimate mangrove forest deforestation rate and area cover [34, 35]. Therefore, search was performed for keyword "mangrove remote sensing." Mangrove remote sensing research publications have increased exponentially over time, although it shows some interesting trends (**Figure 7**). Both mangrove remote sensing and deforestation and degradation figures show higher number of publication after year 2015 that means researchers are using remote sensing technology to estimate several parameters such as biomass, carbon stock, leaf area index, area cover, deforestation rate, etc. from mangrove forest.

Overall mangrove fauna research has been increasing every year (**Figure 8**). Several fauna found in and surrounding mangrove forest area such as fish, crabs, birds, large and small mammals, reptiles, amphibians, etc. These organisms play an important part in ecological function and coastal food web. Search results from Web of Science show that majority of

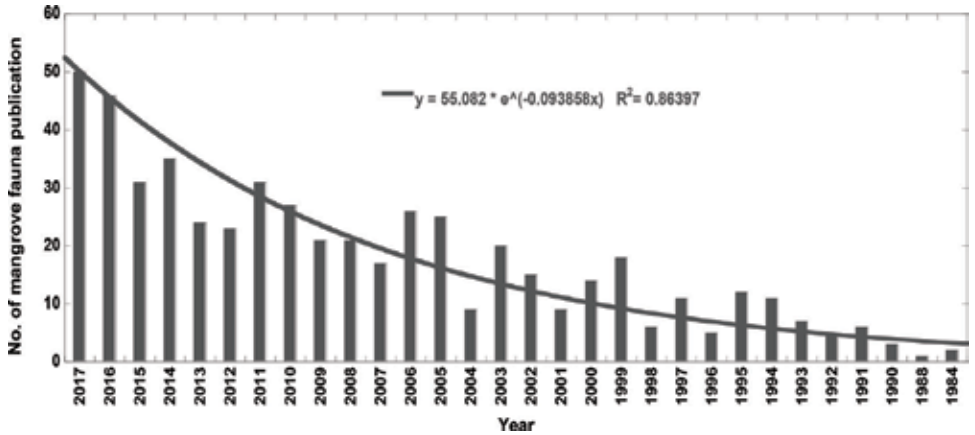

Figure 8. Number of publication records for keyword "mangrove fauna" from 1984 to 2017.

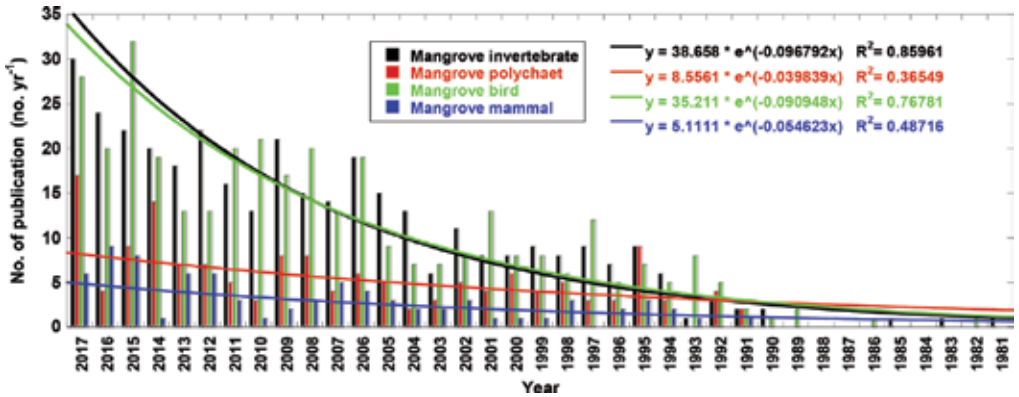

Figure 9. Number of publication records for keywords "mangrove invertebrate," "mangrove polycheat," "mangrove bird," and "mangrove mammal" from 1981 to 2017.

the studies have been conducted on mangrove birds and invertebrates (**Figure 9**) and show exponential increment of publication. Invertebrates, macrofauna (mainly crabs), are an important component of mangrove ecosystem and called ecosystem engineers due to their habit of digging burrows. These invertebrates feed on leaf litter, detritus, plankton, etc. and play a key role in litter breakdown and decomposition of detritus material. Birds are important component in deciding wetland site under Ramsar convention. Most of the mangrove forests are under Ramsar sites. Therefore, mangrove bird research is important in terms of conservation and protection of mangrove forest. On the other hand, mangrove polycheats and mammals show lower and fluctuating publication rate, consequently weak exponential increment (**Figure 9**).

Past studies have showed that literature review could provide important research outputs. In mangroves research, many studies in different fields have been done through literature reviews [36–40].

3. Conclusion

Mangrove research has increased over time around the world in all kind of research areas. From results, it is confirmed that mangrove research is increasing exponentially around the globe. Also number of mangrove researcher is also increasing in the world. There was a time when very few researchers were involved in mangrove forest-related research. The Web of Science search engine can be helpful in quick identification of key research area as well as evolving trends. Also other search engines such as Scopus, Google Scholar, CiteSeer, BioOne, etc., should be taken into account for finer search results.

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Section 2

Mangrove Ecology, Structure and Function

Chapter 2

Mangrove Species Distribution and Composition, Adaptive Strategies and Ecosystem Services in the Niger River Delta, Nigeria

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Additional information is available at the end of the chapter

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Abstract

Mangroves of the Niger River Delta grade into several plant communities from land to sea. This mangrove is a biodiversity hot spot, and one of the richest in ecosystem services in the world, but due to lack of data it is often not mentioned in many global mangrove studies. Inland areas are sandy and mostly inhabited by button wood mangroves (*Conocarpus erectus*) and grass species while seaward areas are mostly inhabited by red (*Rhizophora racemosa*), black (*Laguncularia racemosa*) and white (*Avicennia germinans*) mangroves species. Anthropogenic activities such as oil and gas exploration, deforestation, dredging, urbanization and invasive nypa palms had changed the soil type from swampy to sandy mud soil. Muddy soil supports nypa palms while sandy soil supports different grass species, core mangrove soil supports red mangroves (*R. racemosa*), which are the most dominant of all species, with importance value (I_v) of 52.02. The red mangroves are adapted to the swampy soils. They possess long root system (i.e. 10 m) that originates from the tree stem to the ground, to provide extra support. The red mangrove trees are economically most viable as the main source of fire wood for cooking, medicinal herbs and dyes for clothes.

Keywords: adaptation, deforestation, ecosystem services, west African mangroves

1. Introduction

1.1. Global mangrove species distribution and composition

Mangroves are one of the world's most productive ecosystems. This is because they enrich coastal waters and serve as supermarket of the sea. They are globally distributed and occupy

more than 150,000 km^2, occur in over 123 countries and are made up of more than 73 species and/or hybrids [1–3]. Mangroves are divided into the Indo-West Pacific (IWP) and the Atlantic East Pacific (AEP) groups [4, 5]. They originated from a hot environment [6] and their distribution is influenced by meteorological events [7] such as temperature [8] and precipitation [9]. These climatic parameters influence their distribution to different habitat [10]. Although, tolerance to warm conditions dictates their distribution, they sometimes drift to temperate regions where intense cold weather threatens their survival [11]. Global warming causes mangroves to spread beyond their latitudinal limit [12]. Mangroves are largely restricted to latitudes between 30° north and 30° south. Northern extensions of this limit occur in Japan (31° 22′N°) and Bermuda (32° 20′N); southern extensions are in New Zealand (38°03′S), Australia (38° 45′S) and on the east coast of South Africa (32°59′S) [2]; while there are robust mangrove population on the western coast of Africa with mangroves in Nigeria as one of the most dominant.

Tropical conditions are the best for mangroves, but excessive heat cause rapid evaporation leading to increase in salinity [13], which triggers the succession of salt tolerant mangrove species (e.g. *Avicennia germinans*) over less salt-tolerant species (e.g. *Rhizophora* species) [14]. Increase in temperature affects water body [15]. Temperature greater than 35°C affects root structure, seedling establishment and photosynthetic activity in mangroves [16]. Unrestricted increase in temperature can lead to the migration of species into subtropical salt marsh areas [17] and Arctic pole [18]. Precipitation regulates nutrient up-take and affects productivity [19] and survivability [20] of mangroves. Moderately warm and wet equatorial areas with high rainfall have rich supply of mangrove populations [21]. However, increase in sea level [22] can drown fringe mangroves [13]. In the same vein, global cooling and warming [23, 24] can lead to range shifts and the extinction of organisms [25, 26]. Mangrove propagules are dispersed by tidal currents, but land barriers prevent their free movement [4] leading to a discontinuous distribution. This discontinuity causes intra-specific, morphologic and genetic variation in Rhizophora species [27], which is one of the most dominant mangrove species in the world.

1.2. Ecosystem services of Niger Delta mangroves

The mangrove trees conserve water resources and serve as wind breaks in many communities. Specifically, in the Niger Delta, there are several uses of mangroves by the indigenous people, these include; fire wood, building materials, medicinal products, food baskets and fishing tools etc.

1.2.1. Cooking

Fire wood is a major means of cooking and heating. The firewood is got mostly from the red mangrove tree stems (i.e. Rhizophora species). The trees are first cut into 0.6 m stumps and thereafter chopped into smaller pieces of wood and sold. Fire wood is the preferred cooking method in most rural areas in Nigeria. This is because the wood retains heat for long. Pieces of the wood numbering about 3–5 are gathered and placed under metal tripod stands, and lighted to cook food. The wood ash that comes out after the burning of the wood is used as soil enhancer and disease destroyer in farms when it is spread on the soil surface or on the leaves of crops. It prevents biting and chewing insect pest (grasshoppers and locust) from

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chewing the leaves. The fire wood is also useful in bakery, where larger wood stumps are placed underneath large ovens for baking bread.

1.2.2. Charcoal manufacture

The wood is burnt completely in kiln to form charcoal that is used for outdoor cooking. Charcoal industry is a lucrative business embarked upon by many people in the Niger Delta. The charcoals is measured, put in bags and sold in the market. It is used by a large number of people for outdoor cooking especially during occasions and festivities. It is also used by road side food vendors to roast food items such as plantain, corn, bean balls, pan cakes etc.

1.2.3. Building

The mangrove stems are cut to make stakes. They are also used for construction and building of scaffold. The wood is sawed into different sizes and used as ply wood for building houses. The wood is tough and can be used as roofing boards for houses. However, the use of mangrove for building is restricted because of its high combustibility. Other examples of industrial building materials derived from mangrove include: thatches, bamboo, poles, boats and wooden bridges in local communities. The wood is also used as support pillars and reinforcements for locally built houses and bridges across small rivers or canals. Poles from mangrove are used to connect electric wires, which supplies electricity from one part of the town to another.

1.2.4. Food

The red mangrove propagule is succulent and rich in nutrients and is eaten by crabs (*Goniopsis pelii*). In the Niger Delta people feed on products of animals and insects that live in mangrove forest such as honey combs built by bees in thick mangrove forest. The following organisms are also found in the mangrove forest: mammals, birds, reptiles, insects, roots, stem, flower, honey resins, gum, silk, fabrics, rope, animal oil, and cosmetics. The mangrove forest serves as source of water from streams and lakes. The red mangrove sepal has an enclosure that contains a sweet tasting liquid that is sucked. The tree bark is cut into small bits and used as spices for cooking. The sweet smelling aroma is also used in the manufacture of creams and perfumes; and also bathing soaps that are produced locally.

1.2.5. Medicinal herbs

Tree barks and roots are mixed with other components to produce medicinal herbs that are used to treat some ailments. The bark is chopped into small pieces and put in locally made alcohol to dissolve; lemon is added and left for some time after which it is consumed as medicinal herb for curing several ailments. The mangrove tree bark is boiled with other herbs and used to treat malaria.

1.2.6. Fishery

The mangrove swamps serve as natural fish ponds. The site is dug and surrounded by soil like an embankment with a passageway. During high tides water carrying fishes flows into

the ponds, during ebb tide the water leaves and the fishes get trapped and remain in the embankment. The advantage of this fish pond is that there is a natural exchange of water from the sea, without the use of tap water. The need for external water supply is minimized because of the adjoining water body that supplies constant water to the pond.

1.2.7. Forest products

This includes timber and non-timber products. The timber products are used by the furniture and building industry. Several furniture products are derived from trees cut from the rain forest. Non-timber products include medicinal herbs and pharmaceutical products used locally to treat certain ailments.

1.2.8. Recreation and tourist attraction

Mangrove forests are relaxation points for many citizens who visit the area on site seeing trips. The mangrove forest has a sweet smelling aroma that is therapeutic when one spends time in it. The sea breeze that blows and serenades the trees is a soothing balm that calms a restless nerve. Scientific research is also carried out in the area to identify numerous species found within the forest. The mangrove forest of the Niger Delta contains numerous unidentified species. The forest is a living laboratory that requires further scientific work to identify and classify the species.

1.2.9. Spiritual purpose

The mangrove forest serves as sites for libation and ancestral activities by natives who visit the area to derive some spiritual powers. Big trees are usually not cut, but allowed to grow and serves as points for libation by people that practices African traditional religion. The mangrove forest also serves as hiding place for natives during local wars.

1.2.10. Production of dyes

The tree bark when boiled produces dye used by the clothing industry. The red mangrove tree bark is boiled in hot water to bring out dyes made of red to brown coloration. This is then used to dye fishing net, which help to disguise and attract fishes for higher catch by fishermen.

The mangrove forest is also a region rich in crude oil and gas, which has made Nigeria the largest producer of crude oil in Africa and the sixth largest in the world [28].

1.3. Threats to Niger Delta mangroves

The major threats to mangroves in the Niger Delta are oil and gas exploration, deforestation, dredging, urbanization and Invasive Nypa palm species. Oil exploration began when the first oil well was struck in Oloibiri in the Niger Delta in 1956. Since the striking of this oil well thousands of other oil wells had been drilled resulting to millions of crude oil spillages [28]. The oil spillages had lead to the constant pollution of the mangrove forest leading to the death of numerous mangrove stands [29, 30]. Additionally, the exploratory process involves different stages such as deforestation activities aimed at creating a right of way passage (ROW) for oil pipelines, building

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of boot camps for seismic workers within the forest, etc. leading to the truncation of wildlife activities [31]. Similarly, the use of explosives such as dynamites during exploration for crude oil also led to the death of organisms and the destruction of the forest. Indiscriminate sand dredging is high in the area and had led to the disappearance of many coastal communities because of their conversion from aquatic to a terrestrial environment for the purpose of land expansion to establish residential and industrial quarters. The mangrove forest once destroyed takes up to 15 years or more to re-vegetate as compared to the rain forest that takes 5 years to re-grow. This shows that all aspects of oil exploration are inimical to the mangroves right from the pre-exploratory, exploratory and post exploratory stages. This is because each stage of oil and gas exploration involves hydrocarbon pollution and physical destruction of the mangrove forest. Pollution impacts flora and fauna, for instance oils from spillages clog the roots of mangroves causing outright death through the suffocation of the lenticels, leaf yellowing and defoliation [31, 32]. Pollution has effect on mollusk, crustaceans, echinoderms, polychaetes, cnidarians, oysters, scallops, periwinkles and different species of fishes that inhabit the mangrove forest. Similarly, the immobility of benthic organisms predisposes them to death from pollution. Different species of crabs such as *Callinectes pallidus*, *Uca tangeri*, *Ostrea tulipa* and *Goniopsis pelii* are also affected by pollutants.

Urbanization is also a major threat to the mangroves, this is because population explosion in Nigeria, which is the most populous country in Africa, had led to the migration of a large number of people numbering over 20 million [33] into coastal regions of the Niger Delta to establish houses. Industrialization of wetland areas leads to the urbanization of rural areas that were formerly a habitat for mangroves. Increase in anthropogenic activities around mangrove forest had resulted to the invasion by opportunistic nypa palms (*Nypa fruticans*) and other alien species. The nypa palms were intentionally introduced in 1906 for the purpose of fighting coastal erosion [34]. The palms were originally not a threat to the mangroves, but within the last 30 years due to unabated anthropogenic activities they have become a major threat to mangroves after hydrocarbon pollution [35]. They have currently displaced 5% of the entire mangrove forest in the last 20 years [35] caused mainly by oil and gas exploration, urbanization and deforestation [36], which had opened up the forest to further exploitation. Despite the impacts of the aforementioned factors, mangroves are still resilient to environmental perturbations [37] and have robust growth in the Niger Delta. However, the current threat to mangroves that can lead to their extinction is the interaction of all the factors. It is found that mangroves can survive hydrocarbon pollution by adapting to the contaminated environment through the activities of increased soil fertility via hydrocarbon utilizing bacteria. They can also survive some forms of selective deforestation aimed at harvesting firewood for human use. They can also survive invasion by nypa palm propagules as long as their soil quality is not reduced as a result of the actions of solid and liquid waste. But they would hardly survive when all the aforementioned factors combine and overwhelm them.

1.4. Mangrove species composition in the Niger Delta

There are several species of mangroves in the Niger Delta, but the most dominant ones are the red (*Rhizophora racemosa*), black (*Laguncularia racemosa*) and white (*Avicennia germinans*) mangroves [38]. Button wood mangroves (*Conocarpus erectus*) are also prominent but less studied and is not too common around core mangrove forest. They are mostly found in

inland areas that have sandy soil. They have green leaves and hairy round seeds (**Figure 1c**). The mangroves are mainly fringe forests [39]. This is because they are found at the fringes of the coastlines facing the river. Oil palm trees (*Elaeis guineensis*), mangrove fern (*Acrostichum aureum*) and grass species such as vines, sedges etc. (**Figure 1I**) are found around sandy or disturbed parts of the forest in inland locations. A major factor for their distribution pattern is the nature of the soil, which is less fertile and less saline. Non-mangrove species perform better in soils with low salinity unlike mangrove soil that thrives in highly saline environment [7, 40]. Human activities such as sand filling, reclamation and dredging (**Figure 2**) change the soil from muddy to sandy soil leading to the intrusion of non-mangrove species in mangrove forest.

The white mangroves (*Avicennia germinans*) on the other hand, are the next most dominant after the button wood in sandy areas. The red mangroves are the closest to the seashore whereas the black and white mangroves are more adapted to disturbed soils. They are often found on the edges of shorelines where waste are deposited. In contrast, the red mangroves are mostly found in undisturbed pure swampy soils than mixed or contaminated soils. This is because presence in soils contaminated by waste impairs the growth of red mangroves. An example of a disturbed soil is the sand filled mangrove forest in Buguma, Niger Delta, Nigeria. This area was sand filled in 1984, and since then no mangrove had ever grown on it. Rather the dominant species found

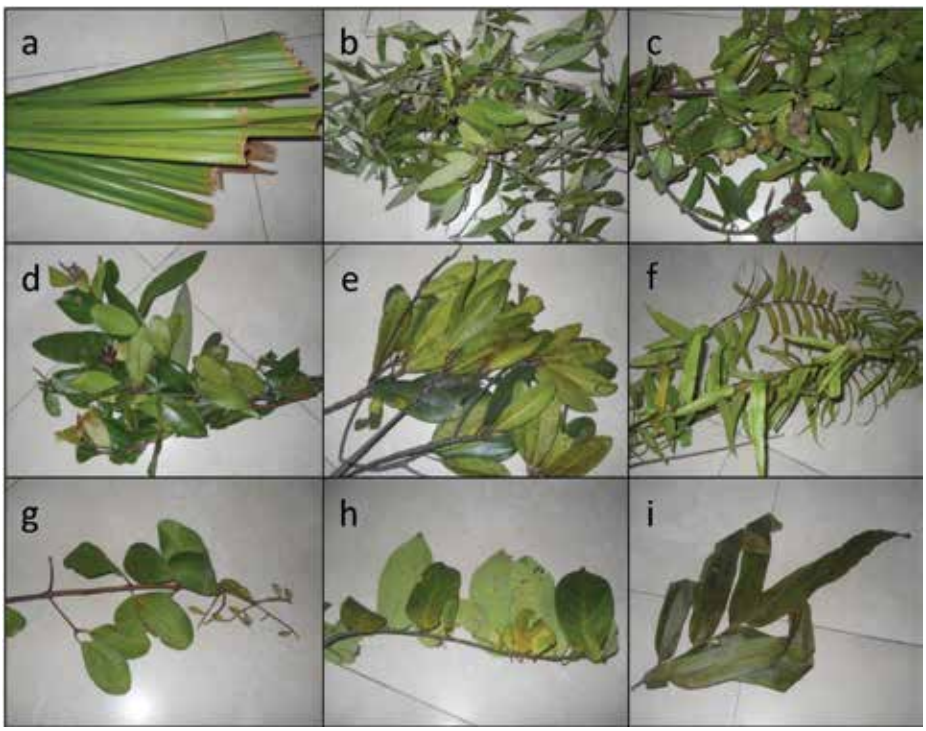

Figure 1. Different mangrove and non-mangrove species found in mangrove swamps affected by anthropogenic activities (dredging and sand filling). (a) Nypa palm (*Nypa fruticans*), (b) black mangroves (*Laguncularia racemosa*), (c) button wood (*Conocarpus erectus*) (d) herb (e) red mangrove (*Rhizophora racemosa*) (f) mangrove associated fern, (g) white mangrove (*Avicennia germinans*), (h) *Heritiera littoralis* (I) mangrove fern (*Acrostichum aureum).*

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Figure 2. Dredged and sand filled mangrove forest in Buguma, Niger Delta, Nigeria. There are still some mangroves that can be seen at the foreground. On the left of the picture is the fence of a secondary school. No mangrove tree has ever grown in this area since the sand filling in 1984. The area is now occupied by weeds and other alien plant species.

are a variety of non-mangrove species in both the seaward and landward areas. The landward area has sandy soil that has large percentage growth of grass species such as corn vine (*Dalbergia ecastaphyllum*), coco plum (*Chrysobalanus icaco*) etc. Because of the proliferation of anthropogenic activities around mangrove forest some grass species had taken over the area. Examples of other species present include carpet grass (*Axonopus compressus*), elephant grass (*Pennisetum purpureum*), guinea grass (*Panicmum maximum*), goose grass (*Eleusine indica*) and goat weed (*Ageratum conyzoides*). A major observation during field work is that mangroves when cut never grow back rather the area from where they are cut is over taken by weeds [28] which forms gradients around the wetland soil. Oil and gas exploration also affect species composition in mangrove forests [35]. For example, industrial activities had led to a permanent change in soil and species composition, which accelerates the proliferation of weeds and other alien species. The weed when they grow becomes the hiding place for foreign insects and rodent pest, which later invade the mangroves.

1.5. Data gaps

Combinations of biotic and abiotic factors had made the mangroves one of the most unique, but less studied systems in the world. The problem of data gap in Africa is often cited in many literatures with little done to correct this trend. This work therefore, brings to fore the distribution and composition of mangroves and non-mangroves species in two locations in the Niger Delta to enable scientist in other regions of the world to have a better understating of the largest mangrove forest in Africa. The emphasis of mangrove study in the past has been the effect of pollution on mangrove forest, but no mention was made of species composition and distribution. This is the reason why this study is embarked upon to help bridge the data gap. This study thus intends to achieve the following objectives;

1.5.1. Objectives

1. To determine the distribution, composition and structural characteristics of mangroves
2. To evaluate the adaptive strategies of mangroves vis-a-vis their significance to the environment.

2. Materials and methods

2.1. Study area

The Niger Delta region is situated in the southern part of Nigeria and bordered to the south by the Atlantic Ocean and to the East by Cameroon. It occupies a surface area of about 112,110 km^2. It represents about 12% of Nigeria's total surface area and it is predicted that by the year 2020 its population would have exceeded 45 million inhabitants, which is almost two third of the entire population of Nigeria (i.e. 200 million). The region is made up of nine of Nigeria's constituent states (i.e. 37) (**Table 1**):

States	Land area (km^2)	Population	City capital
Abia	4877	5,106,000	Umuahia
Akwa Ibom	6806	5,285,000	Uyo
Bayelsa	1107	2,703,000	Yenagoa
Cross River	21,930	4,325,000	Calabar
Delta	17,163	5,681,000	Asaba
Edo	19,698	4,871,000	Benin
Imo	5165	5,283,000	Owerri
Ondo	15,086	4,782,000	Akure
Rivers	10,378	7,679,000	Port Harcourt
Total	112,110	45,715,000	

Source: Adjusted from [41].

Table 1. Land area and population of people in different states of the Niger Delta, Nigeria.

The Niger Delta region makes up 4% of Nigerian population. There is an annual growth rate of 3.5% The population of youths below 30 years (62%) far exceed that of adults of 30–69 years (36%) and older adults above 70 years (2%). The life expectancy is about 50 years. There is resurgence in population of people migrating into the mangrove forest areas to seek for habitation in the last 20 years. The consequence of this situation is the clearing of more mangrove forests.

2.2. Climatic conditions

Mangroves in the Niger River Delta, Nigeria are the largest in Africa, and the third largest in the world. It is estimated to cover between 5000 and 8500 km^3 [42]. It has a tropical monsoon climate and rainfall occurs almost all throughout the year, except November, December and January. Mean annual rainfall ranges from over 4000 mm in the coastal towns, and decreases inland to 3000 mm in the mid-delta area; and slightly less than 2400 mm in the northern parts of the region. In the north western portions including Edo and Ondo States, annual rainfall ranges from 1500 to 2000 mm, respectively. The two seasons that prevail in the Niger Delta are the wet (February–October) and the dry (November–January) seasons with a break in August,

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known as the "August break". During the dry season harmattan winds also called the North East Trade winds blow particles of dust from the Sahara Desert to the coastal maritime regions in the Niger Delta. The monthly temperature ranges between 26 and 30°C. Temperatures are generally high in the region and fairly constant throughout the year. Average monthly maximum and minimum temperatures vary from 28 to 33°C and 21 to 23°C, respectively. The warmest months are February, March and early April in most parts of the Niger Delta Region. The coolest months are June through to September during the peak of rainfall during the wet season. The soil is swampy and grades from red to brown as a result of iron deposition [38]. The soil compaction ranges from 0.25–0.75 tonnes/cm, while the pH ranges from 5.0–7.0.

2.3. Sample collection

A study on species distribution was conducted between seaward and landward sites in Buguma. Along a 20 m transect running across the middle of the plot, eight equally spaced points were identified and soil samples collected and species composition and diversity indices estimated from seaward to landward locations. The soil samples were collected with a hand held augur (Germany) and placed in a black cellophane bag. Leaf samples were collected at each point and placed in an ice cooler, and sent to the laboratory for physico-chemical analysis. The different plant communities were identified by a plant taxonomist.

2.3.1. Species occurrence and stand structure

Floristic diversity, which is the percentage occurrence of mangrove species present around the forests, was determined within a 5 × 5 m^2 sub-plots within a 20 × 20 m plot in Buguma and Okrika in the Niger Delta. The dbh for trees with small girth were measured with a vernier caliper at an accuracy of 0.01 cm while the stems of larger girth were measured with tapes (Forestry suppliers Inc., Jackson, MS). The tree heights were randomly measured within the plot with EC II Haglof clinometers at an accuracy of 0.1 m.

2.3.2. Stand structural characteristics

The stand basal area, which is the summation of all individual basal areas per unit ground area, was calculated as described by [43]. The area of the main plot, 400 m^2 (i.e. 20 × 20 m), and the area of the sub-plots, 25 m^2 (i.e. 5 × 5 m) were used as the conversion factor of 1 hectare [44]. The outcome of this calculation is in [45].

The importance value (I_V) of the mangroves was calculated using the equations of [43]:

The importance value is a quantitative parameter used to show the significance of each species within a stand, and it includes the summation of relative density, relative frequency and relative dominance.

2.3.3. Above ground biomass (AGB)

The allometric method was used to estimate the plot AGB, since biomass was an indicator of the productivity of a mangrove stand [45, 46]. This method is used for estimating tree weight from field verifiable structural indices such as diameter at breast height (dbh) and tree height (h) [46]. The amount of standing biomass in mangrove forest is a function of the systems productivity

[45]. The development of site and species specific allometric relationship is best done using harvesting method [47]. But this method was not used because of its negative effect on the environment. The above ground biomass was therefore, calculated following the equations developed by [48] and presented in 4 studies of [45].

This equation is the Model 1 (diameter-height-wood density) mangrove biomass regression model. The wood specific density (ρ) for African mangroves from the Global Density Database was used in the calculation [49–51]. A total of five dominant mangrove species were taxonomically identified in the study locations and their wood specific densities (ρ) recorded as follows: *R. racemosa* (0.96 g cm^{-3}), *R. mangle* (0.98 g cm^{-3}), *A. germinans* (0.90 g cm^{-3}), *R. harrisonii* (0.86 g cm^{-3}) and *L. racemosa* (0.61 g cm^{-3}). These specific densities were put into the Model 1 mangrove regression model to calculate the plot AGB.

2.4. Soil sample analysis

A comprehensive physicochemical analysis of soils collected from Buguma and Okrika was done at the laboratory where standard methods were observed to analyze the parameters.

2.4.1. Soil organic carbon (Walkley-Black method)

A representative soil sample was collected and grinded into fine particles, such that it can pass through 0.5 mm sieve and air dried. Soil samples were weighed in duplicates of 75 g and transferred to 250 ml Erlenmeyer flask. 10 ml of $K_2Cr_2O_7$ solution was accurately pipetted and dispensed into each of the flasks and swirled gently to disperse the soil. 20 ml of concentrate H_2SO_4 was added rapidly and directing the stream into the suspension. The soil and the reagents were mixed by swirling the flask gently for 1 min. The beaker was rotated again and the flask was allowed to stand on a sheet of asbestos for about 30 min, thereafter, 100 ml of distilled water was added. Then, 3–4 drops of indicator were added and titrated with 0.5 ml of ferrous sulphate solution. As the end point is approached, a greenish caste was observed which later changed to dark green. Thereafter, ferrous sulphate was added, drop by drop until the color changed sharply from blue to red (maroon color) in reflected light against a white background. The blank titration was prepared in the same manner using the above mentioned steps but without soil to standardize the dichromate.

The result was obtained using the formula of [52].

$$\%\text{Organic Carbon in Soil} = \frac{\text{Blank Titre Value-Sample Titre Value}}{\text{Weight of Air-dried Soil (g)}} \quad (1)$$

2.4.2. Soil pH and conductivity

pH meter was used to check the acidity and alkalinity of the soil in situ. Conductivity was measured in field using conductivity meter.

The KH_2PO_4 Extraction Method was used to analyze sulphate content of the soil.

2.4.3. Sulphate and phosphorus analysis

The KH_2PO_4 Extraction Method was used to analyze sulphate content of the soil. 2 g of soil with one tea spoon of carbon black and 40 ml of extracting solution were added into 125 ml of

Erlenmeyer flask, and mechanical shaker was used to shake the mixture for 30 min. The suspension was later emptied into a funnel containing Whatman No. 40 Paper to obtain a clear filtrate. The solution was stored and phosphorus was determined using Calorimetric Method [53].

2.4.4. Metal analysis

A portion of 0.25 g of air dried sediment samples were weighed into a Teflon inset of a microwave digestion vessel and 2 ml concentrated (90%) nitric acid (Sigma-Aldrich, Dorset, UK) were added. The metals were extracted using a microwave accelerated reaction system (MARS Xpress, CEM Corporation, Matthews, North Carolina) at 1500 W power (100%), ramped to 175°C in 5.5 min, held for 4.5 min, and allowed to cool down for 1 h. The cool digest solution was filtered through the Whatman 42 filter paper and made up to 100 ml in a volumetric flask by adding de-ionized water.

For the water samples, 2 ml concentrated (90%) nitric acid (Sigma-Aldrich) was added to 0.2 ml water and the volume was made up to 10 ml with de-ionized water (X 5 dilution). Metal concentrations were analyzed by inductively coupled plasma mass spectrometry (ICP MS: model X7, Thermo Electron, Winsford-Cheshire, UK).

All chemicals and reagents used were of analytical grade and of highest purity possible. Analytical blanks were prepared with each batch of the digestion set and analyzed (one blank for every set of six samples) in the same way as the samples. The analytical methodologies were confirmed using certified reference materials for sandy clay (CRM 049-050, Sigma-Aldrich RTC, Salisbury).

3. Results

3.1. Species composition and diversity indices

Most locations in the Niger Delta have similar mangroves species composition. Some mangrove species found include: *Rhizophora harrisonii* and *Laguncularia racemosa*. The three most commonly found mangrove species are: *Rhizophora racemosa*, *Rhizophora mangle*, and *Avicennia germinans*. Species diversity indices indicates that among the mangroves *Rhizophora racemosa* had the highest abundance and species diversity (**Table 2**) while for the palm species, the nypa palm dominated (**Table 3**) and for the grass species, *Dalbergia ecastophylum* had the highest diversity (**Table 4**).

3.2. Species distribution

Species distribution from seaward to landward areas indicates that core mangrove species were found in the seaward side, whereas the non-mangrove species were found in the landward direction.

3.3. Heavy metal and nutrient concentrations distribution along a transect

There was gradation of heavy metal concentration along the established 20 m transect. It shows that the concentration of metals from landward to seaward directions remained unchanged while Zinc (Zn) concentration along transect fluctuate.

Scientific name	Common name	Abundance	Proportion (P_i)	Ln (P_i)	P_i Ln(P_i)
Rhizophora mangle	Red	5	0.21	−1.561	−0.328
Rhizophora racemosa	Red	8	0.33	−1.109	−0.366
Rhizophora harrisonii	Red	2	0.08	−2.526	−0.202
Avicennia germinans	White	6	0.25	−1.386	−0.347
Laguncularia racemosa	Black	3	0.13	−2.040	−0.265
Total		24		H	1.508

Table 2. Shannon wiener diversity indices (H) of major mangrove species in the Niger Delta, Nigeria.

Scientific name	Common name	Abundance	Proportion (Pi)	Ln (P_i)	P_i Ln(P_i)
Nypa fruticans	Nypa palm	5	0.83	−0.186	−0.154
Elaeis guineensis	Date palm	1	0.17	−1.772	0.366
Total		6		H	0.52

Table 3. Diversity indices (H) of palm species commonly found around most mangrove forest in the Niger Delta, Nigeria.

Scientific name	Common name	Abundance	Proportion (P_i)	Ln (P_i)	P_i Ln(P_i)
Dalbergia ecastophylum	Corn vine	6	0.24	−1.427	−0.343
Chrysobala musicaco	Coco plum	4	0.16	−1.833	−0.293
Paspalum	Silt grass	2	0.08	−2.526	−0.202
Scleria verrucosa	Bush knife	1	0.04	−3.219	−0.129
Combretum racemosum	Christmas tree	3	0.12	−2.120	−0.254
Osbeckia tubulosa	Melastomataceae	1	0.04	−3.219	−0.129
Mariscus longibracteatus	Sedge	1	0.04	−3.219	−0.129
Acrostichum aureum	Aquatic fern	1	0.04	−3.219	−0.129
Scleria naumanniana	Bush knife	1	0.04	−3.219	−0.129
Lycopodium cernuum	Fern	1	0.04	−3.219	−0.129
Alchornea laxiflora	Christmas bush	1	0.04	−3.219	−0.129
Syzygium guineense	Myrtaceae	3	0.12	−2.120	−0.254
Total		25		H	2.249

Table 4. Shannon wiener diversity indices (H) of weed species commonly found around mangrove forest in the Niger Delta, Nigeria.

Nutrient contents varied along the 20 m transect from seaward to landward directions. There was an increase in sulphate (SO_4) and potassium (K) content while there was a decrease in Calcium (Ca), Magnesium (Mg), Manganese (Mn) and Phosphorous (P) contents.

Study location	Conductivity µs/cm	pH	TOC (%)	P (mg/kg)	SO_4^{2-} (mg/kg)	Cd (mg/kg)	Pb (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Mn (mg/kg)	Ca (mg/kg)	K (mg/kg)	Mg (mg/kg)
OK1	1133	5.94	1.989	0.07	25	0.06	6.21	4.86	1.26	1.52	33.28	54.95	229.48
OK2	783	6.4	1.716	0.03	28	0.001	0.001	1.26	0.001	0.44	45.17	38.31	143.73
OK3	9920	5.97	3.315	0.09	60	0.001	0.001	2.6	0.001	4.71	36.95	334.8	513.2
Mean	3945.33	6.10	2.34	0.06	37.67	0.02	2.07	2.91	0.42	2.22	38.47	142.69	295.47
SD	5177.17	0.26	0.86	0.03	19.40	0.03	3.58	1.82	0.73	2.22	6.09	166.58	193.37
SE	2989.04	0.15	0.49	0.02	11.2	0.02	2.07	1.05	0.42	1.28	3.52	96.18	111.64

Table 5. Soil physico-chemical characteristics of different mangrove forest in Okrika, Niger Delta, Nigeria. OK refers to Okrika.

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Study location	Conductivity µs/cm	pH	TOC (%)	P (mg/kg)	SO_4^{2-} (mg/kg)	Cd (mg/kg)	Pb (mg/kg)	Zn (mg/kg)	Cu (mg/kg)	Mn (mg/kg)	Ca (mg/kg)	K (mg/kg)	Mg (mg/kg)
BG1	308	6.53	2.808	0.15	18	1.34	19.14	83.97	19.28	51.84	1149.1	133.85	737.35
BG2	186	6.83	2.145	0.1	15	0.93	22.82	88.55	38.85	62.55	1156	157.05	715.49
BG3	19,280	6.58	3.939	0.24	240	0.001	0.001	8.4	0.001	4.77	282.85	407.4	794.61
Mean	6591.33	6.65	2.96	0.16	91.00	0.76	13.99	60.30	19.38	39.72	862.65	232.77	749.15
SD	10988.9	0.16	0.91	0.07	129.05	0.69	12.25	45.01	19.43	30.74	502.13	151.68	40.86
SE	6344.43	0.09	0.52	0.04	74.51	0.40	7.07	25.99	11.21	17.75	289.91	87.57	23.59

Table 6. Soil physico-chemical characteristics of different mangrove forest in Buguma, Niger Delta, Nigeria. BG refers to Buguma.

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A detailed physico-chemical analysis of the study locations is presented in **Tables 5** and **6**.

3.4. Stand structure and above ground biomass

Stem diameter of the mangrove trees ranged from 0.01 to 16 cm. *Avicennia germinans* had the largest diameter among species. Tree height ranged from 0.02 to 6.71 m. The average diameter and average tree height for most locations are not significantly different from each other.

4. Discussion

Rhizophora racemosa was the most dominant species in all locations. This is in line with the outcome of previous studies done in the Niger Delta [40]. The importance value (I_v) of *R. racemosa* (i.e. 52.02) was the highest for all locations. It is similar to the value derived by [54] in south-eastern Nigeria (i.e. 55.6). The next most dominant species of mangroves are *R. mangle* followed by *A. germinans* [45].

The dominance of the red mangroves (i.e. *Rhizophoraceae* family) is because they grow best in core mangrove soil. They are mostly old growth forest that had been growing for the past 20–30 years without disturbance. They have large diameter and grow beyond 6 m in height. The trees grow in groups and are self-sustaining and support each other. Because of the large sizes of the stem they are often used for firewood and charcoal. Constant destruction of the mangroves by humans had, however, made them to regenerate and grow afresh, making them have less significant wood for charcoals production. Clear cutting lead to renewed sprouting of fresh mangroves, which unifies regeneration [55]. Hydrocarbon pollution and selective deforestation lead to uneven growth. Nevertheless, the growth in height and stem diameter is greater in younger mangrove forest than in older mangrove forest [56]. The forest is also cut to create room for building residential and industrial quarters.

Baseline data on biomass will help to recognize importance of mangroves in Nigeria. Biomass differences among mangrove forests are indicator of healthy and unhealthy forest. Mangrove forest in unprotected areas seems to show unhealthy condition or fragmentation and degradation due to illegal logging and aquaculture [57, 58]. Thus, management effort of rehabilitating degraded forest must be done to improve carbon sequestration and productivity in unprotected mangroves forest.

Four kinds of soils found in mangrove forest in the Niger Delta include: are mud, chikoko-wet, chikoko-dry and sandy soils. Muddy soils is fine to the touch, light brown in color, wet, and mixed with litter. It can be molded into shapes because of its high plasticity and low porosity. This soil allows the growth of few weeds, and few mangrove species. The chikoko-wet is dark brown in color, rough to the touch, forms a semi mold, and often wet and has medium plasticity and low porosity. This soil is the best for the growth of red, black and white mangroves. The chikoko-dry is coffee-brown in color, rough to the touch, has particulate matter and forms no mold. It contains litter material, and has low plasticity and medium porosity. This soil does not support the growth of many plant species because of its dryness. The sandy soil is whitish to dark brown in color, rough to the touch, forms no mold, and has low plasticity, but high

porosity. This soil strictly allows only grasses and other weed species grow on it. They are often found in dredged or sand filled areas.

Mangroves have low growth in muddy soil because the soil suffocate their lenticels, which may lead to death. The case is, however, different for the weeds, which have better growth in muddy soil. A species composition study done in a sand filled area indicates that in a 20 m transect starting from the seaward to the landward direction; there was a significant difference in the number of species found. Similarly, there was a significant difference in soil physico-chemistry at eight points along the transect. The result indicates that the sandier the soil the more the number of weeds, while the swampier the soil the more the population of red mangrove trees (**Table 2**).

The breathing root system of mangrove is built for survival in anaerobic soils. That is why the mangroves thrive in areas where other species fail that soil types influence mangrove growth. For instance, results from a fieldwork I embarked on indicates that total organic content (TOC) was higher in farm (1.99 ± 0.01%) and Nypa palm (1.87 ± 0.01%) soils than in mangrove soils (1.01–1.48%). Similarly, soil types influence the height of mangrove and nypa palm seedlings ($P < 0.001$), but did not influence diameter of seedlings ($P > 0.05$). Mangrove propagules grew best in farm soils. This shows that mangrove distribution is strongly influenced by soil types. Therefore, the more the soil type changes as a result of anthropogenic activities the more it harbors foreign species, which are non-mangroves. In addition, tidal fluctuation and soil moisture content affects the amount of organic matter in sediments [59].

Changes in heavy metals and nutrients can also influence the distribution of mangroves and other plant species in a wet land area. In a study carried out in dredged and sand filled site in Buguma Niger Delta, Nigeria, the result indicates that apart from zinc, which fluctuated, other heavy metals did not vary significantly along a 20 m transect from sandy to mangrove soil ($P > 0.05$). Mangroves play environmental role by acting as a biofilter of heavy metals [60]. Lastly, maintaining high diversity of mangroves is crucial to ensure the health and productivity of coastal zones [60].

4.1. Adaptive strategies of mangroves

There are several adaptive features in mangroves [61] including some that are peculiar to the Niger Delta, Nigeria. The mangrove develops long root system that can easily be mistaken for a tree branch. They grow up to 3 m in height, and grow out from tree branches to the ground. This helps to provide extra support for the trees. The adventitious roots do not only grow from the base, but grow from the top of the trees to the ground. The giant roots support and provide extra surface area for atmospheric respiration during high tides when the ground roots are submerged in water. The branches hardly submerge during high tide or flooding because of the nature of the root system, which grow above the water level. The red mangrove trees are more dominant and more adapted to core mangrove soils. The red mangrove propagules have limited growth in sandy or mixed soils. They are mostly adapted to wet chikoko soil, which is slightly muddy.

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The red mangroves (e.g. *Rhizophora mangle*) are viviparous and have spear-like propagules that germinate while still attached to the tree. This is an adaptation for quick deployment and growth especially when they fall on swampy soils. The base of the propagule contains root cells, which begin to grow immediately it touches the soil or water. However, if the propagules fall on hard surface it lies horizontal, but if it falls in water it would be carried away by tidal currents. The seeds, nevertheless survive being swept away by water current because of its buoyancy, as compared to the nypa palm seeds that are round and are partially submerged when carried by tidal currents.

The torpedo shape of the mangrove propagule enables it to float upright i.e. bottom down and heads up when submerged in water. This allows easy soil implantation and growth.

Rootlets of the white mangrove trees protrude from oxygen-depleted soils like spikes to take in oxygen. This is a way of boosting their survival in a difficult and marshy environment. This characteristic is most often exhibited by the black and white mangroves, but not the red mangroves. This is because white and black mangroves are mostly found in disturbed environments, such as dump sites and sand filled areas. The stems of the red mangroves are elastic and are adapted to wear and tear. The stems and roots form a network that prevents the free movement of animals and humans within the forest. They also restrict the movement of humans and machinery during exploratory activities.

The leaves of the red mangroves (*Rhizophora germinans*) are leathery and succulent and have some xerophytic [62] and schlerophyllic attributes. The epidermis has thick outer walls which enables them to withstand both dry and wet conditions. During the dry season from October to January, the leaves do not fall, and do not undergo rapid transpiration and evaporation, thus preventing desiccation. The mangroves rather look robust, fresh and evergreen in both dry and wet seasons. High litter fall usually occur in the dry season unlike in other areas where the rate of litter fall was higher in wet season. Studies had shown that seasonal changes and hydrocarbon pollution are the two major causes of litter fall and litter accumulation in the Niger Delta, Nigeria. The highest rate of litter fall was recorded in the dry season, between November and March. This is because of reproductive activity (i.e. fruiting and flowering) and harmattan winds that occur mainly during the dry season. The litter enriches the soil and supplies the raw materials needed for decomposition [63]. This leads to the constant enrichment of the soil, which makes the mangrove forest rich in biodiversity.

The mangrove soil is red in color and has life-saving gas that breathes life into the entire mangrove ecosystem. The soil has numerous fiber-like materials that hold and reinforce the soil against water erosion and tide. The combination of nutrients and red soil water with fibrous materials is what has made the mangrove a biodiversity hot spot. Therefore, if these qualities are destroyed as a result of human activities the red mangrove population will decline leading to succession [14] and entry of foreign species [64]. The surface of an undisturbed mangrove soil is slimy and facilitates the movement of creeping and swimming organisms such as mud skippers during low or ebb tides. The slimy and soft nature of the top soil also acts as a defensive mechanism to prevent the free movement of man and

animals on the forest floor. The soil has some holes, which serve as air pockets and safe sanctuaries for threatened organisms (e.g. crabs, mudskippers).

A symbiotic relationship does exist between the red mangrove trees and black ants. Large number of black ants are always found on the leaves, branches and stems of trees, which serve as a source of food for the ants while the ants in turn provide protection for the tree against intruders. Termites also build huge termitarium on the tree trunks, which further provides extra security for the plants by warding off intruders and predators. The ants are entomophagous because they feed on other insects along their path. The ants also attack humans that climb to exploit the trees.

The stems of the mangrove trees are very rigid and could withstand severe external impact or fracture during wind storm. It is also extremely difficult to cut down the trees with a machete. The trees are often cut with chain saw or brought down with bulldozers. The mangroves grow in groups, which gives them extra protection from wind storms. The closeness of the trees to each other also leads to the accumulation of large amount of ground litter materials that decompose to drive the nutrient cycle of the forest [14].

Tree climbing skill is exhibited by red mangrove crabs (*Goniopsis pelii*) to hide from ground predators and evade capture. The crabs eat mangrove leaves thereby contributing to litter fall, which help to enrich the mangrove soil.

The mangrove forest is rich in biodiversity and has organism such as monkeys, guinea fowl, periwinkle, mudskipper, crabs (*Goniopsis pelii*), birds (i.e. cranes) and insects [3]. The whole mangrove system is built to withstand stressful conditions. For example, its roots are natural air pumps that suck in oxygen from the atmosphere. The roots are also one of the largest above ground root systems possessed by any plant in the world. The roots provide extra support for growth in soft soil. The mangrove seeds are highly buoyant, which enables them to float, travel and colonize vast areas without drowning. The tenacity of their stems make their wood to be suitable for the production of charcoal and fire wood for cooking in most African communities. The wood have high combustibility and high fire retention capability. The mangrove forest serves as home for many rural dwellers, who build their houses right inside the forest because it provides protection from flood, tsunami or hurricanes.

In addition to plant and animal resources the Niger Delta mangrove forest is rich in crude oil. Most oil and gas exploration activities do occur within the mangrove forest. These exploratory activities have decimated the mangroves in many locations, which may lead to extinction if this trend is not stopped [4, 5]. Over the years the mangroves had survived many environmental disturbances such as hydrocarbon pollution, deforestation, urbanization, and invasive species by adapting to very difficult conditions.

Mangroves are adapted to hydrocarbon pollution: This is because series of studies and field observations have shown that mangroves growing in highly polluted plots had better structural characteristics, above ground biomass and species composition than mangrove trees growing in lowly polluted soil [45, 54]. It has been difficult to provide answers to the cause of this trend, but of recent it was discovered that the robust growth of mangroves in highly polluted plots is as a result of decomposition and nutrient cycling from excess defoliations as a result of oil and gas exploration. The reason is that oil spill leads to increase in litter fall, which covers the soil surface, and decomposes to enrich the soil. This condition leads

to the proliferation of hydrocarbon utilizing bacteria, which detoxifies the soil and increase the soil fertility leading to a positive feedback such as increase in nutrient turnover. This leads to the rapid growth of mangroves in highly polluted soils. This study is supported by other studies which revealed that the rate of herbivory of crabs and insects on mangrove leave was higher on trees growing in highly polluted soils than in trees growing in lowly polluted soils.

5. Conclusion

Mangrove of the Niger Delta, Nigeria is one of the most productive systems in terms of biodiversity, and ecosystem services in the world, but because of lack of data it is often not mentioned in many literatures. This chapter has brought to light the distribution of different species of mangroves between landward and seaward areas and the effect of soil physicochemistry on mangrove species distribution. *Rhizophora* species i.e. red mangroves are the most dominant species and is often found in the seaward areas whereas the white mangroves and the button wood mangroves are found in the landward locations. The positions of the different species of mangroves in the coastal areas had given them the ability to adapt to their difficult environment. The red mangrove of the Niger Delta has one of the longest above ground root systems, which it uses for support and respiration. The stem is also used for fire wood and charcoal production. The mangrove despite its usefulness to man and the environment has faced a lot of anthropogenic disturbances, which if not curtailed will lead to the final extinction of the mangroves.

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Chapter 3

The Comparison of Vascular Epiphytes Diversity Related to their Occurrence in Natural and Artificial Mangrove Channels, Greenfields, Eastern Coast of Nicaragua

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Additional information is available at the end of the chapter

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Abstract

The eastern Nicaraguan coasts bordered by mangrove forests are often negatively affected by catastrophic events. One of the most destructive was hurricane Joan in 1988, which damaged as much as 80% of the forests. Though neotropical mangrove woodlands are not famous for their high species richness, vascular epiphytes occurring in the mangrove canopies are characterized by high biodiversity. The research presented in this study was focused on vascular epiphytes found in a private Nicaraguan reservation Greenfields. The main aim of the work presented here was to compare two parts of same-age mangrove area surrounding a water channel that runs through the forest stands in the reservation. The biodiversity observed in the initial natural part of the water channel was compared with the biodiversity observed in the artificial part at the end of the channel. In total, there were identified 13 epiphyte species belonging to 5 families on both banks. The Shannon-Wiener index amounts to 1.63 and Simpson index equates to 0.7. In natural channel, there was Shannon-Wiener index of 1.77 and Simpson index 0.75 and for the artificial part it was 0.82 and 0.46. The most common vascular epiphyte species was *Tillandsia bulbosa* belonging to *Bromeliaceae* family; there were exactly recorded 141 occurrences of this specie which amounts to more than a half of all the individual epiphytes examined in the research.

Keywords: mangrove flora, vascular epiphytes, species diversity, red mangroves, Greenfields, Nicaragua, hurricane Joan

1. Introduction

Mangroves are notable amphibious ecosystems with narrow habitat specificity. They are adapted to coping with harsh conditions in coastal brackish water. Owing to their ability to persist in extreme environmental conditions such as salinity, anoxic soil conditions or tidal inundation, mangroves form a very important transition between terrestrial and aquatic ecosystems.

The effect of tropical cyclones and mangrove roles in the process of tidal inundation is essential for the proper functioning of the mangrove ecosystems. Periodic destruction of Caribbean mangrove forests by cyclonic storms is proposed as one explanation for their characteristically low structural complexity as well as the lack of typical climax components in the vegetation [1]. Hurricane Joan toppled or snapped in southeastern Nicaragua 80% of the trees and completely destroyed 500,000 hectares (1,200,000 acres) of canopy [2]. Meteorological data are not available for the Greenfields but data from Bluefields 25 km away from there show records of sustained wind speeds of more than 200 km h^{-1}. Rainfall totalled more than 400 mm for the period between October 21 and 23, 1988 [3]. Therefore, Greefields was attacked seriously, and the mangrove vegetation was completely changed. One of the after effects of the hurricane attack was the start of mangrove regeneration which occurred naturally with only minor artificial intervention. However, the human interventions to the natural succession of the ecosystems were as a minor, at the same time, the end part of the water channel was constructed as a prolongation of the natural one. This meant in fact the most significant human influence on the new ecosystem development in relation to the hurricane Joan affects in the area of Greenfields.

Mangrove habitats have relatively low levels of species richness compared to other tropical habitats such as, for example, tropical rain forests [4]. In the American tropics, only 10 species of mangroves have been recognized [5]. In general, floristic diversity equates directly to structural diversity and function of mangroves. The same factors which limit species presence and growth also affect the functions and benefits of particular mangrove stands such as shoreline stabilization, primary production, and habitat for a range of dependent organisms [6]. Regardless of what is the level of species diversity, mangroves are characterized by many specific life strategies and adaptations. Mangrove uniqueness is derived from their pneumatophore arthropod assemblages together with aerial roots which are responsible for the root fixation mostly in estuarine water exposed in anaerobic sediments.

Epiphytes, as for trees, are generally distributed mostly on branches and trunks; however, minor occurrence was also noticed on the aerial roots. The bulk of the epiphytic biomass in the Pacific and many other areas is on branches and although studies of epiphytes on main trunks can be informative, and trunks are not necessarily representative of branches [7]. Vascular epiphytes are a conspicuous part of tropical rainforest canopies, representing a large fraction of plant biodiversity [8] and forest nutrient capital [9].

Many epiphytes also grow on mangrove trees: these include an assortment of creepers, orchids, ferns, and other plants, many of which cannot tolerate salt and therefore grow only high in the mangrove canopy [10]. In Ref. [11], there was mentioned that most vascular epiphytes are

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intolerant of salt; thus, one encounters only a limited range of species in the black mangal, while the range is relatively high in the canopy, and in areas transitional to adjacent terrestrial communities where the epiphytes are more characteristics. On the other hand, in Ref. [12], Benzing and Davidson wrote that halophytism has not been reported so far in epiphytes, but a certain level of salt tolerance has. This observation is further proved by Griffiths' note [13] with an example of *Tillandsia paucifolia* growing on *Rhizophora mangle* in South Florida which contained quantities of sodium up to several percent of shoot dry weight. Species of vascular plants associated with mangroves whether as climbers or true epiphytes are the same as those that occur in adjacent terrestrial communities. They are unable to tolerate high salt levels and therefore do not penetrate deeply into the mangrove habitat. There are, however, some apparent exceptions. Some bromeliads, for instance, have succulent leaves and seem to accumulate salt within their tissues. This suggests that they have evolved a degree of salt tolerance parallel to the mangrove trees on which they grow [14]. Benzing and Davidson [12] made a special study of the effects of salt on some epiphytic bromeliads that can occur in Mangroves in South Florida: despite the statement that they can be "dense" on mangroves, it is suggested that *Rhizophora mangle* supports few or no epiphytes because of an axenic bark response, even though seedlings of *Tillandsia pauciflora* can be experimentally germinated on its bark if well-watered.

More than half (about 55%) of the epiphytes live in Americas (New World), in part because neither *Bromeliaceae* nor *Cactaceae* ranges beyond this region except all terrestrials. The responsibility for this asymmetry lies with the heavily epiphytic pantropical families (e.g., *Araceae, Gesneriaceae,* and *Orchidaceae*), a majority of which experienced their robust arboreal radiations in Neotropic woodlands [15].

Atwood [16] estimated that 73% of all species of *Orchidaceae* family are epiphytic; however, considering the relative numbers of epiphytic to terrestrial species validly described since 1986, that percentage has risen. Some species are temporarily submerged during periodic flooding. Although there are no truly marine orchids, some species of *Brassavola, Myrmecophila, Dendrobium*, and other genera are epiphytic on mangroves in estuaries; many others have adapted to salt spray and soil salinity in established coastal dunes [17–19].

Epiphytes and epizoites generally have an adverse effect on the mangroves on which they grow because they block lenticels and impede gas exchange [20]. Mangrove forests occupy about 15 million hectares of tropical and subtropical coastline worldwide. Although they amount to only 1% of the total area of tropical forests, mangroves are highly productive ecosystems rich in biodiversity consisting of a wide variety of plant species that provide important habitats for a wealth of fauna and flora [21].

Within the mangrove environment, most plant species are relatively widely dispersed. However, major differences in the environmental connections also occur, particularly in relation to water, salt, nutrients and light, and it seems clear that the sharp boundaries between areas dominated by different species are often the direct result of competition [22].

It seems no known epiphyte species are exclusive to mangroves. Most bromeliads extend over large altitudinal ranges, nevertheless bromeliads are characteristic epiphytes of mangroves in

tropical and subtropical regions of Central and South America [22]. Common mangrove epiphytes include *Aechmea bracteata* and some species of genera Tillandsia [23].

There is a significant deficiency of information focused on the epiphytes diversity in mangrove forest. One of few studies focused on the assessment of the plant diversity was carried out in Malaysia, but in general, this assessment targets to the quantitative study of the mangrove vegetation primarily [24]. Another study has been done in more similar conditions in Brazil focusing on the diversity and distribution of epiphytic bromeliads in mangroves. This study aimed to assess the diversity of epiphytic bromeliads in a subtropical mangrove, evaluating their distribution and relationship with their host trees [25].

Presented study aimed to characterize and analyze vascular epiphytes species occurring in mangroves and their comparison on the example of Greenfields, East Nicaragua. The research was centered around a hypothesis which suggests that there is more significant level of species richness in natural mangrove channels in comparison with channel constructed artificially. To verify this thought, an observation was held which focused on the measurement of species diversity.

2. Materials and methods

2.1. Study site and plant survey

The study area is located in Nicaragua, South Caribbean Coast Autonomous Region approximately 2 km south of Kukra Hill town, 12°13′ N, 83°44′ W. The research area is a part of a private forest reservation owned by Gaudens Pfranger, which was established to support nature conservation and protection of endangered species. The area is connected to the sea by meandering water channel leading through the mangrove stands. These coastal ecosystems border an adjacent terrestrial biome—a tropical rain forest stand (see **Figure 1**).

Figure 1. Location of study area and map of the channel (Greenfields, Nicaragua).

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The entire forest stands including the mangrove forests in the east coast were destroyed by hurricane Joan in 1988. Although this event may thus appear catastrophic at the first sight, it in fact, triggered a system of regenerative mechanisms leading to necessary succession. Existing water channels surrounded by mangrove ecosystems were reserved and afterwards were established new artificial ones. The artificial channels were excavated in the original mangrove area and in fact opened the previous mangrove stands. Occurring secondary mangrove forests originated from previous mangrove stands was starting their redevelopment by the regeneration after the hurricane attack in 1988. Now they are dominated by red mangroves with prevailing *Rhizophora mangle* in species composition, as was also found in the present study. All the surveyed trees were determined as *Rhizophora mangle*. All mangroves are as was mentioned secondary forest stands, and current forest age is approximately of 30 years.

2.2. Methods

The research took place during a period from May 2015 to July 2015 and was conducted on the banks of a 2-km long mangrove channel in which first part (1200 m) is of natural origin, while the subsequent part (800 m) is artificial, as it was constructed shortly after the hurricane attack. The age of the mangrove stand was considered to be approximately the same (roughly 30 years), considering the concurrent natural regeneration after the hurricane attack and visual homogeneity of the forest stand (homogeneous DBH, mean value 12 cm and tree height, mean value 5.5 m). There was no undergrowth layer under the canopy. Considering that the forest stands on the banks of these two parts are in almost the same age, grow in similar environmental conditions, and the same habitat, it was concluded that the two channel parts could be compared to each other. The density of the forest stand was visually approximated (for mean approximately 30 mangrove stems per 100 m^2) and was recognized as similar as well as the distance between adjacent trees.

The average height of the mangrove forest stand was 5–6 m in total and spread over 22 ha. Due to the high density of the forest stand, the research was carried out according to the following design. A channel leading through the mangrove stand was divided into 20 sectors, each 100 m long. Two edge trees situated directly within the channel bank at the end of each sector were marked and surveyed: one tree on the right side of the channel and one tree on the left side. These trees were determined into the species and epiphytes occurring there were determined as well. Each mangrove tree was surveyed in an appropriate way. In the case of epiphyte occurrence on higher sprays, it was necessary to climb the tree for the purpose of determining the epiphyte species. Additionally, canoes were used in the process of determining the epiphyte species on the lower branches. This two-tree design was chosen due to the enormous number of epiphyte individuals that can be found in the majority of mangroves.

There were two parameters recorded and evaluated in the research: occurrence of epiphytic individuals and vascular epiphytes' diversity. The recorded values were matched with the channel sector where they had been collected, and therefore the parameters were studied at the background of the particular part's origin.

The diversity was analyzed using of two types of diversity indexes—Simpson index [26] and Shannon-Wiener index [27].

3. Results and discussion

Fourty trees were examined in the mangrove channel which was divided into twenty transect, each one hundred meters long. All these tree individuals were determined as *Rhizophora mangle*, which in agrees with conclusions of the available sources stating that more than 40% of the stand on the Nicaraguan Atlantic coasts is formed by red mangrove [28].

Consequently, there were two trees chosen at the end of each 100 m sector, that is, 20 trees on the right bank and 20 on the left bank in total, and the number of epiphytes found on these trees was recorded. Through this method, there were 273 vascular epiphytes found in total. The distribution of the vascular epiphyte individuals is presented in **Table 1**. As was mentioned above, epiphytes prefer habitats on branches rather than on trunks or aerial roots. In agreement with this observation, all the recorded vascular epiphytes occurred on the branches, while no vascular epiphytes were found on the mangroves' stems, which is in agreement with conclusions of Pike's study [7].

Furthermore, it was also observed that there were differences in epiphyte distribution depending on the origin of the channel. The data obtained in the first 1200 m long part of the mangrove channel show a significantly asymmetric distribution of vascular epiphytes (presented in **Table 2**) in comparison to the shorter (800 m) artificial part of the channel (presented in **Table 3**). An

No.	Species	Family	No. of individuals	Natural water channel		Artificial water channel	
				Left side	Right side	Left side	Right side
1	*Tillandsia bulbosa Hook.*	*Bromeliaceae*	141	39	51	36	15
2	*Tillandsia caput- medusacae E. Morren*	*Bromeliaceae*	28	18	10	-	-
3	*Catopsis berteroniana (Schult. & Schult. f.) Mez*	*Bromeliaceae*	26	-	8	15	3
4	*Oncidium* sp.	*Orchidaceae*	19	9	10	-	-
5	*Vriesea* sp.	*Bromeliaceae*	16	4	8	2	2
6	*Tillandsia utriculata L.*	*Bromeliaceae*	11	10	1	-	-
7	*Peperomia* sp.	*Piperaceae*	8	6	2	-	-
8	*Tillandsia anceps G. Lodd.*	*Bromeliaceae*	8	3	5	-	-
9	*Aechmea bracteata (Sw.) Griseb.*	*Bromeliaceae*	7	4	3	-	-
10	*Anthurium trinerve Miq.*	*Araceae*	4	2	2	-	-
11	*Encyclia alata (Bateman) Schltr.*	*Orchidaceae*	3	2	-	1	-
12	*Brassavola* sp.	*Orchidaceae*	1	-	1	-	-
13	*Polypodium fraxinifolium Jacq.*	*Polypodiaceae*	1	-	1	-	-

Table 1. The distribution of the vascular epiphyte individuals.

The natural mangrove channel												
Segment of the channel (km)	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2
Right bank (no. of epiphytic individuals)	0	8	2	6	0	1	1	9	23	0	7	32
Left bank (no. of epiphytic individuals)	0	6	7	17	5	18	1	4	7	1	5	39

Table 2. Distribution of vascular epiphyte in the natural part of the channel.

The artificial mangrove channel							
Segment of the channel (km)	1.3	1.4	1.5	1.6	1.7	1.8	1.9
Right bank (no. of epiphytic individuals)	6	0	0	0	0	0	35
Left bank (no. of epiphytic individuals)	8	1	0	0	0	0	6

Table 3. Distribution of vascular epiphyte in the natural part of the channel.

amount of 73% of all vascular epiphytes were found in the natural channel. However, this is a quit high value, it would be unwise to base any conclusion on this number, as it is necessary to take into consideration the asymmetry between lengths of the natural and the artificial parts of the channel. Therefore, the comparison of biodiversity was based on the following indexes in order to prevent the difference in length from influencing the results.

As the research also focused on epiphyte species diversity, the observed epiphytes were determined into species and families and were evaluated according to their localization within the channel parts. There were 13 epiphytic species and 5 families found in the whole mangrove channel (**Table 1**). The most abundant occurrence was observed for *Tillandsia bulbosa*, *Bromeliaceae* —exactly 141 individuals—which is a number representing more than a half of all the epiphytes that were found here, more precisely 52% (see **Table 1**). The survey led to the discovery that the vast majority of occurrences belong to family *Bromeliaceae*. Seven species belonging into *Bromeliaceae* family were observed in the mangroves, namely, *Tillandsia bulbosa* Hook., *Tillandsia caput-medusae* E. Morren, *Catopsis berteroniana* (Schult. & Schult. f.) Mez, *Oncidium* sp., *Vriesea* sp., *Tillandsia utriculata* L., *Peperomia* sp., *Tillandsia anceps* G. Lodd., *Aechmea bracteata* (Sw.) Griseb., *Anthurium trinerve* Miq., *Encyclia alata* (Bateman) Schltr., *Brassavola* sp., and *Polypodium fraxinifolium* Jacq (**Table 1**). *Orchidaceae* was detected as the family with the second most abundant occurrence and was represented by genera *Oncidium*, *Brassavola,* and *Encyclia alata (Bateman) Schltr.* Epiphytes belongs to family *Orchidaceae* were not found in artificial mangrove channel with the exception of one individual *Encyclia alata (Bateman) Schltr. (***Table 1***).* All the plant species were determined according to the taxonomy used in Flora de Nicaragua [29].

To the comparison of two parts of the mangrove channel in consideration of their origin was to detect essential difference between natural and artificial channel. The species distribution as well as the frequency of occurrence was lower in the artificial channel. There were only four vascular epiphytes species determined in the artificial channel: *Tillandsia bulbosa Hook., Catopsis berteroniana (Schult.* & *Schult. f.), Mez, Vriesea sp.*, and *Encyclia alata (Bateman) Schltr.*

	Simpson index	Shannon-Wiener index
Mangrove channel total (2 km)	0.7	1.63
Natural channel (1.2 km)	0.75	1.77
Artificial channel (0.8 km)	0.46	0.82

Table 4. Comparison of biodiversity indexes results.

For the comparison of the two channel parts, there were two types of indexes used to determine the biodiversity—Simpson and Shannon-Wiener indexes (see **Table 4**). Diversity indices provide more information about community composition than simply species richness.

Based on the collected data, it was found that the values of Simpson and Shannon-Wiener indexes differ depending on the origin of the mangrove channel where the data were collected. The results showed that the epiphytes were abundant on the surveyed mangrove trees in both of natural and artificial channels. The Shannon-Wiener index equals to 0.7 and Simpson index equates to 1.63 (**Table 4**).

In the natural channel, the Shannon-Wiener index was 1.77 and Simpson index 0.75, while for the artificial part, it was 0.82 and 0.46 (**Table 4**). Comparing Simpson index 0.75 for the natural channel and 0.46 for the artificial channel could indicate higher value of evenness of natural mangrove channel (1 is a maximum value—being complete evenness). In case of Shannon-Wiener index, the relative abundances of different species were also taken into account. There should be noticed as well as in the first index higher value in the case of natural channel 1.77 a 0.82. Considerably small value of Shannon-Wiener index could point out the small amount of species, H decreases dramatically as the number of species decreases.

All researched epiphytes were present on the mangrove branches. This fact can be caused by the high level of tidal inundation in a narrow water channel, which does not allow to colonize the basal part of trees or also by the effortless colonization of horizontal parts of mangroves.

4. Conclusion

Based on the results presented above, the following statements can be summarized:

- The diversity of epiphytic communities within the study area is taking into account the results of used indexes relatively high where the diversity of epiphytes located in the natural part of the channel is approximately two times higher than in case of artificial one as was expected definitely. This is very important finding especially when the mangrove ecosystems are generally known as the ecosystems with relatively low species richness [4].
- The epiphytic communities located in the natural channel mangrove forests served (and probably still serves) as a refugium for the new developing epiphytic communities in the artificial part (no epiphytic species different than those which originated in the natural part was found there).

- Even after 30 years of developing the new epiphytic communities in mangrove forests surrounding the artificial part of the channel the diversity is not on the level of the natural one there; however, the abiotic determining abiotic conditions (esp. light conditions) are seemed the same.
- After 30 years of development, the current status of new epiphytic communities located in the mangroves of artificially constructed water channel are on the level of approximately 50% (60% as for Simpson index and 46% as for Shannon-Wiener index) of the fully developed mature epiphytic communities of the mangroves located by the natural one. This fact can be highlighted as an important in the consequences of generally accepted opinion of fast forest community development in tropic areas.
- The differences in the epiphytes distribution are mainly determined by the light conditions on the "stand walls" (i.e., vertical edges) which are in case of natural channel long time opened contrary to the case of artificial channel opened only for 30 years. The main result which authors want to point out is that even after this period the new epiphyte community (in artificial channel) still does not reach the diversity level of original natural one (natural channel).

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Chapter 4

Cameroon Mangrove Forest Ecosystem: Ecological and Environmental Dimensions

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Abstract

This study examined the ecological effects of local scale mangrove exploitation through surveys, empirical field experiments, modeling and questionnaires. The ecosystem "health" was assessed by parameterising a mass-balance model (ECOPATH with ECOSIM). The results suggest that forest exploitation affects mangrove forest structure and two-third of the canopy gaps were caused by human activities. Regeneration was affected, and more seedlings were recorded in canopy gaps compared to closed canopy areas. A total of 1358 crabs were collected to assess it population structure, 770 females (56.7%) and 588 males (43.3%), belonging to 13 species. The family Sesarmidae contains 5 species (38.5%), while Grapsidae 2 species (30.8%), Ocypodidae 1 species (15.4%) and to each of the families Portunidae and Gecarcinidae (7.7% each). *Uca tangeri* (Ocypodidae) and *Goniopsis pelii* (Grapsidae) were the two dominant species, constituting 44.1 and 21.9%, respectively, of the total sampled crabs. Propagules predation was a major source of mortality for mangrove. An average of 65.9% of the propagules was predated and most were found to be non-viable. The Ecopath analysis suggests that the Cameroon mangrove ecosystem is relatively healthy and moderately mature. This analysis allowed a reasonable model representation of the Cameroon mangrove system, as the model viability was determined by using the sensitive analysis function.

Keywords: crabs, West Africa, anthropogenic pressure, canopy gaps, propoagule recruitment, ecopath model

1. Introduction

Mangrove forests are one of the unique features of intertidal zones throughout tropical and subtropical regions of the world and cover an area of approximately 15 million hectares

worldwide [1]. In recent years, these ecosystems have been extensively studied. The basic botany of mangrove has been described by Tomlinson [2]. An overview of mangrove ecology, distribution and biology has been described in [3–5].

Cameroon mangrove forests are found east and west of Mount Cameroon with smaller formations dispersed along the estuaries of the other rivers. The main stands of trees are the Rio-del-Rey and the Cameroon Estuary, respectively (**Figure 1**). The latter covers an estimated surface area of about 75,000 ha (approximately 50 km of coastline), while the former covers an estimated surface area of 175,000 ha (approximately 60 km of coastline from the River Sanaga to the Bimbia estuary).

The floristic composition of Cameroon mangrove is characteristic of the Atlantic mangroves of West Africa. It is dominated by *Rhizophora* and comprises mostly three species, *R. mangle*, *R. harrisonii* and *R. racemosa* [3]. The pioneer species *Rhizophora racemosa* constitute 90–95% of the mangrove area [6]. Other mangrove species include *Avicennia germinans*, which occurs on the higher elevation fibrous clay or sandier soils, *Laguncularia racemosa* and *Conocarpus erectus*, *Acrostichum aureum*, *Pandanus candelabrum* and the introduced *Nypa fruticans* [3, 6].

Human activities in coastal areas such as physical alteration of the habitat, over-exploitation of the resources and pollution cause significant pressure on the environment. These pressures have increased steadily as the human population increases. Coastal areas, including mangroves, are characterised by high productivity creating important nurseries for offshore fish,

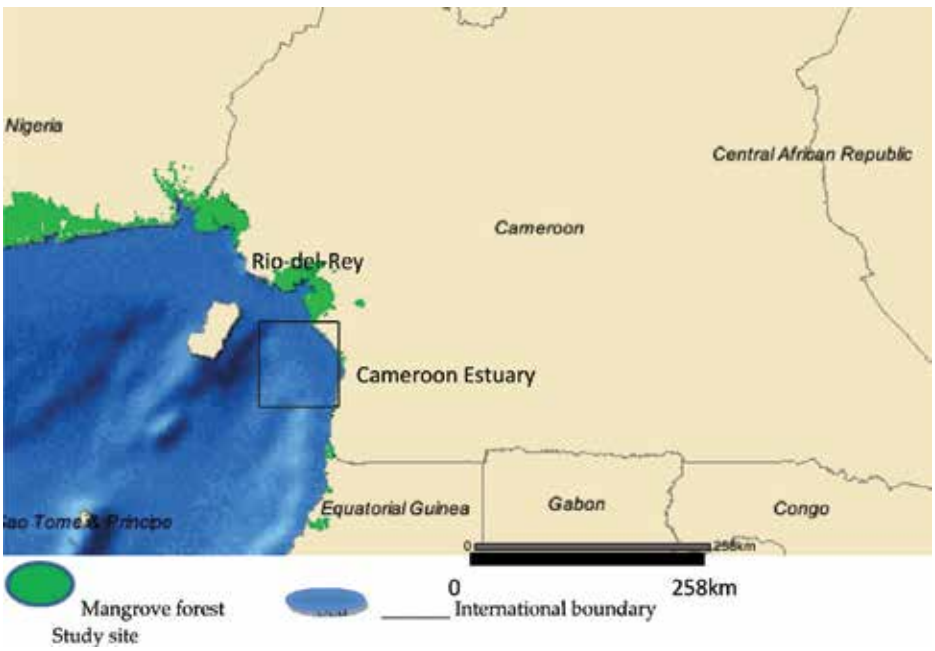

Figure 1. The Cameroon coastline showing mangrove forest locations (Adapted from UNEP –WCMC, 2005).

but they are among the most exploited ecosystems [7]. Frequent, but low intensity, smallscale anthropogenic disturbance, such as firewood extraction, may strongly affect forest structure and species composition in tropical forests [8, 9].

Mangrove crabs are probably the most prominent and significant biotic components of mangrove ecosystems in terms of species richness and their ecological engineering role [10–12]. Their distribution is influenced by biotic and abiotic factors, such as water salinity, temperature, food availability and preference, sediment properties, vegetation type, interspecific competition and predation [13, 14]. The most common crabs in mangroves are either Fiddler crabs (Family Ocypodidae, genus *Uca*) or Sesarmid crabs (Family Grapsidae, subfamily Sesarmidae) [15].

The ecological role of crabs in terms of the functioning of the mangrove ecosystem is thought to be significant [16]. Energy assimilated by crabs plays a significant role in nutrient recycling [17], crabs aerate the soil by burrowing [18], increase nutrient content by burying organic matter, decrease toxic sulphide and ammonium concentrations within the sediment [19], reduce pore water salinity by flushing water through burrows [20] and create a microhabitat for other fauna [21]. Despite the vital role played by crabs in the mangrove ecosystem, data on crabs in some areas remain patchy in Cameroon.

Several species of mangrove macrofauna are known to consume plant materials, including crabs [22–24]. Among these, crabs are thought to be major consumers and to be a key source of leaf and seedling mortality in mangroves [25].

Ecosystem health is a concept that sets new goals for environmental management, and its definition and assessment methods are still being perfected [26]. According to Costanza [27], ecosystem health represents a desired endpoint of environmental management. The advances in this concept are evident from the fact that it is now recognised that a reflexive relationship exists between human systems and natural ecosystems in that the health of one is dependent on the health of the other [28]. According to Rapport et al. [29], healthy ecosystems must not only be ecologically sound, but must also be economically viable and able to sustain healthy human communities.

There are different approaches for assessing ecosystem health, and one is ecological modelling, used as a tool to describe complex system-level metrics related to health. Specifically, I use the mass balance model Ecopath [30]. This model represents trophic networks that connect species (functional groups) in a system, and the magnitude of flows of materials and higher-level indices within the different functional groups can be calculated from the complex network, which can in turn be related to ecosystem health.

1.1. Research framework and objectives

The research framework in which the present study fits involves a number of separate sections, each of which constitutes a piece of the entire study. The discussion links all of these sections, specifically, the objectives are to assess: (a) the mangrove use and structural effects of local-level cutting of Cameroon mangrove forests, (b) the distribution, diversity and abundance

of mangrove crabs in Cameroon mangroves, (c) the ecological effect of mangrove crab herbivore feeding preferences in Cameroon mangrove forests, (d) to examine mangrove community function in terms of trophic linkages, in which a mass-balance model (ECOPATH with ECOSIM) is parameterised and explored.

2. Methodology

To assess mangrove, use and structural effects of local–level cutting of Cameroon mangrove forests data of forest characteristics were collected. I employed the quadrat/census plot method [12].

To assess the floristic composition and stand structure, data were collected on tree species composition, diameter at breast height (dbh), tree height, seedlings, canopy cover, gaps, gap size, stumps and snag (dead stems). In each plot, every tree was numbered, marked and measured (>1.0 m tall) and seedlings (<1.0 m) recorded [13]. The diameter at breast height (dbh) of each tree stem was measured at 1.3 m or above the highest prop root, following [12]. Tree height was measured using marked bamboo poles and clinometers. Evidence of human cutting was also recorded. Data for local uses were collected in villages in the study area, selection of the study site was on the basis of their accessibility, cooperation and background knowledge of village communities utilising mangrove forest. They are assumed representative of the larger mangrove community.

Data were collected by focus group discussion. Five group meetings were carried out per village, first with the chief and the village councillors, followed by three separate meetings with elderly fishermen and one meeting with the elderly women. Data collection was through in-depth interviews and systematic filling out of questionnaires and direct observation of everyday life during village visits. Answering of the questions was done through participatory rapid appraisal method (PRA). The participants were allowed to discuss among themselves and every person's opinion was relevant, until they reached a consensus. In some circumstances, they were given 20 stones to distribute them into categories, to reflect their views.

The questionnaire was mainly structured, with a few semi-structured questions. Elderly residents with a long residency history were chosen in order to explore perceptions of mangrove forest status. More males were interviewed because of the gender bias that exists in the division of labour in this region. Men alone are involved in fishing and harvesting wood, while women assist in wood transportation as well as fish smoking.

Increased participation and some degree of reliability of the interviewee to provide information was enhanced as follows:

1. Contact with the chief of each village before starting data collection;
2. High degree of socialisation with the interviewee during sampling;
3. The use of a field guard (interpreter).

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The approach of administering the questionnaires was made flexible enough to accommodate questions and answers, with the aim of making the process more interactive, friendly and to obtain as much information as possible. Interviews were conducted in English, French and the local dialect, but the filling out the answers to the questions was done in English. The information gathered allowed an evaluation of the uses of the mangrove vegetation and ecosystem, an assessment of the mangrove area and the socio-economic profile of local communities.

Direct observation alone was carried out where a group refused to answer some questions or tried to give deliberately false answers based on my personal judgement and the opinion of the local interpreter.

To assess the distribution, diversity and abundance of mangrove crabs, data were collected at low tide when crabs are more active. Data on crab species present were recorded using 10 × 42 binoculars. Subsequently, crab species were collected by hand for 15–30 min. On approaching the crabs, it immediately retreated to their burrows or took refuge. To offset any bias in favour of collecting slow-moving species, more time and effort was allocated to catching the larger, faster-moving crabs. This may introduce another bias, but previous experience has shown that this gives a more representative overall assessment of species composition [31]. A 1-m^2 quadrat was placed randomly and excavated to a depth of 30 cm and all crabs collected. This excavation method is thought to offer a more reliable estimate of crab density [32]. The crabs were sedated in iced water for a few minutes, washed and stored in 70% alcohol, later identified, weighed (wet weight) and carapace width measured. All the specimens collected were stored carefully to ensure that no appendages were lost due to stress, and identified with the aid of field keys [33–35]. To assess the ecological considerations of mangrove crab herbivore feeding preferences, the level of damage to and preference for mangrove leaves and propagules was studied. Propagule predation was studied by tethered propagules independently with a 50-cm length of nylon twine, the other end of which was tied to a piece of wood on the forest floor. The propagules were spaced far enough apart so that the tethers could not get tangled. The length of each propagule was measured, and propagules individually tagged. The propagules were checked from a distance using binoculars over a 6-h period, after which they were checked once a day for 1 week. All observations were carried out during low tide when the crabs are very active.

Predation status was recorded following [22]: (1) when the epicotyl was eaten (2) when 50% of the hypocotyl was lost (3) when the propagule was pulled into the burrow of crab. Each propagule was classified as viable (capable of growth, i.e. ≤50% of propagule eaten), non-viable (incapable of growth, i.e. >50% of propagule eaten) and missing (when lost). Signs of snail predation were also recorded.

Leaf predation for all the three mangrove species in Cameroon (*Laguncularia*, *Avicennia* and *Rhizophora*). Fresh and senescent leaves were gathered, fresh leaves by harvesting from trees, whilst senescent leaves (yellow and easily abscised) were either picked from the forest floor or harvested from the tree. Ten replicate leaves (fresh and senescent) of each species were tethered with a nylon string 50 cm in length with the other end tied to approximately

5 m of string and tagged. The leaves were tied randomly and far apart to avoid tangling. The leaf surface was measured by tracing around the edge on graph paper. Leaves were checked after 24 h, damage recorded, and it was noted whether the leaves were found on the surface or in a crab burrow. Leaves that were in a burrow were removed by gently pulling on the attached string.

Additional data on leaf predation were gathered from crabs predating within the canopy. Crabs were seen residing on tree trunks, branches and the prop roots. They were observed climbing mangrove trees, usually early in the morning to feed on leaves and by midday they all moved back down, moving up the tree again early in the evening and down again by late evening. An average of 5 crabs was found on a single tree. Young trees (1.5–2 m tall, dbh 2.3–5 cm) of each species (*Laguncularia*, *Avicennia* and *Rhizophora*) were observed from a close distance for about 5 hours and crab feeding activities and presence of crab damage recorded. The percentage of the leaves with damage was used to calculate the damaged leaves per plant, and these values were averaged for each species within the sample area.

To evaluate ecosystem structure, its function and organisation, I applied the Ecopath with Ecosim model (www.ecopath.org) to the Cameroon mangrove estuarine system. Selected ecosystem indicators that could be used to monitor ecosystem status or health were analysed using a set of ecosystem goal functions, representative of Odum's attributes of ecosystem maturity [36]. The attributes represent three different aspects of ecosystem development: (1) complexity in community structure, (2) community energetics and, (3) overall community homeostasis.

The steps and governing principles of the general approach of Ecopath and Ecosim have been described in detail in [30, 37], and can be accessed at http://www.ecopath.org. The detail modelling approach (Ecopath with Ecosim) can be accessed at [35, 36, 38, 39].

For this study, the selection of functional groups to represent the Cameroon mangrove food web was a product of a collaborative process. A number of stakeholders and experts (including myself) participated in the discussion to produce functional groups based on the following criteria:

- The species must be representative and abundant
- The species must be relevant to the overall aims of the study
- There must be some relevant data for those species (although not necessarily for the Cameroon mangrove forest).

In the final iteration, based on these criteria, 26 functional groups were selected for this model (**Table 1**): 13 fishes, 3 kinds of birds (11 species), groupings of 3 crabs, mangroves, phytoplankton, zooplankton, detritus, benthos, shrimps and insects. All the species within a functional group have ecological similarities, defined by similarities in diet, production and consumption rates, life history, and habitat associations, but also sometimes on value-driven criteria, such as commercial status or importance for subsistence users. Because of the nature of the Cameroon mangrove forest, where mangrove wood products are used extensively as source of energy to smoke fish, it is important therefore to consider the mangrove forest as a

primary producer and make the link with fishing pressure. The functional group benthos was included because of its contribution to the diets of other groups.

The input parameters for each group were: the biomass (B), the production/biomass ratio (P/B), the consumption/biomass ratio (Q/B) and ecotrophic efficiency (EE). Input parameters were estimated from the field or extracted from the literature, either from studies done within a similar mangrove ecosystem (in Central Atlantic region) or on the West Africa continental shelf. The diet matrix was constructed by designating the percentage of each prey that occurs in each predator's diet. Diets were derived mostly from the scientific literature, except for crab's groups

1.	Mangrove	*Rhizophora* spp., *Avicennia* spp., *Laguncularia racemosa*
2.	Phytoplankton	Diatoms, dinoflagellates and others
3.	Zooplankton	Neritic copepods, bivalve larvae, ostracods, mysids, nauplii, fish eggs and others
4.	Shrimps	*Peneaus* spp., *Parapenaeopsis atlantica*, *Penaeus notiali*
5.	Mangrove crabs	Sesarmid species
6.	Fiddler crabs	*Uca* species
7.	Other crabs	*Scylla serrata*, *Cardisoma carnifex* and others
8.	*Ilisha africana*	
9.	*Pseudotolithus* spp.	*P. senegalensis*, *P. typus* and *P. elongates*
10.	*Pentanemus quinquarius*	
11.	*Sardinella maderensis*	
12.	*Brachydeuterus auritus*	
13.	*Dreprane africana*	
14.	*Arius* spp.	*A. heudelotii* and *A. parkii*
15.	*Pomadasys jubelini*	
16.	*Galeoides decadactyl*	
17.	*Raja miraletus*	
18.	*Lutjanus* spp.	*L. goreensis* and *L. dentatus*
19.	*Mugil curema*	
20.	*Caranx* spp.	*C. senegallus*, *C. hippo* and *C. senegalensis*
21.	Shorebirds	Finfoot (*Podica senegalensis*), Avocet (*Recutrvirostra avosetta*), White-footed plover (*Charadrius marginatus*), Common Green shank (*Tringa nebularia*), Common sandpiper (*Actitis hypoleucos*).
22.	Birds of prey	Black kite (*Milvus migrans*), Fish eagle (*Haliaeetus vocifer*), Palm nut vulture (*Gypohierax angolensis*), Harrier hawk (*Polyboriodes typhus*)
23.	Insectivorous birds	Grey flycatcher (*Musicapa cassini*), Pied crow (*Corvus albus*)
24.	Benthos	
25.	Insects	
26.	Detritus	Organic matters and associated like bacteria

Table 1. Descriptions of some functional groups of the mangrove ecosystem in Cameroon.

	Prey	Predator																						
		3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
1	Mangrove	—	—	0.6	0.5	0.9	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	0.9	0.1
2	Phytoplankton	0.8	0.1	0.1	—	—	0.3	—	—	0.4	0.2	0.3	0.2	—	—	—	—	0.8	—	—	—	—	—	0.5
3	Zooplankton	—	0.4	—	0.05	—	0.3	0.4	0.1	0.2	0.4	0.3	0.2	0.6	0.2	0.05	0.1	—	0.6	—	—	0.05	—	—
4	Shrimps	—	—	—	0.05	—	—	—	—	—	—	—	—	—	0.1	0.05	0.2	—	—	—	—	0.05	—	—
5	Mangrove crabs (Sesarmidae)	—	—	—	—	—	—	—	—	—	—	—	0.1	—	0.1	0.05	0.1	—	—	—	—	—	—	—
6	Fiddler crabs (*Uca*)	—	—	—	—	—	—	—	—	—	—	—	0.1	—	0.1	0.05	0.1	—	—	—	—	—	—	—
7	Other crabs	—	—	—	—	—	—	—	—	—	—	—	0.1	—	0.1	0.05	0.1	—	—	0.1	—	—	—	—
8	*Ilisha africana*	—	—	—	0.05	—	—	0.3	0.05	—	—	—	—	—	—	0.1	0.05	—	—	—	0.1	—	—	—
9	*Pseudotolithus* spp.	—	—	—	0.05	—	—		0.05	—	—	—	—	—	—	0.1	—	—	—	—	0.1	—	—	—
10	*Pentanemus quinquarius*	—	—	—	—	—	—			—	—	—	—	0.05	—	0.1	—	—	—	—	0.1	—	—	—
11	*Sardinella maderensis*	—	—	—	—	—	—	0.2	0.1	—	—	—	—	—	—	0.1	0.05	—	—	—	0.1	—	—	—
12	*Brachydeuterus auritus*	—	—	—	—	—	—	—		—	—	—	—	—	—	0.1	—	—	—	—	0.1	—	—	—
13	*Dreprane africana*	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	0.1	—	—	—	—	0.1	—	—	—
14	*Arius* spp.	—	—	—	—	—	—	—	0.05	—	—	—	—	0.05	—	0.1	—	—	—	—	0.1	—	—	—
15	*Pomadasys jubelini*	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
16	*Galeoides decadactylus*	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
17	*Raja Miraletus*	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
18	*Lutjanus* spp.	—	—	—	—	—	—	—	0.05	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
19	*Mugil curema*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.05	—	—	—
20	*Caranx* spp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
21	Shorebirds	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
22	Birds of prey	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

	Prey	Predator																						
		3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**
23	Insectivorous birds	—	—	—	—	—	—	—	—	—			—	—	—	—	—	—	—	—	—	—	—	—
24	Benthos	—	0.1	0.1	0.2	—	0.1	0.1	0.4	—	0.1	0.4	0.3	0.1	0.4	0.05	0.3	—	0.4	0.9	—	—	—	—
25	Insects	—	—	—	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	0.05	0.9	—	—
26	Detritus	0.2	0.4	0.2	0.1	0.1	0.3	—	—	0.2	0.3	—	—	0.2	—	—	—	0.2	—	—	—	—	0.1	0.4
		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2. Diet composition.

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where stomach content analysis was carried out. The degree of confidence, that the parameters are appropriate for the Cameroon is expressed through the data pedigree coding option.

Diet information for crabs was obtained directly from stomach content analysis Literature data were used for all other functional groups (**Table 2**).

2.1. Balancing the model

After entering all the basic inputs into the Ecopath model, the first step is to check if the outputs are sensible, in other words, whether the biomasses of all groups can be supported by their consumption rates and the productivities of their prey. Detailed on how to balance the model can be accessed at [36, 37] in the Ecopath manual. Once the model was balanced, various ecosystem attributes were evaluated, these attributes include those given in [36, 40], allowing inferences to be drawn about the health of the ecosystem.

3. Results

3.1. Mangrove use and structural effects of local-level cutting

A total of 3167 individual trees, 423 stumps and 103 snags were recorded. *Rhizophora* (Red mangrove) was the dominant species (83.6%) followed by *Avicennia* (Black mangrove) at 9.1% and *Laguncularia* (White mangrove) at (7.1%).

3.2. Cameroon mangrove forest structure

Mangrove forests differed structurally, due to a combination of anthropogenic and natural factors. The mean tree density and seedling density, the mean diameter at breast height (dbh) and basal areas are presented in (**Table 3**).

3.3. Canopy gaps

A total of 257 gaps were recorded during the study. Human influence was responsible for most of the gaps created (**Table 4**). An average gap size of 3.1 m^2 was recorded. The average gap density of 27.4 was recorded overall. The relationship between seedlings and canopy was examined as an alternative way to estimate the effect of exploiting forest on mangrove

Characteristics	Average
Tree density (n/100 m^2)	16.0 (20.2)
Diameter at breast height (dbh) of stem (cm)	23.8 (19.7)
Stem basal area (m^2/ha)	60.1 (29.8)
Gap size (m^2)	0.32 (0.3)
Seedling density (n/100 m^2)	23.5(40.1)

Table 3. Summary of selected ecological characteristics with mean values and standard deviation (in parentheses).

	Average
Canopy gap density (n/100 m²)	27.4
Canopy density (n/100 m²)	72.3
Gap size (m²)	3.1
Human cause (%)	66.3
Non-human cause (%)	33.6

Table 4. Canopy gaps.

regeneration. Significantly more seedlings were observed in canopy gaps compared to closed canopy areas (T = 3.5, P = 0.008). *Rhizophora* seedlings were more abundant in canopy gap than in closed canopy areas (T = 2.4, P = 0.04), whilst *Avicennia* and *Laguncularia* were not (**Table 5**).

3.3.1. Forest species composition

The size-frequency distributions of all mangrove species are represented in **Figure 2**. All three-species showed a higher concentration of stems in small size classes (<25 cm). Compared to *Rhizophora*, *Avicennia* is completely absent from size classes greater than 95 cm, and *Laguncularia* from classes more than >25 cm.

3.4. Local uses of mangrove wood

All mangrove species are used by the villagers for different purposes. The principal uses are sources for fuelwood and poles for construction (**Figure 3**) and the most preferred species are Rhizophora species (*Rhizophora racemosa*, *Rhizophora harrisonii*) and *Avicennia germinans*. They are preferred because of their slow burning properties, resilience and availability. One of the most interesting properties of mangrove wood is that it burns well when fresh, so the process of drying the wood is not necessary. This property contributes to make it a favourable choice of fuel wood. All the tree parts (branches, stem and roots) are used as fuelwood, mostly for fish smoking.

Poles for construction are used mostly for building houses, bridges, fences and fish smoking barns (**Table 6**). The preferred species for construction is *Avicennia germinans*; because of it resilience property and mostly tree stem of different sizes are used.

3.5. Distribution, diversity and abundance of mangrove crabs

A total of 1358 crabs were collected over the study period, 770 females (56.7%) and 588 males (43.3%) (**Table 7**) belonging to 13 species. Of the 13 species, 5 belonged to the family Sesarmidae (38.5%), 4 species to the family Grapsidae (30.8%), 2 species to the family Ocypodidae (15.4%) and 1 species to each of the families Portunidae and Gecarcinidae (7.7% each). *Uca tangeri* (Ocypodidae) and *Goniopsis pelii* (Grapsidae) were the two-dominant species, constituting 44.1 and 21.9% respectively of the total sampled crabs. *Uca tangeri* dominated the mudflat in zone four, whilst *Goniopsis pelii* dominated zone one (disturbed young forest).

Species	Canopy gap	Closed canopy	t-values	P-values
Rhizophora	863	375	2.4	0.04
Laguncularia	220	59	1.2	0.25
Avicennia	161	93	1.2	0.16
Total	1244	527	3.5	0.01

Table 5. Seedling abundance of different mangrove species in open and closed canopies.

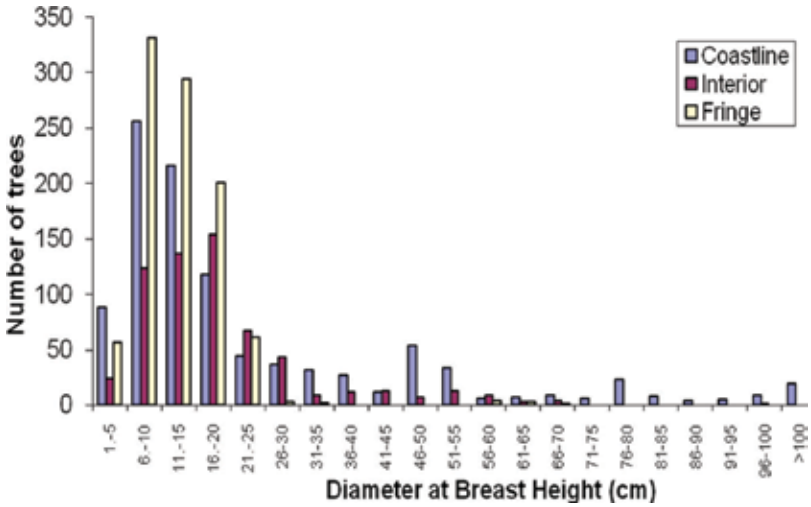

Figure 2. Size-frequency distribution of (dbh) of *Rhizophora, Avicennia* and *Laguncularia* species.

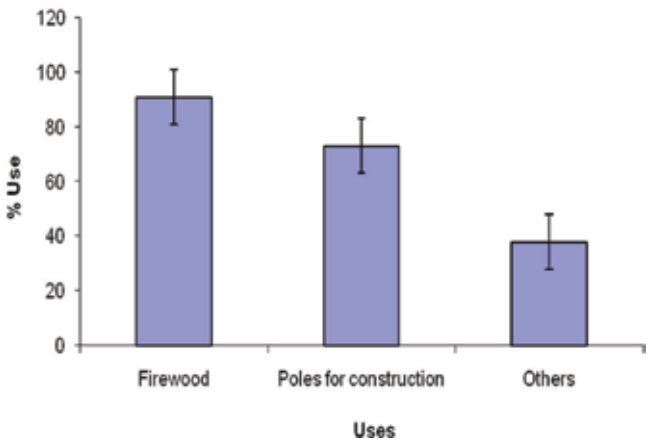

Figure 3. Different uses of mangrove wood as revealed by local users.

The size range for *Uca tangeri* was 0.1–5.5 cm, *Goniopsis pelii* 0.2–7.8 cm and *Sesarma* species 0.2–5.6 cm carapace width (CW) (**Figure 4a–c**). The size frequency distribution differed from normality, for *Goniopsis pelii* (KS = 2.902, P = 0001), *Uca tangeri* (KS = 2.56, P = 0.0001),

Tree	Local names	Uses
Avicennia	Black matanda	Furniture, fencing poles, firewood, construction poles, canoe anchors, poles for building bridges and fish smoking barns, paddles, fishing traps, roof supports, axe handles and resting beds
Rhizophora	Red matanda	Firewood, poles for building bridges and fish smoking barns, construction poles, fencing poles, resting bed, canoe anchors, fishing traps, and paddles
Laguncularia racemosa	White matanda	Firewood, poles for fences and furniture

Table 6. Local uses of mangrove trees in the sampled villages.

Family	Species	Female	Male	Total
Portunidae	*Portunus validus* (*Neptunus alidus*)	2	2	4
Sesarmidae	*Metagrapsus curvatus*	24	20	44
	Sesarma (*Perisesarma*) *huzardi*	28	17	45
	Sesarma (*Chiromantes*) *elegans*	21	9	30
	Sesarma (*Perisesarma*) *alberti*	17	8	25
	Sesarmine species	27	22	49
Gecarcinidae	*Cardisoma* species	39	28	67
Grapsidae	*Goniopsis pelii* (*G. cruentata*)	171	167	338
	Grapsus grapsus	49	60	109
	Pachygrapsus transversus	7	21	28
	Pachygrapsus spp.	8	4	12
Ocypodidae	*Ocypode africana*	50	20	70
	Uca tangeri	322	212	534
	Total	770	588	1358

Table 7. Number of crabs collected.

and *Sesarma* species (KS = 1.59, P = 0.013). All three of the most abundant species were better described by a bimodal rather than a unimodal distribution (**Figure 4a–c**). *Goniopsis pelii* shows a bimodal distribution with highest modal size ranging from 2 to 2.25 cm carapace width and a probable second mode at 6 cm, 2–2.3 cm carapace width for *Sesarma* species and *Uca tangeri* shows a bimodal distribution with highest modal sizes ranging from 1.5 to 1.75, 2 to 2.3, and 2 to 2.25 cm carapace width.

3.6. Relationship between carapace width and wet weight for *Uca tangeri* (Ocypodidae) and *Goniopsis pelii* (Grapsidae)

Uca tangeri (Ocypodidae) and *Goniopsis pelii* (Grapsidae) were the most abundant crabs associated with Cameroon mangroves. Estimating their biomass is essential in order to evaluate their importance to the system. Carapace width and wet weight were therefore determined for *Uca tangeri* and *Goniopsis pelii*. The relationships are as follows:

Goniopsis pelii WW biomass = 1.2588 (CW) $^{1.9095}$ (R^2 = 0.58) and *Uca tangeri* WW biomass = 1.1209(CW) $^{2.0917}$ (R^2 = 0.6619) (**Figure 5**).

3.7. Ecological effect of mangrove crab herbivore feeding preferences

Propagule predation by crabs occurred in all of the mangrove species ranging from 61.6 to 69.1% (**Table 8**). The effect of crab predation on propagules did not differ among mangrove species. The majority of propagules were found to be non-viable after predation and some were lost by being washed away by high tide (**Figure 6**). There was a significant difference between the number of non-viable and viable propagule (T = 2.13, df = 4, P = 0.002) with majority being non-viable. Some propagules were predated by gastropods, but the extent of this was minimal.

The percentage of leaves consumed by crabs varied among mangrove species (**Figure 6a**). *Rhizophora* species was the most consumed and *Avicennia* was the least, although this was not significant between species (ANOVA, F = 2.3, P = 0.24). Senescent leaves were preferred more than fresh leaves for all species (**Figure 7a**), and there was a significant difference in the percentage consumed of fresh and senescent leaves (T = 4.3, df = 2, P = 0.02). The majority of leaves

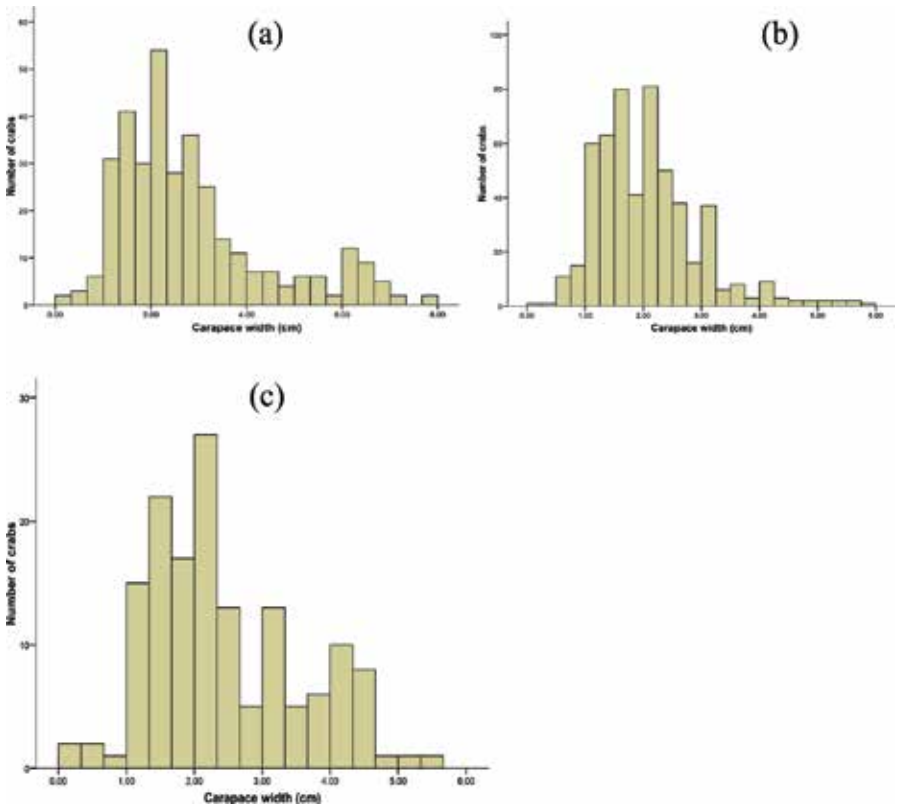

Figure 4. (a) Size (carapace width) frequency distribution of *Goniopsis pelii*, all zones combined. (b) Size (carapace width) frequency distribution of *Uca tangeri*, all zones combined. (c) Size (carapace width) frequency distribution of *Sesarma* species, all zones combined.

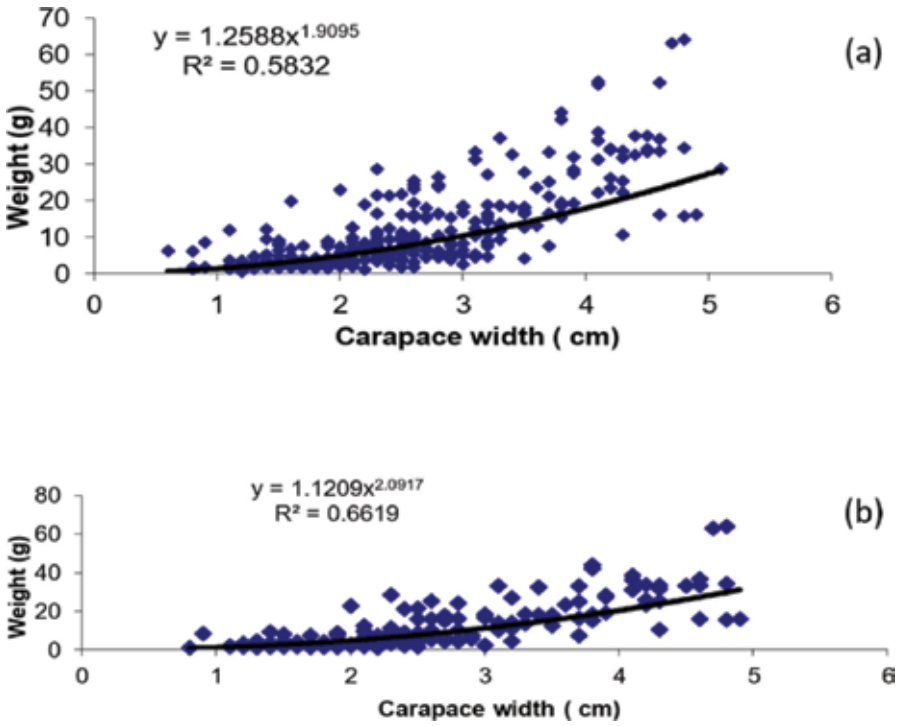

Figure 5. Relationship between carapace width and weight for (a) *Uca tangeri* (b) *Goniopsis pelii*.

Species	Average (%)
Rhizophora racemosa	69.8
Rhizophora mangle	66.3
Rhizophora harrisonii	61.6

Table 8. Summary of the percentage of propagules predated by crabs.

were taken into burrows (**Figure 7b** and **Table 9**), and they had been substantially grazed when recovered from those burrows. There was no leaf breakage during removal from the burrows.

3.8. Mangrove community function in terms of trophic linkages

The structure and network analysis parameter estimates for the model are shown in **Table 10**. These parameters include trophic estimates, biomass estimates, production/biomass estimates, consumption/biomass estimates, production/consumption ratios, gross efficiency estimates and omnivory index estimates. The Cameroon mangrove food web (as depicted here) consists of 3 trophic levels and 17 sublevels, which range from 1.0 to 3.74. The trophic level (TL) is an important index because it identifies an organism's food preferences. The highest values correspond to insectivorous birds, followed by the fish *Pentanemus quinquarius* and *Pseudotolithus* spp., whilst the lowest values correspond to the primary producer; mangrove, phytoplankton and detritus.

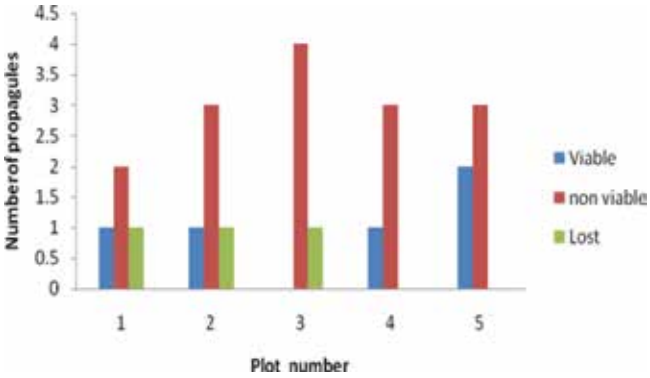

Figure 6. Number of propagules per plot killed by crabs, lost or still viable after predation.

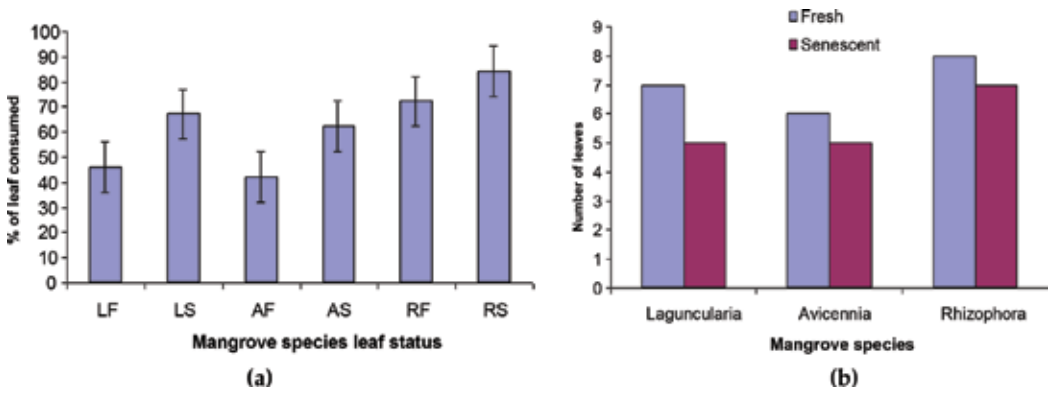

Figure 7. (a) Percentage of leaf material consumed by crabs for each mangrove species. LF = Laguncularia fresh, LS = Laguncularia senescent, AF = Avicennia fresh, AS = Avicennia senescent, RF = Rhizophora fresh, RS = Rhizophora senescent. (b) Number of leaves taken down crab burrows.

Species	Leaf status	n	Number taken down burrows
Laguncularia	Fresh	10	7
	Senescent	10	5
Avicennia	Fresh	10	6
	Senescent	10	5
Rhizophora	Fresh	10	8
	Senescent	10	7
Total		60	38

Table 9. Total number of leaves taken down crab burrows for each species and leaf status.

Summary statistics and basic flows and indices are shown in **Table 11**. The complexity in community structure is measured by the omnivory index (OI) [38]. The OI value for this study is 0.143 which is quite low when compared with Vega-Cendejas and Arreguín-Sánchez

	Habitat							
	TL	**Area (km²)**	**Biomass (t/km²)**	**P/B**	**Q/B**	**EE**	**P/Q**	**OI**
1 Mangrove	**1.00**	1.000	60.870	15.000	—	**0.564**	—	—
2 Phytoplankton	**1.00**	1.000	34.400	180.000	—	**0.712**	**0.313**	—
3 Zooplankton	**2.00**	1.000	27.130	15.000	160.000	**0.129**	**0.280**	—
4 Shrimps	**2.50**	1.000	0.417	5.380	19.200	0.950	**0.161**	**0.250**
5 Mangrove crabs (*Sesarmidae*)	**2.10**	1.000	2.400	2.250	14.000	**0.422**	**0.058**	**0.090**
6 Fiddler crabs (*Uca*)	**2.41**	1.000	1.300	5.500	95.000	**0.319**	**0.091**	**0.452**
7 Other crabs	**2.00**	1.000	2.500	2.000	22.000	**0.456**	**0.550**	—
8 *Ilisha africana*	**2.50**	1.000	1.993	3.006	55.000	0.950	**0.101**	**0.250**
9 *Pseudotolithus* spp.	**3.22**	1.000	1.780	0.648	6.400	0.950	**0.179**	**0.159**
10 *Pentanemus quinquarius*	**3.29**	1.000	0.294	1.775	9.900	0.950	**0.030**	**0.151**
11 *Sardinella maderensis*	**2.40**	1.000	1.015	1.260	42.200	0.950	**0.016**	**0.290**
12 *Brachydeuterus auritus*	**2.50**	1.000	1.615	1.026	63.000	**0.780**	**0.101**	**0.250**
13 *Dreprane africana*	**2.70**	1.000	1.396	0.820	8.100	**0.134**	**0.187**	**0.210**
14 *Arius* spp.	**2.65**	1.000	2.570	1.140	6.100	**0.440**	**0.187**	**0.303**
15 *Pomadasys jubelini*	**2.80**	1.000	0.289	0.731	7.700	**0.760**	**0.095**	**0.160**
16 *Galeoides decadactylus*	**2.99**	1.000	0.869	0.828	9.700	**0.223**	**0.085**	**0.284**
17 *Raja Miraletus*	**3.33**	1.000	1.645	0.560	6.900	**0.008**	**0.081**	**0.146**
18 *Lutjanus* spp.	**3.14**	1.000	2.017	0.770	4.300	**0.010**	**0.179**	**0.102**
19 *Mugil curema*	**2.00**	1.000	1.858	1.367	21.800	**0.350**	**0.063**	—
20 *Caranx* spp.	**2.80**	1.000	0.415	0.655	24.300	**0.083**	**0.027**	**0.160**
21 Shorebirds	**3.00**	1.000	0.021	0.160	65.000	**0.000**	**0.002**	—
22 Insectivorous birds	**3.74**	1.000	0.150	0.100	10.000	**0.000**	**0.010**	**0.167**
23 Birds of prey	**3.03**	1.000	0.022	12.000	60.000	**0.000**	**0.200**	**0.012**
24 Benthos	**2.00**	1.000	12.000	15.000	80.000	**0.571**	**0.188**	—
25 Insects	**2.00**	1.000	20.600	12.000	30.000	**0.054**	**0.400**	—
26 Detritus	**1.00**	1.000	10,000,000	—	—	**0.308**	—	**0.274**

TL: trophic level; **B**: biomass (t/km²); **P/B**: annual production/biomass ratio; **Q/B**: annual consumption/biomass ratio; **EE**: ecotrophic efficiency; **P/Q** annual production/consumption ratio; **OI**: omnivory index

Table 10. Basic input and model estimated output **(bold)** of the Cameroon mangrove estuary.

Parameter	Value	Unit
Sum of all consumption	6723.632	t/km^2·year
Sum of all exports	3305.708	t/km^2·year
Sum of all respiratory flows	3810.424	t/km^2·year
Sum of all flows to detritus	4775.025	t/km^2·year
Total system throughput	18,615	t/km^2·year
Sum of all production	893	t/km^2·year
Total net primary production	7105.1	t/km^2·year
Total primary production/total respiration	1.865	t/km^2·year
Net system production	3294.4	t/km^2·year
Total primary production/total biomass	38.6	t/km^2·year
Total biomass/throughput	0.01	t/km^2·year
Total biomass (excluding detritus)	184.2	t/km^2·year
Connectance index	0.3	t/km^2·year
System omnivory index	0.143	t/km^2·year
Ascendancy (flow bits)	9929.2	
Relative ascendancy	0.25	
Overhead (flow bits)	19117.1	
Overhead (%)	48	
Capacity (flow bits)	39661.3	
Transfer efficiencies	6.3	
Finn's cycling index (FCI %)	2	
Finn's mean path length	1.717	
Flow to detritus		
Zooplankton	2050.348	t/km^2·year
Phytoplankton	1785.893	t/km^2·year
Mangrove	397.640	t/km^2·year
Insect	357.515	t/km^2·year

Table 11. Summary statistics and basic flows and indices.

[41] who estimated OI of 2 for the Yucantan Peninsula in Mexico. The low OI value may be due to some groups being highly specialised and environmental conditions might alter the availability of prey.

3.8.1. Community energetics

Attributes of ecosystem maturity and stability include connectivity index (CI), total system throughput (T), system total primary production/total respiration ratio (PP/R), primary production/biomass ratio (PP/B), and biomass over throughput (B/T). The connective index (CI) is the number of actual links to the number of possible links for a given food web [38].

According to Christensen et al. [42], food web structure changes from linear to web like as the system mature. Hence, CI is correlated with maturity [42]. The Cameroon mangrove CI is 0.174 which is close to the value 0.191 reported by Villanueva et al. [43] for Ebere lagoon in Ivory Coast and lower than 0.3 reported by Vega-Cendejas and Arreguín-Sánchez [41] for Yucantan Peninsula in Mexico.

The total system throughput (T) is the size of the entire system in terms of flow [42, 44]. A high T value means the system is capable of growth, suggesting the system is full of energy and resilience. The Cameroon mangrove system T value is 18,615 t/km^2·year, relatively high compared to 3049 reported for Golfo de Nicoya (Costa Rica), 6240 reported for Ebere logoon (Ivory Coast) and 10,558 reported for Craeté mangrove estuary (Brazil) [45, 46].

Total system primary production and total respiration ratio (PP/R) shows the balance between production and consumption. When the PP/R ratio is close to 1, this indicates a mature ecosystem [40, 43]. When the PP/R ratio is greater than 1, production exceeds respiration and indicates the system is in an earlier development stages. When PP/R is less than 1, this indicates the system is accumulating a lot of organic matter. The Cameroon mangrove PP/R value is 1.865, low when compared with other values from tropical ecosystems.

The transfer efficiency for the Cameroon mangrove system is 6.4%, which is low compared to 9.8% reported for Yacatan Peninsula (Mexico) and 14.9% reported for Golfo de Nicoya (Costa Rica) [41, 45], meaning that the system is relative inefficient to recover after disturbance. The model estimate of primary production/biomass of 38.6 compared to 23.9 reported by Walters et al. [45] for Craeté mangrove estuary (Brazil), the system was reported to be relatively mature, hence this indicates that the Cameroon system is mature and may therefore be relatively stable.

Flow indicators related to "overall community homeostasis", which describes the size and the degree of organisation with which the material is being processed within the system, is within the range of most mangrove or estuary ecosystems. These are closely linked to ecosystem efficiency, maturity and development [44]. These indicators include ascendancy (9929.25) and relative ascendancy (0.250).

Energy use and matter recycling in the system are important processes in ecosystem functioning [40] and are measured as Finn's cycling index (FCI) and Finn's mean pathway. The model estimated value for FCI is 2 which are relatively low compared to 5.5 for Golfo de Nicoya (Costa Rica) and Finn's mean pathway of 1.717 estimated by the model is also relatively low compared to 3.4 and 4.4 reported for Craeté mangrove estuary (Brazil) and Yacatan Peninsula (Mexico). This indicates that the Cameroon system is immature.

4. Discussion

Few studies have examined the ecological impacts of small-scale exploitation of mangrove with the aim of assessing ecological and environmental dimensions. Small-scale cutting of mangrove in the Caribbean reduces the abundance of large trees, but greatly increase the density of smaller trees [47]. Cutting of mangroves in the Philippines resulted in stunted and shrubby tree growth [46], but other studies have shown otherwise. For instance, Nurkin [48]

suggests that small-scale mangrove exploitation has an insignificant effect on mangrove forest structure. In the present study, the impact of small-scale mangrove wood exploitation created large forest gaps.

Not surprisingly, the canopy gaps created by trees cut were relatively small, the largest gap size measured for this study was 72.2 m^2, but the mean gap size was much smaller at 0.32 m^2, relatively small when compared to findings from other mangrove studies. For example, Ewel et al. [49] recorded a mean gap size of 158 m^2 for mangrove in Kosrae Micronesia, though the author deliberately ignored gap sizes less than 10 m^2. Smith et al. [19] observed gap sizes of mature mangrove forest in Australia of 40–120 m^2, but it is possible that he overlooked gaps of less than 10 m^2. By contrast, Walter [7] found a smaller mean gap size on 2.6 m^2 for Philippines mangroves and studies of other forest types have shown that such small canopy gaps have an important effect on the forest structure [50, 51].

Exploitation of mangrove wood product was not completely species selective in this study, but *Rhizophora* was the preferred species for fuelwood and for poles for construction. There is evidence that wood exploitation might have changed *Rhizophora* stem size distribution.

Mangroves are thought to recover quickly after disturbance [47], but the evidence is mixed. Thus, Ewel et al. [49] found no differences in gap regeneration as a result of selective logging in Kosrae. Clarke and Kerrigan [25] found that canopy gap had a strong influence on the abundance of mangrove seedlings, and the most sensitive species was *Rhizophora*, which shows a significant difference in gap regeneration. Smith [52] observed significant recruitment of *Rhizophora* species in gaps [53]. According to Feller and Mckee [50] gap size does not influence *Rhizophora* regeneration.

According to Smith [52] mangrove seedlings regenerate quickly in large numbers in the canopy opening. In the present study, the relatively low seedling density coupled with the small canopy size might suggest that the Cameroon mangrove canopy is relatively closed. This is supported by large canopy density and may imply that the Cameroon mangrove forest structure is relatively healthy.

This study suggests that mangrove resources play an important role in the economic and social life of most local communities within the mangrove area, resulting to significant level of dependency of the local communities on the mangrove resources. The framework of dependence include: pole for building houses, fuelwood for smoking fish, timber building of band, resting beds, bridges, anchor for canoe, pole for fish trap and fences. Among the fabric of uses, the most significant use was fuelwood for fish smoking. The use of mangrove wood as fuelwood mostly for charcoal and cooking has also been reported in Kenya, Vietnam and Malaysia as well [54]. The peculiarity in this study is that fuelwood is used predominantly used for smoking fish and this process is an important economic activity in the area.

In the present study, local mangrove wood exploitation is an important form of ecological disturbance and a potential threat to forest health. Although forest alteration is not dramatic, impacts on species composition and regeneration are apparent. Whilst dramatic changes in mangrove forest species composition and ecosystem health have been seen in many places, due to anthropogenic influences, hence, small-scale exploitation like that seen here, might contribute significantly to long-term environmental problems if not properly managed.

The mangrove forest habitat is unique and rich in crab species. Thirty-nine crab species have been recorded in West and Central Africa mangroves [55]. In this study 13 species were identified belonging to two dominant groups, grapsid and fiddler crabs. All the species in the present study are found in mangroves elsewhere in the Central African region and common genera such as *Uca* and *Sesarma* tend to occur in mangrove habitats worldwide. The distinctness of the Central African mangrove fauna lies in the relative importance of particular families. For example, four to six species of *Uca* are found in all other mangrove regions, but only one species, the widespread *Uca tangeri*, has been reported in Central African mangroves [56].

Environmental factors such as vegetation, substratum, salinity and tidal exposure have been reported to influence the distribution of mangrove crabs [14, 57], with vegetation playing an important role. Environmental conditions were not formally measured in the present study, but the distribution of crab species did differ in the study area. The size frequency distribution of the major species in this study seems bimodal, skewed to the right. Similar distributions have been reported from Mozambique [58] and South American mangrove areas [27]. This distribution suggests that the crab populations recorded here have good recruitment.

According to Mantelatto et al. [59], sexual dimorphism is a result of females being smaller having reduced somatic growth compared to males, because they devote more energy to gonad development. Also larger male crabs are more successful in copulating with females, and win more intra-specific fights [60].

Grapsid and sesarmid crabs are clearly predators of mangrove propagules. *Sesarma* and *Metapograpsus* spp. have been reported predating *Rhizophoraceae* and *Avicennia* propagules [22, 62]. In the present study, 66.7% of the propagules were predated leaving 50% non-viable. This high predation pressure could affect natural restoration of mangrove forest in Cameroon.

Seedling establishment (i.e. type of planting strategy, horizontal or vertical) may also influence predation rate. In the present study, horizontally planted propagules were predated more heavily. This might be because the crabs face difficulties handling vertical propagule due to their size and weight. Although seedling establishment type and tides might influence recruitment, selectivity of crabs might also alter natural restoration of mangrove seedlings in a species-specific way [10]. In the present study, propagule predation did not differ significantly between crab species, but the dominant species foraging on plant material was *Goniopsis pelii.*

In the present study, the average percentage of the leaves consumed was high (71.3%), and similarly high leaf consumption rates have been reported in Australia [23, 61]. The "swept" appearance of the forest floor observed during this study might be as a result of a combination of tidal inundation and high crab activity in the region, and any addition of leaves for crabs (as done here) will be consumed rapidly. Removal of leaves by tide action may be the reason for the large number of leaves dragged into burrows (as well as avoiding predation).

The ecopath model analysis allowed a reasonable model representation of a Cameroon mangrove system. Model viability was determined by using the sensitive analysis function i.e. pedigree index [42]. The sensitivity analysis suggests that parameterisation of groups within the model is most sensitive to decreases in biomass estimates and that the impact of changes in the parameters of one group on another is influenced by the trophic dependency of the impacting group on the impacted group. The impacts of an increase in biomass in one group

on other groups within the systems can be shown using a mixed trophic impact plot. This can be used to get an overall indication of the sensitivities and responses to reduced biomass in one group on another and dependent upon them.

The viability value of 0.52 estimated by the model is an indication that the model was tightly fitted, as the simulation values have remarkably little difference from the original input. The balanced model parameter estimates indicate a mixture of a mature and immature system. The mature indices include: total system throughput (T) that is the sum of all flows (consumption, respiration, export and flow into detritus) is 18,615 t/km^2·year, appears to be high when compared to other values from tropical coastal system. The system primary production/respiration (PP/R) ratio estimated by the model is 1.87 indicating that the system is relatively developed [38].The high ascendancy value of 9929.2 and relative ascendancy of 0.250 indicate that the system is mature. However, the relative ascendancy of 0.250 reported by Vega-Cendejas and Arreguín-Sánchez [41] for Yucatan Peninsula (Mexico) was considered high by the author. The total system biomass value is 184.193 t/km^2·year which appears high fits well within the range of other tropical systems [38].

The model results show that more than 98.6% of the flows to detritus is from TL 1 and 2, these levels playing a significant role in supporting the energy utilised by higher TL groups, and indicate a detritus-based food web and bottom-top control system, which is typical of a mature system.

System energy and matter recycling is an important process in ecosystem functioning [40], and the model low estimate of Finn's cycling index (FCI) and Finn's mean pathway of 1.983 and 1.717, respectively, is indicative of an immature system.

5. Conclusion

In the present study, has shown that local mangrove wood exploitation is an important form of ecological disturbance and a potential threat to forest health. Although forest alteration is not dramatic, impacts on species composition and regeneration are apparent. Whilst dramatic changes in mangrove forest species composition and ecosystem health have been seen in many places, due to anthropogenic influences, hence, small-scale exploitation like that seen here, might contribute significantly to long-term environmental problems if not properly managed. Furthermore, it revealed that Cameroon grapsid and sesarmid crabs consumed large amounts of mangrove plant material, both leaves and propagules, and this may have significant ecological consequences for ecosystem structure and function.

The above system parameters provide a mixed picture of the maturity stage of the Cameroon mangrove ecosystem. Some indicate the system is immature and others that it is mature. It could be concluded that the overall health of the system is sustainable.

Nevertheless, to establish a truly holistic, ecosystem-based approach to the management of the Cameroon mangrove forest, social and economic indicators need to be included and local users, the beneficiaries of the services delivered by the forest, need be included at all stages in the management process and this process need more research.

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Section 3

Mangrove Physiology

Chapter 5

Salt Compartmentation and Antioxidant Defense in Roots and Leaves of Two Non-Salt Secretor Mangroves under Salt Stress

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Additional information is available at the end of the chapter

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Abstract

The effects of increasing NaCl (100–400 mM) on cellular salt distribution, antioxidant enzymes, and the relevance to reactive oxygen species (ROS) homeostasis were investigated in 1-year-old seedlings of two non-salt secretor mangroves, *Kandelia obovata* and *Bruguiera gymnorhiza*. *K. obovata* accumulated less Na^+ and Cl^- in root cells and leaf compartments under 400 mM NaCl compared to *B. gymnorhiza*. However, *B. gymnorhiza* leaves are notable for preferential accumulation of salt ions in epidermal vacuoles relative to mesophyll vacuoles. Both mangroves upregulated antioxidant enzymes in ASC-GSH cycle to scavenge the salt-elicited ROS in roots and leaves but with different patterns. *K. obovata* rapidly initiated antioxidant defense to reduce ROS at an early stage of salt stress, whereas *B. gymnorhiza* maintained a high capacity to detoxify ROS at high saline. Collectively, our results suggest that salinized plants of the two mangroves maintained ROS homeostasis through (i) ROS scavenging by antioxidant enzymes and (ii) limiting ROS production by protective salt compartmentation. In the latter case, an efficient salt exclusion is favorable for *K. obovata* to reduce the formation of ROS in roots and leaves, while the effective vacuolar salt compartmentation benefited *B. gymnorhiza* leaves to avoid excessive ROS production in a longer term of increasing salinity.

Keywords: *Bruguiera gymnorhiza*, *Kandelia obovata*, reactive oxygen species, antioxidant enzymes, X-ray microanalysis

1. Introduction

Mangrove plants form a dominant ecosystem in tropical and subtropical coastlines [1]. *Bruguiera gymnorhiza* is widely distributed in tropical and subtropical area, from the southeastern coast of Africa through Asia to Australia and the southwestern Pacific [2]. *Kandelia obovata* is distributed mostly in the transition regions from tropical to subtropical coastlines of southern China, Taiwan, and the southern islands of Japan [3]. Climatic factors affecting the vegetative and reproductive phenology of *B. gymnorhiza* and *K. obovata* growing in subtropical regions were assessed in recent years. Temperature, day length, and rainfall are suggested to be the important external controlling factors of leaf initiation in *B. gymnorhiza* [4]. Leaf litterfall of the subtropical mangrove *K. obovata* was correlated to monthly day length and maximum wind speed [5]. Flowering of *K. obovata* was influenced by monthly sunshine hour and monthly mean air temperature [6]. While in *B. gymnorhiza*, flowering phenophase was linked with rainfall and relative humidity [4]. *B. gymnorhiza* and *K. obovata* are two major mangrove species along southern China coastlines. *B. gymnorhiza* is a frontline species and mostly occurs in high-saline zones compared with *K. obovata*, which grows in low-saline creeks in mangrove areas [7].

The most striking feature of mangroves is the capacity to withstand high salinity concentrations [8–11]. In general, secretor and non-salt secretor mangroves both exhibited a high capacity to maintain Na^+ homeostasis under sodium chloride (NaCl) stress [7, 12–15]. Root flux recordings showed that *B. gymnorhiza*, *K. candel* (or *K. obovata*, non-salt secretors), *Aegiceras corniculatum*, and *Avicennia marina* (secretors) retained an obvious Na^+ exclusion under NaCl treatment [7, 13–16]. Hydrogen peroxide (H_2O_2), nitric oxide (NO), and calcium (Ca^{2+}) mediated Na^+/H^+ antiport across the PM, thus contributing to control ionic homeostasis in the two non-salt secretor mangrove species [7]. Recently, multiple signaling networks of extracellular ATP (eATP), H_2O_2, Ca^{2+}, and NO in the mediation of root ion fluxes were established in salt-stressed *K. obovata* and *A. corniculatum* [15]. Salt exclusion by roots is the most important salt-tolerant mechanism in woody plants [17–22] and herbaceous species [23–24]. Although mangrove roots could effectively exclude salt ions under NaCl stress, Na^+ and Cl^- taken up by roots would eventually transport to shoots via the transpiration stream during a long-term salt exposure [16, 20–22]. Jing et al. found that Na^+ extrusion capacity in *K. candel* roots declined with the prolonged duration of salt exposure [16]. As a result, large amount of Na^+ accumulated in roots was transported to shoots [12, 16]. Excessive Na^+ accumulation in leaves leads to oxidative stress by the production of reactive oxygen species (ROS) in trees [25–27]. Similarly, salt-induced oxidative stress has been widely shown in herbaceous species [28–35]. In mitochondria and chloroplasts, superoxide anions (O_2^-) are generated as a by-product of electron transfer to O_2 via photosynthetic and respiratory electron transport chain [36, 37]. The active O_2^- leads to subsequent formation of H_2O_2 and hydroxyl radicals ($OH^{\bullet -}$) through chemical and enzymatic reactions [36, 37]. Salt induced an oxidative stress in chloroplast and mitochondria of pea leaves [28–30, 34]. In poplars, great buildup of Na^+ and Cl^- in chloroplasts may directly cause ion toxicity and induce the subsequent oxidative stress [26, 38]. X-ray microanalysis results showed that the inability for the restriction of Na^+ entry into the chloroplasts leads to an uncontrolled oxidation in *Populus popularis* [26, 38]. Salt-resistant plants may maintain ROS homeostasis through limiting ROS production by a protective salt partitioning. Evidence presented elsewhere suggests that NaCl-stressed sorghum plants preferentially

partition Cl^- into leaf sheaths relative to blades [39]. The preferential accumulation of Cl^- in the sheath would lessen the effect of salinity on photosynthetic processes in the leaf blade. Furthermore, X-ray microanalysis of various cell types in leaf sheaths and blades revealed that Cl^- was preferentially accumulated in epidermal vacuoles, relative to mesophyll vacuoles in salt-tolerant barley and sorghum [39, 40]. The high Cl^- concentration in the leaf blade mesophyll cells of a barley cultivar (cv. Clipper) suggests that the lower salt resistance of this cultivar is directly related to the degree of Cl^- exclusion by these cells [40]. Thus, it can be inferred that compartmentalizing salt ions in cell layers of leaf blade would reduce the perturbation of salt on photosynthetic processes in photosynthetically active mesophyll, especially the electron transport processes in chloroplasts. As a result, ROS is less produced [26, 27]. Although salt increased H_2O_2 in *K. candel* leaves, the ROS-induced necrotic lesions were not seen during the period of stress [16]. In addition to ROS scavenging by both enzymatic and nonenzymatic antioxidants, it is possible that mangrove plants could attenuate oxidative stress by a reasonable salt compartmentation in cells. However, this needs further investigations, e.g., by X-ray microanalysis, to clarify.

Under salt stress, the antioxidant defense system serves to remove reactive oxygen species (e.g., $O_2^{\bullet -}$ and H_2O_2) in the chloroplast, mitochondria, and cytosol. Superoxide dismutases (SODs) are considered to be the first defense line against $O_2^{\bullet -}$ and the reaction product [41, 42]. H_2O_2 is further detoxified through a reaction catalyzed by an ascorbate-specific peroxidase (APX), glutathione peroxidase (GPX), and catalase (CAT). APX utilizes ascorbate (AsA) as its specific electron donor to reduce H_2O_2 to water with the concomitant generation of monodehydroascorbate (MDAsA), a univalent oxidant of AsA [43]. CAT, an enzyme that splits hydrogen peroxide to yield oxygen and water, is an important part of the antioxidant defense [44]. GPX efficiently catalyzes the reduction of hydrogen peroxide and organic hydroperoxides by glutathione [45, 46]. In addition to these antioxidant enzymes that can directly scavenge toxic oxygen species, glutathione reductase (GR), which regenerates glutathione (GSH) that has been oxidized during ROS scavenging, is also implicated in redox homeostasis control [47]. The contribution of antioxidant defense to salt tolerance has been confirmed in crop species [32, 33, 48, 49] and woody plants, e.g., poplars [25–27] and mangroves [8, 10, 50, 51]. Takemura et al. detected an increased activity of SOD and CAT in *B. gymnorhiza* at high salt [50]. Parida et al. found that the elevation of antioxidant enzymes, APX and guaiacol peroxidase, was able to scavenge salt-induced H_2O_2 in *B. parviflora* [51]. Therefore, the capacity for regulating ROS homeostasis serves as one important component for salt tolerance in mangroves.

Analyses of isoforms of antioxidant enzymes showed species differences in antioxidant defense system against salt treatment. Plants generally have three SOD isozymes: Cu/Zn-SOD in the cytosol and chloroplasts, Mn-SOD in mitochondria, and Fe-SOD in chloroplasts [52]. Activity of CuZn-SOD I and CuZn-SOD II, the two dominant SOD proteins in poplar leaves, was not detectable in *P. popularis* (salt-sensitive) after 16 days of salt stress, while there were no marked inhibitory effects of NaCl on the two SOD isoenzymes in *P. euphratica* (salt-resistant) during the observation period [26]. Furthermore, genetic differences were found in the timing of APX and CAT response to increasing salinity. Salt treatments increased activity of CAT and APX isoenzymes in the two poplar species, but their activity increased earlier in *P. euphratica* than in *P. popularis* [27]. In mangrove, a certain number of SOD isoenzymes (Mn-SOD, Fe-SOD),

guaiacol peroxidase isoenzymes, and GR isoenzymes were preferentially elevated by NaCl in *B. parviflora* [51]. The induction of antioxidant enzymes might be the result of salt-induced gene transcription. Northern blot analysis revealed that the transcript level of cytosolic Cu/Zn-SOD was increased after a few days of NaCl treatment [50]. Similarly, NaCl was shown to increase *KcCSD* expression in *K. candel* leaves [16]. Proteomic analysis of *K. candel* leaves revealed that SOD abundance increased in response to high NaCl at 450–600 mM [53]. Furthermore, overexpression of copper/zinc superoxide dismutase from mangrove *K. candel* in tobacco enhances salinity tolerance by the reduction of reactive oxygen species in chloroplast [16].

We have previously shown species differences between secretor and non-salt secretor mangroves in root salt exclusion and leaf gas exchange response to salt treatment [7, 12, 15]. The object of this study is to investigate the effect of NaCl on the pattern of cellular salt compartmentation, variations in antioxidant enzymes, and their contributions to ROS (in particular, $O_2^{\bullet -}$ and H_2O_2) homeostasis maintenance in non-salt secretor mangroves.

2. Salt compartmentation and antioxidant defense

2.1. Plant materials and salt treatment

K. obovata hypocotyls developed from fruits turned into mature propagules, which began to drop in March and continued dropping until May [6]. Mature and developing propagules of *B. gymnorhiza* were found throughout the year, but the abundance of mature propagules was highest in summer and lowest in winter [4]. In early March, 200 of propagules of *K. obovata* and *B. gymnorhiza* were obtained from Dongzhai Harbor in Hainan Province of China (latitude 19°51′N and longitude 110°24′E). Propagules were collected from the surface of soil or seawater during the ebb tide. Single hypocotyls were planted in individual pots (15 cm in diameter and 18 cm in height) containing sand and placed in a greenhouse at Beijing Forestry University, Beijing, China (latitude 39°56′N and longitude 116°20′E). The pots were fertilized with 1000 ml half strength Hoagland nutrient solution every 14 d. Seedlings were raised from March to August under nonsaline conditions. The relative humidity was maintained at 60–70%, and photosynthetically active radiation (PAR) varied from 400 to 1200 μmol m^{-2} s^{-1}. Salt treatment was carried out when the fourth pair of leaves came out from the apex of the growing shoots (mid-August) [12].

NaCl concentration started from 100 mM and increased stepwise by 100 mM [12], reaching 400 mM and remained at this salinity until the terminal of experiment. Increasing NaCl saline was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM), respectively. Control plants were kept well watered with no addition of NaCl. PAR was 400–1200 μmol m^{-2} s^{-1}, and air temperature was 20–35°C over the duration of experiment. On day 2, day 5, day 9, and day 14, leaves and roots were sampled for ROS ($O_2^{\bullet -}$ and H_2O_2) determination and total activity measurements of antioxidant enzymes, i.e., superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), and glutathione reductase (GR). For SOD and CAT isoenzyme analyses, leaves and roots were sampled at day 3, day 6, day 10, and day 15. Three replicated plants per treatment were harvested at each sampling

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time. At the final harvest time, roots and upper mature leaves were sampled from control and stressed plants and used for X-ray microanalysis.

2.2. $O_2^{\bullet -}$ and H_2O_2 levels in roots and leaves

$O_2^{\bullet -}$ production rate was typically higher in roots than in leaves in control plants of the two species (**Table 1**). High salinity (400 mM NaCl) increased root $O_2^{\bullet -}$ production rate by 82 and 83% in *K. obovata* and *B. gymnorhiza*, respectively, but the salt-induced rise of $O_2^{\bullet -}$ was absent in the two mangroves when NaCl concentration was below 300 mM (**Table 1**). The same trend was observed in leaves, but the NaCl-induced increase of $O_2^{\bullet -}$ was only observed in *B. gymnorhiza* leaves at 400 mM NaCl (**Table 1**).

Increasing NaCl stress did not significantly elevate root H_2O_2 levels in either species; rather, a significant reduction of H_2O_2 was observed in *B. gymnorhiza* when NaCl saline ranged from 100 to 300 mM (**Table 1**). An abrupt rise of H_2O_2 occurred in *K. obovata* leaves when plants were subjected to 400 mM NaCl, although H_2O_2 remained less than controls at low salt (100–200 mM, **Table 1**). However, salinized *B. gymnorhiza* maintained a H_2O_2 level similar to control leaves despite of a NaCl increase, from 100 to 400 mM (**Table 1**).

In general $O_2^{\bullet -}$ production and/or H_2O_2 levels in roots and leaves were enhanced by high salinity (400 mM NaCl) in the two mangrove species, although root and leaf ROS levels were usually downregulated after exposure to a lower salinity (100–200 mM NaCl), e.g., O_2^{-} and H_2O_2 in *B. gymnorhiza* roots and H_2O_2 in *K. obovata* leaves (**Table 1**). Similarly, NaCl-induced increase of H_2O_2 was observed in leaves of *B. parviflora* [51] and *K. candel* [16] under hydroponic conditions. In this study, the moderate ROS increment induced by 400 mM NaCl caused no oxidative burst in both species, suggesting that stressed plants of *K. obovata* and *B. gymnorhiza* maintained ROS homeostasis throughout the duration of salt exposure. Our data showed that salt compartmentation and antioxidant enzymes contributed to ROS homeostasis in both species but with different patterns under NaCl stress (see below).

2.3. Salt compartmentation and ROS production

2.3.1. Salt compartmentation within root and leaf cells

In this study, SEM-EDX analysis was performed on cross sections of *B. gymnorhiza* and *K. obovata* roots. Na^+ and Cl^- were detectable in root cells of no-salt controls (**Table 2**). Under salt conditions, Na^+ and Cl^- levels significantly increased in the tested structures, i.e., epidermis, exodermis, cortex, endodermis, and stelar parenchyma (**Table 2**). The long-term salt treatment with increasing NaCl saline (100–400 mM, 15 d) significantly increased the content of salt ions by 0.6–9.6 (Na^+) and 0.5–5.1 fold (Cl^-), although Na^+ and Cl^- levels were typically higher in *B. gymnorhiza* than in *K. obovata* in all measured structures (**Table 2**).

In leaf cells of control plants, TEM-EDX data showed an evident Na^+ and Cl^- in epidermis, mesophyll, and xylem vessels (leaf vascular bundle), but *B. gymnorhiza* exhibited 28–195% higher Na^+ than *K. obovata* in all measured cell compartments, such as xylem vessel, epidermal wall and vacuole, mesophyll wall and vacuole, and chloroplast (**Table 3**). NaCl (400 mM) treatment markedly increased Na^+ and Cl^- concentrations in the apoplastic space and vacuoles

Treatment	*K. obovata*				*B. gymnorhiza*			
	Leaf		Root		Leaf		Root	
	H_2O_2	$O_2^{-\bullet}$	H_2O_2	$O_2^{-\bullet}$	H_2O_2	$O_2^{-\bullet}$	H_2O_2	$O_2^{-\bullet}$
Control	17.63 ± 6.00a	1.16 ± 0.12a	10.04 ± 1.98a	5.77 ± 1.00a	5.93 ± 0.91a	0.61 ± 0.07a	17.50 ± 0.17a	3.44 ± 0.56a
NaCl (100 mM)	2.37 ± 0.60b	1.35 ± 0.11a	7.76 ± 2.56a	6.26 ± 0.99a	11.53 ± 4.96a	0.47 ± 0.08a	1.43 ± 1.91b	2.35 ± 0.22a
Control	16.48 ± 4.10a	1.11 ± 0.07a	4.95 ± 1.86a	4.03 ± 1.35a	3.33 ± 1.12a	0.50 ± 0.29a	31.43 ± 4.79a	3.63 ± 0.58a
NaCl (200 mM)	1.50 ± 0.05b	1.26 ± 0.04a	3.20 ± 1.02a	4.34 ± 1.25a	9.01 ± 4.52a	0.69 ± 0.28a	4.79 ± 1.57b	2.68 ± 0.02a
Control	10.97 ± 1.23a	0.67 ± 0.09a	13.10 ± 2.07a	1.54 ± 0.09a	15.93 ± 4.50a	0.48 ± 0.07a	26.44 ± 4.98a	1.81 ± 0.60a
NaCl (300 mM)	11.47 ± 5.10a	0.84 ± 0.12a	13.93 ± 2.34a	1.78 ± 0.13a	23.13 ± 1.10a	0.69 ± 0.29a	4.66 ± 0.35b	1.89 ± 0.52a
Control	11.60 ± 5.80b	1.76 ± 0.41a	8.05 ± 1.08a	1.69 ± 0.06b	19.12 ± 1.18a	0.71 ± 0.09b	10.39 ± 2.15a	2.65 ± 0.09b
NaCl (400 mM)	41.38 ± 8.97a	1.76 ± 0.31a	11.62 ± 3.09a	3.08 ± 0.46a	22.90 ± 3.40a	1.08 ± 0.13a	16.07 ± 3.31a	4.85 ± 0.52a

$O_2^{-\bullet}$ production rate was measured as described by Wang and Luo [54] and Wang et al. [27]. Briefly, leaf and root tissues (ca. 0.5 g) were homogenized in a 3-ml ice-cold buffer [50 mM potassium phosphate, pH 7.0, 1.0 mM EDTA, 1% (w/v) PVP] and then centrifuged at 10,000 × *g* for 20 min at 4°C. A 1.0 ml of extract was mixed with same volume of 50 mM sodium phosphate buffer (pH 7.8) and 10 mM hydroxylammonium chloride. The mixture was kept at 25°C (water bath) for 20 min and then centrifuged at 1500 × *g* for 10 min. Then, 1.0 ml of the mixture was mixed with same volume of 17 mM sulfanilic acid and 7.0 mM 1-naphthylamine. After incubation at 25°C for 20 min, 3.0 ml ethyl ether was introduced to the mixture, shaken to uniform, and centrifuged at 1500 × *g* for 5 min. Absorbance of the water phase at 530 nm was then recorded. For blank controls, the same amount of 50 mM sodium phosphate buffer (pH 7.8) was added into the reaction system instead of the enzyme extract.

Measurement of H_2O_2 content was performed according to Patterson et al. [55], Liu et al. [56], and Wang et al. [27] with modifications. In brief, leaf and root tissues (ca. 0.5 g) were ground to a fine powder in liquid N_2 and then homogenized in 3.0 ml precooled acetone. The homogenate was centrifuged at 10,000 × *g* for 20 min at 4°C. A 1.0 ml supernatant, 2.5 ml extractant (CCl_4:$CHCl_3$ = 3:1, v/v), and 2.5 ml redistilled water was mixed and centrifuged at 5000 × g for 5 min at 4°C. Then, 2.0 ml water phases in the supernatant were divided into two aliquots of 1.0 ml. One was taken as blank control and the other was used to examine H_2O_2 concentration. For the blank control, catalase was introduced to a concentration of 3.0 U ml^{-1} and then kept at 30°C for 10 min. Same amount of solution with inactivated catalase (by high temperature) was added into the H_2O_2 extract. Then, 1.0 ml of 0.2 M sodium phosphate buffer (pH 7.8) and colorimetric reagent, 1.0 ml of 0.2 mM Ti(IV)-PAR, were introduced to both series [57]. The color was developed at 45°C for 20 min and then allowed to equilibrate with room temperature for 20 min. Finally, the absorbance at 508 nm was recorded, and concentration of H_2O_2 was given based on the established standard curve.

Each value (±SE) is the mean of three plants, and values in the same column followed by different letters are significantly different ($P < 0.05$) between control and NaCl treatment.

Table 1. Effects of NaCl on H_2O_2 (nmol g^{-1} fw) levels and $O_2^{-\bullet}$ production rates (nmol min^{-1} mg^{-1} pro) in leaves and roots of *K. obovata* and *B. gymnorhiza*.

Compartment	Treatment	*K. obovata*		*B. gymnorhiza*	
		Na^+	Cl^-	Na^+	Cl^-
Epidermis	Control	2.98 ± 0.30b	5.35 ± 1.26b	10.3 ± 4.46b	24.3 ± 1.76b
	NaCl	7.36 ± 2.19a	32.8 ± 3.94a	16.0 ± 3.82a	44.9 ± 1.96a
Exodermis	Control	1.05 ± 0.23b	12.1 ± 2.12b	7.76 ± 1.78b	27.2 ± 4.46b
	NaCl	11.1 ± 1.24a	23.6 ± 4.72a	23.9 ± 3.33a	51.4 ± 2.14a
Cortex	Control	0.70 ± 0.34b	7.71 ± 1.05b	12.6 ± 3.54b	34.2 ± 1.42b
	NaCl	5.39 ± 1.36a	43.7 ± 2.65a	26.3 ± 3.32a	51.2 ± 3.50a
Endodermis	Control	1.39 ± 0.97b	10.2 ± 0.37b	15.8 ± 4.90b	35.9 ± 3.08b
	NaCl	4.84 ± 0.96a	49.3 ± 1.64a	31.0 ± 5.82a	57.3 ± 5.14a
Stelar parenchyma	Control	1.56 ± 0.58b	6.96 ± 1.33b	17.1 ± 2.19b	24.8 ± 2.46b
	NaCl	5.80 ± 1.12a	38.6 ± 2.51a	35.3 ± 7.89a	48.2 ± 4.51a

K. obovata and *B. gymnorhiza* roots were sampled from control and stressed plants after 15 days of increasing NaCl treatment (100–400 mM). Cellular Na^+ and Cl^- contents were measured by SEM-EDX according to Sun et al. [58]. Briefly, roots with tips were washed free of soil particles and rapidly frozen in liquid nitrogen, vacuum freeze-dried at −100 °C for 24 h, and then slowly allowed to equilibrate to room temperature (ca. 22°C) for 24 h. Freeze-dried roots were gold coated in a high vacuum sputter coater and analyzed with a Hitachi S-3400 N scanning electron microscope equipped with an energy-dispersive X-ray detector (EX-250, Horiba Ltd. Kyoto, Japan). Probe measurements of samples were taken with a broad electron beam covering the whole cells that were randomly selected in the epidermis, exodermis, cortex, endodermis, and stele. Na^+ and Cl^- levels were expressed as a percentage of the total atomic number for all the major elements (K^+, Na^+, Ca^{2+}, Mg^{2+}, and Cl^-) detected from the cell samples.
Each value (±SE) is the mean of three plants, and 5–12 measurements (for each compartment) were taken from each root. Values in the same column followed by different letters are significantly different ($P < 0.05$) between control and NaCl treatment.

Table 2. Salt distribution in root cells of *K. obovata* and *B. gymnorhiza*.

of the two species but with the exception of Cl^- in *K. obovata* (**Table 3**). In comparison, the fractions of Na^+ and Cl^- in the xylem vessel, cell wall, and vacuole were 30–196% higher in stressed *B. gymnorhiza* as compared to *K. obovata* (**Table 3**). However, NaCl stress did not significantly increase Na^+ and Cl^- concentrations in the chloroplast of two mangroves (**Table 3**).

Vacuolar compartmentation in mesophyll was clearly seen in stressed *B. gymnorhiza*, in which the Na^+ and Cl^- concentrations were higher in the vacuole than in the chloroplast (**Table 3**). Noteworthy, *B. gymnorhiza* preferentially accumulated 73–94% higher Na^+ and Cl^- in vacuoles of epidermal cells as compared to mesophyll vacuoles (**Table 3**). In contrast to *B. gymnorhiza*, vacuolar fractions of Na^+ and Cl^- in stressed *K. obovata* remained the same as that of chloroplast, and vacuolar Na^+ and Cl^- in epidermis was similar to that in mesophyll vacuole regardless of treatments (**Table 3**).

2.3.2. Salt compartmentation and ROS production in roots and leaves

X-ray microanalysis data show that Na^+ and Cl^- were evident in root and leaf cells of control plants in the two mangroves (**Tables 2** and **3**), presumably originated from hypocotyls as propagules were collected from the surface of soil or seawater in coastal habitats of mangrove

Compartment	Treatment	*K. obovata*		*B. gymnorhiza*	
		Na^+	Cl^-	Na^+	Cl^-
Xylem vessels (leaf vascular bundle)	Control	131 ± 102b	633 ± 48a	309 ± 22b	576 ± 101b
	NaCl	246 ± 4a	636 ± 101a	729 ± 119a	1069 ± 254a
Epidermal wall (abaxial and adaxial)	Control	266 ± 96b	725 ± 181a	403 ± 22b	812 ± 101b
	NaCl	377 ± 110a	945 ± 71a	840 ± 119a	1305 ± 254a
Mesophyll wall (palisade and spongy)	Control	228 ± 35b	669 ± 224a	420 ± 46b	545 ± 67b
	NaCl	336 ± 27a	926 ± 170a	904 ± 287a	1445 ± 418a
Epidermal vacuole (abaxial and adaxial)	Control	75 ± 71b	495 ± 282a	221 ± 42b	646 ± 23b
	NaCl	183 ± 133a	558 ± 285a	509 ± 125a	1148 ± 121a
Mesophyll vacuole (palisade and spongy)	Control	86 ± 14b	510 ± 123a	123 ± 16b	531 ± 33b
	NaCl	134 ± 31a	634 ± 31a	263 ± 6a	664 ± 3a
Chloroplast (palisade and spongy)	Control	103 ± 18a	532 ± 129a	182 ± 69a	640 ± 89a
	NaCl	141 ± 15a	681 ± 45a	145 ± 57a	494 ± 101a

K. obovata and *B. gymnorhiza* leaves were sampled from control and stressed plants after 15 days of increasing NaCl treatment (100–400 mM). Standard procedures required for sample preparation and X-ray microanalysis were followed as described in Fritz [59, 60]. In brief, leaf segments, 2–3 mm long and 1–2 mm wide, were cut with a razor blade along the smaller veins adjacent to the central vein and immediately placed into aluminum sample holders and rapidly frozen in a 3:1 mixture of propane:isopentane at the temperature of liquid nitrogen. Samples were vacuum freeze-dried at −60°C for 72 h and then slowly allowed to equilibrate to room temperature (ca. 22°C) over a period of 24 h. Then, samples were stored over silica gel until infiltration in plastic. Freeze-dried leaf samples were transferred into vacuum-pressure chambers and infiltrated in ether at 27°C overnight before infiltrating with plastic. The plastic used was a 1:1 mixture of styrene (Merck Schuchardt) and butyl methacrylate (Sigma-Aldrich) containing 1% benzoyl peroxide stabilized with 50% phthalate. Infiltration with plastic was carried out in the following steps: 1:1 ether:plastic for 24 h, 1:3 ether:plastic for 24 h, and finally 100% plastic for 24 h. Following infiltration, samples were transferred into gelatin capsules and polymerized at 60°C for 12 h, then transferred into 35°C oven, and polymerized for at least 7 days. After polymerization, agar samples were cut into 1-μm-thick sections using dry glass knife with an ultramicrotome (Ultracut E, Reichert-Jung, Vienna, Austria). The slices were mounted in copper grids (mesh 50), coated with carbon, and stored over silica gel until analysis.
Leaf sections were analyzed in a Phillips EM 420 electron transmission microscope (Eindhoven, the Netherlands) with the energy dispersive system EDAX DX-4 (EDAX International, Mahwah, NJ 07430, USA). The operating parameters were as follows: accelerating voltage was 120 kV; take-off angle was 25°; and the time for collecting X-rays was 60 live seconds. Probe measurements were made on xylem vessels in the bundle, spongy, and palisade mesophyll, adaxial, and abaxial epidermis. The following structures were examined: cell wall, vacuole, and chloroplast (mesophyll), and magnification was at ×6350. Probe measurements of cell walls were taken with a long and narrow electron beam, and measurements of vacuole and chloroplasts were taken with a broad electron beam covering the target structures. For each section, 10–20 measurements were taken from each compartment. The X-ray spectra were processed with EDAX DX-4 software after manual fitting of the background. Concentrations of Na^+ and Cl^- were determined by analytical calibration standard of NaCl that established according to Fritz and Jentschke [61].
Values in the same column followed by different letters are significantly different ($P < 0.05$) between control and NaCl treatment.

Table 3. Salt compartmentation within leaf cell compartments of *K. obovata* and *B. gymnorhiza*.

forest. Mangrove propagules absorbed salt ions when they contacted seawater [7, 12]. Na^+ and Cl^- increased in cell compartments of roots and leaves (**Tables 2** and **3**). This indicates that the salt ions taken up by roots transported to shoots under NaCl stress [12, 16, 22]. Our data show that there were marked differences in the pattern of salt compartmentation in the two mangroves. *K. obovata* exhibited a high capacity to exclude NaCl from root and leaf cells, whereas

B. gymnorhiza are notable for (1) vacuolar compartmentation in mesophyll cells and (2) preferential accumulation of Na^+ and Cl^- in epidermal vacuoles, relative to mesophyll vacuoles (**Table 3**). The ability to extrude Na^+ from root cells of *K. obovata* likely results from an active Na^+/H^+ antiport driven by H^+ pumping activity of PM H^+-ATPase [7, 15]. Salt compartmentation in vacuoles likely depends on active transport of salt ions across the tonoplast. Salinity may increase the activity of vacuole H^+ pumps, thus making a contribution to the compartmentation of toxic ions into the vacuoles via Na^+/H^+ antiporter systems [62–64]. Mimura et al. found that the elevated concentrations of Na^+ and Cl^- in swelling vacuoles were correlated with the salt-induced activation of tonoplast H^+-ATPase in suspension-cultured cells of *B. sexangula* [65]. We suggest that the two mangrove plants may maintain ROS homeostasis through limiting ROS production by a protective cellular salt compartmentation, in addition to scavenging ROS by antioxidant enzymes in a longer term of increasing salinity (see below). In brief:

a. Salt exclusion and ROS production in *K. obovata*: NaCl treatment increased Na^+ in the leaf apoplast and vacuole of epidermis and mesophyll, but did not elevate Cl^- in *K. obovata* (**Table 3**). Moreover, the absolute values of Na^+ and Cl^- in these measured compartments were lower in *K. obovata* than in *B. gymnorhiza* under 400 mM NaCl (**Table 3**). Result suggests that *K. obovata* plants had a higher capacity for NaCl exclusion, presumably due to the salt uptake and transport restrictions in roots (**Table 2**) [7, 12, 15]. Effective salt exclusion is a benefit for *K. obovata* to reduce ROS production. We have shown that the inability to exclude NaCl favored the formation of $O_2^{\bullet -}$ and H_2O_2, which causes an oxidative burst in leaf cells of a salt-sensitive poplar, *P. simonii* × (*P. pyramidalis* × *Salix matsudana*) (*P. popularis* cv. '35–44') [26, 27, 38].

b. Vacuolar salt compartmentation and ROS production in *B. gymnorhiza*: *B. gymnorhiza* leaves exhibited a more pronounced salt accumulation than *K. obovata* (**Table 3**), resulting from a higher root-to-shoot salt transport [12]. Noteworthy, *B. gymnorhiza* preferentially accumulated Na^+ and Cl^- in epidermal vacuoles, instead of mesophyll vacuoles (**Table 3**). Similar findings were observed in leaf sheaths and blades of sorghum and barley in which Cl^- was preferentially accumulated in most cell layers, particularly the adaxial epidermal cells [39, 40]. The evident Cl^- exclusion from photosynthetically active mesophyll would lessen the effect of salinity on photosynthetic processes, especially the electron transport in chloroplasts in the mesophyll. Moreover, fractions of Na^+ and Cl^- remained higher in mesophyll vacuole than in the cytoplasm (**Table 3**), which may inhibit the enhancement of NaCl on the formation of $O_2^{\bullet -}$ and H_2O_2 in the cytosol, chloroplasts, and mitochondria. NaCl was found to favor the formation of $O_2^{\bullet -}$ and H_2O_2 in chloroplasts and mitochondria of pea cultivars [28, 29]. Accordingly, we hypothesize that the *B. gymnorhiza* limits ROS production by preferential accumulation of Na^+ and Cl^- in epidermal vacuoles, as well as vacuolar compartmentation in mesophyll cells.

2.4. Antioxidant enzymes contributed to ROS homeostasis

2.4.1. Activity of antioxidant enzymes in roots and leaves

Under no-salt control conditions, total activity of measured antioxidant enzymes roots and leaves, SOD, APX, CAT, and GR, varied markedly during the observation period (**Tables 4**

and **5**). This was presumably resulted from genetic difference of seedlings and variations in light intensity and air temperature. In our study, natural PAR was 400–1200 μmol m^{-2} s^{-1}, and air temperature was 20–35°C over the duration of experiment. In general, activities of antioxidant enzymes in roots and leaves were not reduced upon increasing saline (with a few exceptions) but upregulated in both species (**Tables 4** and **5**). Noteworthy, there were species differences in antioxidant defense to increasing salinity. Activity of each component in the measured antioxidant defense system, SOD, APX, CAT, and GR, drastically increased in *K. obovata* roots at 300 mM NaCl, while the same trend was observed in *B. gymnorhiza* roots at 400 mM (**Table 4**). Furthermore, *B. gymnorhiza* leaves showed a higher increase of SOD, APX, and CAT at 400 mM NaCl as compared to *K. obovata* (**Table 5**). SOD of *K. obovata* was upregulated after salt exposure, but the response is quite variable in roots and leaves. Root SOD activity was increased by 100 and 300 mM NaCl, while leaf activity was increased by 200 and 400 mM (**Tables 4** and **5**). SOD activity in roots and leaves of *B. gymnorhiza* did not increase after exposure to 100–300 mM NaCl (**Tables 4** and **5**). The variable response of antioxidant enzymes to salt treatment was also seen in GR. It exhibited a marked elevation in *B. gymnorhiza* leaves at 100 mM NaCl, whereas the steady increase of GR in *K. obovata* was observed at a salt concentration of 300 mM (root) and 400 mM (leaf) (**Tables 4** and **5**).

SOD isoenzymes and CAT isoenzymes in roots and leaves were analyzed by native PAGE. In root extracts, three dominant SOD isoenzymes were detected in *K. obovata* roots, whereas there were two SOD isoforms in *B. gymnorhiza* (**Figure 1A** and **B**). KCN and H_2O_2 inhibited the activity of these isoenzymes in the two species, indicating they were CuZn-SOD isoforms (**Figure 1A** and **B**). NaCl did not restrict activity of all SOD isoforms in *K. obovata* roots during the period of salt treatment (**Figure 1C**), but a marked elevation of CuZn-SODs was observed in *B. gymnorhiza* at 300–400 mM NaCl (**Figure 1D**).

Three dominant SOD isoenzymes were detected in control leaves of both species but with different patterns (**Figure 2A** and **B**). KCN and H_2O_2 inhibited activity of two SOD isoenzymes in both genotypes, indicating that these were CuZn-SOD isoforms (**Figure 2A** and **B**). Another SOD isoform was defined as Mn-SOD since it was resistant to both inhibitors (**Figure 2A** and **B**). Activity of SOD isoenzymes in *K. obovata* leaves was increased by a lower salt, e.g., Mn-SOD at 100 and 200 mM NaCl and Cu/Zn-SOD1 and Cu/Zn-SOD2 at 200 NaCl mM (**Figure 2C**). *B. gymnorhiza* upregulated both Mn-SOD and Cu/Zn-SODs at a higher salt, 300–400 mM NaCl (**Figure 2D**).

Native PAGE of root extract showed three CAT isoenzymes in *K. obovata* and two in *B. gymnorhiza* (**Figure 3**). Increasing NaCl, from 100 to 400 mM, did not restrict activity of all CAT isoforms in both species, although activity of CAT isoforms in control roots fluctuated over the observation period (**Figure 3**). Compared with *K. obovata*, *B. gymnorhiza* exhibited typically a higher activity of CAT1 and CAT2 regardless of treatments (**Figure 3**).

Three and four CAT isoenzymes were identified in *K. obovata* and *B. gymnorhiza* leaves, respectively (**Figure 4**). Salt markedly enhanced the activity of CAT2 in *K. obovata* at 200 mM; however, the enhancement of NaCl on CAT2, CAT3, and CAT4 in *B. gymnorhiza* was observed at 300–400 mM NaCl (**Figure 4**).

Treatment	*K. obovata*				*B. gymnorhiza*			
	SOD	**CAT**	**APX**	**GR**	**SOD**	**CAT**	**APX**	**GR**
Control	246.9 ± 25.0b	138.1 ± 21.2a	270.0 ± 22.3a	33.7 ± 15.2a	133.3 ± 9.0a	27.8 ± 4.8a	130.2 ± 7.8a	12.9 ± 2.9a
NaCl (100 mM)	406.4 ± 21.5a	136.2 ± 11.1a	272.3 ± 22.2a	15.7 ± 3.3a	125.2 ± 7.3a	45.1 ± 19.0a	144.1 ± 18.6a	20.7 ± 3.1a
Control	108.0 ± 20.2a	152.9 ± 21.4a	249.7 ± 46.5a	49.9 ± 8.0a	149.0 ± 31.3a	43.3 ± 2.9a	377.1 ± 34.1a	19.1 ± 5.6a
NaCl (200 mM)	112.2 ± 61.2a	151.9 ± 27.2a	181.4 ± 15.4a	77.6 ± 12.2a	148.6 ± 17.9a	46.7 ± 10.1a	369.4 ± 94.6a	30.4 ± 13.8a
Control	148.4 ± 1.7b	28.9 ± 6.2b	119.8 ± 16.4b	17.4 ± 6.0b	98.4 ± 17.4a	26.4 ± 1.8a	120.8 ± 27.7a	30.0 ± 9.4a
NaCl (300 mM)	377.4 ± 32.9a	60.71 ± 8.0a	343.7 ± 96.4a	49.4 ± 11.4a	121.8 ± 28.1a	27.8 ± 1.2a	178.1 ± 47.7a	29.8 ± 6.5a
Control	193.8 ± 88.8a	35.1 ± 6.3a	62.2 ± 5.7a	17.9 ± 3.6a	132.6 ± 11.8b	109.0 ± 16.3a	218.1 ± 55.6b	23.7 ± 2.3b
NaCl (400 mM)	244.4 ± 64.1a	54.6 ± 18.6a	77.8 ± 4.5a	26.1 ± 0.5a	232.4 ± 19.5a	132.6 ± 1.7a	361.6 ± 80.7a	59.8 ± 15.0a

K. obovata and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. NaCl saline was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Roots of control and salinized plants were harvested at day 2, day 5, day 9, and day 14, respectively. Three replicated plants per treatment were harvested at each sampling time. Roots (ca. 0.5 g) were ground in cold mortars using liquid nitrogen and homogenized in a 3.0-ml ice-cold extraction buffer [50 mM potassium phosphate, pH 7.0, 1.0 mM EDTA, 1%(w/v) PVP]. The extracts were centrifuged at 10,000 × *g* for 20 min at 4°C and used for the assays of superoxide dismutase (SOD), catalase (CAT), and glutathione reductase (GR). For ascorbate peroxidase (APX) measurement, 1.0 mM ascorbic acid (ASC) was added into the enzyme extraction buffer [27]. Protein concentration in the supernatant was determined according to Bradford [66] using bovine serum albumin as standard.

Total SOD activity was assayed as described in Giannopolits and Ries [67] with modifications. The reaction mixture contained 1.8 ml potassium phosphate (50 mM, pH 7.8), 0.3 ml L-methionine (130 mM), 0.3 ml nitroblue tetrazolium salt (750 μM), 0.3 ml Na_2EDTA (100 μM), 30 μl enzyme extract, and 0.3 ml riboflavin (20 μM). The cocktail was mixed and then illuminated by cool white fluorescent lamps (30 μmol m^{-2} s^{-1}) for 6 min. For blank controls, a 30 μl potassium phosphate buffer (50 mM, pH 7.8) was added into the reaction system instead of the enzyme extract. The increase in absorbance at 560 nm, due to the formation of formazan, was recorded. SOD activity was calculated as $A_{enzyme} - A_{control}$. One unit of SOD is defined as the amount of enzyme that causes a 50% inhibition of the aforementioned reaction in comparison with a blank sample.

Total CAT activity was determined spectrophotometrically by measuring the rate of H_2O_2 consumption (extinction coefficient 39.4 mM^{-1} cm^{-1}) at 240 nm for 3 min [44]. The reaction mixture (3.0 ml) contained 50 mM potassium phosphate (pH 7.0) and 2% H_2O_2. Immediately, after the addition of 30 μl enzyme extract, the initial linear rate of decrease in absorbance at 240 nm was used to calculate the activity. One unit is defined as the amount of catalase decomposing 1.0 μmol of hydrogen peroxide per minute at pH 7.0 at 25°C. In blank controls, the same amount of 50 mM sodium phosphate buffer (30 μl, pH 7.0) was added into the reaction system instead of the enzyme extract.

Total APX activity was assayed as described in Mishra et al. [68]. The reaction mixture (3.0 ml) contained 50 mM potassium phosphate (pH 7.0), 15 mM ascorbic acid, and 30 mM H_2O_2 and 30 μl enzyme extract. The reaction at 25°C was initiated by the addition of H_2O_2. APX activity was immediately measured by recording the decrease in absorbance at 290 nm (extinction coefficient 2.8 mM^{-1} cm^{-1}) for 2 min. One unit of APX is defined as the amount of enzyme required to consume 1.0 μmol of ascorbate per min. Correction was done for the low, nonenzymatic oxidation of ASC by H_2O_2 [69]. In blank controls, a 30 μl potassium phosphate buffer (50 mM, pH 7.0) was added into the reaction system instead of the enzyme extract.

Total GR activity was determined at 25°C by measuring the rate of NADPH oxidation [47]. The reaction mixture (3.0 ml) contained 50 mM potassium phosphate (pH 7.8), 2.0 mM Na_2EDTA, 0.15 mM NADPH, 0.5 mM oxidized glutathione (GSSG), and 50 μl of enzyme extract. NADPH was added to start the reaction, and the decrease in absorbance at 340 nm (extinction coefficient 6.2 mM^{-1} cm^{-1}) was recorded as soon as the reaction began. Corrections were made for the background absorbance at 340 nm, without the addition of NADPH. One unit of GR is defined as the amount of enzyme that oxidizes 1.0 μmol of NADPH per min. For blank controls, a 50 μl potassium phosphate buffer (50 mM, pH 7.8) was added into the reaction system instead of the enzyme extract.

Each value (±SE) is the mean of three plants, and values in the same column followed by different letters are significantly different ($P < 0.05$) between control and NaCl treatment.

Table 4. Effects of increasing NaCl on activity of SOD, CAT, APX, and GR in roots of *K. obovata* and *B. gymnorhiza*.

Treatment	*K. obovata*				*B. gymnorhiza*			
	SOD	**CAT**	**APX**	**GR**	**SOD**	**CAT**	**APX**	**GR**
Control	49.1 ± 8.6a	107.4 ± 6.5b	62.0 ± 2.2a	16.5 ± 3.1a	38.1 ± 3.0a	69.3 ± 24.7a	58.7 ± 1.1a	5.8 ± 0.6b
NaCl (100 mM)	67.5 ± 17.6a	138.9 ± 7.5a	76.4 ± 5.4a	20.0 ± 3.1a	32.6 ± 4.5a	37.5 ± 9.0a	64.9 ± 7.5a	10.4 ± 1.5a
Control	61.2 ± 5.9b	223.9 ± 3.3a	102.9 ± 1.9a	25.8 ± 3.4a	52.2 ± 4.2a	88.7 ± 8.2a	181.2 ± 19.5a	22.5 ± 0.2a
NaCl (200 mM)	83.8 ± 5.0a	205.7 ± 22.8a	90.7 ± 16.5a	32.0 ± 2.6a	42.2 ± 7.9a	89.1 ± 9.9a	179.0 ± 10.1a	9.7 ± 1.6b
Control	66.2 ± 8.6a	135.6 ± 21.8a	83.6 ± 6.4a	22.1 ± 6.4a	32.0 ± 4.9a	118.0 ± 1.4a	130.5 ± 12.4a	18.9 ± 3.3a
NaCl (300 mM)	64.4 ± 10.9a	150.5 ± 29.1a	47.3 ± 4.7b	16.0 ± 1.0a	46.4 ± 6.6a	125.2 ± 2.1a	60.4 ± 11.7b	12.9 ± 3.3a
Control	52.2 ± 13.9b	331.3 ± 4.0a	111.9 ± 6.4a	19.9 ± 1.2b	30.6 ± 9.4b	75.9 ± 5.1b	116.1 ± 15.7b	9.5 ± 1.4a
NaCl (400 mM)	74.8 ± 4.2a	356.6 ± 15.1a	129.8 ± 2.5a	36.8 ± 4.1a	59.7 ± 8.6a	250.7 ± 29.6a	213.9 ± 16.3a	7.4 ± 2.1a

K. obovata and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. NaCl saline was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Roots of control and salinized plants were harvested at day 2, day 5, day 9, and day 14, respectively. Three replicated plants per treatment were harvested at each sampling time. Leaf tissues (ca. 0.5 g) were ground in cold mortars using liquid nitrogen and homogenized in a 3.0-ml ice-cold extraction buffer [50 mM potassium phosphate, pH 7.0, 1.0 mM EDTA, 1%(w/v) PVP]. The extracts were centrifuged at 10,000 × *g* for 20 min at 4°C and used for the assays of superoxide dismutase (SOD), catalase (CAT), and glutathione reductase (GR). For ascorbate peroxidase (APX) measurement, 1.0 mM ascorbic acid (ASC) was added into the enzyme extraction buffer [27]. Protein concentration in the supernatant was determined according to Bradford [66] using bovine serum albumin as standard. Methodologies for total activity of SOD, CAT, APX, and GR are shown in **Table 4** legend.

Each value (±SE) is the mean of three plants, and values in the same column followed by different letters are significantly different ($P < 0.05$) between control and NaCl treatment.

Table 5. Effects of increasing NaCl on activity of SOD, CAT, APX, and GR in leaves of *K. obovata* and *B. gymnorhiza*.

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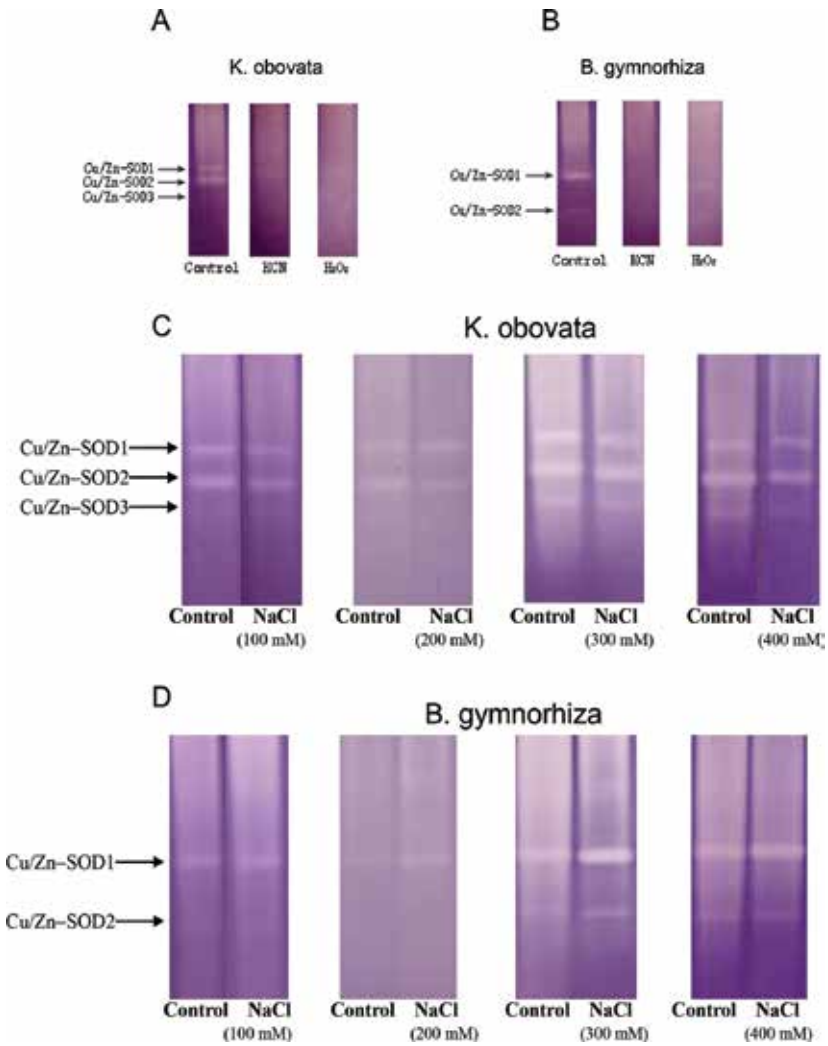

Figure 1. Identification of root SOD isoenzymes and effect of increasing NaCl on SOD isoforms in roots of *K. obovata* and *B. gymnorhiza*. (A and B) Identification of root SOD isoenzymes. Different isoforms of SOD in *K. obovata* and *B. gymnorhiza* were determined by incubating the gels with 5 mM H_2O_2 to inhibit both Cu/Zn-SOD and Fe-SOD or with 5 mM KCN to inhibit only Cu/ZnSOD [70]. Meanwhile, Mn-SOD activity was obtained since it is resistant to both inhibitors, H_2O_2 and KCN. (C and D) NaCl effects on SOD isoforms. *K. obovata* and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. Increasing NaCl was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Control plants were kept well watered with no addition of NaCl. Roots of control and salinized plants were harvested at day 3, day 6, day 10, and day 15, respectively. Three replicated plants per treatment were harvested at each sampling time. The three replicates were extracted independently and ran on three different gels, a representative one of which is shown in the figure. Electrophoretic separation for CAT and SOD was performed at 4°C using the Laemmli (1970) buffer systems [71]. Prior to loading onto the gels, crude protein extracts were mixed with 10% glycerol (v/v) and 0.25% bromophenol blue. Separating gel (10%) and stacking gel (3.9%) were used for native PAGE of SOD isoenzymes. SOD isoenzymes were visualized by the activity staining [72]. In each track 20 μg of soluble protein was applied to native polyacrylamide gel electrophoresis at 4°C. The gels were run at a constant current, 35 mA at 4°C for no longer than 6 h. Immediately, after electrophoretic separation, gels were incubated in staining buffer (50 mM potassium phosphate buffer, pH 7.8, 0.1 mM EDTA, 28 mM TEMED, 0.003 mM riboflavin, and 0.25 mM NBT) for 30 min in the dark at room temperature. Thereafter, gels were exposed to two fluorescent tubes (20 W each) until the SOD bands became visible (SOD bands appeared as light bands on a blue background).

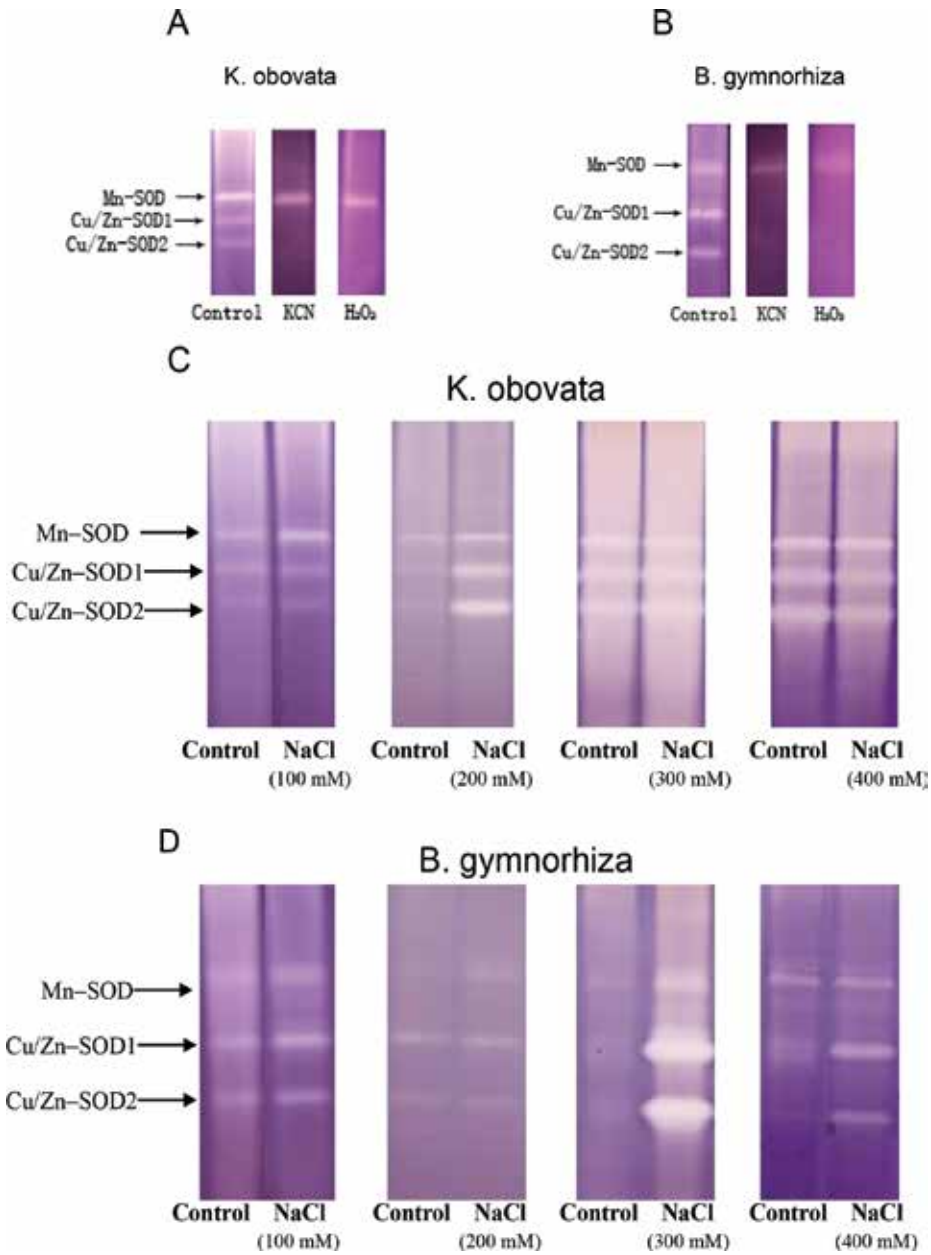

Figure 2. Identification of leaf SOD isoenzymes and effect of increasing NaCl on SOD isoforms in leaves of *K. obovata* and *B. gymnorhiza*. (A and B) Identification of leaf SOD isoenzymes. (C and D) NaCl effects on SOD isoforms. *K. obovata* and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. Increasing NaCl was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Control plants were kept well watered with no addition of NaCl. Leaves of control and salinized plants were harvested at day 3, day 6, day 10, and day 15, respectively. Three replicated plants per treatment were harvested at each sampling time. The three replicates were extracted independently and ran on three different gels, a representative one of which is shown in the figure. In each track 40 μg of soluble protein was applied to native polyacrylamide gel electrophoresis at 4°C. Electrophoretic separation for SOD isoforms is shown in **Figure 1** legend.

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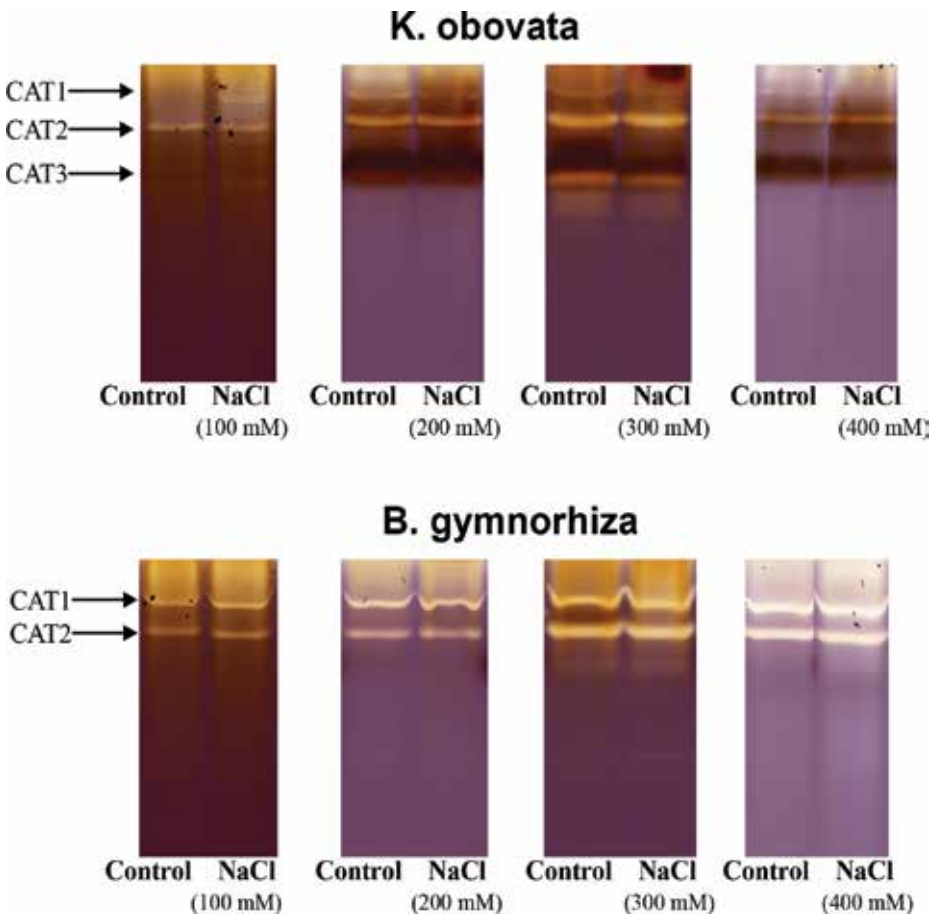

Figure 3. Effect of increasing NaCl on CAT isoforms in roots of *K. obovata* and *B. gymnorhiza*. *K. obovata* and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. Increasing NaCl was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Control plants were kept well watered with no addition of NaCl. Roots of control and salinized plants were harvested at day 3, day 6, day 10, and day 15, respectively. Three replicated plants per treatment were harvested at each sampling time. The three replicates were extracted independently and ran on three different gels, a representative one of which is shown in the figure. Stacking gel (3.9%) and separating gel (7.5%) containing 0.5% soluble starch were used for native PAGE of CAT isoforms. In each track 20 μg of soluble protein was applied to native polyacrylamide gel electrophoresis at 4°C. The activity staining procedure for catalase was followed as per Thorup et al. [73] with modifications. Immediately, after electrophoresis as described above, the gel was incubated in a solution containing 18 mM sodium thiosulphate and 679 mM H_2O_2 for 30 s at room temperature (25°C). The gel was then rinsed with distilled water and incubated in 90 mM potassium iodide solution acidified with 0.5% glacial acetic acid. Finally, negative bands, representing CAT enzymes, appeared on the blue background of the gel.

2.4.2. Salt-elicited antioxidant enzymes contributed to ROS homeostasis

Salt-elicited antioxidant enzymes contributed to ROS homeostasis in the two mangroves but with different patterns. Salinized *K. obovata* exhibited an early and rapid antioxidative defense as compared to *B. gymnorhiza*. After exposure to 100–200 mM NaCl, total SOD activity in *K. obovata* leaves marked increased coincident with the increase of Cu/Zn-SOD1, Cu/Zn-

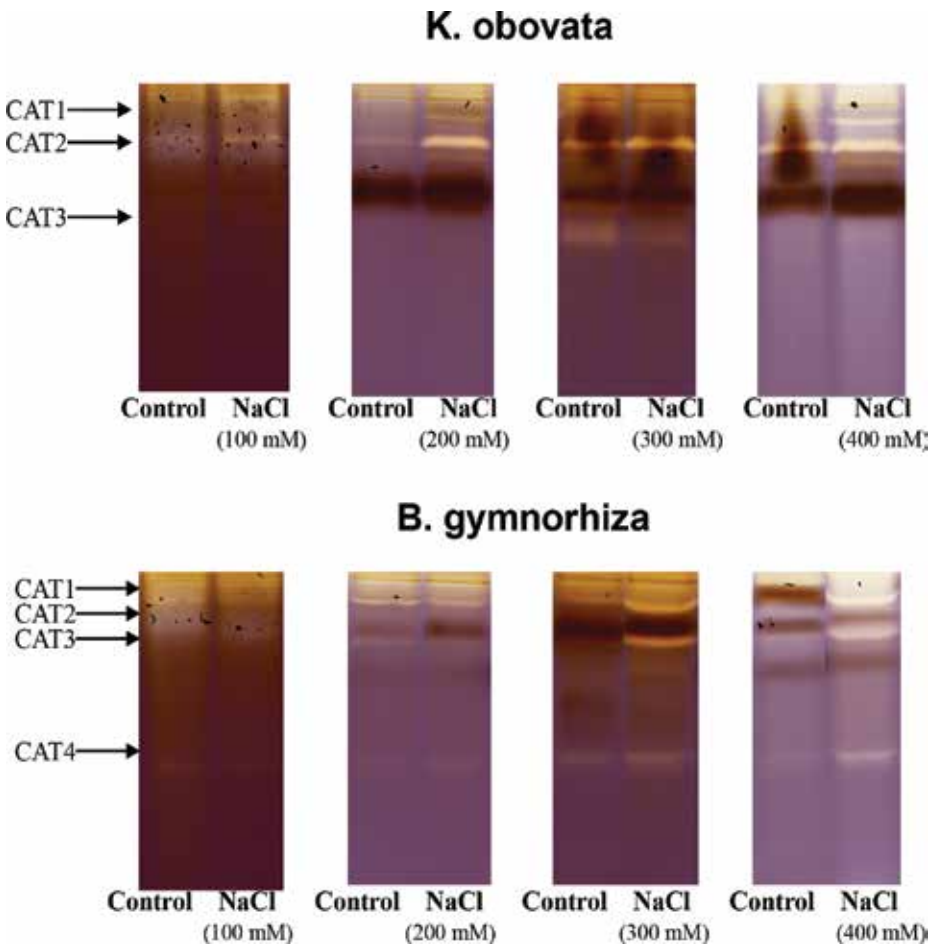

Figure 4. Effect of increasing NaCl on CAT isoforms in leaves of *K. obovata* and *B. gymnorhiza*. *K. obovata* and *B. gymnorhiza* plants were subjected to increasing NaCl treatment. Increasing NaCl was applied at day 1 (100 mM), day 3 (200 mM), day 6 (300 mM), and day 10 (400 mM). Control plants were kept well watered with no addition of NaCl. Leaves of control and salinized plants were harvested at day 3, day 6, day 10, and day 15, respectively. Three replicated plants per treatment were harvested at each sampling time. The three replicates were extracted independently and ran on three different gels, a representative one of which is shown in the figure. In each track 40 μg of soluble protein was applied to native polyacrylamide gel electrophoresis at 4°C. Electrophoretic separation for CAT isoforms is shown in **Figure 3** legend.

SOD2, and Mn-SOD (**Table 5**, **Figure 2**), even though Fe-SOD was not detected as that reported in other mangroves [51]. CAT in *K. obovata* leaves resembles the trend of SOD, and the increased activity was presumably due to the rise of CAT2 (**Table 5**, **Figure 4**). This is inconsistent with a previous report conducted on *B. parviflora* in which NaCl induced a decrease of CAT activity [51]. In the present study, the coincident increase of CAT with SOD in *K. obovata* reveals an elevated capacity to detoxify both $O_2^{\bullet -}$ and H_2O_2 that is caused by NaCl, which is required for rapid removal of ROS and thus avoids oxidative damage. Likewise,

we found that a salt-resistant *Populus* species, *P. euphratica*, was able to enhance active oxygen detoxification by increasing antioxidant enzymes at an early stage of salt stress, thus preventing an oxidative burst [26]. Protein abundance of SOD in *K. obovata* leaves might increase under a high level of NaCl [53]. Furthermore, Jing et al. showed that NaCl increased *KcCSD* transcription in *K. candel* leaves [16]. Thus, it could be inferred that *K. obovata* would upregulate the gene expression of antioxidant enzymes to deal with a long-term saline stress.

Salt-induced elevation of antioxidant enzymes in *B. gymnorhiza* was usually found at high salinity. SOD, APX, and CAT in roots and leaves of *B. gymnorhiza* were all upregulated by 400 mM NaCl (**Tables 4** and **5**). Native PAGE analyses showed that the elevation of leaf SOD in salinized *B. gymnorhiza* resulted from the increase of all detected SOD isoforms, Mn-SOD, Cu/Zn-SOD1, and Cu/Zn-SOD2 (**Table 5** and **Figure 2**), whereas the rise of SOD activity in roots was mainly the result of Cu/Zn-SODs (**Table 4** and **Figure 1**). A similar trend was found in salt-stressed *B. parviflora* in which a significant enhancement of SOD was observed in leaves, mainly due to an increase in Mn-SOD and Fe-SOD2 [51]. NaCl-induced activity of CAT in *B. gymnorhiza* leaves was due to the increase of CAT2, CAT3, and CAT4 (**Table 5** and **Figure 4**).

Noteworthy, both *K. obovata* and *B. gymnorhiza* maintained evident activity of each CAT isoform in root tissues at 400 mM NaCl (**Figure 3**), showing a constant and stable capacity to control H_2O_2 levels. This may partly explain the finding that root $O_2^{\bullet -}$ increased by 82–83%, whereas there was no corresponding changes in H_2O_2 when *K. obovata* and *B. gymnorhiza* were subjected to 400 mM NaCl (**Table 1**).

3. Conclusions

We conclude that both *K. obovata* and *B. gymnorhiza* maintained ROS homeostasis as external NaCl saline increased from 100 to 400 mM but via different pathways:

i. *K. obovata* restricted the increase of salt influx, which is necessary to avoid abrupt increase of ROS. Moreover, *K. obovata* was sensitive to lower salt stress and rapidly initiated antioxidant defense to scavenge active oxygen species by, at least in part, components of the ASC-GSH cycle, e.g., SOD, APX, CAT, and GR. The Na^+/H^+ antiport system and proton pumps, which accelerate the salt exclusion across the plasma membrane, need to be further investigated.

ii. *B. gymnorhiza* maintained higher capacity to detoxify ROS at high salinity; furthermore, the effective vacuolar salt compartmentation in mesophyll cells and the preferential accumulation of Na^+ and Cl^- in epidermal vacuoles may benefit *B. gymnorhiza* plants to reduce ROS production in the mesophyll. Together with antioxidant mechanisms, both enzymatic and nonenzymatic, the critical balance between ROS production and ROS detoxification is remained under salt stress. To elucidate the mechanism underlying the vacuolar compartmentation, critical ion channels and transporters in the vacuolar membranes need to be identified in future investigations.

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Conflict of interest

The authors declare that there is no conflict of interest.

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Section 4

Mangrove Faunal Ecology

Chapter 6

Diversity and Distribution of Polychaetes in Mangroves of East Coast of India

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Additional information is available at the end of the chapter

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Abstract

This research article reports an exhaustive account on the mangrove-associated polychaetes. Polychaetes are an important component in marine benthic communities and they play a major ecological role in mangrove ecosystem. This article gives an overview of polychaete diversity associated to five major mangrove forests of east coast of India (Muthupettai, Pichavaram, Coringa, Bhitarkanika and Sundarban). The results of this survey indicated that the physicochemical parameters did not vary much except a few parameters that showed only marginal variations. With regard to the macrobenthic organisms, the polychaetes topped the list. Crustaceans were found to be the next dominant group in the order of abundance and followed by gastropods and bivalves of the total benthic organisms collected. The results of the statistical analysis revealed that the parameters such as salinity, pH, silt, clay, total organic carbon (TOC), total nitrogen (TN) and total phosphate (TP) were manifested as best match in determining benthic fauna distributions followed by TOC, slit, clay and TP. The maximum number of polychaete species was recorded from Sundarban mangroves (68 species) and minimum in Muthupettai mangroves (39 species).

Keywords: environmental factors, macrofauna, population density, statistical analyses, southeast coast of India

1. Introduction

Mangroves are unique coastal ecosystem contributing as a rich store house of biodiversity. Mangrove forests are extremely important coastal resources [1] which play a pivotal role in socio-economic development. It also plays a major role as nursery ground for juveniles of a plethora of fin and shell fishes. A total of 54 mangrove species belonging to 20 genera and

16 families are reported globally [2]. The most dominant families among mangroves are Avicenniaceae, comprised of one genus and eight species and the Rhizophoraceae having 16 genera and approximately 120 accepted species [3–5]. According to FAO [6] the mangrove area worldwide is estimated to cover from 12 to 20 million hectares. According to Giri *et al*. [7], the mangroves are found in Asia (42%), Africa (20%), North and Central America (15%), Oceania (12%) and South America (11%). In India, the total area under mangrove cover is 4,445km^2, of which about 60% is found on the east coast, 23% on the west coast and the remaining 17% in Andaman & Nicobar Islands [8]. Three types of mangroves habitats, namely deltaic, backwater- estuarine and insular are reported to occur in India. The deltaic mangroves are luxuriantly present on the east coast (Bay of Bengal) where the gigantic rivers make mighty deltas such as the Gangetic, the Mahanadi, the Godavari and Cauvery deltas. The backwater-estuarine types of mangroves exist along the west coast (Arabian Sea), and are characterized by typical funnel-shaped estuarine system of major rivers (Indus, Narmada, Tapti, etc.) or occur in the backwaters, creeks, and neritic inlets. The insular mangroves are present in Andaman and Nicobar Islands, wherein many tidal estuaries, small rivers, neritic inlets, and lagoons support a rich mangrove flora. The mangroves in east coast are large and widespread owing to the nutrient-rich alluvial soil formed by the rivers-Ganga, Brahmaputra, Mahanadi, Godavari, Krishna and Cauvery- and a perennial supply of freshwater along the deltaic coast coupled with smooth and gradual slope which provides larger for colonization of mangroves [9].

Annually, mangroves approximately sequester 22.8 million metric tons of carbon, covering 0.1% of the earth's forests, which is accounting for 11% of terrestrial carbon into the ocean [10] and 10% of the terrestrial dissolved organic carbon exported to the ocean [11]. Despite its enormous benefits, which biodiversity commands, the mangroves have always been given least importance from the point of view of benthic biodiversity by the scientific community.

Benthic communities are either epibenthic or infaunal invertebrates [12, 13] that occur at the soil surface or at the surface of bottom entities, and within the substrate, respectively (Encyclopedia Britannica, Inc. 2015). Benthic fauna are divided into two major groups namely macrofauna and meiofauna. The macrofauna are those organisms which are in the size range of more than 0.5 mm or 500 micron and the meiofauna are the fauna which are less than 0.5 mm but greater than 0.062 mm or 62 microns [12]. They are an important component that influences the productivity of the habitat, and thereby helps in recycling of nutrients and in turn promotes primary productivity [14]. Macro-benthos also help in decomposition and the breakdown of particulate organic material by exposing them to microbes and their waste materials contain rich nutrients forming food for other consumers. Of the various macro benthic taxa, polychaetes constitute the most dominant group constituting about 80% of the total macro benthic community and their diet include microbial, meiobial, and organic substances [15]. Polychaetes are secondary producers of mangroves subsoil habitat production, which is essential for tracing the biotic stability of the area from fisheries point of view [16]. For example, decomposition, the fundamental process wherein the dead organic matter and leaf litter is broken down into CO_2 and simple inorganic molecules which take place through polychaetes in the benthic environment. Added to the utilities stated above, polychaetes are also used as most veritable marine organisms for the

detection of pollution and are considered as the taxonomic group with the highest level of sensitivity to perturbation of the soft substrata [17].

No comprehensive study has been undertaken so far on benthic biodiversity in general and polychaete taxonomy in particular in the mangroves of east coast of India. Taking cognizance of the facts stated above, a case study on the diversity and distribution pattern of polychaetes in five major mangroves of east coast of India is posted in this article.

2. Material and methods

2.1. Study area

For the present investigation, survey was conducted in five different mangrove ecosystems of east coast of India. The description of the study area is detailed in the following section (**Table 1** & **Figure 1**).

The water, sediment and macrofaunal samples were collected seasonally from five major mangrove ecosystem of east coast of India during 2013–2014. In each mangrove, three stations representing i) Land ward zone, ii) core mangrove, and iii) Seaward zone, were fixed and thus altogether 15 stations were sampled:

Name of the mangroves	Station code	Locations	
		Latitude (N)	Longitude (E)
Muthupettai	MUT-1 (LW)	10° 18′ 4.96″ N	79° 22′ 27.59″ E
	MUT-2 (CM)	10° 18′ 10.27″ N	79° 22′ 26.51″ E
	MUT-3 (SW)	10° 18′ 14.64″ N	79° 22′ 25.28″ E
Pichavaram	PIC-1 (LW)	11° 26′ 0.49″ N	79° 48′ 29.06″ E
	PIC-2 (CM)	11° 25′ 46.06″ N	79° 48′ 2.05″ E
	PIC-3 (SW)	11° 25′ 56.45″ N	79° 48′ 16.14″ E
Coringa	COR-1 (LW)	16° 49′ 29.16″ N	82° 20′ 44.74″ E
	COR-2 (CM)	16° 47′ 42.17″ N	82° 20′ 11.73″ E
	COR-3 (SW)	16° 45′ 7.86″ N	82° 19′ 58.86″ E
Bhitarkanika	BIT-1 (LW)	20° 42′ 0.96″ N	87° 0′ 56.96″ E
	BIT-2 (CM)	20° 44′ 40.07″ N	86° 53′ 35.99″ E
	BIT-3 (SW)	20° 42′ 43.98″ N	86° 52′ 39.13″ E
Sundarbans	SUN-1 (LW)	21° 44′ 53.02″ N	89° 9′ 29.38″ E
	SUN-2 (CM)	21° 50′ 55.37″ N	89° 5′ 12.46″ E
	SUN-3(SW)	22° 3′ 27.36″ N	89° 2′ 23.73″ E

LW = Landward zone, CM = Core mangrove zone, SW = Seaward zone.

Table 1. Geographical location of sampling stations in various mangrove ecosystems covered.

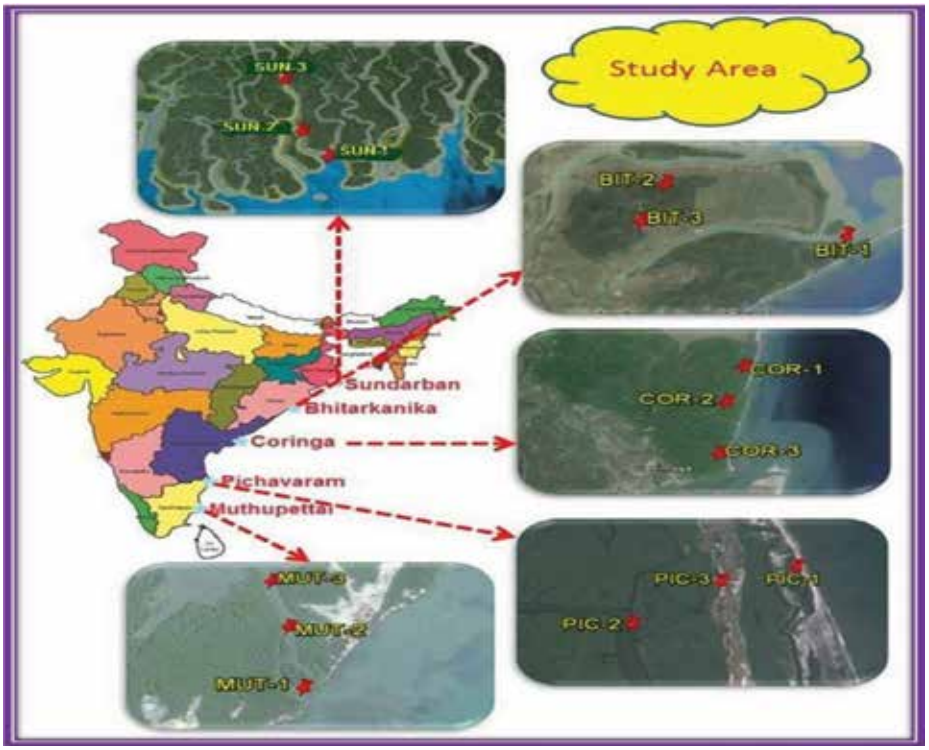

Figure 1. Map showing the various mangrove ecosystems studied in or around east coast of India.

The major mangrove forests selected for the present study are the following:

i) Muthupettai mangroves (Lat.$10^0$18′N; Long.$79^0$49′E) are located on a lagoon environment. They are situated 400 km south of Chennai and lie on the southern part of Cauvery deltaic region along the southeast coast of India. Mangroves spread to an area of about 6800 ha, in which *Avicennia marina* is the single dominant mangrove species accounting for about 95% of the vegetative cover.

ii) Pichavaram mangroves (Lat.$11^0$27′N; Long.$79^0$47′E) are situated amidst the Vellar estuary in the north and the Coleroon estuary in the south. These are a repository of rare, endemic and endangered species of mangroves. In this mangrove, about 81 species belonging to 41 families have been recorded.

iii) Coringa mangroves (Lat. 16° 44′ to 16°53′ N and Long. 82°14′ to 82°22′ E) are located south of Kakinada Bay, Andhra Pradesh state, India. Coringa mangroves receive freshwater from Coringa and Gaderu rivers, distributaries of Gautami Godavari River, and neritic waters from Kakinada bay.

iv) Bhitarkanika mangroves cover an area of 650 km^2 in the river delta of the Brahmani and Baitarani rivers of Odisha state. Next to Sundarbans, Bhitarkanika (Lat. 20°4′ to 20°8′ N; 86°45′ to 87°50′ E) is the second largest viable mangrove ecosystem in India harboring more than 70 species of mangrove and its associates.

v) Sundarban is one among the world's largest delta covering 10,200 sq.km of mangrove forest, spread over India (4200 sq. km of Reserved Forest) and Bangladesh (6000 sq.km approx. of Reserved Forest). The total area of Sundarban region in India is 9600 sq. km, which constitutes the Sundarban Biosphere Reserve, West Bengal. India.

2.2. Collection of water and sediment samples

The environmental parameters such as pH, salinity, temperature and dissolved oxygen (DO was measured following the modified Winkler's method [18] in the site itself. The sediment nutrient parameters such as total nitrogen (TN) was estimated by following the method of Strickland and Parsons [18], total phosphorous (TP) by following the method of Menzel and Corwin [19]; and total organic carbon (TOC) by following the standard method of El Wakeel and Riley [20].

2.3. Biological sample (field and lab routines)

In each station, three replicate samples were collected using Peterson grab. This type of grab is considered to be the most efficient gear in obtaining the good penetrative samples in shallow water environments. The grab employed was found to take a sample covering an area of $0.1m^2$. The procedure adopted for sampling was following the method of Mackie [21]. After collecting the samples, they were emptied into a plastic tray. The larger organisms were handpicked immediately from the sediments and then sieved through 0.5 mm mesh screen. The organisms retained by the sieve were placed in a labeled container and fixed in 5–7% formalin. Subsequently, the organisms were stained with Rose Bengal solution (0.1 g in 100 ml of distilled water) for greater visibility during sorting. All the species were sorted, enumerated and identified to the advanced possible level with the consultation of available literature. The works of Fauvel [22] and Day [23] and http://www.marinespecies.org/polychaeta/ were referred for identification.

2.4. Statistical analyses

The data were approached to various statistical methods namely univariate, graphical/distributional and multivariate methods available in PRIMER (Ver. 7.) statistical software [24]. The data were analyzed for diversity index (H') using the method of Shannon – Wiener's formula [25]; for species richness (d) using the formula of Margalef [26] and species evenness (J') using Pielou [27].

Cluster analysis was done to find out the similarities between the samples/stations/regions. The most commonly used clustering technique is the hierarchical agglomerative method. MDS (non - metric Multi-Dimensional Scaling) [28, 29], was used to find out the similarities (or dissimilarities) between each pair of entities to produce a 'map', which would ideally show the interrelationships of all.

The principal component analysis-Bi-plot (PCA-Bi-plot), a multivariate procedure capable of providing a data reduction and easy visualization through the Pearson correlation between the physicochemical parameters and sampling stations were performed using XLSTAT-Pro version 5.1.4. Canonical Correspondence Analysis (CCA) was also done to relate the abundance of benthic species with linear combination of environmental variables [30, 31].

Canonical Correspondence Analysis (CCA) allows to obtaining a simultaneous representation of the sites, the objects, and the variables in two or three dimensions that is optimal for a variance criterion [30]. To confirm the results obtained through CCA, BIO-ENV procedure [32] was also employed. A weighted Spearman rank correlation coefficient ($\varrho\omega$) was used to determine the harmonic rank correlation between the biological variable and all possible combinations of the environmental variables.

2.5. Results

2.5.1. Environmental variables

The mean values of physicochemical parameters recorded at each sampling station are summarized in **Table 2**. The temperature ranged between 20.43°C and 33.67°C with maximum at Muthupettai and minimum at Sundarbans; salinity values varied between 12.3 psu and 33.12 psu with maximum at Muthupettai and minimum at Sundarbans; pH values fluctuated between 7.10 and 8.23 with maximum at Pichavaram and minimum at Sundarbans; Dissolved Oxygen ranged between 3.80 and 8.23 mg/l with maximum at Bhitarkanika and minimum at Pichavaram. Total nitrogen value ranged between 3.48 and 5.98 μg/g with maximum at Muthupettai and minimum at Sundarbans; Total phosphate value ranged between 0.88 and 1.74 μg/g with maximum at Coringa and minimum at Bhitarkanika; TOC (Total organic carbon) in sediment ranged between 6.45 and 16.52 μg/g with maximum at Sundarbans and minimum at Coringa mangroves. The level of sand in sediment ranged between 47.9% and 78.64% with maximum at Pichavaram and minimum at Sundarban mangroves; Silt in sediment ranged between 10.1 and 31.4% with maximum at Sundarbans and minimum at Bhitarkanika mangroves and the clay content ranged between 6.5 and 23.8% with maximum at Sundarbans and minimum at Pichavaram mangroves.

2.5.2. Principal component analysis

The PCA was performed using physicochemical parameters to set a well defined distinction between the stations and the parameters. The PCA drawn for five mangroves showed 85.67% variance of the total axis wherein the first axis (F1) explained up to 62.47% of the total variance and F2 axis explained only 23.20% of the total variance. When the results were viewed, the parameters such as salinity, pH, Silt, Clay, TN, TP and TOC got positively correlated with MUT-1, PIC-1, BIT-2, PIC-2, SUN-2 and SUN-3 and MUT-1 while water temperature, DO and sand were negatively correlated with stations MUT-3, PIC-3, BIT-1, BIT-3, SUN-1, COR-1, COR-2 and COR-3 (**Figure 2**).

2.5.3. Biological entities

2.5.3.1. Species composition of macrofauna

In the present study, organisms of the following five groups were recorded in the benthic samples collected: 1. polychaetes, 2. crustaceans, 3. bivalves, 4. gastropods and 5. 'others.' As many as 97 species of macrofauna were recorded from 5 mangrove ecosystems of the present

Parameters	Muthupettai		Pichavaram		Coringa		Bhitarkanika		Sundarbans	
	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
Temperature ^{0}C	26 ± 0.02	33.67 ± 0.41	26.33 ± 0.23	30.50 ± 0.52	22.5 ± 0.21	29.17 ± 0.29	23.5 ± 0.32	29.33 ± 0.40	20.43 ± 0.31	31.17 ± 0.29
Salinity (psu)	29.34 ± 0.19	33.12 ± 0.68	18.80 ± 0.43	30.33 ± 0.32	17.5 ± 0.17	29.40 ± 0.31	12.5 ± 0.21	21.77 ± 0.7	12.3 ± 0.45	27.07 ± 0.73
pH	7.13 ± 0.35	7.85 ± 0.47	7.33 ± 0.21	8.23 ± 0.15	7.18 ± 0.32	7.67 ± 0.28	7.2 ± 0.09	7.47 ± 0.14	7.10 ± 0.23	7.7 ± 0.21
DO mg/l	5.34 ± 0.86	6.37 ± 0.41	3.80 ± 0.53	5.23 ± 0.10	4.06 ± 0.18	6.45 ± 0.05	4.33 ± 0.18	7.27 ± 0.34	4.06 ± 0.63	6.33 ± 0.42
TN μg/g	4.69 ± 0.52	5.98 ± 0.78	4.78 ± 0.24	5.03 ± 0.46	4.22 ± 0.78	4.75 ± 0.15	3.76 ± 0.26	5.01 ± 0.09	3.48 ± 0.21	5.41 ± 0.34
TP μg/g	1.12 ± 0.17	1.45 ± 0.28	1.30 ± 0.24	1.62 ± 0.09	0.95 ± 0.05	1.74 ± 0.14	0.88 ± 0.03	1.32 ± 0.08	1.02 ± 0.19	1.47 ± 0.15
TOC mgC/g	9.86 ± 0.07	16.36 ± 0.43	9.98 ± 0.90	16.36 ± 0.22	6.45 ± 0.35	14.4 ± 0.51	7.5 ± 0.07	15.54 ± 0.42	6.55 ± 0.41	16.52 ± 0.13
Sand %	56.4 ± 0.36	67.18 ± 0.05	63.55 ± 0.41	78.64 ± 0.45	64.01 ± 0.28	70.45 ± 0.32	67.6 ± 0.27	75.41 ± 0.09	47.9 ± 0.98	52.1 ± 0.29
Silt %	22.99 ± 0.51	33.22 ± 0.54	14.08 ± 0.64	29.83 ± 0.21	12.34 ± 0.78	21.35 ± 0.17	10.1 ± 0.43	12.32 ± 0.24	26.1 ± 0.29	31.4 ± 0.46
Clay %	9.01 ± 0.86	12 ± 0.02	6.5 ± 0.56	10.5 ± 0.09	12.21 ± 0.45	18.2 ± 0.27	14.34 ± 0.74	20.78 ± 0.15	18.2 ± 0.32	23.8 ± 0.19

Table 2. Physicochemical parameters recorded in five different mangroves ecosystem of east coast of India.

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study. Of these species, polychaetes were found to be the largest component in the collection with 68 species. Crustaceans emerged as next dominant group in the order of abundance with 11 species. The bivalves and gastropods came next in the order with 8 and 6 species respectively and the group 'others' came last in the order with 4 species.

In Muthupettai mangroves, a total of 69 species were recorded. Among these, 39 species belonged to polychaetes, 10 species to crustaceans, 8 species each to bivalves and gastropods and 4 species to group 'others.' With respect to Pichavaram mangroves, a total of 88 species of macrofauna were recorded. Among these, there were 59 species of polychaetes, 10 species were crustaceans, 8 and 7 species were bivalves and gastropods respectively and 4 species of 'others.'

Regarding Coringa, 77 species of macrofauna were found. Among these, 50 species of polychaetes, 9 species of crustaceans and 8 and 7 species of bivalves and gastropods and 3 species of 'others' were recorded. Coming to Bhitarkanika mangroves, 81 species of macrofauna were found. Among these, 54 species of polychaetes, 10 species of crustaceans and 7 species each of bivalves and gastropods and 3 species of 'others' were recorded.

Coming to Sundarban mangroves, 97 species of macrofauna were found. Of these, 68 species of polychaetes, 11 species of crustaceans and 8 and 6 species of bivalves and gastropods respectively, and 4 species of 'Others' were recorded.

Among the polychaetes, *Amphinome* sp., *Ancistrosyllis* sp., *Brada villosa, Capitella capitata, Chone collaris, Cossura coasta*, *Eunice* sp., *Euclymene* sp., *Glycera unicornis, Goniada* sp., *Hyboscolex longiseta*, *Notomastus aberans, Perinereis* sp., *Phylo* sp., *Pherusa monroi, Pista cristata, Polydora capensis, Cirratulus* sp., *Laonice cirrata, Maldane sarsi,. Magelona cincta, Malacoceros indicus, Nephtys dibranchis, Nereis diversicolor, Prionospio pinnata, Prionospio sexoculata, Sabella* sp., *Spio filicornis, Sternaspis scutata* and *Syllis gracilis* were found to be the commonly occurring species in the samples collected in five mangrove ecosystems. With respect to crustaceans, *Apseudes* sp., *Grandidierella* sp., *Gammarus* sp., *Urothoe* sp., *Angeliera* sp., *Mirocerberus* sp. and *Campylaspis* sp. showed consistency

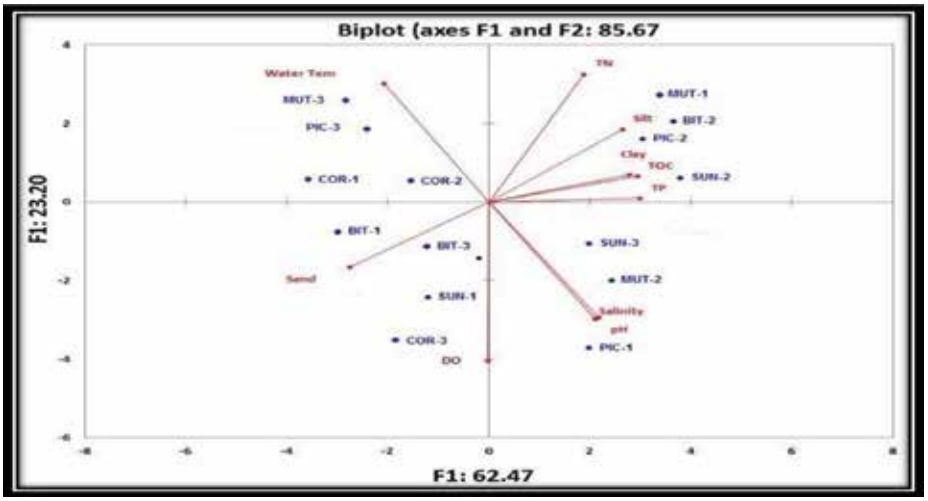

Figure 2. Principle component analysis – Biplot drawn for the relation between physico chemical parameters and stations in five mangrove ecosystems.

S. No	Polychaetes	S-1	S-2	S-3	S-4	S-5	S. No	Polychaetes	S-1	S-2	S-3	S-4	S-5
1.	*Amphinome* sp.	*	*	*	–	*	35.	*Nereis diversicolor*	*	*	*	–	*
2.	*Ancistrosyllis* sp.	*	*	*	*	*	36.	*Nereis* sp.	*	*	*	*	*
3.	*Boccardia polybranchia*	*	–	*	*	–	37.	*Notomastus aberans*	*	*	*	*	*
4.	*Brada villosa,*	*	–	*	*	*	38.	*Notomastus latericeus*	–	–	*	–	*
5.	*Capitella capitata*	*	*	*	*	*	39.	*Notoproctus pacificus*	*	–	*	*	*
6.	*Chone collaris*	*	*	*	–	*	40.	*Orbinia angrapequensis*	*	*	*	*	–
7.	*Chone letterstedti*	*	–	*	*	*	41.	*Paraonidea sp*	*	*	*	–	*
8.	*Cirratulus sp.*	*	*	*	–	–	42.	*Paraonis sp.*	*	*	*	*	–
9.	*Cirrophorus branchiatus*	*	*	*	*	*	43.	*Perinereis* sp.	*	*	*	*	*
10.	*Cossura coasta*	*	–	*	*	*	44.	*Perinereis falsovariegata*	*	–	*	*	*
11.	*Dendronereis arborifera*	–	*	*	*	*	45.	*Pherusa monroi*	*	–	*	*	*
12.	*Euclymene .oerstedii*	*	–	*	–	–	46.	*Phylo* sp.	*	*	*	*	–
13.	*Euclymene sp.*	*	*	*	–	*	47.	*Pista cristata*	*	–	*	*	*
14.	*Eunice sp*	*	*	*	*	*	48.	*Platynereis dumerilii*	*	–	*	*	*
15.	*Eurythoe complanata*	*	*	*	*	*	49.	*Polydora sp.*	*	*	*	*	*
16.	*Eurythoe parvecarunculata*	*	–	*	*	–	50.	*Polyphysia crassa*	*	–	*	–	*
17.	*Exogone clavator*	–	*	*	*	*	51.	*Prionospio cirrifera*	*	*	*	*	*
18.	*Fabrica filamentosa*	*	–	*	–	*	52.	*Prionospio pinnata*	*	*	*	*	*
19.	*Glycera benguellana*	*	–	*	*	*	53.	*Prionospio sexoculata*	*	–	*	*	*
20.	*Glycera longipinnis*	*	*	*	–	*	54.	*Prionospio sp*	*	–	*	–	–
21.	*Glycera unicornis*	–	*	*	–	*	55.	*Prionospio cirrobranchiata*	*	*	*	*	*
22.	*Goniada emerita*	*	*	*	*	*	56.	*Prionospio pinnata*	*	–	*	–	–
23.	*Hyalinoecia tubicola*	–	–	*	*	*	57.	*Prionospio saldanha*	*	*	*	*	*
24.	*Hyboscolex longiseta*	*	–	*	*	–	58.	*Sabella* sp.	*	*	*	*	*
25.	*Laonice cirrata*	*	*	*	*	*	59.	*Sabellaria intoshi*	*	*	*	*	*
26.	*Lumbrineris albidentata*	–	–	*	*	*	60.	*Scolelepis squamata*	*	–	*	*	–
27.	*Magelona cincta*	*	*	*	–	–	61.	*Spio filicornis*	*	*	*	*	*
28.	*Malacocerous indica*	*	*	*	*	*	62.	*Spiophomianes soderstromi*	*	–	*	*	–
29.	*Maldane sarsi*	*	–	*	–	*	63.	*Sternaspis scutata*	*	*	*	*	*
30.	*Megalomma quadrioculatum*	–	–	*	*	*	64.	*Streblosoma persia*	*	–	*	–	*
31.	*Megaloma* sp.	–	*	*	*	*	65.	*Syllis benguellana*	*	*	*	*	*
32.	*Minuspio cirrifera*	*	–	*	–	–	66.	*Syllis gracilis*	*	*	*	*	*
33.	*Neanthes* sp.	*	*	*	*	*	67.	*Syllis sp.*	*	*	*	*	*
34.	*Nephtys dibranchis*	–	–	*	*	*	68.	*Terebellides stroemi*	*	–	*	*	*

*presence

–absence

S-1, Pichavaram; S-2, Muthupettai; S-3, Sundarban; S-4, Coringa; S-5, Bhitarkanika

Table 3. Distribution and diversity of polychaete in different mangrove ecosystems of east coast of India.

in their occurrence in the entire mangrove ecosystem. With respect to bivalves, *Anadara rhombea*, *Crassostrea madrasensis*, *Katelysia opima, Meretrix meretrix*, *Meretrix casta*, *Perna indica*, and similarly among gastropods, *Cerithidea cingulata, Nassarius stollatus*, *Turritella acutangula* and *Murex trapa* were recorded frequently. Group "others" constitute fish larvae, s*ea urchins,* crab and foraminiferans. The common macro benthic species recorded in various stations of five mangrove ecosystems is shown in **Table 3** & **Figure 3**.

2.5.3.2. Population density of macrofauna

The results of population density recorded in five mangroves are given in the following section: In Muthupettai mangroves, the population density of benthic macrofauna varied from 417 to 3545nos/m^2 with the maximum was noticed during summer and minimum during monsoon. Coming to Pichavaram mangroves, the density of benthic organisms varied between 451 and 5645 nos/m^2 with during summer and minimum during monsoon. Regarding Coringa mangroves, the density of benthic organisms ranged from 386 to 4262 nos/m^2 with maximum during summer and minimum during monsoon. Coming to Bhitarkanika mangroves, the density of benthic organisms varied between 433 and 4862 nos/m^2 with maximum during summer and minimum during monsoon. With respect to Sundarban mangroves, the density of organisms varied from 511 to 6845 nos/m^2. The minimum density was recorded monsoon and maximum during summer. Among the mangroves, the maximum density of macrofauna was recorded in Sundarbans (6845 nos/m^2) during summer and minimum in Muthupettai (3545nos/m^2) during monsoon (**Figure 4**).

Figure 3. Polychaete species recorded in five different mangroves ecosystem from east coast of India.

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2.5.3.3. Percentage composition of benthos

The percentage composition of macrofauna recorded in five different mangroves ecosystems are given below:

In Muthupettai, when the results of percentage composition of benthic fauna were viewed, polychaetes constituted the maximum with 54% of the total benthic organisms followed by crustaceans with 14%, bivalves with 12%, gastropods with 13% each and group 'others' with 7% to the samples collected in Muthupettai mangroves. With respect to Pichavaram mangroves, polychaetes continued to emerge as the dominant group in terms of abundance with a percentage occurrence of 56%. Crustaceans ranked second with a percentage contribution of 15%. Gastropods, bivalves contributed 11%, 12% respectively and 'others' with 6% to the total benthic organisms recorded.

Regarding Coringa, as in other mangroves, polychaetes continued to be the dominant group with 61%, followed by crustaceans, bivalves, gastropods and 'others' with 13%, 12%, 9% and 5% respectively. Coming to Bhitarkanika mangroves, polychaetes remained as the dominant group with a percentage contribution of 53%. Crustaceans were found to be the next dominant group with a percentage contribution of 13%. Gastropods, bivalves and 'others' contributed 8%, 11% and 5% respectively to the total benthic organisms collected. In Sundarban mangroves, polychaetes topped the list in terms of abundance with a percentage of 62%. Crustaceans

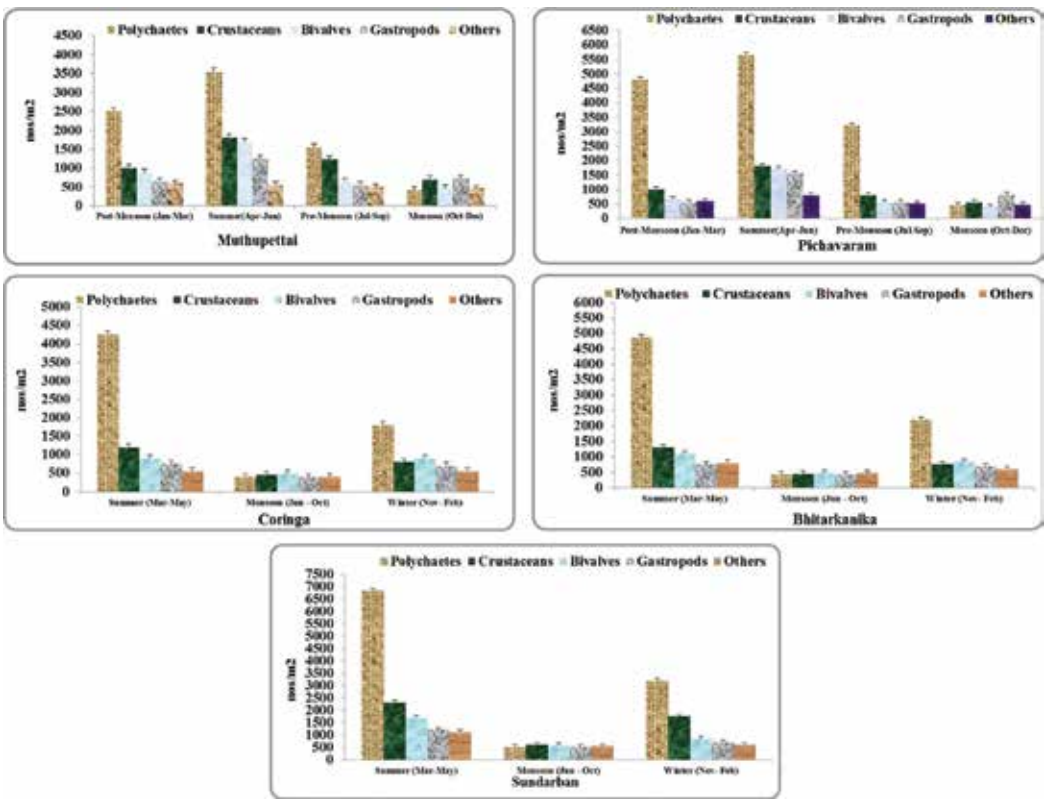

Figure 4. Population density of benthic faunal groups recorded in five different mangroves ecosystems of east coast of India.

formed second dominant group with a percentage contribution of 15%. Gastropods, bivalves contributed with 7% and 10% respectively and 'others' with 6% of the total benthic organisms (**Figure 5**).

2.5.3.4. Diversity indices

The Diversity indices (mean value) recorded at each sampling station is summarized in **Table 4**. The species diversity varied from 3.018 to 4.476 with maximum in Sundarbans and minimum in Muthupettai mangroves; species richness fluctuated from 3.216 to 4.194 with maximum in Sundarbans and minimum in Coringa mangroves; with respect to Pielou's evenness, it varied from 0.852 to 0.991 with maximum in Bhitarkanika and minimum in Coringa mangroves.

2.5.3.5. Cluster analysis

The seaward stations (MUT-1, PIC-1, COR-1, BIT-1 and SUN-1) in all the mangroves got grouped at the highest level of similarity followed by stations of core mangrove zone (MUT-2, PIC-2, COR-2, BIT-2 & SUN-2) and stations of landward zone (MUT-3, PIC-3, COR-3, BIT-3 & SUN-3) got grouped to form cluster based on the species composition with the exception of a few outliers (stations), which might be due to the species commonality between zones. This

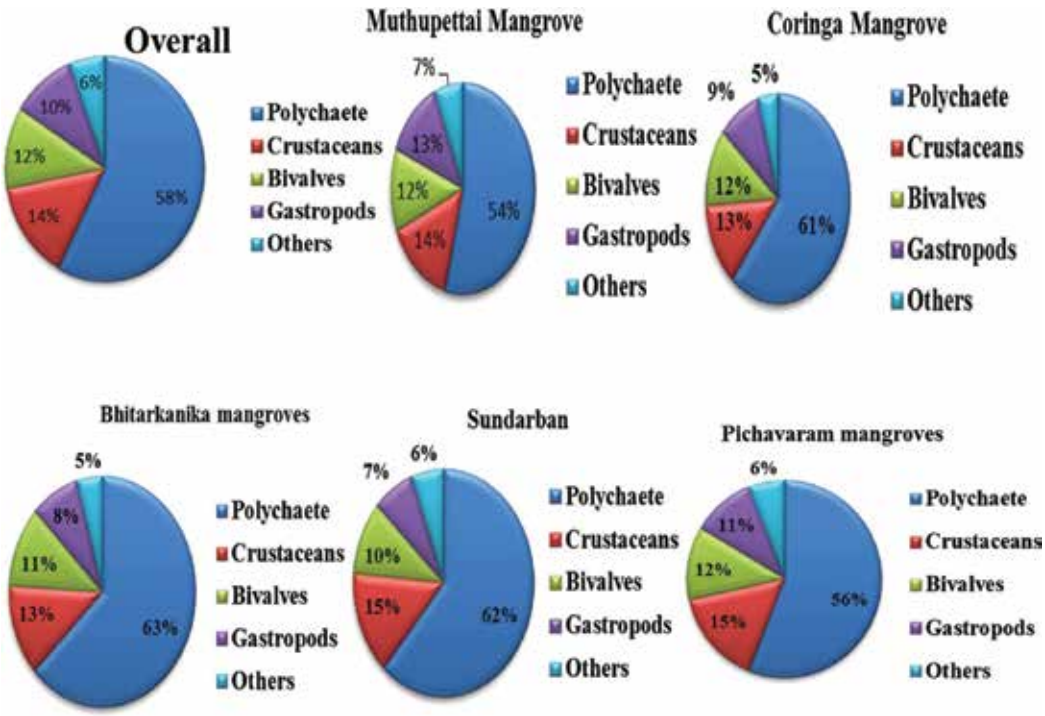

Figure 5. Percentage composition of benthic faunal groups recorded in five different mangroves ecosystem from east coast of India.

Stations	Diversity (H′)		Richness (S)		Evenness (J′)	
	Min	Max	Min	Max	Min	Max
Muthupettai	3.018	4.193	3.564	4.094	0.872	0.969
Pichavaram	3.214	4.414	3.487	4.182	0.854	0.976
Coringa	3.364	4.279	3.216	4.105	0.852	0.965
Bhitarkanika	3.214	4.389	3.314	4.216	0.854	0.991
Sundarbans	3.386	4.476	3.316	4.194	0.872	0.981

Table 4. Diversity indices recorded in five different mangrove ecosystems from east coast of India.

fact was further confirmed through MDS, and the results also revealed the same pattern of groupings as recognized in cluster analysis (**Figure 6**).

2.5.3.6. Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) was done to ascertain the relationship between the physicochemical parameters and benthic faunal density. The CCA drawn for five mangrove ecosystem showed 91.43% variance of the total axis wherein the F1 axis showed 74.56% and F2 axis 16.87% of the total variance. The environmental parameters such as salinity, Silt, Clay, TOC, TP and TN were showing strong correlation with the benthic faunal diversity, while other parameters like water temperature, depth, sand and DO had weak correlation with the benthic faunal distribution (**Figure 7**).

2.5.3.7. BIO-ENV (biota-environment matching)

In the BIO-ENV procedure, which was employed to measure the agreement between the rank correlations of the biological (Bray–Curtis similarity) and environmental (Euclidean distance) matrices, ten environmental variables were allowed to match the biota. The results of best

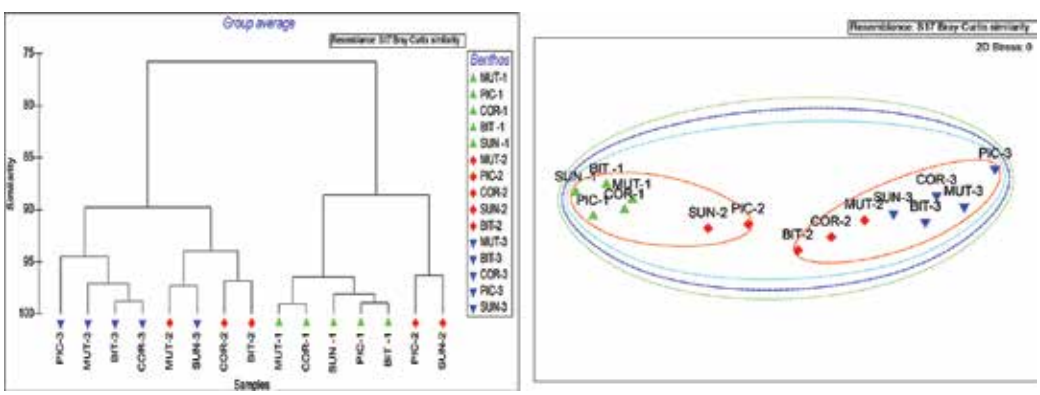

Figure 6. Dendrogram and MDS for the benthic faunal data collected in various mangrove ecosystems during 2013–2014.

combinations are given in **Table 5**. In this case, as evidenced in CCA plot, salinity, silt, clay, TOC, total nitrogen and total phosphorous were featured as the major variables explaining the best match (0.90) with faunal distributions followed by pH, TOC and total nitrogen were also got manifested in the second best variable combinations in determining the faunal distribution in the mangrove ecosystems.

2.6. Discussion

Composition of benthic communities and their role varies from one habitat to another depending upon the water and sediment characteristics of the mangroves. The distribution of mangrove fauna in relation to water quality has been described quantitatively [33]. Among the five mangroves, the maximum temperature was recorded at Muthupettai during summer and minimum in Sundarbans, which could be ascribed to the effect of atmospheric cooling. Similar conclusion was also drawn earlier by Bolam *et al*. [34] in UK continental shelf waters and in shelf waters of southeast coast of India [35]. The temperature levels recorded presently are comparable with the study made by Kathiresan [36] who reported the temperature range of 28–31°C.

The high salinity values observed during summer compared to other seasons is might be due to low rain fall and the rise in atmospheric temperature resulting in high evaporation rate of the surface water. Similar seasonal variations were observed by Manokaran [35] in the inshore waters of Parangipettai and Cuddalore; by Murugesan *et al*. [37] in Tuticorin coastal waters and Rahaman *et al*. [38] in Sundarbans mangroves; Sivaraj *et al*. [39] in Vellar-Coleroon estuarine system.

In the present study, the maximum pH of 8.23 was recorded during summer and minimum of 7.1 was recorded during wet season. Hydrogen-ion concentration was found to vary among

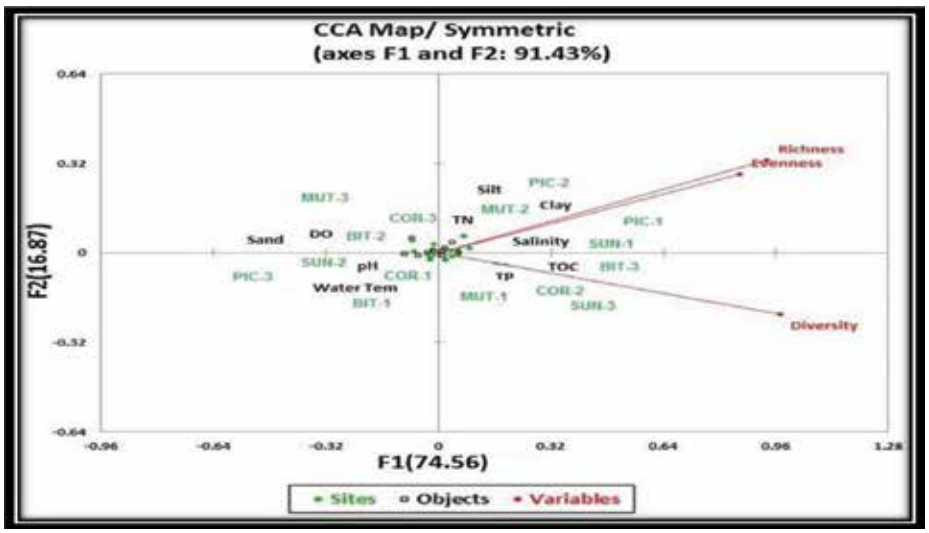

Figure 7. Canonical correspondence analysis drawn for the correlation between benthic faunal composition and environmental variables in five mangrove ecosystems.

S. No.	No. of variables	Best variable combinations	Correlation (ρω)
1.	6	Salinity–Silt–Clay–TOC–Total Nitrogen–Total Phosphorous	0.90
2.	5	Sand–Clay–pH–TOC–Total Nitrogen	0.89
3.	5	Sand–Silt–Clay–Total Phosphorous–TOC	0.88
4.	5	Silt–Clay–DO–Salinity–Total Phosphorous	0.76
5.	4	Temperature–Salinity–Clay–Silt	0.70

Table 5. Harmonic rank correlations (ρω) between faunal and environmental similarity matrices in various stations (mangroves).

the five mangroves and was alkaline throughout the study period. Higher pH observed in summer season could be attributed to the removal of CO_2 by the photosynthetic organisms and the lower pH during monsoon season could be due to the dilution of saline water with fresh-water inflow from nearby sources as has been reported by Murugesan *et al*. [37].

Coming to dissolved oxygen, (DO) it varied from 3.80 to 7.27 mg/l with the maximum (7.27) during wet season and minimum 3.80 was recorded during dry season. All the stations of various mangroves showed the similar seasonal pattern in the distribution of dissolved oxygen with minimum value during dry months and maximum during wetter months. The relatively low DO values observed in the summer are attributed to the entry of high saline waters in to the mangroves, as well as fluctuations in temperature and salinity, which in turn affect the dissolution of oxygen [40]. This fact is in close agreement with earlier studies done elsewhere [38, 41].

Mangrove ecosystems are able to store large amounts of organic carbon [42]. In the present study, the maximum TOC of 16.52mgC/g was recorded at SUN-12 during dry season and minimum of 6.45mgC/g was recorded at COR-13 during wet season. As noticed in temperature and salinity, all the stations showed similar seasonal pattern in the distribution of organic carbon content with maximum value during dry months and minimum during wet months. Similarly, Hasrizal *et al*. [43] studied the seasonal changes of organic carbon content in the surface sediments of the Terengganu near shore coastal area of Malaysia with maximum value during postmonsoon and summer seasons and they also opined that the sediment characteristics and the organic carbon concentration are largely influenced by southwest and northeast monsoons.

In the present study, total nitrogen content showed striking seasonal variation with maximum TN (5.98 μg/g) was recorded during monsoon and minimum (3.48 μg/g) during dry season. Likewise, the maximum TP (1.73 μg/g) was recorded during wet season and minimum (0.88 μg/g) was recorded during dry season. The maximum values in wet season might be attributed to the higher amount of rainfall and river runoff as has been reported earlier by Sreedevi [44]. Similarly Kamykowski and Zentoura [45] also opined that the accumulation of nitrite in the near bottom samples depends on diffusion from sediments as well as mechanisms such as nitrification near the sediment and water interface. Similar observation was made by Gouda and Panigrahy [46] in Rushikulya estuary, Orissa, east coast of India. Manikoth and Salih [47] recorded high nitrogen concentration during monsoon season in the Vembanad estuarine complex, southwest coast of India. Joshi and Ghose [48] studied nutrient

characteristics of Sundarban mangroves. Martin *et al*. [49] studied on the benthic fauna in a tropical estuary of Cochin backwaters and Sekar *et al*. [50] in Pichavaram and Muthupettai mangroves in relation to nutrient characteristics.

Studies on the sediment composition are of paramount importance in benthic ecology. The comprehensive knowledge on the sediment composition is a pre-requisite and inevitable one to understand the benthic ecology [51]. The nature of the substratum has a profound effect on the bottom fauna and conversely, the benthos can influence the sediment characteristics. Gray and Snelgrove and Butman [52, 53] posted the information regarding the relationship between sediments and benthic organisms. They also pointed out that the grain size distribution of the sediments is of great importance in determining the distribution of benthos. Snelgrove and Butman [53] also concluded that the relationship was a complex interaction of the seabed flow and sediment characteristics and that could explain the distribution of organisms across all sedimentary habitats.

The correlation between the physicochemical parameters and benthic faunal density for the surveyed five mangrove ecosystem showed that the environmental parameters such as salinity, Silt, Clay, TOC, TP and TN were showing strong correlation with the benthic faunal diversity, while other parameters like water temperature, depth, sand and DO had weak correlation with the benthic faunal distribution. Similar variables combination were reported earlier by Sundaray *et al.* in Mahanadi River [54]; Satheeshkumar *et al*. [55] in Pondicherry coast; Sivaraj *et al*. [56] in Nandgoan coastal waters; Sivaraj *et al*. [41] in Vellar-Coleroon estuarine system.

Percentage contribution of benthic species composition of the present study showed in the order of polychaetes, crustaceans, bivalves, gastropods and groups 'others'. The dominance of polychaetes in terms of density and species composition in diverse ecological niche is due to their high degree of adaptability to a wide range of environmental factors. Similar preponderance of polychaetes has been observed earlier by Kumar [32] in Cochin backwaters; Prabha Devi [57] in Coleroon estuary, and Ansari *et al*. [58], in Mandovi estuary. Athalye and Gokhale [59] reported the dominance of polychaetes followed by gastropods, bivalves, and hermit crabs in Thane creek, Mumbai. The dominance of polychaetes might be due to the fact that firm substrate provided by roots and dense canopy of the mangroves which also provide protection against desiccation [60]. Similar dominance of polychaetes was also reported in other tropical waters [61, 62].

In a study conducted by Harkantra and Parulekar [63], polychaetes outnumbered the other faunal groups where the substratum was mainly composed of mud. Bhat and Neelakandan [64] also observed maximum number of polychaetes in the clayey-silty substratum, the fine particles of mud and clay substratum, which retains more water than coarse particles (sand and gravel). Such fine deposits or particles are commonly composed of decomposable organic constituents. As the organic content represents an important direct or indirect food source for benthic organisms, elevated organic matter may result in an enhancement of benthic faunal diversity [52, 65]. Therefore, it is clear that polychaetes abound in finer sediments as noticed by the above referred researchers. This fact also corroborates the results of present study. The population density of

macrofauna is governed by various environmental variables such as temperature, salinity, sediment type, organic carbon level in the sediments besides tidal action [66]. Monsoon months registered low density followed by gradual increase in postmonsoon and peaked during summer season, which are in agreement with the results of Sekar *et al*. [38, 50].

The population density recorded presently is comparable with the following studies made in the back waters along the east and west coasts of India: Harkantra *et al*. [66] (50–3175 nos. m^2); Jegadeesan [67] (158–4138 nos. m^2) in Coleroon estuary; Murugan [68] (80–3142 nos. m^2) in Uppanar backwaters; Thangaraj [69] (50–2172 nos/m^2) and Murugesan [70] (635–5125 nos. m^2) in Vellar estuary; Muthuvelu [71] (40–8028 and 40–8328) in Parangipettai and Cuddalore coastal waters; Sekar *et al*. [50] (78–119 ind./1 cm^2) in Pichavaram and Muthupettai mangroves; Sivaraj [41] (254 to 6124 nos. m2 and 654 and 7845 nos. m^{-2}) in Vellar and Coleroon estuary.

In the present study, a marked seasonal variation in the Shannon diversity was found with minimum diversity value (3.018) in Muthupettai mangroves during monsoon and maximum (4.476) in Sundarbans mangroves during dry season. Similar range of diversity values was recorded earlier in Vellar estuary [71]. Shillabeer and Tapp [72] stated that the estuarine and mangrove environment is far more dynamic than the fully marine and therefore, there may be a wide range of variations in the benthic diversity of an estuary.

As in the species diversity, species richness values were also low during wet season and high during dry season, which might be due to adaptability to high salinities at high temperatures than at low temperatures [73], as a result more marine forms are able to flourish in tropical waters [74]. The trend with respect to richness values of the present study is evident in the studies made by Raveenthiranath Nehru [14] in Coleroon estuary and Sebastin Raja [14] in Sunnambar estuary; Palanisamy and Anisa [51] in Pondicherry coastal waters. With respect to evenness (J'), it largely followed the trend of species diversity.

With respect to classification and ordination techniques, the stations of marine zone (seaward) grouped at the highest level of similarity followed by stations of core mangrove zone and stations of fresh water zone (landward zone) grouped to form clusters based on the species composition. The physicochemical parameters such as salinity, Silt, Clay, TOC, TP and TN in landward zone and core mangrove were found relatively similar and it highly influenced the benthic faunal diversity, while in seaward zone the trends of the same parameters varied significantly and it didn't affect the distribution and diversity of the benthic fauna. The MDS results also largely followed the trend of dendrogram. Investigation similar to this was carried out by Sivaraj *et al*. [41] who made a comparative study of Vellar-Coleroon estuarine system using macrobenthic communities through cluster analysis. The stress value observed in MDS plot is comparable with the studies [75–77].

Canonical Correspondence Analysis (CCA) was done to ascertain the relationship between the physicochemical parameters and benthic faunal density. Similar combinations of environmental variables influencing benthic faunal distribution was reported in Nandgaon coastal waters, Maharashtra, India [56]; Sivaraj *et al*. [41] in Vellar-Coleroon estuarine

system. This fact was further confirmed through BIO-ENV, which yielded the combinations of six environmental entities (salinity–silt–clay–TOC–TN–TP) as best match 'defining' the faunal distributions. The associated coefficient of environmental to biotic similarity was 0.90. True to this, studies [39, 71] reported the similar combinations of environmental variables influencing the benthic faunal distribution. Clarke and Ainsworth [62] also reported the organic carbon-sediment particle size, to constitute the best match explaining the distribution of meiobenthic organisms. Similarly, Mackie *et al*. [78, 79] reported the combination as silt-clay-organic carbon forming the best match in explaining the faunal distribution. The combinations recognized in the above referred studies corroborate the results of the present study.

Comparing our own data with the studies made elsewhere in mangroves of other Asian countries, a few inferences could be drawn. In our study, as many as 68 species of polychaetes were recorded from 5 mangrove ecosystems of the present study. The density and number of species recorded presently is comparable with the works carried out in mangroves of other Asian countries barring a few variations in their density and diversity which might be due to the dynamic nature of the mangrove environment. Shillabeer and Tapp [72] stated that the mangrove environment is far more dynamic than the fully marine and therefore, there is every possibility in the variations in the occurrence of species. Similarly, there was no pronounced variation with respect to commonality in the species occurrence between our data and data of others. With regard to representation of polychaete families, by and large the representatives from Errant polychaetes were found to outnumber compared to sedentary counterparts. The similar dominance of errant polychaetes could be seen invariably in the works done in the mangroves of other Asian countries.

3. Conclusion

Based on the foregoing account, it is concluded that the present study yielded quite a good amount of information on the benthic biodiversity in general and polychaete taxonomy in particular in the mangroves of east coast of India. As there was no comprehensive report on the polychaetes of mangroves of east coast of India, comparison was done only based on the available sporadic reports and thus a clear –cut inference could not be drawn.

On the other hand, studies related to taxonomy of benthic fauna is limited as the researchers worldwide did not evince much interest in this line besides the enrolment of a new generation of benthic taxonomists has also been poor in the recent past. There are several reasons for this: (i) indifferent attitudes, both in society and educational systems, and (ii) organisms that are "invisible" from the perspective of immediate economic and medical interest to man and more importantly poor funding from the Government. To achieve this, an intensive collaboration of benthic researchers among the Asian countries is need of the hour, as it will throw an important beam of light on the Polychaete taxonomy in the mangroves with a view to formulate management strategies and also to arrive at meaningful conclusions for the policy makers.

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Section 5

Mangrove Geochemistry

Chapter 7

Morphology, Physical and Chemical Characteristics of Mangrove Soil under Riverine and Marine Influence: A Case Study on Subaé River Basin, Bahia, Brazil

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Abstract

The preservation of mangrove ecosystem requires knowledge on soil Morphology, Physical and Chemical Characteristics, for understanding the requirements for their sustainability and preservation. Seven pedons of mangrove soil, five under fluvial and two under marine influence, located in the Subaé River basin were described and classified. Samples of horizons were collected for physical and chemical analyses, including Pb and Cd. The moist soils were suboxidic, with Eh below 350 mV. The pH of the pedons under fluvial influence ranged from moderately acid to alkaline, and pedons under marine influence was around 7.0. Mangrove soils under fluvial influence were characterized with the highest Pb and Cd concentrations in the pedons, which could be perhaps due to it closeness to the mining company Plumbum, while the lowest Pb concentrations was registered in the pedon furthest from the factory. Because the pedons had at least one metal above the reference level they were considered potentially toxic. The soils were classified as Gleissolos Tiomórficos Órticos (sálicos) sódico neofluvissólico, according to the Brazilian Soil Classification System and as Thiomorphic orthic Gleysol (salic) sodicluvissol (potentially toxic, very poorly drained) according with FAO. The pedon under marine influence was classified in the same subgroup, but the metal concentrations met the acceptable standard.

Keywords: pedogenesis, hydromorphism, heavy metals, contamination, pollution

1. Introduction

1.1. The mangrove soils

Mangrove forests are tropical and subtropical ecosystem characterized by the presence of plant species adapted to high temperatures and organic matter content, and fluctuating salinities and oxygen conditions.

Mangroves provide ecosystem services of great social, economic and environmental importance. They are nurseries for several species of birds, fish and shellfish; they hold a complex community supporting benthic organisms that live in salt water and, they are sources of substantial part of the proteins (shellfish, crustaceans and fish) consumed or marketed by the riverside communities [1]. Despite their ecologic, social and economic functions, and benefits to coastal communities, mangroves are disappearing worldwide at the rate of 1–2% per year due to industrial development, rapid urbanization, population growth and anthropogenic activities [2].

Geology, oceanography, biology, geomorphology and pedology researchers, among others, classify the mangrove substrate as sediments or soils [3]. Hereafter, the mangrove substrate will be referred to as soil because it meets the criteria used by the Soil Survey Staff [4]. That is, they have the capacity to support life (i.e. microorganisms such as bacteria and macro organisms such as plants), filter water, recycle and purify waste and to provide food for the populations that leave riverside. Mangrove soils occur in coastal environments of tropical and subtropical regions and they are originated from sedimentary material deposited by river and marine actions or from the alteration of the sedimentary substrate (parent material). The sediments are further altered by organisms adapted to flood, anaerobic and salt conditions [3, 5–7].

Mangrove formation in different regions of the globe is related to sedimentation processes occurring in the Quaternary Period, as well as to the relative variations of sea level, in marine regressions and transgressions of the last 8–12 thousand years before the present [3, 7–9].

The textural, physical and geotechnical parameters, clay minerals, and pollen records in sediments from a paleo-delta, in southwest coast of India, throw insights on climate change and environment of deposition during the Holocene. Variations in the textural characteristics of sediments evaluated reveal a change in depositional environment of deltaic facies, apparently from marine to fluvial environment during mid-Holocene marine regression. Further, sand and silt mixture in the upper part of borehole suggests that fluvial environment was influenced by the variation in the intensity of monsoon [10].

With the end of the Holocene, the last transgression began, and the sea drowned the valleys excavated by hydrography and reworked the Pleistocene sediments forming Holocene sediments, which filled lagoons, bays and coastal strands [6]. Evaluation of major delta processes indicates that deceleration in sea-level was the key factor in Holocene delta formation [9].

Once formed, these points and islands sheltered on their inner side protected areas that from lagoons evolved to swamp areas with mangroves [8]. The sediments deposited in the marshy areas underwent to general pedogenic processes of addition, removal, transformation, translocation of

materials and energy, and specific processes related to aggradation, salinization, gleization, sulfurization, bioturbation and paludization that result in the formation of different mangrove soils.

The local sedimentation processes depends on the geological, geomorphological, climatic and vegetation factors, quantity and quality of the mineral and organic materials fluvio-lacustre and marine deposited of each region [3]. There exist a significant interaction among highland, estuary (physiographic basin), ocean and atmosphere, as a result of local influence and environment specific factors such as climate, relief, and organisms altered formation processes. The sediments deposited in the fluvio-marine plains of calmer regions, over time transform into soils through pedogenetic process [3, 11].

Mangroves ecosystems are located in lower landscape environments. The soils formed in mangroves ecosystems are located in lower landscape because of that they are constantly receiving fluvial and marine additions of mineral and organic material to their surface (aggradation) [12]. The sediment accumulation is facilitated by vegetation, especially by mangrove species with complex root system and by flocculating salinity effect that leads to the deposition of fine clay particles carried out by rivers. The rates of sediment deposition in mangrove environments in different part of the world vary according to the characteristics of the local [13]. According to [14] it is difficult to determine the rate of mud sedimentation beneath mangroves the author observed deposition rates from 1 to 8 mm $year^{-1}$, in different regions. The more common rate of vertical accumulation is close to 5 mm $year^{-1}$ [15].

The primary contribution of the Mekong tropical delta helped to understand the stratigraphy and history of the formation of mud inland deposits on time scales of centuries and millennia [8]. The sediment accumulation ranges from 0.47 [16] to 10 cm $year^{-1}$ [8]. The energy of the rivers, ocean waves and currents, downstream relief features, root density of mangrove species, among other factors determines an uneven and unstable sedimentation pattern. The sedimentary or crystalline nature of the rocks occurring in the basins that drain the mangrove environments influence: the mineralogy and the texture of the deposited material [3]; the distribution and extension of quaternary deposits [6, 14, 17]; the distribution of the particle size of the mangrove soils [18]; and the geomorphology of the coastal region.

The frequent floods in the mangrove soils by marine salt water trigger the process of salinization. Because of the high concentrations of Na^+ in the marine water many mangrove soils have high rate of sodium saturation coupled with high salt concentrations [12]. Another effect of constant flooding of mangrove soil by fluvial and marine influence is the reduction of oxygen supply and high biological oxygen demand (BOD). These two factors will result in the formation of an environment with low concentration of oxygen that in turn will influence the chemistry of sulfur and iron.

Sulfates are abundant in sea water and together with Fe are important elements in the biogeochemical cycles of mangrove areas [3]. For sulfur the combination of high organic matter content, reactive Fe sources and a large quantity of sulfates, readily available, makes the mangrove soils an environment conducive to the occurrence of bacterial reduction process of sulfidization. The oscillations of redox conditions, due to seasonality, plant action, fauna or anthropogenic interventions may result in a more oxidizing condition in the soil, promoting sulfide oxidation (sulfurization) [12]. The reduction of iron forms in mangrove soils leads to

the formation of a process known as gleização [19]. Moreover, the reduction condition leads to the accumulation of organic material due to the low energy yield from the main mineralization pathway, replacing the aerobic microbial metabolism in a process called Paludization [12]. Also, variation in hydroperiod and soil moisture content affect the amount of organic matter in the sediments [20].

The high concentration of organic matter in estuarine environments is explained by factors, such as the bioturbation [12] of the local fauna and the contribution of organic material (leaf, branches and roots) from the mangrove vegetation. The concentration of C-organic tend to be higher in the first horizons where there is a greater amount of roots, algae (diatoms) and remains of animal in decomposition [21, 22]. The deposition of these materials associated with the hydromorphism reduces the rate of decomposition of the organic compounds.

1.2. Interaction between mangrove vegetation and soil morphological, chemical and physical characteristics

Soils of mangrove ecosystems are the result of complex interactions between abiotic factors, such as tidal oscillations and biotic factors as the activities of the species and organisms [23]. Soils provide essential nutrients for mangrove species growth and physical structure for plant anchorage and stability. They also influence wildlife conservation, and balance the environmental condition. The soil type and its morphological, physical, chemical and physicochemical characteristics are resultant of interactions between factors such as topography, climate, hydrodynamic processes, tidal margin and long-term sea level changes. Therefore, mangrove soils have a unique history in any environment [15].

Mangrove soils are generally characterized by reducing conditions and highly variable soil salinity [24, 25]. The physiographical position of mangroves within the estuary influence the soil properties (pH, Eh, electrical conductivity) and composition (clay mineralogy, organic matter and metal concentration) greatly affects soil attributes and environmental functions [26, 27]. Mangrove growth is also affected by soil texture, salinity, redox potential, and temperature [28, 29]. The texture of soils is broadly distinguished into sandy loams and silt loams, but there is great variability from one region to another.

In a mangrove environment, soils and vegetation have a strong interaction with each other, resulting both in the formation process of the former and in the characteristic of the growing environment of plants, which develop in communities directly influenced by soil characteristics. The plant species of the mangroves have their development influenced by the physical and chemical soil characteristics [30] which may compromise the growth and structure of species [31]. Texture, potential redox, pH, cation exchange capacity, organic carbon and electro conductivity can influence nutrient uptake by plants, despite the difference of selectivity of each species to remove nutrient from the same environment [32–34].

The concentration of organic matter in mangrove forest varies with the plant species age. There exist interrelationships between mangrove vegetation and soil characteristics. As the species age, the productivity and the production of litter and organic detritus that are deposited in the forest floor and within the soil profile increase [35]. After decomposition of

the organic material the accumulation of organic matter increases. The larger organic matter content of mangrove soils influence the status of nutrient in the soil as well as pH and redox potential soils among others [35].

On the other hand, the distribution of mangrove species along the coast has been attributed to: the eco-physiological response of plants to one or more series of environmental gradients; the combination of factors such as frequency and duration of flooding, substrate flooding, pore water salinity and pore water potential [14] and; the change in the environment deposition during the Holocene, and to neotectonic factors, such as changes in sea level and varied intensity of the southwestern monsoon [10]. Due to this strong interaction and specificities of the estuarine environment, mangroves are considered fragile ecosystems, highly sensitive to changes in the environment, mainly due to anthropic actions, which tend to disrupt the system by modifying the environment.

There are about 50 species of mangroves found in the world adapted to tidal oscillations, temperature, salinity and soil texture. The mangrove species most commonly found are *Rhizophora mangle* (red mangrove), identified by the tangle of aerial roots that promote the exchange of oxygen, *Avicennia germinans* (black mangrove), identified by projections called pneumatophores, projected in the soil surrounding the trunk of the tree and *Laguncularia racemosa* (white mangrove) species that projects salts in its leaves. These species may present high growth rates in soils without nutritional limitations [36]. There is a relationship between the soil characteristics and mangrove species [25, 37]. For instance, *Rhizophora* is found in environments with a more alkaline pH, as well as high levels of N, P and C; *Laguncularia* in soils with sandy loamy texture; and *Avicennia germinans* in environments with lower tidal influence.

As upland soils, the evaluation of mangrove soils may provide suitable indicators of the macrofaunal and nutrient status [38, 39] as well as the effect of anthropogenic impact as indicated by the presence of organic and inorganic contaminants.

1.3. Impact of anthropogenic activities on mangrove

In spite of the increased awareness of the value and significance, the mangroves are threatened worldwide by the risk of disappearing, due to economic and social pressure.

Given the importance of mangrove forests and the impacts of global climate change and anthropogenic activities on this ecosystem, mangroves should be legally protected however, less than 10% fall into this category [40, 41]. According to the Brazilian Law No. 12.727/2012 of the Forest Code [42] classifies the mangrove forests as Areas of Permanent Preservation. In general, the destruction of these forests is linked to anthropic interests, activities and needs such as industrial demand, population growth, or poor coastal management, which reflect the alteration, degradation and loss of the natural habitat of several species [43].

Uncontrolled industrialization and urbanization in coastal regions, has damaged the mangrove ecosystem threaten biodiversity, human health [44, 45] and marine life. Heavy metals are considered as anthropogenic pollutants of great impact on mangrove ecosystems [46]. The effect of heavy metals in mangrove environments is worrying because these ecosystems are a nursery for several species (e.g. fish, crabs, oysters), which are consumed and marketed by

the riverine population. In Brazil and in the world, the effect of metals has been reported on soils, plant species and animals of mangroves [11, 41, 47]. Oil spill can cause lethal impacts to plants by preventing transport of oxygen [48]. Enterprises and activities associated with these pollutants have been observed located closer to mangroves, becoming potential threatening ecosystems [46].

Because they are in environments bordering large human settlements, mangroves are under great pressure of use and occupation across the globe. In addition to being exploited, without a rational system of use and management, plants and animals are collected for different purposes. In addition to that, the mangrove directly affected by: the discharge of solid and liquid wastes from the cities that border the rivers and drain their waters to the sea; and by the disorderly occupation of people who drain and bury the mangrove for expansion of urban centers. In the municipality of Santo Amaro, Bahia, Brazil, in addition to all the previously related problems, the mangroves were contaminated by waste from Pb processing in a factory located on the banks of the Subaé River.

2. Study of case: mangrove soil contamination from lead processing industry

Industrial activities are known for the deleterious effects on mangroves, particularly for the presence of high concentrations of toxic elements such as lead (Pb), cadmium (Cd), mercury (Hg), arsenic (As), and zinc (Zn) that cause adverse effects to fauna and flora of mangrove forests, directly or indirectly affecting human health.

Negative effects of the presence of toxic elements from industrial activities in mangroves have been reported [11], due to galena processing activities in the municipality of Santo Amaro-Bahia. The mining-metallurgical complex installed in 1960, 2.5 km Northwest of the city for the production of lead alloys (Pb), in addition to atmospheric contamination, left a liability of around 500 thousand tons of slag (21% Cd and up to 3% of Pb) that resulted in the contamination of the Subaé River and its estuary due to overflow of the tailings pond.

It is believed that Santo Amaro has the highest urban lead contamination in the world, with serious effects on human health, as indicated by the incidence of metal-induced diseases in the population and by the environment contamination.

Studies indicate that the presence of heavy metals in the mangroves of the Subaé River Basin cause social, economic and health impacts, as the ecosystem is a source of subsistence and income for riverside residents, who may be consuming contaminated fish [49, 50]. Negative effects on the mangroves of Santo Amaro and São Francisco do Conde were reported by [11], which is presented in this study of case. The study characterized and classified mangrove soils from Subaé Basin and evaluated the Pb and Cd distribution in horizons of mangrove.

2.1. Materials and methods

The mangroves evaluated in this study are located in the Subáe Basin, Bahia, Brazil, in the municipalities of Santo Amaro and São Francisco do Conde (**Figure 1**). The Subaé River basin

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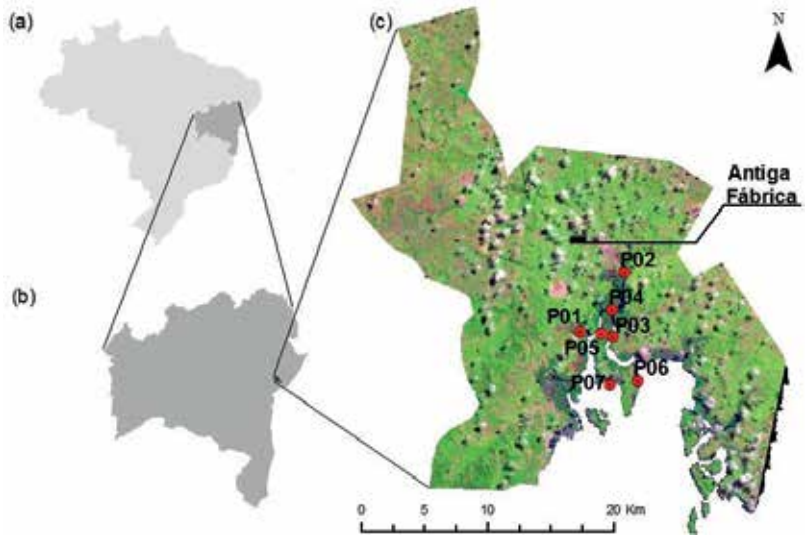

Figure 1. Location of the estuarine zone of the Subaé river, Bahia, Brazil. (a) Location of Santo Amaro in the Brazilian region. (b) Study area in Santo Amaro. (c) Location of the pedons.

is a part of the river basin complex "Recôncavo Norte", located in Northeastern of Bahia, with a total area of 18,015 km^2. This area is drained, aside from the Subaé River, by: Subaúma, Catu, Sauípe, Pojuca, Jacuípe, Joanes, Açu and the secondary rivers from "Baia de todos os Santos" (BTS) and the Inhambupe River [51].

The regional climate is Af (tropical rain forest climate), according to Köppen's classification, i.e., tropical humid to sub-humid and dry to subhumid, with average annual temperature of 25.4°C (maximum average of 31°C and minimum of 21.9°C) and annual average rainfall varying from 1000 to 1700 mm in the rainiest months and from 60 to 100 mm in the driest months [52]. About 2/3 of the territory of Santo Amaro has smooth, wavy relief, coastal plateau, marine and fluvial marine waters.

The region of study is in the Northeaster face from San Francisco craton (Recôncavo Sedimentary Basin), of Meso-Cenozoic age, delimited by a subparallel system of normal faults. The geology of the area is composed by rocks of the following groups: Santo Amaro (Candeias formation: interleaved shale and silt, with levels of limestone and dolomite, sandstone); Island Islands (interleaved shale and sandstone, loam, calciferous sandstone, carbonaceous shale, silicon and calcilutite); and Brotas (Sergi Formation: fine sandstone to conglomerate, conglomerate and subordinate pellet), as well as reservoirs of marshes and mangroves [53].

The sample area mangrove areas, there is a predominance of Vertisols, Argisols, Neosols, in addition to Gleysols [54] are class of soil prevailing in the area. The plant species found in the study area are: *Rhizophora mangle* (Red mangrove, RM), *Laguncularia racemosa* (white mangrove, WM) and *Avicennia schaueriana* (black mangrove, BM). The sample location, the profile code, the prevailing vegetation and the geographical coordinates are shown in **Table 1**.

Mangrove	Identification	Vegetation	Latitude	Longitude
Santo Amaro	P1	WM	0533387 N	8,610,674 E
São Brás	P2	WM and RM	0529852 N	8,606,114 E
São Bento das Lajes	P3	RM and WM	0532483 N	8,605,736 E
Santo Amaro	P4	RM and WM	0532395 N	8,607,834 E
Santo Amaro	P5	RM, WM and BM	0531579 N	8,605,970 E
Ilha Cajaíba	P6	RM and BM	0534697 N	8,602,227 E
Ilha de Araçá	P7	WM and BM	0532211 N	8,601,506 E

Table 1. Geographic coordinates of the profiles and respective vegetation predominant along the Subaé Basin.

2.2. Soil sampling

Based on aerial photography data, the closeness to the factory, field observation, tide tables, and information provided by local fishermen, seven pedons (P) were selected and sampled, of which five pedons represented the fluvial lowland of the Subaé River (P1 to P5) in higher areas and 2 of them in lower areas, closer to the sea (P6 and P7) (**Figure 1**). The pedons P1, P3, P4, P5 and P6 are located at Cajaíba island, which divides the Subaé River into two branches near its mouth, in an anthropic undisturbed environment (P7) as compared with the mangrove forest along the river banks on the continent; and one pedon in the neighboring area of the former Plumbum Mining (P2).

The sites for vertical cuts of soils were defined by following the tide table: when the tide is low, some fluvial dams are formed on the river banks, which enabled the morphological description of profiles and the sampling process, carried out according to [55]. After describing the profiles horizon and layer samples were collected, stored in plastic bags, and maintained in a cold chamber at 4°C, for subsequent chemical and physical analyses.

2.3. Analytical procedures

2.3.1. Oxidation and reduction potential and pH measurements

The oxi-reduction potential (Eh) and pH level of all pedon horizons and layers were measured in the field. The Eh readings (Hanna HI 8424) were obtained by using a platinum electrode and corrected by adding potential of the calomelane reference electrode (+244 mV) and the pH levels were measured with a glass electrode, which was previously calibrated with standard pH solutions at 4.0 and 7.0, after balancing samples and electrodes.

2.3.2. Laboratory

Soil samples were air-dried, around 35°C, crumbled, and ground with a soil hammer mill, using a 2 mm sieve, to obtain air-dried fine soil.

For texture test, soluble salts were previously removed with 60% ethylic alcohol and organic matter by hydrogen peroxide. The pipette method was used with some modifications: 20 g

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of sample was dispersed in 100 mL of water and 10 mL of 1 mol L^{-1} sodium hexametaphosphate [56]. After that samples were kept overnight to settle down in bottom, the samples were shaken for 16 h at 30 rpm in a Wagner agitator, model TE-161, following the other procedures of the method. The samples were assessed to the following chemical properties: electrical conductivity (EC) in the saturation extract; pH in water (1:2.5 soil:solution ratio); exchangeable Ca^{2+}, Mg^{2+} and Al^{3+}, through titration after extraction with a 1 mol L^{-1} KCl solution; Na and K by flame photometry, following extraction through Mehlich-1; H + Al extracted through 0.5 mol L^{-1} calcium acetate at pH 7.0, and determined with 0.025 mol L^{-1} NaOH. Based on the obtained data, it was calculated the sum of bases (S), cation exchange capacity (CEC), and base saturation (V). The phosphorus content was determined by photocolorimetry. All determinations were carried out as described by [56]. Organic carbon was determined by the dry method (muffle) for classification according to [57]. The sulfur content was determined by sample digestion with HCl 1:1, and then calculated by gravimetry after precipitation with $BaCl_2$ [56]. In order to assess the existence of thionic sulfur in the soil, a 0.01 m soil layer, at field capacity, was incubated at room temperature for 8 weeks. Soils with ΔpH [pH(KCl) − pH(H_2O)] values lower than 0.5 units after incubation were considered thionic [57].

Metals were extracted and determined by method 3050B [58], by which 0.5 g of the dry soil fraction was ground in an agate mortar and digested in 10 mL of a HNO_3:H_2O deionized solution, at a 1:1 proportion, with addition of 10 mL H_2O_2 for organic matter oxidation, in a digestion block heated to 95 ± 5°C for about 2 h. Samples were cooled for 15 min, then 5 mL of a HNO_3 solution was added again. To complete digestion, 5 mL of concentrated HCl and 10 mL of deionized H_2O were also added. After digestion, the samples were cooled, filtered, completed to 50 mL and the metals Pb and Cd, determined with an atomic absorption spectrophotometer (model AAS Varian AA 220 FS).

2.3.3. Soil classification

Based on the morphological description and the analytical results, pedons were classified according to the Brazilian System of Soil Classification (SiBCS) [57], the U.S. Soil Taxonomy [54], and the World Reference Base for Soil Resources [59].

3. Results and discussion

The results of morphological and physical analyses of pedons located on a plain relief, directly exposed to tides, under fluvial (P1 to P5) and marine (P6 and P7) influence, from fluvial-maritime sediments, deposited on a sediment rocky mineral (shale), are shown in **Table 2**.

The seven pedons are poorly drained, due to constant flooding by the tide, and, under anaerobiose conditions, they favor the waterlogging process, which affects the removal, translocation, and transformation processes of Fe compounds, resulting in bluish and greenish colors, with red or yellowish mottles in horizons and layers (**Table 2**).

Generally, Gleysols have a massive structure, identified in all horizons and layers of the pedons under study (**Table 2**). Although the consistency was not measured in the field, the flooding condition resulted in very or extremely hard soils when dry. The transition between horizons was

Horizons	Depth	Color		Structure	Transition	Texture class[1]	Sand	Silt	Clay
	cm	Hue	Mottle				g kg^{-1}		
P1—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–8	Gley 1–10 GY 4/1	7. 5 YR 5/6	Massif	Flat and diffuse	Very clayey	16	196	788
2Agn	8–20	Gley 1–10 GY 4/1	7.5 YR 5/6	Massif	Flat and diffuse	Very clayey	29	192	778
3Agn	20–34	Gley 1–10 GY 4/1	7.5 YR 5/6	Massif	Flat and diffuse	Very clayey	39	122	839
4Agn	34–55	Gley 1–10 GY 4/1	—	Massif	Flat and diffuse	Very clayey	66	102	832
P2—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–20	Gley 1 10Y 2.5/1	10YR 4/6	Massif	Flat and diffuse	Medium	459	208	333
2Agn	20–32	Gley 1 10Y 2.5/1	—	Massif	Flat and diffuse	Medium	476	213	311
3Agn	32–61	Gley 1 10Y 3/1	—	Massif	Flat and diffuse	Medium	494	185	321
4Agn	61–83	Gley 1 10Y 4/1	—	Massif	Flat and diffuse	Medium	383	295	322
5Agn	83–102	—	—	Massif	—	Clayey	308	271	421
P3—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–5	Gley 1 5G 4/1	2.5YR 4/8	Massif	Flat and diffuse	Medium	477	254	270
2Agn	5–25	Gley 1 5G 4/1	—	Massif	Flat and diffuse	Medium	609	86	305
3Agn	25–49	Gley 1 5GY 4/1	10 YR 3/6	Massif	Flat and diffuse	Clayey	486	124	390
4Agn	49–71	Gley 1 5G 4/1	—	Massif	—	Clayey	439	209	352
P4—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–7	Gley 1 5G 3/1	Gley 1 5G 2.5 /1 and 7.5 YR 4/6	Massif	Flat and clear	Medium	666	78	255
2Agnj	7–18	Gley 2 10B 3/1	10B 4/1	Massif	Flat and clear	Medium	378	419	203

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Horizons	Depth	Color		Structure	Transition	Texture class[1]	Sand	Silt	Clay
	cm	Hue	Mottle				g kg^{-1}		
3Agnj	18–41	Gley 1 5G 5/1	Gley 2 10GB 4/1 and Gley 1 5G 6/2	Massif	Flat and clear	Sandy	910	3	88
4Agnj	41–60	Gley 1 5G 4/1	—	Massif	Wavy and abrupt	Medium	688	63	249
4Crgnj	60–70	Gley 1 10GY 3/1	2.5 YR 2.5/4	—	—	Medium	648	109	244
P5—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–15	Gley 1 5G 4/1	5YR 4/6	Massif	Flat and gradual.	Very Clayey	26	150	824
2Agn	15–26	Gley 2 10B 4/1	5YR 4/6	Massif	Flat and gradual	Very Clayey	27	233	740
3Agn	26–43	Gley 2 10B 3/1	—	Massif	Irregular and Abrupt	Very Clayey	27	38	935
4Agn	43–60	Gley 2 5 PB 5/1	—	Massif	Irregular and Abrupt	Medium	269	677	54
4Crgn	60–70	Gley 1 5G 5/2	—	Massif	—	Clayey	211	238	551
P6—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–15	Gley 1 5GY 3/1	7YR 3/3	Massif	Flat and diffuse	Medium	439	458	103
2Agn	15–33	Gley 1 10Y 3/1	—	Massif	Flat and diffuse	Silty	86	828	86
3Agn	33–48	Gley 1 5G 3/1	—	Massif	Flat and clear	Very clayey	119	272	609
4Agn	48–60	Gley 1 5G 4/1	—	Massif	—	Very clayey	315	27	659
P7—Gleysol thiomorphic orthic (salic) sodic luvissol, very poorly drained									
Agn	0–9	Gley 1 10Y 3/1	7YR 3/3	Massif	Flat and diffuse	Medium	321	637	42
2Agn	9–17	Gley 1 10Y 4/1	—	Massif	Flat and diffuse	Medium	291	686	24
2Crgn	17–28	Gley 1 10Y 4/1	—	Massif	Flat and abrupt	Silty	100	836	64

[1]Classification according to Embrapa [57].

Table 2. Morphological properties and physical attributes of pedons from mangrove soils in the Subaé river basin, Santo Amaro, Bahia, Brazil.

flat and diffuse (P1, P2, P3, P4, P6, and P7) or gradual (P5), showing sedimentation with layers consisting of material with similar composition and homogenized by the action of organisms.

In mangroves, there is a constant sedimentation of fine dust (silt and clay) brought by tidal variation, which may be explained by the low-energy environment [60]. Texture varied from medium to very clayey, with a predominance of the finer over the sandy fraction (**Table 2**). Also, irregular variation of texture between the soil horizons and layers, in all pedons, indicates major changes in the environmental conditions of the system [61]. Clay in the pedons ranged from 2.4 to 93.5%, showing wide texture variability, to, is a characteristic of mangrove soils [21]. In most horizons and layers from P1 to P5, the pedons influenced by the river, there is a prevalence of the clay fraction, while in the pedons influenced by the sea, P6 and P7, silt and clay are predominant.

3.1. Pedons formed under fluvial influence

From the pedons under fluvial influence, P1 located on the edge of the mangrove of the sampled region was shallowest (0.55 m). All horizons and layers had a 1 10GY Gley color, which indicates a flooded environment and oxidation process promoted by roots and soil microorganisms. Along P1, a more homogenous texture distribution was observed when compared to the other pedons, which may be related to the fact of being in a zone with lower fluvial influence, on the riverbank (continent); therefore, in a more protected environment (**Table 2**).

The deepest pedon was P2 (1.02 m), due to its location at a higher position, so that it is not completely flooded for a long time. The layers and horizons of this pedon had a 1 10Y Gley color in the whole profile, due to its continuous drying cycles, as well as the presence of very fine to thick roots, up to the horizon 5 Agn. The horizon textures of this pedon were medium, and the last was the most clayey, possibly indicating accumulation of particulate material in the aforementioned horizons (**Table 2**).

The pedons P3, P4, and P5 have similar depths (around 0.70 m), with colors varying from 1 5G 4/1 Gley to 2 10B 4/1 Gley and a texture ranging from medium (P3 and P4) to very clayey (P5), indicating pedons formed in accumulation and storage regions, respectively. In P4, a horizon (4 Agnj) with shell deposition was found, attributed to two possible causes: presence of oysters that use the stem and roots of the plant species *Rhizophora mangle* (predominating in the area) as habitat and fall on the ground and are incorporated with time; or as a shell disposal area for the fishermen, still on site, as a result of shell fishing (information provided by local fishermen).

The sequence of Ag horizons or layers was identified in P1, P2, and P3 and the Agr sequence in P4 and P5, with material discontinuity (fluvial nature), evidenced by stratifications, with an irregular texture variation (**Table 2**) and in-depth organic C content, found in all pedons, indicating fluvial sediment storage [59]. In these soils, there are moderate a horizons and the Cr layer of P4 and P5 corresponds to a soft rocky mineral, derived from blue-greenish shales of the island group, also called "green rust" [62].

3.2. Pedons formed under marine influence

Pedons formed under marine were shallower than those formed under fluvial influence (**Table 2**), which is related to a longer submersion time and the location in a marine estuary,

favoring greater particle removal. This behavior is very clear in P7, located in the southern part of the island, in the mouth of "Baía de Todos os Santos", where parental material is almost exposed, in addition to sparse or almost absent presence of vegetation.

Dark brown mottles (7YR 3/3) of horizons Agn of P6 and P7 occur due to oxidation of reduced Fe forms in microenvironments created by roots and soil biota [61, 63]. The texture of these pedons ranged from medium in the surface to very clayey, indicating an alternation of different materials deposited over time (**Table 2**). In P7, high silt percentage may be related to the greater particle deposition in the area, the scarce presence or absence of vegetation, and presence of soft rock at a depth of 0.17 m. The sequence of Agn horizons or layers was identified in P6 and Agn-Crg in P7, for the same reasons as explained for pedons under fluvial influence.

3.3. Chemical properties

The results of chemical analyses of pedons under fluvial (P1–P5) and marine (P6 and P7) influence are shown in the **Tables 3** and **4**. Of the seven pedons, four had only an A horizon (P1–P3, and P6) and three had an A horizon and a C layer (P4, P5, and P7). All pedons are formed by a gley horizon, or a reductive environment, due to tidal movements that maintain the soil waterlogged most of the time.

Profile	Depth	S	pH (H_2O)	pH incubation levels[1]					
	cm	(%)		0[2]	15	30 days	45	60	ΔpH[3]
P1—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–8	3.6	6.7	6.3	6.3	6.6	6.8	4.9	1.4
2Abgnj	8–20	3.6	6.4	7.1	4.0	3.3	3.1	2.5	4.6
3Abgnj	20–34	3.5	6.2	7.1	3.1	3.1	2.9	2.6	4.5
4Abgnj	34–55	3.7	6.1	8.1	4.2	3.9	3.3	3.1	5.0
P2—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agnj	0–20	3.8	5.8	6.3	5.0	3.7	2.7	3.0	3.3
2Agnj	20–32	3.6	6.0	6.1	3.1	2.4	1.7	2.2	3.9
3Agnj	32–61	3.8	5.9	7.0	3.0	2.2	2.1	2.3	4.7
4Agn	61–83	3.6	6.5	7.5	—	—	—	—	—
5Agn	83–102+	3.8	7.0	7.5	—	—	—	—	—
P3—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agnj	0–5	4.0	6.0	7.0	3.7	2.9	2.6	2.4	4.6
2Agnj	5–25	3.9	4.7	6.1	3.4	3.1	3.0	2.9	3.2
3Agnj	25–49	3.8	5.8	7.0	3.0	2.4	2.4	2.3	4.7
4Agnj	49–71+	3.7	6.4	7.5	3.4	2.5	2.6	2.3	5.2
P4—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–7	3.8	6.4	6.6	5.8	5.4	4.7	4.2	2.4
2Agnj	7–18	3.8	4.7	6.6	3.1	2.4	1.7	2.3	4.3

Profile	Depth	S	pH (H_2O)	pH incubation levels[1]					
	cm	(%)		0[2]	15	30 days	45	60	ΔpH[3]
3Agnj	18–41	3.9	5.8	6.9	3.5	2.4	2.2	2.2	4.7
4Agnj	41–60	3.9	4.9	7.0	3.0	2.4	2.2	2.4	4.6
4Crgnj	60–70	3.7	3.6	6.9	2.8	2.5	2.0	2.3	4.6
P5—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agn	0–15	3.8	6.6	6.2	6.5	6.3	6.4	6.4	−0.2
2Agnj	15–26	3.8	5.5	6.3	3.4	2.9	2.7	2.7	3.6
3Agnj	26–43	3.4	5.4	6.7	3.0	2.8	2.6	2.4	4.3
4Agn	43–60	3.7	7.4	7.1	7.0	6.6	6.4	7.3	−0.2
4Crgn	60–70+	3.7	7.6	7.8	7.5	6.4	7.3	7.4	0.4
P6—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained									
Agnj	0–15	3.3	5.8	7.2	4.0	3.1	3.2	3.0	4.2
2Agnj	15–33	3.4	6.5	7.1	3.6	3.4	3.7	3.0	4.1
3Agnj	33–48	3.3	5.5	7.3	3.1	3.0	1.7	2.3	5.0
4Agn	48–60	3.3	5.3	7.2	—	—	—	—	—
P7—Gleysol thiomorphic orthic (salic) sodic luvissol, very poorly drained									
Agnj	0–9	3.9	7.3	7.3	6.6	5.7	5.9	2.9	4.4
2Agn	9–17	3.8	7.2	7.4	6.7	6.4	7.0	7.1	0.3
2Crgn	17–28	3.6	7.0	7.1	6.6	6.6	7.0	7.0	0.1

[1]Sixty-day incubation.

[2]It corresponds to pH value on site, humid sample.

[3]It corresponds to the difference between pH level in the beginning (0) and in the end (60 days).

Table 3. Values for sulfur (S%), $pH_{H_2O,}$ and $pH_{incubation}$ of mangrove soils in the Subaé river basin, Santo Amaro, Bahia, Brazil.

The thiomorphic nature of profiles or layers is determined by the ΔpH value after soil incubation, and soils with ΔpH values >0.5 are identified this way, observed for most of the layers, except for the horizons Agn and 4Agn of P5 and 2 Agn and 2 Crgn of P7. The results for the thiomorphic nature are according to the total S content, higher than the minimum content required (0.75%) to characterize the presence of sulfide materials [64], ranging from 3.3 (2Agnj of P6) to 4.0% (Agnj of P3) (**Table 3**), which is normal for mangrove soils [65, 66].

Organic C contents in pedons formed under fluvial influence (P1, P2, P3, P4, and P5) ranged from 47.0 in the 4 Agn horizon in P2 to 53.4 g kg^{-1} of 4 Agn in P5, with higher nominal values than those of soils formed under tidal influence (45.7 in the 2Crgn layer of P7 at 51.7 g kg^{-1} in the 3 Agn of P6 and Agn horizons of P7) (**Table 4**). However, for both environments, pedons were classified as orthic, because the organic C content was below 80 g kg^{-1}.

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In all pedons, percentage of sodium saturation (PST) values (**Table 4**) (47% in the 2 Agnj horizon of P4 at 69% in the Agn horizon of P1) exceeded the threshold values that classify a soil as sodic

Horizons/layers	Depth	CE	Ca	Mg	Al	H + Al	Na	K	SB	T	V	PST	P	C.org.
	cm	dS m^{-1}	$cmol_c\ kg^{-1}$								%		mg kg^{-1}	g kg^{-1}
P1—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–8	40	3.0	14.0	0.2	3.0	51.2	3.6	71.7	75	96	69	5.3	48.8
2Agn	8–20	38	3.8	15.6	0.2	4.8	52.3	3.3	74.8	80	94	66	5.5	49.8
3Agn	20–34	36	3.6	16.9	0.2	5.6	55.5	3.4	79.4	85	93	65	5.7	51.6
4Agn	34–55	42	4.5	15.5	0.2	7.1	49.0	4.0	73.1	80	91	61	4.9	50.2
P2—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–20	35	2.1	7.6	0.1	5.4	14.9	1.2	25.9	31	83	48	5.2	50.6
2Agn	20–32	35	4.5	4.3	0.1	5.3	19.2	1.2	29.2	35	85	56	5.1	54.0
3Agn	32–61	33	3.2	6.7	0.1	4.6	16.4	1.2	27.5	32	86	51	5.2	51.0
4Agn	61–83	31	2.5	10.0	0.1	1.4	18.1	1.9	32.6	34	96	53	5.2	49.6
5Agn	83–102+	22	3.7	9.6	0.0	1.8	16.0	2.0	31.3	33	95	48	5.4	53.4
P3–Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–5	36	2.7	8.4	0.0	1.9	22.4	1.4	34.8	37	95	61	5.1	50.7
2Agn	5–25	43	2.5	8.0	0.0	8.8	27.7	1.1	39.4	48	82	58	5.0	51.0
3Agn	25–49	44	3.3	10.8	0.0	7.1	35.2	1.6	50.8	58	88	61	4.9	53.0
4Agn	49–71+	38	3.5	11.3	0.1	5.3	39.5	2.0	56.2	61	91	64	5.4	51.9
P4—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–7	31	1.5	5.3	0.0	2.6	18.1	1.1	26.0	29	91	63	5.1	51.6
2Agnj	7–18	27	1.6	4.2	0.7	6.1	11.7	1.1	18.7	25	75	47	5.1	52.1
3Agnj	18–41	30	2.2	4.6	0.0	4.3	12.8	1.2	20.8	25	83	51	5.3	52.9
4Agnj	41–60	29	2.3	7.4	0.5	6.7	19.2	2.2	31.0	38	82	51	5.1	53.1
4Crgnj	60–70	29	7.8	4.6	3.3	12.3	51.2	1.1	64.7	77	84	66	5.1	50.1
P5—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–15	28	2.9	14.1	0.1	3.6	56.5	3.4	76.9	81	96	70	5.2	53.1
2Agn	15–26	20	3.5	14.7	0.2	7.2	42.7	4.8	65.7	73	90	59	5.4	50.2
3Agn	26–43	38	5.1	13.0	0.3	11.1	59.7	4.8	82.7	94	88	64	5.3	52.4
4Agn	43–60	44	8.6	9.8	0.1	0.9	43.7	2.2	64.3	65	99	67	5.6	47.0
4Crgn	60–70+	33	4.9	10.1	0.1	1.0	20.3	3.3	38.5	40	97	51	6.2	52.7
P6—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained														
Agn	0–15	36	3.4	11.3	0.1	6.3	38.4	3.1	56.1	62	90	62	5.7	46.6

Horizons/layers	Depth	CE	Ca	Mg	Al	H + Al	Na	K	SB	T	V	PST	P	C.org.
	cm	dS m^{-1}	$cmol_c$ kg^{-1}								%		mg kg^{-1}	g kg^{-1}
2Agn	15–33	46	6.3	16.2	0.1	5.6	58.7	4.2	85.4	91	94	64	5.1	48.5
3Agn	33–48	41	5.4	19.6	0.6	10.9	70.4	4.5	99.9	111	90	64	5.4	51.7
4Agn	48–60	57	5.5	11.6	0.1	3.7	71.5	5.4	94.0	98	96	73	5.2	50.2
P7—Gleysol thiomorphic orthic (salic) sodic luvissol, very poorly drained														
Agn	0–9	45	4.5	12.8	0.2	2.2	54.4	3.1	74.9	77	97	71	7.1	51.7
2Agn	9–17	48	5.5	10.7	0.2	1.9	58.7	3.0	77.7	80	98	74	5.3	48.7
2Crgn	17–28	42	7.5	15.7	0.2	2.1	67.2	2.8	93.2	95	98	71	5.7	45.7

Table 4. Chemical attributes of pedons in the mangrove in the Subaé river basin, Santo Amaro, Bahia, Brazil.

(PST ≥ 6), which results in clay dispersion and, probably, in soil organic matter dispersion. High Na^+ levels in all pedons, associated with high pH levels, contribute to the halomorphism processes. Excessive salts in the layers or horizons whose EC values ranged from 20 dS m^{-1} (2 Agn of P5) to 57 dS m^{-1} (3 Agn of P6) led to the classification of pedons as salic, since these values are much higher than the threshold values to classify soils as salic (EC ≥ 7 dS m^{-1}) [57] (**Table 4**). The salic nature hinders water absorption by terrestrial plants, but is less relevant for mangrove plants that are adapted to EC levels exceeding those of the classification.

Sorption complex of pedons is dominated by cations $Na^+ > Mg^{2+} > Ca^{2+} > K^+$ and, in almost all horizons and layers, the Mg^{2+} content was higher than Ca^{2+}, which is common in estuarine environments, and may be attributed to pedogenetic processes, such as soluble salt addition, mainly by seawater intrusion and fluvial deposition in a drainage region of fertile soils, as the Vertisols in the region.

Most of the pedons had CEC values between 25 (2 Agnj and 3 Agnj of P4) and 111 cmolc kg^{-1} (3Agn of P6). Cation exchange capacity (T) values between 22.47 and 45.36 cmolc kg-1, in mangrove soils of the Iriri River in "Canal da Bertioga" (Santos, São Paulo, Brazil) [66]. These values are high due to a great contribution of organic matter and a predominance of the Na^+, Mg^{2+}, Ca^{2+}, and K^+.

Although being located in an environment with high deposition of organic and mineral compounds, the studied pedons showed low P availability, with contents from 4.9 (4 Agn of P1) to 7.1 mg kg^{-1} (Agn of P7), compared to the contents in Gleysols (19–35 mg kg^{-1}) in "Bertioga Canal" [66]. The Al content in all pedons was close to zero and the acidity in the environment was due to H, as shown by an evaluation of the difference between potential acidity and exchangeable acidity.

Even the pedons under study presenting similar characteristics, pedons formed under riverine influence showed some different characteristics from those observed for pedons formed under marine influence, as follows.

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3.4. Pedons formed under riverine influence

The pH levels of pedons under riverine influence (P1–P5), assessed in the field, ranged from moderately acid (pH 6.1–6.5) in the 2A horizon of P1 and P3 to moderately alkaline (pH 7.1–8.1) in the 4A horizon of P2 (**Figure 2**). Studying the mangrove soils under riverine influence in the Marapanim river (Pará, Brazil), Amazon Coast, [21] found pH values similar to those obtained in this study. Just as it was observed for physical characteristics, the shallower pedon (P1) and the deepest pedon (P2) showed chemical characteristics different from the others under riverine influence.

The pH level of P1 increased at a greater depth, showing a value within the alkaline range (8.14), attributed to a higher concentration of Na^+, Mg^{2+} and K^+ when compared to the others (**Table 4**). The higher pH values of P2 were registered in the deepest horizons, probably as a result of Mg^{2+} accumulation (**Table 4**), something which may have happened because of closeness to rocks or leaching of the element in the higher layers. Mg^{2+} accumulation and the simultaneous increased pH values at a greater depth, in pedons under riverine influence, was not observed only for P4 (**Figure 2**, **Table 3**). The pH value in P3, P4, and P5 ranged from 6.2 to 7.5, and it tended to increase at a greater depth, something which may be explained by Mg^{2+} and Na^+ accumulation in the profile (**Figure 2**, **Table 3**).

The Eh values of P1 (328–261 mV) and P2 (337–271 mV) were higher in the surface horizons and layers and they decreased at greater depths. According to [61–68], decreased Eh values at greater depths is usual in estuarine environments. Although this proposition is applicable to all of the pedons assessed, it was observed that, in P3 and P4, the horizons with the highest

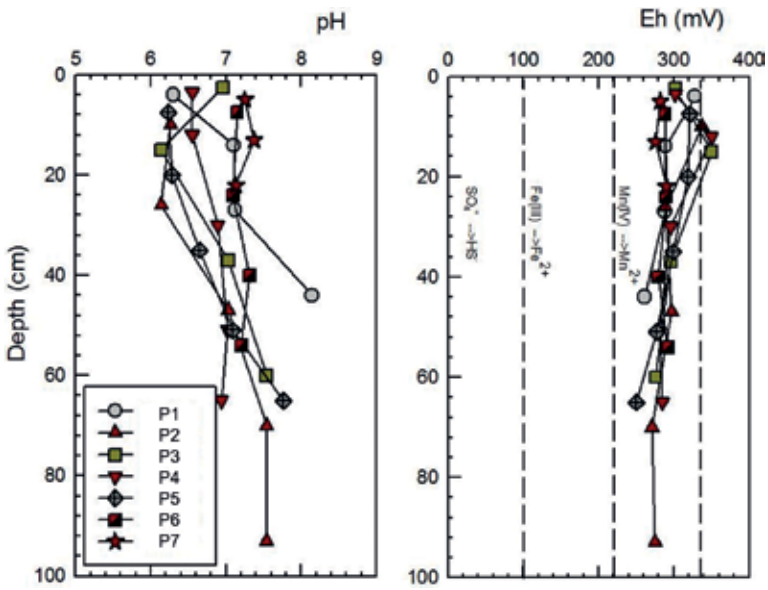

Figure 2. Distribution of pH and Eh in depth in the mangrove soil profiles in the Subaé river basin, Santo Amaro, Bahia, Brazil.

Eh values were concentrated in the subsurface layers (**Figure 2**). Water level fluctuation has led the Eh values to range from 66 to 74 mV. The Eh values in this study ranged from oxic (>300 mV) to suboxic (100–300 mV) (**Figure 2**), in the reduction range from Mn^{4+} to Mn^{2+}, usually between 200 and 300 mV [69] and they do not reach typical values for anoxic environments (Eh < 100 mV, pH 7), as those obtained by other studies [61, 63, 68, 70]. It was observed by [71] substantial variation in the redox conditions for Rhizophora woods in the Cananeia Lagoon System, Brazil, triggering variation in the redox conditions. The suboxic values in this study may be explained by the collection of samples from the edge of mangroves, sites that, according to [72], favor a quicker drainage and, as a consequence, aeration.

The inverse and significant correlation between pH and Eh ($r = -0.705$, $p < 0.001$, $n = 30$), displayed in **Figure 3**, is mainly due to the presence of Fe oxides. The most common electron acceptors in saturated soils, whose reduction tends to buffer Eh for several weeks and, thanks to the proton consumption, they cause an increase in the pH level [73].

The Crgn horizon observed in P4, which indicates the presence of carbonate material (shells), showed a Ca concentration of 7.8 cmolc kg^{-1} (**Table 4**), but one of the lowest pH_{H_2O} levels (3.6%) (**Table 3**), something which may be attributed to the sulfur concentration (3.7%). Sulfur compounds may contribute to decrease the pH levels in the environment, solubilizing some chemical elements [74].

3.5. Pedons formed under marine influence

Pedons under marine influence (P6 and P7) showed pH values around 7.0 along the whole profile (**Figure 2**), something which may be attributed to a higher Ca^{2+} and Mg^{2+} concentration (**Table 4**). Eh values, mainly on the surface of these soils, were lower than those observed for pedons formed under riverine influence. These results confirm the inverse relation between pH and Eh already pointed out.

Eh values of these pedons showed some characteristics different from those observed for the pedons under riverine influence: while the values for pedons under riverine influence

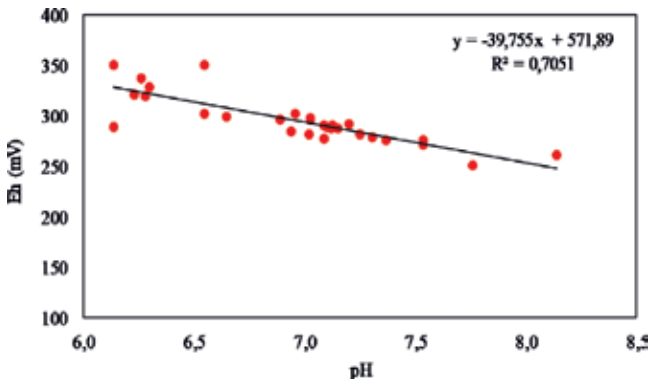

Figure 3. Correlation between Eh and pH in the field of the seven pedons from mangrove soils in the Subaé river basin, Santo Amaro, Bahia, Brazil.

were between 250 and 350 mV, those under marine influence varied: P6 (276–292 mV) and P7 (276–290 mV). These results may be explained by the fact that pedons under marine influence remain submersed for a longer time than those formed under riverine influence. There is no tendency to decrease Eh values at greater depths and the range of Eh values in P6 (13 mV) and P7 (14 mV) is lower than the range for Eh values in the pedons formed under riverine influence.

3.6. Heavy metals

Soils may naturally show high concentrations of heavy metals derived from weathering conditions of the source material rich in these elements or due to anthropogenic influence, through the urbanization and industrialization processes. The environment where mangrove soils are formed, such as those assessed in this study with CEC values between 25 and 100 cmolc kg^{-1} (**Table 4**) had a great capacity to retain metals coming from tidal waters, fresh water, rainwater flow, and atmospheric and anthropogenic precipitation. The presence of metals in mangroves is a matter of concern because this environment is the cradle of several animal species used as human food (fish, crab, oyster, etc.).

The Brazilian environmental legislation does not have specific rules for heavy metal concentrations in coastal environments. In this study, in order to assess the normality level of heavy metal concentrations in pedons under riverine (P1–P5) and marine influence (P6 and P7) (**Table 5**), we used Resolution 420/2009, from the Brazilian National Environmental Council [75], which provides for soil quality criteria and values regarding the presence of chemical substances and it classifies the metal contents observed on the soil as preventive values (the threshold concentration of a certain substance on the soil, which is capable of support its main functions) and investigation values (concentration of a certain substance on the soil above the threshold for potential hazards to human health); and the values established by the National Oceanic and Atmospheric Administration [76], which classify the heavy metal content levels on the soil as background, preventive threshold (TEL) and hazard to the biota for marine sediments (PEL).

3.7. Pedons formed under riverine influence

Lead is among the heavy metals with a greater effect on the aquatic environment, because it is, at the same time, toxic, persistent, and bioaccumulative within the food chain [77]. Among the pedons under study, P1 had the highest contamination degree, with a Pb concentration at all layers above the prevention threshold established by [75] (**Table 5**). The 4 Abgn horizon of P3 also showed lead concentration levels above the prevention threshold. According to the [76] classification, all layers and horizons of pedons formed under riverine influence showed Pb concentration values between 1 and 3.5 times higher than the TEL value. The 4 Crgnj (P4) layer was an exception, since it showed a Pb concentration level below the background. In contrast, Pb concentration value in the 2 Abgn (P1) layer, 111.3 mg kg^{-1}, was very close to the PEL value (112 mg Pb kg^{-1}). The Pb concentration levels registered in P1 are a matter of concern, because the pedon is located at an area frequently used by the riparian population to collect shellfish, both for eating and selling.

Horizon/layer	Pb	Cd	Zn	Mn	Fe
	mg kg^{-1}				dag kg^{-1}
P1—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	85.1 ± 5.7	0.9 ± 0.1	73.4 ± 1.0	128.7 ± 5.0	3.6 ± 0.2
2Abgn	111.3 ± 2.1	1.3 ± 0.1	92.4 ± 0.7	141.2 ± 2.5	5.2 ± 0.0
3Abgn	77.9 ± 2.2	1.2 ± 0.1	95.1 ± 3.5	188.4 ± 0.4	4.6 ± 0.5
4Abgn	82.9 ± 3.1	1.2 ± 0.0	86.4 ± 1.0	235.6 ± 7.5	4.5 ± 0.5
P2—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	58.8 ± 1.8	0.6 ± 0.0	55.2 ± 1.3	90.8 ± 2.0	1.7 ± 0.3
2Abgn	45.9 ± 8.1	0.4 ± 0.1	54.5 ± 2.2	75.7 ± 1.5	1.6 ± 0.2
3Abgn	70.0 ± 8.0	0.8 ± 0.1	55.6 ± 4.7	77.8 ± 1.2	1.9 ± 0.3
4Abgn	55.6 ± 5.5	4.8 ± 7.2	51.4 ± 2.6	99.6 ± 3.9	2.4 ± 0.6
5Abgn	45.0 ± 0.8	0.3 ± 0.0	50.4 ± 3.9	42.8 ± 2.1	2.8 ± 0.1
P3—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	36.5 ± 3.4	0.7 ± 0.1	40.4 ± 0.9	82.6 ± 28.6	1.6 ± 0.1
2Abgn	47.4 ± 2.4	0.6 ± 0.1	43.3 ± 1.1	70.5 ± 1.7	2.1 ± 0.0
3Abgn	53.6 ± 2.4	1.2 ± 0.1	57.8 ± 0.9	98.8 ± 1.3	2.6 ± 0.1
4Abgn	72.5 ± 3.8	1.5 ± 0.2	64.5 ± 1.1	138.2 ± 5.4	2.9 ± 0.3
P4—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	32.0 ± 5.2	0.4 ± 0.2	33.7 ± 1.6	64.0 ± 2.9	1.2 ± 0.1
2Abgnj	35.0 ± 1.9	0.4 ± 0.1	19.5 ± 6.4	39.5 ± 0.2	0.7 ± 0.3
3Abgnj	26.2 ± 2.4	0.4 ± 0.0	23.3 ± 1.5	58.3 ± 1.8	1.0 ± 0.1
4Abgnj	26.6 ± 4.4	0.4 ± 0.0	35.3 ± 1.8	76.1 ± 2.4	1.7 ± 0.0
4Crgnj	14.0 ± 3.6	0.2 ± 0.0	30.9 ± 1.0	98.8 ± 3.8	1.7 ± 0.1
P5—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	54.4 ± 0.6	0.3 ± 0.1	73.1 ± 1.4	241.9 ± 0.2	4.0 ± 0.1
2Abgn	65.5 ± 9.8	0.9 ± 0.2	72.0 ± 3.3	120.3 ± 1.1	3.5 ± 0.0
3Abgn	63.8 ± 7.3	1.4 ± 0.0	73.9 ± 1.7	173.4 ± 2.6	4.2 ± 0.0
4Abgn	45.3 ± 5.4	0.7 ± 0.0	48.2 ± 1.2	240.1 ± 1.8	3.4 ± 0.1
4Crgn	49.5 ± 6.9	1.0 ± 0.1	65.6 ± 0.7	205.8 ± 3.1	4.6 ± 0.1
P6—Gleysol thiomorphic orthic (salic) sodic luvissol, potentially toxic, very poorly drained					
Agn	43.7 ± 5.8	0.6 ± 0.1	52.3 ± 1.8	141.4 ± 9.1	2.8 ± 0.1
2Abgn	29.5 ± 1.3	0.4 ± 0.0	62.4 ± 0.7	252.3 ± 4.9	4.5 ± 0.4
3Abgn	6.2 ± 0.6	0.0 ± 0.0	62.2 ± 3.9	280.4 ± 11.1	3.8 ± 0.5
4Abgn	14.7 ± 4.6	0.0 ± 0.0	59.2 ± 0.1	268.7 ± 1.0	3.9 ± 0.0

Horizon/layer	Pb	Cd	Zn	Mn	Fe
	mg kg^{-1}				dag kg^{-1}
P7—Gleysol thiomorphic orthic (salic) sodic luvissol, very poorly drained					
Agn	9.0 ± 4.3	0.4 ± 0.0	68.2 ± 20.2	229.3 ± 86.5	3.4 ± 0.0
2Abgn	11.9 ± 5.0	0.2 ± 0.1	50.7 ± 2.6	271.3 ± 11.0	2.7 ± 0.1
2Crgn	15.3 ± 0.0	0.3 ± 0.1	54.8 ± 2.4	284.3 ± 7.6	2.9 ± 0.1
CONAMA (2013)					
Prevention	72.0	1.3	300	—	—
NOAA (1999)					
Background	4–17.0	0.1–0.3	7–38	400	0.99–1.8
TEL[1]	30.24	0.6	124.0	—	—
PEL[2]	112.0	4.2	271.0	—	—

[1]TEL: It may affect the biological community.

[2]PEL: It causes some effect on the biological community.

Table 5. Average and standard deviation of heavy metal concentrations in pedons from the mangrove located in the Subaé river basin, Bahia, Brazil and reference values for metals.

Cadmium is a metal of great mobility within the systems and, therefore, it is hard to establish a distribution characteristic for this metal. Cd values in some horizons of pedons under riverine influence, P1 (2 Abgn), P2 (4 Abgn), P3 (4 Abgn) and P5 (3 Abgn), were equal to or higher than the prevention values established by CONAMA [75]. Cd concentrations in the two pedons under marine influence (P6 and P7) were below the prevention values (**Table 5**). The greater presence of Cd in pedons under riverine influence was also confirmed by the NOAA [76] methodology. Only the 5 Abgn (P2), Crgnj (P4), and Agn (P5) layers showed a Cd concentration equal to or lower than the values accepted for background [76].

The other layers or horizons showed Cd concentration values above the TEL limits and the Abgn layer (P2) showed a Cd concentration level that may cause adverse effects to the biota, i.e. a value above PEL (**Table 5**). The highest Cd concentration levels in pedons under riverine influence may be associated with external waste disposal, such as contamination by waste disposed during lead mining, in the municipality of Santo Amaro, or, according to [78], in urban and industrial activities at the Godavari Estuary, India.

Zn concentration levels in the pedons do not pose a potential risk to the biota, with values below the prevention values established by CONAMA [69] and the TEL values established by the NOAA [76], and the concentration values in all of the P4 layers, the pedon least affected by heavy metals, were lower than the background values (**Table 5**).

As they are significant elements in many source materials, it is difficult to differentiate Mn and Fe concentrations having an anthropogenic origin from the natural ones. Mn concentrations in pedons under riverine influence ranged from 39.5 (2 Abgnj of P4) to 240.1 mg kg^{-1} (4 Abgn of P5), values that are below the background established by [76].

Fe concentrations ranged from 0.7 (2 Abgnj of P4) to 5.2 dag kg^{-1} (2 Abgn of P1). In all pedons under study, either of riverine or marine origin, Fe concentration values were above the background threshold values established by NOAA [76], except for the Agn and 2 Abgn (P2) and Agn (P3) layers and all of the P4 layers, which were below the background concentration (**Table 5**).

3.8. Pedons formed under marine influence

Generally, pedons formed under marine influence had heavy metal content levels lower than those in pedons under riverine influence. None of the pedons formed under marine influence showed a Pb concentration value close to the prevention values established by CONAMA [75]. According to NOAA [76], Pb concentrations in the 3 Abgn and 4 Abgn (P6) layers and in the 2 Abgn and Crgn horizons were lower than the background values and only the Agn (P6) layer showed a value higher than the TEL value. Recent study in tropical mangroves showed that mangrove forest act as a biofilter towards heavy metals [79]. Mangrove species compositions change from riverine to marine mangroves due to change in salinity condition and geomorphology. Thus, higher level of species diversity of mangroves is crucial to maintain the health and productivity of coastal ecosystem [79].

Cd concentrations were lower than the threshold value established as background, although in the Agn and 2 Abgn (Pedon 6) and Agn (Pedon 7) layers were higher than the background value (**Table 5**).

Mn concentrations ranged from 141.4 in the Agn horizon of P6 to 284.3 mg kg^{-1} in the 2 Crgn layer of P7, with an increase in the subsurface (**Table 5**). These values were below the background established by NOAA [76]. Mn values in the soils having a marine origin were higher than those obtained in the pedons formed under riverine influence (P2–P4), but similar to P1 and P5 (**Table 5**).

3.9. Soil classification

The morphological, physical, and chemical characteristics determined in the seven pedons, regardless of the riverine (P1–P5) or marine (P6 and P7) influence have enabled us to classify the soils, according to the SiBCS [57], as Gleysol thiomorphic orthic (salic) sodic luvissol. If significant areas having pedons similar to those studied herein are mapped, it may be suggested to the SiBCS the Salic nature as the third category level of the theomorphic Gleysols, due to CE values higher than 7 dS m^{-1} at 25°C (**Table 4**).

Based on the characteristics shown, soils were classified according to the Soil Taxonomy [9] as Entisols (Typic Sufalquents), and pedons P5, under riverine influence, and P7, under marine influence, are classified as Haplic Sufalquents, since they show, in some horizon, at a depth between 20 and 50 cm below the surface, less than 80 g kg^{-1} of clay in the fine soil portion, and the others (P1, P2, P3, P4, and P6) are classified as Typic Sufalquents. According to the system World Reference Base (WRB) [71], soils were not classified as Fluvisols Salic Gleyic (Thionic, Sodic), except for pedon P7, which did not show a salic horizon, therefore, it was classified as Fluvisols Gleyic (Thionic, Sodic).

Soils in all of the pedons, either under riverine or marine influence, showed an identical classification, up to the fourth category level regardless irregular characteristics distribution of

depth, alternation of layers texture and C-org contents, presence of contaminants (heavy metals). It was possible to distinguish only from the fifth category level.

According to Embrapa [57], Gleysols are formed, mainly, due to constant or periodic excessive water, whether they are stratified or not, something which may, many times, lead people to classify these soils as intermediate for Fluvic Neosols. Nevertheless, for the thiomorphic Gleysols there is no definition as intermediate for this class (Fluvic Neosols), at the fourth category level, but, since this is a striking feature of mangrove soils, it was chosen to classify them at the fifth category, in order to suggest the riverine nature, rather than using the texture clustering.

Another characteristic that stands out in soils in the region and has a direct influence on its occupation, use, and management is the presence of heavy metal contaminants, which may occur due to natural factors and processes (source material) or through anthropic processes (introduced into the system by harmful actions). All pedons had heavy metal values higher than those established by the environmental authorities [75, 76], except for P7 (**Table 5**). It is believed that, for this last pedon, the longer distance from the contamination point when compared to the others may have favored its lower concentration.

In the SiBCS, there is no alternative clearly expressed for including heavy metals in the classification, it may be included as a differential characteristic that affects soil use and management for several purposes, also in the fifth category level, based on a chemical attribute that reflects environmental conditions. In the system WRB [59], the prefix Toxic may be used as a formative element for second level units, in some classes, in order to indicate the presence, in any layer within up to 50 cm of the soil surface, of toxic concentrations of organic or inorganic substances that are not the ions Al, Fe, Na, Ca, and Mg.

Based on the classification systems of FAO and the Soil Taxonomy, it was chosen to include the term potentially toxic in the sixth category level, related to the SiBCS, for the soils classes under study having heavy metal concentration above the reference values established by the U.S. National Oceanic and Atmospheric Administration [76]. The pedons under riverine and marine influence were classified as Gleysol thiomorphic orthic (salic) sodic luvissol (potentially toxic, very poorly drained), except for P7, due to the low metal concentration.

4. Final remarks

1. Mangrove soils in the Subaé river basin showed different morphological, physical, and chemical characteristics when they were under riverine and marine influence.
2. Mangrove soils in the Subaé river basin showed holomorphic, hydromorphic, and sulfate-reducing conditions, showing some clayeying, as indicated by the morphological, physical, and chemical characteristics.
3. The highest Pb and Cd concentrations were identified in the pedons under riverine influence, probably due to closeness to the Plumbum Mining factory and the lowest concentrations were found in pedon P7, due to greater distance from the factory.
4. All pedons in the soils under study had concentrations of, at least, one heavy metal (Mn, Zn, Pb, Fe, and Cd) above the minimum value warning (TEL), except for pedon P7.

5. Mangrove soils, regardless of being under riverine or marine influence, were classified as Gleysol thiomorphic orthic (salic) sodic luvissol (potentially toxic, very poorly drained), due to the low metal concentration.

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Mangrove Bioprospect

Chapter 8

Chemistry and Biodiversity of *Rhizophora*-Derived Endophytic Fungi

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Additional information is available at the end of the chapter

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Abstract

Rhizophora are salt-tolerant mangrove flora located in tropical and subtropical intertidal coastal regions. This review summarizes frequently occurring fungal endophytes in *Rhizophora*. In total, 41 families and 64 genera belonging to 23 taxonomic orders of Ascomycota have been reported. Among those discussed here, *Pestalotiopsis*, *Penicillium*, and *Mucor* are the most abundant fungal genera, and they are widely studied. In previous studies, 195 metabolites were encountered in *Rhizophora*-derived endophytic fungi, and their structures are reported within a biogenetic context. Bioassays showed antitumor, antimicrobial, as well as anti-H1N1 activities to be the most notable bioactivities of the secondary metabolites discussed.

Keywords: *Rhizophora*-derived endophytic fungi, biodiversity, secondary metabolites, biological activities

1. Introduction

Endophytic fungi, a polyphyletic group of highly diverse, primarily ascomycetous fungi that spend all or at least for a part of their life cycle inter- or intracellularly colonizing healthy tissues of plants without causing visible disease symptoms [1]. They are found in almost all vascular plants and grass plants [2]. It is worth noting that of the nearly 300,000 plant species that exist on Earth, any given plant is colonized by several to few hundreds of endophytic fungal species. Only a few of these plants have ever been completely studied relative to their endophytic biology [3]. Until recently, extensive work has been conducted on traditionally investigated terrestrial endophytic fungi with biological significance, and these studies mostly concentrated on the tropical and rainforest regions of the world. However, systematic

and comparative approaches to identifying endophytic fungi and their specific location in the plants they colonize, especially in ecological niches such as mangrove endosymbionts growing in high salinity, high temperature, extreme tides, oxygen pressure, high humidity, and light and air limitations, have received considerable attention in recent decades [4, 5]. Hence, it is now generally accepted that the highly complex mangrove ecosystems could act as an effective selector for metabolic pathway evolution via the generation of structurally unprecedented and biologically interesting metabolites of pharmaceutical importance. Such metabolites are believed to be involved in ecological adaptability, defense, communication, and predation [6]. In this review, we summarize the biodiversity of *Rhizophora* endophytic fungi. Additionally, the metabolites encountered in *Rhizophora*-derived endophytic fungi and their structures are reported within a biogenetic context. Special emphasis is placed on the prospect of discovering unique functional metabolites.

2. Endophytic fungi from *Rhizophora*

Mangroves are composed of a large group of salt-tolerant plant communities growing in tropical and subtropical intertidal estuarine zones, which are distributed approximately in the area between 30° N and 30° S latitude [7]. Asia and Australia have the greatest diversity and distribution of mangrove species. Among the 18 million hectares of mangrove forests, more than 40% are found along the Asian coasts, including the South China Sea Coast [10]. The most established mangroves can be found in Bangladesh, Brazil, Indonesia, India, and Thailand [8, 9]. According to the statistical data of the International Society of Mangrove Ecosystem, there are 84 mangrove species globally, belonging to 16 families and 24 genera. Among them, 70 species are true mangroves, pertaining to 16 genera and 11 families. Another 14 species are considered semimangroves, belonging to 8 genera and 5 families [10]. China has 26 species, and 24 of them are distributed in Hainan [11, 12].

Rhizophora is one of the most conspicuous genera of the most widespread mangrove family, the Rhizophoraceae. The genus is relatively old among cosmopolitan mangrove genera, and it has notable discontinued species distributions [13]. In total, eight species comprise the *Rhizophora*, including *R. stylosa*, *R. apiculata*, *R. mucronata*, *R. mangle*, *R. harrisonii*, *R. racemosa*, *R. annamalayana*, and *R. samoensis* (**Table 1**). *R. stylosa*, *R. mucronata,* and *R. apiculata* are mainly distributed in islands and coastal areas bordering the Pacific Ocean and the Indian Ocean, while *R. mangle*, *R. annamalayana*, *R. samoensis*, *R. harrisonii,* and *R. racemosa* are mainly distributed from the eastern Pacific through the American islands to the Atlantic Ocean (**Figure 1**).

Fungi colonized in mangrove forests, which comprise the second largest ecological group of the marine fungi, have specially adapted their own morphological structures and physiological mechanisms to promote the survival of host plants in harsh environmental conditions through long-term endophyte-host interactions [52]. Most mangrove endophytic fungi are facultative halophiles and euryhaline in nature. Since they do not require added salt for growth, they are able to grow at high salt concentrations and show a balanced symbiotic continuum of mutualism with host mangroves [5]. For instance, the halotolerant *Rhizophora stylosa*

Plants species	Distribution	Ref.
R. stylosa	China (Hainan, Guangdong, Guangxi); Philippines; New Caledonia; Fiji (Viti Levu); Australia; Japan (Ryukyu Archipelago)	Hainan plant flora [12]; Xing [14]; Villamayor [15]; Dangan [16]; Morton [17]; Arfi [18]; Chen [11]; Tyagi [19]; Kohlmeyer [20]
R. apiculata	China (Hainan, Guangdong, Guangxi); India; Indonesia; Philippines; Vietnam; Thailand; Singapore; Malaysia	Hainan plant flora [12]; Xing [14]; Selvaraj [21]; Villamayor [15]; Dangan [16]; Rossiana [22]; Clough [23]; Piapukiew [24]; Klaiklay, [25]; Rukachaisirikul [26]; Tan [27]
R. mucronata	China (Taiwan); Vietnam; South Africa; Philippines; Indonesia; India; Thailand; Japan; Singapore; Pakistan	Hainan plant flora [12]; Trinh [28]; Osorio [29]; Villamayor [15]; Dangan [16]; Tarman [30]; Suryanarayanan [31]; Rani [32]; Kandasamy [33]; Rukachaisirikul [26]; Tan [27]; Tariq [34]
R. mangle	Brazil; Venezuela; Dominican Republic; Gua de Ropp; Mexico; America (Florida, Hawaii); Senegal; Gabon; French Guiana; Australia	Boehm [35]; Ferreira [36]; Barreto [37]; Ball [38]; Afzal [39]; Wanderley [40]; Dourado [41]; Godoy [42]; Kohlmeyer [20]
R. harrisonii	Nigeria (Port Harcourt); Ecuador; America; West Africa; Equatorial Guinea; Senegal; Gabon	Hemphill [43]; Twilley [44]; Breteler [45]; Cerónsouza [46]; Cornejo [47]; Afzal [39]
R. racemosa	Nigeria; Ecuador; French Guiana; Gambia; Senegal; Gabon; Togo; America (Hawaii); Mexico	Ukoima [48]; Xavier [49]; Afzal [39]; Osorio [29]
R. annamalayana	India	Elavarasi [50]
R. samoensis	Fiji (Viti Levu); America; Southwest Pacific Islands (Caledonia, Hebrides); Samoa; Marshall Islands	Tyagi [19]; Duke [51]

Table 1. The distribution of ***Rhizophora*** in the world.

endophytic *Pestalotiopsis* sp. is isolated and capable of producing lignin-degrading enzymes. This species secretes over 400 salt-adapted lignocellulolytic enzymes, which enhance the salt adaptation of mangrove hosts [18].

To date, the species of mangrove endophytic fungi identified from a large and diverse ecological group are mostly members of the Ascomycota phylum, with a limited occurrence of basidiomycetes [53, 54]. Since 1955, when Cribb first described endophytic fungi isolated from mangrove roots, several studies on the fungi residing in mangroves along the coastlines of the Indian, Pacific, and Atlantic Oceans have been conducted [55]. Hyde [56] listed approximately 120 fungal species that colonize 29 mangrove plants globally, including 87 ascomycetes, 31 mitosporic fungi, and 2 basidiomycetes. Schmit and Shearer [57, 58] reported 625 mangrove-associated fungi, including 279 ascomycetes, 277 mitosporic fungi, 29 basidiomycetes, 3 chytridiomycetes, 2 myxomycetes, 14 oomycetes, 9 thraustochytrids, and 12 zygomycetes. According to the frequency of their appearance, *Alternaria*, *Aspergillus*, *Cladosporium*, *Colletotrichum*, *Fusarium*, *Paecilomyces*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Phyllosticta*, and *Trichoderma* have been recognized as the predominant culturable mangrove endophytic fungi [59].

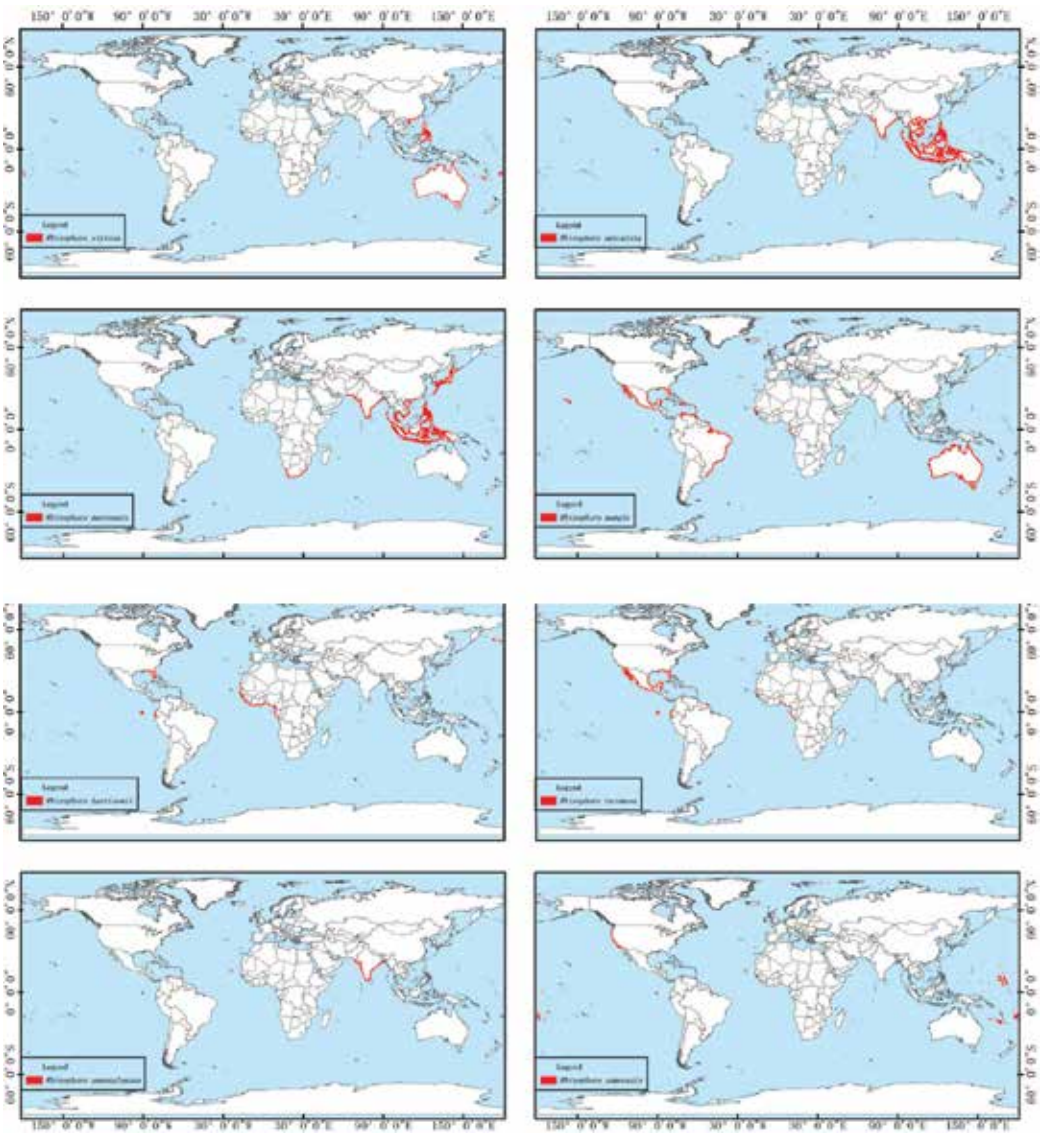

Figure 1. The distribution of *Rhizophora* in the world.

As a relatively underappreciated reservoir of bioresources, endophytic fungi from mangroves have been considered potential pharmaceutical and agricultural resources. Recent studies have investigated the biodiversity and distribution of mangrove endophytic fungi in the South China Sea. The taxonomic identities and diversity of endophytic fungal communities isolated from five species of the genus *Sonneratia* (*S. caseolaris*, *S. hainanensis*, *S. ovata*, *S. paracaseolaris*, and *S. apetala*) and four species of Rhizophoraceae (*Ceriops tagal*, *R. apiculata*, *R. stylosa*, and *Bruguiera sexangula* var. *rhynchopetala*) have been addressed [14].

Identification of biologically interesting metabolites from these endophytic fungi is an important initial step in understanding the role of endophytes to host mangrove plants. According

Plants species	Isolated endophytic fungi	Sampling location	Ref.
R. stylosa	*Aureobasidium*, *Aspergillus*, *Cladosporium*, *Diaporthe*, *Fusarium*, *Guignardia*, *Pestalotiopsis*	China	Xing [14]
	Acremonium, *Alternaria*, *Aspergillus*, *Bionectria*, *Colletotrichum*, *Epicoccum*, *Nigrospora*, *Penicillium*, *Pestalotiopsis*, *Phoma*, *Phomopsis*, *Phialophora*, *Talaromyces*, *Trichoderma*		Hyde [60]
	Chaetomium, *Corynespora*, *Fusarium*, *Geniculosporium*, *Glomerella*, *Guignardia*, *Melanconium*, *Sphaceloma*, *Pestalotiopsis*, *Phoma*		Liu [59]
	Penicillium	Wen Chang	Peng [61]
	Alternaria, *Diaporthe*, *Mucor*	Hainan	Gao [62];Zang [63];Sun [64]
R. apiculata	*Aspergillus*, *Aureobasidium*, *Cladosporium*, *Diaporthe*, *Fusarium*, *Massarina*, *Penicillium*, *Pestalotiopsis*, *Phomopsis*	Dong Zhai Gang	Xing [14];
	Acremonium, *Flavodon*, *Phomopsis*, *Pestalotiopsis*	Thailand	Klaiklay [25];Klaiklay [65, 66];Buatong [67];Rukachaisirikul, [26]
	Acremonium, *Alternaria*, *Aureobasidium*, *Cladosporium*, *Curvularia*, *Drechslera*, *Fusarium*, *Nodulisporium*, *Pestalotiopsis*, *Phialophora*, *Phoma*, *Phomopsis*, *Phyllosticta*, *Pithomyces*, *Glomerella*, *Sporothrix*, *Sporormiella*, *Xylariaceous*	India	Kumaresan [68]
	Acremonium, *Alternaria*, *Cladosporium*, *Chaetomium*, *Penicillium*, *Pestalotiopsis*, *Phialophora*, *Phoma*, *Phyllosticta*, *Pseudeurotium*, *Sporormiella*, *Thielavia*		Suryanarayanan [31]
R. mucronata	*Pestalotiopsis*	Dong Zhai Gang	Xu [69]
	Aspergillus	Indonesia	Tarman [30]
	Phomopsis		Shiono [70]
	Diaporthe, *Neofusicoccum*	South Africa	Osorio [29]
	Acremonium, *Alternaria*, *Aspergillus*, *Botryotrichum*, *Cladosporium*, *Chaetomium*, *Glomerella*, *Nigrospora*, *Pestalotiopsis*, *Phialophora*, *Phomopsis*, *Phyllosticta*, *Sporormiella*, *Trichoderma*	India	Suryanarayanan [31]
	Ascotricha, *Aspergillus*, *Cirrenalia*, *Cladosporium*, *Dicyma*, *Fusariella*, *Paecilomyces*, *Penicillium*, *Phoma*, *Phomopsis*, *Trichocladium*, *Zalerion*, *Zygosporium*		Ananda [71]
R. mangle	*Glomerella*, *Guignardia*, *Nodulisporium*, *Phyllosticta*	Brazil	Wanderley [40]
	Leucostoma		Beau [72]
	Botryosphaeria, *Colletotrichum*, *Coprinellus*, *Cytospora*, *Diaporthe*, *Endothia*, *Epicoccum*, *Fusarium*, *Gibberella*, *Glomerella*, *Guignardia*, *Hypocrea*, *Leptosphaeria*, *Neofusicoccum*, *Penicillium*, *Phomopsis*, *Pichia*, *Trichoderma*, *Xylaria*, *Valsa*		Sebastianes [73]
	Cytospora		Wier [74]

Plants species	Isolated endophytic fungi	Sampling location	Ref.
R. harrisonii	*Pestalotiopsis*	Nigeria	Hemphill [43]
R. racemosa	*Aspergillus, Lasiodiplodia, Paecilomyces, Penicillium*	Nigeria	Ukoima [48]
R. annamalayana	*Fusarium*	Vellar estuary	Elavarasi [50]
R. samoensis			

Table 2. The endophytic fungi isolated from ***Rhizophora***.

to the previous studies, the identification and phylogenetic diversity of mangrove endophytic fungi was largely associated with mangroves located in China, Thailand, Indonesia, Brazil, and India. In total, 26 genera of mangrove endophytic fungi were isolated from *R. stylosa*; 27 genera were isolated from *R. apiculata*; 26 genera were obtained from *R. mucronata*; 23 genera were isolated from *R. mangle*; 1 genus was isolated from *R. harrisonii* and *R. annamalayana* (namely *Pestalotiopsis* and *Fusarium*); and 4 genera of endophytic fungi were isolated from *R. racemosa*. Until now, no studies have been conducted on *R. samoensis*. In comparison with the previous reports, the frequently occurring fungi entophytes in *Rhizophora*, including 41 families and 64 genera belonging to 23 taxonomic orders of Ascomycota have been reported. The fungi of Basidiomycota are rarely found in *Rhizophora*. The dominant endophytic fungi of the *Rhizophora* genus are mainly distributed in *Aspergillus*, *Cladosporium*, *Chaetomium*, *Fusarium*, *Lasiodiplodia*, *Penicillium*, *Pestalotiopsis*, *Phomopsis*, *Phoma*, *Phyllosticta,* and *Trichoderma* (**Table 2**).

3. The secondary metabolites of endophytic fungi of *Rhizophora*

There is a wide range of endophytic fungi in mangroves, and their growing environment is unique. Thus, in the formation of special fungal communities, they will certainly metabolize compounds with rich structures, unlike that of terrestrial fungi. Many of these metabolites provide a rich model structure for the screening of new drugs, which have become increasingly valuable in drug-lead research [5]. A total of 195 metabolites were discovered from *Rhizophora*-derived endophytic fungi reported so far are included. The secondary metabolites of endophytic fungi of mangrove are classified as alkaloids, terpenes, coumarins, chromones, quinones, anthraquinones, peptides, phenolic acids, lactones, and other compounds.

3.1. Alkaloids

Fusarium equisetin AGR12 from *R. stylosa* produced two cyclic acetyl phytotoxin derivatives, equisetin (**1**) and *epi-equisetin* (**2**) [75, 76]. Both equisetin (**1**) and *epi-equisetin* (**2**) exhibit modest antibacterial activity, and equisetin (**1**) had selective antimicrobial activity against some Gram-positive bacteria [77]. The metabolite equisetin was first purified from maize grit medium cultures of *F. equiseti* strain NRRL 5337, and equisetin can inhibit the ATPase activity of mitochondria in rat hepatocytes induced by 2,4-dinitrophenol (DNP) in a concentration-dependent manner.

At a concentration of 8 nmol equisetin/mg protein, the inhibition rate can reach 50% [78]. New cerebroside lipids, chrysogesides A–E (**3–8**), and new pyridone ketones, chrysogedones A and B (**9, 10**), were isolated from the fermentation extract of *Penicillium chrysogenum* PXP-55, isolated from *R. stylosa*. Compound (**6**) exhibited inhibitory activity against *Enterobacter aerogenes* with MIC value of 1.72 μM [61]. The fungus species *Pestalotiopsis* JCM2A4, isolated from the Chinese mangrove plant *Rhizophora mucronata*, is one of the most abundant resources for screening natural products with different biological activities [79]. New N-substituted amide derivatives, pestalotiopamides A–E (**12–16**), and a new succinimide, pestalotiopsoid A (**11**), were isolated from the fermented crude extracts of *Pestalotiopsis* sp. JCM2A4, which was collected from *R. mucronata* [69, 80, 81]. A culture of the fungus *Aspergillus nidulans* MA-143, isolated from *R. stylosa* leaves, yielded six new compounds, and all the compounds contained the structural unit 4-phenyl-3,4-dihydroquinolin-2(1H)-one, aniduquinolones A–C (**17–19**), 6-deoxyaflaquinolone E (**20**), isoaflaquinolone E (**21**), 14-hydroxyaflaquinolone F (**22**), and aflaquinolone A (**23**). The bioactivity results showed that compounds **17–23** had no inhibitory activity against human hepatocellular carcinoma BEL-7402, breast cancer cell MDA-MB-231, leukemia myeloid cell HL-60, or chronic myeloid leukemia cell K652. Additionally, these compounds had no antibacterial activity against *Staphylococcus aureus* or *Escherichia coli*. Compounds **17**, **19**, and **23** exhibited lethal activity against *Artemia salina*, with LD_{50} values of 7.1, 4.5, and 5.5 μM, respectively [82]. About 6 new indole diterpenoid alkaloid derivatives (**24–29**) and 5 known similar metabolites, including 21-isopentenylpaxilline (**30**), paxilline (**31**), ehydroxypaxilline (**32**), emindole (**33**), and paspaline (**34**), were identified from a culture of *Penicillium camemberti* OUCMDZ-1492, isolated from the *R. apiculata*. Among them, compounds **24**, **26–28**, and **30–33** all showed strong H1N1 influenza virus inhibitory activity, with IC_{50} values ranging from 6 to 80 μM [83]. A new paspaline (**34**) and three known analogs, penijanthine A (**35**), paspalinine (**36**), and penitrem (**37**), were isolated from *Alternaria tenuissima* EN-192 from *R. stylosa* stems. Compounds **34–37** had slight antimicrobial activity against *Staphylococcus aureus*, *Escherichia coli*, *Bacillus subtilis*, and *Vibrio anguillarum* [64]. The cultivable *Phomopsis sp*. PSU-MA214 from *R. apiculata* leaves can produce phenylethanol compounds, including phomonitroester (**38**). Compound **38** was initially isolated from *Phomopsis sp*. PSU-D15, which was from another plant of *Garcinia dulcis* [84]. The bioassay test showed that compound **38** had a weak inhibitory effect on breast cancer cells MCF-7 and KB85. The four new quinazolone alkaloid derivatives, aniquinazolines A–D (**39–42**) which were isolated from *Aspergillus nidulans* MA-143 in *R. stylosa*, showed strong lethal activity in shrimp, with LD_{50} values of 1.27, 2.11, 4.95, and 3.42 μM, respectively. Meanwhile, they had no inhibitory activity against hepatoma cell BEL-7402, breast cancer cell MDA-MB-231, leukemia myeloid cell HL-60, and chronic myeloid leukemia cell K562. Moreover, no antibacterial activity against *Staphylococcus aureus* and *Escherichia coli* was observed [82]. Two new indole alkaloids, penioxamide A (**43**) and 18-hydroxydecaturin B (**44**), and a known compound decaturin B (**45**) were isolated from the fermented rice extract of *R. stylosa* endophytic fungi *Penicillium oxalicum* EN-201 [85]. Mucor irregularis QEN-189 was isolated from *R. stylosa*, from which 6 indole diterpenoid alkaloid derivatives and 14 analogs were separated, namely rhizovarins A–F (**46–50, 53**), secopentrem D (**51**), PC-M4 (**52**), penijianthine A (**54**), penitrem A–F (**55–60**), paxilline (**61**), 27-O-acetylpaxillin (**62**), 13-deoxy-27-O-acetylpaxillin (**63**), 10-deoxy-13-deoxypaxilline

(64), and 10β-hydroxy-13-desoxypaxilline (**65**). As for antitumor activity, compounds **46**, **47**, **50**, **55**, **57**, **60**, and **65** had inhibitory activity against lung cancer cell A549, and the IC_{50} values were 11.5, 6.3, 9.2, 8.4, 8.0, 8.2, and 4.6 μM, respectively. They also had inhibitory activity against leukemia cells of HL-60, with IC_{50} values of 9.6, 5.0, 7.0, 4.7, 3.3, and 2.6 μM, respectively [62]. The *Hypocrea virens* of *R. apiculata* is capable of producing isoquinoline alkaloids, 2-methylimidazo[1,5-b]isoquinoline-1,3,5(2H)-trione (**66**) [86] (**Figure 2**).

3.2. Terpenoids

A new sesquiterpene, diaporol A (**67**), with a tricyclic lactone structure; eight new sesquiterpenes, diaporols B–I (**68–75**); drimane; 3*β*-hydroxyconfertifolin (**76**); and diplodiatoxin (77) were isolated from *Diaporthe* sp. of *R. stylosa*. The bioactivity test showed that compounds **67–77** had no cytotoxicity on human gastric cancer cell SGC-7901, breast cancer cell MCF-7, lung cancer cell A549, and hepatocellular carcinoma cell line QGY-7701 at a concentration of 20 μM [63]. Flavodon flavus PSU-MA201 was isolated from *R. apiculata*, from which a known perhydroazulene compound, tremulenolide A (**78**), was separated, and the bioassay test showed that compound **78** exhibited modest antibacterial activity against *Staphylococcus aureus* ATCC25923 and *Cryptococcus neoformans* ATCC90113 with MIC values of 128 μg/mL [65, 66]. A known altiloxin B (**79**) with drimane was isolated from *Pestalotiopsis* sp. of *R. mucronata* [87]. Two known mycotoxins, 8-deoxytrichothecin (**80**) and trichodermol (**81**), were isolated from the *Acremonium* sp. PSU-MA70 of *R. apiculata* [26]. As a plant-derived anticancer drug with a unique mechanism, taxol (**82**) was isolated from *Taxus brevifolia* bark and wood for the first time by American chemists Wani and Wall in 1963 [88, 89]. Subsequently, it has been found that endophytic fungi *Taxomyces* [90], *Pestalotiopsis* [91], *Alternaria* [92], and *Fusarium* [93] could also produce taxol and its analogs. Taxol (**82**) was also isolated from endophytic fungus *Fusarium oxysporum* in *R. annamalayana* [50]. Two new compounds, pestalotiopens A and B (**83, 84**), were separated from the *Pestalotiopsis* sp. JCM2A4 from leaves of *R. mucronata*, and the bioactivity assay revealed that compound **83** was slightly

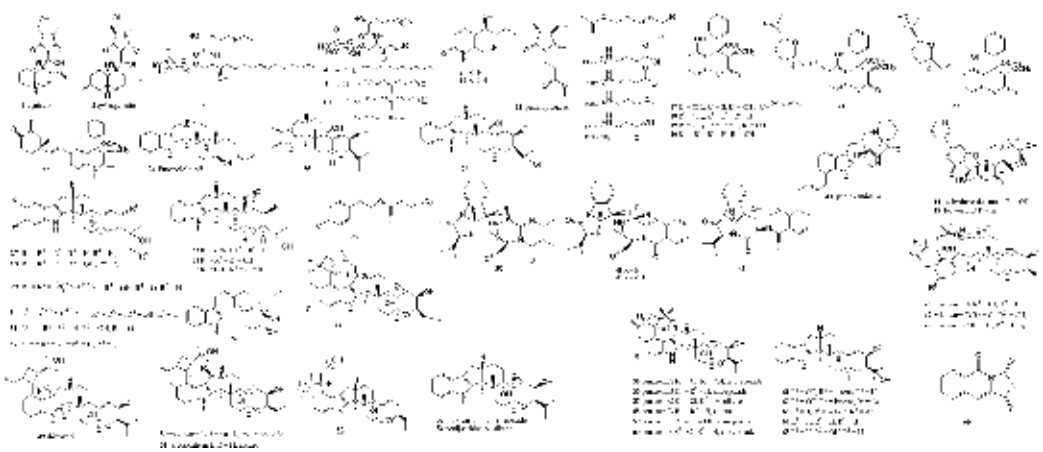

Figure 2. The structures of alkaloids in *Rhizophora*-derived endophytic fungi.

resistant to *Staphylococcus aureus*, *Escherichia coli*, *Enterococcus faecalis*, *Streptococcus pyogenes*, *Pseudomonas aeruginosa*, and *Klebsiella pneumoniae*, with the MIC values ranging from 125 to 250 μM [87] (**Figure 3**).

3.3. Coumarins

A strain of *Pestalotiopsis* sp. was isolated from the leaves of *R. mucronata*, which is an important resource of coumarin compounds. Pestalasins A–E (**85–89**) and one known compound, 3-dydroxymethyl-6,8-dimethoxycoumarin (**90**), were separated from fermentation extracts, and this was the first time that coumarin had been found in the mangrove microbes [69]. A more in-depth study of the chemical constituents of *Pestalotiopsis* sp. led to the discovery of a new isocoumarin derivative, pestalotiopisorin A (**91**) [80]. Seven new structural analogs, acremonones B–H (**92–98**), were isolated from *Acremonium* sp. PSU-MA70, which was from *R. apiculata* [26]. *Pestalotiopsis clavispora* was isolated from the leaves of *R. harrisonii*, and four new polyketide derivatives were separated from endophytic fungi, including pestapyrones A–C (**99–101**), (R)-periplanetin D (**103**), and similanpyrone B (**102**) [43] (**Figure 4**).

3.4. Chromones

Three rare chlorinated chromone derivatives, pestalochromones A–C (**104–106**), were isolated from *Pestalotiopsis* sp. PSU-MA69 in *R. apiculata* [25]. Further studies on the chemical composition of *Pestalotiopsis* sp. from *R. mucronata* led to the discovery of a series of rare lipophilic chromone derivatives, pestalotiopsones A–F (**107–112**), and the known compound, 5-carbomethoxymethyl-heptyl-7-hydroxychromone (**113**). The bioactivity test showed that compound **111** had weak cytotoxic activity against mouse lymphoma cell L5178Y, with an EC_{50} value of 29.4 μM [69]. Four new chromone derivatives, phomopsichins A–D (**114–117**), along with a known compound, phomoxanthone A (**118**), were isolated from the fermentation products of *Phomopsis* sp. 33# from *R. stylosa*. The bioassay results showed that compounds

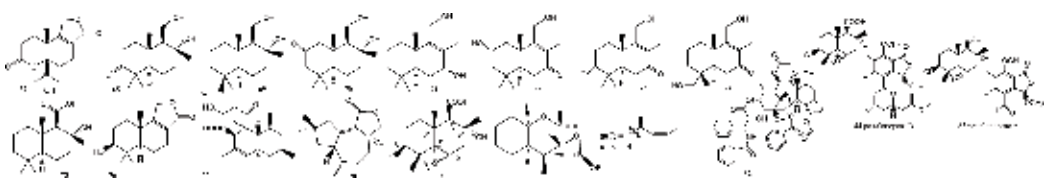

Figure 3. The structures of terpenoids in *Rhizophora*-derived endophytic fungi.

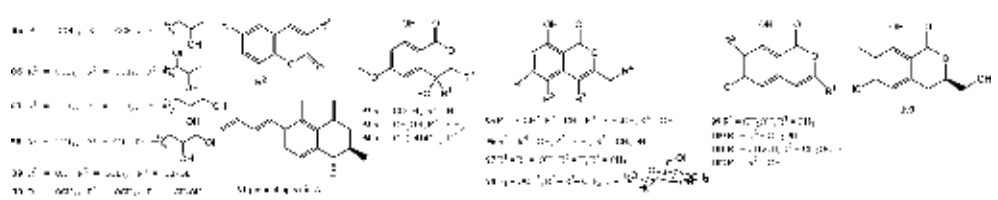

Figure 4. The structures of coumarins in *Rhizophora*-derived endophytic fungi.

114–118 had weak inhibitory effects on acetylcholinesterase (AchE), α-glucanase, DPPH radical and hydroxyl radical, as well as weak inhibitory activity against 18 kinds of plant pathogenic bacteria [94]. A new polyketone derivative, pestalpolyol I (**119**), was isolated from *Pestalotiopsis clavispora* in *R. harrisonii*. The bioactivity test showed that compound **119** had strong inhibitory activity against tumor cells L5178Y, with an IC_{50} value of 4.1 μM. Compound **119** also showed inhibitory activity against leukemia myeloid cells HL-60, hepatoma cells SMMC-7721, lung cancer cells A-549, breast cancer cells MCF-7, and human colon cancer cells SW480, with IC_{50} values of 10.4, 11.3, 2.3, 13.7 and 12.4 μM, respectively [43] (**Figure 5**).

3.5. Anthraquinones

One new tetrahydroanthraquinone derivative, (2R, 3S)-7-ethyl-1,2,3,4-tetrahydro-2,3,8-trihydroxy-6-methoxy-3-methyl-9,10-anthracenedione (**120**) and five known anthraquinones derivatives (**121–125**) were isolated from the endophytic fungi *Phomopsis* sp. PSU-MA214 from *R. apiculata* leaves. Compound **120** had the structure of ethyl tetrahydroanthraquinone, which was weakly cytotoxic to human breast cancer cell MCF-7 and had antibacterial activity against *Staphylococcus aureus* ATCC25923 and methicillin-resistant *S. aureus* SK1 [25]. Three known tricyclic alternarene derivatives (**126–128**) were isolated from the endophytic fungus *Alternaria tenuissima* EN-192 from *R. stylosa* branches, and the antimicrobial activity, tested by filter paper diffusion method, showed that compound **126** had moderate antibacterial activity against *Vibrio anguillarum* [64]. One new xanthone, pestaloxanthone (**129**), was isolated with two known analogs, isosulochrin dehydrate (**130**) and chloroisosulochrin dehydrate (**131**), from endophytic fungi *Pestalotiopsis* sp. PUS- MA69 from *R. apiculata* branches [25]. A known tetrahydrogenated xanthanone dimer, phomoxanthone A (**132**), and a new compound with similar structure, 12-O-deacetyl-phomoxanthone A (**133**), were isolated from a rice fermentation culture extract of the fungus *Phomopsis* sp. IM 41-1 from *R. mucronata*. Two compounds (**132, 133**) had weak antibacterial activity against *Botrytis cinerea*, *Sclerotinia aureus*, *Diaporthe medusaea*, and *Staphylococcus aureus*, while acetylation of the compound had no significant effect on the antimicrobial activity [70]. A known compound, pestaxanthone (**134**), was isolated from *Pestalotiopsis clavispora* from the leaves of the genus *R. harrisonii* [43] (**Figure 6**).

3.6. Peptides

Four known compounds, two ring-phthalocyanines, guangomides A and B (**135, 136**), and two diketopiperazine derivatives, Sch 54794 and Sch 54796 (**137, 138**), were isolated from the

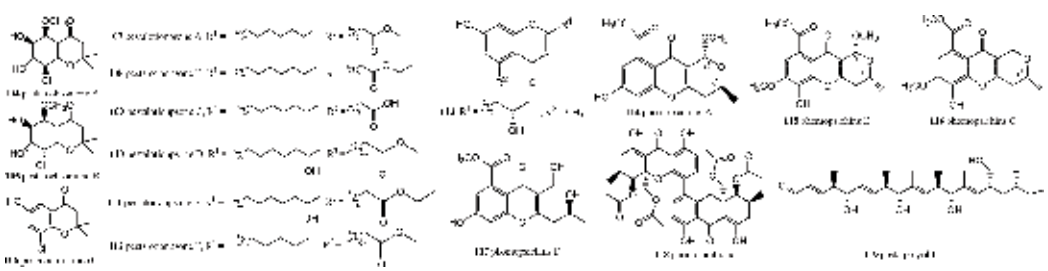

Figure 5. The structures of chromones in *Rhizophora*-derived endophytic fungi.

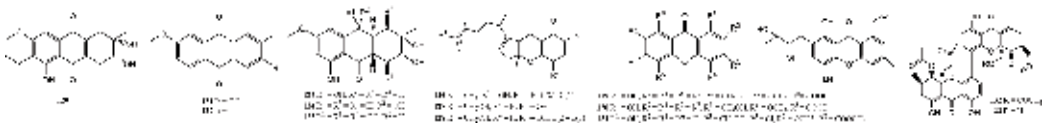

Figure 6. The structures of anthraquinones in *Rhizophora*-derived endophytic fungi.

Acremonium sp. PSU-MA70 from *R. apiculata* [26]. Activity tests showed that compounds **135** and **136** had weak antibacterial activity against *Staphylococcus epidermidis* and *Enterococcus durans* [95] (**Figure 7**).

3.7. Phenolics

In this category, four new diphenyl ether compounds, pestalotethers A–D (**141, 143–145**), and three known compounds, pestheic acid (**142**), chloroisosulochrin (**139**), and isosulochrin (**140**), were isolated from *Pestalotiopsis* sp. PSU-MA69 of *R. apiculata* [25]. A new compound, norpestaphthalide A (**146**), and three known compounds, (R, S)-5,7-dihydroxy-3-(1-hydroxyethyl) phthalide (**148**) and pestaphthalides A and B (**147, 149**), were isolated from *Pestalotiopsis clavispora* in the leaves of *R. harrisonii*. These compounds had no inhibitory effect on leukemia myeloid cells HL-60, hepatoma cells SMMC-7721, lung cancer cells A-549, breast cancer cells MCF-7, and human colon cancer cells SW480 [43] (**Figure 8**).

3.8. Lactones

Five new compounds, including cytosporones J–N (**152–156**), together with known metabolites, dothiorelones A (**150**) and cytosporones C (**151**), were isolated from the *Pestalotiopsis* sp. from *R. mucronata*. Biological tests showed that compound **150** was cytotoxic to human oral epidermoid carcinoma KB cells, lymphoma cells Raji, and human osteosarcoma cells Mg-63. Compounds **151–156** had no significant antitumor activity [69]. In the further study of *Pestalotiopsis* sp. of *R. mucronata*, eight new pyrone compounds, pestalotiopyrones A–H

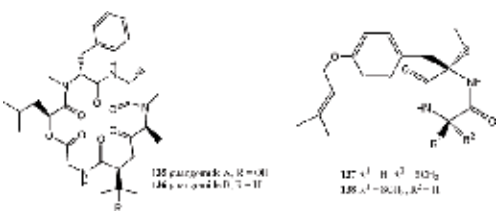

Figure 7. The structures of peptides in *Rhizophora*-derived endophytic fungi.

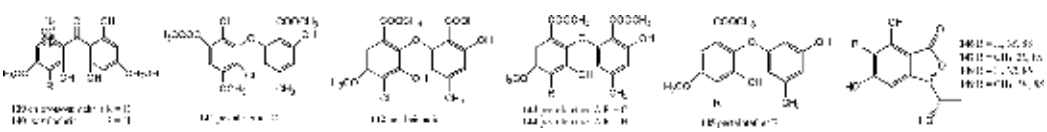

Figure 8. The structures of phenolics in *Rhizophora*-derived endophytic fungi.

(**157–164**); two new compounds, pestalotiollides A and B (**166, 167**); and one known compound, nigrosporapyrone D (**165**), were found in large amounts of fermentation products in the rice culture medium [80]. Three new α-pyrone pestalotiopyrones A–C (**168–170**); two new seiricuprolide macrolides, pestalotioprolides A (**171**) and B (**173**); and two known compounds, seiricuprolide (**174**) and 2′-hydroxy-3′,4′-didehydropenicillide (**172**), were isolated from two endophytic fungi *Pestalotiopsis* sp. PSU-MA92 and *Pestalotiopsis* sp. PSU-MA119 of *R. apiculata* and *R. mucronata* [96]. Among these, compounds **168-170** were repetitive names of pestalotiopyrones A–C [80]. Thus far, the carbon skeleton of phenyleol lactones has been rarely found among natural products [97]. One new butenolactone, pestalolide (**175**), and one known phytotoxin, seiridin (**176**), were found in the fermentation product of endophytic fungi *pestalotiopyrones* sp. PSU-MA69, which was from *R. apiculata*. The bioactivity analysis showed that compound 175 had weak antimicrobial activity against *Candida albicans* and *Cryptococcus neoformans*, with MIC values of 653.06 μM [25]. A new phthalic acid derivative, acremonide (**177**), and one new depsidone, acremonone A (**179**), together with two known substances, (+)-brefelin A (**180**) and 5,7-dimethoxy-3,4-dimethyl-3-hydroxyphthalide (**178**), were separated from the *Acremonium* sp. PSU-MA70, which was isolated from *R. apiculata* [26]. Brefelin A (BFA) is a fungal metabolite that was originally used as an antiviral agent and is now primarily used to study protein transport. It can specifically and reversibly inhibit the Golgi membrane protein protease, prohibiting the linkage of guanine nucleotides to ADP ribosylation factor and, therefore, preventing the transport of proteins from the endoplasmic reticulum (ER) to the Golgi. BFA is also used to inhibit the secretion of cytokine and other proteins as well as enhance the immunostaining of secretory proteins. BFA can activate the neural sheath phosphoric acid cycle, inducing the apoptosis of some tumor cells [98], and it has a weak antibacterial activity against *Candida albicans* NCPF3153 [26]. Three known substances, macrolides pestalotiollides A and B (**181, 182**) and 2-*epi*-herbarumin II (**183**), were isolated from the fermentation extract of *Pestalotiopsis clavispora* from *R. harrisonii*. Bioactivity tests showed that compounds **181–183** had no antitumor effect on leukemia myeloid cells HL-60, hepatoma cell SMMC-7721, lung cancer cell line A-549, breast cancer cell MCF-7, or human colon cancer cell SW480 [43]. In order to effectively control the biosynthesis of *Leucostoma persoonii* from *R. mangle* and stimulate the production of cytosporone compounds, a known antibacterial trihydroxy lactone compound, cytosporone E (**184**), was induced by epigenetic modification [72]. Compound **184** showed a strong anti-infective activity against *Plasmodium falciparum* with an IC_{50} value of 13 μM. Additionally, compound **184** showed strong inhibitory activity against human lung cancer cell A549, with an IC50 value of 437 μM, and a strong inhibitory effect on methicillin-resistant *S. aureus*, with an MIC value of 72 μM [97] (**Figure 9**).

3.9. Others

A new difuranylmethane-derived furan fatty acid, flavodonfuran (**185**), was isolated from the endophytic fungus *Flavodon flavus* PSU-MA201 from *R. apiculata* [65, 66]. Xu isolated a new enoic acid compound, pestalotiopin A (**187**), and two known compounds, 2-anhydromevalonic acid (**186**) and *p*-hydroxybenzaldehyde (**188**), from the *Pestalotiopsis* sp. of *R. mucronata* [80]. Rukachaisirikul and coworkers isolated two known compounds, 4-methyl-1-phenyl-2,3-hexanediol (**189**) and (2R,3R)-4-methyl-1-phenyl-2,3-pentanediol (**190**), from the *Acremonium* sp. PSU-MA70 of *R. apiculata* [26]. One known phenylethanol propionate (**191**) and a known butanamide compound, butanamide (**192**), were isolated from the endophytic fungus *Phomopsis*

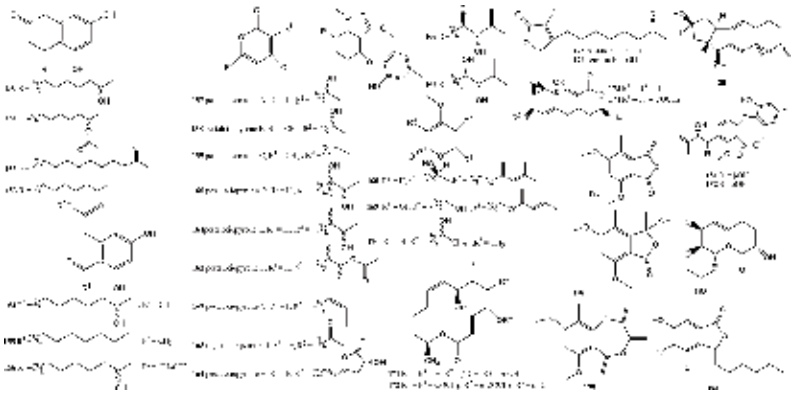

Figure 9. The structures of lactones in *Rhizophora*-derived endophytic fungi.

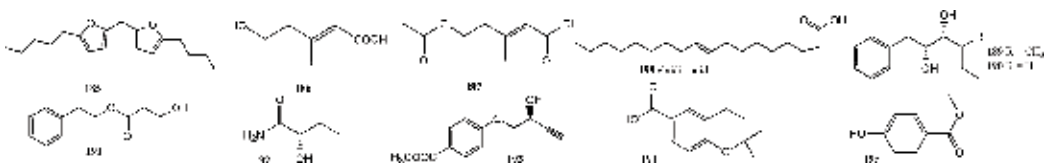

Figure 10. The structures of others in *Rhizophora*-derived endophytic fungi.

sp. PSU-MA214 from *R. apiculata* [25]. (S)-penipratynolene (**193**), DNA-damaging active anofinic acid (**194**), and *p*-hydroxybenzoic acid methyl ester (**195**) were isolated from *Pestalotiopsis* sp. PSU-MA69 of *R. apiculata* [25] (**Figure 10**).

4. Conclusion

In this review, we summarize the distribution of frequently occurring fungal endophytes in *Rhizophora*: 26 genera of mangrove endophytic fungi were isolated from *R. stylosa*; 27 genera were isolated from *R. apiculata*; 26 genera were obtained from *R. mucronata*; 23 genera were isolated from *R. mangle*; 1 genus was isolated from *R. harrisonii* and *R. annamalayana* (namely *Pestalotiopsis* and *Fusarium*); and 4 genera of endophytic fungi were isolated from *R. racemosa*. Until now, no studies have been conducted on *R. samoensis*. In total, the frequently occurring fungi entophytes in *Rhizophora*, including 41 families and 64 genera belonging to 23 taxonomic orders of Ascomycota have been reported. Although the biological potential of endophytic fungi from the abovementioned *Rhizophora* species has not been thoroughly investigated, the core group of fungi can be recognized from different geographic locations. The distribution and molecular phylogeny of the fungi are discussed as well as new findings regarding the chemistry and bioactivity of natural products found in *Rhizophora* endophytic fungi. The *Pestalotiopsis*, *Penicillium,* and *Mucor* genera of endophytic fungi were identified as the most promising fungal groups in terms of chemical diversity. In particular, the *Pestalotiopsis* genus constituted 42.56% of the compounds reported, as shown in **Figure 11**. *R. apiculata* (34.36%) was observed to be the most investigated host plant, followed by *R. stylosa* (33.85%) and *R. mucronata* (23.59%). The chemical identification of metabolites of *R. racemosa* endophytic fungi has not yet been reported (**Figure 11**).

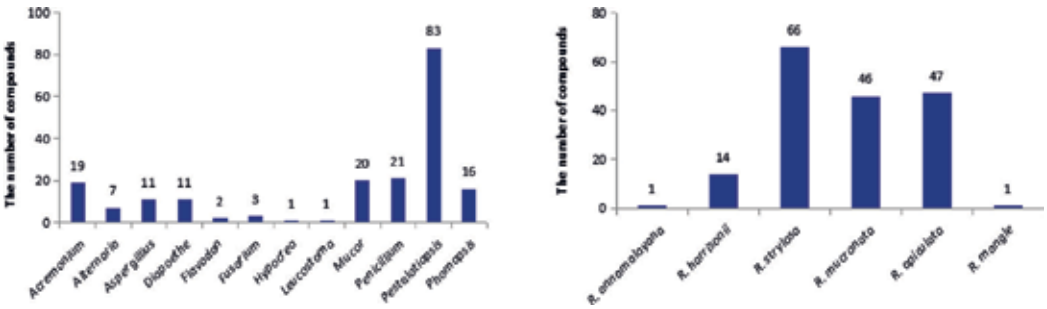

Figure 11. Comparison of metabolite distributions by mangrove endophytic fungal and host *Rhizophora* species.

Some secondary metabolites with unusual structures were identified in *Rhizophora endophytic* fungi. Novel hybrid sesquiterpene-cyclopaldic acid metabolites with unusual carbon skeletons, pestalotiopens A and B (**83, 84**), were obtained from the endophytic fungus *Pestalotiopsis* sp. JCM2A4 isolated from the leaves of the Chinese mangrove, *R. mucronata*. Bioassays revealed that antitumor, antimicrobial, and anti-H1N1 activities are the most notable bioactivities of the secondary metabolites from *Rhizophora endophytic* fungi. Some compounds had significant bioactivities, as exemplified by pestalpolyol 1 (**119**), a novel polyketone derivative isolated from *P. clavispora*. Compound **119** has a strong inhibitory effect on mouse lymphoma cell line L5178Y with an IC_{50} value of 4.10 μM. The indole diterpene alkaloids, rhizovrin A, B, and F (**46, 47, 50**), isolated from endophytic fungi *Mucor irregularis* QEN-189, have strong inhibitory effects on lung cancer cells A549, with IC_{50} values of 11.5, 6.3, and 9.2 μM, respectively, as well as inhibitory effects on leukemia myeloid cells HL-60, with IC_{50} values of 9.6, 5.0, and 7.0 μM, respectively. These findings suggest that *Rhizophora* endophytic fungi offering numerous useful products with medicinal and pathogenic significance have yet to be established.

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Section 7

Mangrove Conservation and Management

Chapter 9

Analysis of the Conservation of Central American Mangroves Using the Phytosociological Method

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Additional information is available at the end of the chapter

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Abstract

Our study of mangrove swamps revealed a total of 120 species, of which 13 are characteristics of mangrove swamps, and 38 of flooded areas with low salt. All the others are invasive species which have taken advantage of the degradation of these natural ecosystems. The scenario is not very different in Laguna de Tres Palos in Mexico. The frequent fires in the low-growing semi-deciduous rainforest (dry forest) have caused intense erosion, with the consequence that the site has silted up. As a result, the first vegetation band of *Rhizophora mangle* is extremely rare. Instead, *Laguncularia racemosa* and *Conocarpus erectus* are dominant, along with a band of *Phragmito-Magnocaricetea* with a high occurrence of *Phragmites australis* (Cav.) Trin., which acts as an indicator of sediment silting. It is extremely frequent for several reasons: as it is the decrease of the salinity of the water, the scarce depth due to the accumulation of sediments and the contamination by the entrance of residual waters of the nearby populations. When the depth and salinity of the water are suitable, the dominant species are *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*.

Keywords: mangrove, conservation, phytosociological method

1. Introduction

Mangrove communities are located in tropical and subtropical areas on different continents between parallel 30° N and 30° S [1]. They are also located in Central America in all the

territories of the Caribbean, Atlantic areas of Brazil and on the Pacific Ocean Coast; Ecuador, Colombia, Panama, Costa Rica, Nicaragua, El Salvador, Guatemala, Mexico, California, Florida. Mangrove ecosystems are important because they serve as a refuge for a high diversity of animal species. However, there are various threats that can damage these ecosystems, and deforestation, sediment clogging, and pollution can cause loss of animal species of high ecological value.

Recently, Mendes and Tsai [2] carried out a study of mangrove swamp sediments in a transect from the outermost to the innermost areas of the mangrove swamp. Specifically, they sampled three points containing the species *Laguncularia racemosa, Avicennia shaueriana,* and *Rhizophora mangle* and analysed a range of physical and chemical parameters as well as microbial activity. This research highlights the need to preserve mangrove areas against deforestation. Research into the deforestation of forests in protected areas [3] of Latin America reveals that this phenomenon increased from 0.04% to 0.10% between 2004 and 2009, with a significant increase in the number of hectares affected. This is due to the

Figure 1. Caribbean mangrove forests (Dominican Republic) with an intense introgression of the invasive species *Eichhornia crassipes.*

Figure 2. Caribbean mangrove forests (Dominican Republic) showing the severe impact of cutting which leads to GHGs emissions.

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Figure 3. Pacific mangrove forests (Mexico). Mangrove swamps threatened by the silting up of the lake basin as a result of the deforestation of the surrounding area. There is currently a severe invasion of *Phragmites australis*.

Figure 4. Mangrove of the Laguna de Tres Palos, Mexico.

density and proximity to the habitat of the rural population and to the decrease in funding for protected areas; however, it is somewhat offset by protection measures in these threatened areas. We recently pointed to the need to establish conservation measures for Central American mangrove swamps [4], as they are facing a number of different threats. One of these is particularly the high rate of sediment deposit caused by the deforestation of surrounding areas which is silting up areas of mangrove; this is the case of several mangrove swamps in Mexico (Laguna de Tres Palos, Acapulco, Mexico). The result is the substitution of the habitat of *Rhizophora mangle* with that of *Laguncularia racemosa*, whose habitat is in turn substituted by *Conocarpus erectus* due to the reduction in the depth of the lake basin, an increased inflow of fresh water and a decrease in salinity. This horizontal dynamic is

accompanied by the proliferation of *Phragmites australis* communities, as a species whose optimal development occurs in sites with shallow standing water with low salinity, quite the opposite of the requirements for mangroves. Mangrove communities should therefore be regarded as fragile owing to the fact that they demand a particular depth of water and salinity. Another danger threatening the mangrove habitat is deforestation by the rural population for use as firewood, charcoal, kindling, and as an energy source. This could be reduced if the per capita income of the population were higher, thereby affording them access to other energy sources. In view of these considerations on the situation of these habitats, our aim is to determine their degree of diversity and state of conservation (**Figures 1–4**). Therefore, we collected phytosociological data, which is essential to understand species diversity and community pattern in Central America. We have also discussed how results from this study can help in conserving mangroves in Central America.

2. Material and methods

We study the diversity and state of conservation of mangrove forests based on the analysis of 16 plant communities distributed throughout Central America (Mexico, Cuba, Dominican Republic) (**Figure 5**) using floristic inventories compiled by several authors [4–6]; this analysis uses over 70 field samplings grouped by ecological, physiognomic and floristic affinity in 16 plant communities. For each sampling, data were taken of the plot size in m2, (40 x 20) coordinates, coverage in percentage, average height of the dominant species and all the species present. Each plant community presents a particular floristic composition; therefore, in the statistical treatment, we will only take into account the flora of each plant association, since

Figure 5. Mangrove areas studied in Central America [4].

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Asociaciones	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Avicennia germinans (L.) L. **	II	IV	V	II	IV	II		V						V	III	V
Laguncularia racemosa (L.) Gaertn.**	V	V	V	II	V	III	IV	I								V
Rhyzophora mangle L.**	V	IV	III	II	I	III	V						V			
Conocarpus erectus L.**	II	II	III	V	III	V	III		V	I		V				II
Batis maritima L.**	II	I	III	I				V							III	II
Dalbergia ecastaphyllum (L.) Taub.*	II	I					V			V						
Rhabdadenia biflora (Jacq.) Muell.Arg.**	II	II	I	II			III	I								
Coccoloba uvifera (L.) L.*	II	I	I	I					V							
Pavonia paludicola Nicols.**	II	I	I				V									
Acrostichum aureum L.*	II	I	II	I												
Annona glabra L. *	II	I	III	I	I											
Bucida buceras L.*	II		II	I												
Bacopa monnieri (L.) Pennell*	I															
Borriria arborescens (L.) DC.*		I	I	I												
Conocarpus erectus L. var. *sericea* (Forst.) Borhidi					I			I								
Crataeva tapia L.*					I	II										
Cydista aequinoctialis (L.) Miers*	I															
Cyperus alternifolius L.*		I														
Cyperus odorata Vahl*	II	I														
Dalbergia berterii (DC.) Urb.*	II															
Echinochloa polystachya (Kunth) Hitchc.*		I														
Eichlornia crassipes (Mart.) Solm**		I														
Eleocharis interstincta (Vahl) R. & S.*		I														
Eleocharis mutata (L.) Roem. & Schult.*		I														
Heterostachys ritteriana (Moq.) Urg.-Sternb.**		I														
Hippomane mancinella L. *	II															
Ipomoea tiliacea (Willd.) Choisy*	I		I	I												
Lonchocarpus palmeri (Rose) *M. Souza**					III											
Ludwigia octavalvis (Jacq.) Raven*		I								II						
Lycium tweedianum Griseb.*	II	I		I												
Machaerium lunatum (L.f.) Ducke*	II	II		I												
Mimosa pigra L.*					I											
Morinda citrifolia L.*	II			I												

Asociaciones	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Nephrolepis multiflora (Roxb) Jarrett ex Morton *	II															
Paspalum geminatum L.*				I												
Phragmites australis (Cav) Trin.*					I	II										
Phyllanthus elsiae Urban**					I											
Pithecellobium lanceolatum (Willd.) Benth.**					I											
Polygonum acuminatum H.B.K.*		I														
Pterocarpus acapulcensis Rose*						II										
Pterocarpus officinalis Jacq.*	II	I														
Rachicallis americana (Jacq.) Ktze.**				I												
Rhynchospora corymbosa (L.) Britton**																
Roystonea hispaniolana L. H. Bailey*	II	I														
Sabal causiarum (Cook.) Becc.*	II															
Salicornia bigelobii Torr.**	I	I														
Sesuvium portulacastrum (L.) L.**	II	I		II				I							III	
Sthalia monosperma (Tul.) Urb.*	II		III													
Typha domingensis Pers.*	II	III		I	I	I										
Bucida palustris Borhidi							III									
Tabebuia angustata Britt.							III									
Roystonea regia (HBK) Cook							I									
Sabal parviflora Becc.							I									
Sarcostemma clausum L.							II	I								
Cissus trifoliata L.							I									
Hohenbergia penduliflora (A. Rich.) Mez.							II									
Tillandsia fasciculata Sw.							II									
Tillandsia usneoides L.							II									
Tillandsia valenzuelana A. Rich.							II									
Baccharis halimifolia L.								II								
Iva cheiranthifolia L.								I								
Distichlis spicata (L.) Greene								I								
Fimbristylis spathacea Roth								I								
Salicornia perennis Mill.								I								
Suriana maritima L.									II							

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Asociaciones	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Cannavalia maritima (Aub.) Thons	I								r	II			r			
Morinda royc L.									r				r			
Caesalpinia bonduc (L.) Roxb.									r	V			r			
Ipomoea alba L.	I									V	II					
Cordia sebesteana L.									r				r			
*Dalbergia brownei (*Jacq.) Urb.										III	V					
Muntingia calabura L.											I					
Panicum purpurascens Raddi										r						
Chamaecrista diphylla (L.) Greene										r						
Cyperus tenuis Sw.										r						
Spilanthes urens Jacq.										r						
Acacia macracantha H. & B. ex Willd			I													
Aristolochia trilobata L	I		I													
Bursera simaruba (L.) Sarg.	I		I													
Calophyllum calaba L.	I															
Capparis flexuosa (L.) L.	I	I	II	I	I											
Cassytha filiformis L.	I															
Cecropia schreberiana Miq.	I															
Chrysobalanus icaco L.	I															
Cissus verticillata (L.) Nicols.	I	I	II													
Citharexylum fruticosum L.				I												
Clusia rosea Jacq.	I															
Corchorus hirsutus L.			I													
Costus speciosus (J.Konig) Sm.																
Crescentia cujete L.	I		I													
Erithalis fruticosa L.	I															
Ficus velutina H. & B. ex Willd.	I															
Guapira discolour (Spreng.) Little				I												
Guazuma ulmifolia Lam.					I					r						
Harrisia nashii Britt. & Rose				I												
Hippocratea volubilis L.	I		I													
Ipomoea pes-caprae (L.) R. Br.	I															
Ipomoea violacea L				I												

Asociaciones	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Leucanea leucocephala (Lam.) De Wit									r				r			
Lonchocarpus domingensis (Turp.) DC.	I		I													
Lonchocarpus pycnophyllus Urb.				III												
Luffa cilindrica L.			I													
Maclura tinctoria (L.) D. Don				I												
Mikania cordifolia (L.f.) Willd.	I	I														
Mucuna pruriens L.					I											
Paullinia pinnata L.	I		I													
Pentalinum luteum (L.) Hansen & Wunderlin				I												
Pereskia quisqueyana Alain				I												
Phoradendron quadrangulare (HBK) J. K. & U.						I										
Pithecellobium unguis-cati (L.) Mart.				I												
Prosopis juliflora (Sw.) DC.				I	I											r
Randia aculeata L.	I		I													
Salpianthus purpurascens (C.ex Lag.) H. et A.					I											
Sapindus saponaria L.				I												
Sophora tomentosa L.	I															
Stigmaphyllon bannisterioides (L.) A. E. Anderson		I														
Terminalia catalpa L.	I															
Thespesia populnea (L.) Soland.	I	I	I	I						II	I					
Vigna luteola (Jacq.) Benth.	I															
Wedelia trilobata (L.) Hitchc.	I															
Zamia debilis L.				I												
Ziziphus rignoni Delp.				I												

1—As. *Machario lunati-Rhizophoretum manglis* Cano et al. 2012. 2—As. *Rhabdadenio biflori-Laguncularietum racemosae* Cano et al. 2012. 3—As. *Sthalio monospermae-Laguncularietum racemosae* Cano et al. 2012. 4—As. *Lonchocarpo pycnifolli-Conocarpetum erecti* Cano et al. 2012. 5—As. *Lonchocarpo sericei-Laguncularietum racemosae* Cano et al. 2012. 6—As. *Crataevo tapiae-Conocarpetum erectae* Cano et al. 2012. 7—*Dalbergio-Rhizophoretum manglis* Borhidi 1991 (Borhidi 1991, Table 97 inv. 1–5). 8—As. *Batidi-Avicennietum germinantis* Borhidi & Del-Risco & Borhidi 1991 (Borhidi 1991, Table 98 inv. 1–6). 9—As. *Conocarpo erectae-Coccoloetum uviferae* Reyes in Reyes & Acosta 2003 (Reys & Acosta 2003, Table 2 inv. 1–6). 10—*Caesalpinio bonduc-Dalbergietum ecastophylli* Reyes & Acosta 2003 (Reyes & Acosta 2003, Table 3 inv. 1–6). 11—*Dalbergietum browney* Reyes & Acosta 2003 (Reyes & Acosta 2003, Table 4 inv. 1–4). 12—*Conocarpetum erectae* Reyes in Reyes & Acosta 2003 (Reyes & Acosta 2003). 13—*Rhizophoretum manglis* Cuatrecasas 1958 (Reyes & Acosta 2003, Table 6 inv. 1–10). 14—As. *Avicennietum germinantis* Reyes & Acosta 2003 (Reyes & Acosta 2003, Table 7 inv. 1–10). 15—As. *Batidi-Avicennietum germinantis* Borhidi & Del-Risco & Borhidi 1991 (Reyes & Acosta 2003, Table 8 inv. 1–3). 16—As. *Laguncurio racemosae-Avicennietum germinantis* Reyes & Acosta 2003 (Reyes & Acosta 2003, Table 9 inv. 1–7).

Table 1. Synthetic table of the plant associations studied.

each association presents its own characteristic species and companions; we add a synthetic index to each species from r, +, I to V, to represent the presence/absence of species in the community. These indices are transformed into Van der Maarel indices [7] for statistical treatment, with the following equivalences: The value r means that the species is very rare, and that it only appears very sporadically, we assign it the same value as +; r, + = 2; value 2 indicates the species is rare and only found in certain isolated inventories in the plant community; I = 3, indicating the species is present in under 40% of the total samplings for the community; II = 4, in 40–55%; III = 5, in 55–70%; IV = 6, in 70–80%; and V = 7, in 90–100% of the total samplings carried out for a particular community (**Table 1**). We then run a series of statistical analyses on the Excel table with the 16 plant communities: cluster (Jaccard's distance) to determine the similarity between communities, diversity (Shannon) for A, B, C and ordination by DCA. We used the statistical packages CAP (Community Analysis Package III) and Past. For the state of conservation, we follow [8].

$$\text{Degree of conservation Gc} = \frac{C \times AM \times (A/Dcar. - A/Dcom.) \times RF \times Sm}{R}$$

1. C = Coverage on a per unit basis
2. AM = Average height of dominant species
3. Acar. – Acom. = Difference between the average values of the abundance indices of characteristics in higher syntaxonomic units in the association and the average values of the association companions.
4. RF = Floristic richness (value 1 if all the species are characteristic; 0.5 if characteristics and companion species are 50%, and 0 where there is no characteristic of the community, signifying that the original community has disappeared.
5. Sm = Minimum area in relation to the area of distribution of the community (subsector, district value: 0.5; sector: 1; subprovince, province: 2; group of provinces: 3.
6. R = Extremely rare phytocoenosis; value 3, rare 2 and normal 1.

   a. **Species that live in humid environments that are temporarily or permanently waterlogged and have high salinity (mangrove forest plants), in environments in which the salinity ranges between 0.2% and 1.3%, according to [9].

   b. *Species that live in humid or temporarily waterlogged environments with or without slight salinity (species in transition between the mangrove forest and neighbouring communities); in this case, the salinity gradient is less than 0.2%. These are species that live in places that are waterlogged with freshwater, as in the case of Gran Estero in the Dominican Republic [10].

   c. Invasive species from nearby communities typical of dry environments. These are species from communities in the surroundings, essentially belonging to the dry forest [11].

3. Results and discussion

This study revealed findings about mangrove community and adjacent vegetation's structure in Central America. This kind of phytosociological studies is ecologically significant and useful in conserving and managing ecosystems. The study identified that deforestation leads to siltation of soil, which can alter vegetation structure in surrounding areas.

3.1. Community analysis

Jaccard's analysis of similarity/dissimilarity shows that coincidences/differences between the plant communities are between 40 and 60%. The highest differences occur between group I (1–7) and group II (9–15) of the cluster (**Figure 6**). This is due to the different floristic composition of the plant communities caused by the influx of invasive species. This cluster analysis is confirmed by applying the DCA analysis (**Figure 7**), which shows two clearly differentiated groups of communities. Group GA in this analysis belongs to communities 9, 10, 11, 12, 13, 14, 15, which are characterised by a low presence—and even the absence—of mangrove species; in contrast, group GB has a very high presence of mangrove species. **Table 1** reveals the presence of 16 species (13.11%), which require strict ecological conditions of salinity and depth, as opposed to 33 species (27.04%) that grow in a low or non-existent salinity gradient, and 73 opportunistic invasive species from neighbouring habitats that penetrate owing to the significant silting of the lake basin (59.83%); this can be seen in the following vegetation profile (**Figure 8**) showing the introgression of dry forest species in the mangrove forest.

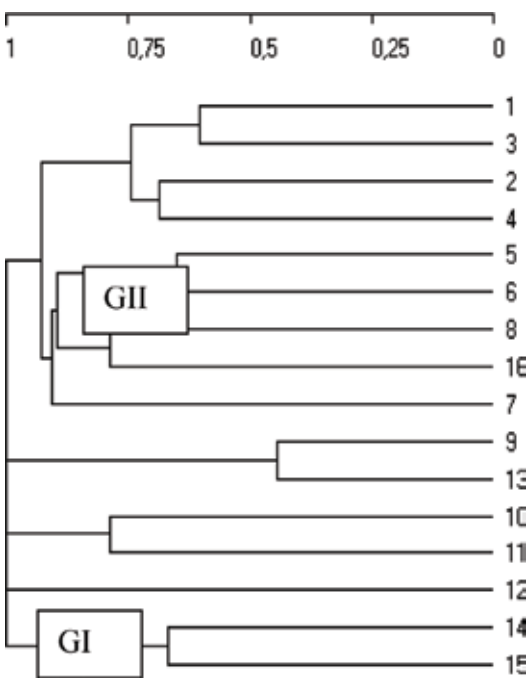

Figure 6. Jaccard similarity/dissimilarity cluster analysis of the 16 plant communities.

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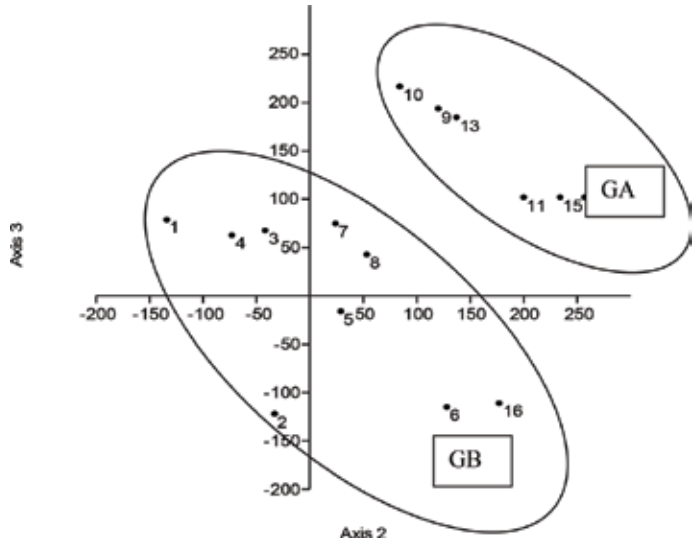

Figure 7. DCA ordination analysis separating the two groups (group GA and group GB) of mangrove communities.

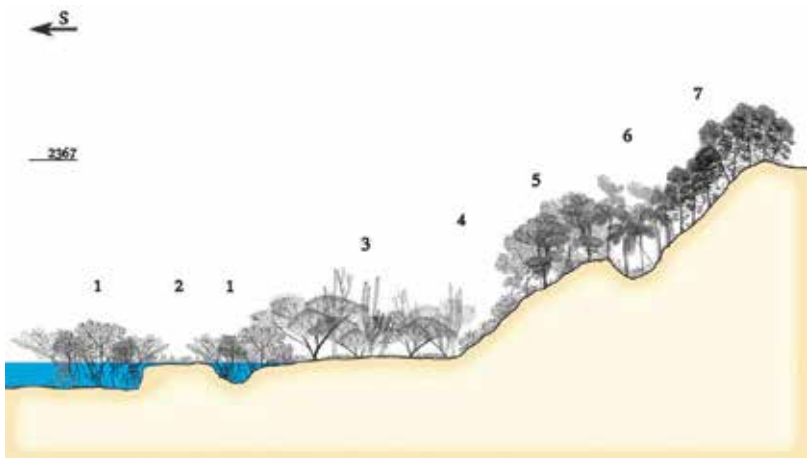

Figure 8. Profile of the vegetation of the cloud forest of Sierra Bahoruco. (1) *Rhabdadenio biflori-Laguncularietum racemosae* and *Lonchocarpo pycnophylli-Conocarpetum erecti.* (2) Salt marshes of *Batidi-Salicornietea.* (3) *Lonchocarpo pycnophylli-Cylindropundietum caribaeae.* (4) *Melocacto pedernalensis-Leptochloopsietum virgatae.* (5) Broad-leaved forest. (6) and (7) Cloud forest of *Prestoea montana.*

The communities in group I of the cluster have 11.68% of characteristic mangrove species, as opposed to 4.96% in group II. Salinity gradient in a given area depends on hydrology of that area. Lugo and Snedaker [12] first formulated the mangrove forest ecological classification system based on physiographic and structural components of mangroves of Florida. This study also showed vegetation groups based on salinity gradient. Modification of environmental parameters, such as salinity, depth of water, as a consequence of clogging, is a cause of change in the structure and diversity of the mangrove [13], and this change implies an

increase in diversity due to a decrease in species specific to the mangrove and an increase in invasive species from nearby ecosystems. By analysing the state of conservation and the diversity of these ecosystems, it can be seen that those with a high Shannon value are not better preserved; on the contrary, the best preserved are those that have few species, but all or most of them are typical of the mangrove ecosystem.

3.2. Diversity analysis

Shannon's diversity analysis was applied to the characteristic mangrove species, the invasive species and the total species in the mangrove forest, and to the 16 plant communities. This was done based on the synthetic table published by ourselves [7]. This table comprises 16 characteristic mangrove plants, 33 plants that grow in areas of wetland and standing water with a low salt content (these are invasive plants in wetland sites), and 73 opportunistic invasive species from nearby areas that penetrate into mangrove forests due to a decrease in the depth of the lake basin as a result of silting.

Table 2 reveals that communities 1–8 have a greater floristic richness than 9–16. There are 10 communities in which the Shannon index ** for characteristic species is greater than 1, and all the other communities have the value zero, signalling that these communities are not rich in mangrove species or have one single species. Paradoxically, in all communities except 12 and 16, the Shannon values for invasive species is equal or are higher than the values for characteristic species. This highlights the negative impact on the mangrove forest, and its substitution by invasive species. There are also anomalous situations such as community 14, where the Shannon value is zero in all cases; or 6, in which the total diversity value, 1.099, coincides with the characteristic species diversity, 1.099, due to the fact that the community has only mangrove species. In practically all cases, the typical floristic richness of characteristics** is very low compared to the floristic richness of invasive species S* + invasive plants, signalling a significant threat for mangrove forests. **Figures 9–11** show that communities 9–15 present a very low species diversity of characteristic mangrove plants, compared to the first communities, which are more diverse. Communities 9, 10, 12, 13 and 14 have a single mangrove species—thus constituting monospecific populations—and in communities 11 and 15 the species** totally disappear.

3.3. Analysis of the state of conservation

To determine the state of conservation of the 16 plant communities studied in Central America, we apply the degree of conservation index (Gc) established by ourselves [8]. The best conserved communities are evidently the most biodiverse, as in these communities (1–8) the floristic richness (Rf) is high, ranging between 0.5 and 0.11; while communities 9–16 have a floristic richness (Rf) of between 0.01 and 0.04. In this second case, community 10 has a value Gc = −0.091, due to the fact that Acar = 1 (average values for the abundance of characteristic species) and Acom = 2.63 (average values for the abundance of companion species). **Table 1** shows that community 10 has a single mangrove species** and 12 S* + invasive plants; in this case, the community is under major threat. However, the other communities −9, 11, 12, 13, 14, 15 and 16– present higher values for Acar than Acom, so the threat of

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Shannon_H (total)	3.965	3.46	3.252	3.503	2.842	2.164	2.733	2.419	2.004	2.502	1.723	1.554	1.537	0	0	1.099
Shannon_H**	2.157	2.34	1.899	2.044	1.881	1.365	1.598	1.703	0	0	0	1.349	0	0	0	1.099
Shannon_H (* + invasive plants)	3.797	3.082	2.978	3.251	2.384	1.6	2.365	1.785	1.887	2.423	1.609	0	1.318	0	0	0
Shannon_H (other invasive plants	3.219	1.609	2.559	2.697	1.609	0	2.286	1.785	1.785	2.241	1.609	0	1.318	0	0	0
Taxa_S_t	54	33	27	34	18	9	16	12	8	13	4	1	6	1	3	5
Taxa_S_**	9	11	7	8	7	4	5	6	1	1	0	1	1	1	0	4
Taxa_S_* + invasive plants	45	22	20	26	11	5	11	6	7	12	4	0	5	0	0	1
Taxa_S_Invasive plants	25	5	13	15	5	1	10	6	6	10	4	0	5	0	0	1
Individual_t	193	114	103	113	65	39	76	45	33	56	17	7	22	7	15	25
Individual_**	41	45	35	33	30	21	30	26	7	3	0	7	7	7	0	22
Individual_* + invasive plants	152	69	68	80	35	18	46	19	26	53	17	0	15	0	0	3
Individual_invasive plants	75	15	41	47	15	3	39	19	19	42	17	0	15	0	0	3

Table 2. Shannon values for characteristic mangrove species and invasive species: number of species and individual per community.

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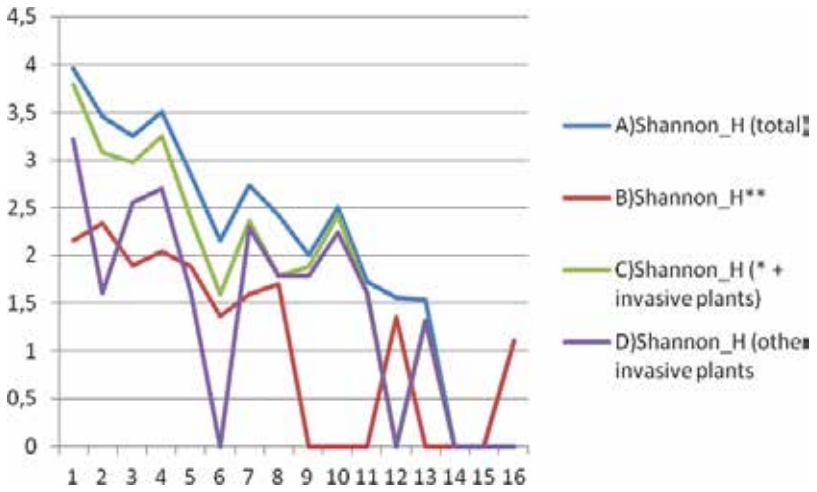

Figure 9. Shannon diversity graph of the four situations. (A) the total species in the community; (B) only characteristic mangrove species; (C) invasive species (both those growing in flooded areas, and invasive species due to the loss of the lake basin); (D) invasive species from nearby communities due to the silting of the lake basin.

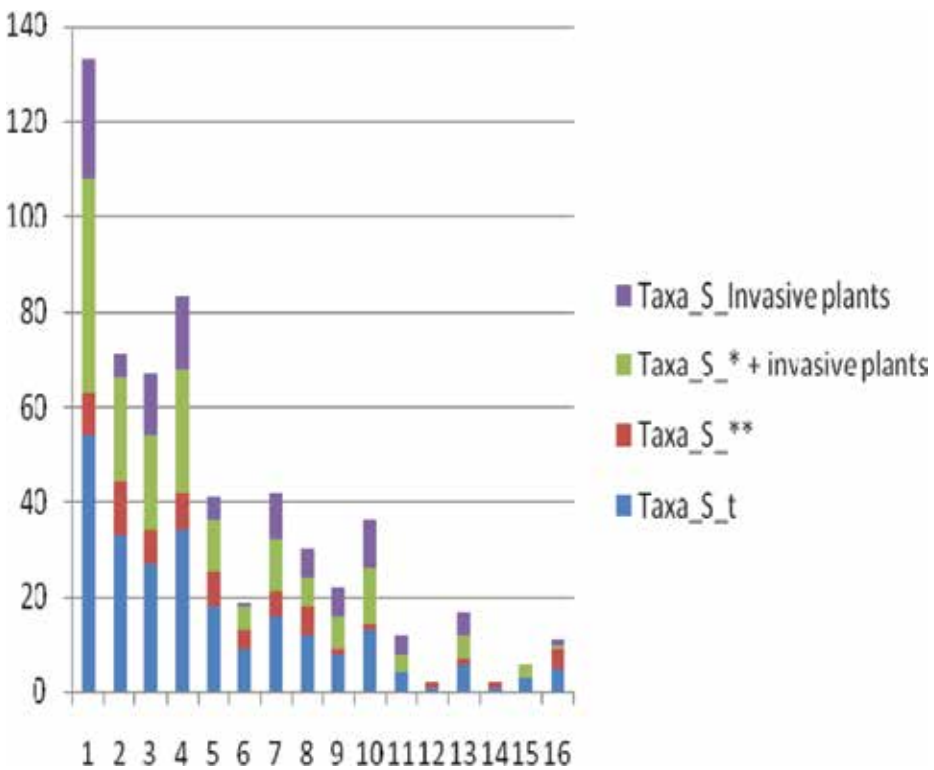

Figure 10. Graph showing the number of characteristic and invasive species.

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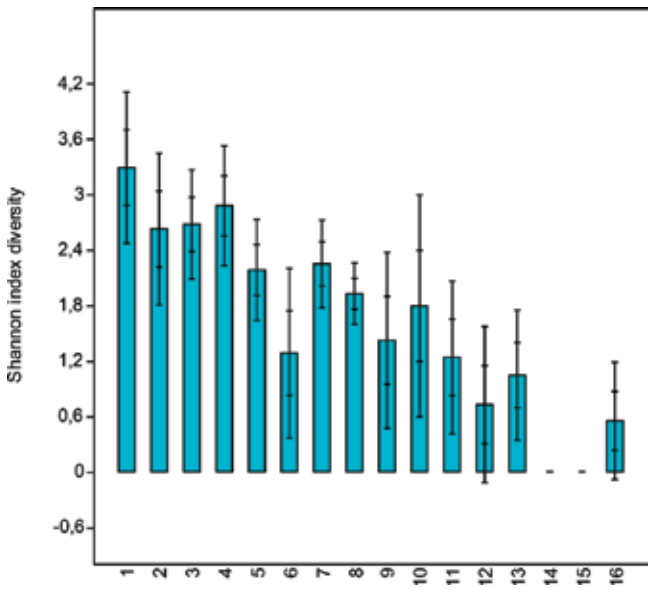

Figure 11. Box plot of the Shannon index.

	C	AM	Aca	Aco	Aca-Aco	Rf	Sm	R	Gc
1	0.948	8.20	2.55	1.37	1.18	0.09	1	2	0.412
2	0.923	7.70	2.09	1.13	0.96	0.11	2	1	1.506
3	0.883	7.20	3.00	1.40	1.60	0.07	3	1	2.150
4	0.880	6.50	2.12	1.07	1.05	0.07	2	1	0.129
5	0.100	10.0	2.28	1.18	1.10	0.07	2	2	0.077
6	0.980	5.20	3.25	1.60	1.65	0.05	2	2	0.420
7	0.920	18.5	4.00	2.00	1.70	0.05	2	2	1.702
8	0.691	6.50	2.33	1.16	1.17	0.06	2	2	0.315
9	0.900	7.00	5.00	1.85	3.15	0.01	2	2	0.198
10	0.800	7.00	1.00	2.63	(− 1.63)	0.01	2	2	(−0.091)
11	0.800	4.00	5.00	1.00	4.00	0.01	2	2	0.128
12	0.900	5.00	4.50	1.00	3.50	0.04	2	2	0.630
13	0.900	8.50	5.00	2.25	2.75	0.01	2	2	0.210
14	0.900	10.0	5.00	0.00	5.00	0.01	2	2	0.450
15	0.691	6.50	5.00	0.00	5.00	0.01	2	2	0.224
16	0.900	12.0	3.50	0.00	5.50	0.04	2	2	1.510

Table 3. Analysis of the degree of conservation of the mangrove communities.

these communities disappearing is negligible or non-existent, with the particularity that communities 14, 15 and 16 have values of Acom = 0 and have no invasive companion species and are thus the best conserved communities. In the first group of communities (**Table 3**), although the floristic richness of ** is high, the Rf of * + invasive plants is also high, implying a significant degree of threat.

The threats that affect the mangrove are several; among which we highlight tourism, industries, infrastructure and deforestation. The methodology used to find out the conservation status of these ecosystems is based on the phytosociological method. With this method, 16 plant communities have been described, which present ecological and floristic differences. Each plant association presents its own characteristic species (Acar), and companion species (Acom) belonging to neighbouring communities. For this reason, and for the first time, we take stock of the relationship between characteristic and companion species, and in response to this, the state of conservation of the plant association. The state of conservation of the mangrove is high when all its species are characteristic, as this ecosystem is poor in characteristic species, its conservation is good, but if it presents a high diversity, it means that it presents many opportunistic companion species, and the state of conservation the mangrove is bad.

4. Conclusions

The floristic diversity presented by some mangrove communities is not synonymous with a good state of conservation, but rather the reverse: this diversity is a cause for concern, as it is due to the high number of invasive species that are difficult to eradicate while the current threats are maintained, in the form of cutting, burning, forest fires, charcoal manufacture, and so on.

Therefore, the best conserved mangrove communities are those which present only typical mangrove species and no companions, even in the case of monospecific populations of *Rhizophora mangle, Laguncularia racemosa, Avicennia germinans, Conocarpu erectus.* The mangrove forest must be regarded as a fragile ecosystem as it demands ecological conditions of depth of water, salinity, and a very specific substrate, and in which any alteration triggers the deviation and substitution of these communities by neighbouring ones.

Based on the results obtained, we propose concrete measures to mitigate and prevent the destruction of the mangrove communities:

1. Not to carry out deforestation in peripheral areas to avoid erosive phenomena and the consequent filling of the lagoon vessel.
2. Deforestation with the aim of obtaining energy (coal) must be prohibited.
3. Implement policies for the integration of rural populations in their environment.
4. Control of mass tourism.

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Mangrove Ecosystem Ecology and Function deals with several aspects of mangrove science, as well as conservation, management, and related policies. The book is divided into six sections and structured into 10 chapters. The first section discusses mangrove ecology, structure, and function; the second section explains mangrove physiology related to salt accumulation; the third section focuses on mangrove polychaetes; the fourth section talks about the bioprospect of mangrove microbes; the fifth section discusses soil geochemistry; and the sixth section elucidates mangrove management and conservation. Researchers from different countries and fields of mangrove ecosystem exploration have contributed their findings. This book would be an ideal source of scientific information to graduate students, advanced students, researchers, scientists, and stakeholders involved in mangrove ecosystem research.

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