STRUCTURAL VARIABILITY OF MANGROVE FORESTS ALONG THE COAST OF KENYA

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University

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To mum, Denise, Davis and Pat.

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LIST OF ABBREVIATIONS/ ACRONYMS

AGB   Above-ground Biomass

ANOSIM   Analysis of Similarities

ANOVA   Analysis of Variance

BA   Basal Area

CI   Complexity index

CSA   Cross Sectional Area

DBH   Diameter at Breast Height

EACC   East Africa Coastal Current

ECC   Equatorial Counter Current

IV   Importance Value

KFS   Kenya Forest Service

KMFRI   Kenya Marine and Fisheries Research Institute

KWS   Kenya Wildlife Service

NEM   North East Monsoon

nMDS   Non-metric Multidimensional Scaling

SC   Somali Current

SEM   South East Monsoon

SIMPER   Percent Similarities Analysis

ABSTRACT

Mangrove forests occur across a diversity of coastal landforms with different geomorphological, climatic and oceanographic influences. These factors influence mangrove structural development and productivity and as a result, the structural development of mangroves varies with the coastal geomorphology. Earlier inventory studies in Kenya suggest that mangroves growing in north of the Tana River have different structural attributes from those growing south of the river. The current study characterised the structure and floristic composition of mangroves in Kenya by describing species composition, basal area (m^2 ha^{-1}), stem density (trees ha^{-1}), importance value index complexity index and above ground biomass (Mg ha^{-1}) across 14 sites spread across the coastline of Kenya. Variability in mangrove floristic composition was tested using analysis of similarities (ANOSIM) and the differences illustrated using non-metric multidimensional scaling (nMDS). Mangrove structural variability was tested using analysis of variance (ANOVA) and comparisons made by performing a post-hoc Tukey pairwise test. A hierarchical cluster analysis was then performed to determine the degree of similarity in mangrove species across the sites based on complexity index, biomass, tree diameter and tree height. To investigate the relationship between mangrove structure and possible drivers of variability, a regression fit model was used. The model described associations between mangrove standing biomass, environmental settings, precipitation, population density, and riverine influence across the sampled sites. *Rhizophora mucronata* was the most important species in most of the sites while *Avicennia marina* was the most important species in the estuarine area of Ungwana Bay. High values of structural complexity were observed in the estuarine and deltaic settings of Ngomeni and Kipini while relatively low levels of structural complexity were observed for the peri-urban mangroves of Mombasa and Mtwapa. Mangrove forest species composition differed significantly across the sampled sites (ANOSIM R: 0.24, p = 0.001). The mangroves of Kipini were significantly different from the rest of the sites. The study revealed significant differences in structural attributes of mangroves growing along the coast of Kenya, specifically, tree diameter [$F_{(13, 34050)}$ =163.01, p=0.000], tree height [$F_{(13, 34050)}$ =1827.28, p=0.000], basal area [$F_{(13, 358)}$ =5.45, p=0.000)], stand density [$F_{(13, 358)}$ =8.68, p=0.000], and standing biomass [$F_{(13, 358)}$ =15.36, p=0.000] across the sampled sites. Environmental settings and population density best explained the variability in mangrove standing biomass. The study suggests that the patterns of mangrove structural variability in Kenya closely follows the patterns of geomorphic variability along the coast. The study concluded that mangroves in Kenya are highly influenced by geomorphological and climatic variability along the coast as well as human influences. These findings are useful for mangrove managers and policy makers and have the potential to guide strategies and actions aimed towards sustainable management of mangrove forests in Kenya.

Chapter One

Introduction

1.1 Background Information

Mangrove forests grow in the intertidal areas of tropical and sub-tropical coasts (Hogarth, 2015; Tomlinson, 2016). In Kenya, these forests occur as pockets in a number of different landforms along the coast. They grow in protected creeks, bays, lagoons, estuaries and small islands along the over 600 km coastline covering an area of about 61,271 ha (GoK, 2017). With an estimated annual economic value of USD 85 million (KES 9.4 billion), mangrove forests in Kenya provide immense benefits to both people and the environment (Save Our Mangroves Now!, 2021). They provide a diversity of wood and non-wood products to adjacent communities and also help support and regulate ecosystem processes and services (GoK, 2017; Rivera-Monroy et al., 2017; Save Our Mangroves Now!, 2021; Erftemeijer et al., 2022).

Mangroves have wide environmental tolerances and are adapted to grow in different environmental conditions within the intertidal area (Alongi, 2009; Hogarth, 2015; Tomlinson, 2016). They grow in habitats with site-specific variations such as inundation classes, water salinity, soil salinity and substrate characteristics and also with regional-scale variations such as climate, oceanography, hydrology, sediment characteristics and even the extent of human disturbance (Mazda et al., 2007; Friess, 2017; Primavera et al., 2019). These factors influence the structure and productivity of mangrove forests and as a result, the structure, distribution and development of mangrove forests varies with the diversity of coastal landforms.

Areas with an abundant supply of resources such as nutrients, freshwater, light and space; a moderate hydroperiod, in terms of frequency, duration and depth of inundation; and areas with minimal effects of regulators such as salinity, pH, metals, and sulphides are very favourable for mangrove growth and development (Twilley & Rivera-Monroy, 2005; Twilley, 2019). Management practices such as conservation and restoration efforts also have the potential to increase mangrove resources and enhance biodiversity (Vierros, 2017). On the other hand, high salinity levels, severe drought and nutrient deficiency may

be limiting to growth (Islam et al., 2019). The influence of human activity may also affect the distribution and productivity of the mangrove forests. The over-exploitation of mangrove resources, conversion of mangroves to other land uses, pollution effects, and climate change negatively influence mangrove distribution and productivity (Tomlinson, 2016).

Mangrove environmental conditions are as a result of the interaction of dominant ecosystem processes such as geomorphology, oceanography and climate as well as anthropogenic influences. These processes act as forcing functions in an area (environmental setting) forming a unique energy signature on the area (Twilley, 1995; Twilley et al., 1996, 2018). Across the globe, studies on the mangrove stands of Australia (Adame et al., 2010), Colombia (Urrego et al., 2009) and Brazil (Estrada et al., 2013; Schaeffer-Novelli et al., 1990, 2000) show that the degree of structural development of mangrove stands will be dependent on the characteristics of the landforms colonized by the trees (Woodroffe et al., 2016).

Mangrove structural variability has also been observed and documented in Kenya. The mangroves growing north of River Tana are structurally more complex in terms of tree height, butt diameter, standing stock and overall biomass compared to those growing south of the river (Ferguson, 1993; Kairo, 2001; Lang'at, 2008). These differences could be attributed to the characteristics of the landforms colonized by the trees in the two regions. However, the statistical evidence of these patterns and influences remains poorly studied. The aim of the current study was to characterise the structure and floristic composition of mangrove forests along the coast of Kenya, compare the structural variability of mangrove formations across selected sites along the coast and discuss the potential causes of these differences.

1.2 Statement of the Problem

Studies on mangrove forest structure in Kenya indicate that the height, basal areas and biomass values of mangroves growing north of River Tana differ from those of mangroves growing in the south. Mangroves growing north of River Tana have greater complexity indices compared to those in the south. However, these studies provide little information on oceanographic processes, geomorphological processes, and climatic influence on

mangrove forests in Kenya. Literature suggests a relationship between mangrove structure and the environmental drivers but it remains unclear what dominant ecosystem processes drive this variability in Kenyan mangrove forests. As a consequence, forest managers lack crucial information regarding the dominant ecosystem processes affecting mangrove growth and development and how these processes drive mangrove growth in various areas along the coast of Kenya. This poses a challenge to mangrove management and restoration efforts.

1.3 Justification

Mangrove ecosystems are dynamic. They are controlled by several interacting factors such as oceanography, hydrology, sediment fluxes, topography of the wetland, and soil and water salinity. Hence, any exploitation of mangrove forests must be subject to very careful planning. The forests should be sustainably managed on an environmentally sound and economically sustainable basis, and they require a specialized form of management. Determining the forces that underlie the patterns of mangrove growth and productivity will help inform forest managers and policy makers on the coastal settings under which mangroves in Kenya grow and their potential effects. This has the potential to help guide strategies and actions aimed towards sustainable management of mangrove forests. Specifically, the review of mangrove harvest plans, and the development of restoration plans could benefit from the findings of this study.

1.4 Research Objectives

1.4.1 General Objective

The main objective of the study is to investigate the structural variability of mangrove forests in Kenya and examine the potential causes of these differences.

1.4.2 Specific Objectives

a. To characterise the mangrove forest structure at multiple selected sites along the coast of Kenya

b. To examine the patterns of variability/similarity in mangrove structure along the coast of Kenya

c. To investigate the relationship between mangrove structural variability and physical environmental drivers

Chapter Two

Literature Review

2.1 The Mangrove Environment

Mangrove habitats are characterized by fluctuating hydroperiods, fluctuating salinity, low oxygen concentration and frequently high temperatures. In order to survive in such environments, mangrove trees have, over time, developed physiological and morphological adaptations such as enhanced anchorage at the roots, development of breathing roots, salt tolerance, salt exclusion and extrusion mechanisms (Lugo & Medina, 2014; Hogarth, 2015; Tomlinson, 2016).

Mangroves typically grow in environments whose salinity ranges between that of fresh water to salinities well above the sea water. The salinity of sea water is approximately 35 g of NaCl/l which means an osmotic potential of -2.5 MPa (Hogarth, 2015). Plants growing in such an environment have to take in water against this pressure. In areas near the landward margin, evaporation raises the salinity above that of sea water making the problem of water acquisition even worse. In such cases, the variation in salinity may be a bigger problem than high salinity itself (Alongi, 2009; Hogarth, 2015).

Because of the variability in salinity across the intertidal area, mangrove forests exhibit distinct zonation patterns that run perpendicular to the shore reflecting different species preferences to inundation frequency (Ellison, 2019). These processes are dependent on the microtopography in relation to sea level position and tidal range. To cope with the salty environment, mangroves employ mechanisms such as salt exclusion at the roots, secretion of excess salts, and tolerance of high tissue salt concentration (Friess, 2016; Ellison, 2019;). *Rhizophora mucronata*, *Bruguiera gymnorrhiza* and *Avicennia marina* possess concentric layers of hypodermal and endodermal cells in the root that act as a barrier during salt exclusion greatly aiding in the process of ultrafiltration. For *Avicennia marina,* 90% of salt is excluded at the root surface, and this rises as the salinity of the environment increases. This is evident from findings by Hogarth (2015) that estimated salt concentration of the xylem sap to be about one-tenth that of sea water.

Even after excluding most of the salt, the concentration of sodium and chloride ions in the tissue of mangrove trees is still higher compared to non-halophytic plants growing in non-saline environments. High salt concentrations inhibit many enzymes. By partitioning solutes within different cellular components, mangroves can protect intracellular enzymes from high salt concentration. Sodium and chloride ions are at high concentrations within cell vacuoles and this way they are excluded from the cytoplasm (Alongi, 2009; Hogarth, 2015). Several mangrove species among them *Avicennia marina*, *Rhizophora mucronata*, *Sonneratia alba* and *Xylocarpus granatum* deposit sodium chloride on the bark of stems and roots. This prevents the salts from interfering with tissue metabolism. *Xylocarpus granatum* also moves salts to the leaves which are then shed when they senesce. *Avicennia marina* possesses salt glands on the leaves and deposits of salt crystals are often clearly visible. The lower surface of the leaf is densely covered with hairs which raise the secreted droplets of salty water away from the leaf surface. This prevents the osmotic withdrawal of water from the leaf tissues (Hogarth, 2015).

In areas that are permanently or periodically inundated, oxygen movement into waterlogged soils is severely limited and as a result, mangrove soils are often virtually anoxic (Lugo & Medina, 2014; Tomlinson, 2016). To cope with this, mangroves growing in waterlogged soils are characterized by aerial roots such as stilt roots and knee roots to enhance respiration. For *Rhizophora mucronata*, stilt roots can grow from the main trunk as much as 2 m above the ground (Naskar & Palit, 2015). In *Bruguiera gymnorrhiza* and *Xylocarpus granatum,* a shallow horizontal root forms knee roots by periodically breaking the soil surface and submerging again. For *Avicennia marina* and *Sonneratia alba*, shallow horizontal roots radiate outwards and at intervals, pneumatophores emerge and stand erect. Pneumatophores supply underground roots with oxygen in anoxic soils. The aerial roots of *Rhizophora mucronata* and the horizontal roots for *Avicennia marina* also provide effective anchorage in fluid and unstable soil (Srikanth et al., 2016).

2.1.1 The Cost of Survival

In order to successfully survive and thrive in the demanding intertidal environment, mangrove require structural and metabolic adaptations. Each of these adaptations bears a

cost in terms of energy and materials. Thus, mangrove trees have to prioritize survival at the expense of maximum growth and productivity.

The process of acquiring and retaining water for mangrove trees is energetically expensive (Hogarth, 2015). At high soil salinities, stomatal conductance is reduced in order to conserve water by reducing transpiration, but this also reduces CO_2 uptake, and subsequently reduces growth. Hence, mangrove trees need to ensure that only sufficient water is expended to maintain the carbon assimilation rate very near the photosynthetic capacity of the leaf (Noor et al., 2015). The construction of structures needed to conserve water such as succulent leaves with thick epidermal walls covered with a waxy cuticle and a dense layer of hairs also carries along with it costs in terms of energy and allocation of materials.

In order to maximize photosynthesis, a leaf must position itself to maximize incident light. However, in a warm tropical coast such as in Kenya, maximizing incident light also maximizes heat gain. For *Rhizophora mucronata*, photosynthesis proceeds rapidly at a temperature of 25°C and declines sharply above 35°C. As a result, mangroves tend to hold their leaves at an angle to the horizontal, so as to reduce heat gain. Cooling is also enhanced by having smaller leaves in order to lose more heat by convection (Naskar & Palit, 2015). Mangrove trees therefore have to choose between maximum photosynthesis and survival in warm tropical coastlines.

The elaborate aerial root structures that enable the mangrove trees to cope with anoxic soils represent costs to the plant. The plant has to allocate resources to build and to maintain these structures. In more anoxic soils, more pneumatophores are produced and the plants incurs even more investment costs. Mangroves therefore cope with environmental stresses of the mangrove environment but they do this at the expense of growth. In extreme conditions, growth may be so restricted that dwarfing occurs (Hogarth, 2015).

2.2 Mangroves of Kenya
In Kenya, there are nine mangrove species (**Table 1**). *Rhizophora mucronata* and *Ceriops tagal* are the most dominant species found in almost all mangrove formations, while *Heriteria littoralis* and *Xylocarpus moluccensis* are the rarest species.

Table 1: Mangrove Species in Kenya. Source: GoK, 2017

Species	Local Name
Rhizophora mucronata	Mkoko
Bruguiera gymnorhiza	Muia
Ceriops tagal	Mkandaa
Sonneratia alba	Mlilana
Avicennia marina	Mchu
Lumnitzera racemosa	Kikandaa
Xylocarpus granatum	Mkomafi
Xylocarpus moluccensis	Mkomafi dume
Heritiera littoralis	Msikundazi

The mangroves in Kenya typically exhibit a distinct zonation pattern from the seaward margin towards the landward margin as a result of inundation, geomorphology and salinity profiles of the intertidal area (**Fig. 1**). *Sonneratia alba* is normally found on the seaward side with large *Avicennia marina* and *Rhizophora mucronate* in the middle zone. *Avicennia marina* expresses a double zonation but is mostly found on the landward side. *Lumnitzera racemosa* normally occurs as a thin fringe on the landward border of mangroves.
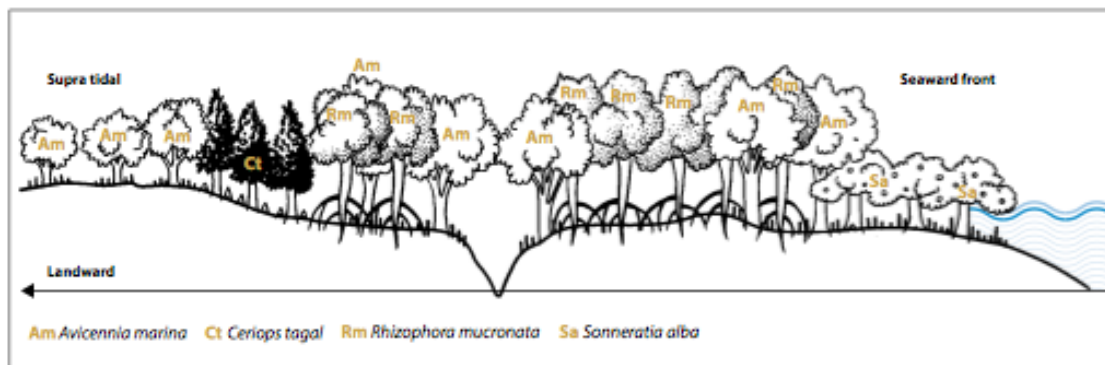
Fig. 1: Mangrove zonation patterns (GoK, 2017).

2.2.1 Distribution of Mangroves in Kenya

The data on mangrove coverage in Kenya has been inconsistent mainly due to the differences in the methods used to map them and the different methodologies used for data comparison. Mangrove cover in Kenya has been estimated to be as low as 32,378 ha from Landsat data by Giri et al. (2010) and as high as 64,426.9 ha using aerial photography (Forest Department of Kenya, 1983). Recent data by the Global Mangrove Watch (2020) estimates the current extent of mangroves in Kenya at 54,430 ha (Erftemeijer et al., 2022). The official figure given by the Kenya Forest Service in the National Mangrove Ecosystem Management Plan (2017-2027) is 61,271 ha. The bulk of these mangroves (61%) are found in Lamu County spanning an area of about 37,350 ha. Tana River County has the least area of mangroves at 3,260 ha, Kilifi County has 8,536 ha, Mombasa has 3,771 ha while Kwale County has 8,354 ha of mangroves.

2.2.2 Mangrove Goods and Services

Mangrove forests in Kenya provide goods and services that are of economic, ecological and environmental value to the society. These forests are harvested for fuelwood and for poles and timber used for construction and boat building (GoK, 2017). At the same time, local communities obtain non-wood mangrove products such as herbal medicines, tannins, honey and fodder from the forests (Bosire et al., 2008; Kairo et al., 2009; GoK, 2017). Besides the food and material resources extracted from mangrove forests, adjacent communities derive other benefits from the forests. Some mangrove areas are sacred sites such as the Kaya forests for the Mijikenda communities and are of great cultural significance. Mangrove ecosystems support research activities and education and also provide opportunities for tourism and recreation (GoK, 2017). For example, the mangrove forest in Gazi supports research and education activities through the Kenya Marine and Fisheries Institute (KMFRI), Gazi Sub-station, and features the Gazi Women Boardwalk, an eco-tourism venture run by the local community (Huff & Tonui, 2017).

Mangrove ecosystems provide ecological services such nutrient cycling, primary production, structural habitat, and soil formation. They support coastal fisheries by acting as nurseries, breeding, spawning, hatching and feeding habitats for fish (Kairo et al., 2009). Over 800,000 people along the coast depend on mangrove-associated fisheries for

their livelihoods (Erftemeijer et al., 2022).The forests play an important role in shoreline protection. The stems and stilt roots of mangroves offer resistance to incoming tides and waves and therefore reduce the hydrologic energy dissipated on coastlines (Alongi, 2009; Kairo et al., 2009; Huxham et al., 2015, 2017; Scheren et al., 2016). This way, the mangroves reduce the risk of flooding to communities that live behind them (Lugo & Medina, 2014). Mangroves are also capable of absorbing pollutants such as heavy metals as well as nutrients and suspended matter and this makes them natural filters that prevent pollutants, sediment and excess nutrients from reaching deeper waters (Tomlinson, 2016).

Despite their relatively low coverage compared to terrestrial forests, mangroves have the capacity to sequester and store carbon that rivals that of tropical terrestrial forests. Recent reports show that mangroves in Kenya sequester approximately 2-3% of the country's total annual emissions from fossil fuels, (about 16 to 18 million tCO_2 per year) (Erftemeijer et al., 2022). Most of the carbon stored in mangrove forests is in the belowground component; the roots and the soil (Inoue, 2019). Mangrove forests therefore have a larger proportion of belowground biomass in comparison to terrestrial forests (Spalding, 2010) and as a result, their carbon density values are reported to be three to four times more than terrestrial forests (Gress et al., 2017). This superior ability to sequester and store carbon per unit area makes mangroves ideal candidates for climate change mitigation and adaptation.

2.2.3 Threats to Mangrove Ecosystems

Mangrove ecosystems provide immense benefits to the communities living near the forests. However, mangrove ecosystems in Kenya are under constant threat. A study by Kirui et al. (2013) revealed that Kenya lost about 20% of its mangrove forests between 1985 and 2010. Conservative figures report a net loss of 2% in the 20 years between 1996 and 2016 (Erftemeijer et al., 2022). The bulk of the losses are in peri-urban areas such as Mombasa (Mohamed et al., 2009). For instance, Tudor creek in Mombasa lost 86.9% of her mangrove forest between 1992 and 2009 (Bosire et al., 2014). Overexploitation of wood resources, land use changes that convert mangrove areas, pollution and sedimentation, diversion and damming of rivers, infrastructure and development, and extreme natural events such as El-Nino rains that trigger massive sedimentation have all

been attributed as threats to the mangrove ecosystem (Abuodha & Kairo, 2001; GoK, 2017; Jennerjahn et al., 2017). Considering sea levels are expected to rise as a result of climate change and that there will be increased pressure on the forests as a result of rapid population growth and increased demand of forest resources and space, the problem of mangrove degradation is expected to worsen if no measures are taken.

2.2.4 Management of Mangrove Forests in Kenya

Mangrove forests in Kenya are gazetted as government forest reserves. The Kenya Forest Service (KFS) is the legal entity mandated to manage all forests in Kenya, including mangrove forests. When these forests occur within Marine Protected Areas, the forests are co-managed with the Kenya Wildlife Service (KWS). Community participation in the management of mangrove forests in Kenya is provided for under the Forest Conservation and Management Act (2016). Currently, there is a National Mangrove Ecosystem Management Plan (2017-2027) in place that provides strategies and guidelines for mangrove management in Kenya. Additionally, the Kenya Forest Service Strategic Plan, updated annually, provides the legal framework for the management of all forest resources in the country. In 2018, the government banned mangrove logging in the country to combat environmental degradation, conserve water towers and mitigate the effects of drought across the country. However, in January 2019, the ban was lifted in Lamu County. This was after the communities appealed to the government on the basis of their dependence on mangroves for their livelihoods (Cece, 2022).

2.3 Mangrove Bio-geomorphology

Bio-geomorphology considers the multiple interactions between ecological and geomorphological processes (Viles, 1988; Viles et al., 2008; Ellison, 2019;). The distribution and development of mangrove species has been influenced by landform processes over long geological time scales (Corenblit & Steiger, 2009; Ellison, 2019). Lugo & Snedaker (1974) describe mangroves as "self-maintaining landscape units that are responsive to long-term geomorphological process". They are open systems, exchanging both energy and matter with terrestrial and offshore coastal ecosystems and their development is facilitated by geomorphic settings that characterize the influences of the physical environment, prevailing processes and their variability (Ellison, 2019).

Attempts to model the function of mangrove ecosystems via energy and material fluxes have revealed high levels of variability in many aspects of mangrove ecosystems (Robertson & Alongi, 1992; Feller et al., 2010). This has led to the development of hierarchical schemes to evaluate the variation in these ecosystems. Some of the most successful schemes are based on geomorphological models such as those developed by Thom (1982), Semeniuk (1985), Woodroffe (1993), and Augustinus (1995). More recently, similar models have been based on the overarching influence of climatic, geomorphological and other environmental features of mangrove forests such as those developed by Twilley & Rivera-Monroy (2005), Ellison (2009) and Worthington (2020). These schemes have been recommended for use in restoring mangrove forests (Rivera-Monroy et al., 2004; Krauss et al., 2008), approximating the value of ecosystem services (Ewel et al., 1998) and assessing the vulnerability to climate change (Lovelock & Ellison, 2007; Gilman et al., 2008). These models are helpful at investigating regional scale factors, but it remains unclear on whether they are sufficient to explain ecological functions within mangroves i.e., microtopographic effects (Twilley, 1995; Feller et al., 2010).

2.3.1 Mangrove Forest Types

Earlier studies classified mangrove species as pioneer or climax species inferring that they were in a successional state leading up to a terrestrial forest through soil accumulation (Watson, 1928; Davis, 1940). Over time, researchers have put forward a new concept to explain the zonation of mangroves. This new concept is that of a steady state landscape that views the zonation of the mangrove ecosystem as a response of external factors rather than a temporal sequence induced by the plants themselves. This concept has been supported by the work of Egler (1952), Macnae (1967), Thom (1967), Walsh (1974), Rabinowitz (1978), Lugo (1980), and Snedaker (1982).

Building on the concept of a steady state landscape, Lugo & Snedaker (Lugo & Snedaker, 1974) classified mangrove forests into five forest types based on the local tidal pattern and terrestrial surface drainage; fringe forests, riverine forests, over-wash forests, basin forests, and dwarf forests.

According to the classification, fringe forests occur along the fringes of protected shorelines and islands and are best defined along shorelines whose elevations are higher than the mean tide. These forests are relatively exposed to tides and waves and may also be affected by strong winds which cause breakage. Riverine forests occur along river and creek drainages and are flushed daily by the tide. This forest type is fronted by a fringe forest which occupies the slope of the drainage way. Over-wash forests occur on small low islands and finger-like projections of larger land masses in shallow bays and estuaries in such a way that the forest obstructs tidal flow and as a result it is usually over-washed at high tide. Basin forests occur in inland areas along drainage depressions that channel terrestrial runoff toward the coast. A variant of basin forests is the hammock forest type that occurs on grounds that are slightly elevated relative to the surrounding areas, in contrast to the depressions associated with the basin type. Dwarf forests are mature forests characterized by individuals less than 1.5 m tall. The individuals are usually dwarfed due to environmental stresses such as nutrient limitations (Lugo & Snedaker, 1974). This classification has been used by to classify mangrove forests in numerous studies (Pool et al., 1977; Cintron & Schaeffer Novelli, 1984; Feller et al., 1999; Schaeffer-Novelli et al., 2000; Adame et al., 2010; Urrego et al., 2014; Ellison, 2019).

2.3.2 Mangroves in Relation to Energy Signatures of Coastal Environments

In his review on the properties of mangrove ecosystems, Twilley (1995) described the ecology of mangroves based on the influence of forcing functions and energy signatures. This description is based on one concept by Odum (1983) for ecosystem ecology on the influence of forcing functions as environmental constraints on the ecological processes of ecosystems. Forcing functions are potential energies of resources outside the boundary of a system. These forcing functions greatly determine the network of energy flow and material cycling that develops within the system (Twilley, 1995). When forcing functions act collectively on a system, they are referred to as the energy signature of that system. In mangrove ecosystems, forcing functions represents forms of energy such as solar radiation, river flows, tides and precipitation and when they act collectively, they form a unique energy signature. The energy signature represents the combination of environmental factors that shape and support the ecological processes that occur within ecosystems (Twilley, 1995). For instance, insufficient solar energy will be a major

constraint on development of maximum biomass in mangrove ecosystems. Fewer tides or a low water turnover results in higher soil salinities and accumulation of toxic substances. The result of this is limited productivity. The maximum production of a mangrove ecosystem will ultimately depend on the cumulative sum of energy associated with the forcing functions of a coastal environment.

The link between the energy signature of an environmental setting and ecological functions such as productivity and nutrient cycling is important for sustainable management of mangrove ecosystems. The concept of energy signatures allows for classification of mangrove environments and this way, comparisons of ecosystem properties among a variety of sites can be made. Understanding how mangrove ecosystems respond to different environmental conditions can also greatly aid in the development of general conceptual models of mangrove ecosystems.

2.3.3 Environmental Settings

The concept of using the energy signature and forcing functions is similar to the concept developed by Thom (1982) of using landform characteristics and environmental processes to describe forest structure and growth. This geomorphic (or physiographic) approach helps explain species distribution and physiognomy by associating plants directly with diverse landform and substrate conditions.

Initially, Thom (1982) identified five basic classes of terrigenous environmental settings based on the relative influence of forcing functions. In a later review, Thom (1984) added three more carbonate environmental settings to the list. An environmental setting is comprised of three essential components; geophysical, geomorphic, and biological. The geophysical component includes factors such as oceanography, and climatic conditions of a region. This includes the general character of sedimentation, the dominance of particular processes (wave, tide, or river), and the topographic expression and composition of particular landforms. The biological component expresses ecological factors arising from the pool of species occurring in a particular region (Thom, 1984). The first two dominant components; geophysical and geomorphic, are the components that are combined to produce an array of physical settings in which mangroves grow.

Thom (1982) describes five settings where terrigenous sediment inputs are dominant. Setting 1 is an allochthonous coast with a low tidal range. The river discharge leads to rapid deposition of sediments and forms deltas that build seawards over flat offshore slopes. Setting 2 is also an allochthonous coast with a high tidal range characterized by strong bidirectional tidal currents. The currents disperse the sediments brought to the coast by rivers and form elongate sand bodies in the offshore zone. Setting 3 is an autochthonous coast characterized by high wave energy and low amounts of river discharge. The slope of the inner continental shelf is steeper and the setting may feature barrier islands and bay barriers. Setting 4 represents a combination of high river discharge and high wave energy. The sand from the river is rapidly redistributed along the shore by waves to form extensive sand sheets. The coastal plain is dominated by sand beach ridges which are narrow discontinuous lagoons with an alluvial plain on the landward side. Setting 5 represents a drowned river valley that has been drowned/ transgressed by a rising sea-level. It remains an open estuarine system since neither marine nor river deposition has been sufficient to infill it.

Thom (1984) describes three additional distinct settings dominated by the accumulation of carbonate. Setting 6 is a low-energy coast where carbonate platforms may slowly accrete due to the accumulation of lime muds and peat. Coral reefs or sand barriers dampen wave energy and the shoreline is indented with mangroves protruding into an extensive shallow water area. In setting 7, mangroves occur behind a mobile but protective sand or shingle barrier. The barrier may consist of coral detritus or shallow peats. Setting 8 is a low-energy embayment that may lack protective barriers. In this setting mangroves occur on carbonate surfaces that have been transgressed by a rising sea-level.

Environmental settings by Thom (1982, 1984) have been used to describe mangrove forests in studies across the world (Cintron & Schaeffer Novelli, 1984; Woodroffe, 1987, 2002; Schaeffer-Novelli et al., 1990, 2000, 2016; Boyd et al., 1992; Woodroffe, 1993; Dunn et al., 2008; Woodroffe et al., 2016). Later studies combine some settings to develop broader classifications for mangrove environmental types. Kathiresan (2004) simplified Thom's classification into three broad categories; Interior mangroves, river-dominated mangroves and tide-dominated mangroves. Twilley & Rivera-Monroy (2005) classify the

settings into deltaic settings, estuarine settings, lagoonal settings and oceanic islands. Balke & Friess (2016) have a simpler classification based on the type of sediment; minerogenic settings and organogenic settings. Worthington et al. (2020) have classified the settings into deltaic, estuarine, lagoonal, open coast and carbonate settings.

In a later review, Twilley et al. (2019) combine the theory of environmental settings by Thom (1982, 1984) and Woodroffe (1993, 2002) and the concept of energy signatures by Twilley (1995) to develop the ecogeomorphology model of mangroves. This is a "hierarchical classification scheme of geomorphological settings and corresponding ecological types" (Twilley et al., 2019). This model describes how patterns of resources, regulators and hydroperiod influence mangrove community structure and ecosystem function by classifying coastal settings into broad categories.

Coastal settings are characterized based on the source of sediment which is as a result of geophysical processes and local geology (Twilley et al., 2019). Clastic/terrigenous sediments are delivered from upland catchments and deposited along the coastal zone. These sediment systems can be classified based on the relative influence of the tides, waves and river on sediment transport. "Muddy coasts" are influenced by substantial river inputs. The sediment could be derived from river basins or from fluid muds transported by nearshore currents and accumulating down-shore from deltaic environmental settings (Woodroffe, 2002; Twilley et al., 2019). "Estuarine coasts" have freshwater and marine sources of sediment that create diverse landforms such as rias and tide and wave-dominated lagoons. The other coastal setting results from in situ processes such as carbon fixation which is primarily the production of mangrove roots and litter and the formation of reef structures and invertebrate shells. This forms peaty or calcareous soils that are a combination of mangrove organic matter and carbonate sediment (Twilley et al., 2019). The other setting is an "arid, climate-dependent arheic coastline type". Using these distinct types of coastal environmental settings, Twilley et al. (2019) have been able to link geomorphological settings and geophysical processes to patterns in mangrove ecosystems.

2.4 Mangrove Structural Variability in Relation to Physical Drivers

The relationship between mangrove tree structure and physical environmental factors has been observed in mangrove forests across many parts of the world. Studies investigating this relationship have been done on the mangrove forests of Brazil (Schaeffer-Novelli et al., 2000), Malaysia (Satyanarayana et al., 2010), Honduras (Castañeda-Moya et al., 2006), Columbia (Urrego et al., 2014), Guinea (Bertrand, 1999), Florida (Castañeda-Moya et al., 2013; Chen & Twilley, 1999), the islands of the Pacific Ocean (Woodroffe, 1987), Vietnam (Fagherazzi et al., 2017) and Australia (Cresswell & Semeniuk, 2018).

Kairo (2001) was among the first ecologists to conduct detailed analysis of mangrove structural variability in various mangrove habitats occurring along the coast of Kenya. The study compared structural attributes of mangrove trees in four pilot areas along the coastline using the environmental settings of Thom (1982), forest types of Lugo & Snedaker (1974) and the forcing functions of rivers, tides, waves and rain (Twilley, 1995). The study observed that basal area values, stand density, canopy height, standing biomass and complexity indices were all significantly higher in the two sites North of River Tana (Northern Swamps and North Central Swamps) than those South of River Tana (Mida Creek and Gazi Bay). The study concluded that the main reasons for the differences were site conditions or 'energy signatures' and human pressure. By using the concept of forcing functions and environmental settings, the study was able to describe how landform characteristics and environmental processes influenced mangrove structural variability along the Kenyan coastline. Although the study only analysed a small number of sites that supported mangrove growth, it was able to provide the first indications as to how dominant physical processes drove mangrove structural variability along the Kenyan coastline. Since the work was constrained by lack of adequate reference data, it recommended further study on the variability of mangrove forest structure and distribution in Kenya and the influence of dominant environmental factors on these systems.

In a later study, Lang'at (2008) attempted to describe mangrove structural attributes in relation to the biophysical features along the coast of Kenya. The study analysed mangrove structural data from more sites than the four done by Kairo (2001). Lang'at

(2008) analysed mangrove structural data for Kiunga, Tana River, Mida Creek, Tudor Creek, Gazi Bay, Shirazi-Funzi Bay, Ramisi and Vanga. The study supported the findings of Kairo (2001) that the mangroves North of River Tana had relatively more complex structure than those growing south of the river. While the study described mangrove structural attributes for the different sites, it did not categorize the different sites into various environmental settings and therefore did not provide a clear relationship between structural variability and the influence of landform characteristics and ecosystem processes.

More recently, Mohamed (2017) did a study assessing the spatial structural variations of mangrove forests along the Kenyan coast by determining mean stem density, mean tree height, mean diameter at breast height (DBH) and pole quality. His findings show that tree height, mean DBH and percentage of poles of merchantable quality were all highest in mangrove formations occurring inside Kiunga Marine National Reserve (KMNR) while the mangroves of Mtwapa had the lowest values of tree height, DBH and percentage of poles of merchantable quality (Mohamed, 2017). However, the study did not analyse physical parameters such as geomorphology and oceanography. The study attributed the high values of KMNR to conservation measures and the low values of Mtwapa to human pressure.

Other than these few national-scale studies on mangrove structural variability in Kenya, a number of studies have attempted to link this productivity to environmental process but they have done so at considerably smaller scales. For instance, a number of studies have analysed mangrove structure and ecosystem processes for the mangroves of Gazi Bay (Dahdouh-Guebas et al., 2004; Kairo et al., 2009; Kihia et al., 2010), Mida Creek (Kairo et al., 2002; Alemayehu et al., 2014), Ngomeni (Bundotich et al., 2009) and Lamu (Alemayehu & Chemuku, 2017). Hence, these studies have linked structure with more local factors such as competition and predation. These factors are important, especially in settings with low physical energy inputs. However, in the use of environmental settings to link ecosystem properties with ecosystem function, Twilley (1995) argues that environmental settings are regional-scale factors affecting the ecology of mangroves and while microtopographic effects might occur, in areas of high energy, the influence of these

local factors on structure and function of mangrove communities is usually insignificant (Twilley, 1995). The current study investigated mangrove structural variability across the entire coastline of Kenya and examined potential causes of these differences using the concept of environmental settings.

Chapter Three

Materials and Methods

3.1 Description of Study Area

The Kenyan coastline stretches over 600 km along the seafront, from the Kenya-Somalia border at Ishakani in the north (1.7°S; 41.5°E) to the Kenya-Tanzania border at Vanga in the south (4.7°S; 39.2°E) (Government of Kenya, 2017). The coastline features sandy beaches, estuaries, protected bays, tidal creeks and a semi-continuous fringing reef system. These areas support the natural growth of mangrove forests (GoK, 2017). The study focused on mangrove ecosystems in 14 sites spread across the five counties of the Kenyan coastline (**Fig. 2**).
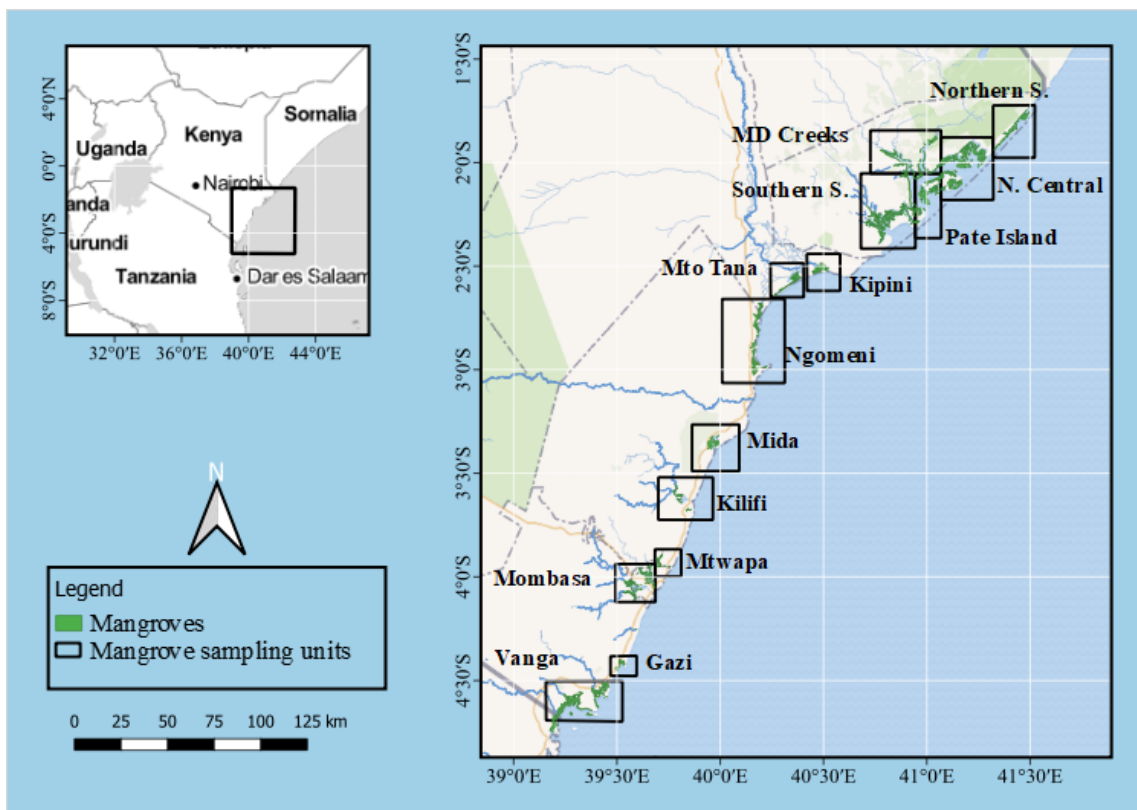
Fig. 2: The 14 study sites along the coast of Kenya. Northern S denotes Northern Swamps; N. Central- Northern Central Swamps; MD Creeks- Mongoni-Dodori Creek Swamps; Southern S- Southern Swamps

Study sites were located in Lamu County at Northern Swamps, Northern Central Swamp, Mongoni-Dodori Creek Swamp, Pate Island Swamp, and Southern Swamp; in Tana River County (Kipini and Mto Tana); Kilifi County (Ngomeni, Mida, Kilifi and Mtwapa); Mombasa County; and Kwale County (Gazi and Vanga) (**Fig. 2**).

The total area of mangroves in Kenya is estimated at 61,271 ha; more than 60% of which occur in Lamu County (GoK, 2017). Kenya's National Mangrove Ecosystem Management Plan (2017-2027) identifies 14 mangrove management units in Kenya (**Fig. 2**). Five of these units – hereafter referred to as 'sites' are in Lamu County: Northern Swamps, Northern Central Swamps, Mongoni and Dodori Creek Swamps, Pate Island Swamps, and Southern Swamps. Three of the sites are in Tana River County: Kipini, Mto Tana, and Ngomeni, while three sites are in Kilifi County: Mida, Kilifi, and Mtwapa. Mombasa County is classified as one unit, while Kwale County has two sites: Gazi and the Vanga-Funzi system (GoK, 2017). This study maintained this classification scheme for ease of reference and comparisons.

The Vanga and Gazi sites are sheltered bays separated by the Shimoni Peninsula with the Vanga site located at the mouth of River Umba. The Mombasa, Mtwapa and Kilifi sites are peri-urban systems characterised by narrow creeks whose origins are drowned river valleys. The Mida site has a similar morphology to Mombasa, Mtwapa and Kilifi but lacks a discharging river/stream. The Ngomeni, Mto Tana and Kipini sites are located in Ungwana Bay, a wide bay in front of the River Tana Delta that is characterised by fringing dune complexes. The Southern Swamps, Pate Island Swamp, Mongoni-Dodori Creeks, Northern Central Swamps and the Northern Swamps sites are in the coastal lagoons and multiple small islands that define the Lamu Archipelago (Oosterom, 1988; Tychsen & Klinge, 2006; GoK, 2017; Government of Kenya, 2017).

3.1.1 Geomorphology

The coastline of Kenya can be broadly classified into three regions on the basis of geomorphology; the northern region, the central region, and the southern region (Oosterom, 1988). **The northern region** lies mainly in Lamu and Tana River Counties and parts of Kilifi County spanning from the Kenya-Somalia border to the mouth of the Sabaki river. It is characterized by wide open bays, reef patches and sheltered lagoons.

The wide, open bays are found in front of the Tana Delta, commonly known as the Ungwana Bay/ Formosa Bay, and near the mouth of the Sabaki River. In between these open bays, the reef patches and sheltered lagoons occur. The open bays are bordered by long beaches and high dune complexes and hence this section can be referred to as a lagoon-barrier and dune ridge coast. The presence of the two perennial rivers (Tana and Sabaki) is one of the reasons why this section is different from the other two sections along the Kenyan Coastline and this is largely as a result of the continuous sediment supply to the shore (Oosterom, 1988; Tychsen & Klinge, 2006; ASCLME, 2012).

The central region lies in Mombasa County and parts of Kwale and Kilifi Counties spanning from just below the mouth of the Sabaki river down to the region between Gazi and Mombasa. This section is characterized by a straight fringing coral reef and has the outward appearance of a cliffed coral reef coast due to the steep cliffs on the landward side. The reef is divided into various segments by narrow tidal outlets of branching bays and/or estuaries. The presence of a continuous reef complex and the presence of steep cliffs in this section can be explained by the protection of the littoral zone by the prominent hills of the coastal range and also by the absence of perennial rivers in the section. The presence of the Giriama Hills and other elevated areas of the coastal range coupled with the lack of perennial rivers have protected the littoral zone from the effects of strong fluvial erosion and sedimentation (Oosterom, 1988; Tychsen & Klinge, 2006; ASCLME, 2012).

The southern region lies in Kwale County spanning from Gazi Bay all the way down to the Kenya-Tanzania border. This section is characterized by wide sheltered bays that lie behind a broken chain of coral reef patches and has the general appearance of an embayed coral reef. In this section, we have three rivers of intermittent discharge namely the Ramisi River, The Umba River and the Mwena River. The character of this drainage system partly explains the difference in configuration of the Northern and Southern regions of the Kenyan coastline. In the northern region, the Tana and Sabaki rivers have a greater discharge and sediment load than the seasonal rivers in the southern region and this in turn has effects on mangrove growth and development (Oosterom, 1988; Tychsen & Klinge, 2006; ASCLME, 2012).

3.1.2 Climate

The Kenyan coast lies in a hot tropical region whose climate system is dominated by the large-scale monsoonal influences of the Western Indian Ocean (Government of Kenya, 2017). It has two distinct monsoon periods, the South East Monsoon between March to May characterized by cooler temperatures and relatively stable weather and the North East Monsoon between October and December which is comparatively dry. Subsequently, annual rainfall follows a strong seasonal pattern with high amounts of rainfall between late March and early June and another peak between October and November rapidly decreasing between October and November (Government of Kenya, 2017). Mean annual total rainfall ranges also vary along the coast ranging from between 500-900 mm yr^{-1} in the North to between 1000-1600 mm yr^{-1} in areas south of Malindi (ASCLME, 2012) (**Fig. 3**). Mean daily temperature ranges between 24-30 ºC while humidity averages about 80% throughout the year (Government of Kenya, 2017).
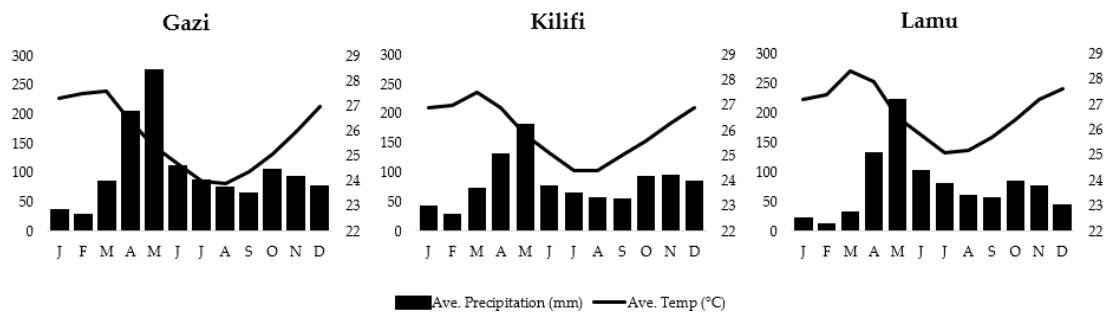
Fig. 3: Average precipitation (mm) and average temperatures (ºC) across three selected sites. Source: KMD, 2020

3.1.3 Oceanography

The tidal regime also varies with swells reaching maximum heights of 6 m during the north east monsoon, and 8 m during the south east monsoon with wave height dropping significantly to 2.5 m during the calm conditions of the inter-monsoon period (March-April). The dominant monsoon-driven currents of the Kenyan Coast are the East Africa Coastal Current (EACC), the Somali Current (SC) and the Equatorial Counter Current (ECC) (Tychsen & Klinge, 2006). The EACC flows northward throughout the year with the width of 160-200 km and a maximum depth of about 400m. The SC is a seasonally reversing current, flowing northward during the SEM and later flowing southward during

the NEM (**Fig. 4**). The reversed Somali Current meets the EACC to form the eastward flowing ECC which flows as an undercurrent (Government of Kenya, 2017). This causes upwellings that are responsible for increased productivity in the north Kenyan coast (Kamau et al., 2020).
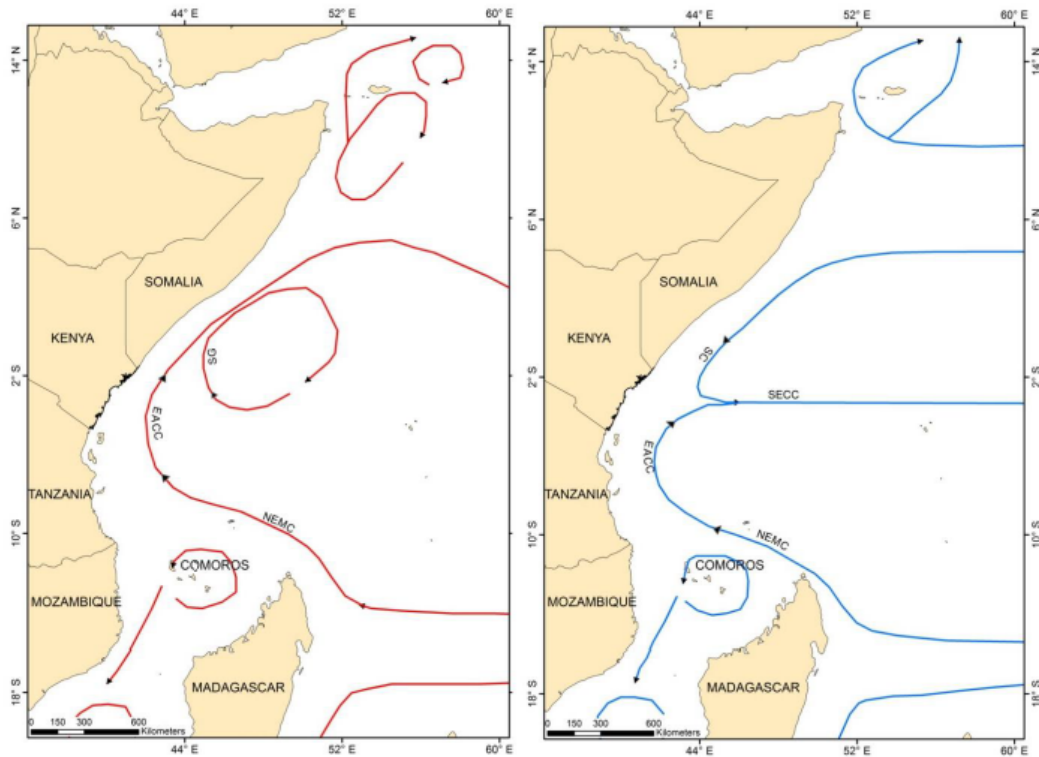
Fig. 4: Major Ocean Currents in the Indian Ocean off the coast of Kenya during SEM (red) and NEM (blue). Source: GoK, 2017.

3.1.4 Hydrology and Drainage

The hydrology of the coast is based on the drainage patterns of perennial and seasonal rivers into the Indian Ocean basin. Two perennial rivers drain into the Indian Ocean, River Tana and the Sabaki River and discharge from the rivers is highly seasonal (**Fig. 5**). Tana River drains into the Indian Ocean near Kipini in north coast of Kenya with a freshwater discharge of about 4 billion cubic meters per year and an annual sediment load of about 6.8 million tonnes (Kitheka et al., 2003). The river branches into a complex deltaic system that opens to the Indian Ocean at Kipini and Mto Tana sites. Several dams have been constructed along the Tana River for hydroelectric power generation and these have

modified the flow and the sediment load of the river (Kitheka et al., 2003). The Sabaki River empties into the Indian Ocean near Malindi town with a freshwater discharge of about 2 billion cubic meters per year and an annual sediment load of between 5 to 13 million tonnes. This is mainly because the river is not dammed (Kitheka et al., 2003, 2005). Both Tana and Sabaki rivers experience a bimodal hydrological cycle. Rainfall peaks in May and November in line with the long and short rainy seasons (Kitheka et al., 2005).

Seasonal rivers that drain into the Indian Ocean are the Mwatate, Mwache and Manjera rivers that rise in the Mwatate Basin in the Taita Hills drain into Port Reitz in Mombasa and the Kombeni and Tsalu rivers discharge into Port Tudor of the Mombasa site. The Rare River, a minor stream of the Voi river, is an intermittent stream that drains into Kilifi Creek. The Ndzovuni River, another intermittent stream also drains into Kilifi. The Ramisi river, with an intermittent discharge, drains into the Ramisi/ Funzi area of Kwale, between the Vanga and Gazi sites. The Umba river that rises in the Pare and Usambara mountains in Tanzania has an intermittent discharge and drains into Vanga in Kwale County. Mwena river, a minor stream of the Umba river also drains into the area.

Several freshwater aquifers are distributed along the coastal area of Kenya mainly within the sedimentary terrains. The largest aquifer system stretches from the north eastern parts of the country in Marsabit and terminates in Lamu, spanning about 250 km, part of which is the Merti aquifer (Kuria, 2013). Other aquifers are the Tiwi and Msambweni aquifers in the southern parts of the coast that stretch over 80 km along the coastline (Mwango et al., 2004; Kuria, 2013; Nijsten et al., 2018; Oiro & Comte, 2019). These aquifers are considered important in maintaining groundwater seepage into mangrove forests (Nijsten et al., 2018) though information on this remains scanty.
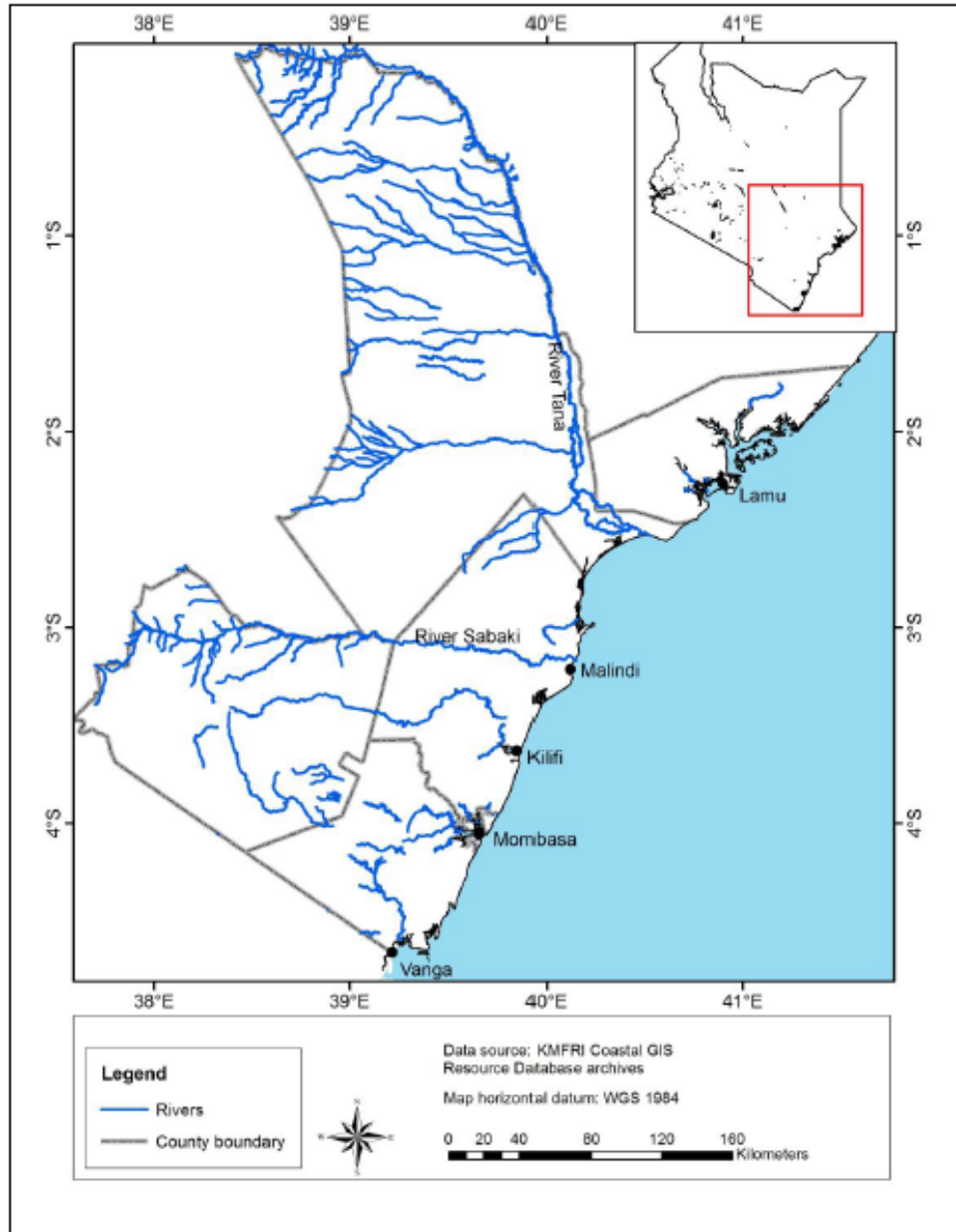
Fig. 5: Drainage networks along the coast of Kenya (Source: GoK 2017).

3.1.5 Demography

The coastal counties of Kenya have about 3.9 million inhabitants which is about 8.4% of Kenya's total population (Kenya National Bureau of Statistics, 2019a, 2019b). More than 60% of this population resides in Mombasa and Kilifi counties. Kilifi County has the highest population along the coast with about 1.4 million inhabitants. Mombasa county

has the highest population density with 5,495 persons per km^2. It is the largest urban centre in the coast with 97 % of the population dwelling within the city. Tana River County has the lowest population density with 8 persons per km^2 (Kenya National Bureau of Statistics, 2019a, 2019b). It is estimated that about 70% of communities living adjacent to mangroves derive their wood requirements from the forest (GoK, 2017).

3.2 Field Sampling & Data Collection

Field assessments on the structural characteristics of mangrove trees were conducted according to the standard, globally-applied "protocols for the measurement, monitoring and reporting of structure, biomass and carbon stocks in mangrove forests" (Kauffman & Donato, 2012). The structural characteristics of mangroves in the 14 sites were assessed using a systematic random sampling design. Belt transects running perpendicular to the shoreline were randomly established. Plots measuring 20 m by 20 m were systematically established along these transects to capture the variability resulting from the zonation of mangroves. Across all the sites, a total of 372 plots were established, representing an overall sampling intensity of 0.3%. Within each plot, all individual mangrove trees with a diameter at breast height (DBH) $\geq$ 2.5 cm were identified and counted. Data on tree height (m) and stem diameter (cm) were collected following the procedures outlined by Kauffman & Donato (2012).

The basal area (BA) of each species; the sum of the cross-sectional areas (CSA) of all trees of the species at breast height, was calculated using equation 1:

$$Basal\ Area\ (m^2\ ha^{-1}) = \frac{Sum\ of\ Cross\ Sectional\ Area}{Plot\ area\ (m^2)} \times 10,000 \qquad (1)$$

The stem density; the number of stems per plot divided by the area of the plot, was calculated using equation 2:

$$Stem\ density\ (trees\ ha^{-1}) = \frac{No.of\ stems\ in\ plot}{Plot\ area\ (m^2)} \times 10,000 \qquad (2)$$

The importance value (IV) of each species; a measure of the relative contribution of each species to the structure of the stand, was calculated using equation 3:

$$IV = relative\ density + relative\ frequency\ + relative\ dominance \qquad (3)$$

The complexity index (CI) of each study site was calculated using equation 4:

$$CI = Number\ of\ species \times basal\ area \times stand\ density \times tree\ height \qquad (4)$$
$$\times 10^{-5}$$

Above-ground biomass (Mg ha^{-1}) was calculated using equation 5:

$$Biomass = 0.251 \times wood\ density\ value\ of\ species\ \times tree\ diameter^{2.46} \qquad (5)$$

We used localised species-specific wood density for the mangroves of Kenya developed by Gillerot et al. (2018) (**Table 2**).

Table 2: Localised species-specific wood density values for the mangroves of Kenya. (Adapted from Gillerot et al., 2018)

Mangrove Species	Wood Density Value
Rhizophora mucronata	0.88
Bruguiera gymnorhiza	0.84
Ceriops tagal	0.85
Sonneratia alba	0.58
Avicennia marina	0.76
Lumnitzera racemosa	0.82
Xylocarpus granatum	0.71
Xylocarpus moluccensis	0.82
Heritiera littoralis	0.84

3.3 Site Classification

To compare the drivers of mangrove variability, mangrove sites were described based on environmental settings, average annual precipitation, population density, and river influence (**Table 3**). The environmental settings described in this study were modified to suit the various landforms of the Kenyan coast. The following categories were adopted: estuarine coasts are sheltered coasts with one or more rivers flowing into them and with a free connection to the open sea and included the Vanga and Mombasa sites; lagoonal

coasts are shallow inland water bodies that are separated from the ocean by a barrier and include the Gazi, Southern Swamps, Pate Island Swamps, and Northern Central sites; tidal creek coasts feature a narrow inlet or estuary that is affected by the flow and ebb of ocean tides and include Mtwapa, Kilifi, Mida, Mongoni-Dodori Creek and Mto Tana sites; deltaic coasts are areas of high river influence with sediment accumulating at the mouth of the river and include Ngomeni and Kipini sites; while open coasts were relatively exposed coasts that are only sheltered from the sea by minor reef segments and reef patches such as the Northern Swamps site.

Table 3: Description of major environmental settings used in the study.

Environmental setting	Description	Major mangrove sites
Estuarine Coasts	Sheltered coasts with one or more rivers flowing into them and with a free connection to the open sea	Vanga, Mombasa
Lagoonal coasts	Shallow inland water bodies that are separated from the ocean by a barrier	Gazi, Southern Swamps, Pate Island Swamps, Northern Central Swamps
Tidal creek coasts	Narrow inlet or estuary that is affected by the flow and ebb of ocean tides	Mtwapa, Kilifi, Mida, Mongoni-Dodori Creek, Mto Tana
Deltaic coasts	Areas of high river influence with sediment accumulating at the mouth of the river	Ngomeni, Kipini
Open coasts	Coasts that are not sheltered from the sea	Northern Swamps

The key characteristics of the sampled sites are summarised in **Table 4**. The average annual rainfall data (1995-2015) was accessed from the Seasonal Climate Analysis map room tool by Kenya Meteorological Department available through this link: (http://kmddl.meteo.go.ke:8081/maproom/Climatology/). The population density was the population density per square kilometre in the administrative units where the mangrove sites occur sourced from the Kenya National Bureau of Statistics (Kenya National Bureau

of Statistics, 2019a, 2019b). The influence of the river on the sites was described in an ordinal scale based on the freshwater discharge levels of the rivers draining into the site. The data was sourced from the environmental sensitivity atlas for the coastal area of Kenya (ASCLME, 2012).

Table 4: Key characteristics of the sampled sites: Environmental settings, Annual average precipitation (mm), Population density per square meter, and River Influence. Southern S denotes Southern swamps, MD Creeks- Mongoni Dodori Creeks, N Central- Northern Central Swamps.

Site	Environmental Setting	Annual Ave. Precipitation (mm)	Population density (persons per sq. km)	River Influence*
Vanga	Estuarine Coast	1109	311	Low
Gazi	Lagoonal Coast	1236	115	Low
Mombasa	Estuarine Coast	1050	6964	Moderate
Mtwapa	Tidal Coast	1090	1627	None
Kilifi	Tidal Coast	954	676	Low
Mida	Tidal Coast	930	537	None
Ngomeni	Deltaic Coast	979	676	High
Mto Tana	Tidal Coast	575	22	Moderate
Kipini	Deltaic Coast	947	58	High
Southern S	Lagoonal Coast	960	77	Low
Pate Island	Lagoonal Coast	960	229	None
MD Creeks	Tidal Coast	960	10	None
N Central	Lagoonal Coast	863	136	None
Northern	Open Coast	560	5	None

*River influence is based on the freshwater discharge levels of the rivers present in a site. High represents a discharge greater than 215 million m^3; moderate (100-215 million m^3); low (<100 million m^3); no influence represents lack of a discharging river.

3.4 Data Analysis

Graphical presentation of data was used to describe the structure of mangroves in Kenya. Multivariate analyses were performed to examine the differences in species composition across the sites based on species abundance. An analysis of similarities (ANOSIM) using the Bray-Curtis similarity index was performed followed by a pairwise post-hoc test with a Bonferroni correction to examine variability in species composition across the sites. The data matrix consisted of the standardized abundance of each tree species at different size-class categories in each site. A percent similarities analysis (SIMPER) was used to determine which tree species contributed the most to the differences found. These differences were then illustrated using a non-metric multidimensional scaling (nMDS) ordination plot. The nMDS was plotted in two dimensions (2D) using the Bray-Curtis similarity index. The structural data was subjected to normality tests before performing a Box-Cox transformation. A One-way Analysis of Variance (ANOVA) followed by a post-hoc Tukey pairwise test was performed ($p<0.05$) to individually compare DBH, height, basal area and stand density and above-ground biomass across the different sites. A hierarchical cluster analysis (unweighted paired group mean average and squared Euclidian distances) was then performed to determine the degree of similarity of species from the 14 sites based on complexity index, biomass, DBH and height. A multiple linear regression with a stepwise selection method was used to fit a model describing associations between standing biomass and the possible drivers of variability (environmental settings, precipitation, population density, and riverine influence). The software, OriginPro 9.0, was used to develop the graphical presentations of the structural data while the multivariate analyses were performed using Paleontological Statistics software (PAST 4) and Minitab 18.

Results

4.1 Species Composition.

All nine mangrove species present in the country were encountered in the study. A total of 34,050 mangrove trees were sampled across various sites in the study. *Rhizophora mucronata* was the most important species in 11 out of the 14 sites studied (78.6%) (**Fig. 6**).

Avicennia marina was the most important species in the estuarine area of Ungwana Bay, which features the Mto Tana and Kipini sites. *Ceriops tagal* was the second most important species across 10 out of the 14 sites (71.4%). A few *Xylocarpus moluccensis* trees were exclusively observed in Mombasa while *Heritieria littoralis* stands were only encountered in Kipini. The *Xylocarpus granatum* of Ngomeni had the highest average DBH at 18.54 ± 1.42 cm while *Sonneratia alba* of Northern Central Swamps were the tallest with a mean height at 14.52 ± 0.25 m. The importance value index (IVI), mean DBH (cm), mean height (m) and mean basal area (m^2 ha^{-1}) of the mangrove species encountered across the sampled sites are detailed in **Appendix 1**.
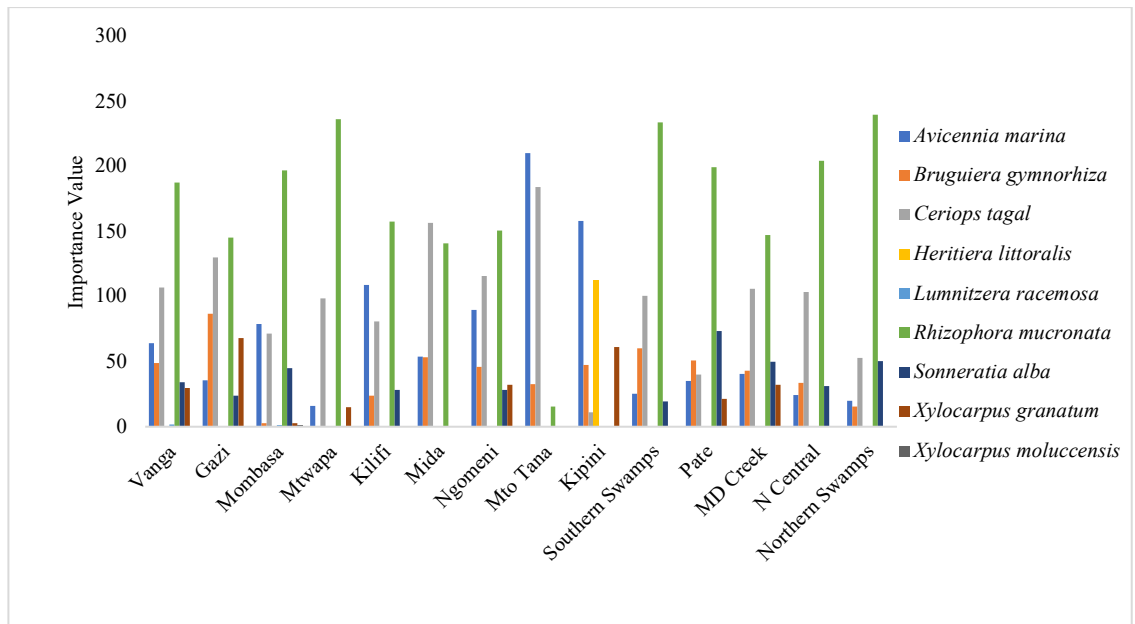
Fig. 6: Importance value (IV) of mangrove species sampled across the sites. MD Creek denotes Mongoni-Dodori Creeks, N Central- Northern central Swamps

Mangrove forest species composition differed significantly across the sampled sites (ANOSIM R: 0.24, p = 0.001). The pairwise post-hoc test with a Bonferroni correction shows Kipini as being significantly different from all the other sampled sites (**Appendix 2**). The ordination plot from the nMDS shows little grouping of sites with the exception of Kipini that appears to form a cluster (**Fig. 7**).
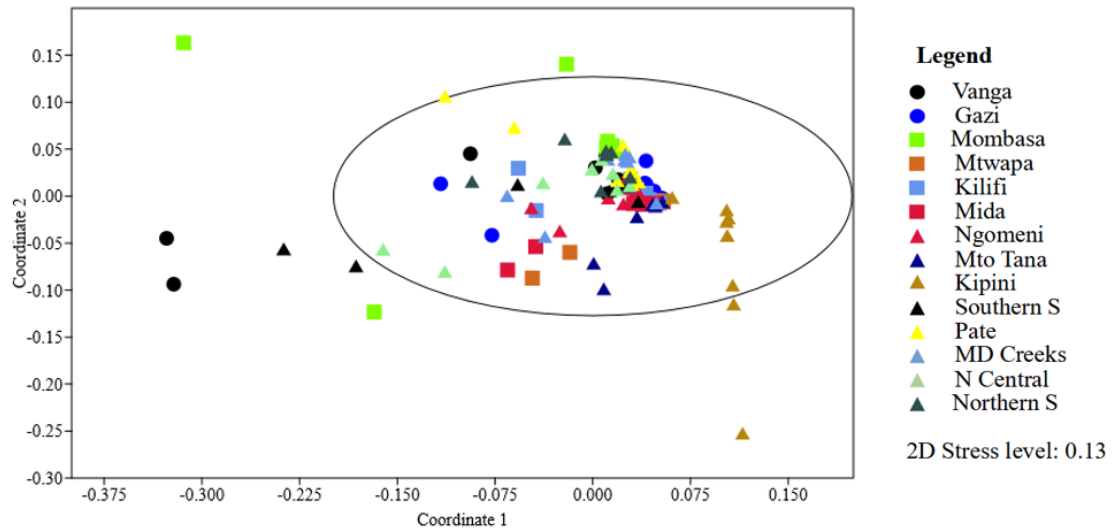
Fig. 7: Non metric multidimensional scaling (nMDS) of sites in two dimensions (2D) based on species abundance. The ellipse shows the 95% confidence interval. The stress level is 0.1304. Southern S is Southern Swamps, MD Creeks is Mongoni-Dodori Creeks, N Central is Northern Central Swamps and Northern S is Northern Swamps.

Table 5: Average dissimilarities and species contributions (percentage contribution and cumulative percentage) to dissimilarity across the 14 sites along the coastline of Kenya as assessed with SIMPER

Taxon	Average dissimilarity	Contribution (%)	Cumulative %
Sonneratia alba	4.395	20.05	20.05
Ceriops tagal	4.306	19.64	39.69
Avicennia marina	3.11	14.18	53.87
Bruguiera gymnorhiza	2.978	13.58	67.46
Rhizophora mucronata	2.473	11.28	78.74
Xylocarpus granatum	2.135	9.739	88.48
Heritiera littoralis	1.672	7.628	96.11
Lumnitzera racemosa	0.6135	2.798	98.91
Xylocarpus moluccensis	0.24	1.095	100

Based on the SIMPER analysis, *Sonneratia alba* (20.1% contribution), *Ceriops tagal* (19.64% contribution) and *Avicennia marina* (14.18% contribution) contributed more than half (53.87%) of the differences observed across the sites (**Table 5**).

4.2 Mangrove Structural Characteristics across the Sites

4.2.1 Mangrove Diameter and Height

The mean values of DBH and height for the different 14 blocks were calculated and reported as mean ± standard error (**Table 6**). The highest mean DBH was recorded for the mangroves of Northern Swamps in Lamu (10.95 ± 0.16 cm) while the mangroves of Mtwapa recorded the lowest mean DBH at 4.29 ± 0.05 cm (**Table 6**).

Table 6: Mean Diameter at Breast Height (DBH) (cm), mean Height (m), and mean aboveground biomass (AGB) (Mg/ha) of the 14 mangrove sites sampled along the coast of Kenya. Values are reported as mean ± standard error. The grouping information from the post-hoc Tukey pairwise comparison post-hoc test at 95% confidence level is reported alongside each variable -the means that do not share a letter are significantly different.

Site	Mean DBH (cm)	Group[*]	Mean Height (m)	Group[*]	Mean AGB (Mg ha⁻¹)	Group[*]
Vanga	7.05 ± 0.09	ef	5.21 ± 0.05	f	199.9 ± 28	cde
Gazi	6.28 ± 0.18	g	4.29 ± 0.10	h	171.9 ± 34.7	defg
Mombasa	5.55 ± 0.06	h	4.21 ± 0.03	h	**76.77 ± 9.61**	f
Mtwapa	**4.29 ± 0.05**	i	**3.06 ± 0.03**	i	89.2 ± 13.4	g
Kilifi	6.53 ± 0.18	fg	3.97 ± 0.09	h	141.9 ± 28.3	cdef
Mida	5.89 ± 0.13	gh	4.89 ± 0.06	g	150.7 ± 27	ef
Ngomeni	8.09 ± 0.22	c	6.04 ± 0.08	e	287.6 ± 70.6	b
Mto Tana	5.95 ± 0.15	gh	4.13 ± 0.10	h	91.2 ± 31.4	fg
Kipini	9.53 ± 0.30	b	7.26 ± 0.14	d	**358 ± 106**	a
Southern Swamps	7.20 ± 0.08	def	5.03 ± 0.03	fg	229.3 ± 21	cde
Pate Island Swamps	9.45 ± 0.21	b	9.71 ± 0.09	b	258.5 ± 36.5	b
MD Creek	7.80 ± 0.18	cd	9.43 ± 0.08	b	183 ± 21.3	bcd
Northern C Swamps	7.42 ± 0.11	de	**11.54 ± 0.06**	a	205.1 ± 21.5	bc
Northern Swamps	**10.95 ± 0.16**	a	7.92 ± 0.09	c	238.5 ± 19.4	a

Generally, the mangroves growing north of the Sabaki river, except the mangroves of Mto Tana, had high mean DBH values (>7 cm) (**Fig. 8**). A similar trend was observed with mean height of the trees (**Fig. 9**).

*means that do not share a letter are significantly different
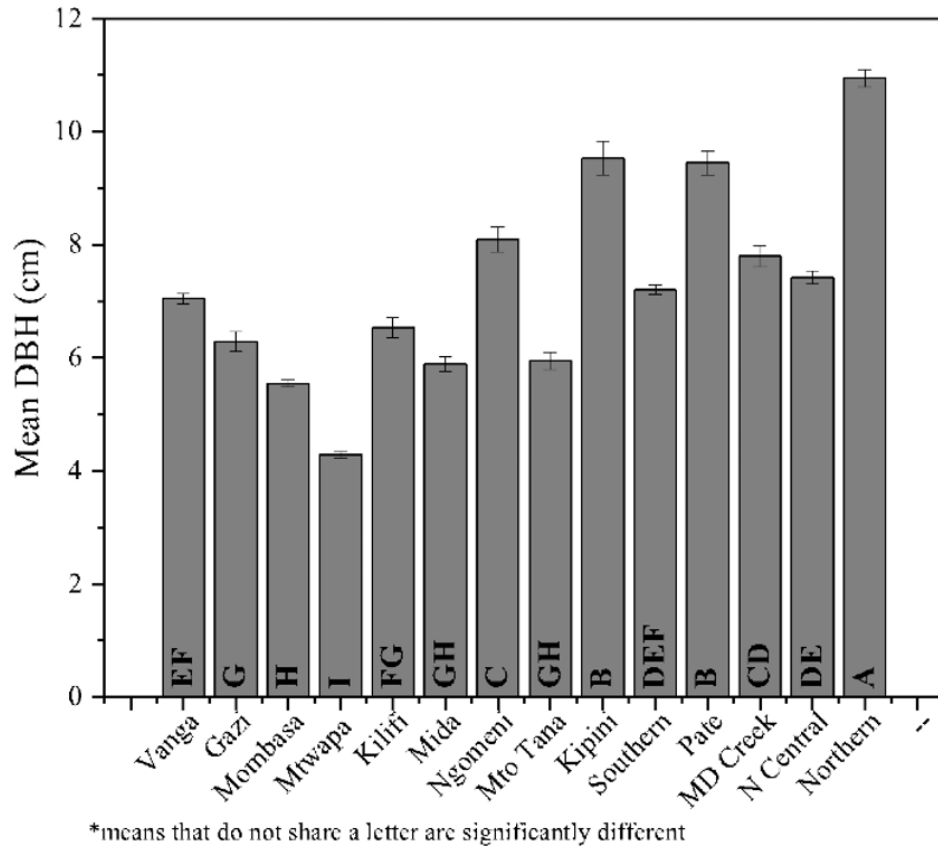
Fig. 8: Mean Diameter at Breast Height (DBH) (cm) of the 14 mangrove sites sampled along the coast of Kenya. Values are reported as mean ± standard error. The grouping information from the post-hoc Tukey pairwise comparison post-hoc test at 95% confidence level is reported alongside each variable -the means that do not share a letter are significantly different. Southern is Southern swamps, MD Creek is Mongoni Dodori Creek, N Central is Northern Central swamps, Northern is Northern swamps

There were significant differences in DBH at p <0.05 between the blocks [F (13, 34050) =163.01, p=0.000]. The lowest mean height for mangrove trees was recorded in Mtwapa (3.06 ± 0.03 m) while the mangroves of Northern Central Swamps in Lamu had the tallest trees on average with a mean height of 11.54 ± 0.06 m. There were significant differences in mean height at p <0.05 between the blocks [F (13, 34050) =1827.28, p=0.000].
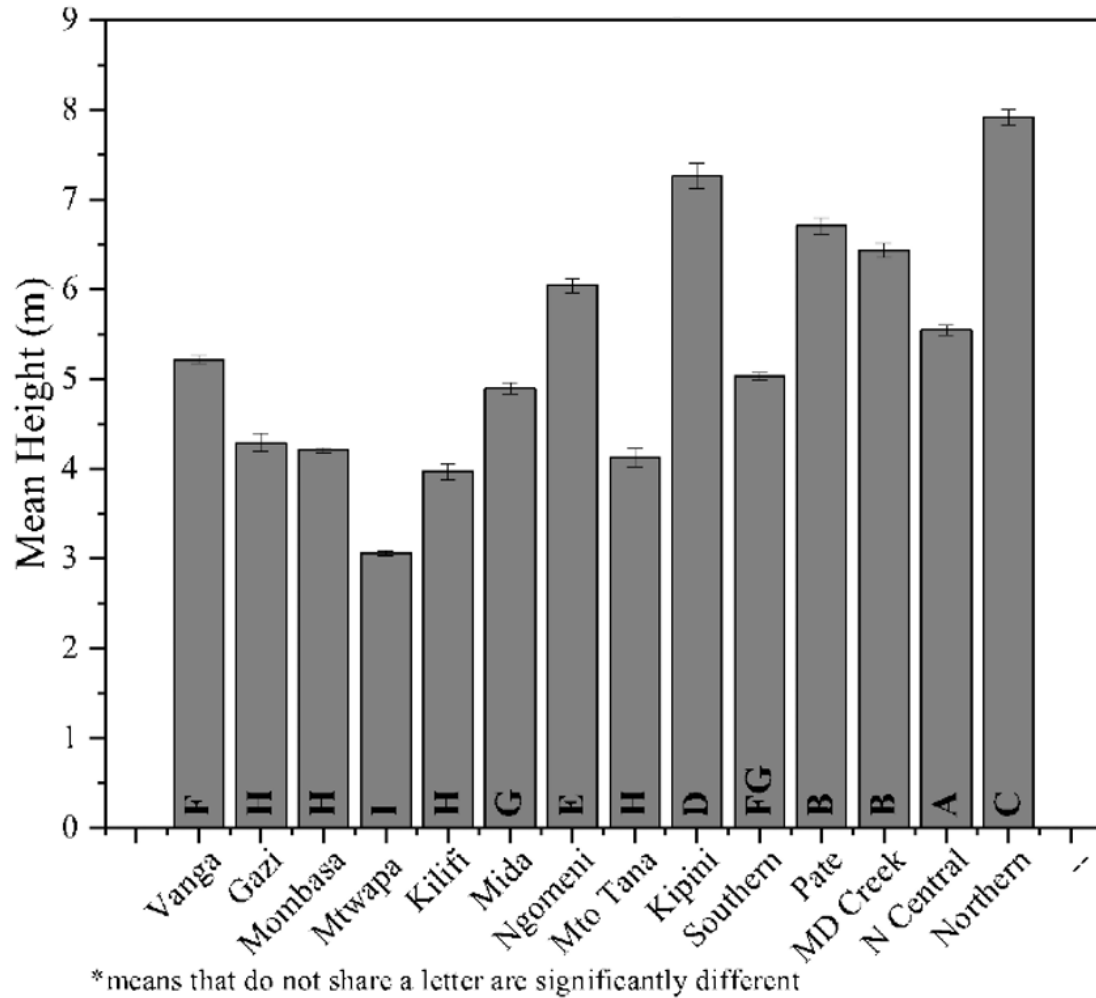
Fig. 9: Mean Tree Height (m) of the 14 mangrove sites sampled along the coast of Kenya. Values are reported as mean ± standard error. The grouping information from the post-hoc Tukey pairwise comparison post-hoc test at 95% confidence level is reported alongside each variable -the means that do not share a letter are significantly different. Southern is Southern swamps, MD Creek is Mongoni Dodori Creek, N Central is Northern Central swamps, Northern is Northern swamps

Mean DBH had a positive correlation with mean height with a Pearson correlation coefficient (r) of 0.668 (p=0.009). Mean DBH also had a strong correlation with biomass (r=0.814, p=0.000) and basal area (r=0.777, p=0.001). Additionally, tree DBH was plotted against tree height in every block on a scatterplot and regression analysis performed to obtain the coefficient of determination (R^2) (**Fig. 10**).
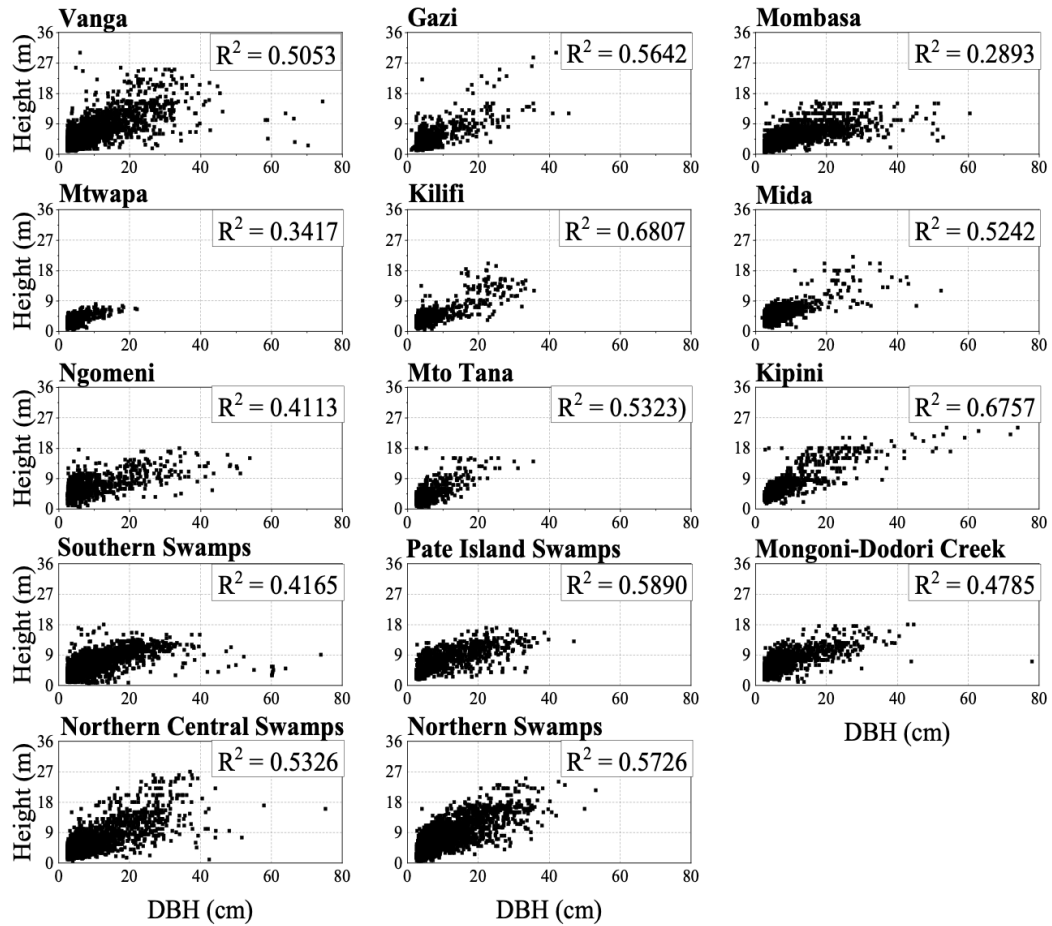
Fig. 10: Height-Diameter distribution of mangrove forests in the 14 sampled sites along the coast of Kenya. R^2 is the coefficient of determination from regression analysis

4.2.2 Stand Density, Basal Area & Complexity Index

The lowest stand density was recorded for the mangroves of Northern Swamps at 1607 ± 129 trees per ha while the highest stand density was for the mangroves of Mtwapa at 7856 ± 2094 trees per ha. There were significant differences in stand density at $p<0.05$ between the blocks [F (13, 358) =8.68, p=0.000]. Stand density was negatively correlated with mean DBH (r = -0.688, p=0.006).

The mean basal area of the mangrove forests was generally high (>15 m² ha⁻¹) for most sites except Mombasa, Mtwapa and Mto Tana (**Table 7**). The mangrove forest of Kipini had the highest mean basal area at 29.78 ± 6.46 m² ha⁻¹ while Mombasa had the lowest

mean basal area at 8.70 ± 0.831 m^2 ha^{-1}. There were significant differences in mean basal area at $p<0.05$ between the sites [F (13, 358) =5.45, p=0.000].

The mangrove forest of Pate Island Swamps was the most structurally complex with a complexity index of 35.79 while the mangrove forest of Mto Tana had the lowest complexity index at 5.15 (**Table 7**). Patterns in complexity index along the sites were similar to the pattern observed for mangrove mean basal area (m^2 ha^{-1}), mean tree DBH (cm) and mean tree height (m). The low complexity index of the forest of Mto Tana exposes the inherent issues affecting the mangroves of this system (**Table 7**).

Table 7: Number of species encountered during the study, mean basal area (m^2/ha), stand density (trees per ha) and complexity Indices (CI) of the 14 sites sampled across the coast of Kenya.

Site	Number of Species	Basal Area (m^2 ha^{-1})	Stand Density (trees ha^{-1})	CI
Vanga	7	19.76 ± 2.26	2987 ± 279	21.54
Gazi	6	20.75 ± 3.60	3730 ± 561	19.92
Mombasa	8	**8.70 ± 0.83**	2113 ± 154	6.19
Mtwapa	4	14.05 ± 2.20	**7856 ± 2094**	13.51
Kilifi	5	15.71 ± 2.25	3418 ± 627	10.65
Mida	4	16.05 ± 1.90	4913 ± 826	15.43
Ngomeni	6	26.06 ± 5.62	3179 ± 554	30.02
Mto Tana	4	11.40 ± 2.90	2739 ± 749	**5.15**
Kipini	5	**29.78 ± 5.88**	2164 ± 391	23.40
Southern Swamps	5	21.69 ± 1.48	3092 ± 213	16.86
Pate Island Swamps	6	26.70 ± 3.38	2302 ± 315	**35.79**
Mongoni Dodori Creek	6	18.44 ± 1.76	2169 ± 296	22.56
Northern Central Swamps	5	19.44 ± 1.42	2496 ± 272	28.00
Northern Swamps	5	22.57 ± 1.47	**1607 ± 129**	14.35
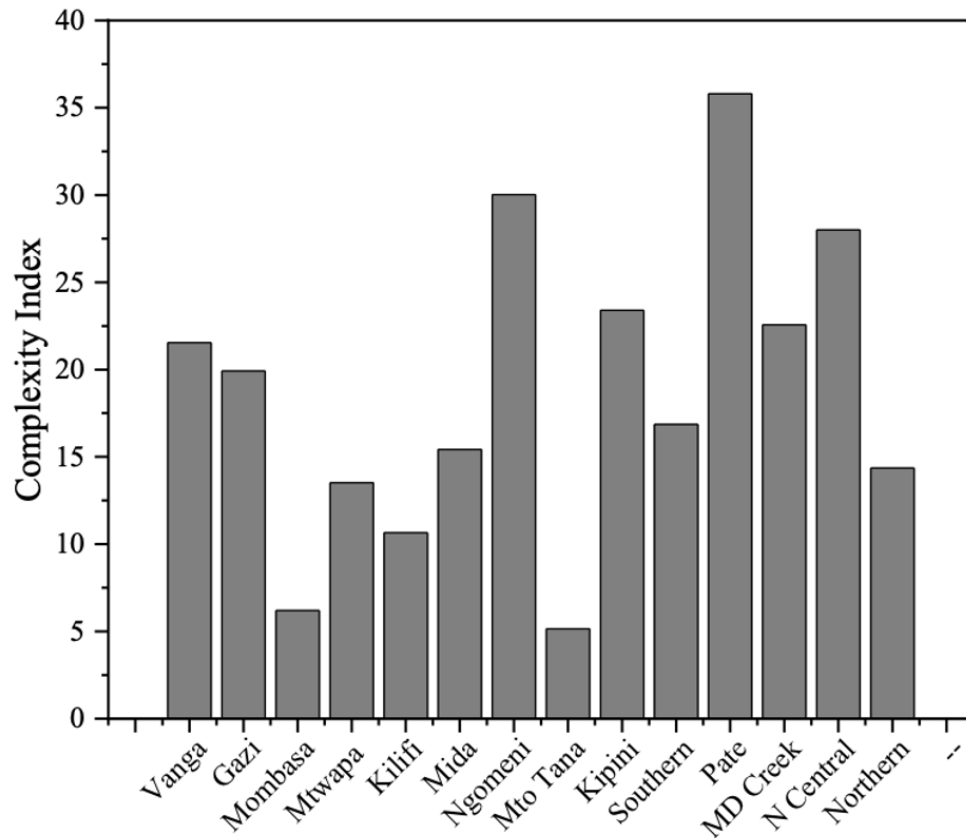
Fig. 11: Bar graph illustrating complexity index values across the sampled sites. Southern is Southern Swamps, MD Creek is Mongoni-Dodori Creek, NC is Northern Central Swamps, Northern is Northern swamps.

4.2.3 Above-ground Biomass

The mangroves of Mombasa had the lowest mean above-ground biomass (AGB) at 76.77 ± 9.61 Megagrams per hectare (Mg ha^{-1}) while the mangroves of Kipini had the highest mean above-ground biomass at 358 ± 106 Mg ha^{-1} (**Fig. 12**). There were significant differences in AGB at $p < 0.05$ between the sites [$F_{(13, 358)} = 15.36$, $p = 0.000$].

The mean above-ground biomass for mangroves growing in the Northern region (Ngomeni, Mto Tana, Kipini, Southern Swamps, Mongoni-Dodori Creek, Pate Island Swamp, Northern Central Swamp and Northern Swamp) was 232.66 ± 12.9 Mg/ha. Those growing in the central region (Mombasa, Mtwapa, Kilifi and Mida) had a mean AGB of 97.17 ± 8.7 Mg/ha while those in the southern region had a mean AGB of 195.13 ± 23.9.

There were significant differences at p<0.05 between the three regions [F (2, 369) = 27.01, p = 0.000]. Post-hoc tests revealed the mangroves growing in the central region were significantly different from those growing in the northern and southern regions.
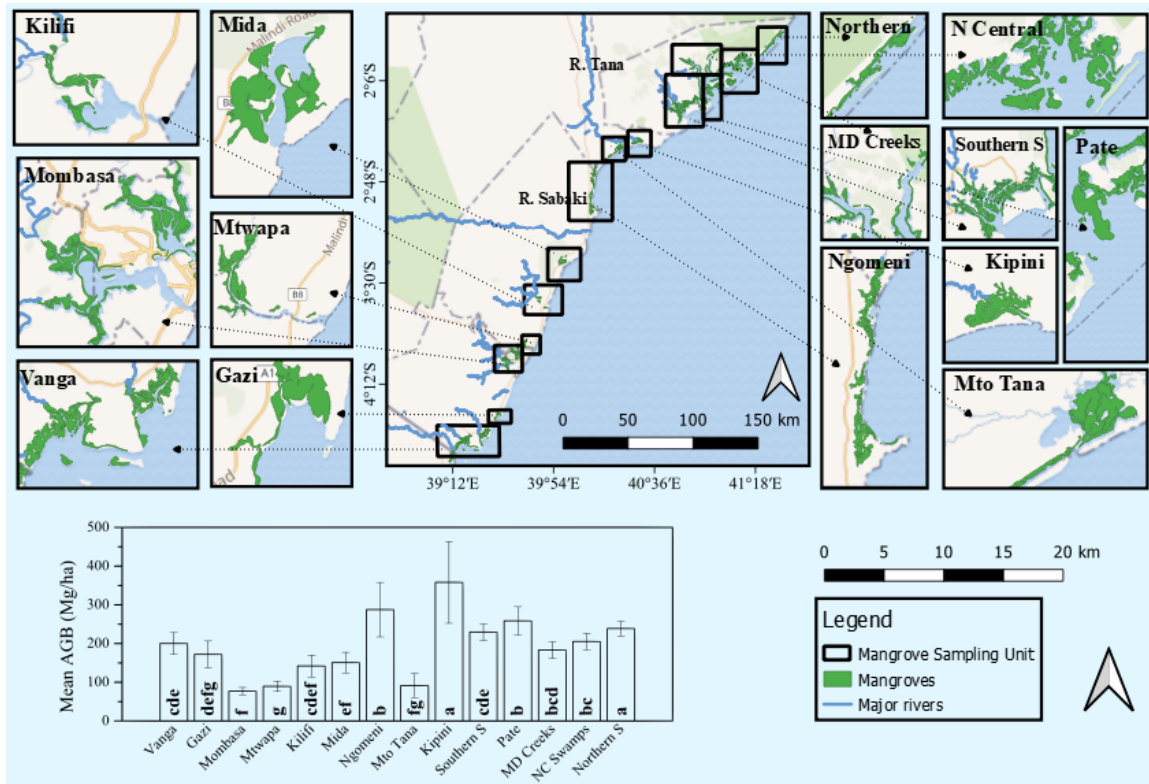
Fig. 12: Map of the 14 mangrove sampling sites along the coast of Kenya featuring mean aboveground biomass (Mg/ha) in each site. The error bars are standard error bars and the letters denote the grouping information from the Tukey Pairwise Comparison Post-hoc test at 95% confidence level -the means that do not share a letter are significantly different. Southern is Southern swamps, MD Creek is Mongoni Dodori Creek, NC is Northern Central swamps, Northern is Northern swamps

4.3 Cluster Analysis & Regression Analysis

The hierarchical cluster analysis using unweighted paired group mean average and squared Euclidian distances on mean AGB (Mg/ha) revealed distinct groupings across the mangrove sites (**Fig. 13**). Kipini, the site that recorded the highest standing biomass, was significantly different from the rest of the sites. Kipini had a unique mangrove floristic composition and had the highest mean standing biomass observed in the study. Mombasa, Mto Tana and Mtwapa, were also shown to be significantly different from the rest of the

sites. These sites had the lowest values of standing biomass and complexity indices recorded in the study. Kilifi and Mida sites, both located in Kilifi County in the central region of the coastline were shown to be similar. These sites share some similarities with the sites of Northern Central swamps, Vanga, Gazi and Mongoni-Dodori creeks, located in the northern and southern regions of the coastline. Ngomeni, Pate Island Swamps, Southern Swamps and Northern Swamps, all located north of the Sabaki river, were also shown to be similar. The multiple linear regression analysis indicated environmental settings and population density best explained the variability in standing biomass. The fit regression model explained 86.74% of the variance in standing biomass.
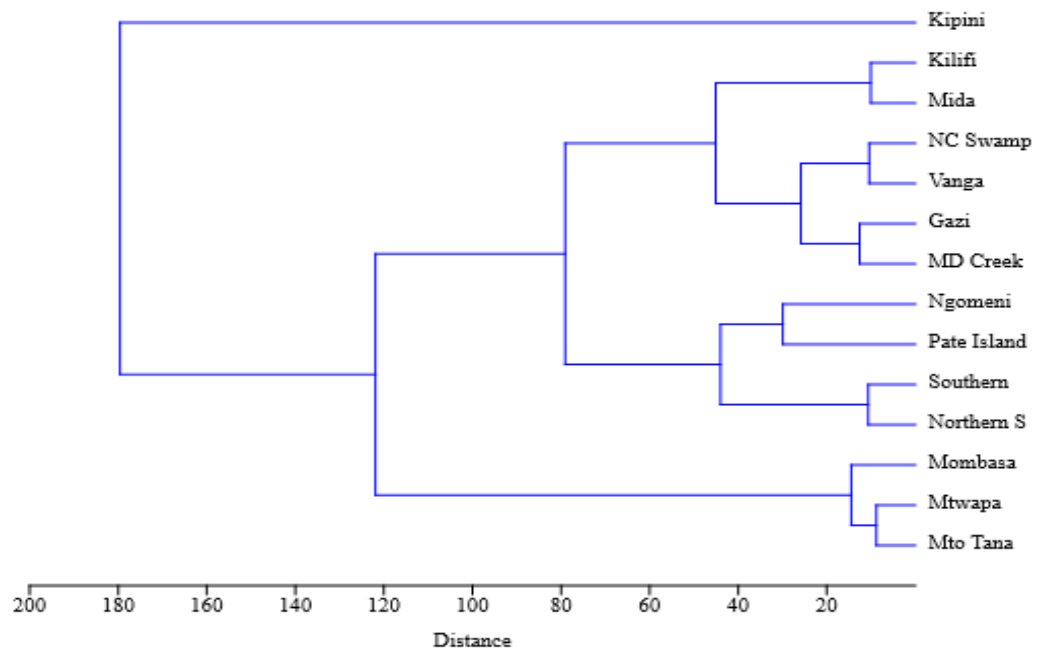
Fig. 13: Dendrogram from the hierarchical cluster analysis across the 14 sampling sites along the coast of Kenya using unweighted paired group mean average and squared Euclidean pairwise distances. Southern is Southern swamps, MD Creek is Mongoni Dodori Creek, NC is Northern Central swamps, Northern is Northern swamps

Chapter Five

Discussion, Conclusion and Recommendations

5.1 Discussion

This study revealed significant differences in mangrove forest structure along the coast of Kenya. High values of standing biomass and structural complexity were observed in the riverine mangroves of the Tana Delta as well as mangroves found in the protected islands of Lamu Archipelago in the northern parts of the coastline. High values of standing biomass were also observed within the sheltered bays of the southern parts of the coastline. In the central region characterised by drowned river valleys, a fringing coral reef and peri-urban settings, relatively lower levels of standing biomass and structural complexity were observed. These patterns of mangrove structural variability closely follow the patterns of geomorphological variability along the coastline. Similar studies carried out on the mangroves of Kenya report an average standing biomass of 119 Mg/ha (Fatoyinbo & Simard, 2013) and 150 Mg/ha (Hutchison et al., 2014). The current study reported a mean standing biomass of 182.86 Mg/ha for the mangroves of Kenya which is close to earlier reported figures, considering these values are from remotely sensed data.

Mangroves in the northern region of Kenya are influenced by the interplay between run-off from River Tana, hydrodynamics and air-sea interactions (Kamau et al., 2020). During the south east monsoon (SEM), high levels of sediment and nutrients are deposited from the Tana and Sabaki rivers into the ocean which creates a pool of nutrients (Kitheka et al., 2005; Kitheka & Mavuti, 2016). This results in elevated nutrient concentrations within the Sabaki estuary and the Tana delta. Nutrient availability is key in enhancing mangrove growth and productivity (Tomlinson, 2016). However, it is probably the maintenance of balance between mineral nutrients and substrate salinity that is relevant, rather than the absolute nutrient levels (Tomlinson, 2016). For instance, the *Heriteria littoralis* dominated forest of the Kipini site at the mouth of River Tana receives copious amounts of freshwater, sediment and nutrients from the hinterland leading to higher productivity and overall biomass (Kitheka et al., 2005; Kitheka & Mavuti, 2016) Conversely, the scrub mangroves growing in the Mto Tana site are majorly composed of dwarf trees due to low freshwater and sediment supply. Currently, the River Tana flows directly into an estuary

at Kipini rather than in the complex system of channels and distributaries leading to its old mouth at Mto Tana. The little freshwater that still flowed into the old delta through the Kalota brook was blocked through the construction of a multi-purpose community dam in 1988 to push the freshwater into their fields and irrigate their crops (Oosterom, 1988). This, together with the presence of solar salt works around the area has ultimately limited mangrove growth in the site.

In the sites north of the Tana river (Southern swamps, Pate Island Swamps, Mongoni-Dodori Creek, Northern Central Swamps and Northern Swamps), the northern flowing EACC moves nutrient rich sediment from the estuaries of the Tana and Sabaki rivers though long-shore transport and is responsible for high productivity in the area (Kamau et al., 2020). These nutrients are later resuspended as the system is perturbated during the north east monsoon (NEM) when the north flowing EACC meets the south flowing Somali Current (SC) causing upwelling and nutrient enrichment (Kamau et al., 2020). The presence of groundwater seepage in the area is another factor that could be driving the productivity of mangroves in the area by providing freshwater into the system (Mwango et al., 2004; Kuria, 2013; Oiro & Comte, 2019). The management system could also be responsible for the luxuriant growth of mangroves in some parts of Lamu. The Northern Swamps mangroves and some parts of Northern Central Swamps fall under the Kiunga Marine National Reserve (KMNR), where commercial exploitation of mangroves is prohibited (Kairo et al., 2002). This could explain the high DBH values observed in KMNR.

Compared to the northern parts of the coastline, nutrient levels in Ramisi and Umba river systems in the southern region are relatively low (Oosterom, 1988). The differences in the sediment loading, nutrient levels and freshwater input between the river systems of the northern and southern regions explains the different levels of productivity between the northern and southern parts of the coastline of Kenya (Oosterom, 1988). In the Vanga area, small, persistent, localized upwelling events occur around the narrow zonal strip that extends between Northern Pemba Island and the mainland, right at the border between Kenya and Tanzania during the NEM. These upwelling events are as a result of the instabilities of the EACC around the chain of islands (Mafia, Unguja and Pemba) and

along the continent's lateral boundary (Halo et al., 2020). Halo et al. (2020) suggest that these upwelling events occur on-shore throughout the annual cycle and are evident by the development of near shore negative wind stress curls and consequent positive Ekman vertical velocities during the NEM. The presence of an intermittent stream (Mkurumudji river), ground water aquifers (the Tiwi and Msambweni aquifers) (Nijsten et al., 2018), as well as intensive community-based mangrove conservation activities could explain the high structural complexity of mangroves in the Gazi site. The carbon offset project, Mikoko Pamoja in Gazi has played a role in the restoration and protection of mangroves in the area (Kairo et al., 2018).

On the other hand, the mangroves in the central region are influenced by the geomorphology of the area as well as human influences. In this region, the transition of the littoral to the paralic zone is marked by a broken chain of prominent hills of the coastal range. The elevated areas of the coastal range and the Giriama hills lands have protected the littoral zone against strong fluvial erosion and sedimentation. This is evident by the development of a continuous reef complex in the littoral zone of the central region (Oosterom, 1988). This coupled with the absence of perennial rivers partly explains the low biomass observed in the mangroves of this region comprising of Mtwapa, Kilifi and Mida. The availability of terrigenous sediments plays a crucial role not only in providing nutrients necessary for mangrove growth but also in providing the necessary accommodation space for mangrove colonization. For instance, the mangroves of Mtwapa and Kilifi occur in an area characterized by steep cliffs on the margin of the land and the ocean with a narrow tidal zone. Hence, there is limited accommodation space available for mangrove colonization.

The dominance of *Ceriops tagal* in Mida resulting from past selective logging of desirable *Rhizophora mucronata* trees (Kairo, 2001) could possibly explain the lower values of standing biomass. *Ceriops tagal* has a relatively lower DBH and mean height compared to the *Rhizophora mucronata* and *Avicennia marina* that dominate the rest of the sites (**Appendix 1**). Overharvesting of mangrove wood products influences the structure of mangrove forests. Unplanned exploitation of mangrove forests could alter the community structure of these forests as the forest moves from a mature forest to a young forest as a

result of the open canopy. Clear-cutting has the potential to alter the overall integrity of the mangrove habitats by altering hydrological patterns and sediment characteristics. The peri-urban mangroves in Mombasa are mainly threatened by human stressors such as overharvesting, habitat conversion, pollution and sedimentation (Mohamed et al., 2009). High values of mangrove standing biomass were observed in estuarine and deltaic sites as well as in sites located in Lamu County (**Table 8**).

Mangroves are facultative halophytes and are more productive in riverine systems with high inputs of freshwater and nutrients (Tomlinson, 2016). There is evidence of longshore transport of nutrients to the mangroves of Lamu area deposited from the Tana and Sabaki rivers (Kamau et al., 2020). This demonstrates linkages between mangrove structural properties and geomorphologically-defined habitats as described by the concept of environmental settings (Thom, 1984; Woodroffe, 1987; Woodroffe, 1993; Worthington et al., 2020). However, relatively lower values of mangrove standing biomass were also recorded for some sites within similar estuarine settings such as Mombasa and Mto Tana. While these areas should have supported high levels of mangrove productivity, the lower biomass values observed could be explained by the presence of human-induced stressors that act to limit mangrove growth and productivity (Mohamed et al., 2009; Oosterom, 1988). This shows that in addition to the interactions between ecological and geomorphological processes, human influence is also a key factor in driving mangrove forest structure in Kenya. A fitting explanation of mangrove structural variability would have to include the feedback processes resulting from the interactions between the forest and the communities living around them. This includes influences that improve the conservation of mangroves (positive feedback) as well as influences that degrade the mangrove ecosystem (negative feedback).

Twilley (1995, 2019) explains that the amount of structure that develops in a mangrove system will be determined by the net energy available to the system – the difference between the energy available to the system – solar, chemical (organic matter and nutrient input) and mechanical energy (wind, tides and waves) and the energy required for maintenance or for overcoming stress- hyper salinity, drought, and actual biomass removal through harvesting. All external factors of coastal systems could be evaluated in

the form of energy and measured in units of energy such as kilocalories or joules and this could be useful in explaining and predicting patterns of mangrove structural development in Kenya. This presents an opportunity for future research.

Table 8: Summary attribute table describing the environmental settings, forcing functions and structural properties of mangroves along the Kenyan coast. (1) denotes the number of species encountered in each site, (2) is basal area (BA) (m^2 ha^{-1}), (3) is canopy height (m), (4) is stand density (SD) (trees ha^{-1}), (5) is standing/aboveground biomass (AGB) (Mg ha^{-1}), (6) is complexity index (CI). Basal area, canopy height, stand density and standing biomass are reported as mean ± standard error. Southern is Southern swamps, MD Creek is Mongoni Dodori Creek, NC is Northern Central swamps, Northern is Northern swamps.

Site	Environmental Setting	Mangrove structural properties					
		(1) Species	(2) BA	(3) Height	(4) SD	(5) AGB	(6) CI
Vanga	Estuarine coast	7	19.7 ± 2.2	5.2 ± 0.1	2987 ± 279	199.9 ± 28	21.5
Gazi	Lagoonal Coast	6	20.8 ± 3.6	4.3 ± 0.1	3730 ± 561	171.9 ± 34.7	19.9
Mombasa	Estuarine Coast	8	**8.7 ± 0.8**	4.2 ± 0.0	2113 ± 154	**76.8 ± 9.61**	6.2
Mtwapa	Tidal Creek	4	14.1 ± 2.2	**3.1 ± 0.0**	**7856 ± 2094**	89.2 ± 13.4	13.5
Kilifi	Tidal Creek	5	15.7 ± 2.3	4.0 ± 0.1	3418 ± 627	141.9 ± 28.3	10.7
Mida	Tidal Creek	4	16.1 ± 1.9	4.9 ± 0.1	4913 ± 826	150.7 ± 27	15.4
Ngomeni	Deltaic coast	6	26.1 ± 5.6	6.0 ± 0.1	3179 ± 554	287.6 ± 70.6	30.0
Mto Tana	Deltaic Coast	4	11.4 ± 2.9	4.1 ± 0.1	2739 ± 749	91.2 ± 31.4	**5.2**
Kipini	Deltaic Coast	5	**29.8 ± 5.9**	7.3 ± 0.1	2164 ± 391	**358 ± 106**	23.4
Southern	Lagoonal Coast	5	21.7 ± 1.5	5.0 ± 0.0	3092 ± 213	229.3 ± 21	16.9
Pate Island	Lagoonal Coast	6	26.7 ± 3.4	9.7 ± 0.1	2302 ± 315	258.5 ± 36.5	**35.8**
MD Creek	Tidal Creek	6	18.4 ± 1.8	9.4 ± 0.1	2169 ± 296	183 ± 21.3	22.6
NC	Lagoonal Coast	5	19.4 ± 1.4	**11.5 ± 0.1**	2496 ± 272	205.1 ± 21.5	28.0
Northern	Open Coast	5	22.6 ± 1.5	7.9 ± 0.1	**1607 ± 129**	238.5 ± 19.4	14.4

[*]CI is equal to: number of species (a) × basal area (b) × stand density (c) × canopy height (d) × 10^{-5}

Mangroves contribute to national carbon emissions and are key players in emissions reduction. Mangrove forests sequester proportionally more carbon than terrestrial systems. While the bulk of this carbon is held within the sediment and the soil, the loss of mangroves and resulting disturbance of the soil horizon either through the direct removal of biomass or land use changes such as conversion of mangrove areas to aquaculture ponds results in extremely high losses with CO_2 equivalent emissions averaging 1802.2 Mg ha^{-1} annually (Kauffman et al., 2018). The current study finds that some mangrove forests in Kenya such as those in estuarine and deltaic settings and the mangroves in the Lamu archipelago have high levels of structural complexity and standing biomass and could potentially form great sites for conservation and management programs such as carbon offset schemes that could further enhance their conservation and provide co-benefits to local communities. However, some of the mangrove habitats in Kenya are threatened by increased population pressure especially the peri-urban mangroves of Mombasa and Mtwapa and this has the potential to reverse the gains resulting from mangrove conservation in other parts of the country. Some of the soil organic carbon that is decomposed as a result of disturbances is returned to the atmosphere as CH_4. CH_4 has a higher global warming potential than CO_2. High CH_4 emissions from mangrove forests can partially offset the CO_2 removed via blue carbon burial by an average of 20% (Rosentreter et al., 2018). These strong anthropogenic influences suggest that reducing disturbances on mangrove forests is instrumental in reducing carbon emissions. Hence, the conservation and restoration of these mangrove ecosystems will play a huge role in mitigating and adapting to climate change.

5.2 Conclusion and Recommendations

Mangrove forests in Kenya that grow in estuarine and deltaic settings exhibit the highest levels of structural complexity. These forests were different from those growing in other areas. Along the coastline, the patterns of mangrove structural variability closely follow the patterns of geomorphological variability. These differences in mangrove structure are statistically significant and they are highly influenced by geomorphological and climatic variability, and the past and present management regimes of the forest.

This spatial variability in structure, species diversity, abiotic environments and even the threats that affect them and this means that a one-size-fits-all management strategy is inappropriate. The management of the mangroves in Kenya should be optimized based on the environmental settings under which they occur and the threats that affect them. From the study, the lowest levels of structural complexity were observed for the peri-urban mangroves of Mombasa and Mtwapa and the mangroves of Mto Tana. There is a particular need for safeguards to protect the peri-urban mangroves of Mombasa and Mtwapa that are under ever-increasing threat. Also, following the findings of the study, intervention measures need to be developed to restore the mangrove system of Mto Tana area. Current levels of protection, particularly through marine protected areas, appear to favour mangrove growth and productivity and therefore may be incentives to increase the coverage and/or the number of these protected areas in order to derive the co-benefits associated with healthy and productive mangrove systems.

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Appendices

Appendix I: Mean DBH (cm), Mean Height (m), Basal area ($m^2\ ha^{-1}$) and importance values (IV) of the various sampled species across the 14 sampled sites. SE is standard error.

Site	Species	Mean DBH (cm)	SE	Mean Height (m)	SE	Basal Area (m^2/ha)	IV
Vanga	*Avicennia marina*	7.71	0.39	4.51	0.18	132.97	64.24
	Bruguiera gymnorhiza	6.33	0.25	5.02	0.12	44.74	49.00
	Ceriops tagal	4.63	0.07	3.39	0.05	96.47	106.92
	Lumnitzera racemosa	3.40	0.35	1.43	0.07	0.07	1.95
	Rhizophora mucronata	7.63	0.13	6.06	0.07	**612.86**	**187.68**
	Sonneratia alba	**18.32**	0.99	**10.36**	0.45	129.58	34.04
	Xylocarpus granatum	7.18	0.34	5.01	0.15	30.78	29.75
Gazi	*Avicennia marina*	**16.41**	2.06	**8.81**	0.73	15.81	35.87
	Bruguiera gymnorhiza	7.94	0.46	5.11	0.26	31.54	87.11
	Ceriops tagal	4.22	0.08	2.75	0.05	30.30	130.40
	Rhizophora mucronata	7.60	0.48	6.53	0.33	**98.15**	**145.44**
	Sonneratia alba	11.41	1.14	6.28	0.37	22.25	24.04
	Xylocarpus granatum	8.65	0.84	5.24	0.35	30.15	68.05
Mombasa	*Avicennia marina*	10.55	0.39	5.69	0.13	178.44	78.99
	Bruguiera gymnorhiza	4.36	0.48	3.41	0.22	0.46	2.85
	Ceriops tagal	4.57	0.13	2.79	0.05	66.74	71.64
	Lumnitzera racemosa	7.55	0.25	3.20	0.40	0.22	1.37
	Rhizophora mucronata	4.57	0.05	4.07	0.03	**277.84**	**196.97**
	Sonneratia alba	**11.85**	0.33	7.11	0.13	145.23	45.24
	Xylocarpus granatum	4.68	0.67	3.52	0.51	0.63	2.89
	Xylocarpus moluccensis	6.50	0.50	**7.45**	0.05	0.17	1.36
Mtwapa	*Avicennia marina*	**11.65**	1.37	**5.03**	0.36	5.15	16.16
	Ceriops tagal	3.73	0.05	2.08	0.03	27.60	98.91
	Rhizophora mucronata	4.42	0.07	3.50	0.03	**91.23**	**236.70**
	Xylocarpus granatum	5.74	0.56	4.02	0.17	2.47	14.89
Kilifi	*Avicennia marina*	**9.93**	0.50	**5.52**	0.28	81.14	108.87
	Bruguiera gymnorhiza	4.09	0.32	3.15	0.21	1.28	23.76
	Ceriops tagal	3.77	0.06	2.08	0.04	17.84	81.18
	Rhizophora mucronata	6.49	0.29	4.43	0.12	**103.23**	**157.68**

Site	Species	Mean DBH (cm)	SE	Mean Height (m)	SE	Basal Area (m²/ha)	IV
	Sonneratia alba	8.67	0.66	4.89	0.21	16.44	28.50
Mida	*Avicennia marina*	11.37	0.98	5.61	0.22	**13.95**	53.86
	Bruguiera gymnorhiza	**11.93**	1.76	**7.08**	0.58	6.83	53.61
	Ceriops tagal	4.29	0.08	3.87	0.06	7.34	**156.59**
	Rhizophora mucronata	7.27	0.25	6.27	0.12	7.87	141.20
Ngomeni	*Avicennia marina*	11.36	0.78	5.46	0.21	**18.45**	89.90
	Bruguiera gymnorhiza	12.20	1.13	7.43	0.43	6.15	45.83
	Ceriops tagal	6.07	0.28	4.86	0.13	4.50	116.14
	Rhizophora mucronata	6.99	0.27	6.55	0.11	11.32	**150.72**
	Sonneratia alba	11.92	0.96	6.64	0.27	13.55	28.50
	Xylocarpus granatum	**18.54**	1.42	**7.81**	0.35	12.77	32.07
Mto Tana	*Avicennia marina*	7.11	0.25	4.28	0.17	**50.79**	**210.19**
	Bruguiera gymnorhiza	**9.61**	1.80	**8.09**	1.24	2.38	32.86
	Ceriops tagal	4.79	0.17	3.85	0.12	26.19	184.45
	Rhizophora mucronata	7.03	1.42	8.00	1.27	0.44	15.35
Kipini	*Avicennia marina*	7.75	0.23	6.61	0.14	105.10	**158.12**
	Bruguiera gymnorhiza	**16.59**	2.55	**10.59**	1.18	26.01	47.35
	Ceriops tagal	3.55	0.19	4.33	0.14	0.50	11.24
	Heritiera littoralis	13.85	0.96	9.11	0.40	**151.03**	112.99
	Xylocarpus granatum	10.32	1.02	6.96	0.34	44.91	61.21
Southern Swamps	*Avicennia marina*	6.89	0.31	3.59	0.13	31.48	25.15
	Bruguiera gymnorhiza	8.13	0.53	4.85	0.12	68.44	60.47
	Ceriops tagal	4.76	0.09	3.21	0.04	97.36	100.74
	Rhizophora mucronata	8.02	0.11	5.81	0.04	**735.87**	**234.07**
	Sonneratia alba	**12.40**	0.75	**7.69**	0.25	42.75	19.56
Pate Island	*Avicennia marina*	12.64	0.83	10.76	0.35	30.59	35.35
	Bruguiera gymnorhiza	4.89	0.14	7.32	0.09	13.58	50.98
	Ceriops tagal	4.49	0.29	7.21	0.21	2.39	40.23
	Rhizophora mucronata	9.18	0.27	9.99	0.12	**190.65**	**199.72**
	Sonneratia alba	**16.34**	0.80	**12.20**	0.26	100.24	73.63
	Xylocarpus granatum	14.94	1.20	10.76	0.43	36.32	21.51

Site	Species	Mean DBH (cm)	SE	Mean Height (m)	SE	Basal Area (m²/ha)	IV
Mongoni-Dodori Creek	*Avicennia marina*	6.40	0.70	7.08	0.36	32.67	40.50
	Bruguiera gymnorhiza	7.17	0.96	8.75	0.40	7.58	43.10
	Ceriops tagal	6.67	0.23	8.91	0.10	56.28	105.90
	Rhizophora mucronata	7.05	0.28	9.70	0.11	**107.80**	**147.33**
	Sonneratia alba	**14.40**	0.59	**12.00**	0.22	64.22	49.90
	Xylocarpus granatum	12.70	1.03	11.31	0.36	26.41	32.03
Northern Central Swamps	*Avicennia marina*	10.35	1.08	9.76	0.26	61.81	24.15
	Bruguiera gymnorhiza	10.65	1.03	12.08	0.30	28.87	33.94
	Ceriops tagal	5.24	0.08	10.03	0.05	106.78	103.71
	Rhizophora mucronata	8.14	0.16	12.52	0.09	**467.67**	**204.26**
	Sonneratia alba	**15.48**	0.75	**14.52**	0.25	92.95	31.38
Northern Swamps	*Avicennia marina*	9.64	0.65	4.78	0.17	24.71	19.93
	Bruguiera gymnorhiza	7.73	0.98	5.91	0.47	6.60	15.40
	Ceriops tagal	6.20	0.18	3.75	0.12	35.43	53.12
	Rhizophora mucronata	11.60	0.19	**9.09**	0.10	**653.74**	**239.98**
	Sonneratia alba	**14.13**	0.49	7.53	0.19	137.10	50.52

Appendix 2: Pairwise *p* value after Bonferroni correction showing the variability in species composition across the 14 sites along the coastline of Kenya as assessed with ANOSIM

	Vanga	Gazi	Mombasa	Mtwapa	Kilifi	Mida	Ngomeni	Mto Tana	Kipini	Southern	Pate	MD Creeks	N Central	Northern
Vanga		0.0217	0.0845	0.0009	0.0104	0.0011	0.0321	**0.0002**	**0.0001**	0.1558	0.2616	0.0902	0.1681	0.014
Gazi	0.0217		0.0008	0.0241	0.009	0.0148	0.1242	**0.0007**	**0.0004**	0.0196	0.0517	0.0639	0.0222	**0.0004**
Mombasa	0.0845	0.0008		**0.0007**	0.0284	0.0013	**0.0004**	0.0011	**0.0002**	0.0314	0.0047	0.0075	0.0482	0.0648
Mtwapa	0.0009	0.0241	**0.0007**		0.0037	0.062	0.0066	0.0168	**0.0002**	0.0013	0.0009	0.0076	0.0058	**0.0004**
Kilifi	0.0104	0.009	0.0284	0.0037		0.0192	0.0765	0.0951	**0.0005**	0.0203	0.006	0.0589	0.0418	0.0091
Mida	0.0011	0.0148	0.0013	0.062	0.0192		0.0306	0.0999	**0.0003**	0.0131	**0.0004**	0.0021	0.0252	**0.0005**
Ngomeni	0.0321	0.1242	**0.0004**	0.0066	0.0765	0.0306		0.0263	**0.0002**	0.0259	0.0088	0.0602	0.0169	0.0008
Mto Tana	**0.0002**	**0.0007**	0.0011	0.0168	0.0951	0.0999	0.0263		**0.0001**	0.001	**0.0001**	0.0034	0.0013	**0.0003**
Kipini	**0.0001**	**0.0004**	**0.0002**	**0.0002**	**0.0005**	**0.0003**	**0.0002**	**0.0001**		**0.0002**	**0.0001**	**0.0004**	**0.0001**	**0.0003**
Southern	0.1558	0.0196	0.0314	0.0013	0.0203	0.0131	0.0259	0.001	**0.0002**		0.0448	0.0365	0.4916	0.0334
Pate	0.2616	0.0517	0.0047	0.0009	0.006	**0.0004**	0.0088	**0.0001**	**0.0001**	0.0448		0.254	0.049	0.008
MDCreek	0.0902	0.0639	0.0075	0.0076	0.0589	0.0021	0.0602	0.0034	**0.0004**	0.0365	0.254		0.0709	0.0087
N Central	0.1681	0.0222	0.0482	0.0058	0.0418	0.0252	0.0169	0.0013	**0.0001**	0.4916	0.049	0.0709		0.1647
Northern	0.014	**0.0004**	0.0648	**0.0004**	0.0091	**0.0005**	0.0008	**0.0003**	**0.0003**	0.0334	0.008	0.0087	0.1647	