Alma Mater Studiorum - Università di Bologna

DOTTORATO DI RICERCA IN

Scienze della Terra, della Vita e dell'Ambiente

Ciclo XXXIII

Settore Concorsuale: 05/A1 - BOTANICA

Settore Scientifico Disciplinare: BIO/03 - Botanica Ambientale e Applicata

COASTAL FORESTS OF KENYA

ECOLOGY, BIODIVERSITY & CONSERVATION

Eastern Africa Coastal forests

Presentata da: Maria Mashirma Fungomeli

Coordinatore Dottorato
Prof. Giulio Viola

Supervisore
Prof. Alessandro Chiarucci

Esame finale anno 2021

Dedication

To my father, Mr Josphat Ezra Fungomeli, for his great wisdom, advice and support.

And to my sisters: Veronica, Pascalia, Justina; and brothers: Robert & Silvano; I will always remain your mother and big sister. With this study, may you be inspired to work hard and strive for the best.

Thank you, for the support and love that kept me going even in the darkest seasons away from the warmth of family, home, friends and country. **God Bless You All!**

To God, I give Glory & Thanks. In Him my Rock, I Believe & Trust.

There is a season for everything under the sun, and a time for every purpose…..Ecclesiastes 3:1

Just when the Caterpillar thought the World was over, it turned into a Butterfly…….

Alma Mater Studiorum - University of Bologna

Coastal Forests of Kenya

Ecology, Biodiversity & Conservation

PhD Thesis

Maria Mashirma Fungomeli

PhD in Earth, Life and Environmental Sciences

Settore Concorsuale: 05/A1 - Botanica

Scientific Discipline:
BIO/03-Applied & Environmental Botany

Supervised by
Prof. Alessandro Chiarucci

PhD Coordinator
Prof. Giulio Viola

Final Exam Year: 2021

Preface

This thesis is the result of a three-year PhD research study, as a collaboration between the University of Bologna in Italy and the National Museums of Kenya in Kenya. The overall study was supervised by Prof. Alessandro Chiarucci. This research has been a great, unique and a challenging platform for me to use *'new-scientific-research lenses'* to bring in new knowledge of a Kenyan coastal forest landscape that I have worked for over eight years in management and conservation under the Coastal Forests Conservation Unit at the National Museums of Kenya.

The study was based at the University of Bologna, with field research sampling visit done in Kenya at the coastal forests of Kenya from November 2018 to June 2019. The field work covered vegetation survey across 25 coastal forest fragments composed of 18 sacred forests and seven forest reserves. In addition to vegetation survey, butterfly survey was carried out only at the Arabuko Sokoke forest as a bio-indicator species of forest fragmentation. The aim was to investigate how plant species diversity influence butterfly diversity and composition. Butterfly farming is taking place in the Arabuko Sokoke forest as a species of conservation value and whose diversity is currently being utilised to support local community livelihoods and advance in the conservation of the forest.

During my PhD period, I participated and presented my work in several conferences, co-supervised students and peer-reviewed scientific articles in international journals as detailed in the research activity report for this thesis. This PhD study platform has greatly built and enhanced my ability in research and science. It has enhanced my confidence and capacity in learning and applying new concepts in ecology, phylogenetic diversity, knowledge of Kenyan coastal forests plant species identification and taxonomy, using statistical R and QGIS softwares, capacity to appropriately design and implement research field surveys. Additionally, it has enhanced my critical thinking, scientific writing skills and peer-review of papers. Importantly, it has enabled in delivering new knowledge and crucial outputs of the coastal forests of Kenya that will form a fundamental reference and application in the conservation strategies. This cements my continued work in these forests on the ecological sustainability, and biodiversity conservation over the long term.

Thesis Organization

This thesis is organised into two parts:

Part I: An overview as a general introduction to the coastal forests of Kenya and threats. It introduces the study area background, study aims, field sampling, study organization and phases.

Part II: The second part consists of seven chapters that are arranged according to research topics and questions and formatted in a structure and outline for publication in peer-reviewed scientific journals. ***Chapter 1*** and ***Chapter 2*** are already published in international peer-reviewed journals, ***Chapter 6*** and ***Chapter 7*** are submitted to journals while ***Chapter 5*** is ready for submission. Finally, ***Chapter 3***, and ***Chapter 4*** are undergoing review by co-authors nearing submission to journals. ***Chapter 1*** consists of a comprehensive review paper of the knowledge gaps of the coastal forests of Kenya. ***Chapter 2*** consists of a database paper of the large-standardised vegetation field sampling work that was done in Kenya and forms the basis of analysis and synthesis in the next chapters. ***Chapter 3*** **to** ***7*** consists of five analytical papers on: forest structure, composition and species diversity; species-area relationship; phylogenetic diversity; conservation-policy paper and vegetation determinants on butterfly diversity respectively. The field vegetation data used in this study is deposited at the sPlot-the Global vegetation database (https://www.idiv.de/en/splot.html) with restricted access for ongoing publishing. Nonetheless, all data description and sampling can be accessed at the Global Index of Vegetation-Plot Databases, Kenya coastal forests vegetation plot-database (https://www.givd.info/ID/AF-KE-001) and from the publication Fungomeli et. al. 2020 https://doi.org/10.3897/VCS/2020/47180. Finally, while I attended different courses during the PhD period, I was inspired by topics that I would wish to take on further with this data. This includes research topics in remote sensing and general detailed spatial analysis in ecology.

Maria Mashirma Fungomeli
April 2021, Bologna, Italy

"You don't have to be great to start, but you have to start to be great" - Zig Ziglar

TABLE OF CONTENTS

Abstract

Aims: the broad objective of this study is to investigate the ecological, biodiversity and conservation status of the coastal forests of Kenya. The coastal forests of Kenya are an intriguing biodiversity hotspot in tropical Africa, presenting rich biodiversity and high endemism. They now exist as indigenous forest islands with varying sizes (10 ha-42000 ha); and two management protection status of forest reserves and sacred forests. Locally, they support local livelihoods while playing a major role as high conservation value ecosystems. However, they face threats from increasing anthropogenic activities and climate change effects. Currently only 10% of the original forest cover is estimated to be left, while only 17% of these is under some kind of protection.

The specific aims of the study are:

(1) to investigate their current conservation status and quantitative trends in plant diversity; **(2)** develop a spatial and standardised vegetation database for the coastal forests Kenya; **(3)** to investigate forest structure, species diversity and composition across the forests; **(4)** investigate the effect of forest fragment area of plant species diversity across the Kenyan coastal forests; **(5)** investigate the phylogenetic diversity across these coastal remnants and within protection status of forest reserves and sacred forests; **(6)** assess vulnerability and provide conservation perspectives informed by our field data and bridge science to concrete policy issues; **(7)** investigate how plant species diversity influence butterfly diversity and composition to use butterflies as bio-indicator species of forest fragmentation.

Study area: Coastal forests of Kenya

Methods: In ***Chapter 1,*** I performed a comprehensive literature and systemic review of the woody plant species diversity of the coastal forests of Kenya. I classified the data into categories of: author and year of study, published or unpublished, survey technique used (plots or checklist) and forest site names. I further categorised forest sites into protection status of forest reserves and sacred forests, and plant species into life forms of trees, shrubs and lianas. I combined the reviewed data with our field sampled data. I performed Species-Area Relationship (SAR) using

the Arrhenius (1921) power function and the Gleason logarithmic model. In ***Chapter 2,*** I performed a field research sampling work in Kenya across forest fragments using 10m x 100m plot, and 5m x 100m subplots. I prepared the vegetation data, cleaned for spelling errors and synonyms, and standardized species taxonomy through The Plant List (www.theplantlist.org), World Flora Online (https://www.worldfloraonline.org) and African Plant Database (https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php/). In ***Chapter 3,*** I extracted environmental and climatic variables, analysed forest structure for basal area and tree stem density. I performed a non-metric multidimensional scaling (NMDS) with fit for environmental variables as vectors for species composition, and PERMANOVA to test for differences in species composition. Species diversity metrics of multiplicative beta diversity partitioning; species accumulation curve and species indicator analysis. I applied statistical tests for significant differences between sacred forests and forest reserves and across all forest sites for species richness and abundance. In ***Chapter 4,*** I calculated rarefaction of species richness to correct for sampling intensity, calculated multiplicative beta diversity and applied multiple regression models for species-area relationship and small island effect. In ***Chapter 5,*** I developed a plant species phylogeny and calculated the phylogenetic tree of the coastal forests of Kenya based on native species, calculated the phylogenetic diversity metrics: Phylogenetic diversity index (PD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), and calculated the null-models of the PD, MPD and MNTD using the independent swap algorithm, and standardised effect sizes (SES) randomization of observed to achieve standardized phylogenetic diversity (sesPD); standardized mean pairwise distance (sesMPD); standardized mean nearest taxon distance (sesMNTD). Statistical tests were applied for significant difference between sacred forests and forest reserves, and correlation models across phylogenetic diversity and threatened species categories; In ***Chapter 6,*** I evaluated and synthesized results of the above four chapters, and compared with existing literature to develop new conservation strategies and propose policy issues of the coastal forest of Kenya; In ***Chapter 7***, I carried out field work using plots measuring 10m x 100m for plants and butterfly diversity in Arabuko Sokoke forest. calculated species diversity metrics of Shannon diversity, Simpson index, and applied general linear regression models (GLM) and Non-metric multidimensional scaling (NMDS) with environmental fit variables, a symmetric Co-correspondence analysis (CoCA) to quantify relationships between plant species community with butterfly species community across the vegetation types. I applied analysis of similarities (ANOSIM) to test for species composition differences in the butterfly community structure among vegetation types and permutational analysis of variance (PERMANOVA) for significant differences between vegetation types, similarity percentages analysis (SIMPER) to determine butterfly species contributing to similarities across vegetation types, Pearson correlation, for butterfly wingspan sizes across vegetation types, and a statistical pairwise *t*-test to compare average wingspan sizes across the vegetation types.

Results: (1) Developed the first quantitative database of the coastal forests of Kenya consisting of 937 woody plant species across 30 forest fragments. There were biases in data scarcity, forest size and variation in sampling methods. **(2)** developed the first large standardised, spatial and geo-referenced vegetation database for the coastal forests of Kenya consisting of 600 plant species, recorded across 25 forest fragments using 158 plots subdivided into 3160 subplots. Overall, it includes 18 sacred forests and seven forest reserves with each forest characterised into details of forest area, geographical location and number of plots sampled per forest patch. (**3)** Species diversity and composition was significant different across forest sites, higher across forest sites (i.e., higher beta diversity) than within single forests, while sacred forests exhibited significant different forest structure, species diversity and composition than forest reserves. Biogeographic factors of elevation, distance from the coast and land use were a major driver of patterns of forest structure, composition and species diversity across the coastal forests of Kenya. (**4)** There was a strong correlation between rarefied and observed values of species richness and diversity. The species-area relationship (SAR) for forest fragment area explained significant variability of plant diversity, a small Island effect (SIE) was not evident across the fragments. **(5)** developed the first phylogenetic diversity (i.e., evolutionary history information) of the coastal forests of Kenya. The forest reserves are insufficient alone to protect the evolutionary history of the Kenyan coastal

forests without taking into account the sacred forests. Some sacred forests exhibited a higher phylogenetic diversity compared to forest reserves. The threatened Red List species contributed a higher evolutionary history of the coastal forests of Kenya and the evolutionary history increased as they become more threatened and extinct. **(6)** Existing conservation and policy gaps emerged as well as the need for conservation strategies and policy approaches founded on both scientific data and the rich biocultural heritage of these forests, emphasized the need for up-to-date scientific monitoring and scaling up protection status of the sacred forests for sustainable conservation is emphasized. **(7)** I recorded 6050 butterfly individuals (86 species, 38 genera and 5 families), and 178 plant species (78 genera and 34 families). A strong correlation between plant diversity and butterfly diversity, butterfly abundances were significant different across vegetation types, Mixed forest exhibited highest butterfly species while forest edge exhibited a higher average species richness and abundance. Main environmental drivers were rainfall of warmest quarter and temperature of warmest month, altitude and distance from the coast.

Conclusions: This study provides for the first time a standardized and large vegetation data and crucial new phase into the conservation of the coastal forests of Kenya. The high beta diversity, correlation to environmental variables and forest structure across forest fragments, suggests the need for a biogeographical conservation approach. Sacred forests exhibited higher forest structure, species composition and phylogenetic diversity, while some forest patches exhibited a higher phylogenetic diversity than taxonomic diversity emphasizing the need to improve protection status and enhance forest connectivity across forest reserves and sacred forests. The high correlation of plant diversity as a direct link to butterfly diversity displays the crucial role of plants in maintaining the rich butterfly diversity and other ecological factors within the Arabuko Sokoke forest and the synergic roles exhibited by the forest edge and mixed forest. The need to consider the forest edge in management strategies and include ecological corridors to enhance sustainable utilization of biodiversity and conservation.

Overview

1.0 General Introduction

1.0 Coastal forests of Kenya

The coastal forests of Kenya are African tropical forests that fall under the global biodiversity hotspots of the Eastern Africa Coastal Forests Biodiversity Hotspot, which includes the coastal forests of Kenya and Tanzania (Figure 1.0; Burgess and Clarke, 2000). Just like many tropical forests, they preserve a rich biodiversity globally. They are an intriguing biodiversity hotspot in the tropical African forest fragments, presenting rich biodiversity and high endemism, in a backdrop of increasing anthropogenic activities; high population; poverty; increased degradation and deforestation; not withstanding climate change effects and erosion of biocultural-traditional values within which over 90% of the Kenyan coastal forest fragments are anchored (Mittermeier et al., 2011; Githitho, 2016; Fungomeli et al., 2020a). Importantly, the Kenyan coastal forests harbour more than 50% of the national threatened and endemic plant species (Wass, 1995).

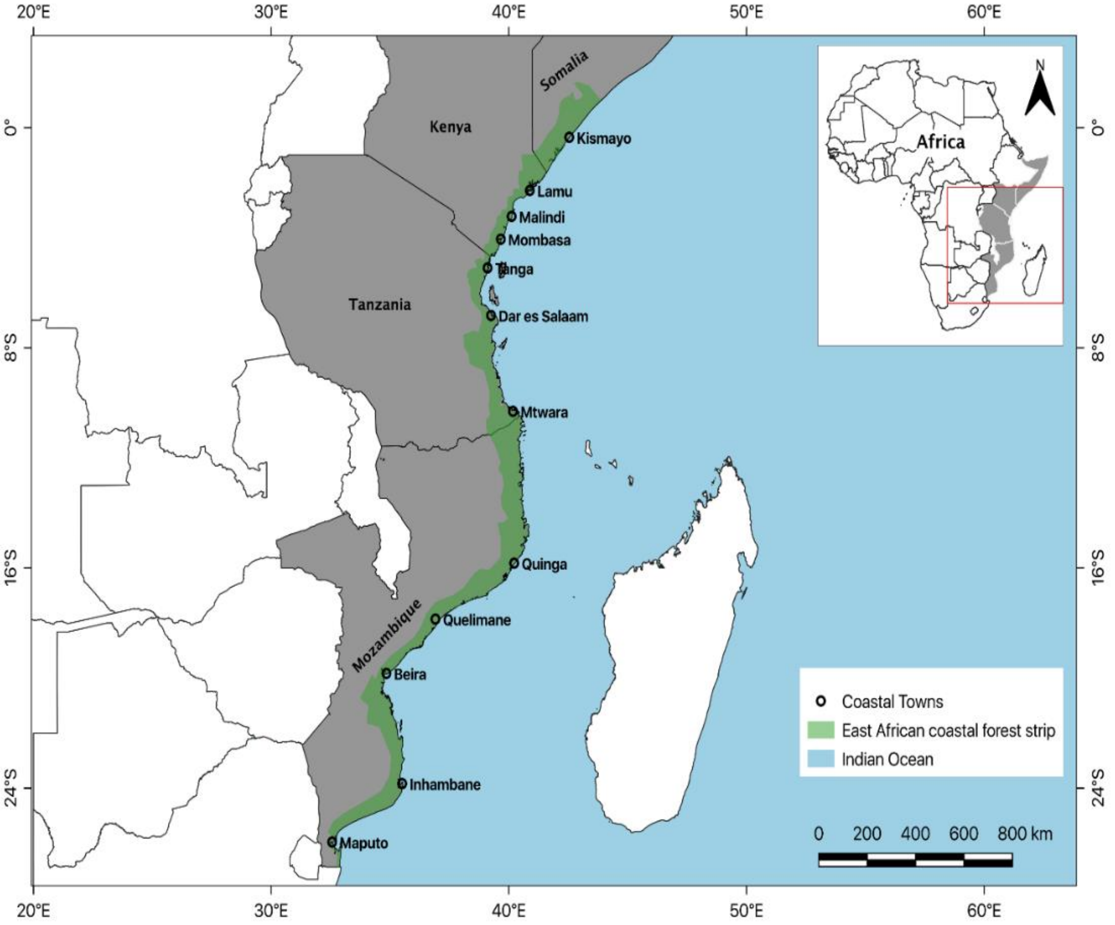


Figure 1.0: A Map of the Eastern African coastal forests, extending from Somalia in the North, through the Kenyan coastal forests, Tanzania and to Mozambique in the South. They form the Eastern African Coastal Forests Biodiversity Hotspot. The green strip depicts the original forest boundary before fragmentation.

Although the Kenyan coastal forests are known to support local livelihoods while playing a major role as high conservation value ecosystems, the threats they face has reduced the ecosystem services and livelihoods-support they can provide.

The Coastal forests of Kenya fall under the Eastern African coastal forest ecoregion as isolated fragments of the once expansive coastal forest within the Swahilian Regional Centre of endemism (Burgess et al., 1998). A major alarm to the Coastal forests is that 10% of the original forest is estimated to be left, and out of these, only 17% are under some kind of protection (Burgess et al., 1998; Burgess and Clarke, 2000). A distinct element of the Coastal forests of Kenya is their wide variation in size (area) from 10 ha to 42,000 ha and a distinct protection status of forest reserves and sacred forests (Figure 2.0). The two largest remaining forests are the Arabuko Sokoke forest (42,000 ha, Figure 2.0, forest site number 19), and Shimba Hills forest (25,300 ha; Figure 2.0, forest site number 25). The forest reserves are officially and legally government protected forests, with support of national conservation and protection policies, while the sacred forests are informally protected by the local communities.

The sacred forests are traditionally, culturally protected and used by the local coastal Mijikenda community as places of traditional religious worship and indigenous rituals (Githitho, 2016). They are cultural heritage forest sites protected by local communities due to their spiritual, religious and cultural practices. They are locally referred to as *'Kayas'* which is a local Mijikenda language word meaning '*homestead*' (Githitho, 2016). These forests have formerly also been used by the local people as burial grounds for their traditional-religious leaders, and so each Kaya sacred forest contains remains of graves which are maintained to date and traditional rituals performed on the graves (Githitho, 2016). Therefore, the sacred forests have ended up being conserved to date as a result of the taboos, religious and other traditional norms in place used by the local communities. These norms and taboos include regulation and prohibition of cutting down trees. As such, sacred forests form the backbone of traditions and indigenous knowledge, while playing a major role in bio-cultural conservation (Robertson, 1987; Githitho, 2016). They largely form the foundation of native forests and represent maintenance of traditions and biodiversity over centuries. However, the current erosion of traditional-cultural values coupled with poverty are a major threat to the sacred forests sustainable conservation. The current situation on the ground in most of the sacred forests shows that the local communities are still actively and willing to continue in conservation, but only if there can be alternative ways to meet and enhance their livelihoods in order to offload direct dependence on the forests and to gain tangible benefits through nature-based solutions (Fungomeli et al. *in press*).

The Kaya sacred forests form a significant number of 90% in number of the remaining Kenyan coastal forests and are composed of native natural forests that protect rare and threatened species found nowhere else in the country (Burgess et al., 1998; Burgess and Clarke, 2000). However, they are often undervalued and underestimated on their ecological value as they occur in small sizes (10ha -75ha), fragmented, remotely located, and isolated (Fungomeli et al., 2020b; Burgess and Clarke, 2000). They are still actively used by local communities to date and form a crucial provision of ecosystem services and support in local livelihoods such as source of water, firewood, charcoal, medicinal plants, provide grazing grounds for domestic animals, and source of food (Kibet 2011; Fungomeli et al., 2020a, 2020b). These uses on one hand form the threats to the survival of the sacred kaya forests, and therefore creating the need for effective strategies to ensure their preservation and conservation is important. The variation in biogeography and location across the coastal forests has enhanced the rich plant diversity within these forest fragments. For example, an interesting notable feature of the sacred forests is also their topography, where most appear as hilly forests areas such as Kaya Chivara; Kaya Jibana; Kaya Kambe; Kaya Mudzimuvya, Kaya Gandini; Kaya Mtswakara and Kaya Dzombo. While others are on flat land such as Kaya Kauma and Kaya Chonyi (Fungomeli et al., 2020b).

A major threat to the Kenyan coastal forests is their very close position within the coast, some within 0.1 km distance from the shore (Figure 2.0; see Fungomeli et al., 2020a). As such, they are surrounded by an expanding tourism with high quest for land and a high surrounding population (Burgess et al., 2000; Matiku, 2003). On the other hand, some forest fragments appear as *'a green oasis'* in the middle of dry and semi-arid surroundings. They are the only green environments within the rural remote dry areas, and so the forest adjacent local people rely on them heavily for their daily needs such as for water, building materials, grazing, fuelwood and medicinal plants (Kibet, 2011, and as also seen during the field sampling survey work). Some examples of very dry and semi-arid forest fragments include Kaya Gandini, Kaya Chonyi and Kaya Mtswakara. They are therefore highly vulnerable to increased degradation, deforestation, encroachment and illegal logging.

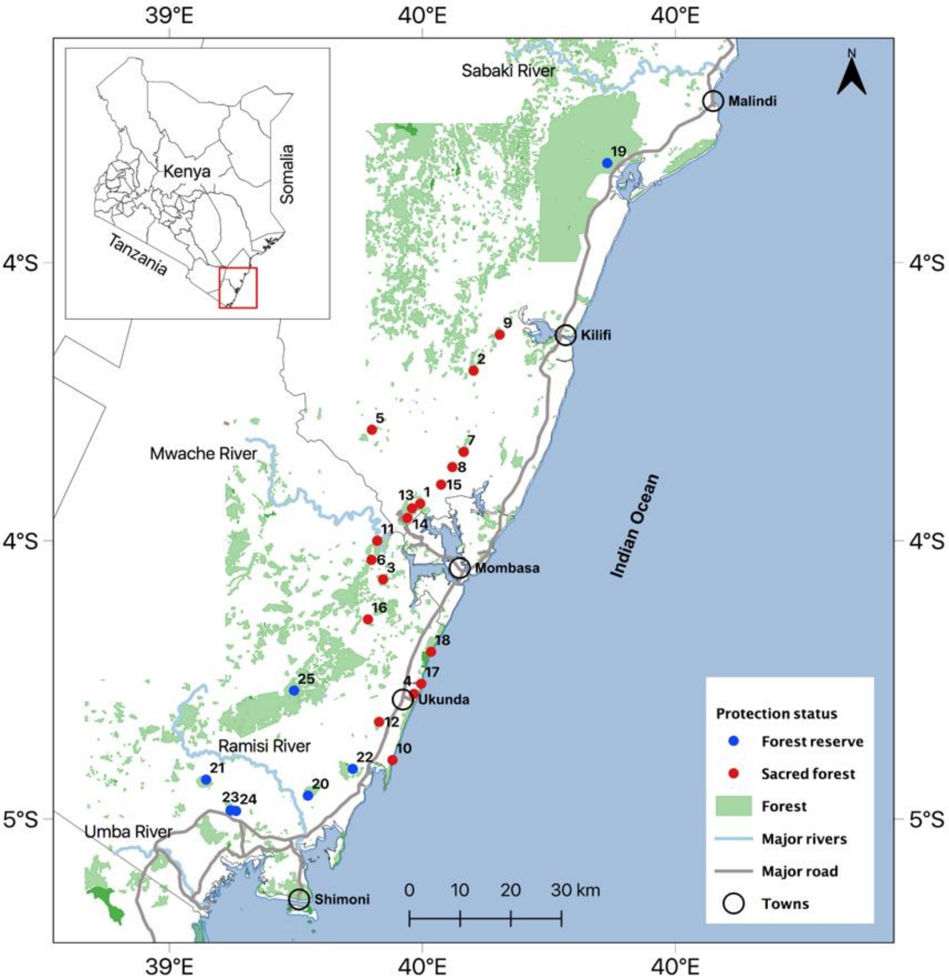


Figure 2.0: A Map of the Coastal forests of Kenya showing the location of the 25 studied forest sites within varying protection status of forest reserve and sacred forests. Forest site names numbered:1=Bomu, 2=Chivara, 3=Chonyi, 4=Diani, 5=Fungo, 6=Gandini, 7=Jibana, 8=Kambe, 9=Kauma, 10=Kinondo, 11=Mtswaka, 12=Muhaka, 13=Muvya, 14=Mwiru, 15=Ribe, 16=Teleza, 17=Tiwi, 18=Waa, 19=Arabuko, 20=Buda, 21=Dzombo, 22=Gogoni, 23=Marenje, 24=Mrima, 25=Shimba.

While it is clear these forests host high values of species richness and endemism (Burgess et al., 1998; Hobohm et al., 2019), and are subject to threats of biodiversity loss and forest cover (Shepheard, 2004;Tabor et al. 2010; Kibet, 2011), most of them have received little or no scientific attention, their vegetation diversity at forest site level is scarce, therefore limiting the capacity to prioritize their conservation at regional and global scales (Fungomeli et al., 2020a, 2020b). The last largest survey was carried out 30 years ago (Robertson, 1987; Robertson and Luke, 1993; Fungomeli et al., 2020a), which was conducted as a plant check list survey (see Fungomeli et al., 2020a). There is no study on the coastal forests of Kenya that has been able to provide a vegetation survey large enough to be used for a comprehensive biogeographical, spatial and ecological analysis and consequently enhance conservation measures. Moreover, their current biodiversity status and trends are still under-studied and some forest fragments remain unexplored. The existing protection status of forest reserves and sacred forests have given a bias to relatively more surveys being conducted on forest reserves, leaving a wealth of unexplored biodiversity in the small fragments of sacred forest sites despite them being higher (90%) in number and spatially distributed (Fungomeli et al., 2020b). It is in this context that this study is based, and we call for their quantitative biodiversity ecological survey that can be a foundation for further analytical synthesis, and the results can be used as a tool to better guide conservation measures (Fungomeli et al., 2020b).

The value of the Kenyan coastal forests goes beyond the biological value. They harbour a wealth of valuable minerals such as titanium and lead. Currently, titanium mining is ongoing at the Kenyan south coast near Buda and Mrima forest reserves (Abuodha, 2002; Burgess et al., 2007; Burgess and Clarke, 2000). Others are silica sands for glass manufacture that was mined in Arabuko Sokoke forest leaving behind old sand quarries (Matiku et al., 1998). Iron, gemstones, and gas are on the list of targeted minerals from these forests (Burgess and Clarke, 2000). Such valuable minerals have become a major target by multinational companies leading to destructive mining causing degradation and deforestation of the coastal forests (Burgess and Clarke, 2000;

Burgess et al., 2007). These multinational companies also target the forests for investment creating a controversy between conservation and economic development (FAO and UNEP 2020). These actions probably contribute to increased deforestation, the loss of species, and the loss of the opportunity to document unique species in undocumented areas (Stropp et al., 2020). The loss of species *sensu lato* leads to loss of ecosystem functions and increased species extinction rate.

Conclusion

African tropical forests, especially the coastal forests of Kenya are the oldest and also most biologically complex ecosystems characterized with high species richness yet not updated in biodiversity data and information is scanty. For example, there are no detailed and reliable studies documented on the flouristic richness of the small sacred kaya forests of the coastal forests of Kenya. Of course, there is more challenges to this ranging from difficulty in accessibility of the sites to financial limitation, but efforts to sample them will add rich information that may not be currently available. We also emphasize on systematic and quantitative ecological survey of the coastal forests of Kenya based on standardised field sampling. Such biodiversity information is crucial to better guide forest management, conservation policy and human interventions at both local, regional and global scales. We look forward to spread the roots of this study and deepen our knowledge and the results into providing a conservation based-model plan of the coastal forests of Kenya.

1.1 Aims of this Study

The broad objective of this study is to investigate the ecological features, biodiversity and conservation status of the coastal forests of Kenya. To achieve this, first, a comprehensive literature review study was carried out to determine the status and to identify the gaps of knowledge (Figure 3.0). Second, a field research sampling work was carried out in Kenya from 28th October 2018-June 2019 with the aim to:

1. Survey woody plant species diversity across a significant number of the presently remaining forest fragments of the coastal forests of Kenya.
2. Survey butterfly species diversity in Arabuko Sokoke forest vegetation zones, and investigate how plant diversity influence butterfly diversity and composition by use of butterflies as bio-indicator species of forest fragmentation.

1.2 Field sampling survey

The field work was carried out across 25 Kenyan coastal forest fragments, composed of 18 sacred forests and seven forest reserves along a spatial scale (Figure 2.0). The data from the field work consists of plant community data recorded in 158 plots subdivided into 3160 subplots. All plots and subplots are geo-referenced and include data on tree species identity, diameter at breast height (dbh) and height. The abundance of shrubs is presented for 316 subplots. A total of 600 taxa belonging to 80 families were recorded, 549 of which were identified to species and 51 to genus level (Fungomeli et al., 2020b). Additionally, forest fragments are characterised into protection status (forest reserves and sacred forests), area (ha), geographical location and number of plots sampled per forest fragment. Species richness and forest structure results are included across forest sites (Fungomeli et al., 2020b). The details of the field survey are included in the second chapter of this thesis as a database paper (Fungomeli et al., 2020b), and subsequently for each research topic and chapter in this thesis.

1.3 Study Organization and phases

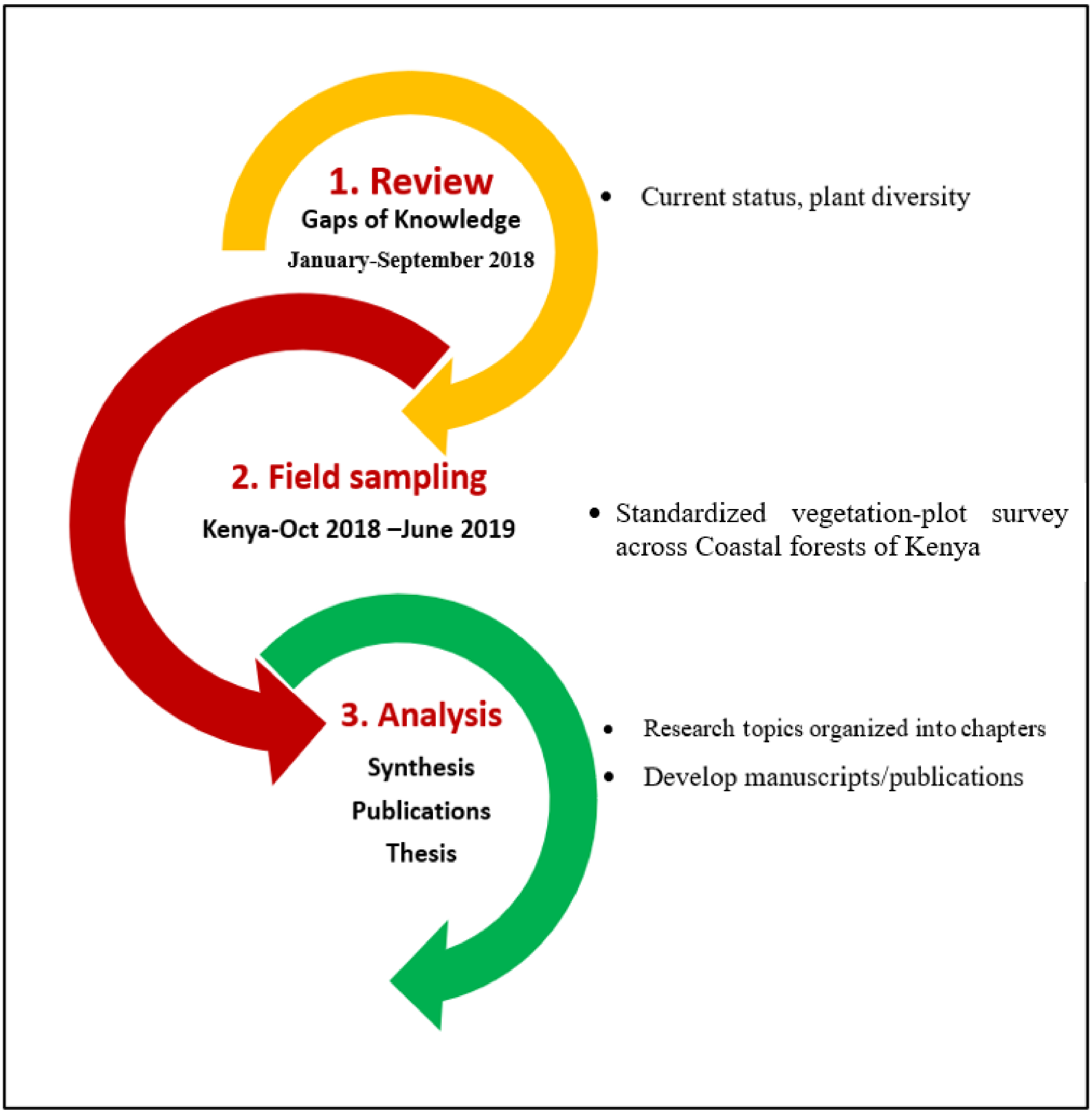


Figure 3.0: Conceptual organization of the entire study and consequent study phases starting from literature review work, to field sampling work and final analysis, synthesis, publications and thesis development. Each phase is marked with the timeline. Details and outcomes for each phase are presented as results referred to as chapters in this thesis.

2.0 References

Abuodha, J.O. Z. (2002) Environmental Impact Assessment of the Proposed Titanium Mining Project in Kwale District, Kenya. *Marine Georesources & Geotechnology*, 20:3, 199-207. https://doi.org/10.1080/03608860290051895.

Azeria, E.T., Sanmartin, I., Stephan, A.S., Carlson, A., Burgess, N.D. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation* 16: 883–912. https://doi.org/10.1007/s10531-006-9022-0.

Burgess, N.D., Clarke, G.P., Rodgers, W.A. (1998) Coastal Forests of Eastern Africa: Status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, 64, 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess, N.D., and Clarke, G.P. (Eds) (2000) *The coastal forests of Eastern Africa*. IUCN, Gland, Switzerland and Cambridge, UK.

FAO (2019) Global Forest Resources Assessment. Rome: FAO.

Fungomeli M, Cianciaruso M, Zannini P, Githitho A, Frascaroli F, Fulanda B, Kibet S, Wiemers M, Mbuvi T, Matiku P, Chiarucci A (2020a) Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, *Plant Biosystems*. https://doi.org/10.1080/11263504.2020.1834461.

Fungomeli M, Githitho A, Frascaroli F, Chidzinga S, Cianciaruso M, Chiarucci A (2020b) A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey* 1: 103-109. https://doi.org/10.3897/VCS/2020/47180.

Githitho, A.N. (2016) Listing The Sacred Mijikenda *kaya* Forests as UNESCO World Heritage Sites: “The Long Journey”, *Journal des africanistes* [En ligne], 86-1, mis en ligne le 10 avril 2018, consulté le 03 October 2019. http://journals.openedition.org/africanistes/4971

Kibet, S. (2011) Plant communities, species diversity, richness, and regeneration of traditionally managed coastal forest, Kenya. *Forest Ecology and Management*, 261: 949-957. https://doi.org/10.1016/j.foreco.2010.11.027.

Lovett, J.C. (1993) Climatic history and forest distribution in eastern Africa. In: Lovett, J.C., and Wasser, S.K., (Eds) *Biogeography and Ecology of the Rain* Forests *of Eastern Africa*. Cambridge: Cambridge University Press, pp. 23-33.

Lovett, J. C. (2008) Biogeography and ecology of the rain forests of Eastern Africa. Cambridge University Press. Great Britain.

Matiku, P. (2003) The Coastal Forests of Kenya: Forest data, threats, socio-economic issues, values, stakeholders, challenges, strategies, investment and enabling environment. *A national synthesis report for the development of the WWF-EARPO Eastern Africa Coastal Forests Ecoregion Programme*, Nature Kenya and WWF, Nairobi, Kenya.

Mittermeier, R.A., Larsen, F.W., Brooks, T.M., Gascon, C. (2011) Global biodiversity conservation: the critical role of Hotspots. In: Zachos, F.E. and Habel, J.C. (Eds), *Biodiversity Hotspots*, Springer-Verlag, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-20992-1.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca G.A.B., Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858. https://doi.org/10.1038/35002501.

Robertson, S.A., and Luke, W.R.Q. (1993) The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi. https://www.africabib.org/rec.php?RID=K00001940.

Robertson, S.A. (1987) Preliminary floristic survey of Kaya forests of coastal Kenya. Reports to the Director NMK and to WWF, Nairobi, Kenya.

Shepheard, W. (2014) Culture and Conservation in the Sacred Sites of Coastal Kenya. [PhD Thesis]. *Durrell Institute of Conservation and Ecology*, University of Kent, Canterbury, United Kingdom. https://kar.kent.ac.uk/48959.

Tabor K., Burgess ND, Mbilinyi BP, Kashaigili JJ, Steininger MK (2010) Forest and Woodland Cover and Change in Coastal Tanzania and Kenya, 1990 to 2000. *Journal of East African Natural History* **99**(1)**:** 19–45.

Wass, P. (Ed.) (1995) *Kenya's Indigenous Forests: Status, Management and Conservation.* IUCN and ODA, Gland, Switzerland and Cambridge, U.K.

Chapter 1

Woody plant species diversity of the Coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot

Chapter published as:

Fungomeli, M.[a,b], Cianciaruso, M.[c], Zannini, P.[a], Githitho, A.[b], Frascaroli, F.[a,d], Fulanda, B.[e], Kibet, S.[f], Wiemers, M.[g], Mbuvi, M.T.S[h], Matiku, P.[i], and Chiarucci, A.[a] (2020). Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot. *Plant Biosystems*. https://doi.org/10.1080/11263504.2020.1834461.

[a]Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy
[b]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Kilifi, Kenya
[c]Department of Ecology, Universidade Federal de Goiás, Goiania, Brazil
[d]Lòm Research, Frosinone, Italy
[e]Department of Biological Sciences, Pwani University, Kilifi, Kenya
[f]Department of Land Resource Management and Agricultural Technology, University of Nairobi, Nairobi, Kenya
[g]Senckenberg German Entomological Research Institute, Muncheberg, Germany
[h]Coast Eco-Region Research Programme, Kenya Forest Research Institute, Gede, Kenya
[i]Nature Kenya, Nairobi, Kenya

Abstract

Aims: The coastal forests of Kenya are global biodiversity hotspots known for rich plant diversity and endemism. They exist as fragmented forest islands, and their current conservation status and quantitative trends in plant diversity are understudied. Our goals were to build a robust basis for future analyses, biodiversity monitoring, and to understand the role of fragment area in determining species richness.

Location: Coastal forests of Kenya.

Methods: We investigated these knowledge gaps by providing a comprehensive literature review and comparing to field data collected using standardized sampling protocol.

Results: We recorded a total of 937 woody species belonging to 88 families in 30 forest patches from reviewed and sampled data. Species richness per site from literature review was affected by biases in data scarcity, forest size and variation in sampling methods. In general, large forests reserves of Shimba hills and Arabuko exhibited a high number of cumulative species compared to smaller forest patches. Species-area relationship showed a significant proportion of species richness per forest was determined by forest area, according to Arrhenius model.

Conclusions: This study is the first to review forest patch woody plant species diversity knowledge gaps in the coastal forests of Kenya, and the resulting comparison provides the first quantitative overview and foundation of these forests.

Keywords: Biodiversity knowledge; coastal forests; conservation; plant species diversity; sacred forests; sampling gaps; species richness; Kenya

1.0 Introduction

The coastal forests of Kenya are part of the global biodiversity hotspots known as the Coastal forests of Eastern Africa, and are known for their rich plant diversity and high levels of endemism (Burgess et al. 1998; Burgess and Clarke 2000; Myers et al. 2000; Hobohm et al. 2019). These forests fall under the Eastern African coastal forest ecoregion as isolated fragments of the once extensive coastal forest within the Swahilian Regional Centre of Endemism (Wass 1995; Burgess et al. 1998). Overall, the Kenyan vascular plant diversity consists of approximately of 7,004 species belonging to 1720 genera and 240 families of which approximately over 50% are found in the coastal forests of Kenya (Beentje 1994). Wass (1995) notes that half of Kenya's threatened woody plants occur in coastal forests. In addition, Kenyan coastal forests have more than 554 strictly endemic plants and 53 strictly endemic animals (Burgess and Clarke 2000). Kenyan coastal forests are presently reduced to a series of over 145 fragmented islands, which widely vary in size and in protection status (Burgess and Clarke 2000). The forests protection status are either being managed as protected forest reserves or sacred forests. The forest reserves are officially and legally government protected forests, while the sacred forests are informally protected by the local communities as cultural, spiritual, and religious places of worship (Metcalfe et al. 2010; Githitho 2016).

Knowledge about status and trends of biodiversity is the baseline for enhancing conservation strategies and detecting the impact of anthropogenic changes (Burgess et al. 2007; Bull et al. 2014; Mihoub et al. 2017). Plant diversity is a crucial factor influencing ecosystem processes and the ecosystem services they provide. The coastal forests of Kenya have played crucial multiple ecosystem services of supporting the livelihoods of the forest adjacent communities, conserving plant species while acting as a sink to carbon and mitigation to climate change effects while conserving biodiversity. FAO and UNEP (2020) estimates that approximately 60% of all vascular plants are found in tropical forests. However, it has been noted that high-quality vegetation data are largely missing for tropical Africa and the region is under-represented in georeferenced open-access databases (Kuper et al. 2006; Collen et al. 2008; Corlett2016; Serra-Diaz et al.2017; Stephenson et al. 2017; FAO and UNEP 2020). As a consequence, we seem to have more knowledge on the biodiversity of temperate areas than of the tropics in general, and African tropical forests in particular (Collen et al. 2008; Corlett 2016). The challenges for Africa to have high-quality data range from the very wide biodiversity with some species still fully unidentified, to access and usability of the data due to uncoordinated data collection. Furthermore, large and numerous forest landscapes make it hard to acquire full data coverage due to limited financial support (Stephenson et al. 2017). As a consequence of these and other limitations, African coastal forest fragments are hardly ever included in global distribution and analyses of biodiversity data.

Failure to include these rich botanical fragments in global monitoring effort is alarming, in the light of the risk they are facing due to climate change, the increasing anthropogenic pressures, and a growing local population (Lovett 1998; Burgess et al. 2007; Lovett 2008; Shepheard 2014; Habel et al. 2017; FAO and UNEP 2020). Climate change is playing a role in species loss and it is estimated that around 40% of the species in Africa might disappear by 2100 due to climatic changes (Sommer et al. 2003; McClean et al. 2005; FAO and UNEP 2020). Growing human population also poses a major threat to biodiversity hotspot areas, as 20% of the world population lives within biodiversity hotspot areas, which cover only around 12% of the Earth's terrestrial surface (Cincotta et al. 2000; FAO and UNEP 2020). Incidences of tree felling, illegal logging and poaching are frequent as forest dependent communities rely on forests for their livelihoods (Matiku et al. 2012; Shepheard 2014; Habel et al. 2017; FAO and UNEP 2020). In this context, close monitoring and assessment, and the availability of up-to-date and high-quality biodiversity data are essential for driving sound conservation of the coastal forests of Kenya by informed policy actions and management strategies.

The present fragmentation and difficult accessibility of the Kenyan coastal forests have made it a challenge to gather a comprehensive knowledge of the patterns of plant species diversity for each forest fragment (Fungomeli et al. 2020). Thanks to a collaboration between the National Museums of Kenya and the Alma Mater Studiorum-University of Bologna we started a research project aiming to depict the major ecological patterns of the plant communities in the Kenyan coastal forests. After the completion of our field survey, a checklist of the plants of the coastal forest of Kenya was published (Ngumbau et al. 2020), but it does not provide data for single forest fragments and can only be used to address general questions. Previous vegetation studies have either been based on the compilation of plant checklists (Robertson and Luke 1993) or targeted the two remaining large forests on the coast which are easy to access (i.e. Arabuko Sokoke and Shimba Hills forests); or sampled single stand forests (Mutangah and Mwaura 1992; Burgess et al. 1998; Burgess and Clarke 2000; Muchiri 2001; Pakia et al. 2003; Lehmann and Kioko 2005; Luke 2005; Pakia 2005; Edwards 2007; Metcalfe et al. 2010; Kibet 2011; Rajat et al. 2017; Wekesa et al. 2017). Nevertheless, some forest fragments remain unexplored and unstudied, and this would probably affect management practices and conservation strategies (Moerman and Estabrook 2006; Ahrends et al. 2011). It is therefore fundamental to provide forest site species references for each forest patch to enhance effective conservation efforts. To our knowledge, no study has provided a sufficiently robust survey of forest site-based data of the Kenyan coastal forests, that can be used for a comprehensive biogeographical, spatial and ecological analysis.

This paper is the first to directly address this knowledge gap, by providing a comprehensive literature review of published and unpublished plant lists, and comparing the existing data to original field data specifically collected to detect plant diversity patterns within and across forest patches. The two main goals of this paper are: i) comparing the plant occurrence data provided by existing literature with those specifically collected by a standardized sampling design; ii) providing a first quantitative overview of the woody species plant diversity of the coastal forests of Kenya by relating the species richness to the forest patch area.

2.0 Materials and Methods

2.1 Study Area

The coastal forests of Kenya are located along the Indian Ocean coastal strip of Kenya (Figure 1.1), in a biodiversity hotspot known as 'Eastern Arc and Coastal Forests of Kenya and Tanzania' (Myers et al. 2000). They fall within the East African coastal ecoregion (ca. 3170 km^2) and are presently found as isolated patches, estimated 145 in number for an approximate area of 787 km^2 (Burgess and Clarke 2000). The Kenyan coastal forests was once a single large forest block (as

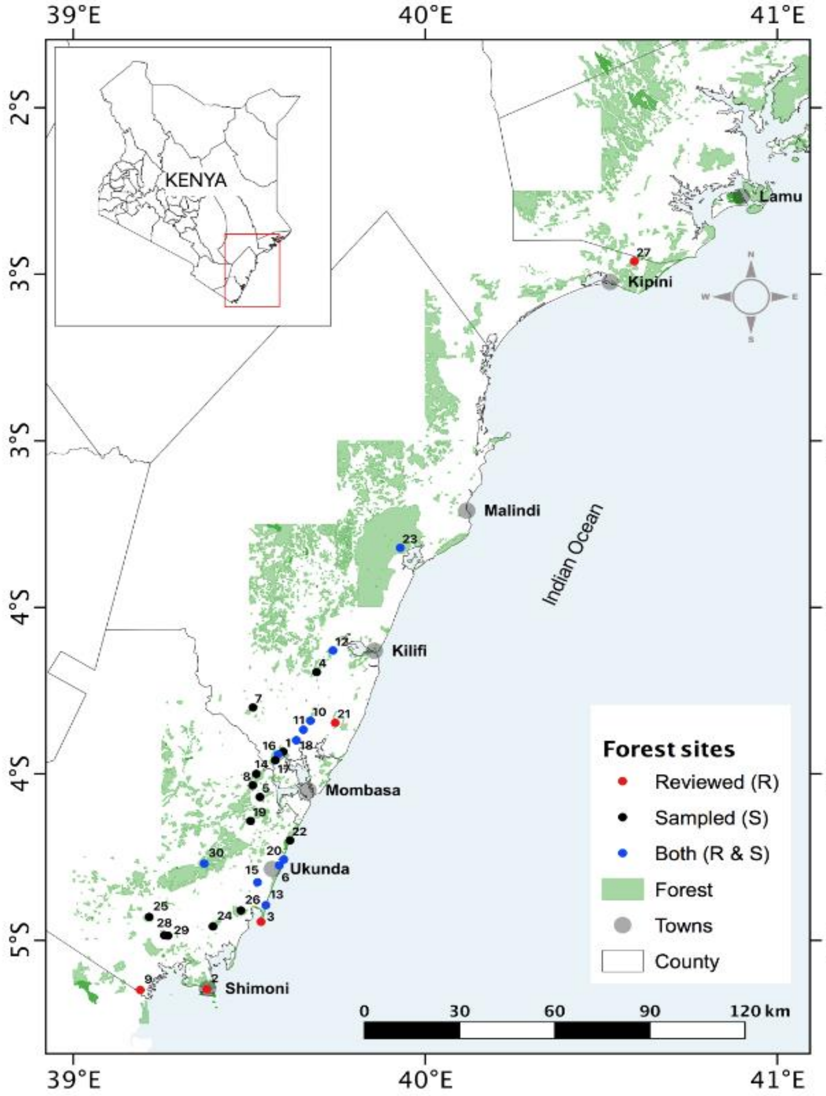


Figure 1.1: Map showing the geographical coverage of the coastal forests of Kenya from reviewed data set and sampled data set forest sites. The green areas depict the original Kenya coastal forest block before fragmentation. The forest sites names as follows: Bomu (1), Cave (2), Chale (3), Chivara (4), Chonyi (5), Diani (6), Fungo (7), Gandini (8), Jego (9), Jibana (10), Kambe (11), Kauma (12), Kinondo (13), Mtswakara (14), Muhaka (15), Muvya (16), Mwiru (17), Ribe (18), Teleza (19), Tiwi (20), Tsolokero (21), Waa (22), Arabuko (23), Buda (24), Dzombo (25), Gogoni (26), Lumshi (27), Marenje (28), Mrima (29), Shimba (30).

shown in the green areas covered by the map Figure 1.1) before fragmentation mainly due to anthropogenic activities (Burgess and Clarke 2000). The climate is tropical with mean annual rainfall ranging from 900 mm to 1200 mm and mean temperatures between 25°C and 30°C (Glover et al. 1954; Moomaw 1960; Burgess et al. 1998; Burgess and Clarke 2000).

There are two larger remaining forest patches: the Arabuko Sokoke forest (420 km^2) and the Shimba Hills forest (253 km^2). In addition, there are over 145 fragmented forest patches of 10-150ha many of which are considered sacred forests and are locally referred to as *'Kayas'* (Figure 1.2, Table 1.1, Githitho 2016; Luke and Githitho 2016). The forests are mainly a mixture of moist and dry forests, with mangrove forests occurring along the shoreline.

Figure 1.2: Kaya Kambe sacred forest, Kenya. One of the Kaya sacred forests remnant patches of the Kenyan Coastal Forests. Photo credit: Steve Okoko Ashikoye.

Table 1.1: The Kenyan coastal forests sites description for forest names, protection status, geographical coordinates and area (ha), species richness resulting from the review data set (SR_R), species richness resulting from sampled data set (SR_S) and cumulative species richness (SR_C) per forest site for the coastal forests of Kenya.

Forest ID	Forest name	Latitude	Longitude	Area (ha)	SR_R	SR_S	SR_C
Sacred forests							
Bomu	Kaya Bomu	-3.93354	39.59635	409	-	154	154
Cave	Three Sisters Cave	-4.64658	39.37975	15	95	-	95
Chale	Kaya Chale	-4.44417	39.53333	50	64	-	64
Chivara	Kaya Chivara	-3.69452	39.69132	150	-	140	140
Chonyi	Kaya Chonyi	-4.06953	39.53038	200	-	62	62
Diani	Kaya Diani	-4.27523	39.58520	20	63	66	96
Fungo	Kaya Fungo	-3.80068	39.51047	204	-	60	60
Gandini	Gandini forest	-4.03443	39.50988	150	-	80	80
Jego	Kaya Jego	-4.64889	39.19028	10	19	-	19
Jibana	Kaya Jibana	-3.84048	39.67382	140	26	195	203
Kambe	Kaya Kambe	-3.86766	39.65363	75	42	109	134
Kauma	Kaya Kauma	-3.62968	39.73778	75	52	77	112
Kinondo	Kaya Kinondo	-4.39427	39.54703	30	79	56	110
Mtswakara	Kaya Mtswakara	-4.00017	39.51997	248	-	64	64
Muhaka	Kaya Muhaka	-4.32568	39.52328	150	72	90	121
Muvya	Kaya Mudzimuvya	-3.94175	39.58190	171	276	85	299
Mwiru	Kaya Mudzimwiru	-3.95913	39.57372	147	-	70	70
Ribe	Kaya Ribe	-3.89922	39.63363	36	66	95	139
Teleza	Kaya Teleza	-4.14147	39.50342	67	-	91	91
Tiwi	Kaya Tiwi	-4.25704	39.59817	10	22	53	61
Tsolokero	Kaya Tsolokero	-3.84670	39.74408	35	29	-	29
Waa	Kaya Waa	-4.19970	39.61565	30	-	43	43
Forest reserves							
Arabuko	Arabuko Sokoke forest	-3.32138	39.92917	42000	291	178	361
Buda	Buda forest	-4.45812	39.39683	670	-	121	121
Dzombo	Dzombo forest	-4.42945	39.21545	650	-	90	90
Gogoni	Gogoni forest	-4.41013	39.47628	832	-	123	123
Lumshi	Lumshi forest	-2.46111	40.59389	1500	82	-	82
Marenje	Marenje forest	-4.48458	39.25906	1480	-	76	76
Mrima	Mrima forest	-4.48573	39.26883	377	-	101	101
Shimba	Shimba Hills forest	-4.26940	39.37208	25300	498	190	555

2.2 Data Collection

We conducted an extensive literature review between February and October 2018, to understand the current ecological status of the vegetation diversity of the coastal forests of Kenya, excluding mangrove forests. We restricted our search to the Kenyan coastal forests and especially those within the Kenyan boundaries of the Swahilian Regional Centre of Endemism. We searched for data from both published and unpublished sources and within conservation organizations working around these forests (Table 1.2). A systematic review of scientific published literature was conducted through databases of Web of Science, Scopus and Google Scholar to capture data sources and technical reports that contained relevant plant list information. We also recorded the methodological approach of the studies, i.e. whether the studies were presenting checklists or plot-based data (Table 1.2). In the first general step, we considered all available data information for all plant species resulting in a list of over 3,000 species. In the second step, we filtered the computed list of all the species to select only woody species. For this purpose, species were classified according to life form following the literature from the Shimba hills annotated dataset (Luke 2005), searches on online herbariums and floras, the African plant checklist online database, and Botanical Information and Ecology Network (BIEN, version 4.1; Maitner 2020). All taxonomic references were in accordance with the African Plant Database (African Plant Database version 3.4.0, 2018). All the data coming from this review made up the *'review dataset'*.

Subsequently, a specific field sampling vegetation survey was designed and carried out by sampling 158 plots, divided into 3160 subplots, distributed across 25 forest patches (Fungomeli et al. 2020). We allocated plots within each forest on the basis of its area. We sampled all allocated plots and subplots within each forest. Each plot measured 10m x 100m, and was further subdivided into twenty subplots of 10m x 5m. All woody plant species present within the plots were identified in the field whenever possible to the species or at least genus level by botanists and with the use of botanical manuals (Noad and Birnie 1990; Beentje 1994; Luke 2005). When onsite identification was not possible, voucher specimens were collected for subsequent herbarium identification. Further details on plot sampling can be found in Fungomeli et al. (2020). The data obtained by this specifically performed field sampling made up the *'sampled dataset'*.

2.2 Data Analysis

For each forest patch, we compiled a list of species drawn from the review dataset and/or the sampled dataset, standardizing nomenclature according to the African Plant Database (2018). For each species, we also recorded details of family and life form (tree, shrub, liana). A species richness value was calculated for each forest patch on the basis of both the species occurrence data available in the review dataset (SR_R) and the sampled dataset (SR_S). Then a combined dataset was obtained by combining the species occurrence data for each forest patch, by merging the plant occurrence data from the two lists and the cumulative species richness per forest patch was consequently calculated (SR_C). For the combined dataset, endemic species were sorted and presented according to Beentje (1994), Burgess et al. (1998), Burgess and Clarke (2000), Luke (2005) and Ngumbau et al. (2020).

We calculated Species-Area Relationships (SARs) for the three data sets (SR_R, SR_S and SR_C), by using the Arrhenius (1921) power function ($S = k \cdot A^z$) and the Gleason (1992) logarithmic model ($S = c + z \cdot log(A)$, where S is the number of recorded species, A is the forest patch area, k and c are the number of species in a forest of unit area as expected by the two models, and z is the increase of the number of species expected by increasing area (different in the two models). We used R^2 and AICc to evaluate the model fitting.

All the analyses and graphs were performed in R-software v.3.6.3 (R Core Team 2020) using the packages *sars* (Matthews et al. 2019), *ggplot2* (Wickham 2016), patchwork (Pedersen 2019), *magrittr* (Bache and Wickham 2014) and *ggrepel* (Slowikowski 2020).

3.0 Results

The *review dataset* was composed by a total of 18 sources (15 published papers, three unpublished reports) and provided plant occurrence data for 16 forest fragments (Table 1.2). The variation in the type of sampling methods used in the review data showed that 12 data sources used the checklist method while six used plots survey technique (Table 1.2). The review dataset resulted into a total of 712 woody species belonging to 348 genera and 77 families (Supplementary material Appendix 1.1, Table 1.1). In total 626 species were identified to species level, while 86 species were only identified to genus level and belonged to 77 genera. The most frequent families in terms of number of species were Rubiaceae (100) and Fabaceae (65) (Table 1.3). Species richness per forest patch in the review dataset showed that the Shimba hills forest reserve was the richest (498), followed by Arabuko Sokoke (291) and Kaya Mudzimuvya (276) while Kaya Jego was the poorest (19) (Table 1.1).

The *sampled dataset* provided plant occurrence data for 25 forest patches (Table 1). This data set recorded 600 woody species belonging to 80 families, 549 of which were identified to species and 51 to genus level, within 43 genera (Supplementary material Appendix 1.1, Table 1.1). The most frequent families in terms of number of species were Rubiaceae (63) and Fabaceae (61) (Table 1.3). Species richness was highest in the Jibana forest (195), Shimba hills (190) and Arabuko (178).

The *combined dataset* provided plant occurrence data for a total of 30 forest patches, split into 22 sacred forests and 8 forests reserves (Figure 1.1). A total of 11 forest patches were covered by both the review dataset and the sampled dataset, while 14 were only covered by the sampled dataset and five by the review dataset (Figure 1.1, Table 1.1). The combined dataset resulted in a total of 937 woody species belonging to 88 families (Supplementary material Appendix 1.1). The number of species shared by the two data set was 375. Trees were represented by 568 species, while shrubs and lianas consisted of 267 and 64 species, respectively. No life form was allocated to the 38 species, which were identified to genus level. Of the 88 plant families, 28 families had

10 or more total species (SR_C), with Rubiaceae and Fabaceae containing the highest number of species (118 and 66, respectively, Table 1.3).

Table 1.2: Published and unpublished sources reporting occurrence data for the woody plant species in the remnant patches of Kenyan Coastal Forests (referred to as "review data set"). Data are shown as author, year of publication and the survey method used in sampling.

Author	Survey technique	Forest surveyed
Published		
Robertson SA, 1987. Preliminary floristic survey of Kaya forests of coastal Kenya. Published in Burgess & Clarke (2000).	checklist	Jego, Jibana, Kambe, Kauma, Ribe & Tiwi
Mutangah JG, Mwaura PK. 1992. A vegetation survey report, Arabuko Sokoke forest management and conservation project. – East African Herbarium, National Museums	plots	Arabuko
Robertson SA, Luke WRQ. 1993. The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi, Kenya	checklist	Arabuko & Shimba
Fanshawe J. 1995. The effects of selective logging on the bird community of Arabuko-Sokoke Forest, Kenya. University of Oxford.	checklist	Arabuko
Burgess ND, Clarke GP, Rodgers WA. 1998. Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. Biological Journal of the Linnean Society. 64: 337-367.	checklist	Arabuko & Shimba
Burgess ND, Clarke GP. editors. 2000. The coastal forests of Eastern Africa. IUCN Publications Services Unit. Cambridge, UK.	checklist	Arabuko, Shimba, Jego, Jibana, Kambe, Kauma, Ribe & Tiwi
Muchiri MN. 2001. Forest inventory report for the indigenous forests in Arabuko Sokoke forest reserve. Kenya Forest Research Institute. Nairobi, Kenya.	checklist	Arabuko
Kibet S. 2011. Plant communities, species diversity, richness, and regeneration of a traditionally managed coastal forest, Kenya. Forest Ecology and Management. 261: 947 - 957.	plots	Muvya
Luke WRQ. 2005. Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. Journal of East African Natural History. 94:5–121.	checklist	Shimba
Lehmann I, Kioko E. 2005. Lepidoptera diversity, floristic composition and structure of three Kaya forests on the South coast of Kenya. Journal of East African Natural History. 94:121-163.	plots	Diani, Kinondo & Muhaka
Pakia M, Cooke JA. 2003. The ethnobotany of the Midzichenda tribes of the coastal forest areas in Kenya: 2. Medicinal plant uses. South African Journal of Botany. 69: 382–395.	checklist	Fungo & Mtswaka
Pakia M. 2005. Plant ecology and ethnobotany of two sacred forests (Kayas) of Kenyan Coast. Die Deutsche Bibliothek, Bayreuth.	checklist	Fungo & Mtswaka
Metcalfe K, French-Constant R, Gordon I. 2010. Sacred sites as hotspots for biodiversity: The three sisters cave complex in coastal Kenya. Oryx. 44: 118–123.	plots	Three sisters cave
Kenya Forest Research Institute. 2016. A field guide to valuable trees and shrubs of Kaya Mudzimuvya forest in Kilifi County, Kenya.	checklist	Muvya
Rajat J, Jefwa J, Mwafaida J. 2017. Survey on indigenous food plants of Kaya Kauma and Kaya Tsolokero in Kilifi County Kenya. Journal of Life Sciences. 11:82–90.	checklist	Kauma & Tsolokero
Wekesa C, Otuoma J, Ngugi, Muturi G. 2017. Floristic composition and structure of Arabuko Sokoke forest. In: Ochieng' D, Luvanda A, Wekesa C, Mbuvi MTE, Ndalilo A. editors. Biodiversity status of Arabuko Sokoke forest, Kenya. Kenya Forest Research Institute, Nairobi, pp. 8-13.	plots	Arabuko
Unpublished		
Moomaw JC, 1960. A study of the plant ecology of the Coast Region of Kenya, East Africa. Government Printer, Nairobi, KE, 62 pp.	checklist	Arabuko, Shimba & Kambe
Thomas, N.R.	checklist	
Edwards WM. 2007. A biodiversity evaluation of Kenya's coastal forest systems. Master's degree research. Durrel Institute of Conservation and Ecology, University of Kent, UK.	plots	Chale, Kinondo & Lumshi

In general, the large forest reserves of Shimba hills and Arabuko exhibited a high number of combined species richness (555 and 362, respectively) compared to the smaller forest patches. The combined data displayed a total of 239 endemic species (Appendix1. 2).

Table 1.3: Distribution of the number of species per family in the review data (SR_R), sampled data (SR_S) and cumulative data set (SR_C) for family >10 total species across the 30 remnant patches of Kenyan Coastal Forests.

Family	**SR_R**	**SR_S**	**SR_C**
Rubiaceae	100	63	118
Fabaceae	66	62	88
Euphorbiaceae	45	31	59
Malvaceae	42	32	56
Apocynaceae	22	20	33
Annonaceae	22	23	31
Moraceae	27	21	29
Rutaceae	20	16	28
Sapindaceae	23	18	27
Lamiaceae	20	16	26
Sapotaceae	20	18	25
Celastraceae	18	14	24
Combretaceae	16	16	24
Capparaceae	14	15	24
Ebenaceae	16	14	20
Acanthaceae	12	12	20
Phyllanthaceae	18	12	19
Salicaceae	14	10	16
Loganiaceae	13	4	14
Boraginaceae	13	5	13
Melastomataceae	11	5	13
Meliaceae	11	9	12
Burseraceae	9	8	12
Anacardiaceae	10	10	11
Rhamnaceae	9	7	10
Ochnaceae	6	8	10
Asparagaceae	4	9	10

Species-area relationships showed that Arrhenius and Gleason models fitted quite similarly for the three data sets, with Arrhenius being always slightly better, according to both R^2 and *AICc* (Table 1.4). The Arrhenius power function produced the best fitting for the review dataset (R^2 = 0.62) and the worst fitting for the sampled dataset (R^2 = 0.38), while the combined dataset yielded intermediate results (R^2 = 0.56). A similar trend was observed for the Gleason model (Table 1.4). For the best fitting model, namely the Arrhenius power function, the k-values were surprisingly similar among the three data sets, with the combined data set showing the highest value, and suggested a species richness value for forest patch of 1km^2 comprised between 82 and 92. On the other hand the z-values were quite different among the three data sets, with the *review dataset* and the *combined dataset* showing the same value of 0.26 and the *sampled dataset* showing a significantly lower value (0.13). The Arrhenius power function, applied to the *review dataset* and the combined dataset, showed Muvya (#16) as the forest patch with the highest positive deviation from the expected value, but this was not confirmed in the *sampled dataset*, in which Jibana (#10) showed the highest positive deviation of species richness (Figure 1.3).

Table 1.4: Fitting of the species-area relationships for the remnant patches of the Kenyan Coastal Forests according to the Arrhenius and Gleason models and by using the data available in the literature (review dataset), newly collected data (sampled dataset) and the merged data (combined data set).

	Arrhenius				**Gleason**			
Data set	**R^2**	**k-value**	**z-value**	**AICc**	**R^2**	**c-value**	**z-value**	**AICc**
Review dataset (n = 16)	0.62	81.98	0.26	191	0.58	103.48	41.45	192
Sample dataset (n = 25)	0.38	86.9	0.13	251	0.37	87.52	14.51	251
Combined dataset (n =30)	0.56	91.18	0.26	345	0.41	105.43	36.74	354

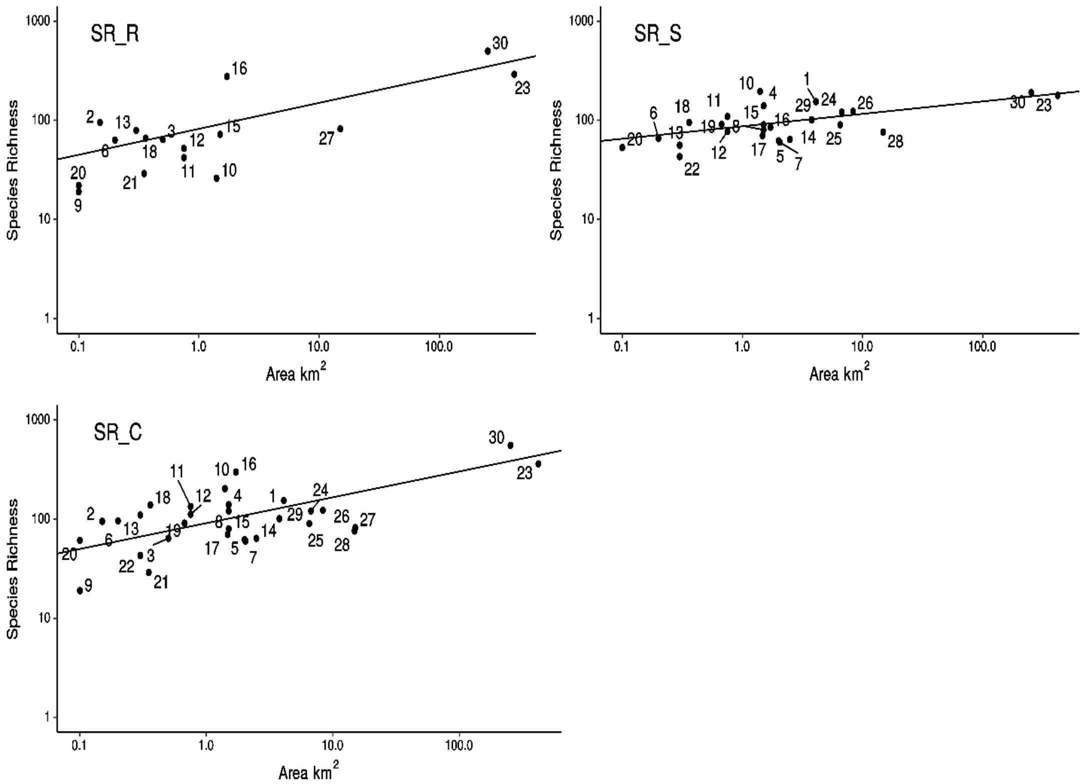


Figure 1.3: Species-area relationships of the woody plant species for the Kenyan Coastal Forests as modelled by Arrhenius power function. The three panels report data sets for the literature data (“review data set” - SR_R), (“sampled data set” - SR_S) and (“cumulative species richness”- SR_C) per forest site for the coastal forests of Kenya.

4.0 Discussion

Biodiversity conservation needs to be supported by the availability and accessibility of high-quality biodiversity data for specific sites, to understand and document spatial and temporal patterns of biodiversity (Collen et al. 2008; Chiarucci et al. 2011). This is particularly important in tropical areas, where biodiversity is rich but few quality data on species occurrence are seldom available. In general, there are three major challenges that affect biodiversity data: availability, accessibility, and data collection methods. The plant occurrence data summarized in this study produced the first list of woody species censused in 30 forest patches solving the challenges of accessibility and availability. To solve the third challenge, specific survey campaigns based on standardized sampling protocols are needed, such as the one we carried out, sampling 25 forest patches with standard and reproducible methods (Fungomeli et al. 2020).

The coastal forests of Kenya have lacked quantitative and standardized scientific surveys covering wide and specific forest patch areas on vegetation communities that can be subjected to full statistical analysis and related to environmental variables for effective biodiversity monitoring (Burgess et al. 1998; Burgess and Clarke 2000). Indeed, further to their description of the lack of large enough data for statistical coverage, Burgess and Clarke (2000) highlighted the lack of quantitative data on vegetation of these forests and the need for several plots to be studied at each forest patch to sample and identify vegetation data; by a thousand of trees that would adequately generate sufficient data for a statistical analysis. This target has now been accomplished by the collection of a unified set of data from 158 transects (Fungomeli et al. 2020), thus opening new opportunities for the forest management and conservation.

The results presented in this study underline how limited is the coverage of available plant occurrence data. In particular, we found that a few and large forest fragments, such as Arabuko Sokoke and Shimba Hills, tend to be a much more common focus of investigation, probably in virtue of their accessibility and widely known due to their size and protection status. In contrast, data were scarcer for the smaller forest fragments (10-75ha), most of which (90%) are sacred forests. This phenomenon is well known in the ecological and biogeographical literature as 'botanist effect', which is specifically used to describe why plant species richness appears to be higher in areas where botanists are disproportionately present as an artefact of a more thorough sampling (Moerman and Estabrook 2006; Pautasso and McKinney 2007; Ahrends et al. 2011). Large forest fragments have also received greater attention for research and biodiversity conservation at a global scale, due to what is often perceived as their greater conservation potential and ability to harbor higher species richness (Hanski and Triantis 2015; Rosch et al. 2015). However, some studies show that several small forest fragments can accommodate higher diversity than single large fragments (Baldi 2008; Hill et al. 2011; Matthews et al. 2014; Rosch et al. 2015; Phillips et al. 2018). In addition, beta diversity between large and small forest sites often constitutes the major components of the total species diversity of a system made by different spatial units (Crist et al. 2003; Chiarucci et al. 2012), so that properly considering the contribution of small forest patches to the global biodiversity picture is fundamental.

Our results may be partly influenced by non-standardized sampling methods in the source review data given that most of the available data are based on descriptive lists rather than a plot-based approach, thus not permitting to depict assembly patterns at the local scale. The results presented here, however allowed us to investigate assembly patterns at the scale of forest patches, using species data obtained by pooling a set of data samples and species lists (Tuomisto 2010; Chiarucci et al. 2011). This dataset represents the largest plant occurrence data set at forest site level for the Kenyan coastal forests available to date and includes both large and small fragments, as they are actually found in the region (Fungomeli et al. 2020).

The Species-Area Relationships (SARs) analysis based on this dataset confirmed the positive correlation between forest patch area and species richness, as predicted by ecological and biogeographical theory (Connor and McCoy 1979; Lomolino 2001; Harte et al. 2009; Dengler et al. 2020). The data available in literature fitted well the SARs, and even better did the cumulative dataset, including the reviewed and newly sampled data. This further shows how completeness of data can affect species richness values of sites and consequently the fitting of species area-models (see e.g. Sastre and Lobo 2009; Petřík et al. 2010). While a relationship between species richness and area clearly emerged, some forest patches diverged quite significantly from the general model, either positively or negatively. This could be an effect of different sampling intensities used to collect the data and of other factors other than just area, such as, for example, habitat diversity (see e.g. Hannus and Numers 2008; Craven et al. 2019). Nonetheless, there is need for a systematic data collection method to rule out bias in data collection method and sampling intensity.

While some studies have suggested that degraded areas within the coastal forests could be reforested by using indigenous and exotic tree species (Mbuvi et al. 2016), we believe that it is first necessary to map and assess the existing natural forest remnants. Only this can provide a robust basis for defining frameworks of forest conservation and management based on the actual ecological value of forests (Chiarucci and Piovesan 2020). A reforestation strategy should be based on the creation of corridors to connect the best preserved and existing forest patches, considering that climate change is a trigger of habitat migrations (Hawn et al. 2018).

Conclusions

This paper provides the first quantitative overview of the woody species plant diversity of the coastal forests of Kenya and offers new analytical and quantitative bases for the conservation strategies of the forests in this biodiversity hotspot. The study clearly demonstrated how scattered and nonhomogeneous was the coverage of plant diversity data for the remaining fragments of the Kenyan coastal forests and assembled the first data set of woody plant occurrences across 30 remnant forest patches ranging in size from 10ha to 42,000ha. The different forest patches preserve diverse species composition, and probably act as refuge for unique species and it is, therefore, fundamental to document species at each patch and conserve a wide range of patches rather than concentrate on large forests. Given the high conservation and endemic value of the Kenyan coastal forests, coupled with the alarming rate of degradation even within areas designated as protected, it is essential that any effort to conserve them ought to be supported by robust data, that forms the baseline for monitoring changes within the ecosystems, a goal that is going to be achieved by newly collected data based on standardized sampling (Fungomeli et al. 2020). This paper lays the foundations for forest site level biodiversity data of the coastal forests of Kenya. It provides the framework to update and include new forest sites not covered within this study.

Acknowledgements

Authors are indebted to the data review sources that led to the compilation of the review dataset. These included both published and grey sources. We thank Dr Wayne Edwards who carried out his vegetation research work on coastal forests of Kenya under funding from the Wild Planet Trust, UK. We acknowledge the botanists and guides in Kenya and the UK team for their support to this research: Erustas Kanga (Kenya Wildlife Service), Willy Kombe (Kenya Wildlife Service), Saidi (Diani Beach botanist), Bakari (Kipini Conservancy botanist), Dr Simon Tollington (Durrel University), Dr Amy Plowman (Wild Planet Trust), Dr Andrew Bowkett (Wild Planet Trust), Dr Natasha De Vere (Wild Planet Trust), Dr Stephen Burchett (University of Plymouth), Dr Wayne Edwards (Wild Planet Trust). We also thank James C. Moomaw and Thomas N.R for their work and data on the coastal forest of Kenya. We thank the online data sources for Moomaw JC (1960) and Thomas NR (1984) through https://edepot.wur.nl/493400. We thank Chiara Lelli for contribution to earlier poster presentation work of the review data. We are grateful to the review data sources of Burgess and Clarke (2000), Burgess et al. 1998, Luke (2005), Kenya Forest Research Institute (KEFRI) and Arocha Kenya online technical reports, that formed source to data from Robertson (1987), Robertson and Luke (1993). We thank the team that led to the field sampled dataset. Our special thanks to Saidi Chidzinga for field sampling and plant specimen identification, Geoffrey Mashauri and Abbas Shariff for assistance in plant identification and knowledge of the Coastal forests. We are grateful to the colleagues who helped in setting the field work, sampling and support during the entire field period: Lawrence Chiro and Abdulrahman Matano of Coastal forests conservation unit-NMK; Joseph Muthini of Kenya Forest Research Institute and George Wara and Blessingtone Magangha of Kenya Forest Service.

Disclosure statement

The authors have declared that no competing interest exist.

Funding

Funding and logistical support for the research work was a concerted effort from various sources. Authors are indebted to University of Bologna, Department of Biological, Geological and Environmental Sciences (BiGEA), the National Museums of Kenya (NMK), International Association of Butterfly Exhibitors and Suppliers (IABES), Nature Kenya and WWF-Kenya for the support received. Marcus Cianciaruso would wish to thank the Fundação de Amparo à Pesquisa do Estado de Goiás, which supported his stay at the University of Bologna during this study.

5.0 References

African Plant Database (version 3.4.0). 2018. Conservatoire et Jardin botaniques de la Ville de Geneve. Pretoria (ZA): Geneva, CH and South African National Biodiversity Institute. [accessed 2018 August 16]. https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php/.

Ahrends A, Rahbek C, Bulling MT, Burgess ND, Platts PJ, Lovett JC, Kindemba VW, Owen N, Sallu AN, Marshall AR, Mhoro BE, et al. 2011. Conservation and the botanist effect. Biol Conserv. 144(1):131–140.

Arrhenius O. 1921. Species and area. J Ecol. 9(1):95–99. Bache SM, Wickham H. 2014. magrittr: a forward-pipe operator for R. R package version 1.5. [accessed 2020 June 9]. https://CRAN.R-project. org/package=magrittr.

Baldi A. 2008. Habitat heterogeneity overrides the species-area relationship. J Biogeography. 35(4):675–681.

Beentje HJ. 1994. Kenya trees, shrubs and lianas. Nairobi (Kenya): National Museums of Kenya. Bruelheide H, Dengler J, Jimenez-Alfaro B, Purschke O, Hennekens SM, Chytry M, Pillar VD, Jansen F, Kattge J, Sandel B, et al. 2019. sPlot: a new tool for global vegetation analyses. J Veg Sci. 30(2):161–186.

Bull JW, Gordon A, Law EA, Suttle KB, Milner-Gulland EJ. 2014. Importance of baseline specification in evaluating conservation interventions and achieving no net loss of biodiversity. Conserv Biol. 28(3): 799–809.

Burgess ND, Balmford A, Cordeiro NJ, Fjeldså J, K€uper W, Rahbek C, Sanderson EW, Scharlemann JPW, Sommer JH, Williams PH. 2007. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. Biol Conserv. 134(2):164–177.

Burgess ND, Clarke GP, editors. 2000. The coastal forests of Eastern Africa. Cambridge (UK): IUCN Publications Services Unit. Burgess ND, Clarke GP, Rodgers WA. 1998. Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. Biol J Linnean Soc. 64(3):337–367.

Chiarucci A, Bacaro G, Filibeck G, Landi S, Maccherini S, Scoppola A. 2012. Scale dependence of plant species richness in a network of protected areas. Biodivers Conserv. 21 (2):503–516.

Chiarucci A, Bacaro G, Scheiner SM. 2011. Old and new challenges in using species diversity for assessing biodiversity. Philos Trans R Soc Biol Sci. 366(1576):2426–2437.

Chiarucci A, Piovesan G. 2020. Need for a global map of forest naturalness for a sustainable future. Conservation Biology. 34(2):368–372.

Cincotta RP, Wisnewski J, Engelman R. 2000. Human population in the biodiversity hotspots. Nature. 404(6781):990–992.

Collen B, Ram M, Zamin T, McRae L. 2008. The tropical biodiversity data gap: addressing disparity in global monitoring. Trop Conserv Sci. 1(2): 75–88.

Connor EF, McCoy ED. 1979. The Statistics and Biology of the SpeciesArea Relationship. Am Nat. 113(6):791–833.

Corlett RT. 2016. Plant diversity in a changing world: status, trends, and conservation needs. Plant Divers. 38(1):10–16.

Craven D, Knight TM, Barton KE, Bialic-Murphy L, Chase JM. 2019. Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. Proc Natl Acad Sci USA. 116(33):16436–16441.

Crist TO, Veech JA, Gering JC, Summerville KS. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of a, b and c diversity. Am Nat. 162 (6):734–774.

Dengler J, Matthews TJ, Steinbauer MJ, Wolfrum S, Boch S, Chiarucci A, Conradi T, Dembicz I, Marceno C, Garc ıa-Mijangos I, et al. 2020. Species–area relationships in continuous vegetation: evidence from Palaearctic grasslands. J Biogeogr. 47(1):72–86.

Edwards WM. 2007. A biodiversity evaluation of Kenya's coastal forest systems. Master's degree research. Canterbury (UK): Durrel Institute of Conservation and Ecology, University of Kent.

FAO and UNEP. 2020. The state of the world's forests 2020. Forests, biodiversity and people. Rome (Italy): FAO Publications.

Fungomeli M, Cianciaruso M, Zannini P, Githitho A, Frascaroli F, Fulanda B, Kibet S, Wiemers M, Mbuvi T, Matiku P, Chiarucci A.2020a. Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, Plant Biosystems. https://doi.org/10.1080/11263504.2020.1834461

Fungomeli M, Githitho A, Frascaroli F, Chidzinga S, Cianciaruso M, Chiarucci A. 2020b. A new vegetation-plot database for the Coastal forests of Kenya. Vegetation Classification and Survey 1: 103-109. https://doi.org/10.3897/VCS/2020/47180

Githitho AN. 2016. Listing the sacred Mijikenda kaya forests as UNESCO world heritage sites: the long journey. J Africanistes. 86:198–217.

Gleason HA. 1922. On the relation between species and area. Ecology. 3(2):158–162. Glover J, Robinson P, Henderson JP. 1954. Provisional maps of the reliability of annual rainfall in East Africa. Q J Meteorol Soc. 80:607.

Habel JC, Casanova ICC, Zamora C, Teucher M, Hornetz B, Shauri H, Mulwa RK, Lens L. 2017. East African coastal forest under pressure. Biodivers Conserv. 26(11):2751–2758.

Hannus JJ, Numers MV. 2008. Vascular plant species richness in relation to habitat diversity and island area in the Finnish Archipelago. J Biogeogr. 35(6):1077–1086.

Harte J, Smith AB, Storch D. 2009. Biodiversity scales from plots to biomes with a universal species-area curve. Ecol Lett. 12(8):789–797.

Hanski I, Triantis K. 2015. Habitat fragmentation and species richness. J Biogeogr. 42(5):989–993. Hawn CL, Herrmann JD, Griffin SR, Haddad NM. 2018. Connectivity increases trophic subsidies in fragmented landscapes. Ecol Lett. 21(11):1620–1628.

Hill JK, Gray MA, Khen CV, Benedick S, Tawatao N, Hamer KC. 2011. Ecological impacts of tropical forest fragmentation: how consistent are patterns in species richness and nestedness? Phil Trans R Soc B. 366(1582):3265–3276.

Hobohm C, Janisova M, Steinbauer M, Landi S, Field R, Vanderplank S, Beierkuhnlein C, Grytnes JA, Vetaas OR, Fidelis A, et al. 2019. Global endemics-area relationships of vascular plants. Perspect Ecol Conserv. 17(2):41–49.

Kenya Forest Research Institute. 2016. A field guide to valuable trees and shrubs of Kaya Mudzimuvya forest in Kilifi County, Kenya. Nairobi (Kenya): Kenya Forest Research Institute.

Kibet S. 2011. Plant communities, species diversity, richness, and regeneration of a traditionally managed coastal forest, Kenya. For Ecol Manage. 261(6):949–957.

Kuper W, Sommer JH, Lovett JC, Barthlott W. 2006. Deficiency in African plant distribution data – missing pieces of the puzzle. Bot J Linnean Soc. 150(3):355–368.

Lehmann I, Kioko E. 2005. Lepidoptera diversity, floristic composition and structure of three Kaya forests on the South coast of Kenya. J East Afr Nat Hist. 94 (1):121–163.2.0.CO;2] .

Lomolino MV. 2001. The species-area relationship: new challenges for an old pattern. Prog Phys Geogr. 25(1):1–21. Lovett JC. 1998. Eastern tropical African centre of endemism: a candidate for world heritage status. J East Afr Nat Hist. 87(1):359–366.2.0.CO;2].

Lovett JC. 2008. Biogeography and ecology of the rain forests of Eastern Africa. Cambridge (UK): Cambridge University Press.

Luke WRQ. 2005. Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. J East Afr Nat Hist. 94 (1):5–120.2.0.CO;2].

Luke WRQ, Githitho AN. 2016. Biodiversity and the Kaya forests. In: Hoorweg J, Muthiga N, editors. Recent advances in coastal ecology: studies from Kenya. Leiden (Netherlands): African Studies Centre; p. 293–301.

Maitner B. 2020. BIEN: tools for accessing the botanical information and ecology network database. R package ver. 1.2.4. [accessed 2020 June 9]. https://CRAN.R-project.org/package=BIEN.

Matiku P, Ogol C, Mireri C. 2012. The impact of participatory forest management on forest integrity and biodiversity in Arabuko-Sokoke forest. Afr J Ecol. 50(2):184–192.

Matthews TJ, Cottee-Jones HE, Whittaker RJ. 2014. Habitat fragmentation and the species-area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. Diversity Distrib. 20(10):1136–1146.

Matthews TJ, Triantis KA, Whittaker RJ, Guilhaumon F. 2019. sars: an R package for fitting, evaluating and comparing species–area relationship models. Ecography. 42(8):1446–1455.

Mbuvi MTE, Wekesa L, Wekesa C, Leley N, Ntabo M, Eshitera A, Karangi M, Manyala P, Okeyo M, Sheikh M, et al. 2016. Capability map for growing high value tree species in the Coast region of Kenya. A guide for farmers, forest managers, extension agents and investors. Print Maxim Nairobi Kenya.

McClean CJ, Lovett JC, Kuper W, Hannah L, Sommer JH, Barthlott W, Termansen M, Smith GF, Tokumine S, Taplin JRD, et al. 2005. African plant diversity and climate change. Missouri Bot Garden. 92:139–152.

Metcalfe K, Ffrench-Constant R, Gordon I. 2010. Sacred sites as hotspots for biodiversity: the Three Sisters Cave complex in coastal Kenya. Oryx. 44(01):118–123.

Mihoub JB, Henle K, Titeux N, Brotons L, Brummitt NA, Schmeller DS. 2017. Setting temporal baselines for biodiversity: the limits of available monitoring data for capturing the full impact of anthropogenic pressures. Sci Rep. 7(1):13.

Moerman DE, Estabrook GF. 2006. The botanist effect: counties with maximal species richness tend to be home to universities and botanists. J Biogeogr. 33(11):1969–1974.

Moomaw JC. 1960. A study of the plant ecology of the coast region of Kenya, East Africa. Nairobi (Kenya): Government Printer. https://edepot.wur.nl/493400.

Muchiri MN. 2001. Forest inventory report for the indigenous forests in Arabuko Sokoke forest reserve. Kenya Forest. Nairobi (Kenya): Research Institute.

Mutangah JG, Mwaura PK. 1992. A vegetation survey report, Arabuko Sokoke forest management and conservation project. Kenya: East African Herbarium, National Museums of Kenya.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature. 403(6772):853–858.

Ngumbau VM, Luke Q, Nyange M, Wanga VO, Watuma BM, Mbuni YM, Munyao JN, Oulo MA, Mkala EM, Kipkoech S, et al. 2020. An annotated checklist of the coastal forests of Kenya, East Africa. PhytoKeys. 147:1–191.

Noad T, Birnie A. 1990. A fully illustrated field guide: trees of Kenya. Nairobi (Kenya): General Printers Ltd. Pakia M. 2005. Plant ecology and ethnobotany of two sacred forests (Kayas) of Kenyan Coast. Bayreuth (Germany): Die Deutsche Bibliothek.

Pakia M, Cooke JA, van Staden J. 2003. The ethnobotany of the Midzichenda tribes of the coastal forest areas in Kenya: 2. Medicinal plant uses. S Afr J Bot. 69(3):382–395.

Pautasso M, McKinney ML. 2007. The botanist effect revisited: plant species richness, county area, and human population size in the United States. Conserv Biol. 21(5):1333–1340.

Pedersen TL. 2019. patchwork: the composer of plots. R package version 1.0.0. [accessed 2020 June 9]. https://CRAN.R-project.org/package= patchwork.

Petřík P, Pergl J, Wild J. 2010. Recording effort biases the species richness cited in plant distribution atlases. Perspect Plant Ecol Evol Syst. 12(1):57–65.

Phillips HRP, Halley JM, Urbina-Cardona JN, Purvis A. 2018. The effect of fragment area on site-level biodiversity. Ecography. 41(7):1220–1231.

R Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/.

Rajat J, Jefwa J, Mwafaida J. 2017. Survey on indigenous food plants of Kaya Kauma and Kaya Tsolokero in Kilifi County Kenya. J Life Sci. 11(2):82–90.

Robertson SA. 1987. Preliminary floristic survey of Kaya forests of coastal Kenya. Nairobi (Kenya): WWF. Robertson SA, Luke WRQ. 1993. The vegetation and conservation status of Kaya coastal forests in Kenya. Nairobi (Kenya): WWF.

Rösch V, Tscharntke T, Scherber C, Batáry P. 2015. Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. Oecologia. 179(1):209–222. Sastre P, Lobo JM. 2009. Taxonomist survey biases and the unveiling of biodiversity patterns. Biol Conserv. 142(2):462–467.

Serra-Diaz JM, Enquist BJ, Maitner B, Merow C, Svenning JC. 2017. Big data of tree species distributions: how big and how good? For Ecosyst. 4(1):1–12.

Shepheard-Walwyn E. 2014. Culture and conservation in the sacred sites of coastal Kenya [PhD thesis]. Canterbury (UK): Durrel Institute of conservation and ecology, University of Kent.

Slowikowski K. 2020. ggrepel: automatically position non-overlapping text labels with ’ggplot2’. R package version 0.8.2. [accessed 2020 June 9]. https://CRAN.R-project.org/package=ggrepel.

Sommer JH, Nowicki C, Rios L, Barthlott W, Ibisch PL. 2003. Extrapolating species ranges and biodiversity in data-por countries: the computerized model BIOM. Rev Soc Boliviana Bot. 4(1):171–190.

Stephenson PJ, Bowles-Newark N, Regan E, Stanwell-Smith D, Diagana M, Hoft R, Abarchi H, Abrahamse T, Akello C, Allison H, et al. 2017. Unblocking the flow of biodiversity data for decision-making in Africa. Biol Conserv. 213:335–340.

Tuomisto H. 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia. 164(4):853–860.

Wekesa C, Otuoma J, Ngugi J, Muturi G. 2017. Floristic composition and structure of Arabuko Sokoke forest. In: Ochieng’ D, Luvanda A, Wekesa C, Mbuvi MTE, Ndalilo A, editors. Biodiversity status of Arabuko Sokoke forest, Kenya. Nairobi (Kenya): Kenya Forest Research Institute; p. 8–13.

Wass P, editor. 1995. Kenya’s indigenous forests: status, management and conservation. Gland (Switzerland): IUCN.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York (NY): Springer-Verlag.

Chapter 2

A new vegetation-plot database for the Coastal Forests of Kenya

Chapter published as:

Fungomeli, M.[1,2], Githitho, A.[2], Frascaroli, F.[1,3], Chidzinga, S.[2], Cianciaruso, M.[4] and Chiarucci, A.[1] (2020). A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey*, 1: 103-109. https://doi.org/10.3897/VCS/2020/47180

[1]Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum- University of Bologna, Bologna, Italy
[2]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Kilifi, Mombasa, Kenya
[3]Lòm Research, Rocca d'Arce, Frosinone, Italy
[4]Department of Ecology, Universidade Federal de Goiás, Brazil

Abstract

Biodiversity data based on standardised sampling designs are key to ecosystem conservation. Data of this sort have been lacking for the Kenyan coastal forests despite being biodiversity hotspots. Here, we introduce the Kenyan Coastal Forests Vegetation-Plot Database (GIVD ID: AF-KE-001), consisting of data from 158 plots, subdivided into 3,160 subplots, across 25 forests. All plots include data on tree identity, diameter and height. Abundance of shrubs is presented for 316 subplots. We recorded 600 taxa belonging to 80 families, 549 of which identified to species and 51 to genus level. Species richness per forest site varied between 43 and 195 species; mean diameter between 13.0 ± 9.8 and 30.7 ± 20.7 cm; and mean tree height between 5.49 ± 3.99 and 12.29 ± 10.61 m. This is the first plot-level database of plant communities across Kenyan coastal forests. It will be highly valuable for analysing biodiversity patterns and assessing future changes in this ecosystem. Taxonomic reference: African Plant Database (African Plant Database version 3.4.0). Abbreviations: DBH = diameter at breast height; GIVD = Global Index of Vegetation-Plot Databases; KECF-VPD = Kenyan Coastal Forests Vegetation Plot Database.

Keywords: Coastal forests, conservation, Global Index of Vegetation-Plot Databases, biodiversity hotspots, Kaya, Kenya, plant species diversity, sacred forests, vegetation plot

GIVD Fact Sheet: Kenya Coastal Forests Vegetation-Plot Database (KECF-VPD)

GIVD Database ID: AF-KE-001			**Last update:** 2020-03-20
Kenya Coastal Forests Vegetation Plot Database		**Web address:** http://www.givd.info/ID/AF-KE-001	
Database manager(s): Maria Fungomeli (maria.fungomeli2@unibo.it); Alessandro Chiarucci (alessandro.chiarucci@unibo.it)			
Owner: Maria Fungomeli, PhD Student-University of Bologna, Dept of Biology, Geology & Envtal Sci. Senior Curator & Research Scientist, Coastal Forests Conservation Unit, Center for Biodiversity National Museums of Kenya e-mail: mfungomeli@museums.or.ke; maria.fungomeli2@unibo.it; fungomaria@yahoo.com			
Scope: A plant species diversity survey of the Coastal Forests of Kenya. The survey covered 25 forests with details of trees and shrubs species, DBH & Height, georeference of sites & transects. Plants were identified to species level where possible otherwise genus level used.			
Availability: according to a specific agreement		**Online upload:** no	**Online search:** no
Database format(s): Excel		**Export format(s):** Excel, Open Document, PDF, CSV file	
Plot type(s): nested plots		**Plot-size range:** 50 to 1000	
Non-overlapping plots: 158	**Estimate of existing plots:** 158	**Completeness:** 100%	**Status:** finished
Total no. of plot observations: 158	**Number of sources (biblioreferences, data collectors):** 0		**Valid taxa:** 600
Countries (%): KE: 100%			
Formations: Forest: 100% = Terrestrial: 100%			
Guilds: [NA]			
Environmental data (%): altitude: 100%			
Performance measure(s): presence/absence only: 100%; number of individuals: 100%; measurements like diameter or height of trees: 100%			
Geographic localization: GPS coordinates (precision 25 m or less): 100%			
Sampling periods: 2010-2019: 100%			
Information as of 2020-03-20 further details and future updates available from http://www.givd.info/ID/AF-KE-001			

1.0 Introduction

Eastern African coastal forests are tropical forests known for their rich biodiversity and high levels of endemism, including a concentration of rare and threatened taxa and high diversity of endemic plant and animal species (Wass 1995; Burgess et al. 1998; Lovett 1998; Burgess and Clarke 2000; Myers et al. 2000; Luke 2005; Azeria et al. 2007). According to Burgess and Clarke (2000), this vegetation type hosts more than 4,500 plant species and 1,050 plant genera, the majority of which are woody. This rich biodiversity has been largely attributed to favourable climatic conditions and a wide range of ecological niches (Moomaw 1960; Lovett 1998; Burgess and Clarke 2000; Montagnini and Jordan 2010). Overall, these forests extend along the coastal edge of Eastern Africa along the Indian Ocean stretching from Somalia in the north, through coastal Kenya and Tanzania, and all the way to Mozambique in the south. They have been defined as the "Swahilian centre of endemism", which constitutes a hotspot of endemism in Africa (Burgess et al. 1998; Luke 2005).

For millennia, Eastern African coastal forests have supported livelihoods both locally and regionally and played a major role as high conservation value ecosystems (Wass 1995). However, they are increasingly facing a number of threats which include a growing population and increased anthropogenic activities such as illegal logging, poaching, charcoal burning and agriculture expansion, all activities leading to increased deforestation (Burgess et al. 1998; Burgess and Clarke 2000; Habel et al. 2017). According to Wass (1995) and Burgess et al. (1998), these threats have had severe impacts and resulted in the heavy fragmentation of once connected forests. Some 10% of the original forest cover is estimated to remain, of which only 17% are under some kind of protection (Wass 1995; Burgess and Clarke 2000). Conserving and sustainably managing the remaining forests of the region requires a developed and enhanced biodiversity monitoring system, which is currently lacking. Developing such a system requires baseline biodiversity data, which are currently scant, limited and outdated.

The Kenyan coastal forests fall within the Eastern African coastal forests. Despite their global significance as biodiversity hotspots (Burgess et al. 1998; Myers et al. 2000; Hobohm et al. 2019), systematic biodiversity data survey based on a standard design are still lacking. The first-ever vegetation survey of the coastal forests of Kenya was carried out in 1987 without using a vegetation plot design (Robertson and Luke 1993), with the aim to create a list of species found in these forests (Robertson and Luke 1993; Luke 2005). A standardized dataset based on vegetation plots and suitable for analyzing spatial and temporal patterns across the whole area does still not exist. Filling this knowledge gap is even more urgent given the continuing deforestation and the uncertainty of future climate change projections. There is need to undertake ecological studies that can provide baseline data required for sound ecological monitoring and evaluation. This paper provides a basic description of a new vegetation-plot database, developed as part of a collaboration between the University of Bologna and the National Museums of Kenya. The database contains data of 25 different forest patches and was developed with the goal to produce a solid sample-based (Chiarucci 2007) overview of the plant communities in the Kenyan coastal forests. The resulting vegetation-plot database represents the first standardized plant data set for these forests and a fundamental tool for future assessments and monitoring of a key biodiversity hotspot.

2.0 Study Area: the coastal forests of Kenya in the context of Eastern African forests

The coastal forests of Kenya are part of the Eastern African coastal forests ecoregion and are isolated patches of evergreen to semi-evergreen closed canopy forests. They present unique remnants of indigenous ecosystems and are part of the North Zanzibar-Inhambane Regional Mosaic, which extends from southern Somalia through coastal Kenya to southern Tanzania, including the islands of Zanzibar and Pemba (Burgess et al. 1998, Burgess and Clarke 2000; Githitho 2004; Peltorinne 2004; Luke 2005), and part of the biodiversity hotspot known as the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et. al. 2000). They stretch from the north to south along the Kenyan coast, and are mostly found on ancient coral reef bed rocks formed as a result of sea level drops. Therefore, they span over a variety of altitudinal gradients and climatic zones. The climatic range of the Kenyan coastal forests is tropical with coastal high humidity (Burgess and Clarke 2000). The annual rainfall follows distinctive rainy seasons and generally increases towards the southern coast and at higher altitudes. The rainfall pattern differs from the north to the south. In the northern region, there are two rainy seasons made of long rains (April to June) and short rains (November to December), while in the south, there is only one long rain season between April and June. However, both south and north regions have an annual rainfall variability where the seasons may vary from year to year. Overall, the mean annual rainfall ranges from 900 mm to 1200 mm (Glover et al. 1954; Moomaw 1960; Burgess et al. 1998; Burgess and Clarke 2000). The mean temperature ranges between 30°C during the dry season (December-March) to 25°C during the long rain season (April-September), with relatively cooler temperatures in the southern coast.

It is estimated that approximately 3,170 km^2 of Eastern African coastal forests remains in Somalia, Kenya, Tanzania, Mozambique, Zimbabwe and Malawi. Approximately 20% of these forests are found in Kenya (Burgess et al. 1998; Burgess and Clarke 2000; Azeria et al. 2007). The number of Kenyan coastal forests patches was estimated to be 107 patches in early 1990s (Robertson and Luke 1993; Wass 1995; Burgess et al. 1998; Burgess and Clarke 2000; Githitho 2004; Luke 2005; Azeria et al. 2007).

The size and protection status of the Kenyan coastal forests is highly variable. The two largest remaining forests are Arabuko Sokoke (42,000 ha) and Shimba Hills (25,300 ha), which are government protected forest reserves (Table 1). Other government protected forest reserves include Marenje (1,480 ha), Gogoni (832 ha), Buda (670 ha), Dzombo (650 ha) and Mrima (377 ha). The other forest remnants spread over small patches (10 to 75 ha) many of which are considered sacred forests and are managed traditionally and culturally by the local communities (Table 2.1). These forest patches are locally referred to as 'Kaya' (Robertson and Luke 1993;

Wass 1995; Burgess and Clarke 2000; Githitho 2004; Luke 2005; Metcalfe et al. 2010; Githitho 2016; Luke and Githitho 2016).

Table 2.1: Overview of the forest sites included in the Kenyan coastal forest vegetation-plot database, with an indication of their protection status, geographical coordinates, area, number of plots and recorded total species richness per forest site.

Forest ID	Forest name	Protection status	Latitude decimal degree	Longitude decimal degree	Area (ha)	Number of plots	Species richness
Arabuko	Arabuko Sokoke forest	Forest reserve	-3.32138	39.92917	42,000	26	178
Bomu	Kaya Bomu	Sacred forest	-3.93354	39.59635	409	8	154
Buda	Buda forest	Forest reserve	-4.45812	39.39683	670	6	121
Chivara	Kaya Chivara	Sacred forest	-3.69452	39.69132	150	8	140
Chonyi	Kaya Chonyi	Sacred forest	-4.06953	39.53038	200	4	62
Diani	Kaya Diani	Sacred forest	-4.27523	39.58520	20	3	66
Dzombo	Dzombo forest	Forest reserve	-4.42945	39.21545	650	6	90
Fungo	Kaya Fungo	Sacred forest	-3.80068	39.51047	204	4	60
Gandini	Gandini forest	Sacred forest	-4.03443	39.50988	150	5	80
Gogoni	Gogoni forest	Forest reserve	-4.41013	39.47628	832	6	123
Jibana	Kaya Jibana	Sacred forest	-3.84048	39.67382	140	8	195
Kambe	Kaya Kambe	Sacred forest	-3.86766	39.65363	75	6	109
Kauma	Kaya Kauma	Sacred forest	-3.62968	39.73778	75	7	77
Kinondo	Kaya Kinondo	Sacred forest	-4.39427	39.54703	30	3	56
Marenje	Marenji forest	Forest reserve	-4.48458	39.25906	1,480	6	76
Mrima	Mrima forest	Forest reserve	-4.48573	39.26883	377	6	101
Mtswakara	Kaya Mtswakara	Sacred forest	-4.00017	39.51997	248	4	64
Muhaka	Kaya Muhaka	Sacred forest	-4.32568	39.52328	150	5	90
Muvya	Kaya Mudzimuvya	Sacred forest	-3.94175	39.58190	171	4	85
Mwiru	Kaya Mudzimwiru	Sacred forest	-3.95913	39.57372	147	4	70
Ribe	Kaya Ribe	Sacred forest	-3.89922	39.63363	36	5	95
Shimba	Shimba Hills forest	Forest reserve	-4.26940	39.37208	25,300	12	190
Teleza	Kaya Teleza	Sacred forest	-4.14147	39.50342	67	6	91
Tiwi	Kaya Tiwi	Sacred forest	-4.25704	39.59817	10	3	53
Waa	Kaya waa	Sacred forest	-4.19970	39.61565	30	3	43

3.0 Data collection

Sampling was based on a nested plot design consisting of 158 rectangular plots located in 25 forests sites of the Kenyan coastal forests spanning along the coastline, from north to south (Figure 2.1). The sampling was carried out from November 2018 to June 2019. The forests are a mixture of evergreen to semi-deciduous forests. During field work, we experienced a mix of wet and semi-dry season while in the field with a lot of light rains. Hence performing part of the fieldwork during the dry season did not affect plants identification, as most plants remained leafy and some flowering while the few deciduous were commonly locally known by botanist and could be easily identified.

To standardize sampling intensity, the number of plots per forest site was approximately proportional to the forest site area, although with some variation due to site accessibility and fragmentation. The location of the plots within each forest site was randomized with minor adaptations due to accessibility. A minimum distance of 200 m between plots per site was maintained to maximize spatial variation. The plots were laid with a north-south orientation, had a standard size of 10 m × 100 m and were further sub-divided into twenty 10 m × 5 m subplots for a total of 3,160 subplots across the entire study system. We sampled and identified at the species level all woody plant individuals with diameter at breast height (DBH) $\geq$ 5 cm (mostly trees) rooted within each subplot. For each tree, besides DBH, we also measured the height with a hand-held clinometer (Suunto PM-5), or a calibrated measuring pole (50 m) in areas with dense forests where clinometer was difficult to use. Woody plant individuals with DBH $<$ 5 cm, mostly shrubs, were sampled and identified in two of the twenty subplots within a plot, where one was randomly selected in the northern half (subplots 1-10) and the second in the southern half (subplots 11-20) of the plot. The abundance of shrub species was assessed by counting the number of individual shoots rooted within the subplot.

Plants were identified on-site to the species or at least genus level by local botanists and with the use of botanical manuals using standard references for the area (Noad and Birnie 1990;

Beentje 1994; Luke 2005). When on-site identification was not possible, voucher specimens were collected for subsequent identification on the lab with the help of herbarium specimens. Finally, Global Positioning Systems (GPS) devices were used for recording the geographical coordinates and altitude of forest sites and plots (start and end points), and shrub subplots.

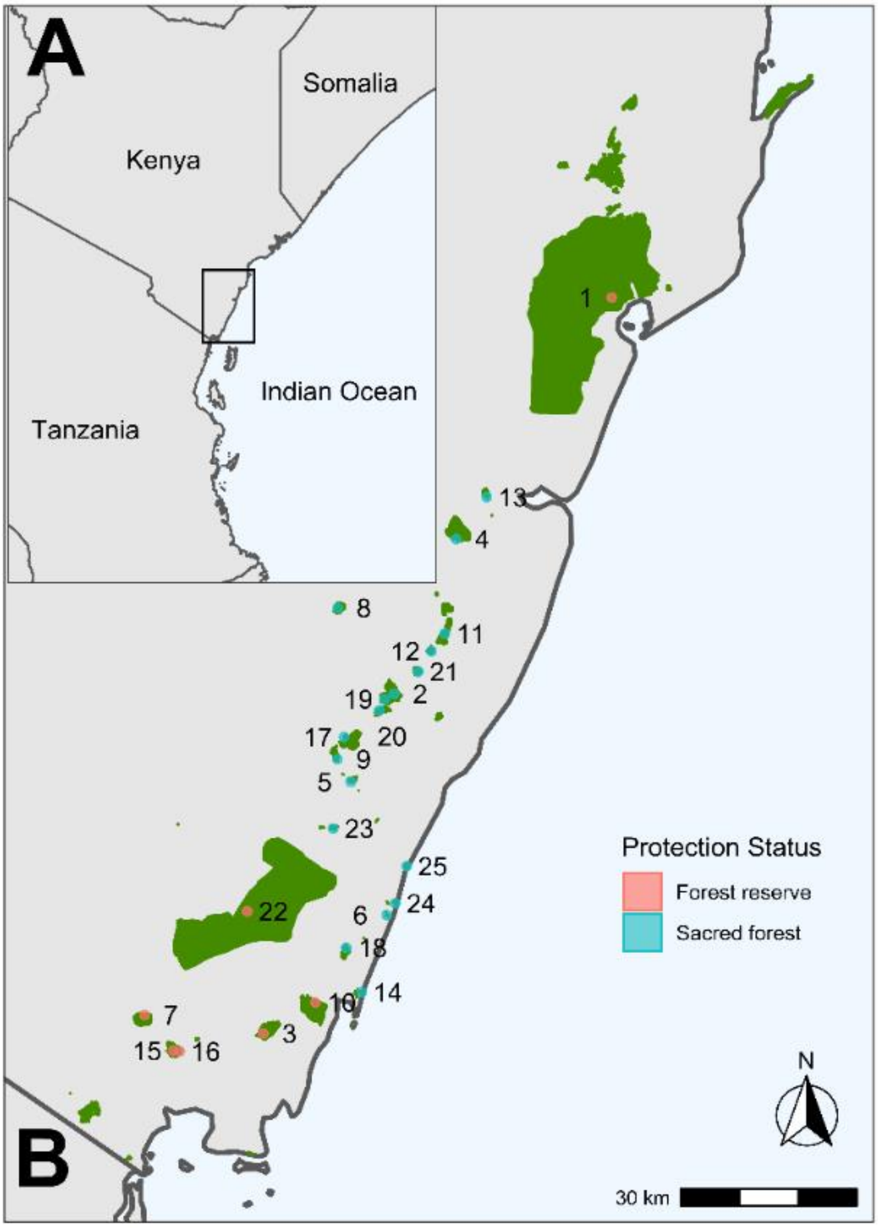


Figure 2.1: **A** Map of Eastern Africa area highlighting the coastal area of Kenya. **B** Coastal forests of Kenya spanning from North to South (all forests identified by green colour with and without numbers), the numbered are the sampled sites with their protection status. 1 = Arabuko, 2 = Bomu, 3 = Buda, 4 = Chivara, 5 = Chonyi, 6 = Diani, 7 = Dzombo, 8 = Fungo, 9 = Gandini, 10 = Gogoni, 11 = Jibana, 12 = Kambe, 13 = Kauma, 14 = Kinondo, 15 = Marenje, 16 = Mrima, 17 = Mtswaka, 18 = Muhaka, 19 = Muvya, 20 = Mwiru, 21 = Ribe, 22 = Shimba, 23 = Teleza, 24 = Tiwi, 25 = Waa.

4.0 Database content

The Kenyan coastal forests vegetation-plot database (KECF-VPD) is registered at the Global Index of Vegetation Database (http://www.givd.info/ID/AF-KE-001). It consists of vegetation data collected in 158 nested plots across 25 forests sites (Table 2.1). The total subplots were 3,160. The sampled forest sites are characterised by different area sizes and protection status, with seven government state forest reserves (377 to 42,000 ha) and 18 sacred sites (10 to 409 ha). Overall, the database includes 40,913 occurrence records relative to a total of 600 distinct taxa belonging to 80 families. 549 species were identified at the specific level and 51 at the genus level belonging to 43 genera. For taxonomy consistency and to avoid misspelt names, plant species names were standardised using the TAXONSTAND package in R statistical software (Cayuela et al. 2017). In total, 19 families had more than 10 species (Table 2.2) with Rubiaceae presenting the highest number of species (63), followed by Leguminosae (61), Malvaceae (34) and Euphorbiaceae (30). Species richness per site varied between 43 species at Waa sacred forest to 195 species at Jibana sacred forest (Table 2.1). The Shimba Hills and Arabuko forest reserves, the largest forest sites, were the richest after Jibana. The number of species increased relative to the area, as expected given the species-area relationship perspective. Some small forest areas, like Jibana, also exhibited high species richness, likely because other factors different from area may have a strong impact in driving local species richness.

The frequency distribution of species richness per plot showed a slightly right-skewed distribution (Figure 2.2), with the highest number of plots harbouring between 35-40 species. The most frequent trees in plots across all sites were *Uvaria acuminata* and *Haplocoelum inoploeum* (Table 2.3). *Hymenaea verrucosa* exhibited the highest mean DBH and height. The shrubs *Monanthotaxis fornicata* and *Synaptolepis kirkii* were among the 20 most frequent woody species in plots (Table 2.3).

Basic forest structure varied across sites (Table 2.4). The highest mean DBH was recorded at Mtswaka sacred forest while the lowest at Chivara sacred forest. Kambe sacred forest exhibited the highest mean height, while Diani sacred forest the lowest. There was a high variation in tree heights from the small to tallest within sites, creating mean heights that would depict a bush rather than a forest, but this is not the case given the large mean DBH recorded. The largest number of tree individuals was sampled at Arabuko and Shimba forest reserves, the largest ones, and where more plots were sampled, while the lowest at Muvya sacred forest.

Table 2.2: List of the most diverse families in the Kenyan coastal forests vegetation-plot database, defined as those having at least 10 different recorded species.

Family	**Number of species**
Rubiaceae	63
Leguminosae	61
Malvaceae	34
Euphorbiaceae	30
Annonaceae	24
Moraceae	23
Sapindaceae	22
Apocynaceae	20
Sapotaceae	18
Rutaceae	17
Celastraceae	16
Combretaceae	16
Lamiaceae	16
Capparaceae	15
Ebenaceae	14
Acanthaceae	12
Phyllanthaceae	12
Salicaceae	11
Anacardiaceae	10

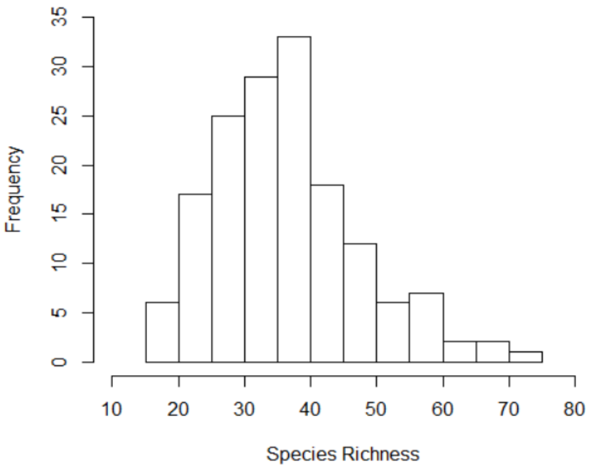


Figure 2.2: Distribution of species richness per plot in the Kenyan coastal forests vegetation-plot database (n = 158 plots).

Table 2.3: List of the 20 most frequent species per plot (n = 158 plots), including family, habit, number of plots in which they have been recorded, and DBH and height (mean ± standard deviation) for species with DBH ≥ 5cm.

Species	**Family**	**Habit**	**Number of plots**	**Mean DBH (±sd) (cm)**	**Mean Height (±sd) (m)**
Uvaria acuminata	Annonaceae	tree	95	7.4 ± 2.13	7.54 ± 7.08
Haplocoelum inoploeum	Sapindaceae	tree	94	11.9 ± 7.46	5.51 ± 2.71
Polysphaeria parvifolia	Rubiaceae	tree	69	5.6 ± 0.57	2.75 ± 0.67
Salacia elegans	Celastraceae	liana	69	7.3 ± 1.87	7.14 ± 2.78
Combretum schumannii	Combretaceae	tree	66	18.5 ± 16.97	9.24 ± 5.74
Hymenaea verrucosa	Leguminosae	tree	66	33.9 ± 21.36	15.73 ± 8.50
Landolphia kirkii	Apocynaceae	liana	66	9.5 ± 3.79	8.21 ± 3.33
Monanthotaxis fornicata	Annonaceae	shrub	66	-	-
Synaptolepis kirkii	Thymelaeaceae	shrub	64	-	-
Cassipourea euryoides	Rhizophoraceae	tree	63	14.7 ± 8.64	8.21 ± 4.02
Asteranthe asterias	Annonaceae	tree	57	6.2 ± 1.60	3.09 ± 1.03
Manilkara sansibarensis	Sapotaceae	tree	57	18.2 ± 11.43	9.41 ± 5.06
Cola minor	Malvaceae	tree	56	12.8 ± 7.79	5.75 ± 3.18
Grewia plagiophylla	Malvaceae	tree	56	12.2 ± 5.71	5.15 ± 2.30
Pyrostria bibracteata	Rubiaceae	tree	56	8.6 ± 5.38	4.25 ± 2.46
Combretum illairii	Combretaceae	liana	54	11.1 ± 13.82	6.00 ± 5.51
Lecaniodiscus fraxinifolius	Sapindaceae	tree	54	20.4 ± 15.06	8.29 ± 5.15
Deinbollia borbonica	Sapindaceae	tree	52	6.7 ± 1.75	2.90 ± 0.66
Allophylus pervillei	Sapindaceae	tree	51	7.0 ± 1.92	3.36 ± 0.83
Suregada zanzibariensis	Euphorbiaceae	tree	51	7.0 ± 2.23	3.83 ± 1.42

Table 2.4: Basic structural data of the Kenyan coastal forest sites expressed as mean (± standard deviation) of the DBH and height, and number of measured trees (n).

Site	Mean DBH (± sd) (cm)	Mean Height (± sd) (m)	n
Arabuko	15.3 ± 12.55	7.73 ± 4.74	2163
Bomu	25.2 ± 22.28	9.99 ± 8.07	275
Buda	16.6 ± 15.14	7.94 ± 6.28	658
Chivara	13.0 ± 9.80	7.26 ± 4.78	539
Chonyi	17.3 ± 15.91	6.79 ± 5.10	216
Diani	16.0 ± 23.26	5.49 ± 3.99	412
Dzombo	18.9 ± 20.84	7.71 ± 5.77	470
Fungo	17.0 ± 14.80	8.74 ± 5.74	208
Gandini	17.3 ± 12.02	7.39 ± 4.45	270
Gogoni	17.5 ± 16.80	7.50 ± 6.10	709
Jibana	18.6 ± 19.45	9.71 ± 7.95	972
Kambe	24.5 ± 25.37	12.29 ± 10.61	274
Kauma	13.4 ± 28.18	7.29 ± 4.67	253
Kinondo	19.5 ± 17.83	9.56 ± 6.92	468
Marenje	16.3 ± 14.18	7.81 ± 5.91	579
Mrima	15.7 ± 15.56	7.12 ± 5.72	485
Mtswaka	30.7 ± 20.71	11.76 ± 7.42	176
Muhaka	24.1 ± 20.97	10.52 ± 8.39	414
Muvya	24.8 ± 20.57	10.69 ± 8.90	110
Mwiru	24.6 ± 20.19	10.64 ± 6.79	153
Ribe	15.5 ± 17.67	7.62 ± 5.74	299
Shimba	15.6 ± 17.16	7.51 ± 6.04	1345
Teleza	17.9 ± 11.03	8.83 ± 5.03	556
Tiwi	14.3 ± 17.73	5.59 ± 3.93	464
Waa	15.8 ± 11.84	6.47 ± 4.10	410

5.0 Conclusion

The KECF-VPD database represents the first vegetation dataset collected according to a standardised plot-based design across Kenyan coastal forests. This database represents a snapshot of the vegetation in a relevant fraction of the existing forest patches in the region. As such, the database provides the best available picture of the current patterns of woody plant biodiversity of these forests. Since the sampling design was based on different scale levels (forest sites, plots and subplots), the database also offers a unique opportunity for exploring the patterns and determinants of plant diversity in the Kenyan Coastal forests across spatial scales. These data will provide a tool and baseline for assessing future changes in the study system.

6.0 Future perspectives

The current KECF-VPD database covers 25 Kenyan coastal forests. There is potential to extend the survey to the remaining coastal forests not covered by this research. The database is presently being explored for analysing species diversity data, in terms of species-area relationships, beta diversity and species composition. A successive phase will also be to develop a biodiversity monitoring platform for these forests. Such a platform could be shared with the institutions, organisations and communities working and living around these forests to promote their conservation and sustainable management. Furthermore, integrating socio-economic aspects into the research would be essential to capture local level forest use by adjacent communities and their attitude towards forest management and conservation.

Data availability

The database is presently stored at the University of Bologna. Its availability is currently restricted to the PhD project within which it was developed. Possible uses by other interested researchers are presently limited on the bases of specific agreement to be discussed with the database administrators. After an embargo period, the data will be contributed to sPlot – the global vegetation plot database (Bruelheide et al. 2019).

Author contributions

A.C conceptualised the idea and provided overall supervision. M.F, F.F and A.C developed the field work sampling design. A.G guided on overall study area briefing, forest sites selection and accessibility. M.F carried out the field work, collected, compiled, standardised data and prepared the manuscript. S.C contributed to field sampling and plant specimen identification. M.C reviewed the species data and verified taxonomy for African and tropical vegetation species. All authors contributed to the final manuscript.

7.0 References

African Plant Database (2019) Conservatoire et Jardin botaniques de la Ville de Genève, Geneva, CH and South African National Biodiversity Institute, Pretoria, ZA (version 3.4.0). https://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php/ [accessed 9 Dec 2019]

Azeria ET, Sanmartin I, Stephan AS, Carlson A, Burgess ND (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. Biodiversity and Conservation 16: 883–912. https://doi.org/10.1007/s10531-006-9022-0

Beentje HJ (1994) Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi, 722 pp.

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, ... Winter M (2019) sPlot: A new tool for global vegetation analyses. Journal of Vegetation Science 30: 161–186.

Burgess ND, Clarke GP, Rodgers WA (1998) Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. Biological Journal of the Linnean Society 64: 337–367. https://doi. org/10.1111/j.1095-8312. 1998.tb00337.x

Burgess ND, Clarke GP [Eds] (2000) The Coastal Forests of Eastern Africa. IUCN, Gland, CH and Cambridge, UK, 443 pp.

Cayuela L, Stein A, Oksanen J (2017) Taxonstand: Taxonomic standardization of plant species names. R package version 2.1. https:// CRAN.R-project.org/package=Taxonstand [accessed 15 July 2019]

Chiarucci A (2007) To sample or not to sample? That is the question for the vegetation scientist. Folia Geobotanica 42: 209–216. https://doi. org/10.1007/BF02893887

Githitho AN (2004) The coastal terrestrial forests of Kenya: A report on resources threats and investments. A report to WWF Eastern coastal forest programme. http://coastalforests.tfcg.org/pubs/CFResource-Ken.pdf [accessed 3 Oct 2019]

Githitho AN (2016) Listing the sacred Mijikenda kaya Forests as UNESCO World Heritage Sites: The Long Journey, Journal des africanistes [En ligne], 86-1, mis en ligne le 10 avril 2018. http://journals.openedition.org/africanistes/4971 [accessed 3 Oct 2019]

Glover J, Robinson P, Henderson JP (1954) Provisional maps of the reliability of annual rainfall in East Africa. Quarterly Journal of the Meteorological Society 80: 1–607. https://doi.org/10.1002/qj.49708034609

Habel J, Constanza I, Zamora C, Teucher M, Hornetz B, Shauri H, Mulwa R, Lens L (2017) East African coastal forest under pressure. Biodiversity and Conservation 26: 2751–2758. https://doi.org/10.1007/ s10531-017-1375-z

Hobohm C, Janišová M, Steinbauer MJ, Landi S, Field R, Vanderplank S, Beierkuhnlein C, Grytnes J-A, Vetaas OR, … Chiarucci A (2019) Global endemics-area relationships of vascular plants. Perspectives in Ecology and Conservation 17: 41–49. https://doi.org/10.1016/j. pecon.2019.04.002

Lovett JC (1998) Eastern Tropical African Centre of Endemism: A Candidate for World Heritage Status. Journal of East African Natural History 87: 359–366. https://doi.org/10.2982/0012-8317(1998)87[359:ETACOE]2.0.CO;2

Luke WRQ (2005) Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. Journal of East African Natural History 94: 5–121. https://doi.org/10.2982/0012-8317(2005)94[5:ACOTPO]2.0.CO;2

Luke WRQ, Githitho AN (2016) Biodiversity and the Kaya forests. In: Hoorweg J, Muthiga N (Eds) Recent Advances in Coastal Ecology: Studies from Kenya. African Studies Centre, Leiden, 293–301. https://www.oceandocs.org/bitstream/handle/1834/9014/ktf70ex1253933-067-20

Metcalfe K, French-Constant R, Gordon I (2010) Sacred sites as hotspots for biodiversity: The Three Sisters Cave complex in coastal Kenya. Oryx 44: 118–123. https://doi.org/10.1017/S0030605309990731

Moomaw JC (1960) A Study of the Plant Ecology of the Coast Region of Kenya, East Africa. Government Printer, Nairobi, 62 pp. https:// edepot.wur.nl/493400

Montagnini F, Jordan CF (2010) Tropical Forest Ecology. Springer, Berlin, 295 pp. https://doi.org/10.1007/b138811

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

Noad T, Birnie A (1990) A Fully Illustrated Field Guide: Trees of Kenya. General Printers Ltd, Nairobi, 350 pp.

Peltorinne P (2004) The forest types of Kenya. In: Pellikka P, Ylhäisi J, Clark B (Eds) Taita Hills and Kenya, 2004 – seminar, reports and journal of a field excursion to Kenya [Expedition reports of the Department of Geography 40]. University of Helsinki, Helsinki, 8–13.

Robertson SA, Luke WRQ (1993) The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi, 425 pp. https:// www.africabib.org/rec.php?RID=K00001940

Wass P [Ed.] (1995) Kenya's indigenous forests: status, management and conservation. IUCN, Gland, CH and Cambridge, UK, 220 pp. https:// portals.iucn.org/library/sites/library/files/documents/FR-014.pdf

Chapter 3

Patterns and community structure of woody plant diversity of the coastal forests of Kenya

Chapter to be published as:

Maria Fungomeli[1,2, *], Frascaroli Fabrizio[1,3], Piero Zannini[1], Marcus Cianciaruso[4], Anthony Githitho[2, ,]
Juri Nascimbene[1] & Alessandro Chiarucci[1]

[1]Biogeography and Macroecology lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy
[2]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Mombasa, Kilifi, Kenya
[3]Lòm Research, Rocca d'Arce, Frosinone, Italy
[4]Department of Ecology, Universidade Federal de Goiás, Brazil

Abstract

Aims: The coastal forests of Kenya are unique tropical forest fragments, globally rich in biodiversity, and species diversity in a matrix of increased adjacent population, degradation and biodiversity loss. A fundamental objective has been to conserve as much of these indigenous forest patches across their spatial distribution. However, there is lack of studies covering a wide range of these forest fragments for a conservation biogeography approach. Here, we investigate patterns and drivers of forest structure, species diversity and distribution of plant communities across a significant number of the presently existing remnants of the Kenyan coastal forests and within protection status of forest reserves and sacred forests.

Location: Coastal forests of Kenya.

Methods: We sampled woody vegetation (trees, lianas and shrubs) in 25 forest fragments composed of 18 sacred forests and seven forest reserves using a total of 158 plots each measuring 10m x 100m. We measured the diameter at breast height DBH>5cm and height, while shrubs were recorded in two subplots of each plot.

Results: We recorded 600 taxa belonging to 343 genera and 80 families. We found forest structure, composition and species diversity to be significantly different across forest sites and between sacred forests and forest reserves. Species accumulation curve and multiplicative beta partitioning showed a significantly higher beta diversity across forest sites than within plots and subplots (alpha diversity). The strongest environmental drivers were mean Shannon land use, mean rainfall, temperature, altitude and distance from the coast respectively.

Conclusions: Our results present for the first time a quantitative information on the coastal forests of Kenya depicting a heterogenous structure across the Kenyan coastal forests. Broad-scale conservation strategies that includes beta diversity across biogeographical and ecological scales of the Kenyan coastal forests are fundamental to maximise biodiversity and more so inclusion of the sacred forests in the protected areas network.

Keywords: Plant species composition**,** species diversity, forest structure, coastal forests, basal area, conservation, Kaya

1.0 Introduction

The coastal forests of Kenya are unique tropical forest fragments, globally rich in biodiversity, endemism and species diversity in a matrix of increased adjacent population, degradation and biodiversity loss (Burgess and Clarke, 2000; Mittermeier et al., 2011). They also contain a high plant diversity making them high conservation value areas while locally supporting livelihoods (Mittermeier et al., 2011). A fundamental objective has been to conserve as much of these indigenous forest patches biodiversity across their spatial distribution. However, there is lack of studies covering a wide range of these forest fragments within a conservation biogeography context. As such, conservation biogeography would provide the understanding of the patterns of species diversity and drivers that determine their geographical distribution across spatial scales for effective conservation plans (Hanski, 2015; Zwiener et al., 2020). A combination of species diversity and forest structure is fundamental for a wholistic approach to management (Chiarucci et al., 2011).

The coastal forests of Kenya are part of the world biodiversity hotspots of Coastal forests of Eastern Africa (Myers et al., 2000), occurring as fragmented patches and supporting a wide range of ecosystem services (Azeria et al., 2007; Mittermeier et al., 2011). Additionally, they occur in two protection management regimes of forest reserves and sacred forests, where the former are protected by state government and the latter locally referred to as *'Kayas'* are considered sacred by the local communities and managed for their religious and cultural practices. Moreover, in terms of their sizes, the forest reserves are relatively large reserves such as the Arabuko Sokoke forest (420,000 ha), Shimba Hills forest (25,300 ha) and Marenje forest (1,480 ha), while the sacred forests appear as highly relatively small patches 10-75 ha (Githitho, 2016).

Patterns of forest structure, composition and species diversity have shown to be influenced by environmental deterministic processes, biotic and abiotic interactions, dispersal limitation and other historical factors (Balsega, 2010; Butaye et al. 2001; Toledo et al., 2012; Tuomisto et al., 2003;). These three factors, however, interact differently or act as combined ecological processes influencing species diversity and composition locally and also across spatial scale. Considerably, in the coastal forests of Kenya fragments, we hypothesize that plant species diversity presently existing within the Kenyan coastal forests is not only determined by natural factors such as environmental drivers, but also by anthropogenic factors such as management practices, disturbance and fragmentation. Moreover, studies have shown that forest structure influences plant species diversity, habitat conditions and general forest productivity (Schweitzer and Dey, 2011). Consequently, species diversity is influenced by multi factors that include micro-habitats, soil type, climate and biotic interactions and these tend to vary with spatial scale (Whittaker, 1967). Inevitably, understanding the underlying factors of plant species diversity and distribution patterns is a crucial step for the conservation and management of plant communities and ecosystems (Toledo et al., 2012).

Due to the to their wide extent in spatial coverage of the Coastal forests of Kenya, they are exposed to various gradients of climatic and ecological conditions, that may drive a variation in plant species diversity and distribution (Ghazoul and Sheil, 2010; Montagnini and Jordan, 2010; Whitmore, 1998). Furthermore, as a result of their increasing anthropogenic disturbance, and increased human population, it has led to ecological degradation, which has reduced the forests of their size and biodiversity (Mittermeier et al., 2011; Shepheard, 2014; Tabor et al., 2010). The final result is the reduction of the once expansive forests into several remnant patches along the coastal strip (Azeria et al., 2007; Burgess and Clarke, 2000; Schweitzer and Dey, 2011). Moreover, the extent of fragmentation, difficulty in accessibility for some fragments, remote rural locations, and high costs of field surveys have made it a challenge to gather a comprehensive knowledge of plant species diversity across the Kenyan coastal forests (see Fungomeli et al., 2020a). Previous vegetation studies have either been based on the compilation of plant checklists (Robertson and Luke, 1993; Luke 2005), or targeted single stand forests (Burgess et al., 1998; Edwards, 2007; Kibet, 2011; Lehman and Kioko, 2005; Luke, 2005; Metcalfe et al., 2010; Muchiri et al., 2001; Mutangah and Mwaura, 1992; Pakia, 2005; Rajat et al., 2017). Nevertheless, some forest fragments remain unexplored and unstudied, living a knowledge gap of their species composition and spatial variation (Fungomeli et al., 2020a, 2020b). To our knowledge, there is no study on the coastal forests of Kenya that provided a vegetation survey large enough to be used for a comprehensive biogeographical, spatial and ecological analysis of the plant communities of the Kenyan Coastal forests, that can also be used as a basis to enhance conservation measures. Furthermore, the existing protection status of forest reserves and sacred forests have given a bias to relatively more surveys being conducted on forest reserves, leaving a wealth of unexplored biodiversity in the small fragments of sacred forest sites despite them being higher in number and spatially distributed (see Fungomeli et al. 2020a, 2020b).

This study provides a plant community analysis based on a systematic vegetation survey across the Kenyan coastal forests biodiversity hotspot. In particular, we investigated patterns and drivers of species diversity and distribution of plant communities across a significant number of the presently existing remnants of the Kenyan coastal forests and within protection status of forest reserves and sacred forests. We aim to understand the variation in species diversity and distribution with the following specific questions:

i. how does forest structure, species composition and diversity vary across the coastal forest sites and within forest reserves and sacred forests?
ii. what are the drivers, both natural and anthropogenic (i.e., distance from the coast, elevation, Shannon land use, and climatic variables) that influence plant community composition across forests patches?
iii. how does species diversity components of alpha and beta diversity determine the variation in plant community composition across forest sites?

We set a hypothesis that forest structure, species composition and diversity will be significantly higher across forest sites and within sacred forests and forest reserves.

2.0 Materials and Methods

2.1 Study Area

The coastal forests of Kenya fall within the biodiversity hotspot known as the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et al., 2000). They are located along the Kenya coastal Indian ocean strip and within the Eastern African forest coastal ecoregion as isolated patches (Figure 3.1a; Figure 3.1b; Burgess and Clarke, 2000; Fungomeli et al. 2020b). Generally, these forest patches are distributed as small patchy remnants of a previously widespread ecosystems type (Azeria et al., 2007). The climatic range is tropical with coastal hot and high humidity. The mean annual rainfall ranges from 900 mm to 1200 mm (Burgess and Clarke, 2000). The mean temperature ranges between 25°C during the long rain season (April-September) to 30°C during the dry season (December-March), with relatively cooler temperatures occur in the southern coast.

Burgess et al. (2000) estimated that about 145 patches existed in the early 1990s. The size of these forests is highly variable, ranging from large national reserves such as the Arabuko Sokoke forest (420,000 ha) and Shimba Hills forest (25,300 ha), to over 50 relatively small patches (10-75 ha), many of which are considered sacred forests and are locally referred to as *'Kayas'* (Figure 3.1b; Figure 3.2; Githitho, 2016; Robertson and Luke, 1993). Previous studies on these Kenyan coastal forests by Kibet and Nyamweru (2008); Kibet (2011); Shepheard (2014; and Tabor et al. (2010) showed that these forests have undergone forest loss, encroachment and degradation, leading to their reduction in size in terms of area and forest cover.

2.2 Data collection

First, we selected 25 forest sites belonging to 18 sacred forests and seven forest reserves spanning along the Kenyan coastline (Figure 3.1b). We sampled vegetation by applying a nested sampling design with three hierarchical levels: subplot level (micro-scale), plot level (stand level), and forest site level. We chose this sampling design in order to maximize spatial scale coverage and partition species diversity across multiple scales from the local scale (plot and subplots) to the regional scale (Chiarucci et al. 2012; Crist et al., 2003; Veech et al., 2002; Veech and Crist, 2010; Whittaker, 1960).

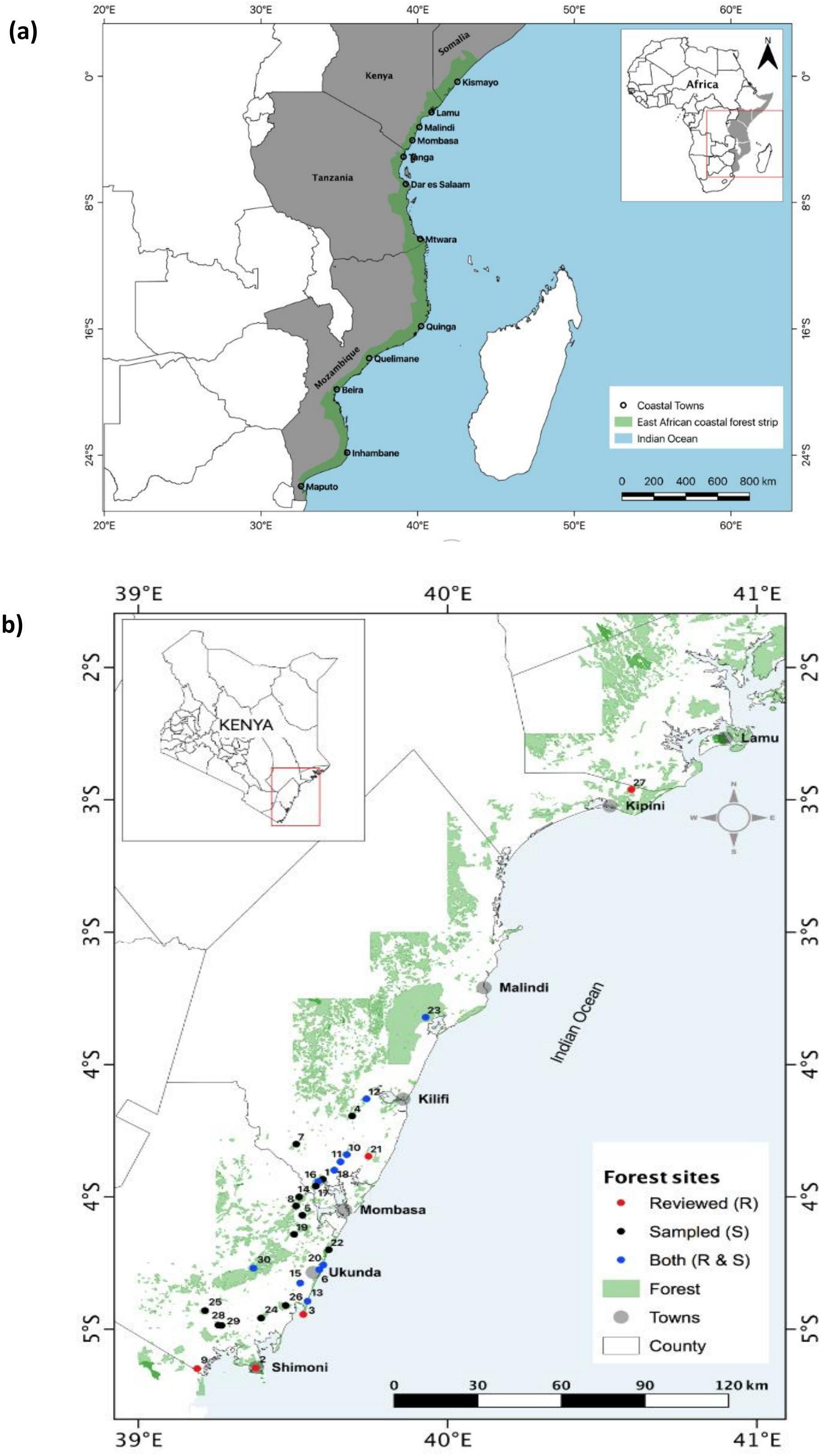


Figure 3.1: A Map of Coastal forests across Eastern Africa and Kenya. **(a):** Eastern African Coastal forests showing the range of coastal forests from Somalia, Kenya, Tanzania and Mozambique. **(b):** A map of the Coastal forests of Kenya showing the location of the 25 sampled forest sites within varying protection status of forest reserve and sacred forests (B). Forest site names numbered:1=Bomu, 2=Chivara, 3=Chonyi, 4=Diani, 5=Fungo, 6=Gandini, 7=Jibana, 8=Kambe, 9=Kauma, 10=Kinondo, 11=Mtswaka, 12=Muhaka, 13=Muvya, 14=Mwiru, 15=Ribe, 16=Teleza, 17=Tiwi, 18=Waa, 19=Arabuko, 20=Buda, 21=Dzombo, 22=Gogoni, 23=Marenje, 24=Mrima, 25=Shimba.

Within the 25 selected forest sites, we sampled a total of 158 plots. The number of plots per forest site was proportional to the log10 of the forest site area, with some variations due to challenges in some forest sites accessibility and fragmentation (Table 3.1; see Fungomeli et al., 2020b). Plot location within each site was randomly positioned by keeping a minimum distance of 200 m among plots and orienting them along a North-South direction. Each plot was 10 m x 100 m and it was further subdivided into twenty subplots of 10 m x 5 m. The geographical location of each plot (start and end points) and subplots were recorded using a Global Positioning Systems (GPS) reader (Garmin eTrex 20x). Within each plot, we recorded woody plant species (trees, lianas and shrubs) rooted therein. All woody species with diameter at breast height (DBH) ≥ 5 cm were sampled and identified within all the 20 subplots and their DBH and height (h) recorded. Shrubs were sampled and identified in two subplots of each plot, by randomly selecting one in the first half of the plots and one in the second half. The abundance of shrub species was assessed by counting the number of individual shoots rooted within a subplot.

Plants were identified on site to the species or at least genus level with the use of botanical manuals using standard references for the area (Beentje, 1994; Luke 2005; Noad and Birnie, 1990; Robertson and Luke, 1993). When onsite identification was not possible, voucher specimens were collected for subsequent herbarium identification at the coastal forest unit and National Museums of Kenya herbarium. Endemic status and life form were determined for all the sampled species across forests sites while the conservation status for each species was determined either as endangered, vulnerable, threatened or least concern according to the conservation status criteria in the ICUN Redlist (IUCN, 2020).

Table 3.1: The Coastal forests of Kenya sites description across protection status for forest name, area (ha) and geographical coordinates (latitude and longitude in decimal degrees), number of sampled plots (No. plots), elevation (m), rainfall (mm), temperature (°C) , distance (km) from the coast and Shannon land use (meanH500) of the 25 sampled forest patches.

Forest ID	Forest name	Area (ha)	Latitude (decimal degrees)	Longitude (decimal degrees)	No. of plots	Elevation range (m)	Mean annual rainfall (mm yr^{-1})	Mean annual temperature (°C)	Distance from coast (km)	Mean Shannon land use (meanH500)
Sacred forests										
Bomu	Kaya Bomu Fimboni	409	-3.93212	39.59415	8	6-215	1121	25.5	9.1	0.64±0.33
Chivara	Kaya Chivara	150	-3.6818	39.69404	8	64-331	1014	25.2	11.3	0.68±0.36
Chonyi	Kaya Chonyi	200	-4.06804	39.53507	4	2-64	1045	25.9	2.9	0.71±0.32
Diani	Kaya Diani	20	-4.27521	39.58598	3	10-24	1162	26.2	0.8	0.76±0.16
Fungo	Kaya Fungo	204	-3.80058	39.5131	4	176-201	989	24.9	24.6	0.66±0.21
Gandini	Kaya Gandini	150	-4.02759	39.50615	5	67-214	1117	25.3	5.3	0.55±0.31
Jibana	Kaya Jibana	140	-3.84361	39.67181	8	81-315	1115	24.9	14.1	0.48±0.41
Kambe	Kaya Kambe	75	-3.86763	39.65274	6	92-180	1142	25.4	14.6	0.61±0.36
Kauma	Kaya Kauma	75	-3.62493	39.73731	7	21-126	1057	25.5	6.3	0.93±0.18
Kinondo	Kaya Kinondo	30	-4.39489	39.53886	3	1-26	1246	26.2	0.2	0.83±0.25
Mtswakara	Kaya Mtswakara	248	-4.00658	39.52517	4	-3-152	1121	25.6	4.0	0.75±0.25
Muhaka	Kaya Muhaka	150	-4.3328	39.52187	5	29-65	1232	26.1	4.4	0.53±0.35
Muvya	Kaya Mudzimuvya	171	-3.94264	39.58194	4	24-220	1096	25.4	8.5	0.77±0.26
Mwiru	Kaya Mudzimwiru	147	-3.95996	39.57615	4	76-266	1084	25.3	6.4	0.75±0.28
Ribe	Kaya Ribe	36	-3.89972	39.63227	5	38-126	1144	25.6	12.4	0.34±0.30
Teleza	Kaya Teleza	67	-4.14031	39.50407	6	151-267	1129	25.3	9.2	0.54±0.23
Tiwi	Kaya Tiwi	10	-4.25503	39.59795	3	4-19	1000	26.2	0.1	1.21±0.21
Waa	Kaya Waa	30	-4.19835	39.61536	3	2-33	1000	26.1	0.1	0.91±0.18
Forest reserves										
Arabuko	Arabuko Sokoke forest	42000	-3.33277	39.88317	26	1-220	903	25.6	0.2	0.46±0.33
Buda	Buda forest	670	-4.45278	39.40407	6	44-99	1346	25.8	7.8	0.17±0.29
Dzombo	Dzombo forest	650	-4.43602	39.21276	6	101-460	1072	25.2	16.5	0.48±0.36
Gogoni	Gogoni forest	832	-4.4204	39.47327	6	2-73	1340	26.2	1.6	0.48±0.40
Marenje	Marenje forest	1480	-4.48485	39.26133	6	73-305	1159	25.3	10.0	0.30±0.30
Mrima	Mrima forest	377	-4.46503	39.30369	6	39-187	1232	25.9	11.6	0.77±0.28
Shimba	Shimba Hills forest	25300	-4.26417	39.38801	12	76-467	1106	24.6	10.6	0.39±0.37

2.3 Data Analysis

2.3.1 Environmental variables

To summarise the ecological factors of each forest site, we extracted environmental variables of elevation, distance from the coast and mean Shannon land use index (meanH500m) from Digital Elevation Models (DEM). In addition, climatic variables of mean annual rainfall and mean annual temperature per forest site were derived from WorldClim database (Fick and Hijmans, 2017).

Figure 3. 2: Kaya Chivara sacred forest, Kenya. One of the sacred Kaya forest remnant patches of the Kenyan Coastal Forests. Photo credit: Steve Okoko Ashikoye.

2.3.2 Forest structure

We characterized forest structure for each forest site by using the measured data for the tree stems with DBH ≥ 5cm and height (m). In particular, we calculated: mean tree density (number of stems ha^{-1}); mean DBH (cm); mean tree height (m) and mean basal area (m^2/ha). To capture a picture of the tallest trees within each forest, a 10% of tallest trees within each forest was extracted and the average value calculated. We finally performed a Kruskal-Wallis test to test for significant differences in forest structure across forest sites and within protection status of forest reserves and sacred forests.

2.3.3 Species composition

In order to visually explore species composition and patterns of variation across all forest sites and also within protection status of sacred forests and forest reserves, we employed a non-metric multidimensional scaling (NMDS, Kruskal, 1964) based on Bray-Curtis dissimilarities using the ‘*metaMDS*’ function in ‘vegan’ R package (Oksanen et al. 2018). Plant species abundances were square-root transformed prior to the analyses to reduce effects of dominant species. Transformed community abundances were then used to generate a Bray-Curtis dissimilarity matrix (Bray and Curtis 1957). We then overlaid the forest site centroid and the environmental variables per forest site to visualize the distribution of species composition in relation to the environmental variables using ‘*envit*’ function in ‘vegan’ R package (Oksanen et al. 2018). Environmental variables were related to the first two axes of NMDS (NMDS 1 and NMDS 2) using multiple regression at 999 permutations and relationship quantified by the coefficient of determination (R^2) and P-value statistical test. We tested for species composition differences in species community structure by an analysis of similarity ANOSIM (Clarke, 1993) using the *‘anosim’* function of the ‘vegan’ R package, for statistically significant differences between species composition of forest sites and within protection status. The analysis of similarity ANOSIM yields a test statistic (R), which compares observed dissimilarities, where R ranges between 0 to 1, where 0 means completely different, and 1 means completely equal species composition. A permutational analysis of variance (PERMANOVA) was subsequently applied to test the significant effect of forest sites and protection status on species composition (Anderson, 2001) based on 999 permutations using the *“adonis”* function in vegan R package (Oksanen et al., 2018). Plant species contributing to similarities across vegetation types were determined using similarity percentages analysis (SIMPER) based on 999 permutations. All calculations were performed in R software (R Core Team 2020) using ‘vegan’ R package (Oksanen et al. 2018).

A species rank abundance curve was computed for all the species in relation to the cumulative number of recorded individuals, while a commonness rank curve was computed to display the frequency distribution of species in relation to the occurrences across plots.

Rare species (unique) and duplicate species were analysed for species frequency occurrence across forest sites. We calculated unique species as species occurring only in one forest site, and duplicate species as species occurring in two forest sites. Finally, for each forest site, we calculated total endemic and IUCN Red List species. Endemic species and ICUN Red List species were compared across forest sites to determine their conservation status.

2.3.4 Species diversity

Vegetation was analysed by species diversity indices of species richness and Shannon-Weiner diversity index H’ (Magurran, 1988). For each forest site, we calculated the average species richness and Shannon’s index per plot, and the total species richness per site. We tested for species richness and abundances significant differences across forest sites and between protection status by use of a multiple comparison Kruskal-Wallis test.

A multiplicative diversity partitioning (alpha, beta and gamma) was performed to compare how species diversity of alpha and beta diversity (β-diversity) varied across sampling scales. This was applied at each scale of sampling taken as hierarchies of subplots, plots and forest site level to the total diversity of the entire data set for all forest sites (Crist and Veech 2006; Veech and Crist 2010; Chiarucci et al. 2011). To quantify this, we used the ‘*multipart’* function in R-vegan package and we obtained the values expected by chance by 999 permutations obtained by randomising all the elements of the lower hierarchical level. The partitioning gave information on species diversity which included the total cumulative species, the average species richness of the samples and the difference in species richness between the first sample points and for each sampling level. A successive nested accumulation curve determines the size of each component of species richness across forest sites.

Species accumulation (Gotelli and Colwell 2001) curves were computed for forest sites across plots. This was performed first by calculating the mean of number of species (and its standard deviation) per plot. Then all combinations were randomised and the mean cumulative number of species was calculated. The data was then grouped into protection status groups of forest reserves and sacred forests. The accumulation curves for each group was then computed by finding the mean and standard deviations of the cumulative number of species from 999 permutations of the data by exact method (Chiarucci et al. 2008). Accumulation curves were plotted for the two groups by species richness against number of plots.

Species Indicator analysis was performed to assess the statistical relationship between species occurrence within forest sites grouped across forest reserves and sacred forests. Only species that showed a significant statistical association ($\alpha < 0.05$) were considered within the two groups. The calculation was subjected to 999 permutations and performed by use of '*multipatt*' function in the 'indicspecies' package of the R software (De Cáceres and Legendre, 2009; De Cáceres et al., 2010). All the data statistical analysis and graphs were performed using R-software (R core Team 2020) and maps performed using Qgis (QGIS Development Team, 2018).

3.0 Results

3.1 Environmental variables

Elevation ranged from a minimum of 9 m at Tiwi to a maximum of 467 m at Shimba Hills (Table 3.1). Mean annual temperature was quite homogenous ranging from 24.6°C - 26.3°C, while mean annual rainfall showed a bit larger variation from 903 mm -1346 mm. Distance from the coast varied from 0.1km (Tiwi and Waa), to 16.5 km (Dzombo). Mean Shannon land use (meanH500m) landscape diversity ranged from 0.17 ± 0.29 to 1.2 ± 0.21 (Table 3.1).

3.2 Forest structure

We recorded a total of 12,878 woody stems with a DBH of ≥ 5cm across the 25 sampled coastal forests of Kenya. Tree density (n ha^{-1}) showed high variation across sites, with the highest values recorded at Kinondo, Tiwi, Diani, Waa and Jibana sacred forests while the lowest values were recorded at Muvya and Bomu sacred forests (Table 3.2). There was a significant difference of forest structure across forest sites and within protection status ($P < 0.001$).

Forest sites also varied greatly in terms of tree size, with the highest mean values of DBH recorded at Mtswaka, Bomu and Muvya, while the lowest values recorded at Kauma and Chivara sacred forests (Table 3.2). Tree species that recorded highest DBH values include *Adansonia digitata* and *Ricinodendron heudelotii* respectively while lowest by *Entada abyssinica.* When comparing the tree density across DBH classes and within sacred and forest reserves, sacred forests displayed higher densities for trees with a DBH ≥80cm (Table 3.2).

In terms of tree height, forest sites differed both in terms of average values and tallest trees (Table 3.2). In particular, the highest mean values of tree height were recorded at Kambe, Mtswaka and Muvya sacred forests, while lowest were recorded at Tiwi and Diani sacred forests. Focusing on the tallest trees of each forest site, Kambe and Muvya emerged with the extremely high values, while Waa and Tiwi for very low values. To be highlighted, Jibana and Kambe forests contained tallest tree height of 60m and 52m respectively, while Waa and Gandini had their highest trees at 24.5m and 20m. The tallest tree species included *Terminalia chebula*, *Ricinodendron heudelotii* while lowest by *Cynometra suahanlesis*.

Similarly, to tree height, the mean basal area per site displayed a statistically significant difference (*P-value = 0.001*) across forest sites and between sacred forests and forest reserves. The variation across forest sites showed highest values at Kaya Diani and Kinondo, and lowest at Kauma and Chivara sacred forests. Furthermore, sacred forests displayed a significant higher mean basal area compared forest reserves that showed intermediate values and all within the same range (Table 3.2).

Table 3.2: Forest structure of the Coastal forests of Kenya for trees with a diameter at breast height (DBH) ≥ 5 cm showing the mean tree density per hectare (N/ha), mean DBH (cm), mean tree height (m), mean basal area per plot (m^2/ha) and height of the 10% tallest trees (m) per each of the 25 studied forest patches in the Kenyan Coastal Forests. All the values for the first four variables report the mean ±sd of the measured trees, while for the last variable (10% tallest trees) the mean and range of values is given.

Forest site	**Tree_density ($N\ ha^{-1}$)**	**Tree DBH (cm)**	**Tree Height (m)**	**Height of the 10% tallest trees (m)**	**Basal Area Mean ($m^2\ ha^{-1}$)**
Sacred forests					
Bomu	388.8 ± 158	25.21 ± 22.28	10.0 ± 8.1	27.2 (21.7-37)	3.05 ± 1.77
Chivara	690 ± 119.5	13.05 ± 9.8	7.3 ± 4.8	19 (12-38)	1.41 ± 0.71
Chonyi	550 ± 95.6	17.26 ± 15.91	6.8 ± 5.1	18.5 (15-25)	2.33 ± 0.61
Diani	1373.3 ± 206	16.03 ± 23.26	5.5 ± 40	15.2 (10-28)	8.59 ± 3.87
Fungo	560 ± 224.9	16.96 ± 14.8	8.7 ± 5.7	22.2 (16-30)	2.07 ± 1.22
Gandini	554 ± 146.9	17.3 ± 12.02	7.4 ± 4.5	16.4 (14.1-20)	1.88 ± 0.37
Jibana	1216.2 ± 219.7	18.56 ± 19.45	9.7 ± 7.9	29.6 (18-60)	6.88 ± 3.32
Kambe	461.7 ± 193.4	24.51 ± 25.37	12.3 ± 10.6	36.5 (28-52)	4.46 ± 2.24
Kauma	404.3 ± 105.2	11.83 ± 9.3	7.3 ± 4.7	17.9 (15-25)	0.64 ± 0.30
Kinondo	1560 ± 70	19.53 ± 17.83	9.6 ± 6.9	27.1 (18-42.5)	8.56 ± 1.49
Mtswaka	445 ± 66.1	30.7 ± 20.71	11.8 ± 7.4	27.1 (22-34)	4.73 ± 1.69
Muhaka	832 ± 80.4	24.08 ± 20.97	10.3 ± 7.7	27.6 (20.1-45.5)	6.62 ± 1.58
Muvya	332.5 ± 125.5	24.83 ± 20.57	10.7 ± 8.9	31.7 (25-38)	2.24 ± 1.03
Mwiru	420 ± 90.6	24.6 ± 20.19	10.6 ± 6.8	25.7 (20-38)	3.01 ± 0.73
Ribe	616 ± 183.4	15.51 ± 17.67	7.6 ± 5.70	23.6 (15-32)	2.59 ± 1.02
Teleza	930 ± 342.5	17.87 ± 11.03	8.8 ± 5	19.7 (15-34.5)	3.21 ± 1.73
Tiwi	1546.7 ± 297.4	14.27 ± 17.73	5.6 ± 3.9	15.1 (10.5-28)	6.28 ± 2.70
Waa	1370 ± 348.7	15.76 ± 11.84	6.5 ± 4.1	15.4 (12.5-24.5)	4.17 ± 3.07
Forest reserves					
Arabuko	839.2 ± 360.2	15.26 ± 12.55	7.7 ± 4.7	18.7 (15-40)	2.55 ± 1.09
Buda	1098.3 ± 112.3	16.57 ± 15.14	7.9 ± 6.3	21.9 (17-38)	4.34 ± 1.10
Dzombo	785 ± 64.4	18.88 ± 20.84	7.7 ± 5.8	21.4 (15-40)	4.86 ± 3.18
Gogoni	1181.7 ± 146.3	17.46 ± 16.28	7.5 ± 6.1	21.7 (16-35)	5.29 ± 0.54
Marenje	973.3 ± 204.7	16.27 ± 14.18	7.8 ± 5.9	21.8 (16-35)	3.53 ± 0.98
Mrima	808.3 ± 234.2	15.69 ± 15.56	7.1 ± 5.7	20.4 (15-38)	3.10 ± 1.66
Shimba	1120.8 ± 294.4	15.58 ± 17.16	7.5 ± 60	22.8 (15-48)	4.71 ± 2.62

3.3 Species composition

We recorded 600 taxa belonging to 343 genera and 80 families. Overall, 549 taxa were identified to species level and 51 to genus level. The most frequent families, in terms of number of species, were Rubiaceae (with 63 species), Fabaceae (with 61 species) and Malvaceae (with 34 species. The life form spectrum was composed of 395 trees, 129 shrubs and 36 lianas (Table S3.1). Among these, 525 were native and 29 alien species, with a total of 237 endemic species and 176 listed as threatened species in the IUCN Red List. All forest patches hosted both endemic and threatened species, with Jibana sacred forest and Shimba Hills forest reserve recording the highest values (Table 3.3).

Species composition varied across forest sites and between the different protection of forest reserves and sacred forests. The NMDS showed a large but not complete overlap of species composition between sacred forests and forest reserves, with the former ones having a wider range of species composition (Figure 3.3). The main environmental drivers that influenced species composition were mean Shannon land use (meanH500, *P-value* = 0.001), mean rainfall (*P-value* = 0.001), distance from the coast (*P-value* = 0.011), temperature (*P-value* = 0.018) and altitude (*P-value* = 0.062) respectively. The ANOSIM revealed a statistically significant difference in species composition within forest sites (*P-value* = 0.001, R^2 = 0.86) and between protection status (*P-value* = 0.001, R^2 = 0.16). Furthermore, PERMANOVA analysis showed significant differences in species composition within all the forest sites (F = 5.26, R^2 = 0.46, *P-value* = 0.001) and between forest reserves and sacred forests (F = 11.64, R^2 = 0.04, *P-value* = 0.001). Finally, SIMPER results revealed an overall dissimilarity of 0.88 contributed by 124 species of species composition differences between protection status.

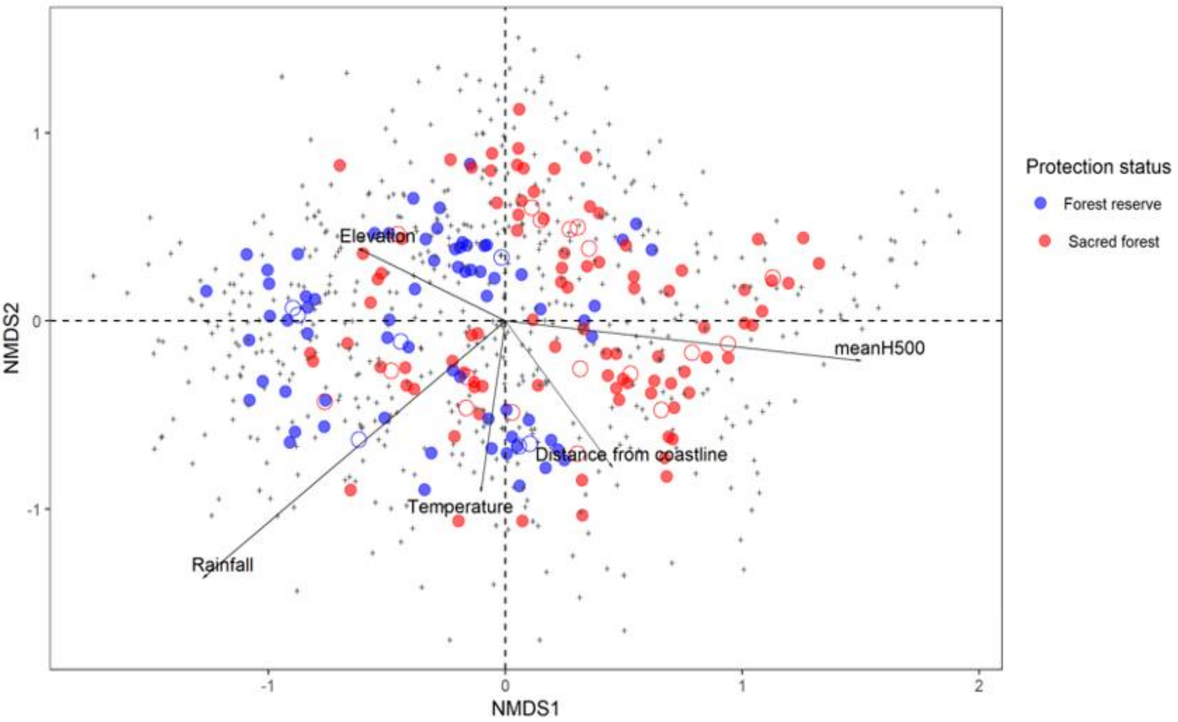


Figure 3.3: Non-metric Multidimensional Scaling (NMDS) for species composition and environmental variables across the coastal forests of Kenya within the 25 sampled forest patches. The solid filled circles of blue and red are the forest plots grouped into protection status of forest reserves and sacred forests. The open circles are the forest sites centroids, while the grey plus sign ('+') indicates species. Environmental variable values meanH500 = mean Shannon landscape land use, distance from coastline, temperature, rainfall and elevation.

Rank abundance curve for the whole set of data showed S*corodopholeus fischeri* as the species with the highest proportion of all recorded individual species, followed by *Julbernardia magnistupulata, Croton pseudopulchellus, Lecaniodiscus fraxinifolius, Ludi mauritiana* and *Cynometra webber* (Figure 3.4a). The rank frequency curve results showed *Uvaria acuminata* as the most common frequent species followed by *Haplocoelum inopleum, Polysphaeria parvifolia, Salacia elegans, Hymenea verrucosa, Monanthotaxis fornicata* and *Combretum schumannii* respectively (Figure 3.4b).

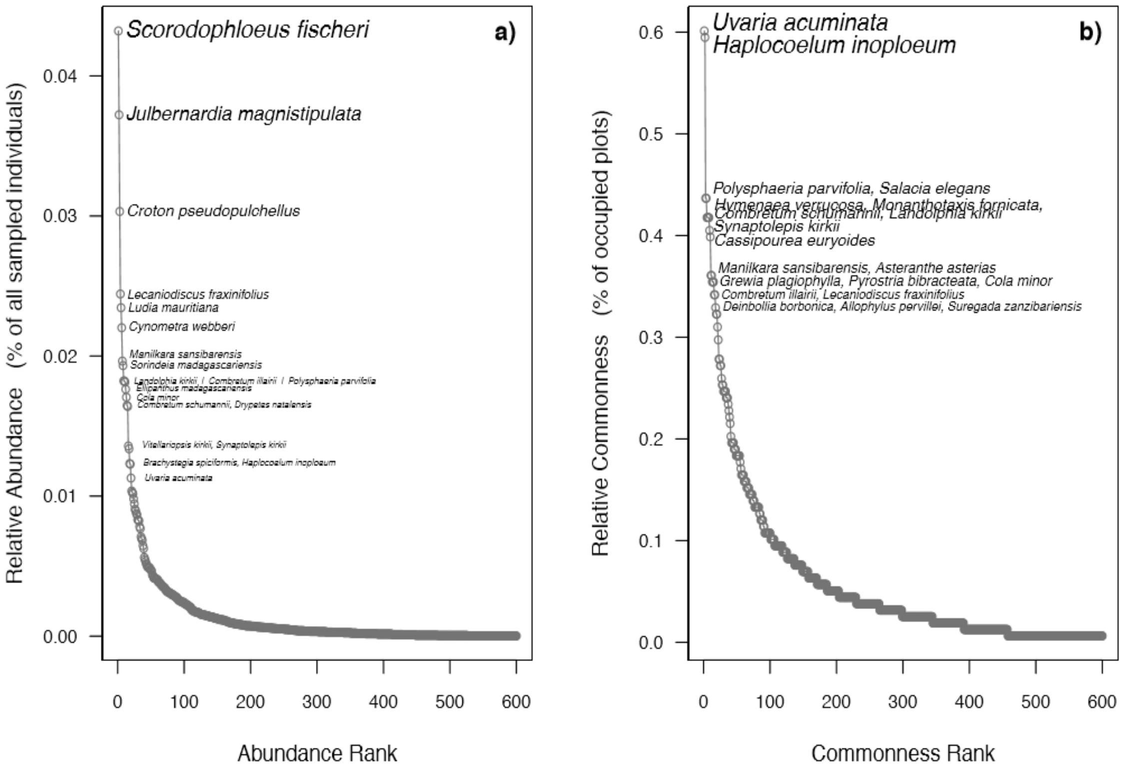


Figure 3.4: Species abundance and commonness within the Coastal forests of Kenya for: **(a)** Species abundance rank across forest sites for all sampled species. **(b)** commonness rank of species within sampled plots across the 25 sampled forest patches of the Coastal forests of Kenya.

Assessment of rare (unique) and duplicate species across forest sites shows 50% of the species were restricted to one or two forest sites, while there was no species occurring in all sites (Table 3.3). *Grewia plagiophylla* and *Uvaria acuminata* occurred in 22 forests out of the 25 studied forest sites, compared to *Deinbollia borbonica*, *Combretum illairii*, *Haplocoelum inoploeum* and *Salacia elegans* which occurred in 21 while only *Polysphaeria parvifolia* in 20 forest sites. Unique and duplicate species represented on average 7.7% and 13.5% of the species per site respectively (Table 3.3). Shimba hills forest reserve followed by Jibana forest and Arabuko forest were the sites with highest proportion of unique and duplicate species (Table 3.3).

Table 3.3: Species diversity of the Coastal forests of Kenya for average species richness per plot, Shannon index (average per plot), cumulative species richness per site (Cum-SR), number of rare species (as unique species occurring in one forest site only) and duplicate species occurring in two forest sites only), number of endemic species and number threatened species (IUCN Red List) of the 25 studied forest patches in the Kenyan Coastal forests.

Forest site	Mean species richness per plot	Shannon Index (av/plot)	Cum-SR	Unique species	Duplicate species	Endemic species	Threatened species
Sacred forests							
Bomu	36.5 ± 9.5	2.82	154	13	31	68	58
Chivara	37.8 ± 12.0	2.72	140	13	20	74	50
Chonyi	37.5 ± 16.8	2.78	62	0	5	33	18
Diani	31.3 ± 4.9	2.83	66	5	7	31	23
Fungo	35.0 ± 9.7	2.77	60	5	8	27	19
Gandini	41.6 ± 4.1	3.05	80	4	5	41	30
Jibana	34.1 ± 12.6	2.74	195	25	44	100	69
Kambe	33.8 ± 5.5	2.78	109	13	25	54	32
Kauma	33.1 ± 6.6	2.71	77	14	18	42	30
Kinondo	36.0 ± 16.5	2.64	56	7	9	25	14
Mtswaka	37.5 ± 3.5	2.92	64	6	7	38	28
Muhaka	36.2 ± 5.7	2.68	90	4	6	51	27
Muvya	45.8 ± 19.3	3.01	85	2	7	50	32
Mwiru	33.3 ± 5.9	2.62	70	3	8	34	26
Ribe	35.4 ± 4.6	2.72	95	4	10	42	39
Teleza	38.2 ± 20.4	2.83	91	1	5	50	26
Tiwi	50.7 ± 12.4	3.25	53	0	2	24	18
Waa	39.3 ± 18.0	2.81	43	4	7	21	17
Forest reserves							
Arabuko	36.0 ± 8.7	2.71	178	20	33	90	54
Buda	37.7 ± 6.6	3.01	121	6	16	61	38
Dzombo	36.3 ± 11.2	2.65	90	5	8	47	32
Gogoni	33.7 ± 13.0	2.68	123	11	20	66	46
Marenje	42.0 ± 18.4	2.72	76	10	11	41	27
Mrima	33.0 ± 9.9	2.64	101	5	10	50	33
Shimba	37.3 ± 12.7	2.79	190	30	46	96	62

3.4 Species diversity

Jibana sacred forest was the richest site in cumulative species richness, followed by Shimba Hills and Arabuko forest reserve, while Waa forest was the lowest (Table 3.3). The average species richness per plot ranged from 31.3 ± 4.9 at Diani to 50.7 ± 12.4 at Tiwi. A Kruskal-Wallis test showed overall significant differences of species richness and abundance across forest sites and within protection status (*P-value* < 0.0001*)*. Species richness within protection status and across forests was statistically significant (Figure 3.5; chi-square =102.7, df=1, *P-value* <0.0001, and chi-square =517.1, df=24, *P-value* <0.0001 respectively), while species abundance showed significant difference within protection and across forest sites respectively (chi-square=73.7, df=1, *P-value* <0.0001, and chi-square=498.4, df=24, *P-value* <0.0001). Additionally, a multiple comparison Kruskal-Wallis test identified 136 and 149 forest site groups as statistically significant different in species richness and abundance respectively. On average, half of the species per site were endemic (range 44.2% -59.4%) and more than one third per site were listed as threatened species (range 25.0% - 43.8%).

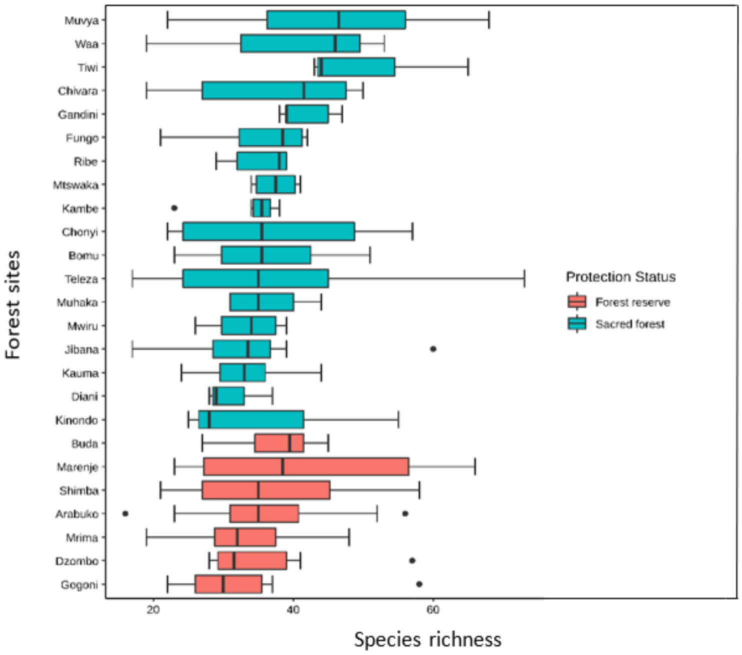


Figure 3.5: Comparison of the mean species richness per plot across forest sites, and grouped into protection status of forest reserves and sacred forests across the 25 sampled forest sites of the coastal forests of Kenya.

The combination of species accumulation curve and additive beta partitioning showed a high significant difference ($P < 0.05$, ***) of beta diversity (β-diversity) across sampling scales as expressions of alpha, beta and gamma in subplots, plots and forest sites (Figure 3.6). Additive beta diversity at finer scales (across subplots within plots and across plots within forest sites) was significantly lower than expected by random expectations, while it was significantly higher at the broader scale (across forest patches), suggesting the major role of geographic gradients and spatial distance.

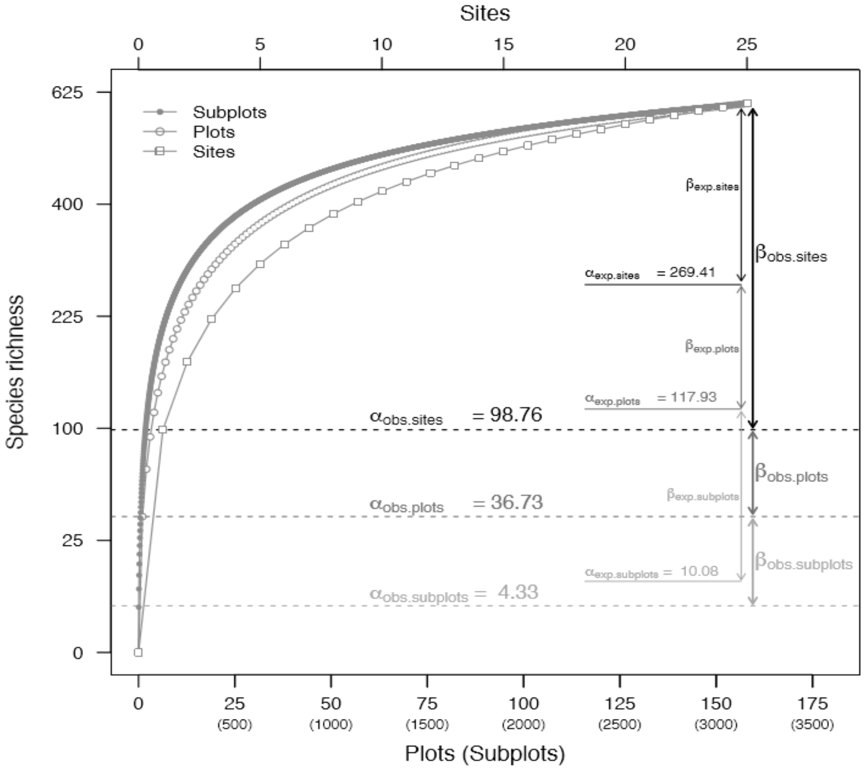


Figure 3.6: Multiplicative beta partitioning within sampled plots, subplots and forest sites across the 25 sampled forest patches of the Coastal forests of Kenya.

Species accumulation curves showed the sacred forest sites accumulating significantly ($p < 0.05$) a higher species richness of new species over the sampled plots than forest reserves. Both accumulation curves start rising at relatively and divert from half the species richness to reach different asymptote curves (Figure 3.7).

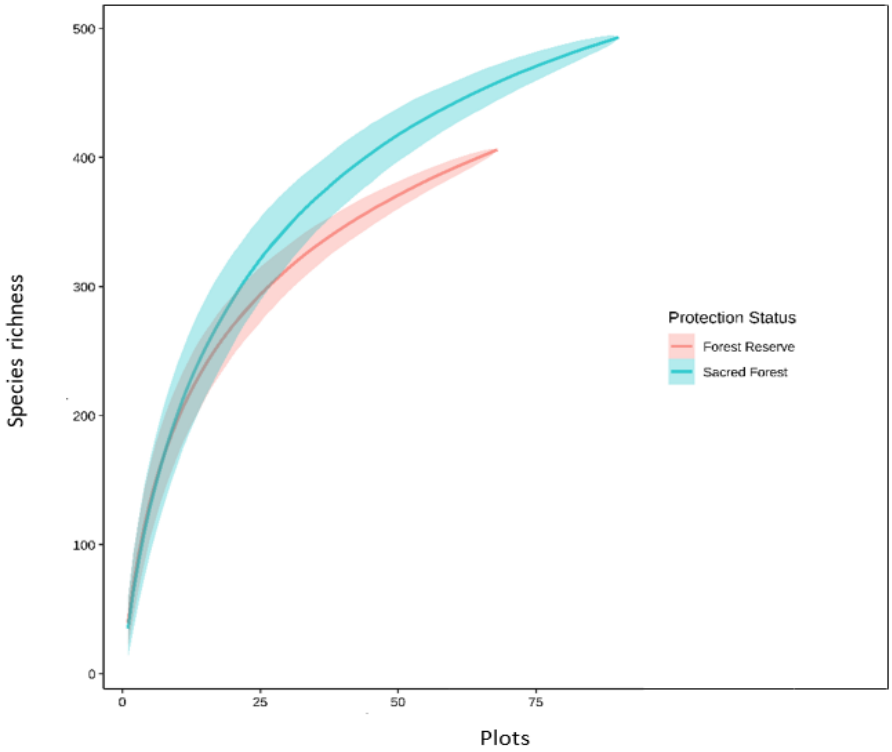


Figure 3.7: Species richness accumulation curves of the coastal forest of Kenya corresponding to forest patches grouped into protection status of forest reserves and sacred forests within the 25 sampled forest patches. The shaded areas represent 95% confidence intervals. Sacred forests exhibit species richness significantly greater than forest reserves.

Results of the species indicator analysis showed a total of 115 species that were statistically significantly associated at all forest sites within forest reserves and sacred forests groups ($\alpha < 0.05$, Appendix 3.1). Forest reserves contained 75 species with species of high stat values as *Landolphia kirkii* and *Synaptolepis kirkii* while sacred forests contained 40 species with *Cussonia zimmermannii* and *Chazaliella abrupta* with highest stat values.

4.0 Discussion

To our knowledge, there is no study on the coastal forests of Kenya that has been able to provide a vegetation survey large enough for comprehensive biogeographical, spatial and ecological analysis across forest structure and species diversity until the current study. Our results provide a standardized systematic vegetation survey across the Kenyan coastal forests biodiversity hotspot. In particular, we investigated the patterns and drivers of forest structure, community composition and plant diversity across the Kenyan coastal forest fragments with varying protection status of sacred and forest reserves.

We found that forest structure, composition and species diversity in the coastal forests of Kenya shows a strong variation and are spatially structured across the large geographic scale gradient of the 25 studied coastal forests of Kenya. On one hand, our results present for the first time a quantitative information on the coastal forests of Kenya forest structure, species diversity and distribution patterns across a spatial scale. On the other, our analysis shows a high variation in forest structure, composition and species diversity across the coastal forests of Kenya depicting a heterogenous structure across environmental and ecological factors. In particular, species accumulation curve and beta partitioning for alpha, beta and gamma diversity within sampled plots, subplot and forest sites showed a higher species richness variation across forest sites (beta diversity) than within plots and subplots (alpha diversity). Additionally, forest structure varied greatly across forest sites, where sacred forest sites exhibited a relatively higher forest structure, species composition and species diversity. Our results display the strongest environmental drivers were altitude, mean Shannon land use and distance from the coast. In contrast however to our expectations, some relatively high elevated forest patches exhibited a high species richness, although this may not be surprising for the low elevation range of the Kenya coastal forests (19 m – 467 m) where species can be well mixed (Lovett, 1998). Mean annual temperature showed an influence on plant species composition and distribution despite its small temperature changes across the forests.

Overall, our results can be explained and attributed to reflect widely the heterogenous structure of the coastal forests of Kenya that are spread across hills and flat forests and exposed to different micro-habitats and climate (Burgess and Clarke, 2000). Our findings are consistent with earlier studies of the Kenyan coastal forest fragments as composed of a heterogenous vegetation structure and high plant diversity (Burgess and Clarke, 2000; Lovett, 1998; Luke, 2005). The heterogeneity can be attributed to a complex of biotic and abiotic influences ranging from their different geology, soils, climatic variation, fragmentation and topography (Ghazoul and Sheil, 2010; Newton and Echeverría, 2014; Stein et al. 2014). Other ecological factors such as soil type, pH and geology which were not considered in this study could explain further the structure, composition and plant species diversity of the coastal forests of Kenya.

Forest structure

With respect to forest structure, our results show a strong observed pattern which exhibited high values of mean DBH, height and basal area across forest sites. In particular, we found a highest mean basal area, tree density, mean tree height and highest tree sizes (DBH) in sacred forests compared to the forest reserves. Canopy heights variation shows ranges of high canopy values of upto 40m to 60m in some forests. These results give an indication that sacred forests are composed of old growth forests compared to the forest reserves that can be classified as regenerating (Wood et al., 2019). Additionally, a vegetation structure study carried out in Tanzania by Lowe and Clarke (1995) showed that forests with a low tree stem density were associated with a history of disturbance. Studies have shown that, the intensity of disturbance influences with highly disturbed forests in terms of logging may influence forest structure and species diversity (Busck-Lumholt and Treue, 2018). Generally, the reduction in basal area and stem density in some forests can be attributed to overexploitation of the forest resources through human activities. Most of the reported human activities in these forest areas are among others illegal logging, encroachment and clearance for agriculture, fuel wood extraction, charcoal production and grazing of domestic animals, medicinal plants extraction, building materials (Busck-Lumholt and Treue, 2018; Kibet 2011; Shepheard, 2014).

Although our results show a general high forest structure (basal area, tree heights and tree density) better exhibited within the smaller forest patches many of which are sacred forests than forest reserves, a study by Tabor et al. (2010) shows there is generally a higher forest cover change in the coastal forests of Kenya (53 km^2 forest cleared between 1990-2000), with higher forest loss in the unprotected areas than protected areas such as the forest reserves. At this reported rate of clearance, there is certainly a general higher risk of species loss and extinction rate for threatened, rare and endemic species especially in the smaller forest patches with relatively less protection level. Considerably, we found both forest reserves and sacred forests showed dominance of tree density with smaller DBH classes, with forest reserves exhibiting intermediate values of mean DBH classes, height and basal area and all in the same range category. A dominance of the smaller DBH classes is a potential indicator of good forest health as it supports possible natural forest regeneration (Franklin et al., 2006; Kibet, 2011).

Species composition

While there was no species that was distributed over the entire forest sites, more than 50% of all species were restricted to only one or two forest sites. Observation of species that occurred in 22 out of the 25 studied forest sites included *Grewia plagiophylla* and *Uvaria acuminata*, while *Deinbollia borbonica*, *Combretum illairii*, *Haplocoelum inoploeum* and *Salacia elegans* occurred in 21 forest sites and only *Polysphaeria parvifolia* in 20 forest sites. These species may be termed as more 'generalists species' occurring in a wider range of ecological habitats. A further observation on unique species per forest site showed Shimba hills forest reserve with 30 unique species only occurring in one forest site and 46 species found within two sites, followed by Jibana and Arabuko forest sites. These results reflect these forest sites as exhibiting 'specialist species', with restricted range, but also could be explained as a case of endemic, rare and threatened species that occur in these forest sites as supported by Burgess et al. (1998), Burgess and Clarke (2000) and Luke (2005) who demonstrate that the coastal forests support high numbers of endemic species that are mostly narrow-range and restricted to single forest sites.

Comparing species composition between sacred forests and forest reserves, our results show that sacred forests had a large species composition that included more than 80% of the forest reserves as displayed by the NMDS and the species accumulation curve. These results can be attributed to the old-growth forest nature exhibited by the forest structure of the sacred forests and further supported by the results of the indicator species analysis with significant number of species in the sacred forests. Our results are consisted with other studies that have shown sacred forests have been reported to contain a higher variation in species richness level that can be explained by the forest ‘age’ as they play a big role as ecological corridors (dos Santos et al., 2007; Rosch et al., 2015).

Our results show that species composition variation across forest sites can also be explained by environmental factors, where altitude, temperature, mean Shannon land use (H) and distance from the coast were the strongest variables influencing composition. Other studies on tropical forests have found that generally, temperature is known to play an important role in influencing species diversity in tropical habitats (Wright, 2010; Zhang et al., 2014), where a slight change in temperature influences plant species composition and diversity. Distance from the coastline exhibited an effect on species composition. This could be explained by the proximity to the coast which offers marine-ecological influence with better moisture and soil wet conditions to support better vegetation growth compared to further inland where climate conditions change to drier (Lovett, 1993; Lovett, 2008). Additionally, generally climate closer to the ocean is characterized by better rainfall patterns compared to further inland and such areas would also be dominated by plant species that are tolerant to a mix of salinity and high humidity levels (Lovett,1993). Finally, altitude played a role to influence plant community composition and structure despite a short range. These results can be explained and supported by other studies on the African tropical forests who found altitude to play a major role in distribution of tree species and was thought to be through a strong relationship with rainfall where rain was higher in higher elevation forests (Eilu et. al., 2004).

Species diversity

We found a strong variability in species richness and diversity across the coastal forests of Kenya, with a strong variation across the geographical scale. There was a high variation of the Shannon Index per site while diversity partitioning showed a stronger diversity variation is exhibited between forest sites (beta diversity), than within sampling plots (alpha diversity). Such a strong pattern of beta diversity may be attributed to the variation in biogeographic factors combined with different species dispersal mechanisms, where the geographical variation of the Kenya coastal forests from the low altitude and coastal dry forest of Arabuko Sokoke on the North to the relatively high altitude and moist forests at the South such as Shimba hills are enabling environments in driving a higher beta diversity at forest site scale. Our results are in support of other study findings that have shown plant species diversity in tropical forests varies greatly across forests due to variation in biogeography, habitat and disturbance (Corlett, 2016; Dauby et al. 2014; McGlynn, 2010; Whitmore, 1998). Additionally, species diversity across the forest sites could be as a result of different geological substrate formations as shown by studies, experienced over the last 200 million years (Burgess and Clarke, 2000). At the Kenyan coastal forests, the geological formations range from rocks to alluvial deposits. Moreover, most forests are found on plains, while some on hill-tops, plateaux, marine and lacustrine deposits which may influence different species within the habitats (Burgess and Clarke, 2000).

Considerably, Jibana sacred forest exhibited higher species richness followed by Shimba hills forest reserve. Both sites are found on relatively moist areas with higher rainfall compared to the other forest patches. Nonetheless, higher species richness at Jibana sacred forest can be attributed to the relatively different substrate formed on a jurrassic limestone while Shimba hills is formed on ancient sands (Burgess and Clarke, 2000). However, in contrary, other studies within the area have shown Shimba hills forest to be the richest forest fragment in the Kenyan coastal forests (Luke, 2005; Robertson and Luke 1993). These results discrepancies might be explained by the lack of biogeographical standardised sampling approach in which former studies were based on plant checklist (see Fungomeli, 2020b; Scheiner et al., 2011). In addition, our study sampled woody plant species across the Kenyan coastal forest patches, which could result to the differences (see Fungomeli et al., 2020a). Moreover, other factors such as area where the 'habitat diversity' hypothesis argues the increase of the number of species with area due to increased micro-habitats enabling niches could explain the results by other studies on the higher species richness and diversity in Shimba hills (MacArthur and Wilson, 1967; Rozenweig, 1995).

Although sacred forests are traditionally protected by the communities, they are still heavily used by the forest adjacent communities for their daily household needs, which may influence spatial patterns and community composition in the Kenyan coastal forests. Additionally, in most cases, the sacred Kaya forests are mostly located in very remote areas and more often spread around arid to semi-arid areas and appear to be the only green area of forest and pasture land that is surrounded farmlands and high population (Alados et al., 2004; Franklin et al.,2006; Kibet, 2011). This scenario is observed in forest patches such as Kaya Mtswakara, Kaya Gandini, Kaya Chonyi, Kaya Chivara, Kaya Mudzimwiru and Kaya Mudzimuvya sacred forest sites (Githitho 2016). Our results emphasize the need for a better management and scaling-up of protection measures in support of these smaller forest patches which still contribute to a high forest cover regionally and consequently globally while discharging crucial ecosystem services.

In general, analysis of species richness across the forest patches showed that the sacred forests exhibited a higher species richness compared to forest reserves which can be attributed to several factors ranging from the higher forest structure exhibited by the sacred presenting them as old growth forests which consequently harbours and conserves higher species richness especially in fragmented forests. These results are in support of other findings from studies that sacred forests exhibit high levels of biodiversity and they protect rare and threatened species (Campbell, 2004; Kibet, 2011; Kokou et al., 2008; Sanou et al., 2013).

Several studies on tropical forests have shown that biogeographical environmental factors play a major role in species richness and diversity. Moreover, species diversity is also largely affected by climate change, soil conditions, and human activities. Furthermore, the plant community structure has been shown to be as a result of stochastic and environmental deterministic process (Corlett, 2016; McGlynn, 2010). Our sampling was mainly field based and therefore contained variations more related to local factors, that may not have been well captured by the extracted broad-scale environmental variables. Subsequently, we infer our results of the variation in the coastal forests of Kenya forest structure, composition and species diversity to be as an influence of a combination of these factors.

Conclusion

Overall, our results present for the first time the spatial variation in forest structure, composition and species diversity across the coastal forests of Kenya which remain relatively limited in quantitative documentation across numerous forest patches. In particular, we found that biogeographic factors were a major driver of patterns of forest structure, composition and species diversity across the coastal forest of Kenya. More importantly, our results present interesting insights of a higher species composition and diversity across forest sites than within a forest. Therefore, the biodiversity of the coastal forests of Kenya is rich when accounted across forest fragments than on single sites emphasizing for conservation of the rich biodiversity across geographical scale. These results account for the different biogeographic climatic factors enhancing species diversity at different forest sites as a result of the heterogeneous structure across the forest fragments. Our results emphasize the importance of a biogeographical and ecological conservation-plan model of the coastal forests of Kenya. Management and conservation of the coastal forests Kenya like many other tropical forests globally is a growing challenge. This documentation and understanding the patterns of composition and biodiversity distribution of the coastal forests of Kenya is crucial for use in monitoring and preventing further loss of species while using the data to predict climate change effects. These results present a crucial tool that can also be used to re-evaluate previous conservation efforts which were either based relatively more concentrated on the forest reserves or on endemic species leaving out other smaller forest patches which still exhibit high species richness while supporting critical ecosystem services. Nonetheless, our results also show that human activities have contributed to the degradation of these forest fragments especially more so at the local scale and these seem more pronounced at the sacred forests. As such, our results call for scaling-up of protection measures in the sacred forests, and develop broad-scale conservation strategies while taking into account monitoring the extraction and use by the adjacent local communities, and integrate regional biodiversity drivers for the effective sustainable management and conservation of these forest fragments. As better illustrated by Mittermeier et al. (2011), conservation actions are more local in many respects, but this has to be supported and informed by data of trends and status of local biodiversity.

5.0 References

Alados, C.L., ElAich, A., Papanastasis, V.P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D. and Cabezudo, B. (2004) Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecological Modelling*, 180, 523-535.

Anitha, K., Joseph, S., Ramasamy, E.V. and Prasad, S.N. (2009) Changes in structural attributes of plant communities along disturbance gradients in a dry deciduous forest of Western Ghats, India. *Environmental Monitoring and Assessment*, 155, 393–403, https://doi.org/10.1007/s10661-008-0442-z.

Azeria, E.T., Sanmartin, I., Stephan, A.S., Carlson, A. and Burgess, N.D. (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, 16, 883–912. https://doi.org/10.1007/s10531-006-9022-0.

Barthlott, W., Hostert, A., Kier, G., Kuper, W., Kreft, H., Mutke, J., Rafiqpoor, M.D. and Sommer J.H. (2007) Geographic patterns of vascular plant biodiversity at continental to global scales. *Erdkunde*, 61, 305-315.

Beentje, H.J. (1994) Kenya Trees, Shrubs and Lianas. National Museum of Kenya, Nairobi, Kenya.

Butaye, J., Jacquemyn, H. and Hermy, M. (2001) Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. *Ecography*, 24, 369-380.

Busck-Lumholt, L.M. and Treue, T. (2018) Institutional challenges to the conservation of Arabuko Sokoke Coastal Forest in Kenya. *International Forestry Review*, 20, 488-505. https://doi.org/10.1505/146554818825240665.

Burgess, N.D., Clarke, G.P. and Rodgers, W.A. (1998) Coastal Forests of Eastern Africa: Status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, 64, 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess, N.D. and Clarke, G.P. (Eds) (2000) *The coastal forests of Eastern Africa*. IUCN, Gland, Switzerland and Cambridge, UK.

Campbell, M. O. (2004) Traditional forest protection and woodlots in the coastal savannah of Ghana. *Environmental Conservation*, 31, 225–323.

Chiarucci, A. (2007) To sample or not to sample? That is the question for the vegetation scientist. *Folia Geobotanica*, 42, 209–216. https://doi.org/10.1007/BF02893887.

Chiarucci, A., Bacaro, G., Filibeck, G., Landi, S., Maccherini, S., & Scoppola, A. (2012). Scale dependence of plant species richness in a network of protected areas. *Biodiversity and Conservation*, 21, 503–516. https://doi.org/10.1007/s10531-011-0196-8

Chiarucci, A., Bacaro, G., Rocchini, D. (2008) Quantifying plant species diversity in a natura 2000 network: Old ideas and new proposals. *Biological Conservation*, *141*, 2608-2618. https://doi.org/10.1016/j.biocon.2008.07.024.

Chiarucci, A., Bacaro, G., Rocchini, D., & Fattorini, L. (2008). Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. Community Ecology, 9(1), 121–123. https://doi.org/10.1556/ComEc.9.2008.1.14

Chiarucci, A., Bacaro, G. and Scheiner, S.M. (2011) Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions: Biological Sciences, 366*, 2426-2437. https://doi.org/10.1098/rstb.2011.0065.

Clinebell, R.R., Phillips, O. L., Gentry, A.H., Stark, N. and Zuring, H. (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, 4, 56-90. https://doi.org/10.1007/BF00115314.

Corlett, R.T. (2016) Plant diversity in a changing world: Status, trends, and conservation needs. *Plant Diversity,* 38, 10-16. https://doi.org/10.1016/j.pld.2016.01.001.

Crist TO, Veech J.A., Gering, J.C. and Summerville KS (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of a, b and c diversity. *American Naturalist,* 162, 734–74.

Crist, T. O. and Veech, J.A. (2006) Additive partitioning of rarefaction curves and species–area relationships: unifying alpha-, beta-, and gamma-diversity with sample size and habitat area. *Ecology Letters*, 9, 923–932.

Dauby, G., Hardy, O.J., Leal, M., Breteler, F. and Stevart, T. (2014) Drivers of tree diversity in tropical rain forests: new insights from a comparison between littoral and hilly landscapes of Central Africa. *Journal of Biogeography,* 41, 574–586. https://doi.org/10.1111/jbi.12233.

De Cáceres, M., Legendre, P. and Moretti, M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos,* 119,1674-1684.

De Caceres, M., Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*. URL http://sites.google.com/site/miqueldecaceres/

Dos Santos K., Kinoshita L.S. and dos Santos F.A.M. (2007) Tree species composition and similarity in semideciduous forest fragments of south eastern Brazil. *Biological Conservation,* 135, 268-277. https://doi.org/10.1016/j.biocon.2006.10.027.

Edwards, W.M. (2007) A biodiversity evaluation of Kenya's coastal forest systems. Master's degree research. *Durrel Institute of Conservation and Ecology*, University of Kent, UK.

Eilu, G., Hafashimana, D.L.N. and Kasenene, J.M. (2004) Density and species diversity of trees in four tropical forests of the Albertine Rift, Western Uganda. *Diversity and Distributions,* 10, 303-312. https://doi.org/10.1111/j.1366-9516.2004.00089.x

Fick, S.E. and Hijmans, R.J. (2017) Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology.*

Franklin, J., Wiser, S.K., Drake, D.R., Burrows, L.E. and Sykes, W.R. (2006) Environment, disturbance history and rain forest composition across the islands of Tonga, Western Polynesia. *Journal of Vegetation Science*, 17, 233–244.

Fungomeli, M., Cianciaruso, M., Zannini, P., Githitho, A., Frascaroli, F., Fulanda, B. *et al*. (2020a) Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, Plant Biosystems, https://doi.org/10.1080/11263504.2020.1834461.

Fungomeli, M., Githitho, A., Frascaroli, F., Chidzinga, S., Cianciaruso, M. and Chiarucci, A. (2020b) A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey*, 1: 103-109. https://doi.org/10.3897/VCS/2020/47180.

Ghazoul, J. and Sheil, D. (2010) *Tropical rain forest ecology, diversity, and conservation*. Oxford: Oxford University Press.

Githitho, A.N. (2016) Listing The Sacred Mijikenda *kaya* Forests as UNESCO World Heritage Sites: "The Long Journey", *Journal des africanistes* [En ligne], 86-1[accessed 07 August 2019]. http://journals.openedition.org/africanistes/4971.

Gotelli, N.J. and Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecological Letters*, 4, 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Habel, J.C., Casanova, I.C.C., Zamora, C., Teucher, M., Hornetz, B., Shauri, H., Mulwa, R.K., Lens, L. (2017) East African coastal forest under pressure. *Biodiversity and Conservation*, 26, 2751–2758.

Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C., Iverson, L., Currie, D. J., *et al*. (2001) Global change in forests: Responses of species, communities, and biomes. *Bioscience*, 51, 765-779. https://doi.org/10.1641/0006-3568(2001)051[0765:GCIFRO]2.0.CO;2

Hanski, I., & Triantis, K. (2015) Habitat fragmentation and species richness. *Journal of Biogeography,* 42, 989-993. https://doi.org/10.1111/jbi.12478.

Hill, J.L. and Curran, P.J. (2001) Species composition in fragmented forests: conservation implications of changing forest area. *Applied Geography,* 21, 157-174.

IUCN (International Union for the Conservation of Nature and Natural Resources) (2020). The IUCN Red List of Threatened Species: 2020 Categories and Criteria (version 3.1). https://www. redlist.org/info/categories_criteria2020.html (last accessed 12 August 2020].

Kruskal, J.B. (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1-27.

Kibet, S. (2011) Plant communities, species diversity, richness, and regeneration of traditionally managed coastal forest, Kenya. *Forest Ecology and Management*, 261, 949 -957. https://doi.org/10.1016/j.foreco.2010.11.027.

Kibet, S. and Nyamweru, C. (2008) Cultural and biological heritage at risk; the case of the Rabai Kaya forests in coastal Kenya. *Journal of Human Ecology,* 24, 287-295. https://doi.org/10.1.1.563.4827.

Kobal, M., Kastelec, D. and Eler, K. (2017) Temporal changes of forest species composition studied by compositional data approach. *iForest*,10,729-738. https://doi.org/10:3832/ifor2187-010.

Kokou, K., Adjossou, K. and Kokutse, A. D. (2008) Considering sacred and riverside forests in criteria and indicators of forest management in low wood producing countries: The case of Togo. *Ecological Indicators*, 8, 158-169. https://doi.org/10.1016/j.ecolind.2006.11.008.

Lehmann, I. and Kioko, E. (2005) Lepidoptera diversity, floristic composition and structure of three Kaya forests on the South coast of Kenya. *Journal of East African Natural History*, 94, 121-163.

Lovett, J.C. and Wasser, S.K. (Eds) (1993) Biogeography and Ecology of the Rain Forests of Eastern Africa. Cambridge: Cambridge University Press, UK.

Lovett, J.C. (1993) Climatic history and forest distribution in eastern Africa. In: Lovett, J.C., and Wasser, S.K., (Eds) *Biogeography and Ecology of the Rain* Forests *of Eastern Africa.* Cambridge: Cambridge University Press, pp. 23-33.

Lovett, J. C. (2008) Biogeography and ecology of the rain forests of Eastern Africa. Cambridge University Press. Great Britain.

Lovett, J.C. (1998) Eastern tropical African centre of endemism: A candidate for world heritage status. *Journal of East African Natural History*, 87, 359-366.

Luke, W.R.Q. (2005) Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. *Journal of East African Natural History*, 94, 5-121. https://doi.org/10.2982/0012-8317(2005)94[5:ACOTPO]2.0.CO;2.

MacArthur, R.H. and Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ. Google Scholar.

MacFarlane, D.W., Kinzer, A.T. and Banks, J.E. (2015) Coupled human-natural regeneration of indigenous coastal dry forest in Kenya. *Forest ecology and management,* 354, 149-159. https://doi.org/10.1016/j.foreco.2015.06.026.

Metcalfe, K., Ffrench-Constant, R. and Gordon I. (2010) Sacred sites as hotspots for biodiversity: The Three Sisters Cave complex in coastal Kenya. *Oryx*, 44, 118-123.

McGlynn, T. (2010) Effects of Biogeography on Community Diversity. *Nature Education Knowledge,* 3, 42.

Mittermeier, R.A., Larsen, F.W., Brooks, T.M. and Gascon, C. (2011) Global biodiversity conservation: the critical role of Hotspots. In: Zachos, F.E. and Habel, J.C. (Eds), *Biodiversity Hotspots,* Springer-Verlag, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-20992-1.

Montagnini, F. and Jordan, C.F. (2010) Tropical forest ecology. Berlin: Springer. https://doi.org/10.1007/b138811.

Muchiri, M.N. (2001) Forest inventory report for the indigenous forests in Arabuko Sokoke forest reserve. Kenya Forest Research Institute, Nairobi, Kenya.

Magurran, A.E. (1988) Ecological Diversity and its Measurement. Croom Helm Ltd. Australia.

Mutangah, J.G. and Mwaura, P.K. (1992) A vegetation survey report, Arabuko Sokoke forest management and conservation project. East African Herbarium, National Museums of Kenya.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858. https://doi.org/10.1038/35002501.

Newton, A.C. and Echeverría, C. (2014) Analysis of anthropogenic impacts on forest biodiversity as a contribution to empirical theory. *Forests and global change*, 417-446. https://doi.org/10.1017/CBO9781107323506.019.

Noad, T. and Birnie, A. (1990) A Fully Illustrated Field Guide: Trees of Kenya. General Printers Ltd, Nairobi, Kenya.

Pakia, M. (2005) Plant ecology and ethnobotany of two sacred forests (Kayas) of Kenyan Coast. Die Deutsche Bibliothek, Bayreuth.

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Rajat, J., Jefwa, J. and Mwafaida, J. (2017) Survey on indigenous food plants of Kaya Kauma and Kaya Tsolokero in Kilifi County Kenya. *Journal of Life Sciences*, 11, 82-90.

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Robertson, S.A. and Luke, W.R.Q. (1993) The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi. https://www.africabib.org/rec.php?RID=K00001940.

Rösch, V., Tscharntke, T., Scherber, C. and Batáry, P. (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia*, 179, 209-222.

Rosenzweig, M.L. (1995) Species diversity in space and time. Cambridge University Press, Cambridge.

Sanou, L., Devineau, J.L. and Fournier, A. (2013) Floristic communities and regeneration capacity of woody species of the wooded shrines of the Bwaba cultural area (Department of Bondoukuy, West Burkina Faso). *Acta Botanica Gallica*, 160, 77-102. https://doi.org/10.1080/12538078.2013.797366.

Schweitzer, C.J. and Dey, D.C. (2011) Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-cumberland plateau escarpment region, USA. *Forest Ecology and Management*, 262, 1729-1741. https://doi.org/10.1016/j.foreco.2011.07.020.

Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlinn, D.J. and Willig, M.R. (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, 81, 195-213. https://doi.org/10.1890/10-1426.1.

Shepheard, W. (2014) Culture and Conservation in the Sacred Sites of Coastal Kenya. [PhD Thesis]. *Durrell Institute of Conservation and Ecology*, University of Kent, Canterbury, United Kingdom. https://kar.kent.ac.uk/48959.

Stein, A., Gerstner, K. and Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880. https://doi.org/10.1111/ele.12277.

Tabor, K., Burgess, N.D., Mbilinyi, B.P., Kashaigili, J.J., Steininger, M.K. (2010) Forest and Woodland Cover and Change in Coastal Tanzania and Kenya, 1990 to 2000. *Journal of East African Natural History*, 99, 19-45.

Toledo, M., Pena-Claros, M., Bongers, F., Alarcon, A., Balcazar, J. and Chuvina, J. *et al.* (2012) Distribution pattern of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*,100,253-263. https://doi.org/10.1111/j.1365-2745.2011.01890.x.

Tuomisto, H., Ruokolainen, K., Aguilar, M. and Sarmiento, A. (2003) Floristic patterns along a 43-km long transect in an Amazonian rain forest. *Journal of Ecology*, 91, 743-756. https://doi.org/10.1046/j.1365-2745.2003.00802.x.

Marcilio-Silva, V., Zwiener, V.P. and Marques, M.C.M. (2017) Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest. *Diversity Distributions*, 23, 1110-1119. https://doi.org/10.1111/ddi.12616.

Veech, J.A. and Crist T.O. (2010) Toward a unified view of diversity partitioning. *Ecology*, 91, 1988-1992.

Veech, J. A., Summerville, K. S., Crist, T. O. and Gering, J. C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99, 3-9.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279-338. https ://doi.org/10.2307/1943563.

Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Reviews of the Cambridge Philosophical Society*, 42, 207-264. https://doi.org/10.1111/j.1469-185x.1967.tb01419.x.

Whitmore, T.C. (1998) *An Introduction to Tropical Rain Forests*. *2nd Edition.* Oxford University Press, New York.

Wood, A., Tolera, M., Snell, M., O'Hara, P. and Hailu, A. (2019) Community forest management (CFM) in south-west Ethiopia: Maintaining forests, biodiversity and carbon stocks to support wild coffee conservation. *Global Environmental Change*, 59, 101980. https://doi.org/10.1016/j.gloenvcha.2019.101980.

Wright, S.J. (2010) The future of tropical forests. *Annals of the New York Academynof Sciences*, 1195, 1-27. https://doi.org/10.1111/j.1749-6632.2010.05455.x.

Zhang, Y., Han, C. and Taylor, A. (2014) Multiple drivers of plant diversity in forest ecosystems. *Global Ecology and Biogeography*, 23, 885-893. https://doi.org/10.1111/geb.12188.

Zwiener, V.P., Padial, A.A. and Marques, M.C.M. (2020) The mechanisms explaining tree species richness and composition are convergent in a megadiverse hotspot. *Biodiversity and Conservation*, 29, 799-815. https://doi.org/10.1007/s10531-019-01910-9.

Chapter 4

Species-area relationship and small-island effect of the plant diversity in the coastal forests of Kenya

Chapter to be published as:

Maria Fungomeli[1,2, *], Piero Zannini[1, *], Fabrizio Frascaroli[1,3] & Alessandro Chiarucci[1]

[1]BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy
[2]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Mombasa, Kilifi, Kenya
[3]Lòm Research, Rocca d'Arce, Frosinone, Italy

Abstract

Aims: In tropical areas, forest fragmentation is a primary driver of biodiversity loss due to habitats isolation, area reduction, deforestation and degradation. The coastal forests of Kenya are a biodiversity hotspot existing as fragmented forest islands, left from a once continuous forest. Understanding how species diversity is affected by area is a fundamental question in ecology and is crucial to assess the long-term effects of fragmentation and predict species extinctions.

Location: Coastal forests of Kenya- biodiversity hotspot

Methods: Using our standardized vegetation data, we examine the effect of forest fragment area and small Island effect of plant diversity in the Kenyan coastal forests by approaching a sSecies-Area Relationship (SAR) and Small Island Effect (SIE) using a range of alternative regression models. Best-fit model was selected based on the lowest Akaike's Information Criterion corrected for sample size (AIC_c).

Results: We found a significant relationship between rarefied and observed values of species diversity, which suggests that species richness values were not inflated by the different sampling effort across forest sites. Additionally, we found that the area of forest fragments explained a significant portion of the variability of species richness confirming the important role of forest fragment as a driver of diversity. The best fit model was the Arrhenius power model, which fitted better with a lower AIC_c value. Finally, a SIE was not evident in our study.

Conclusions: We show a strong effect of area on the highly fragmented Kenyan coastal forests. From our results, the SAR model indicates that species conservation seems to be more effective in fragments that are larger. We however argue that, species extinctions and extinction debts are likely to be higher in smaller fragments compared to larger fragments and therefore the need to design conservation-based strategies taking into account both the large and small forests in a landscape approach in order to avoid species loss.

Keywords: Coastal forests, fragmentation, small-island effect**,** species extinction, species-area relationship

1.0 Introduction

Understanding how species diversity is affected by area is a fundamental question in ecology (Lawton 1999; Lomolino 2000) and is crucial to assess the long-term effects of fragmentation and inform future conservation strategies. Such knowledge can be used to predict species extinction debts and species extinctions as a result of habitat loss and aid in the design of appropriate management and conservation strategies (Drakare et al., 2006; Halley et al., 2016; He & Hubbell, 2011).

According to the Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967; Whittaker & Fernandez-Palacios, 2007), area is the main determining factor of the number of species in isolated ecosystems, such as in real islands (e.g., Lomolino & Weiser, 2001, Triantis et al. 2012), but also in forest fragments (e.g., May & Stumpf 2000; Marshall et al. 2009). The species-area relationship (hereafter SAR), has been used in ecology to describe patterns of species richness in relation to area, whereby the number of species increases with area (Arrhenius, 1921; Rosenzweig, 1995; Lomolino, 2000) and larger forest fragments host a higher number of species (Triantis et al., 2006; Dengler, 2010; Sfenthourakis and Panitsa, 2012; Gaston and Blackburn, 2000; Pärtel et al., 2016; Schrader et al., 2020). As such, SAR is a crucial biodiversity conservation tool also used to predict species losses as result of habitat fragmentation (He and Hubbell, 2011; Matthews et al., 2014a). Below a certain threshold, area can become a poor predictor of the species richness of isolated units, as they can be subjected to a 'small-island effect' (SIE). The SIE occurs in small islands, mainly due to stochastic processes, as species richness does not increase with increasing island area but varies independently of the island size, - or increases at a lesser rate than in larger islands (Triantis et al., 2006; Burns et al., 2009; Dengler, 2010; Sfenthourakis and Panitsa, 2012; Pärtel et al., 2016; Schrader et al., 2020). Although first developed with regards to island biogeography, the SIE can arguably be applied to small habitat fragments to describe the effects of extreme fragmentation in previously continuous habitats (Wang et al., 2018). Forest fragmentation is a primary driver of biodiversity loss mainly caused by habitat isolation, area reduction, deforestation and degradation (Laurance et al., 2002; FAO and UNEP, 2020). Many tropical forests now exist as remnant forest fragments, within an intensively transformed landscape matrix, largely as a consequence of human activities and the effects of globalization (Fahrig, 2003; Laurance et al., 2002).

Species-area relationship has been employed through a number of models (see Dengler 2010 and Triantis et al., 2012) is computed by fitting function models. The most widely applied models are the power function $\boldsymbol{S = cA^z}$ (Arrhenius, 1921; Mathews et al., 2014; Dengler et al., 2020), which is sometimes adopted in its log-log transformation, and the semi-log function $\boldsymbol{S = c + z \cdot log(A)}$ (Gleason, 1922), where: $\boldsymbol{S}$ = species number, $\boldsymbol{A}$ = the sampled area, $\boldsymbol{c}$ = the number of species present in one-unit area, $\boldsymbol{z}$ = the rate of increase of species richness with increasing area, or slope of the SAR in the log-log transformation of the model. SIEs, instead, are detected through segmented (i.e., breakpoint) regression models (Burns et al., 2009; Schrader et al., 2020). If a SIE is detected, the model fitting for small area units differs from the model fitting of large areas, and the slope is expected to be zero or lower in smaller areas (MacArthur and Wilson, 1967; Lomolino and Weiser, 2001; Dengler 2010; Matthews et al., 2014b; Wang et al., 2018).

Studies of SAR and SIE have developed over time and provided extensive investigations of deterministic curves, process-driven models (degrees of models), statistical methodology, sampling models, and applications on multiple taxa to understand various patterns in ecology (Azeria et al., 2007; Muggeo, 2008; Burns et al., 2009; Dengler, 2010; Sfenthourakis and Triantis, 2009; Tjørve & Tjørve, 2011; Triantis et al., 2012; Wang et al., 2015; Mathews et al., 2014b; Mathews et al., 2019). However, no study to our knowledge has investigated the effects of area and SIE on the species diversity within the Coastal forests of Kenya fragments.

In this study, we use a range of alternative models to examine the relation between forest fragment area and plant diversity, and possible presence of SIE, across 25 fragments of the Kenyan coastal forests. Among African tropical forests, the coastal forests of Kenya are a biodiversity hotspot consisting of an ‘archipelago of forest patches’ left from a once continuous forest that extended over tropical Africa (Lovett, 1998; Burgess and Clarke, 2000; Burgess et al., 2004; Azeria et al., 2007). They exhibit conservation values in virtue of their rich biodiversity and high rates of endemism (Burgess et al., 1998; Burgess and Clarke, 2000; Lovett, 1998; Myers et al., 2000). However, these values are threatened by the high pressure of deforestation and increasing fragmentation (Burgess and Clarke, 2000; Burgess et al., 2004).

Here, we focus on different spatial scales, based on our field survey that applied standardized sampling to forest fragments widely differing in areal extent. To build on the general hypothesis that species richness is affected by the size of the forest fragment, we aim to test the role of SAR and SIE in controlling plant species diversity across the Kenyan coastal forest fragments. Specifically, we aim to test the following hypotheses: i) forest fragment area controls the plant species diversity both in terms of cumulative species richness (gamma richness) and variance in species composition (beta diversity); ii) below a certain fragment size, species diversity is not related to forest area and varies in a stochastic way, as predicted by the Small Island Effect (SIE).

2.0 Materials and Methods

2.1 Study Area

The coastal forests of Kenya are part of the biodiversity hotspot known as the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et al., 2000). They are located along the Kenya coastal Indian ocean strip within the Eastern African coastal ecoregion (Figure 4.1, see Fungomeli et al., 2020b), as isolated patches covering approximately 787 km^2 (Burgess and Clarke, 2000). The climate is tropical with coastal heat and high humidity (Burgess and Clarke, 2000). The mean annual rainfall ranges from 900 mm to 1200 mm while mean annual temperature is comprised between 25° C- 30° C (Burgess and Clarke, 2000).

The area of the Kenyan coastal forests is highly variable, with only two large remaining fragments, Arabuko Sokoke forest (420 km^2) and Shimba Hills forest (253 km^2), and a number of small or very small patches (0.1 - 0.75 km^2, Figure 4.1), many of which are considered sacred forests and are locally referred to as *'Kayas'* (Githitho, 2016; see Fungomeli et al., 2020b). The forests are mainly a mixture of moist and dry forests, with mangrove forests occurring along the shoreline.

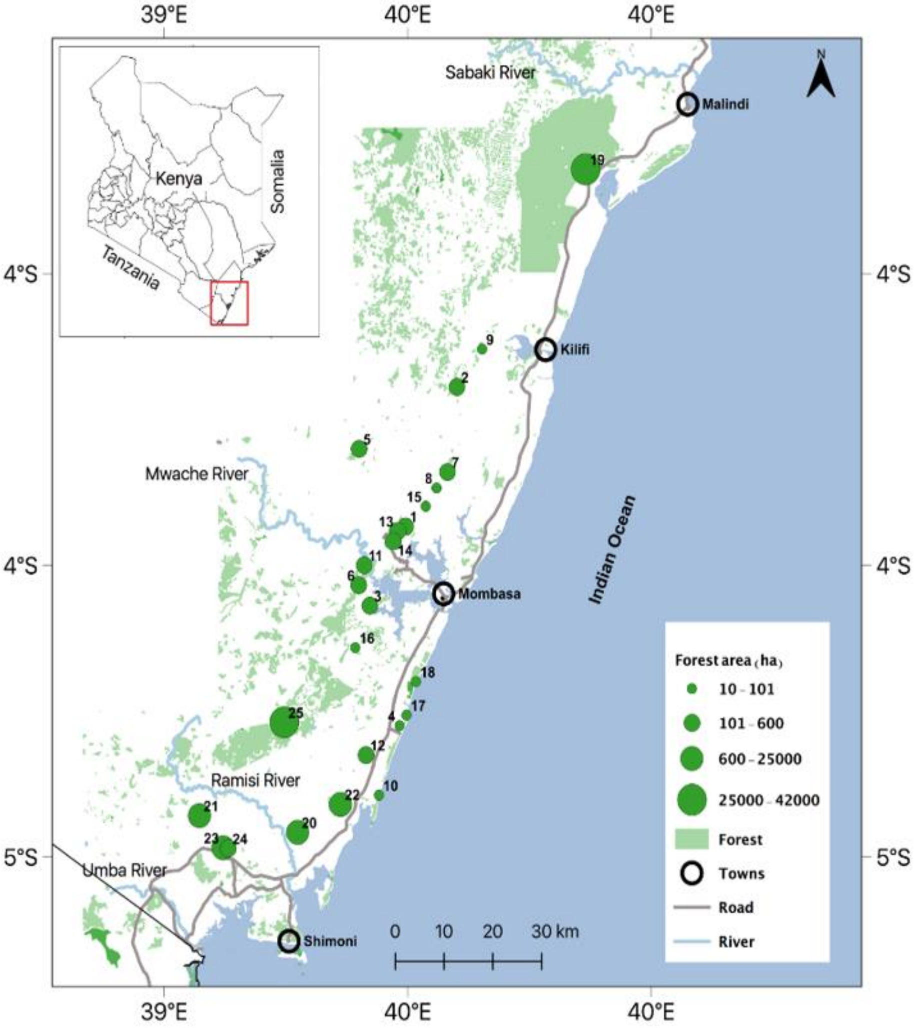


Figure 4.1: Map and locations of the 25 studied sites in the Coastal forests of Kenya, showing forest area. Forest site names numbered 1-25: 1=Bomu, 2=Chivara, 3=Chonyi, 4=Diani, 5=Fungo, 6=Gandini, 7=Jibana, 8=Kambe, 9=Kauma, 10=Kinondo, 11=Mtswaka, 12=Muhaka, 13=Muvya, 14=Mwiru, 15=Ribe, 16=Teleza, 17=Tiwi, 18=Waa, 19=Arabuko, 20=Buda, 21=Dzombo, 22=Gogoni, 23=Marenje, 24=Mrima, 25=Shimba.

2.2 Data collection

We sampled 25 forest fragments (Table 4.1), covering the whole areal spectrum and ranging from the very small Kaya Tiwi site (0.1 km^2) to the largest site in the area, the forest of Arabuko Sokoke (420 km^2). We sampled woody plant species in each forest fragment by using a number of plots within each fragment based on forest area (Table 4.1; see Fungomeli et al. 2020b) and maintaining a 200 m as minimum distance between plots. Each plot measured 10 m x 100 m and was subdivided into twenty contiguous subplots of 10 m x 5 m.

We measured and identified all the woody plant individuals rooted within each subplot with DBH (diameter at breast height) ≥ 5 cm, recorded their DBH and height (h). For shrubs, we recorded number of shoots by using two subplots randomly selected within the first half and the second half (subplots 1-10 and 11-20, respectively) of each plot. Plants were identified in the field whenever possible to the species or genus level. When onsite identification was not possible, voucher specimens were collected for subsequent herbarium identification.

2.3 Data Analysis

2.3.1 Rarefaction

To measure plant species diversity per forest fragment, we used estimates of gamma richness to refer to the species richness per forest fragment. Gamma diversity per forest fragment was calculated by rarefaction according to the following procedure: the first step was to account for the difference in sampling effort across the 25 forest fragments as revealed by the deviations emerging from a linear relation between the log area and the number of plots per forest fragment. To account for this, we used sampled-based rarefaction (Gotelli & Colwell, 2001) by using the analytical formula (Chiarucci et al., 2008) to interpolate a standardized value of species richness per site for a number of plots perfectly proportional to the log of forest fragment area. In this way, we achieved a standardized number of species per each forest fragment, based on a comparable sampling approach, related to forest area, that was used as a conservative measure of the of the forest fragment gamma richness (Table S4.1).

Table S4.1: Coastal forests of Kenya Rarefied values across forest sites for number of plots (rarPlots), species richness (rarS), and Beta diversity multiplicative (rarBmulti) across the 25 studied forest fragments.

Forest site	nPlots	rarPlots	S	rarS	Bmult	rarBmulti
Arabuko	26	5.8	178	100.4	5.0	2.8
Bomu	8	3.3	154	91.2	4.1	2.4
Buda	6	3.6	121	96.0	2.5	2.0
Chivara	8	3.8	140	97.5	3.7	2.6
Chonyi	4	3.0	62	53.8	2.2	1.9
Diani	3	1.6	66	49.4	1.6	1.2
Dzombo	6	3.4	90	69.0	2.7	2.1
Fungo	4	3.0	60	50.2	2.6	2.2
Gandini	5	2.7	80	58.9	2.4	1.8
Gogoni	6	3.9	123	102.0	2.6	2.1
Jibana	8	3.0	195	125.6	3.1	2.0
Kambe	6	2.3	109	57.7	3.5	1.9
Kauma	7	2.5	77	43.7	3.3	1.9
Kinondo	3	3.0	56	56.0	1.8	1.8
Marenje	6	3.1	76	56.8	2.4	1.8
Mrima	6	3.2	101	76.2	2.7	2.1
Mtswaka	4	3.2	64	57.7	2.1	1.9
Muhaka	5	2.8	90	71.0	2.2	1.7
Muvya	4	3.0	85	71.1	2.7	2.2
Mwiru	4	2.8	70	59.1	2.2	1.8
Ribe	5	2.4	95	61.5	2.8	1.8
Shimba	12	5.5	190	135.6	4.2	3.0
Teleza	6	2.3	91	51.4	3.0	1.7
Tiwi	3	1.6	53	40.9	1.5	1.2
Waa	3	1.9	43	34.2	2.0	1.6

Species diversity metrics of alpha and gamma species richness are computed directly from the field data records, while β-diversity has to be calculated by either use of multiplicative or additive partitioning methods (Chiarucci et al., 2010; Crist et al., 2003; Crist & Veech, 2006; Gering et al., 2003; Jost, 2010; Marcilio-Silva et al., 2017; Veech et al., 2002; Veech & Crist, 2010). Here, we apply multiplicative beta partitioning to SAR model (Crist & Veech, 2006; Veech & Crist, 2010; Chiarucci et al., 2008). Therefore, beta diversity was calculated as the traditional multiplicative diversity (Whittaker 1960; Whittaker, 1972; Jost, 2007) by using the ratio between the rarefied gamma richness per forest fragment and the mean number of species per plot, used as an unbiased estimate of alpha diversity within forest fragment. To check for potential bias introduced by the different sampling effort in each forest fragment, the rarefied measures of gamma and beta diversity were compared to those based on the observed data through ordinary linear regressions (Table S4.1).

2.3.2 Species-area relationship (SAR) and Small Island effect (SIE)

To test our hypotheses and evaluate what model best describes different species-area relationships and the possible presence of SIE, we fitted nine different models to gamma diversity. First, we fitted baseline models of Arrhenius power function (Arrhenius, 1921; *S* vs *A*), the Gleason semi-log function (Gleason, 1922; *S* vs *LogA*) and the log-log Arrhenius function (*LogS* vs *LogA*) by means of "*sar_power*", "*sar_loga*" and "*lin_pow*" functions, respectively from the *"sars*" R package (Mathews et al., 2019). Second, to model for the presence of SIE, we fitted two SIE models: the *two-slopes* and *left-horizontal* models, to each of the above three baseline models. The *left-horizontal* segmented model infers that the slope is flat (=0) till breakpoint, while *two-slope* models infers a model with two different slopes on the left and right of the breakpoint.

Then, we selected one or two best-fit models for each variable combination (pairs), based on Akaike's Information Criterion (AIC) score corrected for sample size (AIC_c, Suguira 1978) calculated using "*MuMln"* R package). The best model-fit was adopted if the AIC_c values were lowest.

3.0 Results

General data

The data we collected in the 25 forest fragments included 600 species belonging to 336 genera and 80 families (Table 4.1). The recorded gamma richness per forest ranged from 43 to 195, while average species richness per plot ranged from 31.3 ± 4.9 to 50.7 ± 12.4 (Table 4.1).

Table 4.1: Coastal forests of Kenya fragments description and species diversity within sacred forests and forest reserves for forest site names, area (ha), number of plots, average species richness (± sd) and cumulative species richness (gamma richness) per forest site across the 25 studied forest fragments of the coastal forests of Kenya.

Forest ID	Area (ha)	No. of plots	Average species richness	Gamma species richness
Sacred forests				
Bomu	409	8	36.5 ± 9.5	154
Chivara	150	8	37.8 ± 12.0	140
Chonyi	200	4	37.5 ± 16.8	62
Diani	20	3	31.3 ± 4.9	66
Fungo	204	4	35.0 ± 9.7	60
Gandini	150	5	41.6 ± 4.1	80
Jibana	140	8	34.1 ± 12.6	195
Kambe	75	6	33.8 ± 5.5	109
Kauma	75	7	33.1 ± 6.6	77
Kinondo	30	3	36.0 ± 16.5	56
Mtswaka	248	4	37.5 ± 3.5	64
Muhaka	150	5	36.2 ± 5.7	90
Muvya	171	4	45.8 ± 19.3	85
Mwiru	147	4	33.3 ± 5.9	70
Ribe	36	5	35.4 ± 4.6	95
Teleza	67	6	38.2 ± 20.4	91
Tiwi	10	3	50.7 ± 12.4	53
Waa	30	3	39.3 ± 18.0	43
Forest reserves				
Arabuko	42000	26	36.0 ± 8.7	178
Buda	670	6	37.7 ± 6.6	121
Dzombo	650	6	36.3 ± 11.2	90
Gogoni	832	6	33.7 ± 13.0	123
Marenje	1480	6	42.0 ± 18.4	76
Mrima	377	6	33.0 ± 9.9	101
Shimba	25300	12	37.3 ± 12.7	190

Observed and rarefied species richness

The rarefied and observed values of gamma richness and beta diversity were highly related (R^2 = 0.867, $P < 0.0001$ and R^2 = 0.696, $P < 0.0001$, respectively; Figure 4.2), suggesting that, overall, species diversity values per forest site were not inflated by the different sampling efforts. At the same time, a certain variation existed, justifying the use of rarefied measures.

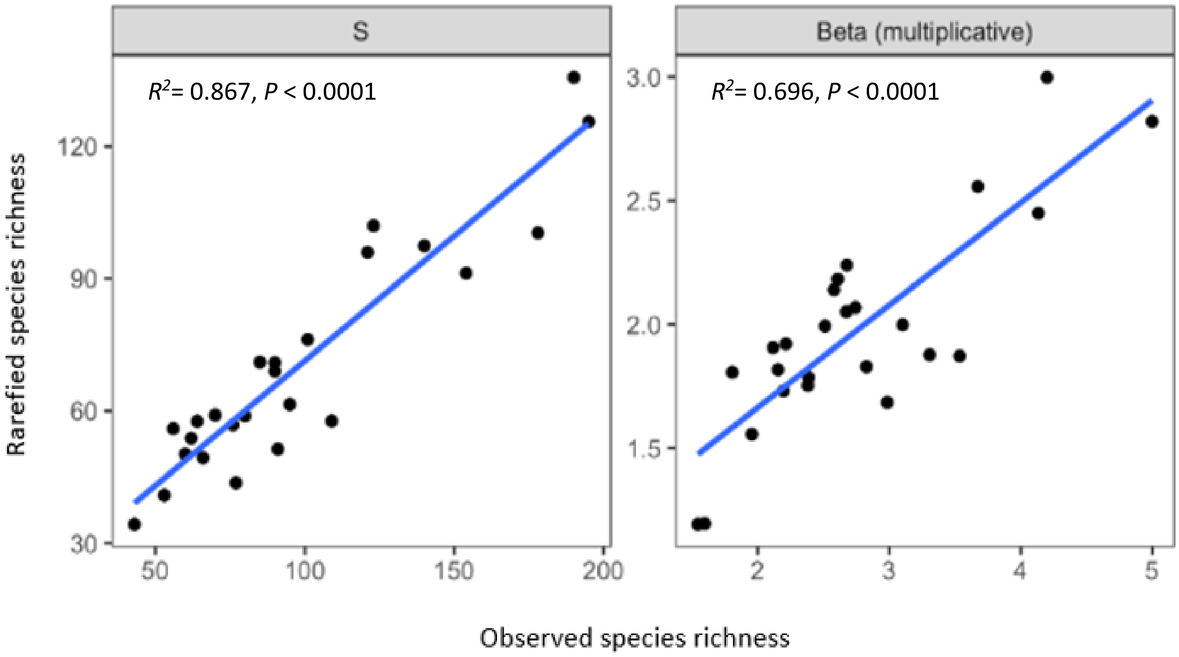


Figure 4.2: Relationship between the rarefied and observed gamma diversity for species richness (S), and beta multiplicative diversity across the 25 surveyed forest fragments in the Coastal forests of Kenya.

Effect of forest patch area on plant species diversity-SAR

Forest patch area explained a considerable proportion of the variability of rarefied species richness as based on the best-fit models (Table 4.2). In particular, the Arrhenius power function model performed the best across the fragments, showing the lowest AIC_c (248.179). Therefore, despite the amount of explained variability was quite limited (R^2_{Adj} = 0.449), the hypothesis of an effect of forest fragment size on gamma richness is supported by our analyses.

Table 4.2: Variables and model fitting for the species-area relations (SAR) and Small Island Effect (SIE) for the coastal forests of Kenya (n=25), using Arrhenius power function, Gleason model and log-transformed Arrhenius power function, and SIE models of *two-slopes* and *left-horizontal* models, where *C*= intercept, *Z* = slope, S=species richness, A=Area. The best fitting models are based on low Akaike information criterion corrected for sample size (AIC_c) and R^2 adjusted (R^2_{Adj}).

Variable	**Model**	**C**	**Z_1**	**Z_2**	**Threshold**	**R^2_{Adj}**	**AIC_c**
S-A	*Arrhenius*	82.998	-	0.141	-	0.449	248.179
	Two-slopes	75.480	5.183	-0.073	25.17	0.449	254.181
	Left-horizontal	91.157	-	0.265	0.17	0.298	258.171
S-Log(*A*)	*Gleason*	82.076	-	16.712	-	0.448	248.206
	Two-slopes	82.298	25.807	44.905	2.51	0.463	253.549
	Left-horizontal	59.43	-	40.038	0.30	0.475	250.912
Log(S)-Log(A)	Log-Log (*Arrhenius*)	77.851	-	0.155	-	0.444	-24.928
	Two-slopes	83.946	0.250	0.143	0.63	0.427	-19.244
	Left-horizontal	59.156	-	0.155	0.17	0.444	-22.071

Small Island Effect-SIE

The models used to fit SIE did not show any improvement compared to their reference models, as highlighted by their higher values of the AIC_c statistic (Table 4.2; Figure 4.3). Therefore, the hypothesis of a small island effect on forest fragments below a certain threshold was rejected by our analysis. Further, the *left-horizontal* and *two-slopes* models showed patterns that were not distinguishable nor ecologically meaningful with respect to their reference SAR models (Table 4.2; Figure 4.3).

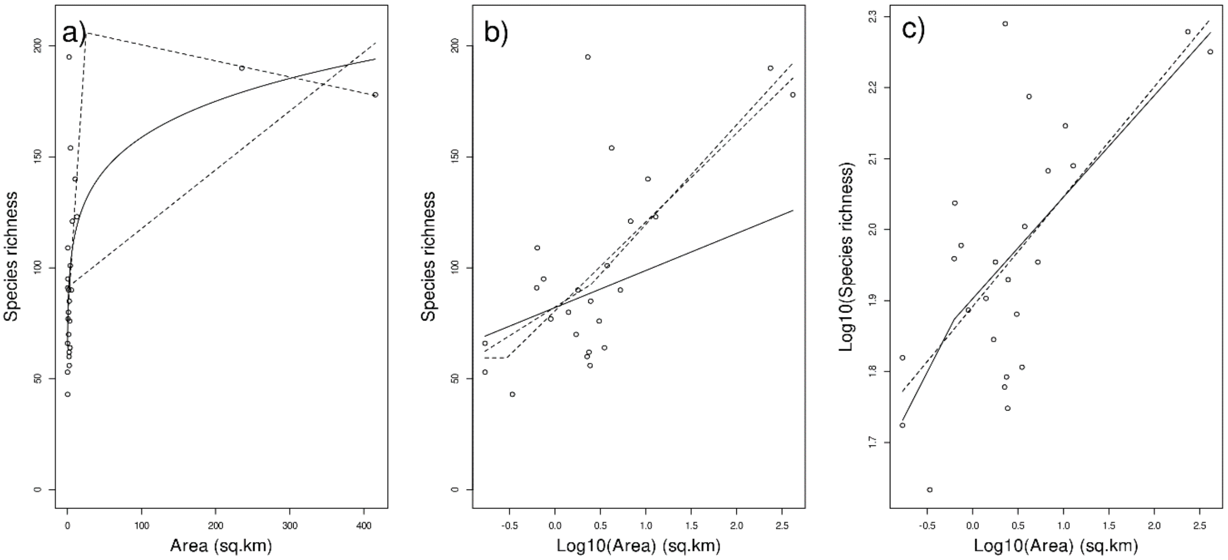


Figure 4.3: Species-Area Relationship (SAR) and Small Island Effect (SIE) of the 25 surveyed fragments in the Coastal forests of Kenya. Graphical output of the fitting models predicting the measures of species diversity on the basis of forest patch area. **(a)** S-A, **(b)** S-LogA and **(c)** LogS-LogA. where S=species richness, A=Area. The best fitting models are shown by continuous solid line, while other models are shown by dotted lines. The best fitting models are based on low Akaike information criterion (AIC_c) and R^2 adjusted (R^2_{Adj}). Note that in the third panel (**c**), the *Log-Log Arrhenius* and *Left-horizontal* are both present but indistinguishable due to the log-transformation and similar coefficients (see Table 4.2).

4.0 Discussion

The species-area relationship (SAR) provides an ecological platform to assess the long-term effects of fragmentation on species diversity. To our knowledge, this is the first study to investigate effects of area on species diversity in the coastal forests of Kenya. Our study found three main results. First, we found a significant relationship between rarefied and observed values of species diversity, which suggests that species richness values per forest site were not inflated by the different sampling effort across forest sites. Second, we found that the area of forest fragments explained a significant portion of the variability of species richness confirming the important role of forest fragment as a driver of diversity. Third, we did not detect any significant SIE, suggesting that area increase has similar effects on species richness also in case of very small forest fragments.

4.1 Fragment area explained significant variability of species diversity

We found that the forest fragment area explained a significant variability of species diversity as based on the models. These results were reflected on the diversity measures of gamma and multiplicative beta diversity across the Kenyan forest fragments. This confirms the first hypothesis about the significant role of forest fragment area on the various species richness. These results largely confirm the SAR which suggests that species diversity and population size is a function of area and which increases with increase in area (Rosenzweig, 1995). However, the unexplained variability (above 50%) can be explained as resulting from other environmental factors across the biogeographical scale. These variables may include the different forest management in protection status of forest reserves and sacred forests, both abiotic and biotic gradients, heterogeneity and disturbance (Lomolino and Weiser 2001; Mittelbach and Schemske, 2015; Wang, et al., 2018). Nevertheless, our results are largely supported by the findings of Kallimanis et al. (2008) who show that increased species richness is correlated with area. We therefore depict patterns of species diversity across the Kenyan coastal forest fragments and show the significant role of forest fragment area on species diversity.

4.2 Performance of the various models on species diversity and area

The species-area relationship (SAR) model fitting varied across models, with variation in mean species richness per unit area (*c-values*), the rate of increase of species accumulation with increased area (*z-values)* and Akaike's Information Criterion score corrected for sample size (AIC_c) among models. The best fit model was the Arrhenius model, which fitted better with a lower AIC_c value followed by Gleason (248.179 and 248.206 respectively). Notably, the difference in the AIC_c values for Arrhenius and Gleason models was minimal (0.027). Our results are consistent with other studies that have shown the Arrhenius model (power model) to be widely the best model across true island isolates in the Island species-area relationships (ISAR; Dengler et al., 2020; Matthews et al., 2016; Triantis et al., 2012). Furthermore, Arrhenius model showed mean species richness to area (*c* =83 species) with a slope value of 0.141 (*z*-value), which show a higher slope value depicting a high habitat diversity among fragments. Additionally, the *z*-values are within the SAR theoretical expectation range (0.07 - 0.4) of Island-area relationships (Rosenzweig, 1995; Triantis et al., 2012; Whittaker & Fernández-Palacios, 2007).

Theoretically, larger *z*-values imply a quick accumulation of species as area increases therefore also implying a higher rate of species turnover (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007). However, the *z* and *c*-values are also further affected by ecological factors such as dispersal, landscape heterogeneity, scale, disturbance, endemism and life form for plants (Halley et al., 2016; He & Hubbell 2011; Hobohm et al., 2019; Schrader et al., 2020). For example, studies have shown that *z*-values increases with fragments isolation and increasing extinction rates, while it decreases with disturbance and latitude (Hobohm et al., 2019; Qian et al., 2007; Triantis et al., 2012). On the other hand, the different *c*-values imply differences in species richness across fragments which add up to account for the species pool. In the broad sense (*sensu lato*), interpretation of *c* and *z*-values values and implications for conservation calls for attention in application for biodiversity conservation. In this respect, our study landscape is characterised by a biodiversity hotspot with high species richness against high endemism, rare species and disturbance which all act simultaneously and may explain the *z*-value exhibited.

4.3 Small Island Effect (SIE) on species richness

A small Island effect (SIE) did not emerge in our results due to the higher AIC_c values exhibited by the *left-horizontal* and *two slopes models* with respect to the reference SAR models, so our second hypothesis is rejected. A fundamental explanation which has favoured large fragments and more so the SAR is that large fragments contain high number of species and stable habitat conditions and therefore species extinction risk is very low (MacArthur and Wilson 1967). Nevertheless, in ecology, SIE are used to predict species extinctions resulting from habitat loss (Lomolino & Weiser 2001; Whittaker & Fernandez-Palacios 2007). The Kenyan coastal fragments exhibit high species richness across, and falls within a matrix of endemic, rare and threatened species, while evidently against a backdrop of anthropogenic effects and heterogeneity which may increase species extinction threats. Therefore, also considering the small forest fragments in our study area, our results call for further consideration and analysis on species extinction and extinction debts across this Kenyan biodiversity hotspot (Halley et al., 2016).

Our results challenge the conventional *a priori* assumption that smaller and isolated forest fragments, across spatial scales, biogeographic gradients and more so within the complex tropical rich habitats (also biodiversity hotspot areas) would exhibit a SIE (Zhang et al., 2016). To some extent, this is perceived to be pronounced in shaping tropical biodiversity that tend to have high number of species and high number of rare and threatened species, where species variation is hard to explain using environmental variables only (Zhang et al., 2016). However, overall, there is ongoing debate to understand the underlying factors controlling SIE when using 'area' *per se* as the main driving factor which can be hard to dis-entangle from general drivers of species distribution at different spatial scales (Dengler 2010; Triantis et al. 2006; Triantis and Sfenthourakis 2012; Wang et al. 2015; Yu et al. 2020). Potentially, the SIE are explained by stochastic factors and processes (immigration, colonization, dispersal, mortality) which also work simultaneously with deterministic factors to influence community dynamics and predict species extinction (Stegen et al., 2012; Zhou & Ning, 2017). Furthermore, Triantis et al. (2006) argues that detection of the existence of SIE should consider both parameters of the most complex and diverse biomes of the world, and therefore, multiple interactions of ecological factors, heterogeneity and drivers of species richness acting at different scales may have a greater effect on detection of SIE beyond forest 'area' (Wiens 1989; Whittaker et al. 2001; Triantis et al. 2006).

4.4 Conclusion and implications for conservation

The Kenyan coastal forests exist in a highly fragmented nature, heterogeneity, and in a mix of protection status of forest reserves and sacred forests. The forests reserves which are exhibited by larger fragment areas seem to benefit by virtue of their large size and probably from sound protection and conservation measures. On the other hand, the small size fragments, most of which are the sacred forests, exhibit different levels of species richness with some fragments plotting above and some below the SAR curves. From our results, the SAR model indicates that species conservation seems to be more effective in fragments that are larger (Lomolino & Weiser, 2001; Wang, et al., 2018). We however argue that, species extinctions and extinction debts are likely to be higher in smaller fragments compared to larger fragments (Halley et al., 2016; Volenec & Dobson, 2019), and therefore the need to consider conservation planning of the smaller fragments in a landscape approach. This approach is further supported by our phylogenetic diversity analysis of these fragments where the smaller forests exhibited higher amount of threatened and endemic species, with a high phylogenetic diversity (Fungomeli et al. *in prep*).

5.0 References

Arrhenius, O. (1921). Species and area. *Journal of Ecology*, 9, 95-99. https://doi.org/10.2307/2255763.

Azeria, E.T., Sanmartin, I., Stephan, A.S., Carlson, A., & Burgess, N.D. (2007). Biogeographic patterns of the East African coastal forest vertebrate fauna. *Biodiversity and Conservation*, 16, 883-912. https://doi.org/10.1007/s10531-006-9022-0.

Azovsky, A. I. (2011). Species-area and species-sampling effort relationships: disentangling the effects. *Ecography*, 34, 18-30. https://doi.org/10.1111/j.1600-0587.2010.06288.x

Baldi, A. (2008). Habitat heterogeneity overrides the species–area relationship. *Journal of Biogeography*, 35, 675-681. https://doi.org/10.1111/j.1365-2699.2007.01825.x

Beentje, H.J. (1994). Kenya trees, shrubs and lianas. National Museums of Kenya, Nairobi, KE, 722 pp.

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, . . ., Winter M (2019) sPlot: A new tool for global vegetation analyses. Journal of Vegetation Science 30: 161–186. https://doi.org/10.1111/jvs.12710019.

Burgess, N. D., Clarke, G. P., & Rodgers, W. A. (1998). Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society*, 64, 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess, N. D., Clarke, G. P. (eds) (2000). The coastal forests of Eastern Africa. IUCN, Gland, CH and Cambridge, UK. Google Scholar.

Burgess, N. D., Hales, J., Underwood, E., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T., Newman, K., & Hales, J. (2004). Terrestrial ecoregions of Africa and Madagascar: a conservation assessment. Island Press.

Burns, K.C., McHardy, R.P., & Pledger, S. (2009). The small-island effect: fact or artefact? *Ecography*, 32, 269-276. https://doi.org/10.1111/j.1600-0587.2008.05565.x

Cayuela L, Stein A, Oksanen J (2017) Taxonstand: Taxonomic standardization of plant species names. R package version 2.1. URL: https://CRAN.R-project.org/package=Taxonstand [accessed 15 July 2019].

Cencini, M., Pigolotti, S., & MunÕz, M.A. (2012). What ecological factors shape species-area curves in Neutral Models? *PLoS ONE* ,7, e38232. https://doi.org/10.1371/journal.pone.0038232.

Chiarucci, A., Bacaro, G., Rocchini, D., & Fattorini, L. (2008). Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. *Community Ecology*, 9, 121-123. https://doi.org/10.1556/ComEc.9.2008.1.14.

Chiarucci, A., Bacaro, G., Arévalo, J. *R.*, Delgado, J. *D., &* Fernández-Palacios, J.M. (2010). Additive partitioning as a tool for investigating the flora diversity in oceanic archipelagos. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 83-91. https://doi-org.ezproxy.unibo.it/10.1016/j.ppees.2010.01.001.

Crist, T. O., Veech, J. A., Gering, J. C., & Summerville, K. S. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta, and gamma diversity. *American Naturalist*, 162, 734-743. https://doi.org/10.1086/378901

Crist, T.O., & Veech, J.A. (2006). Additive partitioning of rarefaction curves and species–area relationships: unifying α-, β- and γ-diversity with sample size and habitat area. *Ecology Letters*, 9: 923-932. https://doi.org/10.1111/j.1461-0248.2006.00941.x

Dengler, J. (2010). Robust methods for detecting a small island effect. *Diversity and Distributions*, 16, 256-266. https://doi.org/10.1111/j.1472-4642.2010.00646.x

Dengler, J., Matthews, T. J., Steinbauer, M. J., Wolfrum, S., Boch, S., Chiarucci, A., Conradi, T., Dembicz, I., Marcenò, C., … Biurrun, I. (2020). Species-area relationships in continuous vegetation: Evidence from Palaearctic grasslands. *Journal of Biogeography*, 60, 72-86. https://doi.org/10.1111/jbi.13697.

Drakare, S., Lennon, J.J. & Hillebrand, H. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters*, 9, 215-227. https://doi.org/10.1111/j.1461-0248.2005.00848.x

FAO and UNEP (2020). The State of the World's Forests 2020. Forests, biodiversity and people. Rome. https://doi.org/10.4060/ca8642en.

Fahrig L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst*. 34, 487-515. https://doi.org:10.1146/annurev.ecolsys.34.011802.132419.

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40, 164-1663. https://doi.org/10.1111/jbi.12130

Fletcher, R.J., Diham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F. P.L., Ries, L., Prevedello, J.A., Tscharntke, T., Laurance, W.F., Lovejoy, T. & Haddad, N.M. *(*2018*)*. Is habitat fragmentation good for biodiversity? *Biol Conserv* 226*:*9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Fungomeli, M., Githitho, A., Frascaroli, F., Chidzinga, S., Cianciaruso, M., & Chiarucci, A. (2020a). A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey*, 1, 103-109. https://doi.org/10.3897/VCS/2020/47180.

Fungomeli, M., Cianciaruso, M., Zannini, P., Githitho, A., Frascaroli, F., Fulanda, B., Kibet, S., Wiemers, M., Mbuvi, T., Matiku, P. & Chiarucci, A. (2020b). Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, *Plant Biosystems*, https://doi.org/10.1080/11263504.2020.1834461.

Gaston, K., & Blackburn, T. (2000). *Pattern and process in macroecology.* Blackwell Science Ltd. Willey publisher. https://onlinelibrary.wiley.com/doi/book/10.1002/9780470999592.

Gentile, G., & Argano, R. (2005). Island biogeography of the Mediterranean Sea: The species-area relationship for terrestrial isopods. *Journal of Biogeography*, 32, 1715-1726. https ://doi.org/10.1111/j.1365-2699.2005.01329.x

Gering, J. C., Crist, T. O., Veech, J. A. (2003). Additive Partitioning of Species Diversity across Multiple Spatial Scales: Implications for Regional Conservation of Biodiversity. *Conservation Biology*, 17, 488-499. https://doi.org/10.1046/j.1523-1739.2003.01465.x

Githitho, A. N. (2016). Listing the sacred Mijikenda Kaya Forests as UNESCO World Heritage Sites: The Long Journey, *Journal des africanistes [*En ligne], 86-1, http://journals.openedition.org/africanistes/4971 [accessed 7 July 2019].

Gleason, H. A. (1922). On the relation between species and area. *Ecology*, 3, 158-162. https://doi.org/10.2307/1929150

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Green, J., Holmes, A., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M. & Beattie, A.J. (2004). Spatial scaling of microbial eukaryote diversity. *Nature*, 432, 747-750. https://doi.org/10.1038/nature03034

Halley, J.M., Monokrousos, N., Mazaris, A.D., Newmark, W.D. & Vokou, D. (2016). Dynamics of extinction debt across five taxonomic groups. *Nature communications,*7:12283 https://doi.org/10.1038/ncomms12283

Hanski, I., & Triantis, K. (2015). Habitat fragmentation and species richness. *Journal of Biogeography,* 42, 989-993. https://doi.org/10.1111/jbi.12478

He, F., & Hubbell, S.P. (2011). Species–area relationships always overestimate extinction rates from habitat loss. *Nature*, 473, 368-371. https://doi.org/10.1038/nature09985

Hobohm C, Janišová M, Steinbauer MJ, Landi S, Field R, Vanderplank S, Beierkuhnlein C, Grytnes J-A, Vetaas OR, …, Chiarucci A (2019). Global endemics-area relationships of vascular plants. *Perspectives in Ecology and Conservation* 17: 41–49. https://doi.org/10.1016/j.pecon.2019.04.002

Hrdina, Aleš & Romportl, Dušan. (2017). Evaluating Global Biodiversity Hotspots – Very Rich and Even More Endangered. *Journal of Landscape Ecology*. https://doi.org/10. 10.1515/jlecol-2017-0013

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427-2439. https://doi.org/10.1890/06-1736.1

Jost, L. (2010). Independence of alpha and beta diversities. *Ecology*, 91, 1969-1974. https://doi.org/10.1890/09-0368.1

Kallimanis, A. S., Mazaris, A. D., Tzanopoulos, J., Halley, J. M., Pantis, J. D., Sgardelis, S. P. (2008). How does habitat diversity affect the species-area relationship? *Global Ecology and Biogeography*, 17, 532-538. https://doi.org/10.1111/j.1466-8238.2008.00393.x.

Kraft, N. J. B. et al. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science* 333, 1755-1758. https://doi.org/10.1126/science.1208584.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76(1), 5. https://doi.org/10.2307/3545743.

Laurance, W., & Bierregaard, R. (eds) (1997). Tropical forest remnants: ecology, management, and conservation of fragmented communities. Chicago, IL: University of Chicago [Google Scholar].

Laurance W.F et al. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* 16, 605-618. https://doi.org/10.1046/j.1523-1739.2002.01025.x.

Lawton, J. H. (1999). Are there general laws in ecology? *Oikos*, 84, 177-192. https://doi.org/10.2307/3546712.

Lomolino, M.V. (2000). Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, 27, 17- 26. https://doi.org/10.1046/j.1365-2699.2000.00377.x

Lomolino, M.V. & Weiser, M.D. (2001). Towards a more general species-area relationship: diversity on all islands, great and small. *Journal of Biogeography*, 28, 431-445. https://doi:10.1046/j.1365-2699.2001. 00550.x.

Lovett, J. C. (1998). Eastern Tropical African Centre of Endemism: A Candidate for World Heritage Status. *Journal of East African Natural History*, 87, 359-366. https://doi.org/10.2982/0012-8317.

Luke, W. R. Q. (2005). Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. *Journal of East African Natural History*, 94, 5-121. https://doi.org/10.2982/0012-8317.

MacArthur, R.H. & Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373-387. https://doi.org/10.2307/2407089

MacArthur, R.H. & Wilson, E.O. (1967). The theory of island biogeography. Princeton University Press, Princeton, NJ. Google Scholar.

Marcilio-Silva, V., Zwiener, V.P., Marques, M. C. M. (2017). Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest. *Diversity Distributions*, 23,1110-1119. https://doi.org/10.1111/ddi.12616.

Marshall, A. R., Jørgensbye, H. I. O., Rovero, F., Platts, P. J., White, P. C. L., & Lovett, J. C. (2009). The species-area relationship and confounding variables in a threatened monkey community. *American Journal of Primatology*, 71, 1-12. https://doi.org/10.1002/ajp.20787.

Matthews, T.J., Cottee-Jones, H.E.W., & Whittaker, R.J. (2014a). Habitat fragmentation and the species-area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, 20, 1136-1146. https://doi.org/10.1111/ddi.12227

Matthews, T. J., Steinbauer, M. J., Tzirkalli, E., Triantis, K. A., & Whittaker, R. J. (2014b). Thresholds and the species–area relationship: A synthetic analysis of habitat island datasets. *Journal of Biogeography*, *41*, 1018–1028. https://doi.org/10.1111/jbi.12286

Matthews, T. J., Guilhaumon, F., Triantis, K. A., Borregaard, M. K., & Whittaker, R. J. (2016). On the form of species-area relationships in habitat islands and true islands. *Global Ecology and Biogeography*, *25*, 847–858. https://doi.org/10.1111/geb.12269

Matthews, J., Triantis, K. A., Whittaker, R. J., & Guihaumon, F. (2019). sars: An R package for fitting, evaluating and comparing species-area relationship models. *Ecography*, 42, 1446-1455. https ://doi.org/10.1111/ ecog.04271

May, R. M., & Stumpf, M. P. H. (2000). Species-area relation in tropical forests. Science, 290(5499), 2084–2086. https://doi.org/10.1126/science.290.5499.2084

Mittelbach, G.G., & Schemske, D.W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, 30 (5), 241-247. https://doi.org/10.1016/j.tree.2015.02.008

Moomaw JC (1960). A study of the plant ecology of the Coast Region of Kenya, East Africa. Government Printer, Nairobi, KE, 62 pp. https://edepot.wur.nl/493400.

Montagnini F, Jordan CF (2010). Tropical forest ecology. Springer, Berlin, DE, 295pp. https://doi.org/10.1007/b138811

Muggeo, V. M. R. (2008). Segmented: An R package to fit regression models with broken-line relationships. *R News*, 8, 20-25.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858. https://doi.org/10.1038/35002501

Noad, T., & Birnie, A. (1990). A fully illustrated field guide: trees of Kenya. General Printers Ltd, Nairobi, KE, 350 pp.

Phillips, H.R.P., Halley, J.M., Urbina-Cardona, J.N., & Purvis, A. (2018). The effect of fragment area on site-level biodiversity. *Ecography*, 41, 1220-1231. https://doi:10.1111/ecog.02956

Qian, H., Fridley, J. D., & Palmer, M. W. (2007). The latitudinal gradient of species-area relationships of vascular plants of North America. *The American Naturalist*, 170, 690-701. https://doi.org/10.1086/521960

Robertson, S. A., & Luke, W. R. Q (1993). The vegetation and conservation status of Kaya coastal forests in Kenya. WWF, Nairobi, KE, 425 pp. https://www.africabib.org/rec.php?RID=K00001940

Rosenzweig, M.L. (1995). Species diversity in space and time. Cambridge University Press, Cambridge.

Schrader, J., König, C., Triantis, K. A., Trigas, P., Kreft, H., Weigelt, P., & Sandel, B. (2020). Species-area relationships on small islands differ among plant growth forms. *Global Ecology and Biogeography*, 29, 814-829. https://doi:10.1111/geb.13056

Sfenthourakis, S., & Triantis, K. A. (2009). Habitat diversity, ecological requirements of species and the Small Island Effect. *Diversity Distribution*, 15, 131-140. https://doi:10.1111/j.1472-4642.2008.00526.x

Sreekar, R. et al. (2018). Spatial scale changes the relationship between beta diversity, species richness and latitude. *R. Soc.open sci.* 5, 181168. https://dx.doi.org/10.1098/rsos.181168

Stegen, J.C., Lin, X., Konopka, A.E. & Fredrickson, J.K. (2012). Stochastic and deterministic assembly processes in subsurface microbial communities. *The ISME Journal* 6, 1653-1664. https://doi.org/10.1038/ismej.2012.22

Sugiura, N. (1978). Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics-Theory and Methods*, 7, 13-26. https://doi:10.1080/03610927808827599

Tjørve, E. (2009). Shapes and functions of species–area curves (II): a review of new models and parameterizations. *Journal of Biogeography*, 36, 1435– 1445. https://doi.org/10.1111/j.1365-2699.2009.02101.x

Tjørve, E., & Tjørve, K.M.C. (2011). Subjecting the theory of the small-island effect to Ockham's razor. *Journal of Biogeography*, 38, 1836-1839. https://doi:10.1111/j.1365-2699.2011.02534.x

Tulloch AIT, Barnes MD, Ringma J, Fuller RA, Watson JEM *(*2016*)*. Understanding the importance of small patches of habitat for conservation. *Journal of Applied Ecology* 53*:*418–429. https://doi:10.1111/1365-2664.12547

Triantis, K.A., Vardinoyannis, K., Tsolaki, E.P., Botsaris, I., Lika, K. & Mylonas, M. (2006). Re-approaching the small island effect. *Journal of Biogeography*, 33, 915- 923. https://doi.org/10.1111/j.1365-2699.2006. 01464.x

Triantis, K.A., & Sfenthourakis, S. (2012). Island biogeography is not a single-variable discipline: the small island effect debate. *Diversity Distributions*, 18, 92-96. https://doi:10.1111/j.1472-4642.2011.00812.x

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012), The island species–area relationship: biology and statistics. *Journal of Biogeography*, 39: 215-231. https://doi:10.1111/j.1365-2699.2011.02652.x

Veech, J. A., Summerville, K. S., Crist, T. O., & Gering, J. C. (2002). The additive partitioning of species diversity: recent revival of an old idea. *Oikos*, 99, 3-9. https://doi.org/10.1034/j.1600-0706.2002.990101.x

Veech, J. A., & Crist T.O. (2010). Toward a unified view of diversity partitioning. *Ecology*, 91, 1988-1992. https://doi.org/10.1890/09-1140.1

Volenec, Z.M., & Dobson, A. P. (2019). Conservation value of small reserves. *Conservation Biology*, 34(1), 66-79. https://doi.org/10.1111/cobi.13308

Wang, Y., Wu, Q., Wang, X., Liu, C., Wu, L., Chen, C., … Ding, P. (2015). Small-island effect in snake communities on islands of an inundated lake: The need to include zeroes. Basic and *Applied Ecology*, 16, 19-27. https ://doi.org/10.1016/j.baae.2014.10.006.

Wang, Y., Chen, C., & Millien, V. (2018). A global synthesis of the small-island effect in habitat islands. Proceedings of the Royal Society B: *Biological Sciences*, 285, 20181868. https://doi.org/10.1098/rspb.2018.1868.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3, 385-397. https ://doi.org/10.2307/2389612.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279-338. https ://doi.org/10.2307/1943563.

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21, 213-251. https ://doi.org/10.2307/1218190

Whittaker, R. J., Willis, K. J. & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453-470. https://doi.org/10.1046/j.1365-2699.2001.00563.x

Whittaker, R.J. & Fernández-Palacios, J.M. (2007). *Island Biogeography. Ecology, Evolution and Conservation* (2nd edition). Oxford University Press.

Whittaker, R.J., & Matthews, T.J. (2014). The varied form of species-area relationships. *Journal of Biogeography*, 41, 209-210. https://doi.org/10.1111/jbi.12256

Yu, J., Li, D., Zhang, Z., & Guo, S. (2020). Species-area relationship and small-island effect of bryophytes on the Zhoushan Archipelago, China. *Journal of Biogeography*, 47, 978-992. https://doi.org/10.1111/jbi.13790.

Zhang, X., Pu, Z., Li, Y., & Han, X. (2016). Stochastic processes play more important roles in driving the dynamics of rarer species. *Journal of Plant Ecology*, 9(3), 328–332. https://doi.org/10.1093/jpe/rtv058.

Zhou J, Ning D. 2017. Stochastic community assembly: does it matter in microbial ecology? *Microbiol Mol Biol Rev* 81: e00002-17. https://doi.org/10.1128/MMBR.00002-17.

Chapter 5

Phylogenetic diversity of the Coastal forests of Kenya:

Role of sacred Kaya forests and IUCN Red List in the conservation of evolutionary history of a biodiversity hotspot

Chapter to be published as:

Maria Fungomeli[1,2*], Alessandro Chiarucci[1], Arianna Balacchi[1] & Marcus Cianciaruso[3]

[1]Biogeography and Macroecology Lab, Dept. of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy
[2]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Mombasa, Kilifi, Kenya
[3]Department of Ecology, Universidade Federal de Goiás, Brazil

Abstract

The Kenyan coastal remnant forest fragments are a biodiversity hotspot valued for their rich biodiversity and endemism, in a backdrop of increased fragmentation and species extinction threats. However, there is lack of studies on the evolutionary history of these forest fragments limiting our capacity to mitigate species loss and maintain ecosystem services function. Here, we investigate the phylogenetic diversity across these coastal fragments, within protection status; within threatened species categories of IUCN Red List; endemic species; and implications for their conservation.

By using our data collected in a standardized and intensive sampling, we calculated phylogenetic diversity metrics such as mean pairwise distance (MPD); mean nearest taxon distance (MNTD) and Faith's Phylogenetic diversity (PD). Then we calculated null models as standard effect sizes (ses) of sesMPD, sesMNTD and sesPD.

Our results present for the first time the picture of the evolutionary history of the plant species in the coastal forests of Kenya. We show that the forest reserves are insufficient alone to protect the evolutionary history of the Kenyan coastal forests without taking into account the sacred forests. Additionally, some sacred forests exhibited a higher phylogenetic diversity compared to forests reserves. The sacred forest fragments play a vital role in conserving distinct evolutionary lineages; offer seed sources for biologically unique species and therefore connectivity between sacred and forest reserves is crucial for enhanced dispersal. The threatened Red List species contributed to a higher evolutionary history and this increased as they become more threatened. Our results suggest the need to adopt a phylogenetically informed conservation approach that compliments the current taxonomic diversity. Moreover, conservation measures should protect Red List species to avoid greater loss of evolutionary history.

Keywords: biodiversity conservation, coastal forests, endemic species, kaya forests, mean nearest taxon distance, sacred forests, threatened species, tropical forests.

1.0 Introduction

Tropical forest fragmentation forms a key contributor to global species extinction crisis. This extinction crisis challenge is more pronounced in a biodiversity hotspot with already existing high numbers of endemic, rare and threatened species such as the coastal forests of Kenya. The Kenyan coastal forest fragments have been valued for their rich biodiversity that they support in terms of number of species, threatened (IUCN Red List), endemic and rare species. However, to the best of our knowledge, there is lack of knowledge of how much evolutionary history biodiversity they preserve beyond species counts. Traditionally, biodiversity conservation has widely been based on species counts (species richness, species diversity) without taking into account the phylogenetic diversity which would be a better measure of biodiversity (Cadotte et al., 2010; Chiarucci et al., 2011; Laity et al., 2015; Mazzochini et al., 2019; Miller et al., 2018; Pellens & Grandcolas, 2016). Inevitably, with the uncertain future of increasing anthropogenic changes and climatic change effects, conserving the phylogenetic diversity of the coastal forests of Kenya will essentially not only play an important role in decreasing the potential to general species loss, and more for endemic and threatened species, but also contribute to maintaining the ecosystem function and stability, and have a better understanding of ecological and evolutionary focused knowledge (Arroyo-Rodriguez et al., 2012; Jin & Qian, 2019). Phylogenetic diversity indices would allow to shelter most distinctive species and also include greater number of species in fewer areas (Arroyo-Rodriguez et al., 2012).

The IUCN Red List of threatened species and endemic species have been globally used to show the conservation status of biological diversity and species extinction risk (IUCN, 2020). This has served as a crucial conservation tool used to guide conservation measures, actions and policy (IUCN, 2020). However, this global conservation status measure uses species-counts criteria to evaluate their status regionally and globally, without considering species evolutionary history. In this case, phylogenetic diversity would make an enhanced guidance to combining community ecology and biodiversity conservation more effective (Pellens & Grandcolas, 2016). Furthermore, due to the increasing fragmentation, isolation and deforestation of tropical forests, integrating the evolutionary history would maximize outputs on the already conservation costs within the wake of limited resources allocated to conservation activities. For example, as mostly experienced in most biodiversity conservation organizations, most often there is limited or lack of funding, and not enough resources neither enough time to conserve species one by one. It is therefore necessary to maximize the return on investment in conservation by combining ecology and evolutionary history (Laureto & Cianciaruso, 2017; Margules & Pressey, 2000; Pellens & Grandcolas, 2016; Winter et al., 2013).

The coastal forests of Kenya are globally rich tropical remnants known to harbor high number of threatened species and endemism making them one of the most important areas for conservation (Burgess & Clarke, 2000; Fungomeli et al., 2020a; Myers et al., 2000). They fall within the Eastern Africa coastal forests as remnants of forest patches under different sizes and different forms of protection status. They fall under two management regimes: forest reserves and the sacred forests. The forest reserves are officially and legally government protected forests while the sacred forests are informally protected by the local communities (Githitho, 2016). These sacred forests are traditionally used by the coastal Mijikenda community as places of worship and locally referred to as *'Kayas'*, which in the local language means '*homestead*' (Githitho, 2016). Therefore, the sacred forests have ended up being conserved to date as a result of the taboos, religious and other traditional norms in place used by the local communities. The two largest remaining Kenyan coastal forest patches are the Arabuko Sokoke forest reserve (420km^2) and the Shimba Hills forest reserve (253km^2), while the rest of the forests are spread in relatively small fragments ranging between 10 ha and 450 ha, many of which are considered the sacred forests (Table 5.1; Figure 5.1; Figure 5.4).

Nevertheless, the coastal fragments in Kenya where most threatened species are found are declining due to agriculture, mining and tourism (IUCN, 2020). Most fragments are fairly isolated and tend to be threatened by increased degradation through human activities such as illegal logging, poaching and clearance for agriculture leading to loss of biodiversity as a major threat to sustainable conservation of these forest remnants (Kibet, 2011).

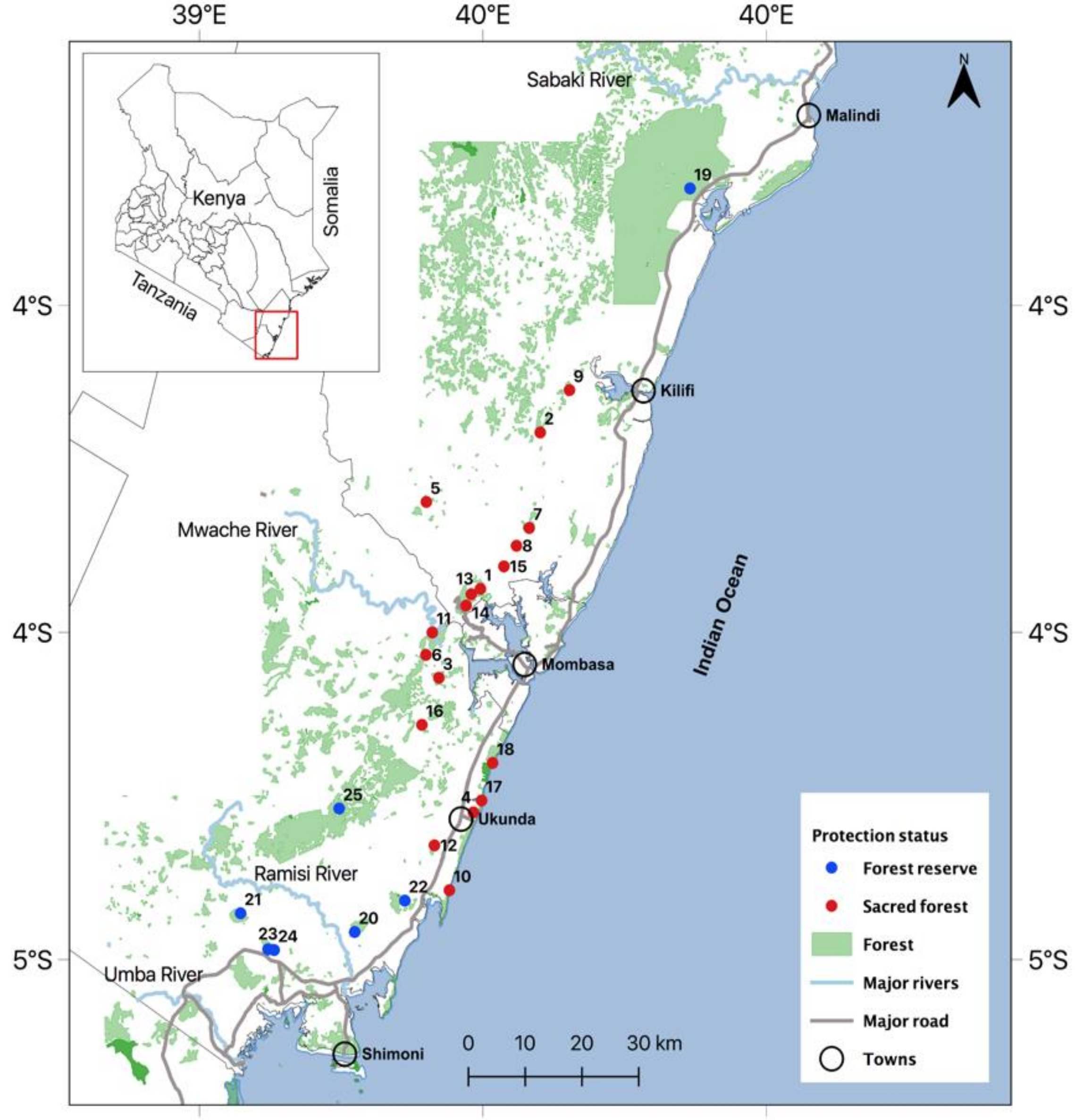


Figure 5.1: Coastal forests of Kenya map of the sampled forest fragments, classified into protection status of forest reserves and sacred forests. The forest size (area) can be seen in Table 5.1. Forest site numbers: 1=Bomu, 2=Chivara, 3=Chonyi, 4=Diani, 5=Fungo, 6=Gandini, 7=Jibana, 8=Kambe, 9=Kauma, 10=Kinondo, 11=Mtswaka, 12=Muhaka, 13=Muvya, 14=Mwiru, 15=Ribe, 16=Teleza, 17=Tiwi, 18=Waa, 19=Arabuko, 20=Buda, 21=Dzombo, 22=Gogoni, 23=Marenje, 24=Mrima, 25=Shimba.

The analysis and application of phylogenetic diversity information in conservation of forest fragments is an increasingly crucial attempt to optimize the preservation of evolutionary history with conservation efforts across spatial scales (Cadotte et al., 2010; Faith, 1992; Pellens & Grandcolas, 2016). The application of this to the Kenyan coastal fragments drives the question and understanding of how much of biodiversity is being protected from an evolutionary point of view? This situation pauses the question of whether incorporating the evolutionary history into conservation measures of the coastal forests would aide into better prioritization of the current conservation measures and strategies?

To sustain and prioritise the conservation of the coastal forests of Kenya, it is vital to understand the phylogenetic diversity these forest remnants exhibit across forest sites, within protection status, and within threatened and endemic species along a spatial gradient. In this study, we examine the phylogenetic diversity across 25 Kenyan coastal forest remnants and implications for their conservation. Specifically, we aim to answer the following questions: (i) Are there differences in the phylogenetic diversity between forest reserves and the sacred forests? In this case, how does the evolutionary diversity (evolutionary history) among species analyzed vary across the protection status? (ii) What is the contribution of the IUCN Red List species and endemics to the phylogenetic diversity of the Kenyan forest fragments? As such, do endemic and threatened species in the coastal forest sites have more or less phylogenetic diversity than expected by chance?

2.0 Materials and Methods

2.1 Study area

The coastal forests of Kenya are located along the Indian ocean coastal strip of Kenya (Figure 5.1), as biodiversity hotspot known as “Eastern Arc and Coastal Forests of Kenya and Tanzania” (Myers et al., 2000). They fall within the Eastern African coastal ecoregion (ca. 3170 km^2) and are presently found as isolated patches, estimated 145 in number for an approximate area of 787 km^2 (Burgess & Clarke, 2000; Fungomeli et al., 2020a). The coastal forests of Kenya spread from the south coast in Kwale county, through Mombasa county, to the north coast in Kilifi, Lamu and Tana river counties

(Figure 5.1). They range in size from as low as 10 ha to 42,000 ha across various climatic and elevation gradients (Figure 5.1). Some forests are found on hill tops such as Kaya Chivara, Kaya Jibana, Kaya Dzombo, Kaya Mudzimuvya and Shimba hills forest, whereas others are found in lowland areas such as Arabuko Sokoke forest. Additionally, some forests occur on the shore line such as Kaya Tiwi, Waa and Kaya Kinondo, while Kaya Fungo and Dzombo are located the furthest distance from the coast at 24.6 km and 16.5 km respectively (see Fungomeli et al., 2020b). The climate is tropical with mean annual rainfall ranging from 900mm to 1200mm and mean temperatures between 25˚C and 30˚C (Burgess & Clarke, 2000).

Overall, the coastal forests of Kenya are mainly a mixture of moist and dry forests, semi-evergreen closed canopy forests, thickets and bushland. They are also characterised by woodland and coastal evergreen bushland, grassland with mangrove forests occurring along the shoreline (Beentje, 1994; Burgess & Clarke, 2000).

2.2 Data collection

Data used in this study comprised of two sources: i) A field survey across the forest sites of the coastal forests of Kenya that formed our community matrix; ii) A compilation of woody plant species to form the recent published plant checklist of the coastal forests (Ngumbau et al., 2020). A combination of the field data and compiled species formed the phylogeny of the coastal forests of Kenya.

First for the community matrix, we used field sampled data on plant species composition and abundance from 25 forest patches composed of 18 sacred forests and seven forest reserves (Fungomeli et al., 2020b). We sampled woody plant species (trees, shrubs and lianas) within 25 forest sites for a total of 158 plots each measuring 10 m x 100 m, and further subdivided into twenty subplots of 10 m x 5 m. The number of plots per forest site was approximately proportional to the log of the forest site surface area and with variation due to some forest sites accessibility and fragmentation (Table 5.1; see Fungomeli et al., 2020b). A minimum distance of 200 m among plots within a site was ensured in order to cover spatial variation.

Table 5.1: Phylogenetic metrics of the Coastal forests of Kenya across sacred forests and forests reserves showing Area (ha), species richness (SR), observed mean pairwise distance (MPD_obs) and observed mean nearest taxon distance (MNTD_obs) based on native species of the coastal forests of Kenya.

Forest sites	**Area (ha)**	**SR**	**MPD_obs**	**MNTD_obs**
Sacred forests				
Bomu	409	152	220.30	36.54
Chivara	150	136	217.44	63.46
Chonyi	200	62	200.32	73.72
Diani	20	63	209.40	83.66
Fungo	204	59	224.44	117.39
Gandini	150	80	201.40	55.50
Jibana	140	187	227.87	65.81
Kambe	75	107	223.92	75.79
Kauma	75	76	215.42	55.19
Kinondo	30	50	204.01	105.41
Mtswaka	248	63	238.28	99.62
Muhaka	150	88	212.43	70.75
Muvya	171	85	220.75	71.23
Mwiru	147	69	209.87	64.75
Ribe	36	94	218.83	70.41
Teleza	67	90	193.72	93.82
Tiwi	10	52	198.79	104.88
Waa	30	40	202.59	87.63
Forest reserves				
Arabuko	42000	176	225.65	48.26
Buda	670	116	218.98	66.80
Dzombo	650	87	213.60	63.08
Gogoni	832	120	218.23	51.80
Marenje	1480	75	209.51	79.49
Mrima	377	98	201.65	71.77
Shimba	25300	187	214.20	49.87

The general orientation of each plot was set at a North-South direction. We recorded the diameter at breast height (dbh) ≥ 5 cm and height (h) of all trees and lianas species rooted within each plot, while shrubs were sampled and identified in two subplots within each plot (one within 1-10 subplots and second randomly selected within subplots 11-20). The abundance of shrub species was assessed by counting the number of individual shoots rooted within a plot. All plants were identified in the field whenever possible to the species or at least genus level by botanists and with the use of botanical manuals using standard references for the area (Beentje, 1994; Luke, 2005; Noad and Birnie, 1990). When onsite identification was not possible, voucher specimens were collected for subsequent herbarium identification.

Second, for the phylogeny, we built the phylogeny of the coastal forests of Kenya, by compiling a comprehensive plant species by a combination of the field community matrix species and species from the recent published plant checklist of the coastal forests of Kenya (Ngumbau et al., 2020). We removed exotic species and considered only native plant species. We also checked for synonyms and standardised our data for plant names according to The Plant List (TPL, www.theplantlist.org). Our final phylogeny resulted into a total of 1183 native woody species, composed of trees, shrubs and lianas. Whereas, the field sampled data resulted into 596 species belonging to 336 genera and 80 families excluding cultivated exotics. These data formed the community matrix sampled (Figure 5.1, see Fungomeli et al., 2020b).

We further got information and classified all species into the categories of endemic species and IUCN Red List species. Endemic species were classified based on the endemic species references of the area (Beentje, 1994; Burgess et al., 1998; Burgess & Clarke, 2000; Luke, 2005). The IUCN species Red List species threat level were classified according to the global IUCN Red List (2020, www.iucnredlist.org, version 3.1) for the coastal forests of Kenya. We selected four categories of Least Concern (LC), Near Threatened (NT), Vulnerable (VU), and Endangered (EN).

2.3 Data analysis

2.3.1 Phylogenetic tree and hypothesis

We constructed a plant species phylogenetic tree composed of 1183 species belonging to 510 genera and 100 families of woody plant species (trees, shrubs and lianas), in our compiled phylogeny of the coastal forests of Kenya (Appendix 5.1). To create our phylogenetic tree, we used the function '*phylo.maker*' in 'V.PhyloMaker' R package (Jin and Qian, 2019). The 'V.PhyloMaker' is a package to generate phylogenies for vascular plants and is based on the mega-tree 'GBOTB.extended.tre' (GenBank and phylogenetic data from the Open Tree of Life (Smith and Brown, 2018).

We used our species names with genus and family information and extracted the information of root and basal nodes of the genera in the mega-tree GBOTB.extended using '*build.nodes.1'* formula in the *phylo.maker'* function (Jin and Qian, 2019). '*build. nodes.*1' is deemed important to be used if the species of a genus are distributed in more than one cluster, where '*build. nodes.*1'extracts the genus or family-level largest clusters's root and basal node based on the most recent common ancestor of all the tips in the largest cluster of the genus, and defines it as the basal node of the genus (Jin and Qian, 2019). Moreover, in the construction of the phylogenetic tree, we used a 'scenario 3' hypothesis where the tip for a new genus is binded to the half point of the family branch, i.e., the branch between the family root node and basal node (Jin and Qian, 2019).

The tree branch lengths are dated in millions of years and were used to calculate the phylogenetic distance metrics with cophenetic distances. The phylogenetic tree is provided as supplementary material (Figure S5.1). Matching of the phylogeny and our community field matrix was performed using *match.phylo.comm* function in PhyloMeasures R package (Kembel et al., 2010; Tsirogiannis & Sandel, 2015), to ensure all our community matrix species were present in the phylogenetic tree.

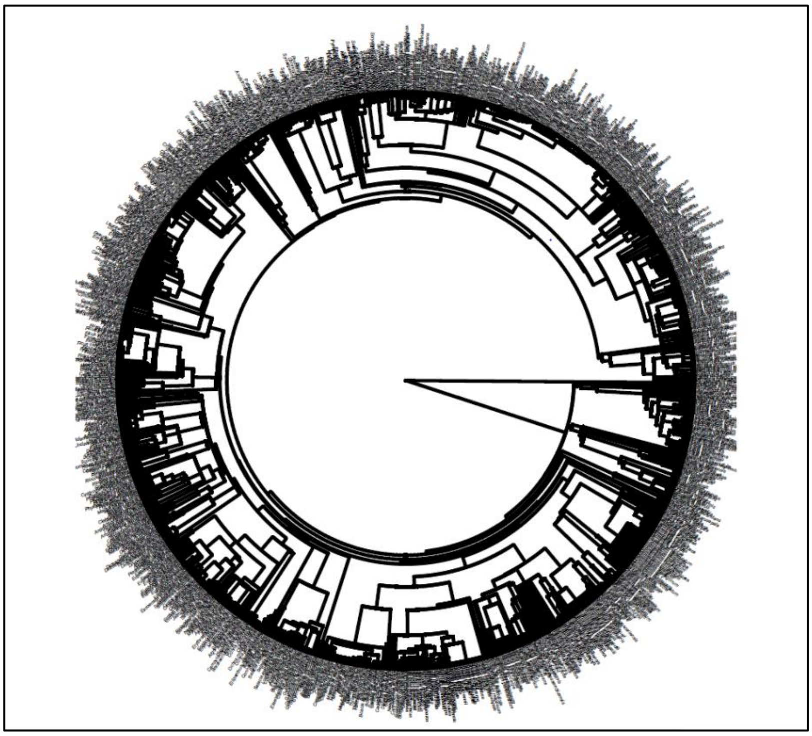


Figure S5.1: Coastal forests of Kenya phylogenetic tree composed of 1183 woody plant species belonging to 510 genera and 100 families.

2.3.2 Phylogenetic diversity metrics of MPD and MNTD in sacred and forest reserves

We calculated metrics that evaluate the evolutionary history present across our forest patches for all native woody species, within forest patch protection status of forest reserves and sacred forests. We calculated diversity metrics as follows: Mean pairwise distance (MPD); Mean nearest taxon distance (MNTD); and Faith's Phylogenetic diversity (PD, Faith, 1992) that showed the general variation in phylogenetic diversity of the coastal forests of Kenya, which was used to answer our first and second question. MPD and MNTD were calculated based on species abundances, and we used these calculations to answer our second question of whether there was a difference in phylogenetic diversity between forest reserves and sacred forests. MPD refers to the average phylogenetic distance (i.e., branch length) among all pairs of species within a community. As such, it is the relatedness between all possible pairs of taxa in an assemblage and it measures the average phylogenetic distance between all combinations of pairs of individuals (including conspecifics), whereas MNTD represents the mean phylogenetic relatedness between each species and its nearest relative in the assemblage (Webb et al., 2002). Therefore, MNTD measures the average phylogenetic distance between an individual and the most closely related non-conspecific individual (Kembel et al., 2010). Accordingly, MPD and MNTD both use the phylogeny as a phylogenetic distance matrix, where MPD reflects phylogenetic structuring across the whole phylogeny while MNTD reflects phylogenetic structure closer to the tips (Kembel et al., 2010).

We used a t-test to test the phylogenetic metric of MPD and MNTD whether they significantly differed across protection status of forest reserves and sacred forests.

2.3.3 Phylogenetic diversity metrics and Standardized effect sizes (sesPD) of IUCN categories and endemic species

Further, we calculated metrics that evaluate the evolutionary within IUCN Red List species and endemic species across the forests. This was based on species presence and absences and we used the null models of PD, i.e., the standard effect sizes (sesPD) to answer our second question of the contribution of IUCN Red list species and endemic species to the phylogenetic diversity of the coastal forests of Kenya. The Faith's phylogenetic diversity (PD) is calculated as the sum of the branch lengths of all species in each one of the forest sites and measures total evolutionary history tracing species back to the root of the tree (Faith, 1992; Tucker et al., 2016; Webb et al., 2008).

We used null models to standardise the PD measurements (standardized effect sizes, sesPD) in order to calculate the observed and randomly expected PD for all species within each forest site. This was in order to derive observed and expected phylogenetic diversity values to answer our second question of the contribution of the IUCN Red List species and endemics to the phylogenetic diversity of the forest fragments.

We considered 999 randomizations, and 5000 iterations using the "independent swap algorithm" (Gotelli, 2000). The independent swap null model is a preferred approach as it randomizes the species richness across the phylogenetic tree tips while maintaining the community matrix species richness per forest site and frequency of occurrence of each species in the 999 randomizations values. To calculate the sesPD, the difference between the observed and expected PD was divided by the standard deviation of the randomized PD using the following equation:

$$\mathrm{sesPD} = \frac{(\mathrm{PD}_{\mathrm{observed}} - \mathrm{PD}_{\mathrm{randomized}})}{\mathrm{SD}_{\mathrm{randomized}}} \qquad \text{(eqn 1)}$$

where $PD_{observed}$ is the original observed PD value, $PD_{randomized}$ is the expected PD of randomized values, and $SD_{randomized}$ is the standard deviation of the respective deviation of the 999 randomized PD values. Positive sesPD values indicate phylogenetic overdispersion (i.e., a higher observed PD than expected by chance), while negative values indicate phylogenetic clustering (i.e., a lower observed PD than expected by chance) (Saraiva et al., 2018; Swenson, 2014; Webb et al., 2008). In this case, we considered significant values when the PD was higher than expected by chance for sesPD values higher than 1.96 (i.e., sesPD > 1.9). All phylogenetic analyses and metrics were performed in R-software, version 3.6.3 (R Core Team, 2020) using the *'ses.pd'* function in *Picante package* (Kembel et al., 2010) and *PhyloMeasures package* (Tsirogiannis & Sandel, 2015 & 2017).

3.0 Results

3.1 Forest reserves and sacred forests Phylogenetic diversity (MPD and MNTD)

Overall, there was no significant difference in the phylogenetic diversity between forest reserves and sacred forests (MPD *P* value=0.80; MNTD *P* value = 0.07; Figure 5.2). These results imply that both forest reserves and sacred forests preserve comparable amount of evolutionary history across the sampled study forests.

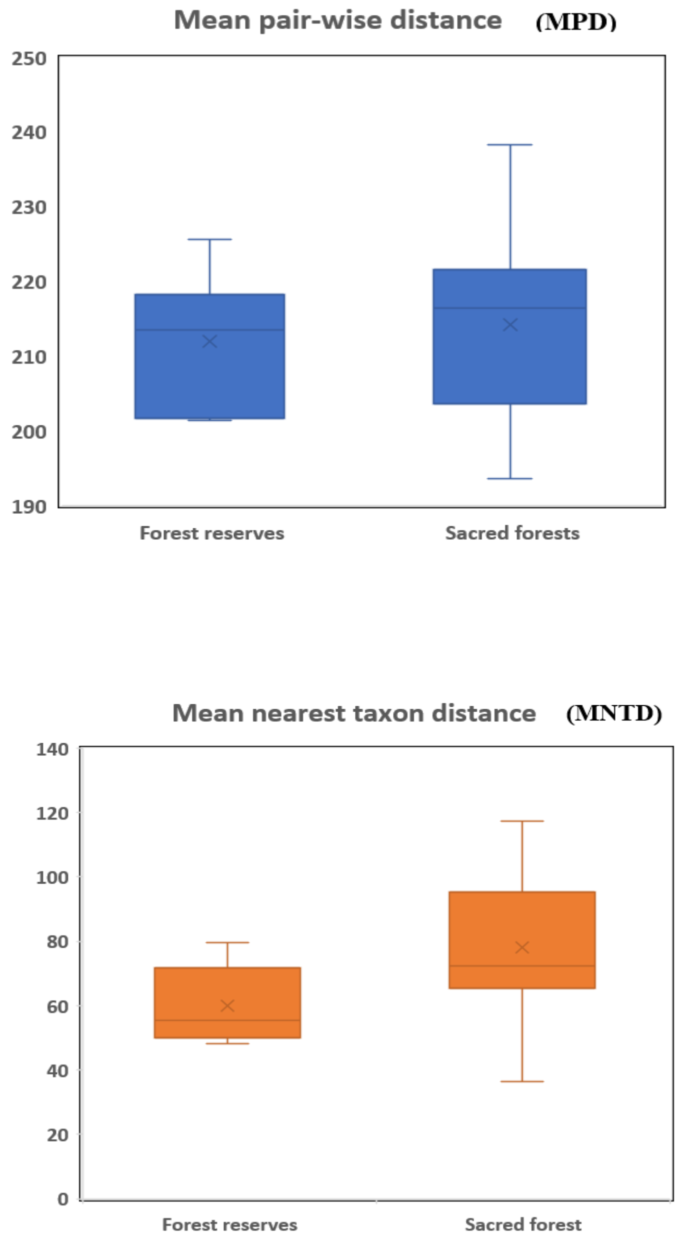


Figure 5.2: Comparison of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) of the coastal forests of Kenya across protection status of forest reserves and sacred forests (statistical tests: MPD *P* value=0.80; MNTD *P* value = 0.07).

3.2 IUCN Red List standardized effect sizes of phylogenetic diversity (sesPD)

We found that the pattern of standardised effect sizes (sesPD) constantly increased for the species of the different IUCN Red List categories from least concern (LC) to endangered (EN) categories (Figure 5.3a). The negative sesPD values indicated phylogenetic clustering showing a lower observed than expected phylogenetic diversity, whereas the positive values of sesPD implied there was phylogenetic overdispersion, which means existence of a higher observed than expected phylogenetic diversity.

Overall, greater the protection status of groups of species in IUCN Red List categories, the higher the phylogenetic diversity with respect to random expectations, i.e., the sesPD were significantly higher than expected by chance (sesPD > 1.9, or < -1.9), and increased as the species became more threatened from the LC to the EN category (Figure 3a). These results suggest that a higher evolutionary history is exhibited by more threatened than less threatened species. On the other hand, the differences across species of the different IUCN Red List categories were not congruent between forest reserves and sacred forests (Figure 5.3b). Mtswakara sacred forest exhibited the highest IUCN category sesPD value, while lowest at Buda forest reserve.

3.3 Endemic species standardized effect sizes of phylogenetic diversity (sesPD)

We found that endemic species standard effect sizes (sesPD) were not different from a random expectation (i.e., most sesPD were within the range +1.96/-1.96). In addition, most sesPD exhibited were negative, while some forest sites had sesPD lower than -1.96 (Bomu, Buda and Mrima), which indicates that endemics are quite closely related (Figure 5.3c).

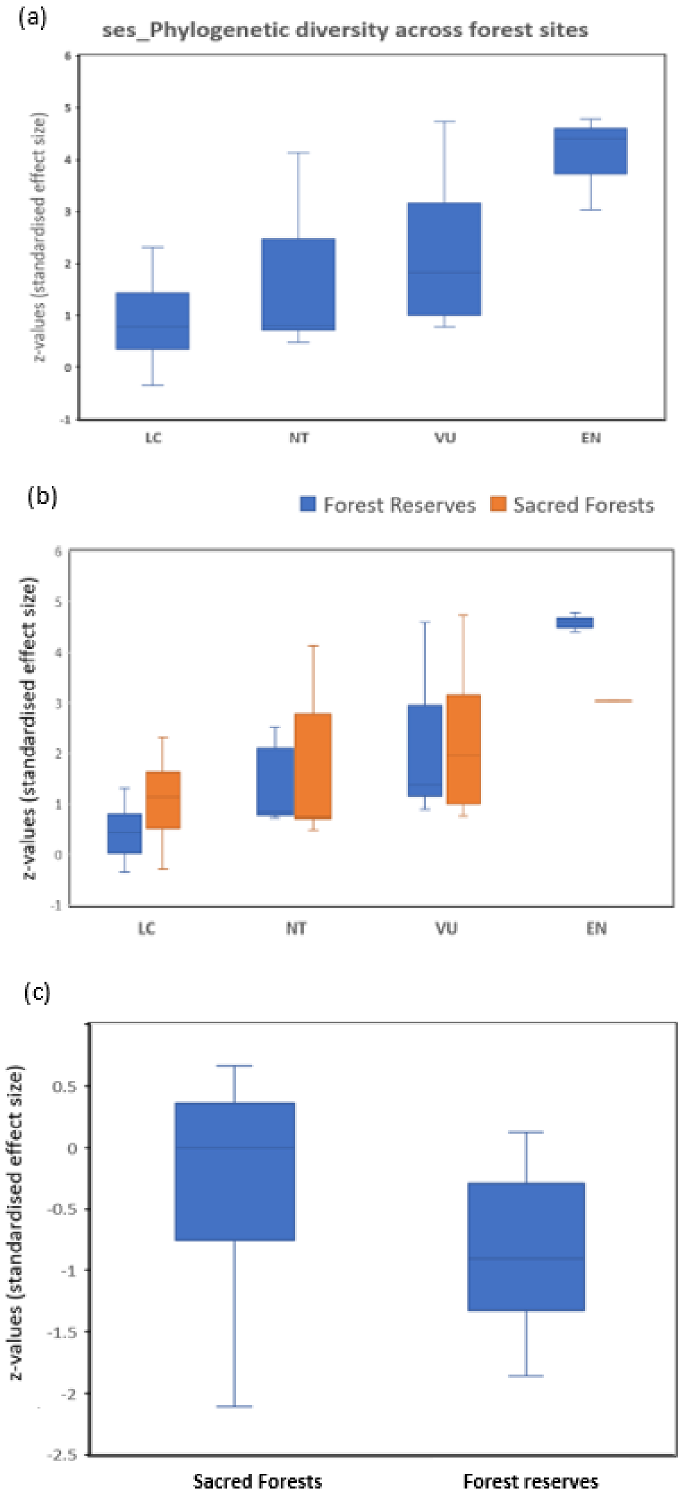


Figure 5.3: IUCN Red List threatened species categories and endemic species standard effect sizes of phylogenetic diversity (sesPD) of the coastal forests of Kenya for: **(a)** IUCN Red List species across all forest sites; **(b)** IUCN Red List species within forest reserves and sacred sites. Species conservation categories: LC=least concern, NT=near threatened, VU=vulnerable, EN=endangered. **(c)** Endemic species within sacred forests and forest reserves. All sesPD values >1.9 or < -1.9 are considered significantly different.

Figure 5.4: Kaya Jibana sacred forest, Kenya. One of the sacred Kaya forest remnants of the coastal forests of Kenya. Photo credit: Steve Okoko Ashikoye.

4.0 Discussion

Biodiversity conservation strategies of fragmented tropical forests faces a challenge to incorporate the biodiversity rich and spatially heterogenous ecosystems for protection. Protecting the phylogenetic diversity is perceived as crucial for effective conservation practices. In this study, we investigated the phylogenetic diversity across the native woody species of the coastal forest fragments of Kenya. To the best of our knowledge, this is the first study to quantitatively investigate the evolutionary history of the coastal forests of Kenya.

Sacred forests & Forest reserves MPD & MNTD

When we compare sacred forests and forests reserves phylogenetic diversity of MPD and MNTD, our results show that averagely, there was no significant difference in the phylogenetic diversity between forest reserves and sacred forests, which suggests they preserve the same amount of evolutionary history. These results can partly be explained by the history of the Kenyan coastal forests where they all once existed as one expansive block of forest landscape before their fragmentation

(Burgess and Clarke, 2000). However, on the other hand, fragmentation and anthropogenic activities may have induced most clearance of the original native vegetation and what remains today could be a secondary re-growth forests of more homogenous vegetation (Lovett, 1998). This is arguably the case when considering most forests in Kenya where they underwent logging for timber by licensed companies in the early 60’s and late 70’s through to early 80’s before a national ban was put in place in early 90s to date (Robertson and Luke, 1993; Wass, 1995).

In general, some sacred forests exhibited a higher phylogenetic diversity compared to forest reserves. For example, the highest MPD and MNTD were exhibited at Kaya Mtswakara and Kaya Fungo sacred forests respectively which implies they have presence of less related species at the terminal structure of the phylogenetic tree. Considerably, higher MNTD values indicate species are distantly related which explains species in the same forest fragment that do not share the same evolutionary history (Kembel et al., 2010; Pellens & Grandcolas, 2016). The sacred forests with higher MPD and MNTD values indicate they are an ancient refugia (Costion et al., 2015; Misher et al., 2014). In general, such forest fragments are known to contain a proportion of evolutionary distinct lineages and therefore a large amount of evolutionary history (Pellens & Grandcolas, 2016). On the other hand, forest fragments with lower MPD and MNTD suggest that they contain a high proportion of species that have originated recently (Collen et al., 2011; Davies & Buckley, 2011; Forest et al., 2007, Mishler et al., 2014; Sairaiva et al., 2018). These results therefore suggest that the forest reserves are insufficient alone to protect the evolutionary history of the Kenyan coastal forests without taking into account the sacred forests. There is therefore need to prioritise and protect the sacred forest fragments as they conserve biologically unique species despite their cultural-traditional protection measures and their small size. However, overall, our results may also be explained by influences of environmental filtering and historical processes that may alter the phylogenetic clustering or phylogenetic over-dispersion across the forest sites (Webb et al., 2002).

Overall, we found that, the Kenyan coastal forests varied in their phylogenetic diversity. Interestingly, comparing the 25 studied forest fragments, we found forest fragments with high observed phylogenetic diversity MPD and MNTD that would not be considered as priority for conservation if based on their species richness only (see Fungomeli et al., 2020a; Fungomeli et al., 2020b where the number of species per forest patch are given and discussed). These fragments include Kaya Waa, Mtswakara and Mwiru sacred forests for MPD while Kaya Tiwi and Kinondo for MNTD. These forest fragments are currently managed and protected by the local communities. They exist in smaller fragment sizes (10 - 670 ha), isolated and spatially distributed while they face a high degradation threat as local communities depend on them for their livelihoods (Kibet, 2011). Our results suggest these forest sites harbour unique vegetation species which may form the foundation under which the evolutionary history of the coastal forests originates (Shapcott et al., 2015; Thuiller, et al., 2015). We highlight an important element to the protected areas and conservation network of the coastal forests of Kenya to carefully uptake and include protection of these forest sites. On a broader scale, our results highly support the use and inclusion of phylogenetic diversity in conservation measures of the coastal forest of Kenya, beyond traditional taxonomic counts (Cadotte, et al., 2010; Faith, 1992; Forest et al., 2007; Miller et al., 2018).

IUCN Red List & endemics

The use of threatened species and endemic species as crucial indicators for priority in habitat conservation has been a criterion that has preserved many habitats and more so the coastal forest of Kenya biodiversity hotspot (Burgess et al., 1998; Margules & Pressey, 2000; Myers et al., 2000; Rodrigues et al., 2004). Our results of the IUCN Red List threatened species showed that, there is an increase in the phylogenetic diversity across forest fragments with increasing threatened species level. Here, we found that with increasing threat level from least concern, near-threatened, vulnerable, to endangered species, there was an increase in the evolutionary history across forest fragments, suggesting that as species became near extinct, they exhibited a higher phylogenetic diversity. Our results suggest that species with higher phylogenetic diversity are closer to extinction. If the species that are presently under higher threat will go extinct, this will lead to a greater loss of evolutionary history than expected by a random extinction of the same number of species. Of particular mention.

These results add a valuable component of phylogenetic diversity for consideration to the conservation planning of these forests. On one hand, we see a complementarity effect of combining both the use of threatened and endemic species with phylogenetic diversity as ecological and phylogenetic diversity criteria (EcoPD), or into what some studies have suggested as evolutionary distinctiveness and globally endangered species (EDGE, Isaac et al., 2007). While on the other hand, we see a crucial new phase of valuing the less valued, small and fragmented sacred forests that exhibit a high phylogenetic diversity (Pellens & Grandcolas, 2016). Nevertheless, there is a challenge to rapidly assess the status of many species and be included in the IUCN Red List, hence we might be losing protection of many threatened species, therefore losing a higher evolutionary history of the Kenyan coastal forests. In this case, protecting specific sites which host higher phylogenetic diversity could help preventing the loss of evolutionary unique species, and conserving as much of the phylogeny life as possible and the retention key ecosystem services and functions (Cadotte, 2009; Chiarucci et al., 2011; Miller et al., 2018; Saraiva et al., 2018).

For the endemic species evolutionary history, both forest reserves and sacred forests have endemics which, in general, do not depart from a random expectation of the amount of PD they should have (i.e., not having sesPD >1.96). Nonetheless, most sesPD are negative and some forest sites have sesPD lower than -1.96 (e.g Kaya Bomu) which indicates that endemics are quite closely related. Although with lower phylogenetic diversity, endemic species face a higher probability of being included in the species Red List of threatened categories as they face higher risk of extinction as a result of increased degradation rates, habitat loss and fragmentation due to human activities. Furthermore, species losses are higher in small fragments (Arroyo-Rodriguez et al., 2012; Saraiva et al., 2018). Any conservation measures should therefore account for the preservation of endemic species.

Overall, our results may also be attributed to the spatial heterogeneity in abiotic and biotic environmental factors across the fragments which need to be taken into account. We note that, spatial heterogeneity influences both species and phylogenetic diversity which in turn influence the ecological processes such as dispersal and competition across forest fragments which may account for the variation in the phylogenetic diversity across the Kenyan coastal fragments (Costion et al., 2015). The Kenyan coastal forest fragments are distributed in a transverse biogeographical scale covering different environmental gradients which may affect both ecological and evolutionary processes (Costion et al., 2015). A further classification of the Eastern African coastal forests biodiversity hotspots positions them as globally biologically richest but most endangered ecoregion, as found in high temperature ecoregion (Mittermeier et al., 2005; Myers et al., 2000). Therefore, in the face of climate change, protecting as much of the evolutionary history as possible is considered a strong strategy to maintain the capacity of these forest ecosystems and species to adapt well to environmental changes and also increase ecosystem functions, such as primary productivity (Cadotte et al., 2009).

Conclusion

This study presents for the first time the evolutionary history and phylogenetic patterns of the coastal forest fragments of Kenya. Our results suggest that the forest reserves are insufficient alone to protect the evolutionary history of the Kenyan coastal forests without taking into account the sacred forests. On the other hand, some sacred forests exhibited a higher phylogenetic diversity compared to forest reserves. Therefore, even small forest fragments could play a vital role in conserving distinct evolutionary lineages; offer seed sources for biologically unique species; as reservoirs of phylogenetic diversity and high levels of evolutionary history. There is therefore need to prioritise and also protect the sacred forest fragments and enhance connectivity to forest reserves. Due to their invaluable bio-cultural significance, the sacred forests can therefore be termed as the ‘cradle of heritage’ for evolutionary history of the coastal forests of Kenya to complement the forest reserves. They therefore form the node of evolutionary history of the Kenyan coastal forests.

The threatened species contribute a higher evolutionary history to the Kenyan coastal forests. Indeed, to avoid extinction and greater loss of evolutionary history, conservation measures should prioritise protection of these species across the coastal forest belt.

Our results present a tool to be used in re-identifying and expanding protection networks to include important forest fragments for conservation along the Kenyan coastal forests. We suggest an extended and review of protection areas and strategies of the Kenyan coastal forests. We emphasize the need to adopt a phylogenetically informed conservation approach model that includes a combination of forest fragments matrix based on conservation on a higher variety of phylogenetic diversity, higher variety of ecological biodiversity in order to explain the ecosystem dynamics and maximize ecological stability. Such a multifaceted biodiversity measure would offer a wholistic approach to combining primary biodiversity components of species diversity and phylogenetic diversity.

5.0 References

Arroyo-Rodríguez, Cavender-Bares, J., Escobar, F., Melo, F.P.L., Tabarelli, M., & Santos, B. A. (2012). Maintenance of tree phylogenetic diversity in a highly fragmented rain forest. *Journal of Ecology*, 100, 702-71. https://doi.org/10.1111/j.1365-2745.2011. 01952.x.

Beentje, H. J. (1994). Kenya trees, shrubs and lianas. National Museums of Kenya, Nairobi, KE, 722 pp.

Burgess, N. D., Clarke, G. P., & Rodgers, W. A. (1998). Coastal forests of Eastern Africa: status, endemism patterns and their potential causes. *Biological Journal of the Linnean Society* 64, 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess, N. D., & Clarke, G. P. (Eds) (2000). The coastal forests of Eastern Africa. IUCN, Gland, CH and Cambridge, UK.

Cadotte, M.W., Davies, T. J., Regetz, J., Kembel, S. W., Cleland, E., & Oakley, T. H. (2010). Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. E*cology Letters*,13, 96-105. https://doi.org/10.1111/j.1461-0248.2009.01405.x.

Cadotte, M. W., Cavender-Bares, J., Tilman, D., & Oakley, T. H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PloS ONE*, 4(5): e5695. https://doi.org/10.1371/journal.pone.0005695.

Chiarucci, A., Bacaro, G., & Scheiner, S.M. (2011). Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society*, 366, 2426-2437. https://doi.org/10.1098/rstb.2011.0065.

Collen, B., Turvey,S. T.,Waterman, C., Meredith, H. M.R., Kuhn,T. S.,Baillie, J.E. M.,... Isaac, N. J. B. (2011). Investing in evolutionary history: implementing a phylogenetic approach for mammal conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1578), 2611-2622. https://dx.doi.org/10.1098/rstb.2011. 0109.

Costion, C. M., Edwards, W., Ford, A. J., Metcalfe, D. J., Cross, H. B., Harrington, M.G., ... Crayn, D. M. (2015). Using phylogenetic diversity to identify ancient rain forest refugia and diversification zones in a biodiversity hotspot. *Diversity and Distributions*, 21(3), 279-289. https://dx.doi.org/10.1111/ddi.12266.

Davies, T. J., & Buckley, L. B. (2011). Phylogenetic diversity as a window into the evolutionary and biogeographic histories of present-day richness gradients for mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1576), 2414-2425. http://dx.doi.org/10.1098/rstb.2011.0058.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61,1-10. https://dx.doi.org/10.1016/0006-3207(92)91201-3.

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Procheș, Ș., Bank, M.V.D., Reeves, G., Hedderson, T.A.J., & Savolainen, V. (2007). Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, 445, 757-760. https://dx.doi.org/10.1038/nature05587.

Fungomeli, M., Cianciaruso, M., Zannini, P., Githitho, A., Frascaroli, F., Fulanda, B., …Chiarucci, A. (2020a). Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot. *Plant Biosystems*, 154(6), 973-982. https://doi.org/10.1080/11263504.2020.1834461.

Fungomeli, M., Githitho, A., Frascaroli, F., Chidzinga, S., Cianciaruso, M., & Chiarucci, A. (2020b). A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey*, 1, 103-109. https://doi.org/10.3897/VCS/2020/47180.

Githitho, A. N. (2016). Listing the sacred Mijikenda *kaya* Forests as UNESCO World Heritage Sites: The Long Journey, *Journal des africanistes [*En ligne]. URL: http://journals.openedition.org/africanistes/4971 [accessed 3 Oct 2019].

Gotelli, N. J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, 81(9), 2606-2621. https://dx.doi.org/10.1890/0012-9658.

Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist*, 169, E68– E83. https://doi.org/10.1086/511334.

Isaac, N.J., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One*, 2, e296.

IUCN (International Union for the Conservation of Nature and Natural Resources) (2020). The IUCN Red List of Threatened Species: 2020 Categories and Criteria (version 3.1). https://www. redlist.org/info/categories_criteria2020.html (last accessed 12 August 2020].

Jin, Y., & Qian, H. (2019). V.PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography*, 42, 1353-1359. https://doi.org/10.1111/ecog.04434.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., …Webb, C. O. (2010). Picante: r tools for integrating phylogenies and ecology. *Bioinformatics,* 26, 1463-1464. https://doi.org/10.1093/bioinformatics/btq166.

Kibet, S. (2011). Plant communities, species diversity, richness, and regeneration of a traditionally managed coastal forest, Kenya. *Forest Ecology and Management*, 261, 947 -957. https://doi.org/10.1016/j.foreco.2010.11.027.

Laity, T., Laffan, S. W., González-Orozco, C. E., Faith, D. P., Rosauer, D. F., Byrne, M., ... Newport, K. (2015). Phylodiversity to inform conservation policy: An Australian example. *Science of the Total Environment*, 534, 131-143. https://dx.doi.org/10.1016/j.scitotenv.2015.04.113.

Laureto, L. M. O., & Cianciaruso, M. V. (2017). Palm economic and traditional uses, evolutionary history and the IUCN Red List. *Biodiversity and Conservation*, 26, 1587-1600. https://doi.org/10.1007/s10531-017-1319-7.

Lovett, J. C. (1998). Eastern Tropical African Centre of Endemism: A Candidate for World Heritage Status. *Journal of East African Natural History,* 87, 359-366. https://doi.org/10.2982/0012-8317.

Luke, W. R. Q. (2005). Annotated check-list of the plants of the Shimba Hills, Kwale District, Kenya. *Journal of East African Natural History,* 94, 5-121. https://doi.org/10.2982/0012-8317.

Margules, C., & Pressey, R. (2000). Systematic Conservation Planning. *Nature*, 405. (6783), 243-253. https://doi.org/10.1038/35012251.

Mazzochini, G. G., Fonseca, C. R., Costa, G. C., Santos, R. M., Ary T. Oliveira-Filho, A. T., & Ganade, G. (2019). Plant phylogenetic diversity stabilizes large-scale ecosystem productivity. *Global Ecology and Biogeography,* 28, 1430-1439. https://doi.org/10.1111/geb.12963.

Mishler, B. D., Knerr, N., González-Orozco, C. E., Thornhill, A. H., Laffan, S. W., & Miller, J. T. (2014). Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nature Communications,* 5, 4473. https://dx.doi.org/10.1038/ncomms5473.

Miller, J. T., Jolley-Rogers, G., Mishler, B. D., & Thornhill, A. H. (2018). Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution,* 56, 663-667. https://doi.org/10.1111/jse.12436.

Mittermeier, R., Gil, P., HoVman, M., Pilgrim, J., Brooks, T., Goettsch-Mittermeier, C., Lamoreux, J., & da Fonseca, G. (2005). Hotspots Revisited: Earth's Biologically Richest and Most Threatened Terrestrial Ecoregions. Agrupacion Sierra Madre, Mexico.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature,* 403, 853-858. https://doi.org/10.1038/35002501.

Ngumbau, V. M., Luke, Q., Nyange, M., Wanga, V. O., Watuma, B. M., Mbuni, Y. M., Munyao, J. N., Oulo, M. A., Mkala, E. M., Kipkoech, S., et al. (2020). An annotated checklist of the coastal forests of Kenya, East Africa. *PhytoKeys*, 147, 1-191. https://doi.org/10.3897/phytokeys.147.49602.

Noad, T., Birnie, A. (1990). A fully illustrated field guide: trees of Kenya. General Printers Ltd, Nairobi, KE, 350 pp.

Pellens, R., & Grandcolas, P. (Eds.) (2016). Biodiversity Conservation and Phylogenetic Systematics, Topics in Biodiversity and Conservation. Springer International Publishing AG Switzerland. https://doi.org/10.1007/978-3-319-22461-9.

R Core Team (2020). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.Rproject.org/.

Robertson, S.A., & Luke W.R.Q. (1993). Kenya Coastal Forests: The Report of the NMK/ WWF Coast Forest Survey. WWF Project 3256: Kenya, Coast Forest Status, Conservation and Management. National Museums of Kenya.

Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., ... Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 9 -12. https://dx.doi.org/10.1038/nature02459.1.

Saraiva, D. D., dos Santos, A. S., Overbeck, G. E., Eduardo, L. G., & Jarenkow, J. A. (2018). How effective are protected areas in conserving tree taxonomic and phylogenetic diversity in subtropical Brazilian Atlantic Forests? *Journal for Nature Conservation*, 42, 28-35. https://doi.org/10.1016/j.jnc.2018.02.002.

Shapcott, A., Forster, P. I., Guymer, G. P., McDonald, W. J. F., Faith, D. P., Erickson, D., Kress, W. J. (2015). Mapping biodiversity and setting conservation priorities for SE Queensland's rainforests using DNA barcoding. *PLoSOne,* 10 (3),1-28. https://doi.org/10.1371/journal.pone.0122164.

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105 (3), 302-314. https://doi.org/10.1002/ajb2.1019.

Swenson, N. G. (2014). Functional and phylogenetic ecology in R. Springer UseR! series. New York: Springer.

The Plant List (2013) The plant list (version 1.1.). https://www.theplantlist.org/. [accessed 15 June 2020].

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., Araujo, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature,* 470, 531-534. https://doi.org/10.1038/nature09705.

Tsirogiannis, C., & Sandel, B. (2016). PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography,* 39, 709-714. https://doi.org/10.1111/ecog.01814.

Tsirogiannis, C., & Sandel, B. (2017). PhyloMeasures: Fast and Exact Algorithms for Computing Phylogenetic Biodiversity Measures. R package version 2.1. https://CRAN.R-project.org/package=PhyloMeasures

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., ... Mazel, F. (2016). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, 92(2), 698-715. http://dx.doi.org/10. 1111/brv.12252.

Wass, P. (Ed) (1995). Kenya's indigenous forests: status, management and conservation. Gland, Switzerland and Cambridge, UK: IUCN. https://portals.iucn.org/library/sites/library/files/documents/FR-014.pdf.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Reviews of Ecology and Systematics*. 33, 475-505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448.

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24(18), 2098-2100. http://dx.doi.org/10.1093/bioinformatics/btn358.

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution*, 28(4), 199-204. https://doi.org/10.1016/j.tree.2012.10.015.

Chapter 6

Conservation of the Coastal forests of Kenya:

A tropical biodiversity hotspot with unexplored biocultural diversity potential

Manuscript submitted to *Perspectives in Ecology and Conservation Journal* (PECON).

Chapter published as:

Maria Fungomeli[1,2,*], Marcus Cianciaruso[3], Fabrizio Frascaroli[1,4], Anthony Githitho[2] & Alessandro Chiarucci[1]. Conservation of the Coastal forests of Kenya: A tropical biodiversity hotspot with Unexplored biocultural diversity potential.

[1]Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Italy
[2]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Mombasa, Kilifi, Kenya
[3]Department of Ecology, Universidade Federal de Goiás, Brazil
[4]Lòm Research, Rocca d'Arce, Frosinone, Italy

Abstract

Sustaining biodiversity of the coastal forests of Kenya is a critical concern in the face of increased degradation and loss of biodiversity due to anthropogenic activities, high population and climate change effects. This paper assesses this vulnerability and provides conservation perspectives informed by a recent vegetation survey of the coastal forests of Kenya, carried out through a standardized protocol. The extensive field survey offers a chance to explore the current status of these forest jewels, develop new conservation strategies and bridge science to concrete policy issues. We suggest policy approaches that take into account both scientific data and the rich biocultural heritage of these forests. Their survival will ultimately be influenced by sound policy actions, management strategies, funding availability and inclusion of local rural communities in conservation efforts. We emphasize the need for up-to-date scientific monitoring and scaling up their protection status for sustainable conservation.

Keywords: biodiversity hotspot, coastal forests, conservation, Kaya sacred forests, Kenya, policy

1.0 The coastal forests of Kenya

The coastal forests of Kenya are part of the Eastern African Coastal Forests Biodiversity Hotspot (Myers et al., 2000; Mittermeier et al., 2011). These forests, which are mainly a mixture of moist and dry forests, with mangrove forests occurring along the shoreline, are found as isolated fragments of the once expansive coastal forest within the Swahilian regional center of endemism (Figure 6.1a; Burgess et al., 1998). The Eastern African Coastal Forest harbour more than 4,500 plant species belonging to 1,050 plant genera and 3,000 animal species in 750 genera (CEPF, 2016). Of these species, the endemics comprise of approximately 1500 plants, six mammals, nine birds, 26 reptiles and 79 butterflies (Burgess et al., 1998). Overall, the Kenyan Coastal forests have more than 554 strictly endemic plants and 53 strictly endemic animals (Burgess and Clarke, 2000). Nationally, the coastal forests of Kenya harbours 50% of the national endemic plants, 60% of birds and 65% of mammals, highlighting the national, regional and global importance of these forest fragments to biodiversity conservation (Burgess and Clarke, 2000; CEPF, 2003).

Despite being a biodiversity hotspot and hosting threatened and endemic tropical fauna and flora (Myers et al., 2000; Mittermeier et al., 2011; CEPF, 2016), these forests are scarcely known in terms of their current biodiversity conservation status and trends, limiting the capacity of effective management policies. Globally, there are 36 hotspots hosting around 50% of endemic plant species, out of which 22 hotspots are located in tropical areas (CEPF, 2016). This paper provides conservation perspectives informed by a recent vegetation survey of the coastal forests of Kenya, carried out via a standardized protocol (Fungomeli et al., 2020a; Fungomeli et al., 2020b). The recent extensive field survey offers a chance to explore the current status of these forest jewels, develop new conservation strategies and bridge science to concrete policy issues and practice. Our current review of the biodiversity hotspot publications shows a relative lack or limited publications on the biodiversity of the Eastern Arc and Coastal Forests of Kenya and Tanzania (Figure 6.2). In this paper, we call the attention to the biodiversity importance of the Kenyan coastal forests and their conservation value at both local, regional and global scale. We present varying protection and conservation challenges and draw insights from a synthesis of recent field survey. We also highlight potential policy actions for enhanced sustainable conservation in the context of the existing socio-cultural and economic set-up surrounding them.

2.0 Protection status of the coastal forest of Kenya

The coastal forests of Kenya now exist as fragmented forest islands largely due to anthropogenic activities (Lovett, 2008). Currently, there are approximately 145 forest fragments covering an area of 787 km^2, stretching from the North to South along the Kenyan coast (Figure 6.1b; Metcalfe et al., 2010). This represents approximately 10% of the original forest cover, of which only 17% are under some kind of legal protection (Burgess and Clarke, 2000; CEPF, 2003). These forest fragments are widely variable in size, ranging from 10 to 42,000 ha. The Arabuko Sokoke forest (42,000 ha) and the Shimba Hills forest (25,300 ha) are the two large remaining Kenyan coastal forests (Figure 6.1b), while the rest of the forests are spread in relatively small fragments ranging between 10 and 450 ha (Figure 6.1).

Another important distinction is between fragments managed as forest reserves and those protected as sacred forests (Figure 6.1b; 6.1c and 6.1d). The forest reserves are officially and legally government protected forests while the sacred forests are informally protected by the local communities. These sacred forests are traditionally used by the coastal Mijikenda community as places of worship and locally referred to as *'Kayas'*, which in the local language means '*homestead*' (Githitho, 2016). As a result of the taboos and other traditional norms in place, these forest patches have been effectively conserved to date (Githitho, 2016) and demonstrate the crucial role of traditional indigenous knowledge in conserving biodiversity of global relevance. As such, kaya forests can be regarded as prominent instances of 'biocultural landscapes', that is, landscapes where biological and cultural elements are inextricably intertwined and mutually dependent (Gavin et al., 2015). Around 39 sacred forests are now inscribed under UNESCO as World Heritage Sites and hence they are protected in collaboration with the government, while over 35 sacred forests remain under local community protection alone (Metcalfe et al., 2010), which can expose them to additional threats and illegal activities. However, inscription as world heritage has not guaranteed their total protection, as highlighted by their increasing degradation (Kibet, 2011; Shepheard, 2014).

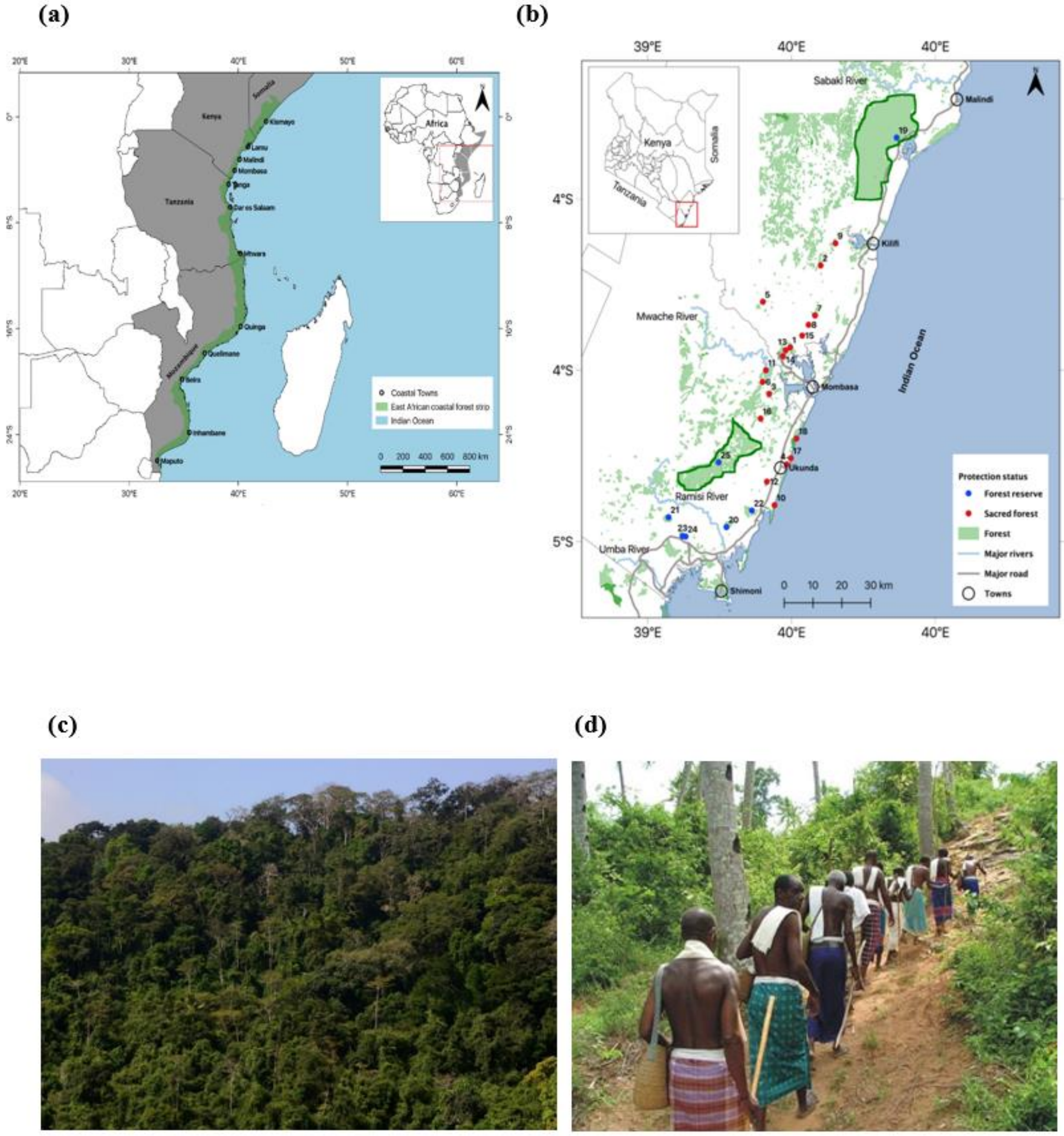


Figure 6.1a: A distribution map of the East African coastal forests. **Figure 6.1b:** Coastal forests of Kenya map and locations of the 25 forests covered in the large standardized vegetation sampling of the coastal forests of Kenya and their protection status. **Figure 6.1c:** Kaya Jibana sacred forest, found on hill top. **Figure 6.1d:** Sacred forest kaya elders in the forest for their traditional, spiritual and cultural-ritual practices (Photo credit: Steve Okoko Ashikoye). 1=Bomu, 2=Chivara, 3=Chonyi, 4=Diani, 5=Fungo, 6=Gandini, 7=Jibana, 8=Kambe, 9=Kauma, 10=Kinondo, 11=Mtswaka, 12=Muhaka, 13=Muvya, 14=Mwiru, 15=Ribe, 16=Teleza, 17=Tiwi, 18=Waa, 19=Arabuko, 20=Buda, 21=Dzombo, 22=Gogoni, 23=Marenje, 24=Mrima, 25=Shimba.

Half of Kenya’s threatened woody plants occur in coastal forests and more so in the sacred forests (Burgess and Clarke, 2000). Studies conducted across the coastal forests indicate that the sacred kaya forests are key refuges for species conservation in a matrix of their cultural heritage importance (Kibet, 2011; Fungomeli et al., 2020a). The integration of data coming from our recent survey shows that, despite their relatively small size, sacred forests harbor a greater number of species, including endemics and threatened species, when compared to the large forest reserves (Fungomeli et al., 2020a). In addition, the forest structure shows that the sacred kaya forests exhibit more old growth forests compared to the forest reserves (Fungomeli et al., 2020a). Further analysis of the plant evolutionary history of the coastal forests of Kenya highlights that sacred forests harbor significantly higher phylogenetic diversity compared to forest reserves (Fungomeli et al. in press). Moreover, the observed phylogenetic diversity for plant species listed in the IUCN Red List was higher than expected by chance and increased as the species become more threatened with extinction (Fungomeli et al. in press). The higher phylogenetic diversity in the sacred forests suggests they have higher numbers of less related species compared to forest reserves, emphasizing their role as refugia and species repositories. Ultimately, failing to conserve the sacred forests would lead to losing more than half of the evolutionary history and natural heritage of the Kenyan coastal forests.

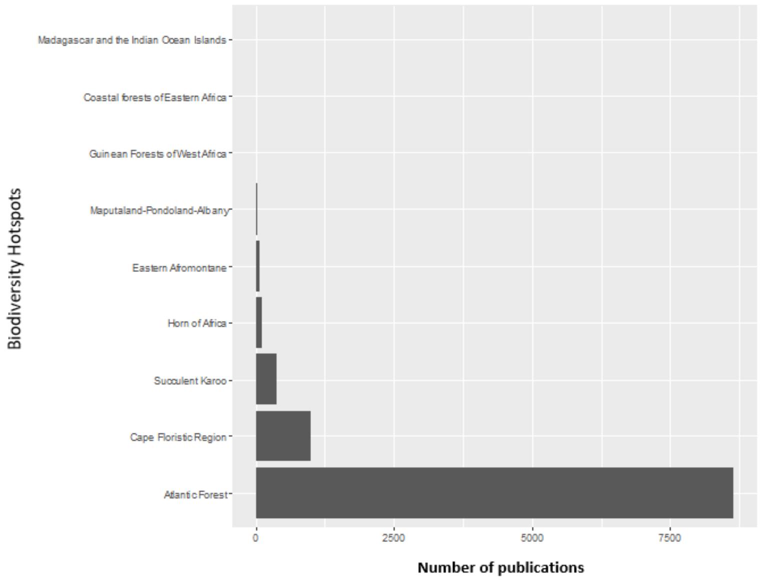


Figure 6.2: Biodiversity hotspots and the number of publications on the African Biodiversity Hotspots and comparative basis with Atlantic forest hotspot.

3.0 Threats to the Kenyan coastal forests

Major threats to the biodiversity of the Kenyan coastal forests come from the growing human population. The Kenyan coastal population has increased from 1.83 million in 1989 to 4.33 million in 2019 (Republic of Kenya, 1989; 2019) and approximately 65% of the population depend directly on these forest for their livelihoods (Matiku et al., 2012). Incidences of tree felling, illegal logging and poaching are frequent as a growing number of people have to rely on forests for their livelihoods (Kibet, 2011; Habel et al., 2017; FAO and UNEP, 2020). Additionally, over 50% of the sacred sites are under threat of clearance with uncontrolled use and increased poaching and reduction in their original area due to encroachment (Tabor et al., 2010; Shepheard, 2014). Strassburg et al. (2020) shows that, the coastal forests of Kenya fall at the top 15% globally as areas that need priority for restoration focusing on biodiversity and climate change mitigation. Many of these forests also harbour a wealth of valuable mineral resources, such as titanium and lead, which have become a major target for multinational companies (Burgess et al., 2007). These companies target the forests for investment creating a controversy between conservation and economic development (FAO and UNEP, 2020). Titanium mining is ongoing at the Kenyan south coast near Buda and Mrima forest reserves (Abuodha, 2002; Matiku, 2003; Burgess et al., 2007). Silica sands for glass manufacture was mined in Arabuko Sokoke forest leaving behind old sand quarries (Matiku, 2003). Iron, gemstones, and gas are on the list of targeted minerals from these forests (Matiku, 2003). These actions pose severe threats in terms of increased deforestation, loss of species, and loss of opportunity to document unique species in undocumented areas (Stropp et al., 2020). Some offset measures have been put in place such as reforestation activities either directly on the degraded forest sites or as agroforestry activities to support plantation of trees by forest adjacent communities on their farms (Matiku et al., 2012). However, as in other cases around the world, it is debatable to what extent similar mitigation activities can offset the original damage produced.

The sacred kaya forests currently face severe erosion of the traditional values and practices, largely caused by urbanization, making biocultural landscape sustainability highly fragile (Githitho, 2016). Generally, conservation of the coastal forests is also challenged by the erosion of traditional values in the case of sacred kaya forests, and by limited capacity and insufficient funding to cover the vast area of forest patches in the case of both forest reserves and sacred forests.

The fragmented nature of these forests increases the threat of species loss and extinction and this effect is more pronounced on the already threatened and endemic species. Moreover, endemism of plants as well as other groups is primarily relictual (Burgess et al., 1998) and single site endemism and disjunct distributions are common (Burgess and Clarke, 2000; CEPF, 2003). This makes it extremely difficult to prioritize the forests in terms of their conservation value. For example, while Arabuko-Sokoke is top for endemic birds and for mammal species richness, it barely makes it into the top ten for plants. Overall, the five most important forests in the East African coastal forests are Rondo (plants and birds), lowland East Usambara and Arabuko-Sokoke (birds, mammals and reptiles), Shimba Hills forest (plants and birds) and Pugu Hills (birds and mammals) (Burgess et al., 1998; Burgess et al., 2000; Lovett, 2008; CEPF, 2016). For this reason, conserving and sustainably managing the remaining forests of the region ultimately requires a developed and enhanced biodiversity monitoring system, which is currently lacking (Fungomeli et al., 2020a). For example, the lack of forest site-level biodiversity quantitative surveys poses a challenge to assess and monitor these forests and their contribution to local, regional, and global biodiversity (Fungomeli et al., 2020b).

4.0 Cultural and economic importance of the coastal forest of Kenya for the society

Local people living around these forests have traditionally depended on them for their daily requirements such as for food, medicinal plants, firewood and building materials (Fanshawe, 1995; Kibet, 2011). Most of these communities practice subsistence farming as the main source of occupation which has become less productive due to unreliable rainfall patterns and climate change impact and therefore increasing dependency pressure on the forest resources (Fanshawe, 1995; Gordon and Ayiemba, 2003; Matiku et al., 2012).

In government protected forest reserves, nature-based enterprises such as butterfly farming, herbal medicine and eco-tourism projects have been introduced both inside and outside the forest, that aim to give incentive and involve the local people living adjacent to these forests to participate in conservation (Gordon and Ayiemba, 2003; Burgess et al., 2007; Matiku et al., 2012). Butterfly farming along the coastal forests has demonstrated a successful link of forest conservation and improving the livelihoods of the forest adjacent rural communities where over US$ 2.0 million in pupae export has been earned in community earnings since 1994 (Gordon and Ayiemba, 2003; Mombasa Butterfly House report, 2019). Through the Kipepeo butterfly project and Mombasa butterfly house, butterfly farming has boosted coastal forests conservation and education through sustainable utilization of butterfly biodiversity involving over 500 butterfly farmers and over 2500 farmers involved in beekeeping. In addition, there is a change of attitudes of the local communities towards forest conservation and enhanced conservation education due to these projects (Gordon and Ayiemba, 2003). As such, the forests provide a base for the sustainable utilization while providing alternative income sources to the rural communities without clearing the forest for agriculture.

Working on linking sustainable forest management and community needs is a smart approach for long term forest survival but extraordinarily complex in nature in meeting short term community needs (Fungomeli et al., 2020b). The current nature-based enterprises leave out more than 65% of the forest adjacent communities without any conservation engagement while they still depend on the forest. Therefore, the need to integrate the socio-economic aspects and capture local level biodiversity data and forest use is essential to ensure conservation and sustainability measures of these fragments (Burgess et al., 2007). In addition, diversifying and introduction of new nature-based activities to the forest adjacent communities would ensure a bigger incentive benefit and increased percentage of engagement of the local population into conservation efforts.

5.0 Potential Policy forums and conservation avenues

Sustaining biodiversity of the coastal forests of Kenya is a critical concern. The forests' status as a biodiversity hotspot should draw attention for conservation efforts and grant them inclusion in both regional and global conservation and policy platforms. However, this has not consistently been the case over the years, creating lapse in enforcing conservation measures.

These forests are currently included in global programs such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), UNESCO World Heritage and the Convention on Biological Diversity (CBD). Under the CBD, for example, Kenya should be obligated to identify, assess and monitor species and habitats, as well as involve local communities and protect their indigenous knowledge and rights to access and benefit from biodiversity (Matiku, 2003). However, as noted by Burgess et al. (2005), most sacred forests are not featured within the protected area database of the UNEP-World Conservation Monitoring Centre (https://www.wcpa.org), either due to their small size or their protection status as community-protected areas. The growing recognition of Other Effective area-based Conservation Measures (OECMs), however, should offer a viable instrument for overcoming the latter issue (e.g., Maxwell et al., 2020).

Other organizations, such as WWF-Kenya, Critical Ecosystem Fund (CEPF) and UNDP, have extensively written and provided information on the coastal forest of Kenya in their technical reports and websites (CEPF, 2003 and 2016; WWF, https://www.worldwildlife.org/ecoregions/at0125). Similarly, we acknowledge the extensive work of the Coastal Forests Conservation Unit under the National Museums of Kenya and together with the Kenya Forest Service, for its continued conservation efforts. However, these efforts have been limited by lack of funding, while engagement in global policy biodiversity platforms has remained lower than it could be desired.

Additionally, there is need for sustainable on-site conservation activities that can engage stakeholders in conservation practices. Moreover, the sacred forests that form 90% by number of the coastal forests present valuable biocultural landscapes, and therefore any conservation measures should be tailored to fit the on-ground complexity of enhancing the traditional-cultural practices, while using that as a platform to boost their continued ecological conservation. In the African tropical forest context, and more so Kenya, forests have played a key role in supporting the livelihoods of local communities for millennia. The focus should be beyond a biodiversity hotspot or a world heritage site and encourage the recognition and inclusion of traditional indigenous knowledge which has played a major role in the sacred forests survival as forest fragments. This means any conservation measures should include and link the local communities to conservation organizations locally and globally. More attention should also be created to inscribe to the world heritage list the majority of the remaining sacred forests which will give them international recognition and global presence for conservation consideration and funding. Additionally, seeking recognition of the sacred Kaya forests as OECMs, would be fitting for the kayas that still have relatively intact and efficient governance structures. In such cases, recognition as Other Effective area-based Conservation Measures (OECM) would grant legal ratification, and therefore protection, if needed, while offering respect of and continuity with the communities' rights, tradition and management. (see Maxwell et al., 2020; Dudley et al., 2018).

Developing strategies for their conservation and protection should include an up-to-date current survey and build on standardized and quantitative protocols (see Fungomeli et al., 2020a) to create a high-quality database for a foundation that allow biodiversity monitoring for the coastal forests of Kenya. Such a database would allow improved and data-informed conservation planning.

An impediment to full biodiversity research of the sacred forests is the prohibition by the elders, and the local culture and taboos governing the sacred forests, where researchers are prohibited to access most deeper parts or certain worship areas within the Kayas. This was also experienced during our vegetation survey (Fungomeli et al., 2020a). To promote access to research information in these forests, a crucial local step would be to establish and support citizen-science research in the sacred forests, in which the local elders or communities are involved and trained in a coordinated research of their own resources. This would lead to a win-win scenario where there is enhanced research access, and for the Kaya elders there is integrated awareness of their culture, and increase protection of biodiversity richness within their forests, while feeding into wider research objectives.

Currently, the Kenya Forest Act 2005 and Kenya Forest Policy 2014 promotes the Kenya Forest Service to involve communities in forest conservation through a model of Community Forest Associations (CFAs) at each forest site. However, the sacred forests are not currently included. This model presents an opportunity to include the sacred forests and boost protection and continuous community engagement.

Integrating and linking educational programs to schools and involve the youths in education and conservation programs would ensure a smooth succession of cultural and conservation values. Inevitably, conservation efforts will only make more impact if they are more localized and executed (Mittermeier et al., 2011). Nevertheless, priority should be to explore innovative ways to reduce forests dependence; tackle illegal activities, restore degraded areas, reduce fragmentation and increase forest connectivity. These proposed approaches will save the many forest fauna that depend on the coastal patches, and continue to preserve their role as biocultural heritage landscapes; species reservoirs; water catchment areas and sustainable livelihoods of the local people.

Conflict of interests

The authors declare no conflicts of interest.

Acknowledgements

We thank the team that led to the large field vegetation sampling of the coastal forests of Kenya. Our special thanks to Saidi Chidzinga for field sampling and plant specimen identification, Geoffrey Mashauri and Abbas Shariff for assistance in plant identification and knowledge of the Coastal forests. We are grateful to the colleagues who helped in setting the field work, sampling and support during the entire field period: Lawrence Chiro and Abdulrahman Matano of Coastal forests conservation unit-NMK; Joseph Muthini of Kenya Forest Research Institute; and George Wara and Blessingtone Magangha of Kenya Forest Service. We also thank the Kaya community and elders for allowing us access and entry to the Kaya forests.

Funding

Funding and logistical support for the research work was a concerted effort from various sources. Authors are indebted to University of Bologna, Department of Biological, Geological and Environmental Sciences (BiGEA), the National Museums of Kenya (NMK), International Association of Butterfly Exhibitors and Suppliers (IABES), Nature Kenya and WWF-Kenya for the support received. Marcus Cianciarusso wishes to thank Fundação de Amparo à Pesquisa do Estado de Goiás (FAPEG/Brazil) that supports his research work.

6.0 References

Abuodha, J.O. Z., 2002. Environmental Impact Assessment of the Proposed Titanium Mining Project in Kwale District, Kenya, Marine Georesources & Geotechnology, 20:3, 199-207. https://doi.org/10.1080/03608860290051895.

Burgess, N.D., Clarke, G.P., Rodgers, W.A., 1998. Coastal forests of Eastern Africa: Status, endemism patterns and their potential causes. Biological Journal of the Linnean Society. 64: 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x.

Burgess, N.D., Clarke, G.P., (Eds) 2000. The coastal forests of Eastern Africa. IUCN Publications Services Unit, Cambridge, UK.

Burgess, N.D., Kuper, W., Mutke, J., Brown, J., et al., 2005. Major gaps in the distribution of protected areas for threatened and narrow range Afrotropical plants. Biodiversity and Conservation (2005) 14: 1877–1894. https://doi.org/10.1007/s10531-004-1299-2.

Burgess, N.D., Balmford, A., Cordeiro, N.J., et al., 2007. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. Biological Conservation. 134(2):164–177. https://doi.org/10.1016/j.biocom.2006.08.024.

CEPF (Critical Ecosystem Partnership Fund), 2003. Ecosystem Profile: Eastern Arc Mountains and Coastal Forests of Tanzania and Kenya Biodiversity Hotspot. https://www.cepf.net [accessed 13 July 2020].

CEPF (Critical Ecosystem Partnership Fund), 2016. Announcing the World's 36th Biodiversity Hotspot: The North American Coastal Plain. https://www.cepf.net [accessed 13 July 2020].

Fanshawe, J., 1995. The effects of selective logging on the bird community of Arabuko-Sokoke Forest, Kenya. University of Oxford.

FAO, UNEP, 2020. The state of the world's forests 2020. Forests, biodiversity and people. FAO publications, Rome.

Fungomeli, M., Githitho, A., Frascaroli, F., et al., 2020a. A new vegetation-plot database for the Coastal forests of Kenya. Vegetation Classification and Survey, 1: 103-109. https://doi.org/10.3897/VCS/2020/47180.

Fungomeli, M., Cianciaruso, M., Zannini, P., et al., 2020b. Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, Plant Biosystems, https://doi.org/10.1080/11263504.2020.1834461.

Gavin, M.C., McCarter, J., Mead, A., et al., 2015. Defining biocultural approaches to conservation. Trends Ecological Evolution,30(3): 140-145. https://doi.org/10.1016/j.tree.2014.12.005.

Githitho, A.N., 2016. Listing The Sacred Mijikenda *Kaya* Forests as UNESCO World Heritage Sites : The Long Journey. Journal des africanistes: 86-1.

Gordon, I., Ayiemba, W., 2003. Harnessing butterfly biodiversity for improving livelihoods and forest conservation: The Kipepeo Project. The Journal of Environment & Development. 12. 82-98. https://doi.org/10.1177/1070496502250439.

Habel, J.C.,Casanova, I.C.C., Zamora, C., et al., 2017. East African coastal forest under pressure. Biodiversity and Conservation. 26(11): 2751–2758. https://doi.org/10.1007/s10531-017-1375-z.

Kibet, S. 2011. Plant communities, species diversity, richness, and regeneration of a traditionally managed coastal forest, Kenya. Forest Ecology and Management 261: 947 -957. https://doi.org/10.1016/j.foreco.2010.11.027.

Lovett, J.C., 2008. Biogeography and ecology of the rain forests of Eastern Africa. Cambridge University Press, Great Britain.

Matiku, P., 2003. The Coastal Forests of Kenya: Forest data, threats, socio-economic issues, values, stakeholders, challenges, strategies, investment and enabling environment. A national synthesis report for the development of the WWF-EARPO Eastern Africa Coastal Forests Ecoregion Programme. Nature Kenya and WWF, Nairobi, Kenya.

Matiku, P., Ogol, C., Mireri, C., 2012. The impact of participatory forest management on forest integrity and biodiversity in Arabuko-Sokoke forest, Kenya. African Journal of Ecology. 50(2):184–192. https://doi.org/10.1111/j.1365-2028.2011.01311.x.

Maxwell, S.L., Cazalis, V., Dudley, N., et al., 2020. Area-based conservation in the 21st century. Preprints, https://doi.org/10.20944/preprints202001.0104.v1

Metcalfe, K., Ffrench-Constant R, Gordon I. 2010. Sacred sites as hotspots for biodiversity: The Three Sisters Cave complex in coastal Kenya. Oryx. 44(1): 118–123. https://doi.org/10.1017/S0030605309990731.

Mombasa butterfly house, https://www.mombasabutterflyhouse.org [Accessed 15 August 2020].

Mittermeier, R.A., Larsen, F.W., Brooks, T.M., et al., 2011. Global biodiversity conservation: the critical role of Hotspots. In: Zachos, F.E. and Habel, J.C. (Eds), Biodiversity Hotspots, Springer-Verlag, Berlin Heidelberg. https://doi.org/10.1007/978-3-642-20992-1.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., et al., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858. https://doi.org/10.1038/35002501.

Republic of Kenya, 2019. National Population and Housing Census, Kenya National Bureau of Statistics, Nairobi.

Shepheard-Walwyn, E., 2014. Culture and conservation in the sacred sites of coastal Kenya. PhD Thesis, Durrel Institute of conservation and ecology, University of Kent, UK.

Strassburg, B. B. N., Iribarrem, A., Beyer, H. L., et al., 2020. Global priority areas for ecosystem restoration. Nature, https://doi.org/10.1038/s41586-020-2784-9.

Stropp, J., Umbelino, B.R.A., Correia, A.J.V., et al. 2020. The ghosts of forests past and future: deforestation and botanical sampling in the Brazilian Amazon. Ecography 43: 979–989. https://doi.org/10.1111/ecog.05026.

Tabor, K., Burgess, N.D., Mbilinyi, B.P et al., 2010. Forest and Woodland Cover and Change in Coastal Tanzania and Kenya, 1990 to 2000. Journal of East African Natural History **99**(1)**:** 19–45. https://doi.org/10.2982/028.099.0102.

WWF-Kenya (World Wildlife Fund), 2020. https://www.worldwildlife.org/ecoregions/at0125 [Accessed 23 August 2020].

Chapter 7

Vegetation determinants on butterfly diversity and composition of a tropical coastal forest, the Arabuko Sokoke forest, Kenya

Manuscript submitted to *Journal of Insect conservation*

Chapter published as:

Maria Fungomeli[1,3*], Martin wiemers[2], Lucia Calderini[1], and Alessandro Chiarucci[1]

[1]Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum- University of Bologna, Bologna, Italy
[2]Senckenberg German Entomological Research Institute, Eberswalder Str. 90, 15374 Müncheberg, Germany

[3]Coastal Forests Conservation Unit, Centre for Biodiversity, National Museums of Kenya, Kilifi, Kenya
[*]maria.fungomeli2@unibo.it

Abstract

Aims: The Arabuko Sokoke forest (ASF) is the largest remaining forest fragment of the coastal forests of Kenya and Eastern Africa, and known for its high conservation value, endemism and, recently, was declared a UNESCO biosphere reserve. The need to regular assess and monitor its biodiversity is fundamental for long-term conservation efforts. We aimed to investigate species diversity patterns of butterflies play a crucial role as indicator of habitat quality and in relation to woody plant diversity across main vegetation types within ASF.

Methods: We sampled butterflies and woody plants within ASF across four major vegetation types: *Cynometra* forest, *Brachystegia* woodland, mixed forest and the forest edge. We recorded butterflies by using 108 walking transects, each of 15mins, evenly distributed across each vegetation. We sampled woody plants by using 26 plots each measuring 10m x 100m. Each vegetation plot was overlaid to one butterfly transect.

Results: We recorded 6050 butterfly individuals during the dry season belonging to 86 species from 38 genera and 5 families. Woody vegetation was composed of 178 species belonging to 78 genera and 34 families. Butterfly species abundance was significantly different across vegetation types, while there was no significant difference in species richness. Butterfly species diversity had a strong correlation with plant species diversity. The main environmental drivers of butterfly species richness were rainfall of warmest quarter and temperature of warmest month, altitude and distance from the coast. In our butterfly trait analysis, average wingspan size was significantly different among vegetation types and lower in *Cynometra* forest than forest edge and Mixed forest.

Conclusions: Overall, our results highlight the crucial role of plant diversity as a direct link to butterfly diversity and the crucial synergic roles exhibited by the forest edge and mixed forest. These results call for inclusion of ecological corridors and can help guide butterfly farming activities in ASF to enhance sustainable utilization of biodiversity and conservation.

Keywords: biodiversity, ecology, habitat quality, plant species, tropical forests

1.0 Introduction

The Arabuko Sokoke forest is the largest remaining forest fragment in the coastal forests of Kenya and Eastern Africa, the rest of which consists of small forest patches spread along the Kenyan coastline (Burgess et al. 1998; Burgess and Clarke 2000); Fungomeli et al. 2020a). It is globally recognized as a world biodiversity hotspot of the Eastern African Coastal Forests of Kenya and Tanzania (Myers et al. 2000), as a centre of endemism hosting a conspicuous number of threatened and endangered species, and was therefore recently declared a UNESCO biosphere reserve (UNESCO 2019). Sustaining biodiversity globally is a critical concern in the face of climate change, increased rate of anthropogenic activities and habitat fragmentation. Anthropogenic pressure and biodiversity loss, together with climate change are heavily impacting tropical forests such as Arabuko Sokoke forest (ASF) in Kenya, which are known to support rich flora and fauna biodiversity trends (Burgess and Clarke 2000; Schweitzer and Dey 2011; Newton and Echeverría 2014; FAO 2018). It is estimated that globally, approximately 90% of butterflies are found in tropical areas, but their ecological role is less studied than in temperate areas, which also applies to the vegetation studies (Bonebrake et al. 2010; see Fungomeli et al. 2020a). Moreover, Arabuko Sokoke forest is rich in plant diversity and butterfly diversity, but little is known of their interaction. The forest is rich in biodiversity, with over 300 butterfly species (four species endemic to the forest of Kenya and Tanzania: *Acraea matuapa, Baliochila latimarginata, Baliochila stygia* and *Charaxes blanda),* 50 rare plant species which are both nationally and globally rare, three rare endemic mammals and home to 230 bird species 15 of which are rare and endemic to the Kenyan coast (Arabuko Sokoke Forest Management Team 2002). The forest also plays a crucial role as a global eco-tourism site, while locally supporting survival of the forest adjacent indigenous people livelihoods who depend on the forest for butterfly farming, collecting medicinal plants, cutting trees for poles and fuelwood. Plants form the local natural resource base and crucial factor upon which all other forest species depend on and more so butterflies.

Butterflies play a crucial role as biogeographical and ecological indicator species of habitat fragmentation, anthropogenic disturbance and climate change effects (Larsen 1993; Heikkinen et al. 2009; Manzoor et al. 2013). Their life cycle highly depends on plants either for breeding (host plants) or food (nectar feeding), and multiple other environmental factors (Collinge et al. 2003; Manzoor et al. 2013). They can serve as indicators for biodiversity in ecological studies due to their sensitivity to even minor changes in habitat conditions or disturbances (Lomov et al. 2006; Bouyer et al. 2007; Dobson 2012). In addition, butterflies play an essential ecological role as pollinators, and herbivores (Courtney et al. 1982; Bonebrake et al. 2010; Rader et al. 2015). Herbivory has been valued as a mechanism that has promoted plant coexistence and diversity, while pollination has enhanced plants life, growth and diversity (Vail 1992; Coley and Barone 1996; Viola et al. 2010). Moreover, their association with particular vegetation types and hostplants, the fluctuation in their richness and abundance according to seasonality and their pervasive presence on the territory makes them perfect study subjects for investigating and monitoring conservation status of ecosystems (Lien 2007; Monastyrskii 2007; Habel et al. 2018). This co-existence inter-play between butterflies and plants offers a unique fundamental contribution to ecosystem functioning while presenting a huge potential in tropical forests biodiversity monitoring (Humpden and Nathan 2010).

Approximately 18,000 butterfly species are known globally, of which 3,600 are found in Africa and around 870 species found in Kenya (Larsen 1991; Larsen 1996). Arabuko Sokoke forest hosts more than 300 of the Kenyan species of butterflies (Ayiemba 1995; Larsen 1996; Arabuko-Sokoke Forest Management Team 2002). The Arabuko forest constitutes an essential part of a world biodiversity hotspot in the Afrotropical ecoregion, situated in a matrix which is subject to increasing anthropogenic pressures, where the remaining forest fragments are threatened by continuous timber extraction and farmland conversion, in combination with climate change effects. The forest is naturally made up of three dominant vegetation types which are: *Cynometra* forest, *Brachystegia* woodland and mixed forest. Some butterfly studies carried out in ASF have looked at the butterfly diversity across the forest and vegetation types or seasonality influence on butterfly diversity

(Ayiemba 1995; Habel et al. 2018). However, to our knowledge, there is no study that has thoroughly investigated the influence of the plant species diversity on butterfly diversity in ASF. Moreover, the need to regular assess and monitor its continued fragmentation and biodiversity is therefore fundamental for long-term conservation efforts (Azeria et al. 2007; MacFarlane et al. 2015; Habel et al. 2017; Busck-Lumholt and Treue 2018). In this study, we investigate the effects of vegetation habitats and plant species diversity on the butterfly species richness and composition in Arabuko Sokoke forest.

In particular, we investigate: (i) how the dominant vegetation types influence butterfly species diversity, composition and abundance in ASF. (ii) how plant species diversity influence or correlate with butterfly diversity and composition (ii) how environmental drivers and butterfly traits of wingspan sizes for butterfly species diversity and composition vary within Arabuko Sokoke forest. We synthesize these results to better guide in the conservation policy formulations for sustainable forest use and management of the forest especially in the dry season when this study was conducted.

2.0 Materials and Methods

2.1 Study Area

The Arabuko Sokoke forest (ASF) is the largest forest fragment remaining within the Kenyan coastal forests covering an area of 42,000 ha, the second being Shimba hills forest (25,300 ha; Figure 7.1a; Burgess and Clarke 2000; Fungomeli et al. 2020a). It is globally valued as a world biodiversity hotspot of the Eastern Arc and Coastal Forests of Kenya and Tanzania (Myers et al. 2000). It is a dry lowland coastal forest that spreads within the two cities of Kilifi in the south and Malindi in the north, positioned between 39°48’E and 40°00’E longitude and between 3°11’S and 3°29’S latitude (Fanshawe 1995; Muchiri et al. 2001). It lays on a flat coastal plain at sea level and the area is divided by a low escarpment which crosses the forest from south-west to north-east (Moomaw 1960; Fanshawe 1995).

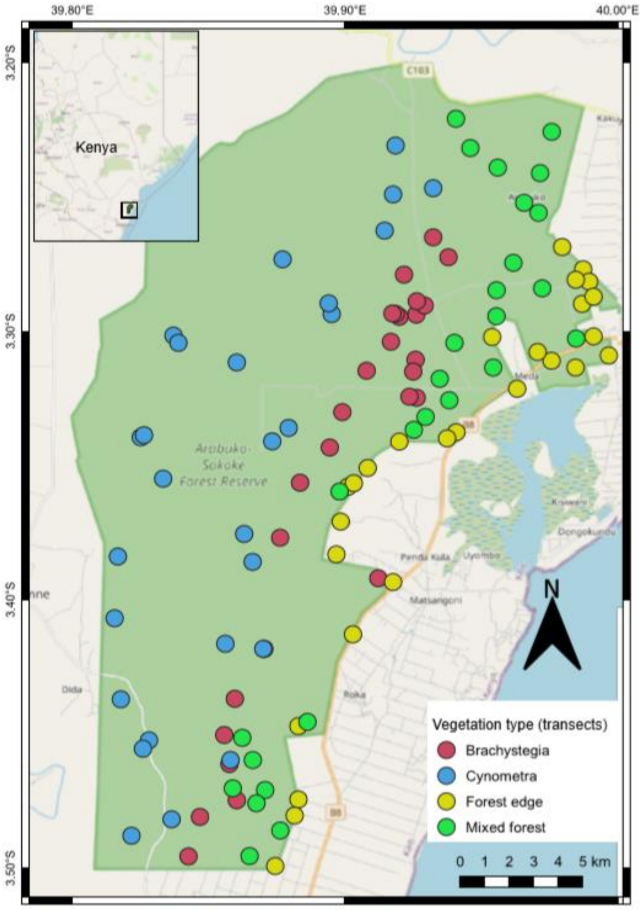


Figure 7.1a: A forest map of Arabuko Sokoke forest, Kenya showing butterfly transects distribution by vegetation type within the four vegetation types of Brachystegia forest, Cynometra forest, Forest edge and Mixed forest.

The climate consists of rainy and dry seasons, with two rainfall seasons of long and short rains. The long rain season occurs from April to July; short rains from October to December while the dry season lasts from December to March (Burgess and Clarke 2000; Omenge 2002). The annual rainfall ranges from 600-1,000mm, with rainfall decreasing from east to west within the forest (Omenge 2002; Habel et al. 2017). Temperature ranges from annual averages of 24-30°C with a high humidity of about 60% annually (Burgess and Clarke 2000). Several water pools exist within the forest during the rainy season with most drying out in the dry season and no rivers within the forest (Fungomeli et al. 2001; Kanga 2002; Muriithi and Kenyon 2002).

Figure 7.1b: The four vegetation types study sites within Arabuko Sokoke forest, Kenya showing **A:** Cynometra woodland; **B:** Brachystegia forest; **C:** Mixed forest; **D:** Forest edge

A distinct feature of the ASF are the distinct soil types and vegetation types within the forest (Figure 7.1b). There are two main types of soil, a light white sandy soil and a heavy red soil (Fanshawe 1995; Muchiri et al. 2001). These soil types have influenced the vegetation types with the dominating red soil of *Cynometra* woodland covering more than two thirds of the forest, whereas the remaining area of the forest is covered by white sandy soils of the mixed forest and *Brachystegia* woodland (Figure 7.1b; Fanshawe 1995). *Cynometra* forest is covered by *Cynometra* species (*Cynometra suhalensis*, *Cynometra webberi*), located within the inland part of the forest; while *Brachystegia* forest is covered by *Brachystegia spiciformis* which occurs in the white dry sandy soils. Lastly, the mixed forest is located in the eastern part of the forest, and is covered by mixed plant species of *Afzelia quanzensis*, *Combretum schumannii*, *Hymenaea verrucosa* and *Manilkara sansibarensis* (Fanshawe 1995; Muchiri et al. 2001; Arabuko Sokoke Management Team 2002).

2.2 Data collection

Field sampling and data collection were conducted during the dry season months (January-April) of 2019 across four vegetation types of ASF. *Cynometra* forest, *Brachystegia* woodland, mixed forest and forest edge (Figure 7.1a; Figure 7.1b; QGIS 2018). Butterflies were sampled by using a standard number of 27 transects measuring 10m x 100m per each vegetation type leading to a total of 108 transects. Butterflies were recorded in each 27 transect by using a standard count technique performed by walking at slow constant pace for approximately 15min. All butterfly species seen on both side of the path were recorded. Each transect was walked two times to be sure of having a complete and exhaustive recording (Pollard 1977; Pollard and Yates 1993). Butterflies were identified and recorded at species level, with the exception of species complexes with very similar species within the genera *Acraea*, *Eurema* and *Neptis*, which were only identified to genus level. Specimens that could not immediately be identified in the field were caught with a sweep net and placed in numbered envelopes or photographed for further identification in the lab. Identification was carried out using the butterfly references for the area (Larsen 1996) and supported by taxonomic counter checks from published sources. All transects were geo-referenced, with details of date, hour of start and end.

Vegetation field sampling was performed by using 26 plots each measuring 10 m x 100 m (same used for butterfly transects hereafter referred to as plots), and internally subdivided into 20 subplots of 10m x 5m. Each vegetation plot corresponded to a butterfly transect. Within the plots and subplots, we identified and measured the height and diameter at breast height (DBH) for each individual woody plant species (trees, lianas and shrub) with DBH $\geq$ 5cm. Plants with DBH<5cm such as small shrubs were identified in two subplots of each plot (see Fungomeli et al. 2020b).

2.2.1 Environmental and climatic variables

To summarize the ecological factors of each vegetation types, we derived environmental variables of elevation and distance from the coastline from elevation models. In addition, we extracted bio climatic data for each plot using WorldClim (Fick and Hijmans, 2017). We focused on factors composed of rainfall and temperature which were extracted as follows: Temperature: mean annual temperature, mean diurnal range, maximum temperature of warmest month, annual range of temperature (warmest to coldest month), mean temperature of wettest quarter, and mean temperature of driest quarter. Rainfall variables per vegetation habitat were extracted as mean annual rainfall, rainfall of wettest and driest month, rainfall of wettest and driest quarter, rainfall of warmest and coldest quarter.

2.2.2 Butterfly traits: wingspan sizes

We compiled and obtained wingspan sizes for our sampled butterfly species from published data sources of Woodhall (2005); Habel et al. (2018); Woodhall (2020); Schmitt (*pers. comm*); Barcode of Life Data System database (https://v3.boldsystems.org); and from the collection of the Senckenberg German Entomological Research Institute, Müncheberg.

2.3 Data analysis

A community matrix was prepared for the butterfly species abundances and another matrix was prepared for the woody plant species across the four vegetation types. We classified each butterfly species according to three ecological feeding habits of oligophagous, monophagous and polyphagous. A further classification into endemic status was assigned to species according to Larsen (1996).

2.3.1 Butterfly species diversity

Butterfly species diversity was analysed in terms of species richness, Shannon index and Simpson index across vegetation types.

Shannon Index: $$H = \sum_{i=1}^{k} p_1 \, ln(p_1)$$

Simpson Index: $$D = 1 - \sum_{i=1}^{k} p_1^2$$

For both of the indices, k represents the total number of species, while p_i indicates the relative abundance of each species that is calculated as n_i/N –(in which n_i indicates the number of individuals of the i-species and N indicates the number of individuals of all the species in the sampling units. Shannon Index when $p_i = 0$ then $p_i - \ln(p_i) = 0$ and the maximum value of the index is $ln(\mathrm{k})$. Higher values of these two indices mean higher diversity within the community.

Butterfly species richness and abundances mean distributions were plotted within vegetation types. We performed statistical tests for butterfly species richness and abundance across vegetation types by multiple pairwise-comparison (pairwise t-test) between the means of groups for analysis of variance (ANOVA) with Bonferroni adjusted P-values. A ranking of butterfly species frequencies was computed per each forest type by using a rank-abundance curve (Whittaker 1965).

2.3.2 Correlation between butterfly and plant species diversity

We applied a symmetric Co-correspondence analysis (CoCA) to quantify relationships between plant species community with butterfly species community across the vegetation types. Co-correspondence analysis is useful for comparing biological communities where observations have been made at the same locations (Braak and Schaffers 2004). We did this by a weighted average of species abundance values for plant species and separately for butterfly species within each of the four vegetation. We used '*coca'* function of the 'cocorresp' R package (Simpson 2009) to correlate using the 'symmetric' method. All graph plotting was performed using R package *ggplot2* (Wickham 2016) and *ggrepel* (Slowikowski 2020).

2.3.3 Butterfly species composition

We square-root transformed butterfly community abundances prior to the analysis to reduce effects of dominant species. Transformed community abundances were then used to generate a Bray-Curtis dissimilarity matrix (Bray and Curtis 1957). We tested for differences in the butterfly community structure among vegetation types using the '*anosim'* function of the 'vegan' R package (Oksanen et al. 2020). We also tested for differences between vegetation types using the permutational analysis of variance (PERMANOVA), using the '*adonis'* function of the 'vegan' R package. All tests were conducted using 999 permutations. Butterfly species contributing to similarities across vegetation types were determined using similarity percentages analysis (SIMPER). The *P*-values in pairwise comparisons were Bonferroni corrected.

2.3.4 Butterfly composition and environmental variables

We performed a non-metric multidimensional scaling analysis (NMDS; Kruskal 1964) based on Bray-Curtis dissimilarities to visualize butterfly species composition among vegetation types and relationships with environmental factors. Butterfly species abundance were square root transformed prior to the analyses. Environmental variables were related to the first two axes of NMDS (NMDS 1 and NMDS 2) using multiple regression at 999 permutations and relationship quantified by the coefficient of determination (R^2) and *P*-value statistical test. All calculations were performed in R software (R Core Team 2020) using the 'vegan' R package (Oksanen et al. 2020) with the '*metaMDS*' function for the NMDS, and the '*envit*' function to fit the environmental variables as vectors.

2.3.5 Butterfly traits: wingspan

Using Pearson correlation, we correlated butterfly wingspan sizes across vegetation types, by first correlating for total abundances in all vegetation types, and then second within each vegetation type. Additionally, a statistical pairwise *t*-test was done to compare average wingspan sizes across the vegetation types. The *P*-values were Bonferroni corrected.

3.0 Results

We recorded a total of 6050 butterfly individuals belonging to 86 species, 38 genera and 5 families across the four vegetation types of Arabuko Sokoke forest (Appendix 7.1). The plant species survey resulted in a total of 178 plant species belonging to 78 genera and 34 families (results already shown in Fungomeli et al. 2020b).

3.1 Butterfly species diversity

The butterfly family Nymphalidae turned out to represent the family with the highest number of species followed by Pieridae, Papilionidae, Lycaenidae and Hesperiidae (Appendix 7.1). The abundance for each family follows the pattern of species richness per family, with a higher abundance of individuals in the Nymphalidae family, followed by Pieridae, Papilionidae, Hesperiidae and Lycaenidae (Appendix 7.1). Analysis on the most abundant butterfly species showed *Phalanta phalanta*, *Appias epaphia*, *Catopsilia florella, Hypolimnas misippus, Coeliades forestan*, as the most frequent species across the vegetation types (Figure 7.2). Butterfly species richness and abundances were strongly correlated (R^2=0.89). Butterfly species feeding habit distribution showed oligophagous and polyphagous species being dominant at the forest edge respectively (Figure 7.3).

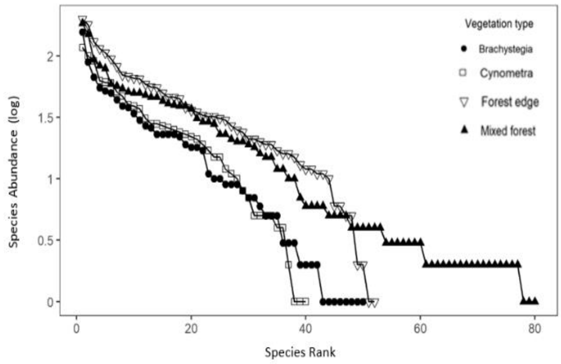


Figure 7.2: Frequency ranking of butterfly species abundance within the vegetation types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in the Arabuko Sokoke forest, Kenya.

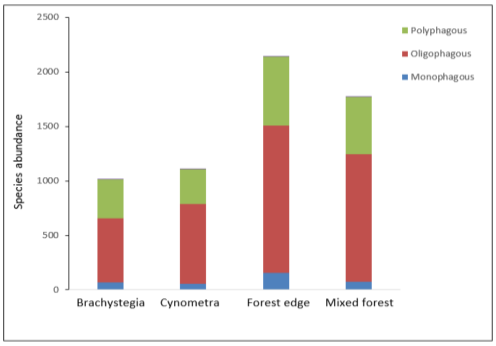


Figure 7.3: Butterfly feeding habits abundance of monophagous, oligophagous and polyphagous across the four vegetation types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in the Arabuko Sokoke forest, Kenya.

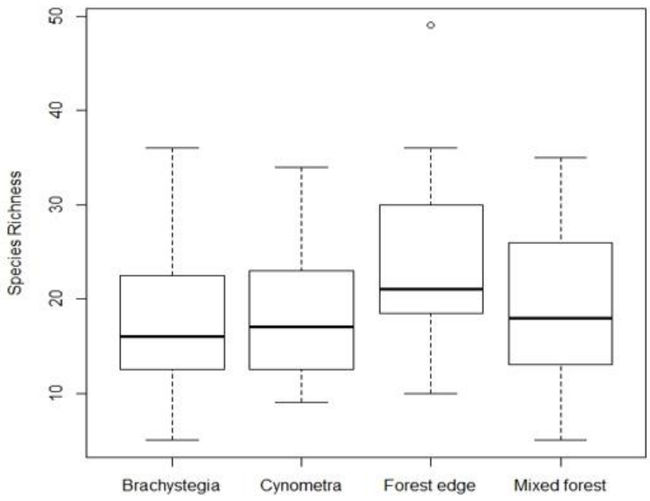
Butterfly species richness and abundances across vegetation types showed mixed forest vegetation had the highest cumulative species richness, followed by forest edge and *Brachystegia,* while *Cynometra* had the lowest value (Table 7.1). Average species richness and species abundance per plot showed some variation across vegetation types with apparently higher values in the forest edge and mixed forest (Figure 7.4). According to ANOVA, species richness was statistically not significant different across vegetation types (P=0.05), while species abundances were statistically different across vegetation types (P=0.001). Furthermore, abundance pairwise comparisons shows a statistically significant higher values between *Cynometra* and Forest edge vegetation (P=0.001) and between *Brachystegia* and Forest edge (*P*=0.013). The diversity indexes were quite similar ranging from 2.57 to 2.87 for the Shannon Index and from 0.9 to 0.93 for the Simpson Index (Table 7.1). Butterfly species abundances were higher in the forest edge, followed by mixed forest (Table 7.1).

Table 7.1: The butterfly species diversity across vegetation types, showing cumulative species richness and abundance, Shannon index and Simpson index per vegetation type in Arabuko Sokoke forest, Kenya.

Species diversity	Brachystegia	Cynometra	Forest edge	Mixed forest
Cumulative species richness	50	40	52	80
Cumulative species abundance	1022	1112	2141	1775
Shannon's H Index	2.57	2.58	2.87	2.66
Simpson's 1-D Index	0.90	0.90	0.93	0.91

Table 7.2: The environmental variables across vegetation types, showing elevation (m), distance from the shore (km) and mean annual temperature (°C) and rainfall (mm) in Arabuko Sokoke forest, Kenya.

Environmental variables	Brachystegia	Cynometra	Forest edge	Mixed forest
Elevation (m)	47.19	111.93	27.81	50.81
Distance from shore (km)	6.60	11.17	3.53	5.51
Mean annual temperature	25.71	25.31	25.84	25.70
Mean diurnal range temp. (mean of monthly)	8.07	8.19	8.03	8.04
Max temperature of warmest month	32.07	31.74	32.14	32.04
Temperature annual range (warmest-coldest month)	11.91	12.01	11.83	11.86
Mean temperature of wettest quarter	25.71	25.30	25.87	25.71
Mean temperature of driest quarter	26.90	26.53	27.03	26.89
Mean annual rainfall	100.28	97.00	102.56	101.64
Rainfall of wettest month	23.40	20.78	24.90	23.78
Rainfall of driest month	1.31	1.51	1.22	1.28
Rainfall of wettest quarter	49.45	44.54	52.43	50.64
Rainfall of driest quarter	7.41	8.43	6.86	7.29
Rainfall of warmest quarter	19.90	19.54	20.29	20.25
Rainfall of coldest quarter	21.90	20.01	23.04	22.93



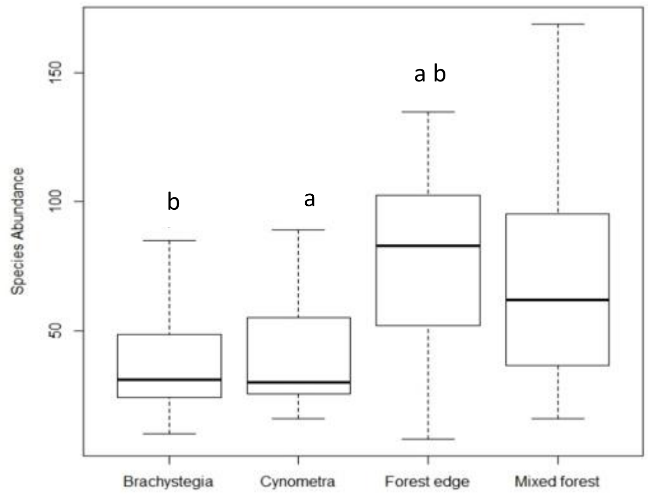


Figure 7.4: Boxplots showing butterfly species richness and abundances comparison across the four vegetation types of Brachystegia, Cynometra, Forest edge and Mixed forest in the Arabuko Sokoke forest, Kenya. Vegetation type with same letter denotes statistically significant differences ($P < 0.01$) between means.

3.2 Correlation between butterfly and plant species diversity

Co-correspondence analysis (CoCA) indicated a correlation between plant and butterfly species composition within the vegetation types, with the correlation coefficients between butterfly community and plant community for Axis 1 and 2 being 0.991 and 0.994 respectively. The first and second axis eigen-values showed the percent contribution of each axis to the total inertia (0.022 and 0.012) which represented a variance of 57.3% and 32.6% respectively, therefore with a total explained variance of 89.9% (Figure 7.5), indicating a high and significant correlation between the community matrices of plants and butterflies.

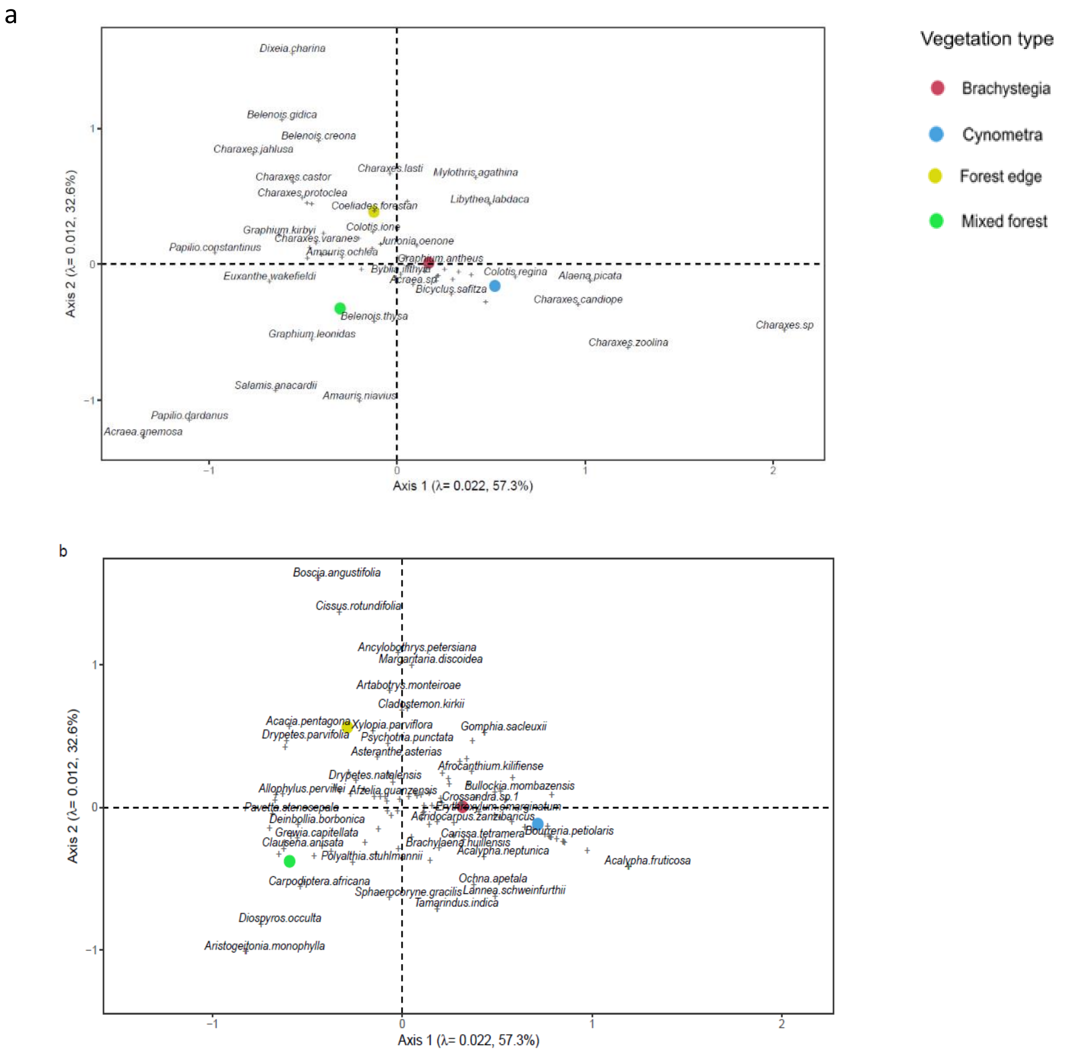
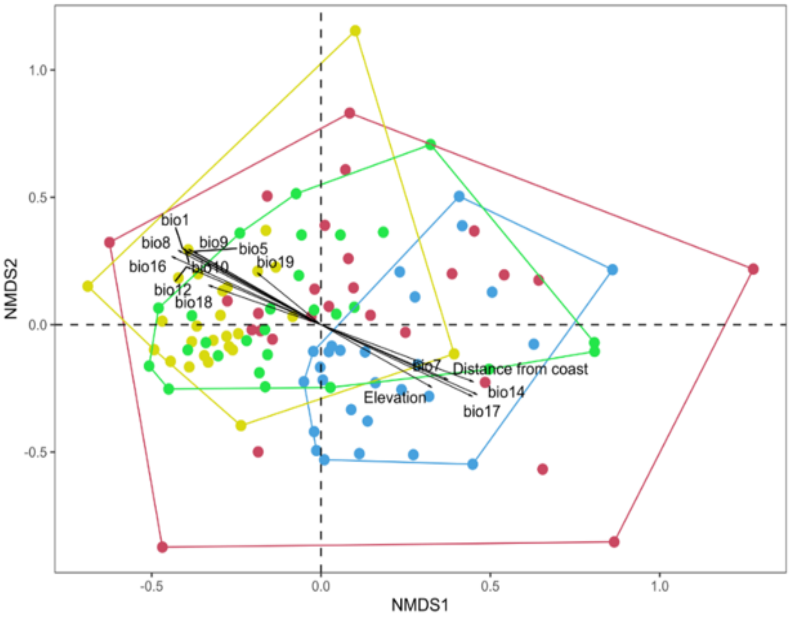


Figure 7.5: A symmetric co-correspondence analysis (CoCA) ordination bi-plot correlation of (a) butterfly species and plant species correlation (b) plant species and butterfly species within the four vegetation types of Brachystegia, Cynometra, Mixed forest and Forest edge in Arabuko Sokoke forest, Kenya. The Axis-1 eigen value of 0.022 explains a variance of 57.3% and Axis-2 eigen value of 0.012 explains a variance of 32.6%. Total explained variance by Axis 1 and 2 is 89.9%.

3.3 Butterfly species composition and environmental variables

The NMDS analysis of butterfly species composition across the four vegetation types did reveal a sort of gradient from the forest edge, mixed forest and *Cynometra*, with the *Brachystegia* vegetation covering a wider NMDS space that overlaps to the previous three types (Figure 7.6). In fact, a pairwise permutational multivariate analysis of variance (PERMANOVA) revealed statistically significant compositional differences in butterfly assemblages within the four different forest vegetation types ($R^2 = 0.07$; $P = 0.006$). Additionally, SIMPER results show species composition differences between vegetation types that contribute to 70% of the observed dissimilarities (Appendix 7.2).



● Brachystegia ● Cynometra ● Forest edge ● Mixed forest

bio1	Mean annual temperature
bio2	Mean diurnal range temp. (mean of monthly (max temp - min temp))
bio5	Max temperature of warmest month
bio7	Temperature annual range (warmest-coldest month)
bio8	Mean temperature of wettest quarter
bio9	Mean temperature of driest quarter
bio12	Mean annual rainfall
bio13	Rainfall of wettest month
bio14	Rainfall of driest month
bio16	Rainfall of wettest quarter
bio17	Rainfall of driest quarter
bio18	Rainfall of warmest quarter
bio19	Rainfall of coldest quarter

Figure 7.6: Non-metric multidimensional scaling (NMDS) and environmental variables relationship for butterfly species composition within the four vegetation types of Arabuko Sokoke forest, Kenya (k=3, stress = 0.23). Different colours represent different vegetation types as follows: *Brachystegia* (red), *Cynometra* (blue), forest edge (yellow), mixed forest (green).

Our results for the NMDS environmental fit shows environmental variables were statically significantly associated with butterfly species composition (*P*-value = 0.001) where the rainfall of driest month (bio14), rainfall of driest quarter (bio 17) influenced more *Cynometra* vegetation, while mixed forest and forest edge were more influenced by mean annual temperature (bio1), mean rainfall of the warmest (bio18) and driest quarter (bio19). Additionally, *Cynometra* vegetation was strongly influenced by elevation and distance from the shore (Figure 7.6, Table 7.2).

3.5 Butterfly traits: wingspan sizes

Finally, results on wingspan sizes showed no significant correlation with species abundances across vegetation types (Figure 7.7). However, the average wingspan sizes in *Cynometra* forest was significantly smaller (*P*<0.01) than in Forest edge and Mixed forest (Figure 7.8).

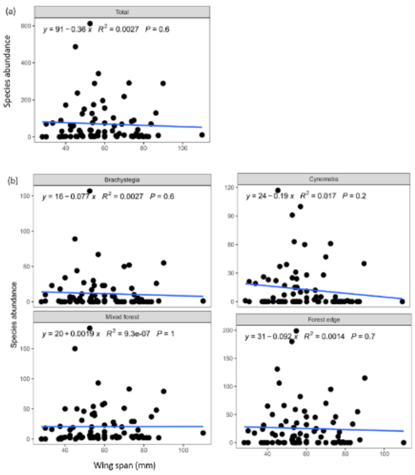


Figure 7.7: Butterfly wingspan sizes correlation across the four vegetation types of Arabuko Sokoke forest, Kenya. Showing wingspan correlation for (a) The total correlation in the four vegetation types (b) the correlation for each vegetation type of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge.

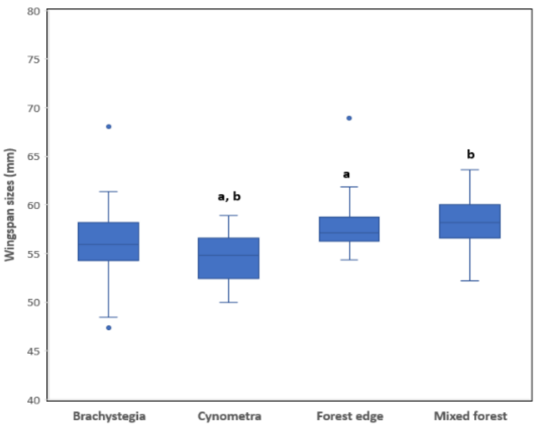


Figure 7.8: Butterfly average wingspan sizes across the four vegetation types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge in Arabuko Sokoke forest. Vegetation type with same letter denotes significant differences (P < 0.01).

4.0 Discussion

In this study, we investigated diversity and composition of butterfly and plant diversity within ASF during the dry season. Butterfly abundances showed a statistically significant difference across the vegetation types while species richness was statistically not significant different at the local (transect) scale while showing quite evident differences in terms of total species richness. On one hand, these results can be attributed to the climatic factors where the forest edge exhibited the highest annual rainfall, and highest wettest quarter followed by the mixed forest. This is further supported by the high significant differences in butterfly abundances between *Cynometra* and Forest edge. These results suggest the influence of rainfall and temperature on butterfly composition although this may also mainly be an indirect effect, with a more direct effect on the vegetation types. Additionally, our results highlight the crucial role of the forest edge as a refuge for feeding and maintaining populations during the dry season, while the mixed forest appears to serve as a host plant reservoir that is used for breeding which explains the high species richness. The synergic roles for butterfly species exhibited by the different vegetation habitats support the relevance of habitat diversity within Arabuko Sokoke forest and provide elements to build a good strategy for management and conservation strategies.

Plant and butterfly species composition were strongly correlated showing a concordant variation across the four vegetation types observed in the forest. These results suggest that plant species composition highly influences butterfly species diversity in Arabuko Sokoke forest. Our results confirm a fundamental direct link between butterflies and plants that make up the habitat in which butterfly live. Plants offer the natural base either as hostplants for larval food, nectar and shade for butterfly survival. Butterfly species diversity and composition are associated with plant species richness, vegetation types, seasonality, and other ecological factors (Larsen 1996). Different butterfly species are selective and have different preference for plant species for breeding (Larsen 1996). Consequently, the high plant species diversity in Arabuko Sokoke forest therefore also explains the high butterfly diversity in this ecosystem. For example, during the larval stages, they feed on host plant leaves, whereas they rely on a wide variety of flowering plants for nectar during their adult stages. Moreover, other butterfly species such as those in the genus '*Charaxes*' feed on fruits and dung in their adult stages (Larsen 1996). In our study, we sampled woody plant species (trees, shrubs and lianas). Our results therefore suggest woody plant diversity as a strong driver of butterfly diversity. This can be attributed to the different micro-climates enhanced by woody plant species enabling improved habitat ecological factors more so during the dry season (Checa et al. 2014). These results are in support of other studies that found butterfly species richness correlated with plant species richness and habitat type (Melo et al. 2019). A study by Steffan-Dewenter and Tscharntke (1997) shows butterfly species richness to be influenced by plant species richness and flower abundance. Additionally, in Arabuko Sokoke forest, some woody plants are known to flower throughout the year, while some only during the dry season. The alternate flowering characteristic of woody plants makes them a stable support for butterfly diversity. Nevertheless, other studies have shown the role of herbaceous plants for adult butterfly feeding (Kitahara et al. 2008).

We observed butterfly species abundance was significantly different across the vegetation types and was higher in the forest edge. This can be explained by the possible presence of micro-habitat niches of both biotic and abiotic resources that support availability of food and flowering plants for nectar feeding, especially during the dry season when most of the forest vegetation is not flowering. This can be further explained by the synergy of crop farming around the forest edge, whereby farming activities promote herbaceous species that cannot be found in the forest during the dry season. These herbaceous plants give a multitude of little flowers which butterflies can feed on during dry periods. This characteristic makes the forest edge a place mainly devoted to feeding, while other vegetation habitats may be preferred for reproductive and oviposition purposes. However, some studies have interestingly reported that butterfly diversity is usually higher in disturbed forests of forest edges than within natural forests (Blair and Launer 1997; Bobo et al. 2006). Moreover, the climatic variables of rainfall especially rainfall of warmest quarter was higher in the forest edge. Additionally, in Arabuko Sokoke forest, the water swamps also characterize the forest edge (Figure

7.1; Fungomeli et al. 2001; Arabuko Sokoke Forest Management Team 2002), where they are located on the Mida area and the Gede forest edge which may offer wetter soil conditions for butterfly feeding and watering. As such, butterflies are spotted in damp areas mud-puddling. Concordantly, a study by Viljur et al. (2020) shows that soil moisture is a direct habitat driver of butterfly species richness with high richness in soils of intermediate moisture. This argument can further support the seasonality effect, as during the dry season the forest edge offers the only available soil moisture source for butterfly communities. Nevertheless, we recorded the most frequent species which show characteristics of their survival during the dry season. For example, *Phalanta phalanta, Catopsilia florella* and *Hypolimnas misippus* have been shown to be strong survival species some of which are migratory, found mostly in open forest formations and also being dry zone species, while *Appias epaphia* are shown to prefer intermediate habitats of between closed forests and forest margins (Larsen 1996).

In addition, the mixed forest is also known for maintaining relatively moist conditions due to the canopy cover and soil conditions (Fanshawe 1995; Muchiri et al. 2001). Of particular mention, the species *Papilio dardanus* was only recorded in vegetation types of mixed forest and the *Brachystegia* forest during this survey. It is a favourite and a preferred butterfly species in Arabuko Sokoke forest for breeding by butterfly farmers around the forest as it fetches a good export price (2.50 US dollar per butterfly pupae). However, it is largely found during the rainy season. Concurrently, from the plant species NMDS (Figure S7.1), we found a dominance of the host plant for the *Papilio dardanus* in the mixed forest. These host plants include plant species of *Clausena anisata, Vepris amaniensis and Vepris trichocarpa* (Larsen 1996). This may explain the presence of host plants and better ecological conditions in the mixed forest. Moreover, the mixed forest is also preferred by elephants, probably because of the abundance of food and the shade provided by the canopy. Elephants droppings also act as a source of minerals and nutrients which butterflies have been seen feeding on during the dry season (Figure S7.2; Larsen 1996). Therefore, this could have been expected as one of the promoting factors for the relatively consistent presence of butterflies in this vegetation habitat. The mixed forest vegetation type can therefore be referred to as the ‘hotspot’ of species diversity in Arabuko Sokoke forest.

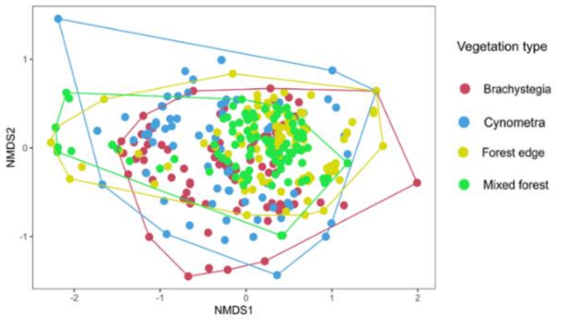


Figure S7.1: Plant species composition non-metric multidimensional scaling within the four vegetation types of Arabuko Sokoke forest, Kenya.

Figure S7.2: Butterflies in Arabuko Sokoke forest, in the mixed forest vegetation type, feeding from elephant dung during the field sampling. Photo credits: Maria Fungomeli

Butterfly wingspan sizes were significantly higher in Forest edge and Mixed forest compared to *Cynometra* forest. This can be attributed to the open-canopy state of the forest edge compared to the closed and dense forest type of the *Cynometra* forest (Hill et al. 2001). Studies have shown that, butterflies with larger wing sizes can be more abundant in forest gaps which exhibit a wide flight area favouring large-size butterflies (Hill et al. 2001). On the other hand, the oligophagous feeding habit was more dominant in the mixed forest, and less across the other vegetation types, giving an indication of being composed of more ‘generalists’ butterfly species.

Conclusion

The different vegetation types have played a synergetic role to maintain the butterfly species diversity and abundance of the Arabuko Sokoke forest. The significant difference in butterfly species abundance and higher values in average species richness and abundance in the forest edge point out the major role it plays as a refuge and feeding zone during the dry season. The importance of the mixed forest as a high plant species diversity spot is highlighted by the higher cumulative species richness found. Moreover, plant species diversity in ASF was strongly correlated to butterfly diversity emphasizing the crucial role of plants in maintaining the rich butterfly diversity and other ecological factors in support of fauna within the forest. These results emphasize the need for different habitat structure to maintain butterfly communities across different seasons, and enhance connectivity of the vegetation types. Therefore, there is the need to consider conservation and management strategies for the forest edge of Arabuko Sokoke forest to maintain the forest biodiversity.

Furthermore, Arabuko Sokoke forest is known for butterfly farming activities carried out by the forest adjacent communities for conservation and education purposes. Our results could help to guide the use of the butterfly diversity with respect to vegetation habitat and seasonality. This could help reduce forest disturbance of certain areas based on seasons and guide sustainable biodiversity utilization and conservation. A repetition of this study during the rainy season is expected to improve our understanding on drivers of butterfly species richness and abundance in ASF.

5.0 References

Arabuko-Sokoke Forest Management Team (2002) Arabuko-Sokoke Strategic Forest Management Plan 2002-2027. Available in Kenya from: Forest Department, Kenya Wildlife Service, Kenya Forestry Research Institute, National Museums of Kenya, Nature Kenya, and in UK from: BirdLife International.

Ayiemba WO (1995) A study of the butterfly diversity of Arabuko-Sokoke Forest, Kenya. Dissertation, University of Nairobi.

Ayiemba WO (2003) The utilisation of Arabuko Sokoke Forest butterflies is sustainable. In: Hoorweg J, Muthiga N (eds) Recent Advances in Coastal Ecology, Studies from Kenya.

Azeria ET, Sanmartin I, Stephan AS, Carlson A, Burgess ND (2007) Biogeographic patterns of the East African coastal forest vertebrate fauna. Biodiversity and Conservation 16: 883–912. https://doi.org/10.1007/s10531-006-9022-0.

Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. Biological Conservation 80:113–125.

Beentje HJ (1994) Kenya Trees, Shrubs and Lianas. National Museums of Kenya, Nairobi, Kenya.

Bobo KS, Waltert M, Fermon H, Njokagbor J, M¨uhlenberg M (2006) From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. Journal of Insect Conservation 10: 29–42.

Barcode of Life Data (BOLD) Systems taxonomy database. https://v3.boldsystems.org [accessed 13 August 2020].

Bonebrake TC, Ponisio LC, Boggs CL, Ehrlich PR (2010) More than just indicators: A review of tropical butterfly ecology and conservation. Biological Conservation 143: 1831-1841. https://doi.org/10.1016/j.biocon.2010.04.044.

Bouyer J, Sana Y, Samandoulgou Y, Cesar J, Guerrini L, Kabore-Zoungran C, Dulieu D (2007) Identification of ecological indicators for monitoring ecosystem health in the trans-boundary W Regional park: A pilot study. Biological Conservation 138: 73-88. https://doi.org/10.1016/j.biocon.2007.04.001.

Braak CJF, Schaffers AP (2004) Co-Correspondence Analysis: A new ordination method to relate two community compositions. Ecology 85:834-846. https://doi.org/10.1890/03-0021.

Braby MF (1995) Reproductive seasonality in tropical satyrine butterflies: strategies for the dry season. Ecological Entomology 20: 5-17.

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr., 27: 325-349. https://doi.org/10.2307/1942268.

Brakefield PM, Larsen TB (2008) The evolutionary significance of dry and wet season forms in some tropical butterflies. Biological Journal of the Linnean Society 22: 1–12. https://doi.org/10.1111/j.1095-8312.1984.tb00795.x

Busck-Lumholt LM, Treue T (2018) Institutional challenges to the conservation of Arabuko Sokoke Coastal Forest in Kenya. International Forestry Review 20: 488-505. https://doi.org/10.1505/146554818825240665.

Burgess ND, Clarke GP, Rodgers WA (1998) Coastal Forests of Eastern Africa: Status, Endemism Patterns and their potential causes. Biological Journal of the Linnean Society 64: 337-367. https://doi.org/10.1111/j.1095-8312.1998.tb00337.x

Burgess ND, Clarke GP (eds) (2000) The coastal forests of Eastern Africa. IUCN, Gland, Switzerland and Cambridge, UK.

Checa MF, Rodriguez J, Willmott KR, Liger B (2014) Microclimate variability significantly affects the composition, abundance and phenology of butterfly communities in a highly threatened neotropical dry forest. Florida Entomologist 97: 1-13. https://doi.org/10.1653/024.097.0101.

Coley PD, Barone JA (1996). Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics, Vol. 27:305-335. https://doi.org/10.1146/annurev.ecolsys.27.1.305.

Collinge SK, Prudic KL, Oliver JC (2003) Effects of local habitat characteristics and landscape context on grassland butterfly diversity. Conservation biology 17:178-187

Courtney SP, Hill CJ, Westerman A (1982) Pollen Carried for Long Periods by Butterflies. Oikos 38:260-63. https://doi.org/10.2307/3544030.

Dobson F (2012) Butterflies act as wildlife indicators, warning us of ecosystem changes. https://www.enn.com/articles/45000

Fanshawe JH (1995) The Effects of Selective Logging on the Bird Community of Arabuko-Sokoke Forest, Kenya. Dissertation, University of Oxford.

FAO (2018) The State of the World's Forests 2018 - Forest pathways to sustainable development. Rome. Licence: CC BY-NC-SA 3.0 IGO. http://www.fao.org/state-of-forests/en/ .

Fick SE, Hijmans RJ (2017) Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology.

Fungomeli M, Cianciaruso M, Zannini P, Githitho A, Frascaroli F, Fulanda B, Kibet S, Wiemers M, Mbuvi T, Matiku P, Chiarucci A (2020a) Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot, Plant Biosystems. https://doi.org/10.1080/11263504.2020.1834461.

Fungomeli M, Githitho A, Frascaroli F, Chidzinga S, Cianciaruso M, Chiarucci A (2020b) A new vegetation-plot database for the Coastal forests of Kenya. Vegetation Classification and Survey 1: 103-109. https://doi.org/10.3897/VCS/2020/47180.

Fungomeli M, Mathenge J, Wairungu S (2001) The economic importance of the Arabuko Sokoke forest water pools to the forest adjacent community as well as forest fauna and flora. Kenya Forest Research Institute, Gede, Kenya.

Habel J, Constanza I, Zamora C, Teucher M, Hornetz B, Shauri H, Mulwa R, Lens L (2017) East African coastal forest under pressure. Biodiversity and Conservation 26: 2751–2758. https://doi.org/10.1007/s10531-017-1375-z

Habel JC, Seibold S, Ulrich W, Schmitt T (2018) Seasonality overrides differences in butterfly species composition between natural and anthropogenic forest habitats. Animal Conservation 21: 405-413. https://doi.org/10.1111/acv.12408.

Hill J, Hamer K, Tangah J, Dawood M (2001) Ecology of tropical butterflies in rainforest gaps. Oecologia 128:294–302. https://doi.org/10.1007/s00420100651.

Heikkinen RK, Luoto M, Leikola N, Po¨yry J, Settele J, Kudrna O, Marmion M, Fronzek S, Thuiller W (2009) Assessing the vulnerability of European butterflies to climate change using multiple criteria. Biodiversity and Conservation 19: 695-723. https://doi.org/10.1007/s10531-009-9728-x

Humpden NN, Nathan GN (2010) Effects of plant structure on butterfly diversity in Mt. Marsabit Forest – northern Kenya. African Journal of Ecology 48: 304–312. https://doi.org/10.1111/j.1365-2028.2009.01151.x.

Kanga EM (2002) A conservation and recovery plan for the Ader`s Duiker *Cephalophus Adersi* in Arabuko Sokoke Forest, Kenya. http://www.wwct. org.uk/userfiles/pagefiles/conservation-research/coastal-east-africa/aders-duiker/Project%20report%202002%20-%20%20Aders'%20duiker%20in%20ASF.pdf

Kitahara M, Yumoto M, Kobayashi T (2008) Relationship of butterfly diversity with nectar plant species richness in and around the Aokigahara primary woodland of Mount Fuji, central Japan. Biodiversity conservation 17: 2713-2734. https://doi.org/10.1007/s10531-007-9265-4.

Larsen TB (1991) The Butterflies of Kenya and their Natural History. Oxford University Press, Oxford. ISBN: 9780198540113.

Larsen TB (1993) Butterfly Conservation Symposium - Keele University, September 1993.

Larsen TB (1996) The Butterflies of Kenya and their natural history. Oxford University Press, Oxford. Catalogue No : 1193. ISBN : 9780198500056

Larsen TB (2005) Butterflies of West Africa. Apollo Books, Stenstrup. ISBN: 9788788757439.

Lien VV (2007) Ecological indicator role of butterflies in Tam Dao National Park, Vietnam. Russian Entomological Journal 16: 479-486.

Lomov B, Keith DA, Britton DR, Hochuli DF (2006) Are butterflies and moths useful indicators for restoration and monitoring? A pilot study in Sydney's Cumberland Plain Woodland. Ecological management and restoration 7: 204-210.

MacFarlane DW, Kinzer AT, Banks JE (2015) Coupled human-natural regeneration of indigenous coastal dry forest in Kenya. Forest ecology and management 354: 149-159. https://doi.org/10.1016/j.foreco.2015.06.026

Manzoor F, Sadat HB, Hina F (2013) Butterflies as indicator of climate change. Zoo's Print 28: 19-21

Martinez-Sanchez N, Barragan F, Gelviz-Gelvez SM (2020) Temporal analysis of butterfly diversity in a succession gradient in a fragmented tropical landscape of Mexico. Global Ecology and Conservation 21. https://doi.org/10.1016/j.gecco.2019.e00847.

Melo DHA, Filgueiras BKC, Iserhard CA, Iannuzzi L, Freita AVL, Leal IR (2019) Effect of habitat loss and fragmentation on fruit-feeding butterflies in the Brazilian Atlantic forest. Canadian Journal of Zoology 97: 588-596. https://doi.org/10.1139/cjz-2018-0202.

Monastyrskii AL (2007) Ecological and Biogeographical Characteristics of Butterflies (Lepidoptera, Rhopalocera) of Vietnam. Entmol. Rev. 87:43. https://doi.org/10.1134/S0013873807010058.

Moomaw JC (1960) A study of the plant Ecology of the Coast Region of Kenya, East Africa. Nairobi. Government Printer. https://edepot.wur.nl/493400.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853-858. https://doi.org/10.1038/35002501.

Muchiri MN, Kiriinya CK, Mbithi DM (2001) Forest Inventory report for the indigenous forests in Arabuko Sokoke Forest Reserve, Arabuko Sokoke Forest Management Project. Kenya Forestry Research Institute, Gede-Malindi, Kenya.

Murithi S, Kenyon W (2002) Conservation of biodiversity in the Arabuko Sokoke Forest, Kenya. Biodiversity and Conservation 11: 1437–1450. https://doi.org/10.1023/A: 1016234224819.

Newton AC, Echeverría C (2014) Analysis of anthropogenic impacts on forest biodiversity as a contribution to empirical theory. Forests and global change (pp. 417-446) Cambridge University Press. http://dx.doi.org/10.1017/CBO9781107323506.019

Noad T, Birnie A (1990) A Fully Illustrated Field Guide: Trees of Kenya. General Printers Ltd, Nairobi, Kenya

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MH, Szoecs E, Wagner H (2020) Vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan.

Omenge PM (2002) The role of butterfly farming in forest conservation and community development in Kenya. https://www.researchgate.net/publication/291147956.

Pollard E (1977) A method for assessing changes in the abundance of butterflies. Biological Conservation 12:115-134. https://doi.org/10.1016/0006-3207(77)90065-9

Pollard E, Yates TJ (1993) Monitoring Butterflies for Ecology and Conservation - The British Butterfly Monitoring Scheme. Chapman & Hall, London.

QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R et al. (2015) Non-bee insects are important contributors to global crop pollination. Proceedings of the National Academy of Sciences, 113: 146-151. https://doi.org/10.1073/pnas.1517092112.

Schweitzer CJ, Dey DC (2011) Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-cumberland plateau escarpment region, USA. Forest Ecology and Management262:1729-1741. https://doi.org/10.1016/j.foreco.2011.07.020.

Simpson GL (2009) cocorresp: Co-correspondence analysis ordination methods. R package version 0.4-1. http://cran.r-project.org/package=analogue.

Slowikowski K (2020) ggrepel: automatically position non-overlapping text labels with 'ggplot2'. R package version 0.8.2. https://CRAN.R-project.org/package=ggrepel.

Steffan-Dewenter I, Tscharntke T (1997) Early succession of butterfly and plant communities on set-aside fields. Oecologia 109, 294-302. https://doi.org/10.007/s004420050087.

UNESCO (United Nations Educational, Scientific and Cultural Organization), Man and the Biosphere programme (2019) Thirty-first session-Sc-19/CONF.231/1_v2. UNESCO Headquarters, Paris.

Vail SP (1992) Selection for over-compensatory plant responses to herbivory: a mechanism for the evolution of plant–herbivore mutualism. The American Naturalist 139:1. https://doi.org/10.1086/285309.

Viljur M, Tiitsaar A, Gimbutas M, Kaasik A, Valdma D, Erki Ounap E, Tammaru T, Tiit Teder T (2020) Conserving woodland butterflies in managed forests: Both local and landscape factors matter. Forest Ecology and Management 462: 118002. https://doi.org/10.1016/j.foreco.2020.118002.

Viola DV, Mordecai EA, Jaramillo AG, Sistla SA, Albertson LK, Gosnell JS et al. (2010) Competition-defence trade-offs and the maintenance of plant diversity. Proc. Natl. Acad. Sci. USA.

Whittaker RH (1965) Dominance and diversity in land plant communities: Numerical relations of species express the importance of competition in community function and evolution. PubMed 147: 250-60. https://doi.org/10.1126/science.147.3655.250.

Wickham H (2016) ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Woodhall S (2005) Field Guide to Butterflies of South Africa Cape Town. South Africa: Struik. ISBN 978-1-86872-724-7

Woodhall S (2020) Field guide to butterflies of South Africa: Second Edition. Bloomsbury Publishing, ISBN: 1472973704, 9781472973702

Appendices

The main field vegetation data across the 25 sampled Coastal forests of Kenya is deposited on sPlot-the global vegetation database repository with restricted access (https://www.idiv.de/en/splot.html) for ongoing publications. Further, the vegetation data description is available and can be accessed at the Global Index of Vegetation-Plot Databases, Kenya coastal forests vegetation plot-database (https://www.givd.info/ID/AF-KE-001) and from the publication article: Fungomeli et. al. 2020 - A new vegetation-plot database for the Coastal forests of Kenya. *Vegetation Classification and Survey* 1: 103-109, https://doi.org/10.3897/VCS/2020/47180.

In addition, all appendices cited in the various chapters are a long species data list. They are therefore deposited on Zenodo data repository: https://doi.org/10.5281/zenodo.4400785, with restricted access to be authorised by author.

The appendices cited are arranged in the following format in the Zenodo data repository:

Chapter number	**Appendix number**	**Tittle**
1	Appendix 1.1	Woody plant species matrix with species name, family and lifeform from reviewed data (SR_R) and sampled plot data (SR_S) of the coastal forests of Kenya.
1	Appendix 1.2	Coastal forests of Kenya endemic woody plant species from the combined data set of reviewed and sampled data of the coastal forests of Kenya
3	Appendix 3.1	Species Indicator analysis for the Coastal forests of Kenya grouped into forest reserves and sacred forests recorded in all 158 sampled plots.
5	Appendix 5.1	Coastal forests of Kenya Phylogeny species composed of 1183 woody species, belonging to 510 genera and 100 families.
7	Appendix 7.1	Arabuko Sokoke forest sampled butterfly species names, with author names, genus and family across the vegetation types of *Brachystegia*, *Cynometra*, Mixed forest and Forest edge.
7	Appendix 7.2	Butterfly species SIMPER composition dissimilarities, species that cumulatively contribute upto 70% of the observed dissimilarities across the vegetation types of Arabuko Sokoke forest.

Co-author Declaration

This declaration states the independent research contribution of the PhD candidate for each paper compiled in the thesis.

Paper No.	**Title and full bibliographic reference**		
Paper I	A new vegetation-plot database for the Coastal forests of Kenya. Fungomeli, M., Githitho, A., Frascaroli, F., Chidzinga, S., Cianciaruso, M., & Chiarucci, A. (2020a). *Vegetation Classification and Survey*, 1, 103-109. https://doi.org/10.3897/VCS/2020/47180.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author and Corresponding author	Study design Field work Data preparation Data analysis and visualization Writing Editing	50% >75% >75% 75% 75% >75%	

Paper No.	**Title and full bibliographic reference**		
Paper II	Woody plant species diversity of the coastal forests of Kenya: filling in knowledge gaps in a biodiversity hotspot. Fungomeli, M., Cianciaruso, M., Zannini, P., Githitho, A., Frascaroli, F., Fulanda, B., Kibet, S., Wiemers, M., Mbuvi, T., Matiku, P. & Chiarucci, A. (2020b). *Plant Biosystems*, 154(6), 973-982. https://doi.org/10.1080/11263504.2020.1834461.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author and Corresponding author	Study design Field work Data preparation Data analysis and visualization Writing Editing	50% >75% 75% 50-75% 50-75% 75%	

Paper No.	**Title and full bibliographic reference**		
Paper III	Patterns and community structure of woody plant diversity of the coastal forests of Kenya. Maria Fungomeli, Frascaroli Fabrizio, Piero Zannini, Marcus Cianciaruso, Anthony Githitho, Juri Nascimbene & Alessandro Chiarucci.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author, Corresponding author	Study design Fieldwork Data preparation Data analysis & visualization Writing Editing	50% >75% >75% 50-75% 50-75% >75%	

Paper No.	**Title and full bibliographic reference**		
Paper IV	Species-area relationships and small-island effect on plant diversity of the coastal forests of Kenya. Maria Fungomeli, Piero Zannini, Fabrizio Frascaroli, & Alessandro Chiarucci		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author equal contributing with second author, and corresponding author	Study design Fieldwork Data preparation Data analysis & visualization Writing Editing	50% >75% 50-75% 50% 50-75% 50-75%	

Paper No.	**Title and full bibliographic reference**		
Paper V	Phylogenetic diversity of the Coastal forests of Kenya: Role of sacred Kaya forests and IUCN Red List in the conservation of evolutionary history in a biodiversity hotspot. Maria Fungomeli, Alessandro Chiarucci, Arianna Balacchi & Marcus Cianciaruso.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author	Study design Fieldwork Data preparation Data analysis & visualization Writing Editing	50-75% >75% >75% 75% 50-75% >75%	

Paper No.	**Title and full bibliographic reference**		
Paper VI	Fungomeli, M., Cianciaruso, M., Frascaroli, F., Githitho, A. & Chiarucci, A. (2020c). Conservation of the Coastal forests of Kenya: A tropical biodiversity hotspot with Unexplored biocultural diversity potential. Submitted to: *Perspectives in Ecology and Conservation*, manuscript number: PECON-D-20-00245.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author and corresponding author	Study design Fieldwork Data preparation Data analysis & visualization Writing Editing	75% >75% >75% 75% 75% >75%	

Paper No.	**Title and full bibliographic reference**		
Paper VII	Vegetation determinants on butterfly diversity and composition of the Arabuko-Sokoke coastal forest, a tropical biodiversity hotspot, of Kenya. Maria Fungomeli, Martin Wiemers, Lucia Calderini, & Alessandro Chiarucci.		
Role of PhD candidate	**Type of contribution**	**Overall contribution (%)**	**Signature of PhD candidate and tutor**
First author and corresponding author	Study design Fieldwork Data preparation Data analysis & visualization Writing Editing	75% >75% >75% 50-75% 75% >75%	

Acknowledgements

First, my deepest gratitude to my supervisor Prof. Alessandro Chiarucci for his great guidance, support and advice throughout this study. Thank you for instilling in me the capacity to work independently, and the many lectures I attended in your classes of Vegetation ecology, Biogeography and Macroecology, and a field trip work to Lipari were a great building block to this study. Thank you for the great work in collaboration with University of Bologna and the National Museums of Kenya in advancing the biodiversity knowledge in the fascinating field of the Coastal forests of Kenya biodiversity hotspot. Thank you too for taking the time away from study to invite me to stay with your family in Tuscany. My special gratitude to Prof. Giulio Viola for his overall coordination and personal support during this study. I also thank the two external examiners and reviewers of this thesis: Prof. Fabio Attore (Italy) and Prof. John Maxwell Halley (Greece) for their comments and suggestions to improve the final quality of the work.

My sincere thanks goes to the different funding sources and field logistical support that immensely helped to accomplish the field work in Kenya, without which this work would not have been possible. Thank you to the University of Bologna, Department of Biological, Geological and Environmental Sciences (BiGEA), the National Museums of Kenya (NMK), International Association of Butterfly Exhibitors and Suppliers (IABES), Nature Kenya and WWF-Kenya for the support received. Great thanks to the National Museums of Kenya for granting me the study leave to accomplish this study. Sincere thanks to Mr Anthony Githitho of Coastal forests conservation Unit-NMK, for his invaluable advice, time throughout the field work and study period.

My sincere and great appreciation to Prof. Marcus Cianciaruso and Dr Martin Wiemers for their lead collaboration in two of the chapters in this study in Phylogenetic diversity and Butterfly diversity respectively. My special thanks to Dr Fabrizio Frascaroli for his patience and time in teaching me statistical analysis in R, and input in statistical analysis. My gratitude to Prof. Duccio Rocchini, Prof. Juri Nascimbene, Dr Giovanna Pezzi and Dr Fabrizio Buldrini for your study advises and collaboration. To my PhD colleagues in the lab: Irene Montanari-thank you for your friendship and

Love, always being there as a family for me throughout my stay in Bologna; to Piero Zannini thank you for the statistical input into the study.

Special thanks to my Kenyan team that worked tirelessly in the field during the field sampling and the collaboration with other forest institutions. I thank Saidi Chidzinga, Geoffrey Mashauri and Abbas Shariff, Lawrence Chiro and Abdulrahman Matano of Coastal forests conservation unit-NMK; Dr Tito Mbuvi and Joseph Muthini of Kenya Forest Research Institute; and George Wara and Blessingtone Magangha of Kenya Forest Service.

I am deeply indebted to Fr Albert Buijs, Chantal Derungs and Caspar Bijleveld for their great support throughout my study without which I would not have managed to spend the study period and stay in Bologna. In you I found true counsellors, motivators, friends, family, parents, and support angels who took me through this study in every single step through the many challenges. Your prayers and support kept me strong in darkest seasons. May God Bless you abundantly.

Finally, great thanks to my family for being with me since the start, always being there, for your prayers and motivation. My special thanks to my sister Veronica Fungomeli, Mr Leornard Mambo Mashanga and Louei -Aurelian Mashanga, for the great responsibility over the family while I was away on study. Ahsante sana! Mungu awabariki!

Above all, I would like to give thanks to The Almighty God for His protection, guidance, provision of wisdom, patience and strength throughout my study period. In the most weary moments and darkest seasons, You gave me strength, comfort and encouragement to keep going. Thank you, Lord!

The Study Journey

Inspired by Nature, Driven by Science

My passion for nature and the years of my work in forest conservation of the Coastal forests of Kenya, was a great inspiration for me to undertake this PhD study of the Coastal forests of Kenya without a full scholarship. This study has resulted into crucial outputs and insights including the first large quantitative vegetation data base of the coastal forests of Kenya. The overall results will mark a new milestone into re-organisation of conservation strategies of these forest fragments.

The great challenge during field work was to access most of these Kenyan coastal forest fragments. Many are located in very remote rural areas; with bad-terrain access roads; long distance covered to access, with several days spent on single forests; dense forests hard to walk; hills and mountains to climb, hostile weather and the dangerous wildlife security issues making access and sampling within forests very difficult. We encountered numerous challenges, and many flat tyres of our vehicle. Not forgetting the huge financial costs involved to carry out such a large survey in a limited time period that left me totally bankrupt.

As such, this PhD study platform has truly tested my determination, built my research and science confidence, enhanced my capacity in delivering results that can enhance the conservation of the coastal forests of Kenya. Thank you to Prof. Alessandro Chiarucci and Prof. Giulio Viola for coordination during the PhD period, and to all collaborating institutions, friends, family and individuals into making this journey a worthwhile.

The rich biodiversity dataset sampled and developed during this study for the coastal forests of Kenya forms a long-term standing quality data. It has the potential to be explored and utilized for great synthesis and publications. I remind anyone using the data to be considerate for ethical scientific collaborations.