POPULATION ECOLOGY AND PHENOLOGICAL RESPONSES OF FOOD-PRODUCING FOREST TREES TO CLIMATE CHANGE: IMPLICATIONS FOR RURAL FOOD SECURITY

By

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ABSTRACT

Tropical rainforests are important ecosystems that provide numerous benefits to humans and are home to a rich diversity of flora and fauna. The Afrotropical rainforests are particularly valuable due to their high biodiversity and provision of essential services such as carbon sequestration and water regulation. However, these forests are facing unprecedented threats from various anthropogenic activities, including habitat loss, fragmentation, degradation, and climate change. While studies have focused on the global and regional impacts of these activities on tropical forests, small-scale, less intense, human activities like foraging are modifying the forest in ways that have not been fully evaluated. This doctoral research project aims to address this knowledge gap by exploring the impact of low-intensity anthropogenic activities and environmental drivers on the species composition, structure, and biodiversity of the Oban rainforest in Nigeria. The project comprises four interconnected research objectives: (1) to analyse the impact of human utilization of tree species for food on the diversity, composition, and structure of food-producing and non-food producing tree species; (2) to assesses how human foraging affects regional-scale tree species biodiversity patterns in Nigeria and Cameroon; (3) to evaluate the effect of climate variability on forest phenology (EVI) in Oban rainforest between 2002 and 2022 and (4) to provide baseline monitoring data on the reproductive phenology (time of budding, flowering and fruiting) of tree species in Oban Forest between May 2020 to May April 2022. Findings show that low-intensity human activities such as foraging can significantly impact tree species assemblages in tropical forests, particularly for edible species, potentially leaving long-lasting footprints. The research highlights the complex interplay that environmental, spatial, and human factors have in shaping tree species dissimilarity in the Nigeria-Cameroon forest region, providing valuable insights on the need for further research to better understand the extent and nature of human impacts on regional forest composition. The remote sensing data shows that precipitation is a as the major driver of changes in EVI with up to seven months lagged response. The timing of the peak in EVI showed potential implications for the livelihoods of forest-dependent communities who rely on forest resources for food and income. The seasonal trend in fruit production, occurred in July and August in the first cycle and in July in the second growing season. Continuous production of flowering buds and flowers was observed throughout the year without indicating a clear seasonal cycle. The results highlight the importance of considering the influence of human activities in understanding the dynamics of tropical forests, and further research is needed to explore the different possibilities and validate the findings fully. There is a need to address some key unknowns and uncertainties in the study, such as the impact of extreme weather events and other variables influencing the tropical forest phenological cycle. Collaborating with local communities, policymakers, and modellers could help address these limitations and provide a more comprehensive understanding of the phenological cycle in the Oban Forest. Long-term monitoring of the reproductive phenology of food-producing tree species is an essential approach to generating ground-based data to better understand the response of phenology to environmental and other factors.

DEDICATION

To my dearest mom,

I dedicate this thesis to you with utmost gratitude and appreciation for all the sacrifices you have made to ensure my success. Your unwavering emotional and financial support has been the cornerstone of my academic journey, and I am forever grateful for it. You have always been my guiding light, my source of strength, and my role model, and I cannot imagine achieving this milestone without your love, prayer, and encouragement.

I also dedicate this thesis to my late dad, who instilled in me a passion for academics that continues to drive me today. Although he is no longer with us, his memory and legacy live on through my achievements, and I know he would be proud of the person I have become.

I hope that this thesis serves as a testament to the love and dedication that both of you have shown me throughout my life. Thank you for everything you have done, and for always believing in me.

With love and gratitude,
Sijeh Agbor Asuk

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CANDIDATE’S CONTRIBUTION

The work presented in this thesis is the result of collaborative research. The specific contributions of the candidate are outlined below.

CHAPTER ONE: INTRODUCTION, was completed by Sijeh Asuk

CHAPTER TWO: IMPACT OF HUMAN FORAGING ON TREE DIVERSITY, COMPOSITION AND ABUNDANCE IN A TROPICAL RAINFOREST

Authorship: **Asuk, S. A.**, Matthews, T. J., Sadler, J. P., Thomas A. M. Pugh, T. A. M., Ebu, V. T., Ifebueme, N. M. and Kettridge, K.

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Candidate’s contribution:

Sijeh Asuk, Nicholas Kettridge, Jonathan Sadler, Tomas Pugh, and Tomas Matthews: conceived research ideas. **Sijeh Asuk**, Vincent Ebu and Nzube Ifebueme: established plots and collected the data. **Sijeh Asuk** led the interpretation and writing of the manuscript with assistance from Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews. Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews: supervised the research and provided feedback. *Biotropica* Associate Editor Jennifer Powers and three anonymous peer-reviewers provided feedback on the manuscript and statistical methods during the manuscript publication process.

CHAPTER THREE: HUMAN FORAGING AFFECTS REGIONAL SCALE TREE SPECIES BIODIVERSITY PATTERNS IN TROPICAL WESTERN AFRICA

Authorship: **Sijeh A. Asuk**, Joseph P. Wayman, Jonathan P. Sadler, Thomas A. M. Pugh, Thomas J. Matthews, Oliver L. Phillips, Simon Lewis, Bonaventure Sonké, Joey Talbot, James Comiskey, Lise Zemagho, Lucas Ojo, Serge Begne, Terry Sunderland, Wannes Hubau, Vincent Droissart, Lan Qie, Martin Gilpin, Murielle Simo-Droissart, Ted Feldpausch, Kelvin Peh, Lindsay F. Banin, Marie Noel Kamdem Djuikouo, and Nicholas Kettridge

Status: To be submitted

Candidate's contribution:

Sijeh Asuk, Nicholas Kettridge, Jonathan Sadler, Tomas Pugh, and Tomas Matthews: conceived research ideas. Data collected by **Sijeh Asuk** was combine with regional plot data collected Oliver L. Phillips, Simon Lewis, Bonaventure Sonké, Joey Talbot, James Comiskey, Lise Zemagho, Lucas Ojo, Serge Begne, Terry Sunderland, Wannes Hubau, Vincent Droissart, Lan Qie, Martin Gilpin, Murielle Simo-Droissart, Ted Feldpausch, Kelvin Peh, Lindsay F. Banin, Marie Noel Kamdem Djuikouo. Data was analysed and interpreted by **Sijeh Asuk** with assistance from Joseph P. Wayman who wrote the GDM model code. Chapter was written completed by **Sijeh Asuk**. Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews supervised the research and provided feedback.

CHAPTER FOUR: THE EFFECT OF AIR TEMPERATURE AND PRECIPITATION ON PHENOLOGY IN AN AFRO-TROPICAL RAINFOREST

Authorship: **Sijeh A. Asuk**, Jonathan P. Sadler, Thomas A. M. Pugh, Thomas J. Matthews, and Nicholas Kettridge

Status: To be submitted

Candidate's contribution:

Sijeh Asuk conceived research ideas, collected and analyzed data, interpreted results, and wrote the manuscript. Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews supervised the research and provided feedback.

CHAPTER FIVE: MONITORING REPRODUCTIVE PHENOLOGY OF FOOD-PRODUCING TREES IN A NIGERIAN RAINFOREST

Authorship: **Sijeh A. Asuk**, Jonathan P. Sadler, Thomas A. M. Pugh, Thomas J. Matthews, Vincent T. Ebu, and Nicholas Kettridge

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Candidate's contribution:

Sijeh Asuk conceived research ideas, managed and coordinated the phenological data collection team in Nigeria in collaboration with Vincent Ebu. **Sijeh Asuk** compiled the data, presented the results, and wrote the manuscript. Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews supervised the research and provided feedback.

CHAPTER SIX: KEY RESEARCH FINDINGS, SYNTHESIS AND FUTURE DIRECTIONS, was completed by the **Sijeh Asuk**. Nicholas Kettridge, Jonathan Sadler, Thomas Pugh, and Thomas Matthews supervised and provided feedback.

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1. **Asuk, S. A.,** Matthews, T. J., Sadler, J. P., Thomas A. M. Pugh, T. A. M., Ebu, V. T., Ifebueme, N. M. and Kettridge, K. (2023) Impact of human foraging on tree diversity, composition, and abundance in a tropical rainforest, Biotropica, 55(1), pp. 232–245.

Conference presentations

1. **Asuk, S.,** Kettridge, K., Sadler, J., Pugh, T., Matthews, T., Ebu, V., and Ifebueme, N. (2021) Does foraging impact tropical forest composition? EGU General Assembly 2021. Online 19-30 April 2021. https://doi.org/10.5194/egusphere-egu21-8867.
2. **Asuk, A. S.,** Kettridge, K., Sadler, J., Pugh, T., Matthews, T. (2019) Population ecology and phenological responses of food-producing forest trees to climate change: implications for rural food security. School of Geography, Earth and Environmental Sciences (GEES) Doctoral Research Conference, 2019. The University of Birmingham, UK. 19-20 April 2019.

LIST OF ABBREVIATIONS

AfriTRON	African Tropical Rainforest Observation Network
BA	Basal Area
CRNP	Cross River National Park
Dbh	Diameter at Breast Height
DCHP	Distance to Closest Human Presence
DNAE	Distance to Nearest Anthropogenic Edge
ECMWF	European Centre for Medium-Range Weather Forecasts
EVI	Enhanced Vegetation Index
GAM	Generalised Additive Regression Model
GDMs	Generalized Dissimilarity Models
GEE	Google Earth Engine
L1P1	Location one, Plot one (up to n^{th})
masl	Meters Above Sea Level
SADs	Species Abundance Distributions
βsim	Simpson’s Similarity Index (turnover resultant beta diversity)
βsor	Sørensen Index of Dissimilarity (total beta diversity)

CHAPTER ONE: INTRODUCTION

1.1. INTRODUCTION

Tropical rainforests are some of the most important ecosystems on the planet (Rajpar, 2018; He et al., 2020; Roberts, Hamilton and Piperno, 2021; Pillay et al., 2022). Their renowned ecological significance spans a broad range of functions and services that are essential for life on Earth. Beyond serving as carbon sinks, mitigating the impacts of climate change, they also play a pivotal role in regulating global weather patterns and local climates (Vauhkonen, 2018; Hong and Saizen, 2019). Across the tropical forest regions of Africa, Asia, Latin America, and the Caribbean, the rich biodiversity of forest plants, fungi, and animals serves as a vital food source, bolstering household food security through ancestral practices (Asprilla-Perea and Díaz-Puente, 2019; Friant et al., 2019; McMichael, 2021). The Afrotropical rainforests, found mainly in Central and West Africa, globally distinguished for their vibrant biodiversity, are home to a myriad of flora and fauna, many of which are yet to be discovered or studied in depth. These forests not only serve as gene banks (Roberts, Hamilton and Piperno, 2021; Pillay et al., 2022) for untapped resources that might be critical for medicine, food, and industry in the future but also function as water catchment areas, ensuring clean and regular water supplies for millions, biodiversity conservation, and the supply of non-timber forest products (Alamgir et al., 2016; Englund, Berndes and Cederberg, 2017; Hong and Saizen, 2019; Mengist and Soromessa, 2019; Kothandaraman et al., 2020; Zeppetello et al., 2020). This makes them among the most valuable and biologically diverse ecosystems.

Forest-dependent rural communities often utilize wild foods as primary alternatives to conventional sources of animal proteins, cereals, tubers, vegetables, and fruits (Asprilla-Perea and Díaz-Puente, 2019; van Loon et al., 2019). In urban areas, they also play a pivotal role in supplementing conventional foods, enhancing overall food availability (van Loon et al., 2019; Kamga et al., 2013; Asprilla-Perea and Díaz-Puente, 2019). Beyond mere consumption, wild foods also offer economic avenues, with many communities relying on activities like hunting, gathering, and cultivation for their subsistence, thereby ensuring food access (Pereira et al., 2010; Friant et al., 2015; Benítez-López et al., 2019; Ember, 2020). Despite the immense significance of tropical forests, they are under increasing threats from high-intensity anthropogenic activities such as logging, agriculture, mining, and urbanization leading to habitat loss, fragmentation, and degradation (Bush et al., 2015; Clement et al., 2015; Piperno, McMichael and Bush, 2015; Levis et al., 2017; Jarzyna and Jetz, 2018; McMichael, 2021; Scerri et al., 2022).

Climate change further exacerbates these threats. The large-scale accelerated loss of tropical forest has been linked to increased local warming of the earth surface (Vargas Zeppetello et al., 2020). Climate change poses significant threats to food security, particularly in regions like Sub-Saharan Africa (Ofori et al., 2021; Tantoh, 2023). As global temperatures rise, the delicate balance of ecosystems is disrupted, leading to a cascade of challenges for agriculture and food production. In Sub-Saharan Africa, where over 95% of agriculture is rain dependent (Mupangwa et al., 2016; Ofori et al., 2021), the implications of climate change are profound. Changes in precipitation patterns, coupled with increased temperatures, can lead to reduced growing seasons, impacting crop yields and livestock productivity (Henrietta et al., 2020; Ofori et al., 2021). Shifts in precipitation patterns and rising temperatures also modifies species composition, ecological interactions, and forest ecosystems services provisioning is being transformed (Jarzyna and Jetz, 2016; McMichael, 2021). Furthermore, the depletion of natural resources, exacerbated by climate change, affects not only agriculture but also fishing activities, wild food, and other vital food sources for many human communities in the region (Jarzyna and Jetz, 2018; McMichael, 2021; Ofori et al., 2021). The frequency and intensity of droughts, a natural phenomenon in Africa, are expected to increase due to climate change, further straining food resources (Bhaga et al., 2020; Ofori et al., 2021). Such droughts have historically led to severe food shortages, affecting millions (Bhaga et al., 2020; Ofori et al., 2021). Additionally, climate change can amplify the spread of pests and diseases, further threatening crop yields (Ofori et al., 2021; Zacarias, 2020). As Sub-Saharan Africa grapples with these challenges, the nexus between water, land, and food resources becomes even more critical, underscoring the need for integrated and adaptive strategies to ensure food security in the face of a changing climate (Ofori et al., 2021).

Growing evidence suggests that less intense, more subtle human impacts may also affect ecological communities and alter what is considered ‘natural’ ecological and biogeographical pattern (Piperno, McMichael and Bush, 2015; Chaturvedi et al., 2017; Levis et al., 2017; Roberts, Hamilton and Piperno, 2021; Singh et al., 2022). One such example is the utilisation of forests for food by forest-dependent human communities, which in some cases has been found to leave lasting impacts on forest ecology and dynamics (Steadman, 1993; Bush et al., 2015; Socolar et al., 2016). There have been many studies on the global and regional impacts of high-intensity anthropogenic activities on tropical forests (McMichael, 2021; Singh et al., 2022; Chaturvedi et al., 2017). However, despite the potential significance of low-intensity human activities like foraging on the forest ecosystem, these impacts have remained understudied, due to the difficulties in measuring and quantifying them (Piperno et al., 2015; Singh et al., 2022; McMichael, 2021). The existing uncertainty in the impact of local-scale phenology-climate relationships in Afrotropical forests (Nakamura et al., 2017) necessitates the need for further research. This would aid proper understanding of the complex relationships between environmental changes, biodiversity, and low-intensity human activities in tropical rainforests, especially the Afrotropical rainforests, to develop effective conservation and management strategies.

Furthermore, leaf phenology (Bush et al., 2020; Bush, 2018) plays a vital role in the life cycle of plants and ecosystem functioning, and it is often synchronised with seasonal changes in environmental factors (Adamescu et al., 2018; Cleland et al., 2007; Gray and Ewers, 2021; Richardson et al., 2013). Variation in the onset of the rainy season, shifts in temperature, and variations in day length can trigger significant phenological events such as when trees flower, when fruits ripen, and when animals migrate or breed, all of which have cascading impacts on the broader ecosystem (Wagner et al., 2017; Yu et al., 2017; Smith et al., 2020; Muller-Landau et al., 2021). Understanding this phenological pattern is vital for many forest-dependent human communities in Africa that depend on forests for their livelihoods (Benítez-López et al., 2019; Friant et al., 2019; Jansen et al., 2020; Mayes et al., 2017). Whether it is the fruiting of a particular tree species that provides food or the flowering of another that offers medicinal value, the lives of these communities are intricately intertwined with the pulse of the forest (Jansen et al., 2020).

The Oban Forest, located in the Oban division of Cross River National Park in South-eastern Nigeria, covers about 3,000 km^2 of the country's land area and is home to a diverse array of tree species, many of which are economically important (Olajuyigbe, 2019; Friant et al., 2019). The forest has been described as one of Africa's most biologically diverse hotspots, with over 4,000 plant species, including many endemic species, and numerous fauna such as primates, elephants, and birds (Agaldo et al., 2016; Nigerian National Park Service, 2019; Aladesanmi, 2022; Olajuyigbe, 2019). Oban Forest plays a crucial role in the socio-economic development of forest-dependent communities by providing timber and non-timber forest products, regulating climate, water, and nutrient cycles, and supporting livelihoods.

Oban Forest is a fundamental source of cultural dietary needs for 39 forest-dependent communities, which rely on them for their livelihoods, such as harvesting non-timber forest products, income generation, and engaging in ecotourism (Ogogo, Asuk and Ikpeme, 2014; Agaldo, Gwom and Apeverga, 2016; Asuk and Nchor, 2018; Friant et al., 2019; Nigerian National Park Service, 2019). Like other tropical forest, the modification of the physiology, composition, and diversity of species in the Oban Forest ecosystems can alter the service provisioning capacity of forest ecosystems and directly or indirectly impact the cultural dietary needs of these communities (Morin et al., 2018; Santos et al., 2018; Ellis et al., 2021; Naif et al., 2020; Montgomery et al., 2020; Bera et al., 2020; Ding et al., 2019).

The strategic integration of wild foods in food security planning can render such interventions more relevant and sustainable. Aligning with ancestral uses of wild foods, policies, programs, and projects can tap into deeply rooted cultural practices (van Loon et al., 2019; Piperno et al., 2015; McMichael, 2021; Levis et al., 2017; Bush et al., 2015). This approach not only ensures a seamless transition but also reduces dependency on conventional foods, which might be challenging to produce, costly, or culturally resisted. However, while the benefits of wild foods in enhancing food security are evident, there are significant challenges that hinder their full integration into policies and programs. One primary concern is the potential negative impact on biodiversity due to indiscriminate and unplanned extraction practices (van Loon et al., 2019; Asprilla-Perea and Díaz-Puente, 2019). Addressing this requires sustainable strategies that can assess the wild food populations' abundance and density, project their sustainability, measure the extraction's impact, and explore cultivation or breeding possibilities. To navigate this, decision-makers must champion systematic, multidisciplinary studies to understand how these forest-dependent communities will be impacted. It is therefore essential to study the complex relationships between environmental changes, biodiversity, and low-intensity human activities in tropical rainforests. This will facilitate the development of sustainable forest management practices that maintain forest health, productivity, and the provision of essential services to local communities (Hong and Saizen, 2019; Asuk et al., 2018). The research gaps that informed this PhD research, the underlying research aim and objectives, a description of the study area and an outline of the thesis structure are described in this chapter.

1.2. RESEARCH GAPS

Tropical rainforests rank among the planet's most biologically rich ecosystems, teeming with an unparalleled diversity of flora and fauna (Rajpar, 2018; He et al., 2020; Roberts, Hamilton and Piperno, 2021; Pillay et al., 2022). These forests play a crucial role in global ecological processes, from carbon sequestration to water purification (Vauhkonen, 2018; Hong and Saizen, 2019). High-intensity human activities such as deforestation and logging in these forests have been well-documented, and their ramifications widely recognized (Lewis, Edwards and Galbraith, 2015; Phillips, Newbold and Purvis, 2017; Roberts et al., 2017). Yet, the subtler impacts of low-intensity anthropogenic activities, such as localized foraging, traditional agriculture, and minor forest produce collection, remain less explored (Lewis, Edwards and Galbraith, 2015; Scerri et al., 2022). Both forms of activities, whether large-scale or small-scale, not only modify the species composition and their life cycles but also impair the broader functions of these ecosystems.

Nigeria's Oban Forest is a prime example of tropical rainforest of significance in Africa. The forest is not merely a reservoir of biological diversity but also plays a pivotal role in sustaining the socio-economic fabric of 39 forest-dependent communities (Ogogo, Asuk and Ikpeme, 2014; Agaldo, Gwom and Apeverga, 2016; Asuk and Nchor, 2018; Friant et al., 2019; Nigerian National Park Service, 2019). Beyond providing timber and other tangible resources, the Oban Forest offers invaluable ecosystem services. It regulates local climate, ensures consistent water supply by acting as a watershed, and recycles crucial nutrients that support both flora and fauna

(Nigerian National Park Service, 2019), which have implications for understanding broader tropical forest landscapes.

While high-intensity impacts on rainforests from activities like logging are widely recognized, the subtle effects of low-intensity human activities, especially those like collecting medicinal plants and traditional shifting agriculture practices, could have significant cumulative impacts over time (Lewis, Edwards and Galbraith, 2015; Santos, Disney and Chave, 2018; Williams et al., 2020; Scerri et al., 2022). Although the Oban Forest presents specific dynamics, understanding the intricacies of these activities could provide insights into how similar actions affect biodiversity and ecosystem stability in other tropical rainforests.

There is also an evident gap in understanding local-scale phenology-climate relationships in Afrotropical forests, such as the Oban Forest. This could shed light on the interaction between changing environments, biodiversity, and human activities. The unique relationship between seasonal changes in plant behaviours (phenology) and local climate variations, especially in Afrotropical environments like the Oban Forest, is understudied. Understanding these interactions can provide more knowledge of how climatic changes might disrupt natural cycles and rhythms in tropical forests worldwide (Dunham et al., 2018; Pezzini et al., 2014; Smith et al., 2020; Stan et al., 2020).

Furthermore, while leaf phenology is known to be essential, its deep-seated role in ecosystem functioning, especially in connection with forest-dependent communities, requires more scrutiny. This is because the timing of leafing, flowering, and fruiting has profound implications for different food web tiers within an ecosystem. In the Oban Forest, how these cycles align with the needs of herbivores, pollinators, and forest-dependent communities holds a broader lesson for understanding ecosystem functionality across tropical forests.

Another area that merits exploration is the interplay between shifts in forest physiology and the dietary and cultural needs of dependent communities. The forest-dependent communities around Oban Forest may have evolved traditional knowledge systems and practices rooted in their forest's health (Agaldo, Gwom and Apeverga, 2016). A study into understanding how the changing in forest, whether due to pests, diseases, or human interventions, could affect these traditions and practices can shed light on the human-nature interdependence prevalent in tropical forests globally.

Lastly, to safeguard the health and productivity of such forests and ensure continued service to local communities, there is a pressing need to better grasp and develop sustainable forest management practices. The Oban Forest faces challenges like illegal logging, encroachment, and habitat fragmentation. Promoting innovative, community-centric sustainable management practices in the Oban Forest could pave the way for similar initiatives in other threatened tropical forests.

By addressing these research gaps within the Oban Forest's framework, the study will enrich the existing knowledge of tropical rainforests. This knowledge lays the foundation for developing conservation strategies and sustainable management practices for tropical forests worldwide. Thus, the research areas identified as priorities for the study (see detailed literature in Chapters Two to Five).

1.3. AIMS AND OBJECTIVES

The general aim of the research is to investigate the factors that affect the biodiversity and phenology of trees in Oban Forest, Nigeria. The project comprises four interconnected research objectives:

(1) to analyse the impact of human utilization of tree species for food on the diversity, composition, and structure of food-producing and non-food producing tree species;

(2) to assess how human foraging affects regional-scale tree species biodiversity patterns in Nigeria and Cameroon;

(3) to evaluate the effect of climate variability on forest leaf phenology (EVI) in Oban rainforest between 2002 and 2022, and;

(4) to provide baseline monitoring data on the reproductive phenology (time of budding, flowering and fruiting) of tree species in Oban Forest between May 2020 to May April 2022.

1.4. STUDY AREA

1.4.1. Oban Forest, Nigeria

The study was conducted in an Afrotropical rainforest in the Oban Division of Cross River National Park (CRNP), Nigeria (Figure 1.1b,d). The forest is situated between longitude 8°10´ and 8°55´ East and latitude 5°00´ and 5°50´ North and covers an estimated area of ~251,345 ha (Olajide et al., 2008; Jimoh et al., 2012; Adeyemi, 2016). In the North, South and West, the forest is bounded by and has a total of 39 forest-dependent / support zone and small-holder agricultural communities, and it is continuous with the Korup National Park and Ejagham Forest Reserve of Cameroon in the East (Agaldo et al., 2016; Jimoh et al., 2012; Adeyemi, 2016; Oluwatosin and Jimoh, 2016).

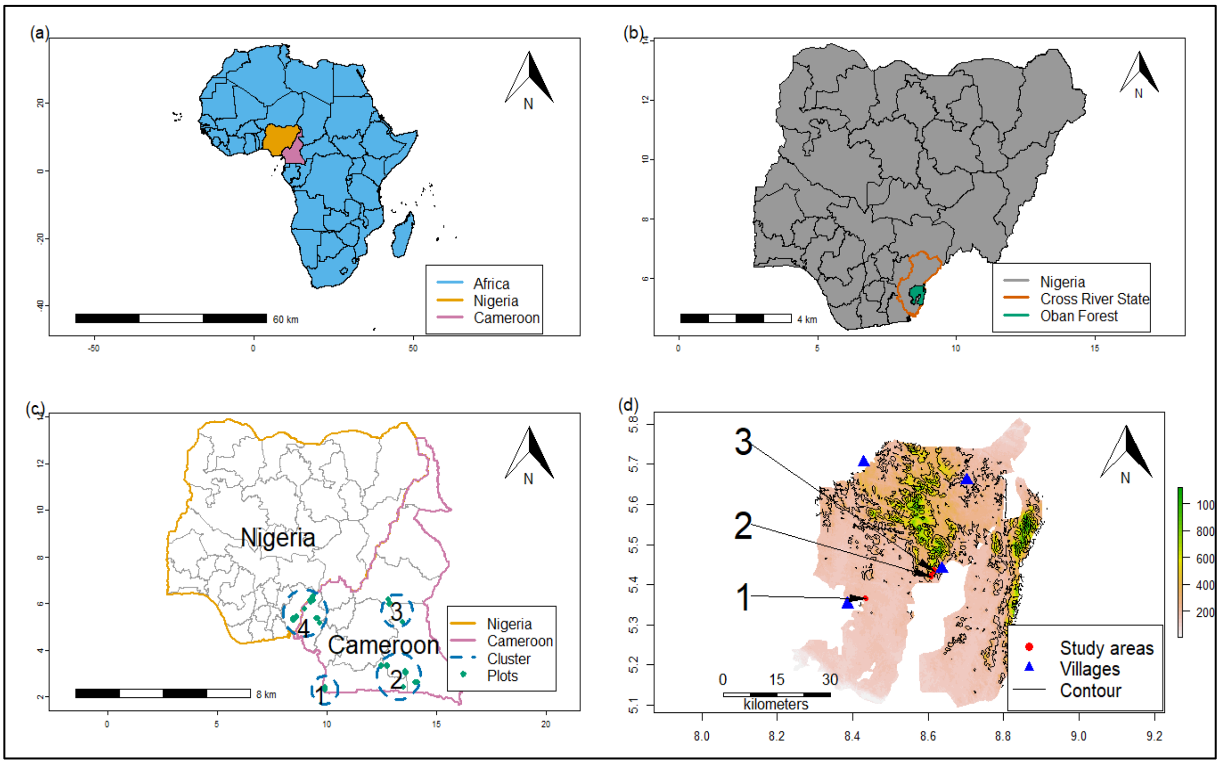

Figure 1.1. The study locations used for the study are shown in the Map. (a) Map of Africa showing Nigeria and Cameroon (b) Map of Nigeria showing location of Oban Forest in Cross River State (c) Map of Nigeria and Cameroon Showing the locations of the plots used for the regional study. Blue circles represent clusters (d) Map of contour map of Oban showing location of plots and villages visited during the study.

The forest vegetation is lowland and submontane moist tropical rainforest with mean annual precipitation ranging between 3,000 mm and 3,500 mm, mean monthly temperature range of 23 °C to 37 °C, rugged terrain and elevation ranging from ~ 100 m to over 1000 m above mean sea level (Jimoh et al., 2012; Aigbe and Omokhua, 2015; Agaldo et al., 2016). The forest is the last stronghold of pristine tropical forest in Nigeria, part of the “Gulf of Guinea biodiversity hotspots of conservation concerns” in West Africa (Agaldo et al., 2016) and known to house many endemic flora and fauna species (Oates et al., 2004). This includes most of the 935 tree species identified in Nigeria (Lock and Keay, 1991), other herbaceous plant species, and rich diversity of butterflies, birds, reptiles, amphibians, and a wide range of mammal species, including ungulates, cats, buffalo, elephants and primates, including the world’s rarest lowland gorillas and others plant and animal species (Asuk et al., 2018). Oban Forest was used as the study location for all chapters except Chapter Three, which included additional plots from Cameroon for the regional analysis.

1.4.2. Forests in Cameroon

The study for Chapter Three was carried out using tree data from 66 plots established in the tropical forests of Nigeria (Oban Forest) and Cameroon, bordering countries in Africa's West and West-Central Africa, respectively (Figure 1.1a,c). The forests of both countries are contiguous via their common borders (Enuoh and Ogogo, 2018; Nigerian National Park Service, 2019). Species composition data used for the study comprised single census tree-by-tree samples collected between 2002 and 2019 from five plots established in Nigeria by Asuk et al (2022a) and 61 plots established in Nigeria and Cameroon, accessed from the forestplots.net database (Lopez-Gonzalez et al., 2011, 2009).

1.5. THESIS STRUCTURE

The presented thesis is based on the paper style alternative to thesis format. The outlined aims, objectives, and research questions/hypotheses are addressed in Chapters Two to Five of the thesis. Each chapter can be regarded as an independent unit and is self-contained however, Chapter Three is a regional study that builds on findings from Chapter Two.

Chapter Two of the thesis explores the influence of human utilization of tree species for food on the diversity, composition, and structure of food-producing and non-food-producing tree species in Oban Forest, Nigeria. The study utilizes tree diameter distribution, stem density, beta diversity patterns, and species abundance distributions (SADs) to assess the effects of human foraging on the forest ecology along an elevational gradient. Chapter Three builds on the findings of Chapter Two by evaluating the impact of low-intensity anthropogenic activities on the assemblage of tree species communities at a local and regional scale, using an analysis of beta diversity. The study utilizes Generalized dissimilarity models (GDMs) and variance partitioning on a regional dataset from tropical forests located in Nigeria and Cameroon to assess the influence of human presence on the beta diversity of forest trees at a regional scale and whether this influence differs between those species used for food and those which are not. Chapter Four aims to aid a better understanding of the impact of environmental drivers on Oban rainforest phenology by evaluating the response of forest leaf phenology to changes in air temperature and precipitation in Oban Forest, Nigeria, between 2002 and 2022. The study utilizes the enhanced vegetation index (EVI), as a proxy for phenology, to evaluate the response of forest leaf phenology to changes in air temperature and precipitation in Oban Forest. Chapter Five provides two years tree phenological monitoring data set for trees in Oban Forest.

These four chapters contribute to knowledge geared toward understanding the impact of anthropogenic activities and environmental drivers on Oban rainforest ecosystems. They will develop more effective conservation strategies to ensure tropical forests' long-term survival and ecosystem services.

CHAPTER TWO: IMPACT OF HUMAN FORAGING ON TREE DIVERSITY, COMPOSITION AND ABUNDANCE IN A TROPICAL RAINFOREST

Published article: Biotropica

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2.1. ABSTRACT

Tropical forest tree communities are structured by a range of large-scale drivers including elevation, certain high-impact anthropogenic activities (e.g., deforestation), and fires. However, low-impact human activities such as foraging may also be subtly but notably altering the composition of tropical forest tree communities. The study assessed the i) differences in species diversity, patterns of relative abundance, and pairwise beta diversity between trees with edible and inedible fruits and seeds along an elevation gradient, and ii) impact of human foraging on the forest tree communities in Oban Division of Cross River National Park, Nigeria. Fifteen permanent 40 by 40 m plots were established along an elevational gradient (120 - 460 m above mean sea level). All trees of 10 cm diameter at breast height (dbh) and above were measured, identified, and, with the aid of structured questionnaires, classified into those with edible and inedible fruits/seeds. A total of 35 edible species with density of 128 stems/hectare and basal area of 11.99 m^2/hectare, and 109 inedible species with density of 364 stems/hectare and basal area of 22.42 m^2/hectare were sampled. However, the evenness of edible and inedible species was similar at pooled and plot levels. For inedible species, there was a positive relationship between pairwise beta-diversity and elevation, and this was driven mainly by turnover. In contrast, edible species exhibited a non-significant trend between elevation and beta-diversity. Thus, the study showed that human foraging of edible fruits may have subtly influenced patterns of species diversity and community structure in this tropical forest.

2.2. INTRODUCTION

Anthropogenic activities leading to large-scale habitat loss are known to have substantially impacted forest biodiversity (Steadman, 1993; Helmus, Mahler and Losos, 2014; Bush et al., 2015; Clement et al., 2015; Piperno, McMichael and Bush, 2015; Stahl, 2015; Levis et al., 2017). However, there is growing evidence that less intense, more subtle human impacts may also affect ecological communities, and in turn alter what is consider to be ‘natural’ ecological and biogeographical patterns (Piperno, McMichael and Bush, 2015; Chaturvedi et al., 2017; ; Singh et al., 2022).

For example, the modern floristic composition and structure of some natural forests, like the Amazonian Forest, have been linked to past human activities in the forest (Levis et al., 2017). These activities, such as cultivation, seed dispersal and propagation, in situ tending of useful resources, and hunting of large mammals that aid in seed dispersal have the capacity to both extend and reduce the abundance and distribution of tree species (Socolar et al., 2016; Levis et al., 2017). However, in contrast to the coarse-scale effects of forest loss and degradation (Swenson et al., 2011; Gallardo-Cruz et al., 2009; Alahuhta et al., 2017; Donoso et al., 2017; García-Navas et al., 2020), smaller scale impacts of anthropogenic activities on ecological patterns in tropical forests are left largely understudied, likely due to the difficulties in measuring and quantifying them. Thus, we still lack a comprehensive understanding of the magnitude and dynamics of impacts from low intensity anthropogenic activity on natural forest ecosystems (Piperno, McMichael and Bush, 2015; Stahl, 2015; Levis et al., 2017).

One widespread example of low intensity activities is the utilization of forests for food by forest-dependent human communities, which in some cases has been found to leave lasting impacts on forest ecology and dynamics (Bush et al., 2015; Socolar et al., 2016; Steadman, 1993). The most important plant parts found to be utilized for food by human communities in tropical countries are underground storage organs, fruits, and leaves (Welcome and Van Wyk, 2020). Friant et al's (2019) examination of dietary differences and associated changes in agriculture-forest frontiers of Cross River State, Nigeria revealed that in addition to human hunting of wild animals, the forest also acts as a source of nuts, seeds and vegetables. These plant foods are thought to comprise a significant component of the daily diets of forest-dependent human communities. Although food-producing tree species have been largely identified and documented in many tropical forest regions, very little is known about the effect of varying degrees of human foraging on their abundance, and distribution in space. The continuous influence of humans on the forest, and at varying intensities, could, in principle, lead to a change in the forest community that might be reflected in contrasting distribution and abundance patterns between different species (Verberk, 2012). Although it is expected that a typical tropical forest ecosystem will comprise a few species with high abundance and many species with low abundance (ter Steege et al., 2013), human activities can alter the species richness of, and the distribution of abundance between, tree species either through preferential planting or conservation of beneficial trees, or through intentionally or inadvertently influencing the propagule pool (McGill et al., 2007; Socolar et al., 2016). Thus, it is important to understand how less overtly destructive anthropogenic activities, such as foraging, can over time influence the species composition, and ultimately function, of the forest.

The hypothesis that harvesting tree-based food products affects community composition and relative abundance can be evaluated through a focus on two commonly studied biogeographical patterns: beta diversity and the species abundance distribution (SAD). Beta diversity is the dissimilarity in species composition between two or more communities (Pound et al., 2019; Anderson et al., 2011), and has been used as an effective indicator for assessing the impact of anthropogenic activities on the composition of species in terrestrial and aquatic ecosystems (Dantas de Miranda et al., 2019; Elo et al., 2018; Kessler et al., 2009; Gradstein et al., 2007; Silva et al., 2018). Changes in beta diversity along elevational gradients has been a particular area of research interest in ecology (Yu et al., 2017; García-Navas et al., 2020; Guerin et al., 2013; Socolar et al., 2016; Nascimbene and Spitale, 2017). Elevation has also been used as a proxy for temperature to assess relationships with plant community diversity (Xu et al., 2017; Nascimbene and Spitale, 2017; Swenson et al., 2011; Gallardo-Cruz et al., 2009) and functional traits of plant species (Yu et al., 2017).

The SAD characterizes the abundance of all species found within a defined community (Matthews and Whittaker, 2015; McGill et al., 2007). It is an important ecological and biogeographical concept because it provides insight on the structure, function, and other less visible aspects of ecological communities (Matthews et al., 2014; Verberk, 2012). Two primary types of empirical SAD shape are commonly observed in nature: logseries (with a dominance of very rare species) and lognormal (dominance of species with intermediate abundance) type shapes. Empirical SADs have been used to study the responses of ecological communities to anthropogenic disturbances such as land-use change and pollution, by evaluating how the form of the SAD changes in response to disturbance (Matthews et al., 2014).

Human foraging in tropical forest could affect the beta-diversity and SAD patterns of tree communities in various ways. For example, during food (seeds and fruits) gathering, forest dependent communities cover a wider area of the forest as well as higher elevational gradients and in the process, promote the dispersal of edible species (McMichael et al., 2017), which may result in increasing their relative abundance and distribution, shifting the SAD from more uneven shapes (which are common in tropical tree communities; ter Steege et al., 2013) to more even shapes, and lowering the spatial beta-diversity of edible species.

While low-intensity food collection should theoretically leave an imprint on beta diversity and the SAD (Adeyemi, 2016; Socolar et al., 2016; Verberk, 2012), higher-intensity activities, such as harvest of trees for timber, would also be expected to leave an imprint on stem diameter and density distributions of the forest (Adeyemi, 2016). However, high-intensity activities should affect species independently of their foraging value to humans, whereas low-intensity foraging should specifically alter the patterns of edible species. Analysis of forest structure can thus provide complementary insights to help narrow the range of possible causes behind changes in beta diversity or SADs.

The present study analyses a tropical forest elevational gradient and utilizes tree diameter distribution, stem density, beta diversity patterns and SADs to assess how the utilization of tree species by humans for food influences the community composition and structure of food producing (herein ‘edible’) and non-food producing (herein ‘inedible’) tree species in Oban Forest of Cross River State, Nigeria. In turn, this enabled us to assess how low-intensity anthropogenic activities have influenced the ecological dynamics of the forest along an elevational gradient. The following hypothesis were tested:

1. Human movement of propagules along the elevational gradient will lead to more even distribution of abundance of edible species compared to inedible species.
2. Edible and inedible species will exhibit different turnover patterns along the elevational gradient in the forest.
3. Tree species utilization along elevational gradient will have different effects on tree stem density and diameter class distributions of edible and inedible trees.

2.3. MATERIALS AND METHODS

2.3.1. Study location

The study was carried out in an area of tropical rainforest located in Oban Division of Cross River National Park (CRNP), Nigeria (Figure 2.1b). The forest is situated between longitude 8°10´ and 8°55´ East and latitude 5°00´ and 5°50´ North and covers an estimated area of ~251,345 ha (Jimoh et al., 2012; Olajide et al., 2008; Adeyemi, 2016). In the North, South and West, the forest is bounded by a number of forest-dependent and small-holder agricultural communities, and it is continuous with the Korup National Park and Ejagham Forest Reserve of Cameroon in the East (Adeyemi, 2016; Jimoh et al., 2012; Oluwatosin and Jimoh, 2016; Agaldo et al., 2016).

The forest vegetation is lowland and submontane moist tropical rainforest with mean annual precipitation ranging between 3,000 mm and 3,500 mm, mean monthly temperature range of 23 °C to 37 °C, rugged terrain and elevation ranging from ~ 100 m to over 1000 m above mean sea level (Jimoh et al., 2012; Aigbe and Omokhua, 2015; Agaldo et al., 2016). The forest is the last stronghold of pristine tropical forest in Nigeria (Agaldo et al., 2016). The Oban Forest is also part of the "Gulf of Guinea biodiversity hotspots of conservation concerns" in West Africa (Agaldo et al., 2016). It is known to house a large number of endemic flora and fauna species (Oates et al., 2004), including most of the 935 tree species identified in Nigeria (Lock and Keay, 1991), other herbaceous plant species, and a rich diversity of butterflies, birds, reptiles, amphibians, and a wide range of mammal species including ungulates, cats, buffalo, elephants and primates, including the world's rarest lowland gorillas and others plant and animal species (Asuk et al., 2018).

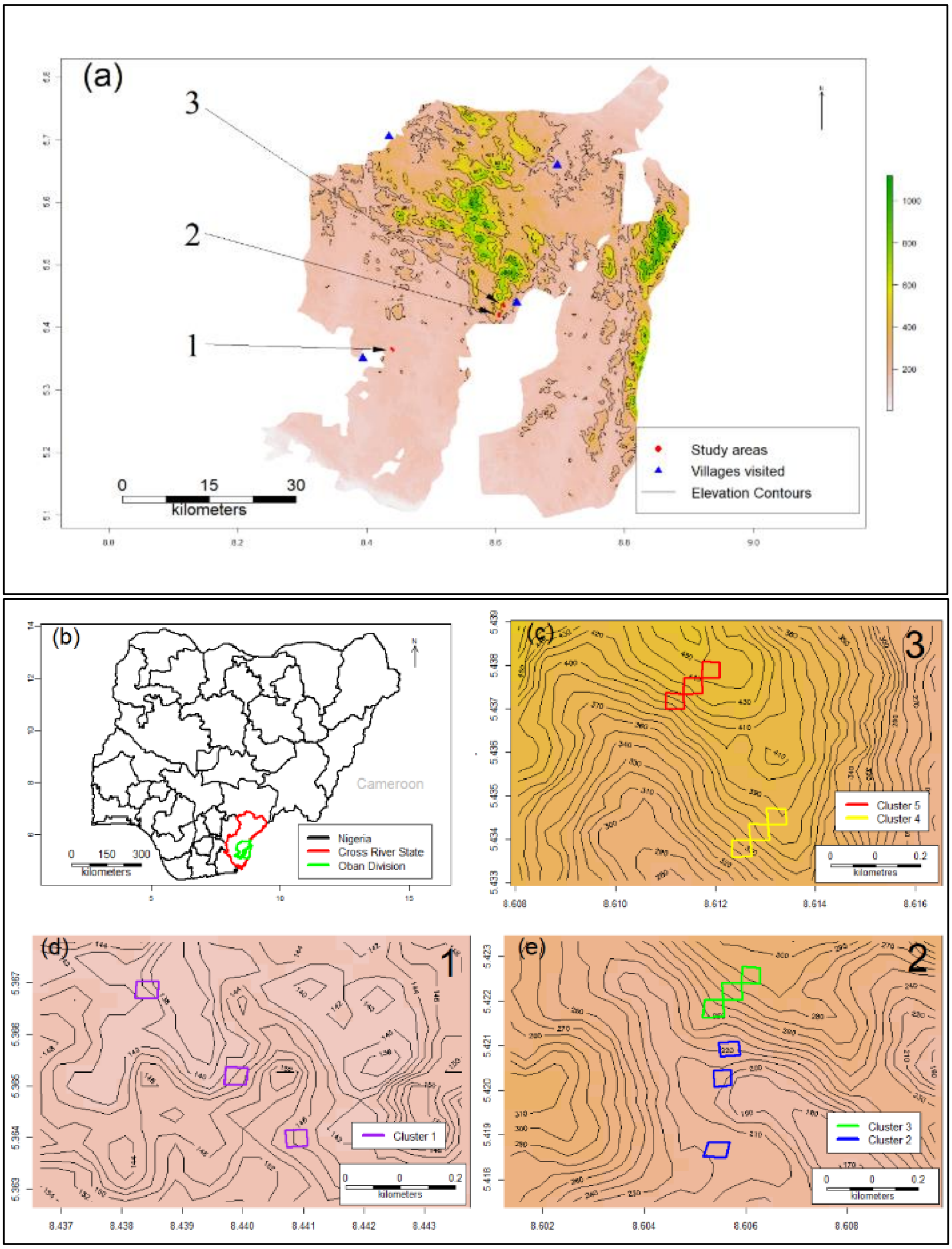


Figure 2.1. Topographic map of Oban Division showing the three areas selected for location of permanent sample plots and forest dependent communities used for the study (a). Map of Nigeria showing the location of Oban Division of Cross River National Park (b). Clusters of plot clusters along elevational band withing the three study areas (c, d, e).

2.3.2. Plot establishment

To assess the impact of elevation on species diversity and the impact of humans along these elevational gradients, plots were established along an elevational gradient rising from about 100 m to 500 m above sea level (Jimoh et al., 2012; Aigbe and Omokhua, 2015; Agaldo et al., 2016). Plot location was also consistent with some additional considerations (see Appendix 2.6.1, section 2.6.1.1 in Appendices from ForestPlots.net (Phillips et al., 2018).

Between 23rd August 2019 and 9th September 2019, along an elevational band of between 100 m and 500 m above sea level, five plot clusters were established in three areas of the forest for the study (see Appendix 2.6.1, Table 2.6.1): one cluster in Erukut, and two clusters in Aking and Osomba each (Figure 1a,c,d,e). Three 40 by 40 m plots with varying elevation were established in each of the clusters, making a total of 15 sample plots (Figure 1c,d,e) with a total area of 2.4 hectares. Due to the steep topography of Aking and Osomba locations, plots were established at closer horizontal intervals based on elevational differences of about 20 m.

2.3.3. Data collection

All trees with a minimum of 10 cm dbh in all 15 plots were measured and tagged with a unique number. The collected data included plot information (plot number and GPS coordinate of the four corners of plots using Garmin eTrex 10 Outdoor Handheld GPS Unit), tree dbh (diameter of a tree at 1.30 m from the base) using a diameter tape and LaserAce 1000 rangefinder for points of measurement too high for a diameter tape, species name, assigned tag number, and species group (edible and inedible species). Measurement of buttress trees, folk trees, leaning trees or trees on a slope was completed using the African Tropical Rainforest Observation Network (AfriTRON) protocol (Phillips et al., 2018). Trees were identified to species level by a field taxonomist and in cases where there was uncertainty in the identification of species, tree locations were noted, and specimens collected and stored in herbarium presses for further taxonomic work.

Information on tree species producing edible fruits, nuts and seeds for humans was collected from four out of 39 forest dependent / support zone communities within the Oban Division of Cross River National Park (Enuoh and Ogogo, 2018; Ewah, 2013) using structured questionnaires (see Appendix 2.6.2 in Supporting Information). Two of the villages, Nsan and Aking were selected based on proximity to the plot while Obutong, and Mkpot were selected to ensure a spread around the National Park. Mixed method interviews (Friant et al., 2019) comprising of group interviews with the council of chiefs, farming / gathering household heads, and individual interviews. The respondents were restricted to those above 25 years of age who had lived in the area long enough to provide information on forest tree species use. The information generated from the interviews was compiled into a comprehensive list and used to categorize tree species into those producing edible products and those which only produce inedible ones (see supplementary information for further details). The study was reviewed and approved by the Humanities and Social Sciences Ethical Review Committee of the University of Birmingham. Consent letters on the collection, use and storage of data by research team, were read to all participants. Only respondent who consented voluntarily participated in the study.

2.3.4. Data processing and analysis

2.3.4.1. Comparing species abundance distributions (SADs) and the evenness of edible and inedible tree species along the elevational gradient

Species abundance distributions were calculated for the different species groups at the community level (i.e., all plots combined) using the ‘sads’ and ‘gambin’ R packages (Prado et al., 2018; Matthews et al., 2020). The histogram form of SAD plotting was used (Matthews and Whittaker, 2014; Connolly and Dornelas, 2011). As an additional SAD test, the gamma-binomial (gambin) model was fitted to the SAD data on a histogram of log-transformed octaves (Matthews and Whittaker, 2014). To create the abundance octaves, $\log_2$ transformation was used to double the abundance class of previous octave (Matthews et al., 2014, 2020). Thus, beginning from 0, each octave had an interval that was twice the preceding one (octave 0 = "1 individual", 1 = "2-3", 2 = "4-7", 3 = "8-15", 4 = "16-31", 5 = "32-63") (Prado et al., 2018; Verberk, 2012; Matthews et al., 2014, 2020). The gambin model is a flexible SAD model with one free parameter (alpha) that provides a metric of SAD shape (Matthews et al., 2014), allowing us to compare the shape of edible and inedible species SADs. 95% confidence intervals around the alpha values were calculated using bootstrapping. As SAD form is known to be affected by sample size, standardized alpha was also calculated by subsampling all samples down to the smallest number of individuals in a plot (Matthews et al., 2014). The number of individuals in the smallest group was randomly sampled from the groups with larger sample size, alpha value calculated and then this process repeated 999 times to generate the mean alpha values and standard deviations (Matthews et al., 2020).

Pielou’s evenness index was used for comparing the evenness between edible and inedible species at the plot level and at the combined (pooled) plot level (Pielou, 1966). Pielou’s evenness index (Eq. 1) was computed using the vegan package in R (Oksanen et al., 2022), and plot level evenness for edible and inedible species were compared using a t-test from the “car” package in R (Fox et al., 2022).

$$J = \frac{H}{log(S)} \qquad \text{Equation 1}$$

Where: J = Pielou's evenness index

H = Shannon's diversity index

S = species richness

2.3.4.2. Beta diversity and spatial species turnover along the elevational gradient

Pairwise beta diversity between all plots along the gradient was calculated using Sorensen's dissimilarity index (β_{sor}). We also analyzed the turnover component of β_{sor}, Simpson's dissimilarity index (β_{sim}), which measures the replacement of species between pairs of plots independently of richness differences (Baselga, 2010; Aspin et al., 2018; Jarzyna and Jetz, 2018). The formulas (Eq. 2 and Eq. 3) for the computed indices are shown below (Baselga, 2010, 2012).

$$\beta_{\mathrm{sor}} = \frac{\mathrm{b+c}}{\mathrm{2a+b+c}} \qquad \text{Equation 2}$$

$$\beta_{\mathrm{sim}} = \frac{\mathrm{min\ (b,c)}}{\mathrm{a+min\ (b,c)}} \qquad \text{Equation 3}$$

Where: a = number of species common to both locations

b = number of species present in the first location but absent in the second location and

c = number of species present in the second site but absent in the first location

The 'betapart' R package was used to calculate the dissimilarity indices using a vector of species incidence (Baselga et al., 2018). The incidence-based pairwise dissimilarities were regressed against elevation using a linear regression model to determine any general trend. Due to the non-independence of the data, Mantel correlation tests were undertaken relating the dissimilarity matrices to a matrix of elevational differences between plots to generate the correlation coefficient (and its significance) and respective confidence intervals, using the ‘ecodist’ package in R (Goslee and Urban, 2017). In addition, to remove any possibility of spatial autocorrelation, a partial Mantel test (Legendre et al., 2015) was conducted using the species dissimilarity metrices, plot elevational matrix and plot distance matrix. This was done using the “vegan” R package (Oksanen et al., 2022). These analyses were undertaken for edible and inedible species separately.

Two null models were run to confirm that the trends in tree beta diversity and turnover with elevation observed in the edible and inedible species category were not due to chance (see details in Appendix 2.6.3). In addition, two sensitivity tests were conducted to check the effect of the ground distance between plots in Erukut and those in Aking and Osomba on the βsor and βsim trends observed in the edible and inedible species categories (see details in Appendix 2.6.3).

2.3.4.3. Stand density, basal area, and diameter size distribution

The dbh of all trees in the study area were transformed using natural logarithms and visualized on a relative density plot using the ggplot2 package in R (Wickham, 2016; RStudio, 2011). Stand density per plot was also computed for each species category. The basal area (BA) and total BA of each measured tree were calculated from their diameter at breast height (Aigbe and Omokhua, 2015; Ojating, 2008).

Linear regression analysis was used to compare the effect of the elevational gradient, and the edible-inedible species category, on tree density (tree per ha) and total basal area (m^2 per ha). Moran’s I test (Moran, 1950) was used to check for spatial autocorrelation in the linear regression residuals. This was done with the ‘DHARMa’ R package (Hartig, 2017). To determine if the slopes and intercepts of the linear regression lines differed between the species categories, for each dependent variable, ANCOVA was used. The ANCOVA models were developed using the “aov” function and type III sums of squares, using the “car” package (Fox et al., 2022) in R (see details in Appendix 2.6.4). R (version 4.0.3) was used for all analyses (RStudio, 2011).

2.4. RESULTS

2.4.1. Summary of site information

We sampled 492 tree stems per hectare, with total basal area density of 34.41 m^2 per hectare across the 15 plots (Table 2.1) (Asuk et al., 2023). The sampled individuals were distributed amongst 144 species in 105 genera and 49 families. Species identified as edible from group interviews with local villagers are shown in the appendix (see Appendix 2.6.5, Table 2.6.5). The total richness in this study was divided into 35 edible species that provided food in the form of fruits and seeds for rural communities and 109 inedible species. Among the edible and inedible categories, 67.35% of families, 75.24% of the genera, 75.69% of the total species richness and 65.15% of the total basal area belonged to the inedible species. The mean BA was higher in edible species (*0.09 (std: 0.37)* m^2) due to the presence of larger stems among the edible species category compared to inedible species. The fifteen most abundant species had a total density of 10 stems per hectare, while the total stem density across all plots was 213 stem/ha. The 15 most abundant species represented 43.29% of the total tree stand, and 23.37% of the total basal area. These prevalent species included 5 edible species making up 26.76% (57 stem/ha) of the stem density and 10 inedible species making up 73.24% (156 stem/ha) stems density.

2.4.2. SADs and evenness of edible and inedible species

2.4.2.1. All plots combined

The SAD of all species combined (Figure 2.2b) showed there were few highly abundant species and a higher proportion of rarer species, with the modal octave containing 2-3 individuals representing the peak of the distribution. The alpha parameter of the gambin model was 3.1 (confidence interval of 2.4-4.4). The alpha parameter of the gambin model was slightly lower for inedible (alpha = 3.1 and confidence interval of 2.2-4.4) compared to edible (4.0 and confidence interval of 2.1-7.1) species. However, the confidence intervals of the two alpha values overlapped. A lower alpha was recorded for inedible category of 1.83 (SD = 0.30 and 95% CI of 1.37-2.41) after standardizing the population of both categories. At this scale, the pooled (all plots combined) evenness index of the edible category was not different from the inedible.

Table 2.1. Summary of total species, tree density per hectare and total basal area in the forest (std = standard deviation)

Variable	Edible	Inedible	Total
Families	16 (32.65%)	33 (67.35%)	49
Genera	26 (24.76%)	79 (75.24%)	105
Total species richness	35 (24.31%)	109 (75.69%)	144
Total stem density (stem/ha)	128 (26.02%)	364 (73.98%)	492
Total Basal Area (m^2/ha)	11.99 (34.85%)	22.42 (65.15%)	34.41
Mean Basal Area (m^2/ha)	*0.59 (std: 0.42)*	*0.39 (std: 0.12)*	
Prevalent species count	5 (33.33%)	10 (66.67%)	15
Prevalent species stem density (stem/ha)	57 (26.76%)	156 (73.24%)	213
Prevalent species basal area (m^2/ha)	2.23 (27.74%)	5.81(72.26%)	8.04

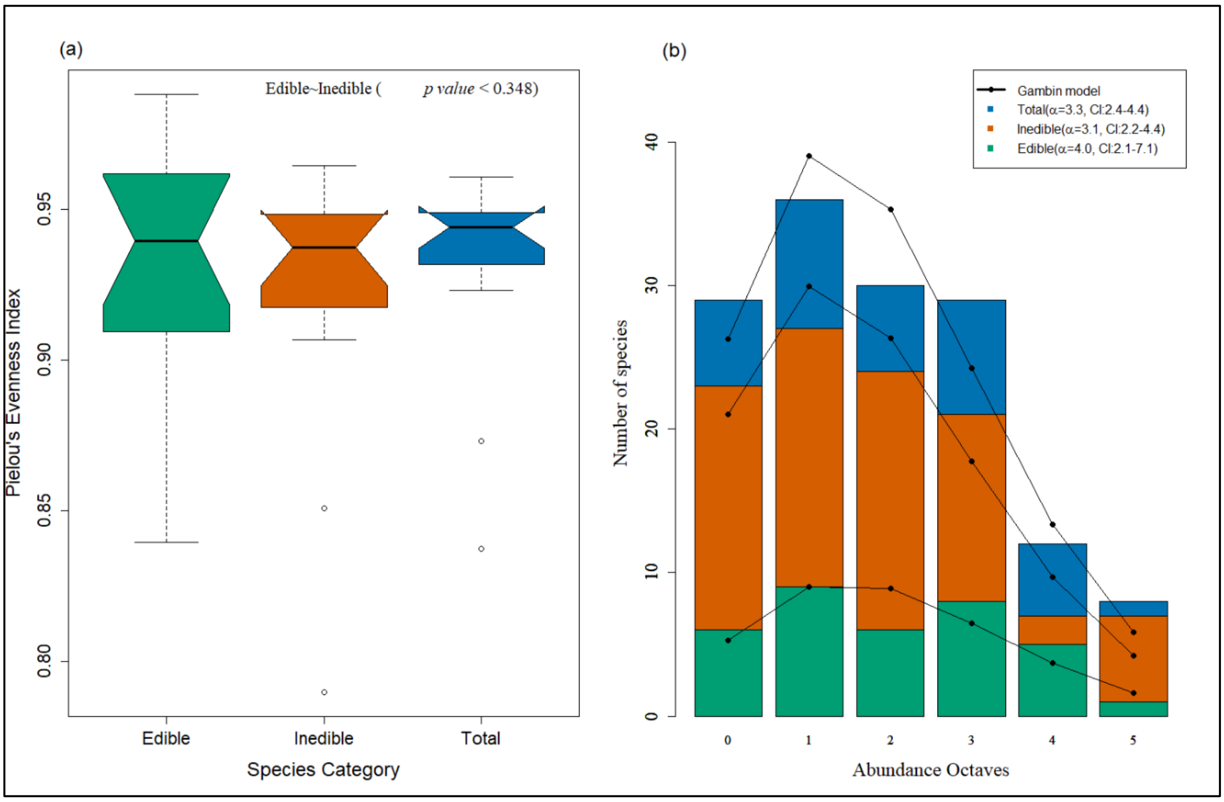


Figure 2.2. (a) Boxplot of plot level Pielou's evenness index for edible, inedible and total species categories (pooled evenness Total = 0.887, Edible = 0.871 and Inedible = 0.869) and (b) a species abundance distribution octave plot with the fit of the gambin model for edible, inedible and all tree species in the forest. (Octaves: 0 = "1 individual", 1 = "2-3", 2 = "4-7", 3 = "8-15", 4 = "16-31", 5 = "32-63"). Note: the brown bars are overlayed on the blue bars while the green bars are overlayed on the brown bars to preserve origin at zero.

2.4.2.2. Individual plots

At the scale of individual plots, Pielou's evenness index (Figure 2a) showed that the edible species had similar (*p value* < 0.348) evenness at the plot level compared to the inedible category. For edible species, evenness ranged from 0.840 to 0.988 while for inedible species it ranged from 0.790 to 0.964.

2.4.3. Beta diversity and the turnover of edible and inedible species along the elevation gradient

2.4.3.1. Relationship between beta diversity and elevation in edible and inedible tree species

Pairwise dissimilarity plots (Figure 3a,d) showed that elevation had a strong positive effect on the differences in composition between plots in the study area when all species were considered together. There was a significant (*p* = 0.001) Mantel correlation value of 0.43 between both total beta diversity (a) and turnover (b) and elevation, indicating that both pairwise total beta-diversity and turnover increased with increasing difference in elevation between plots.

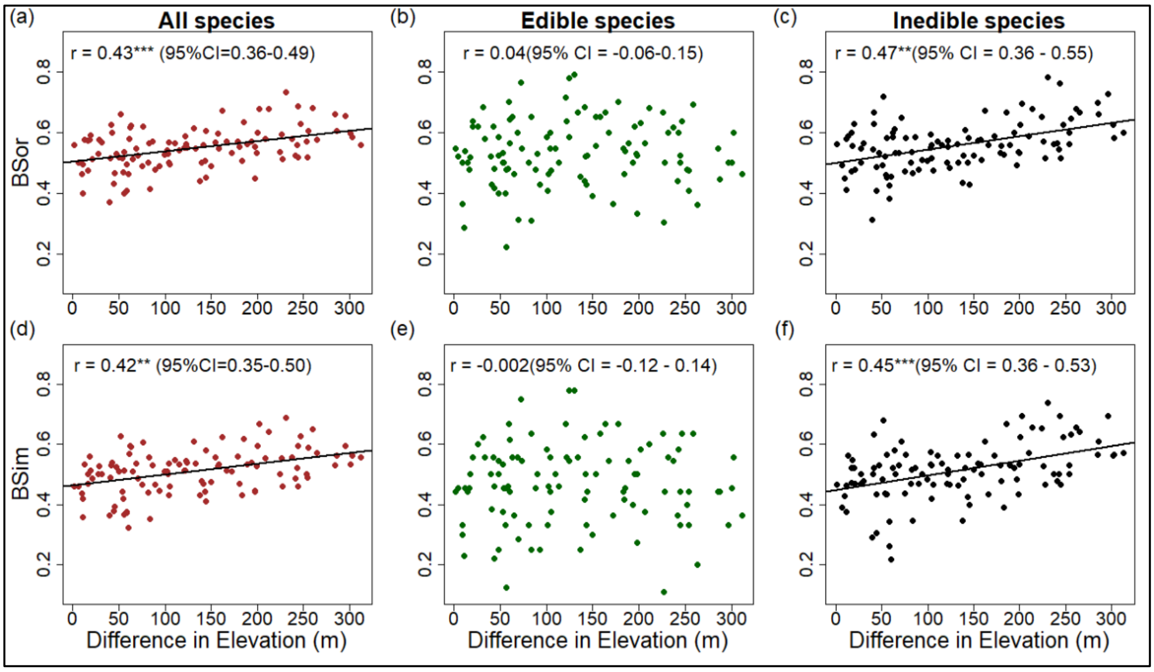


Figure 2.3. Pairwise dissimilarity trend showing the association between both total beta diversity, BSor (a,b,c) and turnover, BSim (d,e,f), and elevation (m) for edible and inedible species in Oban Forest. The r values and confidence intervals (CIs) were generated from Mantel correlation tests. The solid lines show ordinary least squares regression fits, only for significant associations.

Both the pairwise total beta diversity and replacement component for edible species (Figure 2.3b,e) remained constant as the difference in elevation between plots increased. In contrast, inedible species exhibited a significant positive correlation between total beta diversity and the replacement component, and elevation (Figure 2.3c,f). For both the total beta-diversity and turnover plots, the Mantel correlation coefficients for edible and inedible species did not overlap, indicating significant differences in the patterns between the two subsets.

2.4.3.2 Sensitivity test and null model analyses

The sensitivity test to check the effect of the ground distance between plots on the β_{sor} and β_{sim} trends observed (see Appendix 2.6.6, Figure 2.6.1 and 2.6.2), yielded similar trends for both species categories, suggesting that the distance between plots in Erukut from those in Aking and Osomba were not driving the observed patterns. The *p values* from the partial Mantel's test which accounted for spatial autocorrelation in the data yielded similar results as the Mantels test (see Appendix 2.6.6, Table 2.6.6). The fixed-fixed null model analysis (see Appendix 2.6.6, Table 2.6.7) revealed that the Mantel correlations for edible species were not significantly different from observed, but the observed correlations (both β_{sor} and β_{sim}) for the inedible species were significantly higher than expected. The interspecies randomized null model (see Appendix 2.6.6, Table 2.6.6) provided slightly contrasting results. The correlations for the edible species, for both β_{sor} and β_{sim}, were found to be significantly lower than expected, given the null model. Again, the observed correlations for inedible species were higher than expected, although they were not significant.

2.4.4. Effect of tree species utilization on diameter size distribution, tree stem density and BA along the gradient

2.4.4.1. Diameter size distribution

The diameter distribution for all species together, and edible and inedible species separately, all show a reverse J-shaped or negative exponential function characteristic of a natural uneven-aged tropical forest stand (Daniel et al., 2015; Marín et al., 2005), with the number of trees stems decreasing as tree dbh increases (Figure 2.4). The nonlinear relationship between dbh and stem density shown on the curve further indicated that there was regeneration and upgrowth of stems along diameter classes in the forest stand (Daniel et al., 2015; Marín et al., 2005). For lots of the dimeter distribution curves within plots (Figure 2.4b), the edible category (red line) was above the inedible (blue line) around point 4.

2.4.4.2 Tree stand and basal area densities along the elevational gradient

Linear regression models fitted to tree density (tree/hectare) against elevation (m) (Figure 2.5a) indicated a significant relationship only for inedible species. The R^2 value for edible species was 0.02 (intercept = 141.25, slope = -0.05; *p value* = 0.65), while a significant positive association with elevation was observed for inedible species, with an R^2 value of 0.34 (intercept = 283.50, slope = 0.29; *p value* = 0.02). Results from the ANCOVA model (see details in Appendix 2.6.4) with two covariates (species category and elevation) and with tree density as the dependent variable, showed that the slopes of the regression lines differed between the edible-inedible categories (interaction term *F value* = 5.026; *p value* = 0.034). Results from the Moran's I test of spatial autocorrelation for edible and inedible species categories yielded p-values that were greater than 0.05 in all cases, thus indicating that there was no spatial autocorrelation in the residuals (see details in Appendix 2.6.7, Table 2.6.8).

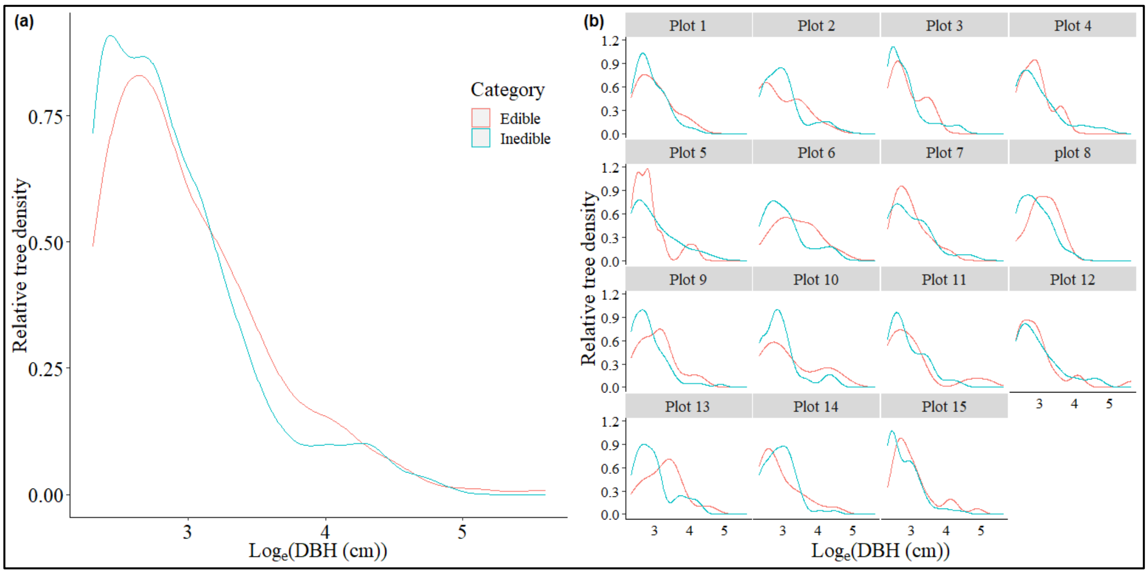


Figure 2.4. Tree diameter size distribution curve showing relative density of tree dbh in Oban Forest. (a) Tree diameter size distribution curve of all measured trees grouped into edible and inedible categories. (b) Tree diameter size distribution curve of trees measured in each plot categorized into edible and inedible.

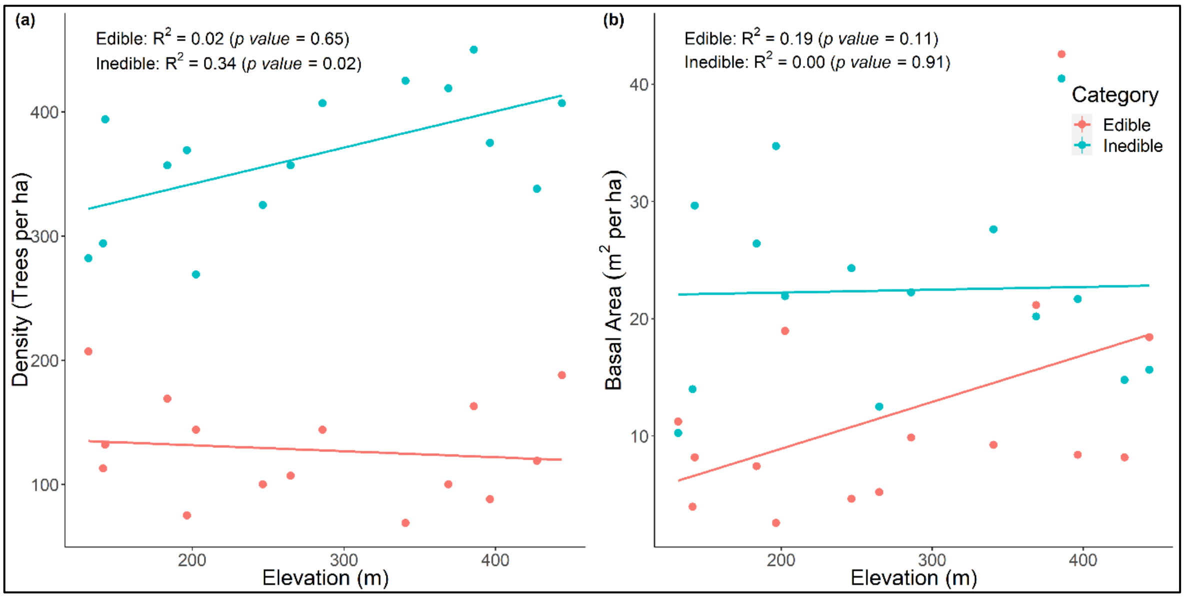


Figure 2.5. Trend in stem density (a) and total basal area per hectare (b) per plot with increasing elevation for edible and inedible species were greater than 0.05 in all cases, thus indicating that there was no spatial autocorrelation in the residuals (see details in appendix 2.6.7, Table 2.6.8).

No significant relationships were recorded between total BA and elevation (Figure 5b) for either category. ANCOVA with species category and elevation as covariates, and total basal area as the dependent variable (see Appendix 2.6.4), showed that the slopes of the regression lines for both categories were not significantly different from each other (interaction term *F value* = 1.421; *p value* = 0.244). Moran's I test yielded a non-significant *p-value*, indicating that there was no spatial autocorrelation in the model's residuals (Appendix 2.6.7, Table 2.6.8).

2.5 DISCUSSIONS

2.5.1. Potential effect of human activities along the elevational gradient on SADs and species evenness

The SAD plots (Figure 2.2) for the total community indicate that the sampled area of the forest exhibited a log-left skewed lognormal distribution type SAD, a pattern commonly observed in tropical forests (Song et al., 2020). Pooled species richness was lower for edible species and higher for inedible species while the Pielou’s evenness index was similar for both categories at pooled and plot levels. However, at the plot level, edible tree species recorded the highest evenness while inedible species recorded the lowest.

Despite the difference in species richness and stand density between both categories, the high evenness in edible category at plot and pooled levels might be due to sample size effects (Mackey and Currie, 2001) or linked to historical impacts of human influence on the abundance of species along the elevational gradient (Wilsey and Potvin, 2000) through tree management, deliberate planting, and conservation for food production (see Section 2.4.3). Conservation efforts have concentrated on the present species richness of the forest but previous an assessment of species abundances shows how the forest species composition and abundance has modified over time (Ellis et al., 2021, 2010; Wilsey and Potvin, 2000). This is further evident in the beta diversity results whereby inedible species exhibited more turnover than edible species.

2.5.2. Difference in beta diversity and turnover in edible and inedible species along the elevational gradient

Elevation is an important variable that affects the distribution of trees in tropical rainforests (Lan et al., 2011). The pairwise beta diversity trends observed here showed that there was a positive association between beta diversity and differences in elevation. The beta diversity and turnover trends of inedible species were similar to that for all species combined. In contrast, the beta diversity of edible species exhibited no trend with elevation (Figure 2.3).

In the absence of human influence, we may expect the constant turnover of species along the elevational gradient due to niche filtering (i.e. the changing of abiotic conditions with increasing elevation) and/or dispersal limitation (Peters et al., 2019). This will result in increased pairwise spatial beta-diversity between plots with increasing elevational distance, which is the pattern observed for inedible species. However, edible species did not exhibit a significant relationship between elevation and pairwise composition. This could be due to tree propagules being spread by humans along the gradient (both purposefully and indirectly), resulting in the spatial homogenization of community composition. However, for the spreading of seeds by humans to have this effect it must mean that i) niche filtering is not a dominant assembly mechanism and instead dispersal limitation is driving tree distributions in this forest (Hubbell, 2001), ii) human-aided dispersal is occurring at such a rate that mass effects (Shmida and Wilson, 1985) are overriding any niche filters, or iii) a combination of the two. Further research is needed to fully explore these different possibilities.

2.5.3. Trends in dbh distribution, tree species density and BA along elevational gradient in the forest

The dbh, BA and stem density distribution shown by certain species categories can indicate the type of human footprint in the forest (de Quesada and Kuuluvainen, 2020). Humans tend to favor propagation and conservation of certain tree species based on their utilization value. Thus, the dbh distribution of edible tree differed from that of inedible trees species (Marín et al., 2005). The interventions of humans include selective conservation, enrichment planting and seed dispersal of desired species, while undesirable species may be harvested.

There was consistency of red line (edible) above blue line (inedible) around point 4 (Figure 2.4), which could be suggestive of a period of disturbance (mortality, gap in the forest that favor height growth or slowed diameter growth) in the inedible category not observed in the edible species category (Aigbe and Omokhua, 2015). However, the variability observed in individual plots of tree dbh also suggests that other variables maybe important. The diameter distribution of trees species can be affected by the mortality patterns in the forest (de Quesada and Kuuluvainen, 2020) or the distribution of species abundance. A study in an old growth forest in Costa Rica, revealed that basal area and density of large trees is expected to increase with elevation (Muñoz Mazón et al., 2020). Even though inedible species had three times the species diversity, three times the stand density of edible species, they only had twice the total BA and a lower mean BA than edible species (see Table 2.1).

The level of impact that foraging by local communities has on forests is likely to be linked to accessibility in some way, although this is not necessarily a simple function of elevation given the activity is low intensity and does not require heavy machinery, and thus foragers have the capacity to cover a wider spatial range and along varying elevational gradients (Jimoh et al., 2012). For example, the villagers interviewed stated that they often foraged in the higher elevations of our gradient. However, there are additional human activities that may be more impactful at different parts of the elevation gradient, which may then influence species composition and distribution across the gradient (Socolar et al., 2016), although these should impact edible and inedible species equally. For instance, logging activities might be limited to more accessible areas at relatively low elevation.

Socolar et al. (Socolar et al., 2016) stated that human activities, taxa, and geographical location can determine the impact pattern on tree species composition and diversity. In a forest area, like the study location used here, with rough terrain, increasing elevational gradient, inaccessible roads, and reasonable distance away from human habitation, forest harvest for timber and/or farming at higher elevation might be difficult (Adeyemi, 2016; Jimoh et al., 2012; Aigbe and Omokhua, 2015; Olajide et al., 2008; Otu et al., 2012). Therefore, while some activities that occurred in the past may have been limited to the lower elevations or unevenly distributed along varying elevations, these activities such as harvesting of timber, farming, nomadic nature of some indigenous settlements, foraging and others could have affected the distribution of tree stand density along the elevational gradient (Adnan et al., 2015; Aigbe and Omokhua, 2015; Jimoh et al., 2012; Asuk et al., 2021). In addition, conservation efforts by indigenous people would favor trees utilized for their seeds, fruits, and others more than those not used for food (Asuk et al., 2021). This would result in trees with food value having bigger girth with greater mean BA per hectare (see Table 2.1) and a more even distribution of stand density with elevation compared to species that may likely have been harvested prior to the creation of the National Park. Furthermore, as humans forage along the elevational gradient, they may be more likely to propagate seeds of desirable tree species at lower elevations in a bid to reduce their foraging distances. Although it is not possible to make a definitive attribution, the difference in BA and stand density trends observed in edible and inedible species for the study area (Figure 2.5) are therefore consistent with the expected impacts of human intervention.

However, it is worth highlighting that, alternative explanations may also explain the observed patterns, or may be acting in tandem with the effects of human foraging (Adnan et al., 2015; Brockerhoff et al., 2017). First, edible, and inedible species may have different trait values, especially if traits are linked with edibility (e.g., traits related with tissue density) (Lueder et al., 2022; Waddell et al., 2020). If edibility-related traits also affect dispersal ability or the ability of species to cope with the abiotic environment (as in tissue density traits), then the edible-inedible comparison may not reflect the effect of humans but that of trait–environment interactions. Similarly, edible species might be functionally similar due to phylogenetic similarities, which are not accounted for in this study. Second, while we classified species as edible based on interviews with local villagers, we cannot discount the role of other animal taxa in dispersing the edible species (Teitelbaum and Mueller, 2019). As data on species traits and interaction networks in the study area are not available, we recommend conducting further study involving abiotic factors and functional traits to validate these findings (Waddell et al., 2020; Lueder et al., 2022).

2.5.4. Implications and additional considerations

The disparity in the trends observed in edible and inedible species could be due to selective dispersal of propagule during foraging, deliberate conservation, and management of desired species by humans for food production. These low-impact activities are theorized to potentially modify the forest species composition overtime leaving observable footprints. Furthermore, large scale disturbance of the forest due to timber harvesting, clear cutting for agriculture, or agroforestry practices are some other factors capable of modifying the forest. These human interactions, that potentially modified the forest prior to the creation of the National Park, might have left some footprints which are still visible in the dbh abundance-size distribution. Even though the forest is now protected, low intensity activities of human may continue to modify the species composition and structure of the forest. This supports the findings of (Aigbe and Omokhua, 2015) (2015) who pointed out that the species composition of the Oban Forest might be recovering from past disturbances from tree mortality which occurred prior to acquiring the National Park status. Notwithstanding the data indicating human impact, Adeyemi (2016) was of the opinion that the hilly terrain, poor road network and large water bodies adjoining the forest may have assisted in reducing pressure on the forest from certain human activities such as logging, thus preserving the current species diversity of the forest. But as pointed out by Levis et al. (2017), some activities such as food gathering encourages forest dependent communities to cover wider ranges thus promoting dispersal of edible species.

The results of this study, along with information of past disturbances that may have occurred in the forest (Adeyemi, 2016; Jimoh et al., 2012; Aigbe and Omokhua, 2015; Olajide et al., 2008; Otu et al., 2012; Agaldo et al., 2016), suggest that low-intensity human activities have influenced the forest species distribution and structure. Earlier research has shown that more than 50 % of the global tropical broadleaf forest show evidence of similar low intensity human impact (Ellis et al., 2010, 2021). Studies in the Amazon forests (Clement et al., 2015; Bush and Flenley, 2007; Piperno et al., 2015) also indicate that low-intensity human activity has modified the forest. Furthermore, studies have shown that indigenous human societies have historically modified the structure and composition of terrestrial biosphere dating back 12,000 years and 75 to 95% of these areas might now be in seminatural states (Helmus, Mahler and Losos, 2014; Williams et al., 2020; Ellis et al., 2021). Much focus has rather been placed on high intensity activities such as logging and it has been shown that many forests are not natural due to human farming, and nomadic settlements in the past. But our result show that even very low intensity foraging, which is not visible from remote sensing and field inventories is also possibly changing forest dynamics, which throws into question whether any forest can be classified as "natural".

As a single case study, care is needed in extending these findings elsewhere and further work at a broader scale will be needed to assess whether these patterns and interpretations hold true more widely across the continent and indeed tropical forests as a whole. In our opinion, the results presented indicate a role of human foraging on the distribution and structure of edible tree species.

2.6. APPENDICES

Appendix 2.6.1. Summary of plot information and location criteria

Table 2.6.1. Mean plot elevation, cumulative plot distances, and clusters located in the three study areas. A total of 15 plots were established within five clusters in three areas (Erukut, Aking and Osomba). Erukut had one cluster with three plots, Aking and Osomba had two clusters with three plots each respectively.

Area	Cluster number	Plot ID	Mean plot elevation	Cumulative plot distance
Erukut	1	L1P1	131.69	0
Erukut	1	L1P2	142.77	246.11
Erukut	1	L1P3	141.34	421.27
Aking	2	L2P1	196.59	19623.46
Aking	2	L2P2	183.65	19801.55
Aking	2	L2P3	202.59	19875.58
Aking	3	L3P1	246.60	19981.15
Aking	3	L3P2	265.00	20046.95
Aking	3	L3P3	286.05	20118.13
Osomba	4	L4P1	385.78	21531.38
Osomba	4	L4P2	368.95	21587.33
Osomba	4	L4P3	340.67	21695.87
Osomba	5	L5P1	443.86	22072.59
Osomba	5	L5P2	427.45	22146.89
Osomba	5	L5P3	396.45	22202.86

Appendix 2.6.1.1. Additional consideration for plot location

Additional consideration for plot location based on ForestPlots.net (Phillips et al., 2018) included:

1. Adequately accessible to facilitate repeated surveys. Due to the rugged terrain of the Oban Forest landscape (Jimoh et al., 2012; Aigbe and Omokhua, 2015; Agaldo et al., 2016), the plots were located in areas of the forest that were between a 15 - 80 minutes' walk from access roads.
2. Long-term security from deforestation and other anthropogenic activities except the collection or gathering of non-timber forest products for food. The plots are situated in the forest of CRNP which was created from existing forest reserves in 1991 (Nigerian National Park Service, 2019). Each month a team consisting of six CRNP and one Wildlife Conservation Society (WCS) staff patrol different areas of the park to ensure the protection of flora and fauna of the forest (Nigerian National Park Service, 2019).
3. Presence of long-term institutional support through a collaborative effort between the National Park Service and WCS for the sustained conservation of the National Park (Nigerian National Park Service, 2019).

Appendix 2.6.2. Qualitative data collection and structured questionnaire used for collection of data on forest tree species utilization in Oban Division, Cross River National Park

Ten percent of the 39 forest-dependent enclave/buffer zone communities in the study area were purposively selected for the study. Structured questionnaire (see below) was utilized to collect data on current utilization of forest tree species for food. Mixed method interviews (Friant et al., 2019) were used to purposively administer the questionnaires to respondents based on the following criteria:

1. Individuals involved in the gathering of fruit/seeds/nuts and farmers
2. Individuals who are at least 30 years and likely to be knowledgeable about forest tree species utilization in the area
3. Individuals who had lived in the area for at least 15 years to give valid information on the study
4. The council of chiefs were interviewed as a group.

The respondents included individuals of all gender and was dependent on the number of individuals who met the criteria above.

QUESTIONNAIRE USED FOR THE STUDY

Community Code: _______ Date of interview_________ Interviewers Name: ___________

DEMOGRAPHIC DATA

Q1. Type of interview

Individual [ ] Group [ ] Number of Respondent in Group: ________

Q2. Age group?

25-34 [ ] 35-44 [ ] Above 45 [ ]

TREE SPECIES UTILIZATION

Q3. What forest tree species and parts are utilized for food in your community?

Species name		Species part utilized for food				
	Fruit	Seed	Nut	Leaf	Flower	Others (specify)

Appendix 2.6.3. Null model Analysis and sensitivity test

Appendix 2.6.3.1 Null model analysis

Two null models were run to confirm that the trends in tree beta diversity and turnover with elevation observed in the edible and inedible species category were not due to chance: a fixed-fixed model and an edible species classification randomization model. We used a fixed-fixed model (quasiswap) which keeps the row and column totals (site richness and species incidence) in a presence-absence matrix constant while randomising which species are found in each plot (Ulrich and Gotelli, 2013, 2010; Ulrich et al., 2007). A null presence-absence matrix was simulated, and the above analyses undertaken using these null data; the process was then repeated 999 times. We then compared the observed ordinary least square regression and Mantel correlation values with the random ones derived from the null models. This was done for β_{sor} and β_{sim} in both the edible and inedible species categories.

A second null model was used to assess similarity in classified species communities relative to randomly assembled species classification in the regional species pool. This was generated by keeping the total number of edible and inedible species found in the regional species pool constant, but randomising which species were classified as edible and inedible. Again, 999 null communities were generated, and the total beta-diversity and species turnover analyses were repeated using these null communities.

Appendix 2.6.3.2. Sensitivity analysis

Two sensitivity tests were conducted to check the effect of the ground distance between plots in Erukut and those in Aking and Osomba on the β_{sor} and β_{sim} trends observed in the edible and inedible species categories. The elevational component of the pairwise dissimilarity index and turnover was replaced with the ground distance of plots from access roads, and the distance between plots. This was done to confirm if the beta diversity and species turnover trends observed could be attributed to elevation and not other factors such as distance of plots from each other or from nearest human settlement. Due to the distance between location "1" and the two other locations (2 and 3) (see Figure 1) and to correct distance outliers, the three plots in location "1" were omitted from the second sensitivity test (involving the distance between plots), leaving twelve plots in total.

Appendix 2.6.4. Analysis of covariance (ANCOVA) model

The first model assessed the effect of elevation on the dependent variables (species density and total basal area per ha) while controlling the effect of species categories (edible and inedible) without accounting for interactions. The second model assessed the effect of elevation on the dependent variables (species density, and total basal area per ha) while controlling the effect of species categories (edible and inedible) and the interactions between the covariates (elevation and species categories). Model one and model two were then compared to determine if the interactions between covariates significantly affected the results. Significant result from the comparison indicates that model two (with covariate interactions) was used for the analysis while not significant results mean model one will be used (see supporting documents).

Appendix 2.6.4.1. Tree density

Table 2.6.2. Results from ANCOVA with density (trees per ha) as dependent variable and elevation and tree category as covariates.

Elements	Sum Square	Df	*F – value*	*P - value*
Intercept	38146	1	19.630	0.000 ***
Elevation	393	1	0.202	0.657
Category	19344	1	9.954	0.004**
Elevation:Category	9766	1	5.026	0.034 *
Residuals	50526	26		

From the ANCOVA results (Table 2.6.2), the covariate, species category was significantly related to density (trees per hectare) (F(1,26) = 9.954, $p < 0.01$). There was no significant effect of elevation (m) on density (trees per hectare) after controlling for the effect of species category (F(1,26) = 0.202, p = 0.657). There was also a significant interaction effect between elevation and species category on tree density (F(1,26) = 5.026, p = 0.034). Thus, density of trees in inedible category are more likely to increase along elevational gradient than in edible species.

Appendix 2.6.4.2. Basal Area

Table 2.6.3. Results from ANCOVA with Total BA (m^2 per ha) as dependent variable and elevation and tree category as covariates.

Elements	Sum Square	Df	*F – value*	*P - value*
Intercept	127.28	1	1.500	0.231
Elevation	150.81	1	1.778	0.194
Category	814.82	1	9.605	0.004 **
Residuals	2290.45	27		

Table 2.6.4. Results from ANCOVA with Total BA (m^2 per ha) as dependent variable and elevation and tree category as covariates with interaction.

Elements	Sum Square	Df	*F – value*	*P - value*
Intercept	1.62	1	0.019	0.890
Elevation	268.55	1	3.215	0.085
Category	414.86	1	4.967	0.035*
Elevation:Category	118.70	1	1.421	0.244
Residuals	2171.75	26		

From Table 2.6.4, species category, significantly effect on Total BA (F(1, 27)= 9.605, p = 0.004). There was no significant effect of elevation on Total BA after controlling the effect of species category (F(1, 27) = 1.778, p = 0.194). The results showed that the regression slope for both categories was not significant.

Appendix 2.6.5. List of species categorized as edible based on utilization of seeds, nuts, and fruits for food

Table 2.6.5. Tree species categorized into edible and inedible species from focused group discussion with local communities

	Family	Genus	Species
1	Anisophylleaceae	Poga	Poga oleosa
2	Annonaceae	Xylopia	Xylopia aethiopica
3	Annonaceae	Xylopia	Xylopia quintasii
4	Burseraceae	Canarium	Canarium schweinfurthii
5	Burseraceae	Dacryoides	Dacryoides edulis
6	Clusiaceae	Allanblackia	Allanblackia floribunda
7	Fabaceae	Angylocalyx	Angylocalyx oligophyllus
8	Fabaceae	Brachystegia	Brachystegia eurycoma
9	Fabaceae	Dialium	Dialium guineense
10	Fabaceae	Parkia	Parkia bicolor
11	Fabaceae	Pentaclethra	Pentaclethra macrophylla
12	Fabaceae	Tetrapleura	Tetrapleura tetraptera
13	Fabaceae	Treculia	Treculia africana
14	Guttiferae	Garcinia	Garcinia mannii
15	Irvingiaceae	Irvingia	Irvingia gabonensis
16	Lamiaceae	Vitex	Vitex doniana
17	Malvaceae	Cola	Cola digitata
18	Malvaceae	Cola	Cola hispida
19	Malvaceae	Cola	Cola lepidota
20	Malvaceae	Cola	Cola rostrata

Table 2.6.5 (cont.). Tree species categorized into edible and inedible species from focused group discussion with local communities

	Family	Genus	Species
21	Malvaceae	Cola	Cola verticillata
22	Myristicaceae	Pycnanthus	Pycnanthus angolensis
23	Olacaceae	Caula	Caula edulis
24	Olacaceae	Olax	Olax subscorpioidea
25	Phyllanthaceae	Maesobotrya	Maesobotrya barteri
26	Phyllanthaceae	Maesobotrya	Maesobotrya dusenii
27	Phyllanthaceae	Uapaca	Uapaca heudelotii
28	Phyllanthaceae	Uapaca	Uapaca staudtii
29	Polygalaceae	Carpolobia	Carpolobia alba
30	Rutaceae	Zanthoxylum	Zanthoxylum zanthoxyloides
31	Sapindaceae	Blighia	Blighia sapida
32	Sapotaceae	Baillonella	Baillonella toxisperma
33	Sapotaceae	Chrysophyllum	Chrysophyllum albidum
34	Sapotaceae	Chrysophyllum	Chrysophyllum dumbeya
35	Sapotaceae	Chrysophyllum	Chrysophyllum welwitschii

Appendix 2.6.6. Sensitivity tests and null model analysis to support the effect of human foraging along elevational gradient of beta diversity

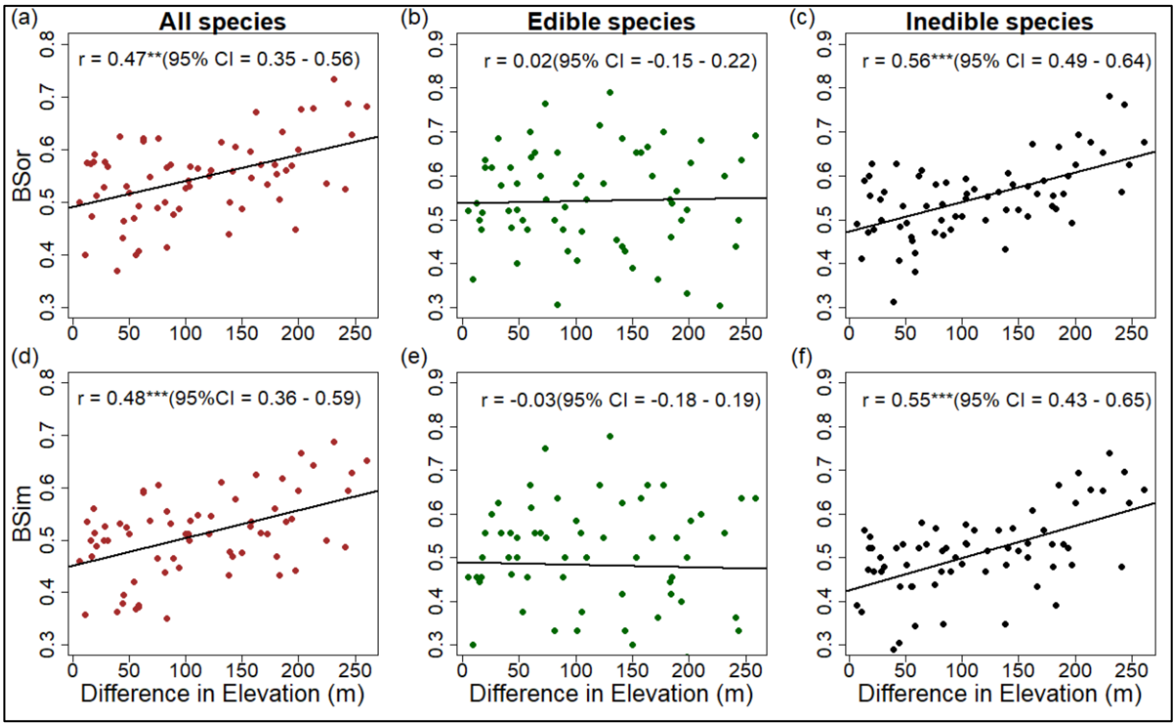


Figure 2.6.1. Pairwise dissimilarity trend showing total beta diversity (a,b c) and turnover (d,e,f) with elevation (m) for edible and inedible species in Oban Forest. Three plots that were furthest away were excluded from this analysis. The r values and confidence intervals (CIs) were generated from Mantel correlation tests. The line shows an ordinary least squares regression for BSor and for BSim for all labelled categories.

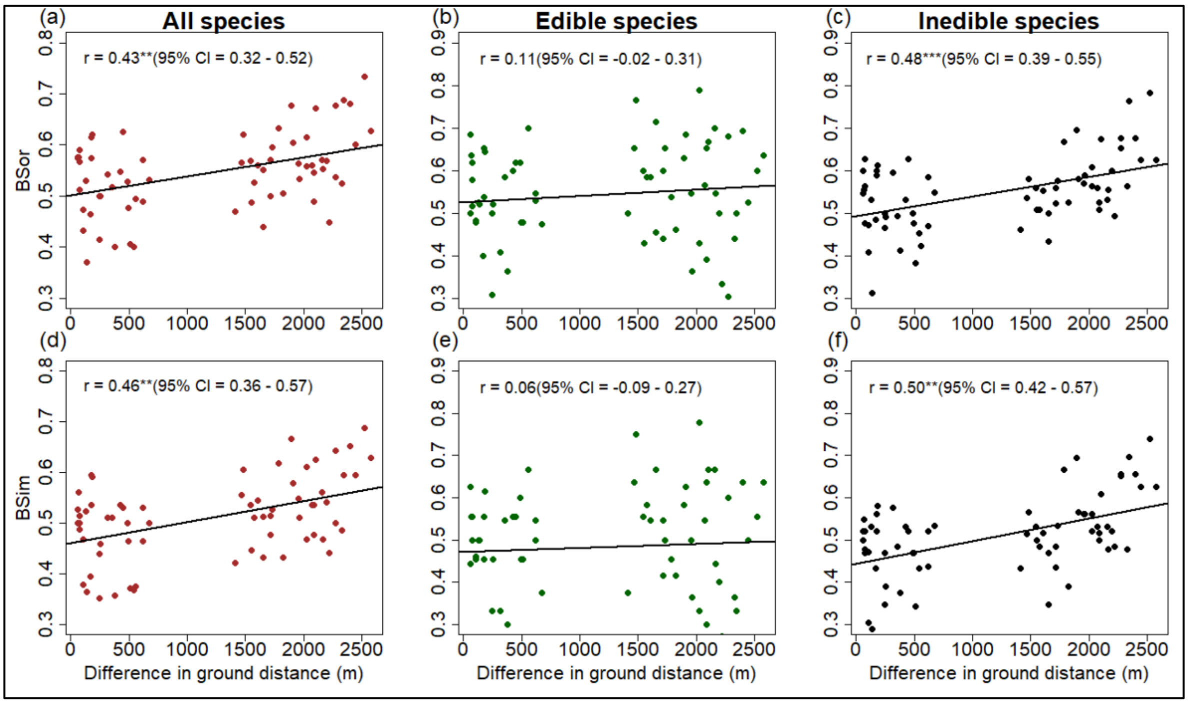


Figure 2.6.2. Pairwise dissimilarity trend showing total beta diversity (a,b c) and turnover (d,e,f) with distance (m) for edible and inedible species in Oban Forest. The r values and confidence intervals (CIs) were generated from Mantel correlation tests. The line shows an ordinary least squares regression for BSor and for BSim for all labelled categories.

Table 2.6.6. Results from partial Mantel's test accounting for partial autocorrelation

Category	Index	Partial Mantel r	*P-value*
All species	βsor	0.423	0.002**
All species	βsim	0.430	0.001***
Edible	βsor	0.086	0.199^{ns}
Edible	βsim	0.043	0.301^{ns}
Inedible	βsor	0.442	0.001***
Inedible	βsim	0.446	0.001***

Table 2.6.7. Two null model analyses of pairwise beta diversity dissimilarity and species turnover in edible and inedible species (β_{sor} = Sorensen's dissimilarity index, β_{sim} = Simpson's dissimilarity index (turnover), SES = standardized size effect, r = mantel correlation, ^{ns} = not significant at 5% probability level, *** = significant at 5% and 1% probability level, ** = significant at 5% and 1% probability level, ** = significant at 5% probability level)

Category	Index	Observed		Null model analysis		
		r (confidence interval)	*P-value*	Mean	SES	*P-value*
Null model one: Fixed-fixed null model						
Edible	βsor	0.04(-0.06-0.15)	0.321^{ns}	0.02	0.21	0.77^{ns}
	βsim	-0.00(-0.12-0.14)	0.50^{ns}	-0.03	0.20	0.80^{ns}
Inedible	βsor	0.47(0.36-0.55)	0.001***	0.01	4.82	0.001^{***}
	βsim	0.45(0.36-0.53)	0.001***	-0.00	4.85	0.001^{***}
Null model two: Interspecies randomized null model						
Edible	βsor	0.04(-0.06-0.15)	0.32^{ns}	0.26	-2.22	0.029^{*}
	βsim	-0.00(-0.12-0.14)	0.50^{ns}	0.26	-2.84	0.004^{**}
Inedible	βsor	0.47(0.36-0.55)	0.001***	0.35	1.90	0.06^{ns}
	βsim	0.45(0.36-0.53)	0.001***	0.35	1.90	0.13^{ns}

Appendix 2.6.7. Testing for spatial autocorrelation

Table 2.6.8. Results from Moran's I test (Moran, 1950; Legendre et al., 2015) *of spatial autocorrelation using residuals from linear regression model of tree density and elevation, and basal area (BA) and elevation. Moran's I test of spatial autocorrelation was done for edible and inedible tree species categories* (Hartig, 2017). *The P-value was greater than 0.05 for all cases thus, the null hypothesis, H0: there is no spatial autocorrelation (Moran's I = 0), was accepted.*

Category	Regression Model	Observed	Expected	sd	*P-value*
Edible	Density ~ elevation	-0.195193	-0.071429	0.179354	0.4902
Inedible	Density ~ elevation	-0.045619	-0.071429	0.181751	0.8871
Edible	BA ~ elevation	0.078606	-0.071429	0.174006	0.3886
Inedible	BA ~ elevation	-0.107592	-0.071429	0.179729	0.8405

Appendix 2.6.8. Data and R code availability

Plot data that supports the findings of this study, list of tree species categorized into edible and inedible species, R codes used for the data analysis and generating presented results and metadata containing description of files and columns are available on DRYAD via the link https://datadryad.org/stash/share/1Y6cJQLWgMaaK1Fiy_doMYtwtJ7ljxskGuOPRvOWWpg. The file Asuk_et_al_raw_plot_data.csv contains plot data for the tree species inventory. Asuk_et_al_dbh_size_distribution.csv contains data on diameter at breast height (DBH) in cm, basal area (square meters), plot number (from 1 to 15) and species category (species). Asuk_et_al_plot_data_summary.csv contains summarized plot data, and Asuk_et_al_Biotropica.R is the R code for generating the results presented in the manuscript.

CHAPTER THREE: HUMAN FORAGING AFFECTS REGIONAL SCALE TREE SPECIES BIODIVERSITY PATTERNS IN TROPICAL WESTERN AFRICA

3.1. ABSTRACT

Anthropogenic activities are altering forest biodiversity and functions at local, regional, and global scales. However, the effects of low-intensity human activities on tropical forest ecosystems are not well understood. In this study, we examined the impact of human presence on the beta diversity of forest trees in the Nigeria-Cameroon forest region, focusing on the differences between edible and inedible species. We used tree data from five plots in Nigeria and 61 plots in Nigeria and Cameroon, collected between 2002 and 2019. We applied Generalized Dissimilarity Models (GDMs) to evaluate the pairwise beta diversity between plots and the role of selected environmental variables in explaining variation in beta-diversity, including the distance of plots to human presence, plot elevation, and stem density. Our analysis showed that human influence was a significant driver of beta diversity in the Nigeria-Cameroon forest region. The turnover component of total beta diversity accounted for most of the tree species dissimilarity. The variables important in driving total beta diversity included geographical distance, plot elevation, stem density, the distance of plots to human presence, and forest species composition. We also found that forest composition was driving the dissimilarity of total beta diversity of edible tree species, which was not seen in inedible species. Stem density was an important variable in the edible tree species models, but not the inedible species models. In contrast, the effect of elevation was significant in the inedible species models but absent in the edible species models. Our findings suggest that human influence is an important driver of beta diversity in the Nigeria-Cameroon forest region. The results highlight the importance of human presence in shaping tree species assemblages in African tropical forests.

3.2. INTRODUCTION

Forest biodiversity and the functions it provides are rapidly changing at local, regional, and global scales due to large-scale habitat loss and modification from anthropogenic activities (Bush et al., 2015; Clement et al., 2015; Helmus et al., 2014; Jarzyna and Jetz, 2018; McMichael et al., 2017; Piperno et al., 2015; Stahl, 2015; Steadman, 1993). Anthropogenic activities such as selective harvesting, illegal logging, clear-cutting for agricultural purposes, foraging of fruit/seed for food, and conservation modify the species composition and distribution of species within the forest (Asuk et al., 2022; Benchimol and Peres, 2013; Elo et al., 2018). However, the impact of anthropogenic activities varies depending on the type, intensity and duration of the activity, the type of species, and the use of species for food, timber, medicine, and others (Adeyemi, 2016; Adnan et al., 2015; Aigbe and Omokhua, 2015; Asuk et al., 2023; Jimoh et al., 2012). For instance, forests subjected to clearcutting prior to the attainment of a “protected” or “reserve” status might be at different stages of regeneration and dominated by fast-growing pioneers (Aigbe and Omokhua, 2015). Also, as nomadic forest human communities migrate from place to place, there is often some level of deliberate planting of preferred tree species, thus affecting the species composition of the forest (Adnan et al., 2015; Aigbe and Omokhua, 2015; Jimoh et al., 2012; McMichael et al., 2017).

Studies of the effects of anthropogenic activities on forest biodiversity have focused primarily on the high intensity impacts, such as deforestation, fragmentation, and degradation (Alahuhta et al., 2017; Donoso et al., 2017; Gallardo-Cruz et al., 2009; García-Navas et al., 2020; Swenson et al., 2011). Growing evidence suggests that low intensity human activities such as foraging for food, selective species conservation, dispersal of seeds of desirable species (e.g., species with fruits eaten by humans) and enrichment planting may be modifying forest ecosystems more than previously thought, and thus potentially affecting the form of different ecological and macroecological patterns (Asuk et al., 2023; Chaturvedi et al., 2017; McMichael et al., 2017; Piperno et al., 2015; Singh et al., 2022). For example, the modern floristic composition and structure of some areas of natural forests in Amazonia have been linked to past low-intensity human activities (e.g., plant cultivation, seed dispersal and propagation, and incidental domestication) (McMichael et al., 2017). However, the general effects of low intensity anthropogenic impacts on spatial ecological patterns in tropical forests are not well understood (Jarzyna and Jetz, 2018; Anderson et al., 2011), likely due to the difficulty in measurement and quantification of such impacts (Asuk et al., 2023; McMichael et al., 2017; Piperno et al., 2015; Stahl, 2015).

One way in which to assess the impact of low-intensity drivers on tropical forest composition is by measuring the effects of human activities such as foraging, preferential planting and deliberate conservation on the total beta-diversity of the forest (Asuk et al., 2023; Biswas and Mallik, 2011; Bush et al., 2015; Roberts et al., 2021; Singh et al., 2022). Beta diversity, which is the dissimilarity in species composition between two or more communities separated in space (Anderson et al., 2011; Pound et al., 2019), has been successfully used as an effective indicator for analysing changes in species composition along spatial and environmental gradients (Anderson et al., 2011; Jarzyna and Jetz, 2018, 2016), including for tropical forest trees (Fontana et al., 2020; He et al., 2020; Ruokolainen, 2002).

While there have been numerous ecological studies of the beta diversity of forest tree species, these have mostly focused on identifying high intensity drivers of change in beta diversity at global scales, as well as mainly being focused on temperate forests, with less work focused purely on tropical forests (Aspin et al., 2018; Barnagaud et al., 2017; Biswas and Mallik, 2010, 2011; Devictor et al., 2010; Fu et al., 2019; García-Navas et al., 2020; Herault et al., 2010;

Jarzyna and Jetz, 2016; Lueder et al., 2022; Swenson et al., 2011; Waddell et al., 2020; Zambrano et al., 2020).

The importance of African Forests cannot be over emphasized; however, these forests remain grossly understudied. In this study, we use a beta diversity framework to evaluate the impact of low intensity anthropogenic activities on local and regional tree species composition in tropical west Africa. A previous local-scale study in Oban Forest, a tropical African rainforest located in Nigeria, assessed the impact of low-intensity anthropogenic activities on tree species diversity by comparing diversity patterns observed in tree species foraged for food and those that were not (Chapter 2)(Asuk et al., 2023). Findings from the study suggested that species composition, the species abundance distribution, beta-diversity, and turnover trends varied according to species utilization (i.e., those utilized for food by humans and those not utilized for food by humans). This points to a potentially pervasive impact of low intensity human foraging practices on tropical forest composition. For example, humans may disperse the seeds of edible species across the landscape and conserve those trees by not cutting them down for timber (due to the fruits/seeds they produce being highly valued as sources of food). Similarly, regarding timber harvest, it has been reported that while trees are cut down, certain trees species with food value are left standing within the forest estate or in old, abandoned farm estates (Asuk et al., 2023; Ellis et al., 2021; Jansen et al., 2020). However, this study was focused on a single national park, and thus whether these effects are more prevalent across tropical ecosystems at large scales is unknown. The present chapter will address this research gap.

Better understanding of the magnitude and dynamics of impacts from low intensity anthropogenic activities on beta diversity on a regional scale or how these activities interact with other drivers is essential if we are to accurately predict the future impacts of humans on tree community composition and dynamics (McMichael et al., 2017; Piperno et al., 2015; Stahl, 2015; Wayman et al., 2021). This study analyses beta diversity using a regional dataset of West African tropical forests which contains presence/absence information of tree species, categorized into edible (produce seeds and fruits eaten by humans) and inedible (not eaten by humans) species, to answer the following question: is there an influence of human presence on the beta diversity of forest trees at a regional scale and does this influence differ between those species used for food and those which are not? It is expected that the impact of humans on the distribution and composition of tree species observed at a local scale (see Chapter Two - Asuk *et al*. 2023) should sum up to what can be seen at the regional scale. However, this might vary based on the level of access human have to the regional forest.

3.3. MATERIALS AND METHODS

3.3.1. Plot and species composition data

The study was carried out using tree data from plots established in the tropical forests of Nigeria and Cameroon, bordering countries located in the West and West-Central regions of Africa respectively (Figure 3.1). The forests of both countries are contiguous via their common borders (Nigerian National Park Service, 2019; Enuoh and Ogogo, 2018). Species composition data used for the study comprised single census tree-by-tree samples collected between 2002 and 2019 from five plots established in Nigeria by Asuk et al. (2022) and 61 plots established in Nigeria and Cameroon, accessible from the forestplots.net database (Lopez-Gonzalez et al., 2011, 2009). The selected plots in Cameroon all measured 100m x 100m except for one that measured 40m x 100m (see Appendix 3.7.1, Table 3.7.1). The plots in Nigeria were smaller than those in Cameroon, measuring 40m x 120m (see Appendix 3.7.1, Table 3.7.1).

The plots were grouped into four spatial clusters based on their spatial proximity (Fig. 3.1). The associated plot metadata also included information on elevation, average plot slope, longitude, and latitude, stand density, forest status and forest composition. Elevation was recorded as the elevation of plots in meters above mean sea level as recorded during field inventories. Average plot slope was the slope of the plot at 20m scale into intervals: flat (0 – 2 degrees), almost flat (2 to 5 degrees), slightly sloping (5 to 10 degrees), moderately sloping (10 to 20 degrees) and steep (greater than 20-degree slope). Geographic data consisted of information on longitude and latitude in meters (UTM) collected during forest inventories (used for generating geographic distance between plots). Stand density, which refers to the number of living individual tree stems per unit area was generated by counting the total number of stems in each plot. To produce forest composition data, the composition of each plot was classified by forestplots.net as either mixed forest, monodominant, or savanna (see Appendix 3.7.1, Tables 3.7.2 and 3.7.3). Forest status data contained information about the status of the forest within the plots in relation to past or present anthropogenic disturbance as described by forestplots.net e.g., old-growth, secondary forest, logged, burned and other mixed classifications (Lopez-Gonzalez et al., 2011).

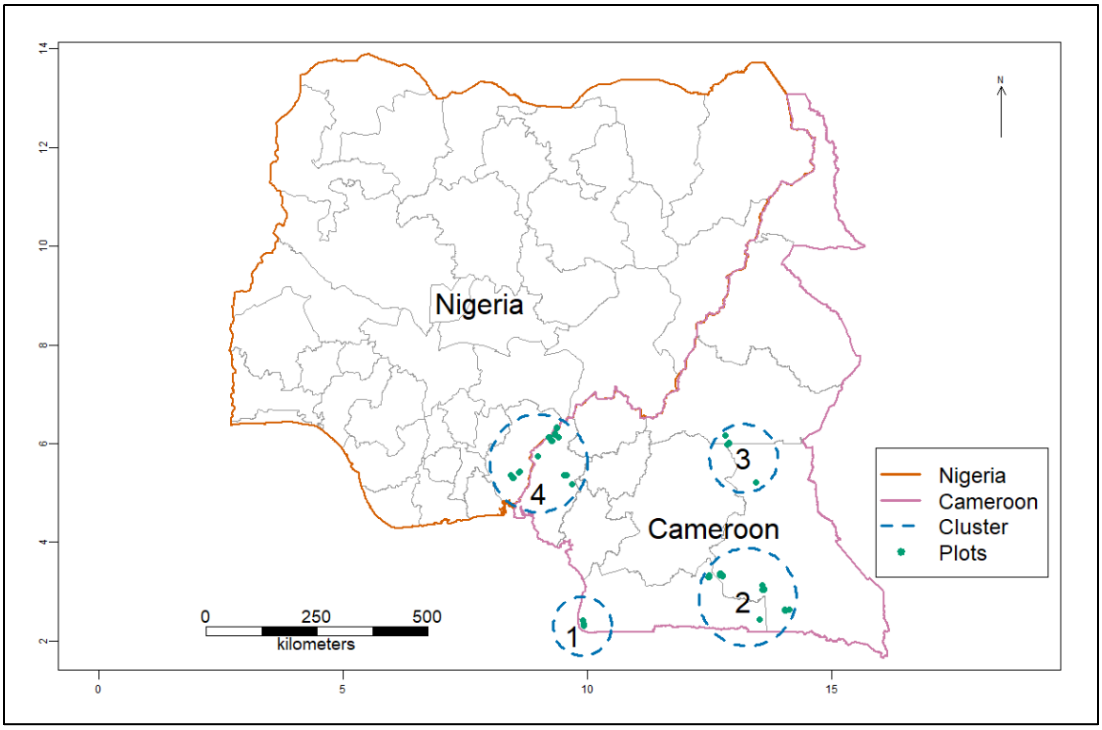


Figure 3.1. Map of Nigeria and Cameroon showing the location of the 66 plots used for the study. The plots were grouped into four spatial clusters (blue broken lined circles), numbered 1 to 4.

3.3.1.1. Plot selection criteria

To reduce any area effect on tree composition and thus ensure justifiable pairwise comparison of the plot data, differences in plot dimension/area (i.e., plots that were much larger/smaller compared to other plots) were reduced. Data from the last tree censuses collected between 2002 and 2019 were filtered from the multiple census tree data for the study. We then selected plots that fell between the size range of 40 by 100 m and 100 by 100 m with mixed and monodominant species composition, in old-growth, and secondary forest ecotones. Specifically, for the Nigerian plots, five clusters of three adjacent plots that were below 100 m by 100 m were merged into plots of size 40 m by 120 m (see Figure 2.1 in Chapter two for more details). This created 66 plots across the whole study region, with an average size of 94.55 m (std. 17.38 m) by 101.52 m (std 5.33 m) and containing a total of 28,299 individual trees. All other plots that did not meet the above criteria were discarded.

As outlined above, due to the geographical distances between plots, the 66 plots were further grouped into four clusters based on the geographic/natural proximity of plots. Cluster one had three plots, cluster two had 25 plots, cluster three had seven plots and cluster four had 31 plots. The distinct cluster groups were coded from 1 to 4 (Fig. 3.1) and cluster identity included as a variable in the Generalized dissimilarity models (GDMs) to check the effect of cross-cluster variation on the models' outcome. Furthermore, the GDMs were also run with data from each of the four cluster groups individually to compare model outcomes.

3.3.2. Species categorization

Tree species were categorized into those with fruits, nuts and seeds that are edible and those that are inedible for human consumption. The categorization was based on a combination of structured questionnaires (see Appendix 3.7.2) administered to four forest dependent / support zone communities within Oban Forest in Nigeria (Chapter 2; Asuk et al., 2023), and secondary data on tree species utilization collected from online databases. These online databases included Useful Tropical Plants database (https://tropical.theferns.info/), PlantUse database (https://uses.plantnet-project.org/en/), Royal Botanical Gardens Kew/Plants of the World

Online database (https://powo.science.kew.org/), PlantZAfrica (http://pza.sanbi.org/), World Agroforestry (https://apps.worldagroforestry.org/usefultrees/), and ebooks and journal publications. Only trees species that were identified to produce fruits, nuts and seeds consumed by humans were classified as edible. All other trees species were classified as inedible.

3.3.3. Human influence/presence

Two variables were used as proxies to assess the impact of humans on the tree species composition in the region (see more details in Appendix 3.7.3):

1. Distance to the nearest anthropogenic edge (DNAE), calculated as the straight-line distance from the plot to the nearest anthropogenic edge of the forest at the time of the census (see more details in Fig. 3.7.1 and 3.7.2 in Appendix 3.7.3). Information on the nearest anthropogenic edge was available for plots in the Oban Division dataset, but few other plots in the forestplots.net dataset. For plots without this information, open street map and Google Earth were used to measure a straight-line distance from the GPS location of the plots to the nearest sign of anthropogenic edge (e.g., farm, settlement, other anthropogenic disturbance). DNAE was used as an indicator to measure the possible presence of high impact human activity in the region.
2. Distance to the closest human presence (DCHP) – calculated as the straight-line distance from the GPS centre point of the plot to the closest identified footpaths, often used to forage for food and for hunting, thus it was used as an indicator for low-impact human activities. The human presence measurement was generated from Open Street Map and validated on Google Earth. Because we had data from censuses carried out in different years, the images on Google Earth were adjusted to coincide with the census year before a measurement was taken (see more details in Fig. 3.7.1 and 3.7.2 in Appendix 3.7.3).

DCHP generally had shorter distances than DNAE and is arguably a more accurate measure of low impact human presence in the forest region.

3.3.4. Data analysis

The data analysis involved three main steps: the generation of a presence-absence matrix of tree species for each plot, calculation of Sorenson's pairwise beta-diversity between plots (partitioned into nestedness and turnover components), and the use of Generalized Dissimilarity Models (GDMs) to identify variables that drive spatial beta diversity. However, the nestedness models failed as none of the explanatory variables explained any variation and, therefore, they were excluded from further discussion. The data were analysed using R (R Core Team, 2022).

3.3.4.1. Presence-absence matrix and beta-diversity calculation

For each plot, a presence-absence matrix was constructed separately for all species, edible species, and inedible species. We then computed the pairwise dissimilarity (beta diversity; Sorensen index) between each plot and every other plot within the dataset for each presence-absence matrix. We then partitioned the pairwise dissimilarity into the turnover (which is independent of nestedness / richness differences) and nestedness components. All beta-diversity components were calculated using the "betapart" package in R (Baselga et al., 2018; R Core Team, 2022).

3.3.4.2. Generalized Dissimilarity Models (GDM)

GDMs and variance partitioning are useful tools for disentangling what proportion of dissimilarity between communities is due purely to the effect of distance between those communities, and what proportion is explained uniquely by environmental (including anthropogenic) differences (Buzatti et al., 2019; Guerin et al., 2013, 2021; He et al., 2020; Wayman et al., 2021).

The “gdm” R package (Ferrier et al., 2007; Mokany et al., 2022) was used to fit the GDMs, which involves modelling the total pairwise beta diversity and the turnover component against the selected environmental variables to assess which predictor variables drive spatial taxonomic dissimilarity in tree species community composition between the plots. GDMs utilize the pairwise dissimilarity from beta-diversity matrices as the response variable and transform this dissimilarity to allow for meaningful comparison with combinations of predictor variables on different scales in the form of site pairwise distances (Mokany et al., 2022). A linear combination of I-spline basis functions fit using non-negative least squares regression was used to transform each predictor variable in the GDM (Mokany et al., 2022). The spline function of each predictor variable is relatively flexible in shape. However, because GDMs assume that dissimilarity can only increase between two sites that become more different in their predictor variables, I-splines are constrained to increase monotonically (Mokany et al., 2022).

We fitted separate GDM models for both total beta diversity and turnover calculated from each of the three presence-absence matrices (all species, edible species only, non-edible species only)(Mokany et al., 2022). These models included all the environmental variables, plot level variables and a measure of distance between each plot. The direct impact of each variable along the dissimilarity gradient was assessed through the application of a permutation and backwards selection approach, enabling the calculation of significance and variable importance (applied using the function ‘gdm.varImp’ within the ‘gdm’ package (Mokany et al., 2022; Ferrier et al., 2007)). This approach first fits a model using all the predictor variables unpermuted (model 1). The rows are then permuted 100 times and a separate GDM is fitted to each. Deviance between the unpermuted and permuted models is then calculated. The process is then repeated for each individual predictor, whilst holding the others constant, to calculate importance scores and significance for each one. The least significant predictor is then dropped, and the permutation is repeated with the remaining predictors until a model is found where all those remaining are significant ($p < 0.05$; model 1).

Geographic distance (the Euclidean distance between sites based on the x and y coordinates) was included as a predictor to account for the direct or indirect likelihood of distance-induced dissimilarity between site-pairs through dispersal limitations (Mokany et al., 2022). However, dissimilarity driven by environmental gradients could get suppressed or wrapped up in the dissimilarity from distance between sites, leading to the variance explained by each to be shared. Therefore, we fitted two more models for each response: one containing only geographical distance (model 2) and one with only environmental predictors (model 3). The shared variance between the environmental predictors and geographical distance was generated using the formula (Ray-Mukherjee et al., 2014) below.

$$V_s = V_{full} - (V_{full} - V_g) - (V_{full} - V_e) \qquad \text{Equation (1)}$$

where V_s is the shared variance explained between the environmental and geographic variables, V_{full} is the total variance explained by the model (model 1), V_g is the variance explained by the model containing only geographic variables (model 2), and V_e is the variance explained by the environmental model only (model 3).

3.4. RESULTS

Across the 66 plots, there were a total of 28,299 individual sampled trees. Gamma diversity across the study area was 708 species in 316 genera, out of which, from a view of human consumption, 208 species were classified as edible, and 500 species were classified as inedible.

3.4.1. Taxonomic beta diversity of the region partitioned into turnover and nestedness components

An alpha diversity of 236 for edible species and 472 for inedible species with 11097 and 17202 stems respectively was observed in the Nigerian-Cameroon forest (Table 3.7.4 in Appendix 3.7.4). The average total pairwise beta diversity between sites was similar (Figure 3.2) for all species (0.739 ± 0.125), edible species (0.729 ± 0.142) and inedible species (0.746 ± 0.128). The turnover component of beta diversity was the main determinant of the overall beta-diversity, while nestedness contributed a very small proportion in the region. For all species, turnover (0.669 ± 0.148) accounted for 90.5% of total beta diversity while nestedness resultant dissimilarity (0.070 ± 0.077) was responsible for 9.5%. For inedible species, turnover (0.672 ± 0.157) was responsible for 90.1% of total beta diversity while nestedness (0.074 ± 0.085) described 9.9% of total beta diversity. Similarly, 89% of total beta diversity for edible species was due to turnover (0.649 ± 0.169) and 11% was due to nestedness resultant dissimilarity (0.080 ± 0.082).

3.4.2. GDM results

As expected, Model 1 (a combination of geographic distance and environmental variables) had the highest variance explained in all, inedible and edible and species groups with 40.9%, 36.8% and 31.8% of variance explained in total beta diversity respectively. Similarly, Model 1 also recorded highest percentage of variance explained in turnover (species replacement) inedible, all and edible species group with 43.5%, 41.6% and 27.74% (Table 3.1). Model 3 (models run with environmental variables only) recorded the second highest variance explained for total beta-diversity with 30.9%, 24.8% and 23.1% (all, inedible, and edible species group respectively), while Model 2 had the least variance explained in total beta-diversity, between 18.3%, 17.4%, and 13.2% for all, inedible, and edible species group respectively (see Table 3.1). A low shared explained variance between geographical distance and environmental predictors was observed, with percentages ranging from 8.3%, 5.4% and 4.57% for dissimilarity due to total beta diversity and 5.85%, 5.8%, and 4.20% in dissimilarity due to turnover in all, inedible, and edible species group respectively (see Table 3.1).

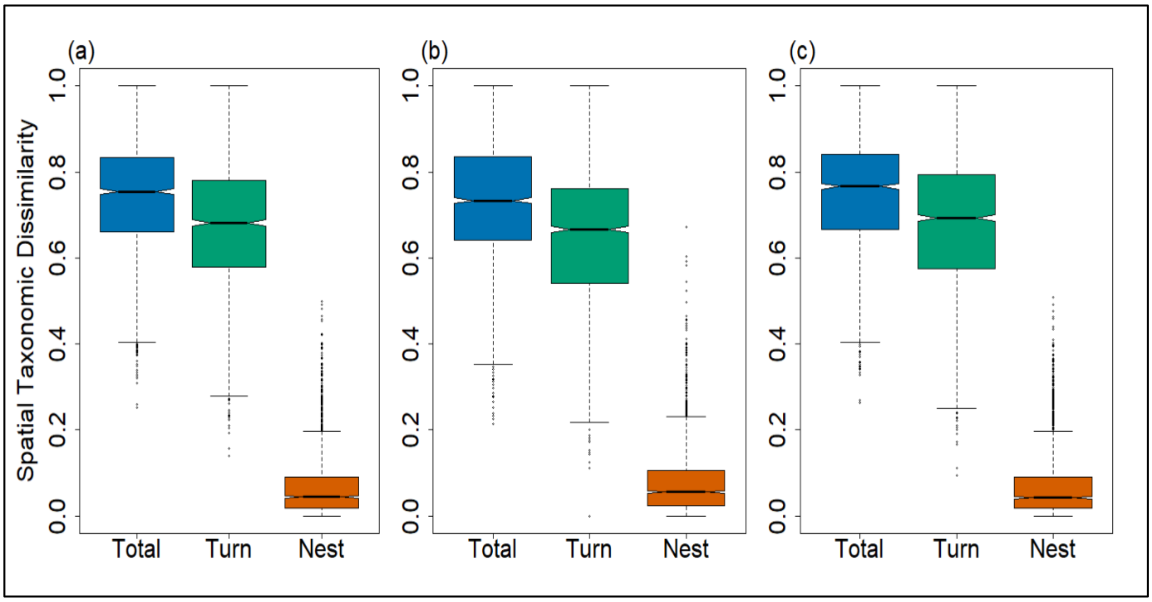


Figure 3.2. Boxplots of pairwise spatial dissimilarity of all (a), edible (b) and inedible (c) tree species found in the region. Plots display total beta-diversity (Total) as well as the turnover (Turn) and nestedness (Nest) components.

Table 3.1. Results from the generalized dissimilarity models analysing the spatial dissimilarity between forest plots. "Total" refers to total Sorenson's beta diversity while "Turn" refers to the Simpson's turnover partition of beta diversity. NA values indicate where variables were non-significant within models. Shared variance (%) was calculated from the variance explained by the full model, the geographic only model, and the environment only model. Model 1 (all the predictor variables), Model 2 (only geographical distance) and Model 3 (only environmental predictors) rows show the percentage deviance explained for the models.

Groups	**All**		**Edible**		**Inedible**	
	Total	**Turn**	**Total**	**Turn**	**Total**	**Turn**
GDM Deviance	104.19	127.37	157.09	208.10	120.16	142.20
Null Deviance	176.20	218.03	230.25	287.99	190.19	251.47
Intercept	0.66	0.50	0.66	0.42	0.71	0.48
Model 1	40.87	41.58	31.77	27.74	36.82	43.45
Model 2	18.26	17.30	13.22	13.19	17.38	15.54
Model 3	30.89	30.13	23.12	18.75	24.83	33.70
Shared Variance (%)	*8.28*	*5.85*	*4.57*	*4.20*	*5.39*	*5.79*
Variable importance						
Geographic (m)	24.38	27.51	27.18	32.36	32.54	22.42
Elevation	19.83	25.23	NA	NA	19.99	26.98
Stem density (stems/ha)	NA	NA	19.31	15.04	NA	NA
DNAE (m)	NA	NA	NA	15.24	NA	NA
DCHP (m)	18.35	24.34	14.07	24.01	21.54	26.65
Forest composition	18.25	NA	26.86	NA	NA	NA

3.4.2.1. Drivers of spatial taxonomic beta diversity across all, edible and inedible species

A total of six variables (geographic distance, elevation, stem density, DNAE, DCHP, forest composition) out of the eight variables imputed in model 1 significantly affected beta-diversity at varying levels of importance across all groups (All, Edible and Inedible) (Table 3.1).

All species models

In the All species model (All; Table 3.1), geographical distance, elevation, DCHP and forest composition were the four significant predictors of total beta diversity in the region. Except for turnover in inedible species, geographical distance had the highest variable importance in all beta diversity and turnover models (Table 3.1). Geographical distance – which had a similar effect on total beta diversity across all the species groups (all, edible, inedible) - had a steeply rising trend (as indicated by the I-splines) which gradually reduced close to its peak (between 200 and 300 km) and then levelled off (Figure 3.3a). In decreasing order of variable importance, the effect of elevation was second with a gentle trend that levelled off between 500 m and 700 m followed by a sharp continuous linear increase (Figure 3.3a), although this increase should be interpreted with caution as it is based on a very small number of plots. DCHP was the third most important predictor of changes in total beta diversity in the All species model, with a small but sudden increase in the first 20 meters followed by a continuous linear increase; however, this linear increase was due to only four points (Figure 3.3a). Forest composition was the least important significant predictor in the All model and had a gentle linear relationship with total beta diversity (Figure 3.3a). The turnover resultant beta diversity model had three significant variables: geographical distance, elevation and DCHP, in order of decreasing importance (Figure 3.4a). The trends in these variables, as shown by the I-splines, were similar to those observed for total beta diversity.

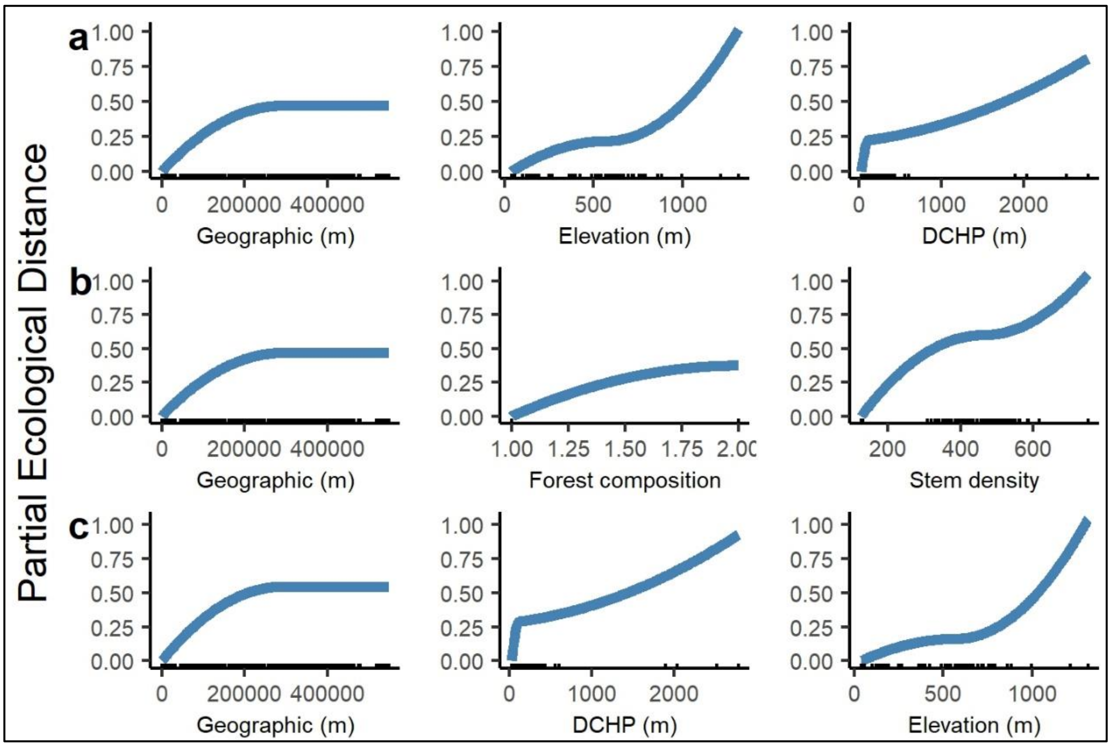


Figure 3.3. Plotted I-splines of the three variables with highest importance scores from the GDMs analysing the spatial relationship between geographic gradients, environmental variables, and tree species composition. Plots on row (a) are the Total Sorensen's beta-diversity for the entire region, (b) are the Total Sorensen's beta-diversity for the edible species category, and (c) Total Sorensen's beta-diversity for the inedible species. Plots are organized from left to right in order of increasing importance.

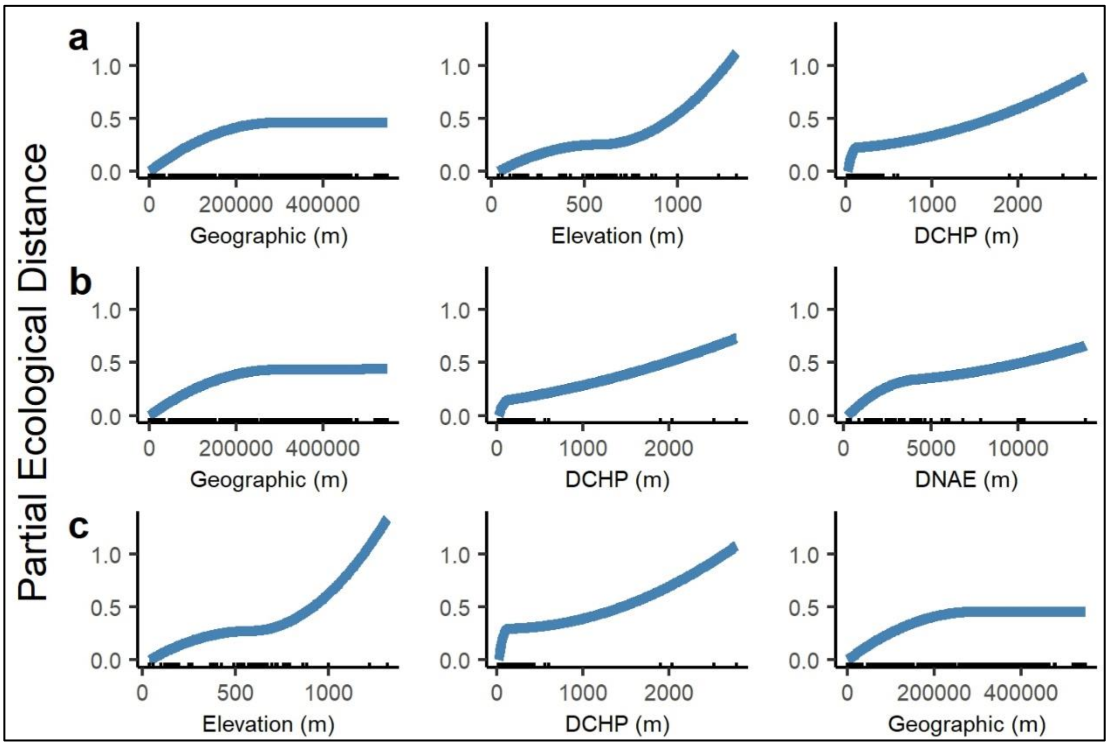


Figure 3.4. Plotted I-splines of the three variables with highest importance scores from the GDM analysing the spatial relationship between the turnover component of Sorensen's beta diversity and geographic gradients, environmental variables, and tree species composition. Plots on row (a) are for all species, (b) are for the edible species category, and (c) for the inedible species. Plots are organized from left to right in order of increasing importance.

Edible species

For edible species, total dissimilarity in community assemblage was significantly influenced by geographical distance, forest composition, stem density and DCHP, in order of decreasing variable importance (Table 3.1). The I-splines indicated that the relationship between geographic distance and total beta diversity had an initial steep linear trend that then plateaued. Forest composition exhibited a slight linear trend, while stem density had a steeper linear trend (Figure 3.3b). DCHP exhibited a very steep initial rise, followed by a continuous linear increase (Figure 3.4b). The turnover resultant beta-diversity of edible species was driven by four significant variables: geographical distance (most important variable), DCHP, DNAE and stem density (least important variable) (Table 3.1), although DNAE and stem density had similar importance scores. The I-splines indicated that the relationship between geographic distance and total beta diversity had an initial steep linear trend that then remained constant at the peak just as seen in total beta diversity. Both DCHP and DNAE exhibited positive roughly linear relations with beta diversity, however caution should be taken as most of the trend in DCHP was driven by four points (Figure 3.4b).

Inedible species

The models for total and turnover resultant beta-diversity using the inedible species data produced the same three significant predictors of dissimilarity, but with varied importance values (Table 3.1). The significant predictors with the highest variable importance for the total beta diversity of inedible species were geographic distance, DCHP and elevation, in order of decreasing importance. Geographic distance increased (based on the I-splines) with a steep linear trend and then remained constant at its peak. DCHP exhibited a very steep initial rise followed by a continuous linear increase while elevation showed a gentle trend that leveled off at about 600m followed by a sharp continuous increase (Figure 3.3c). Inedible turnover resultant beta-diversity models showed that elevation had the highest variable importance, followed by DCHP and geographical distance. However, the variable importance values for DCHP (26.65) and elevation (26.98) were similar.

Total beta diversity models for edible and inedible species had two common variables that were significant (geographical distance and DCHP). While there were differences in the variable importance hierarchy, the maximum I-spline values for these variables were higher when using the inedible species data than for the edible data.

3.4.2.2. Effects of spatial clusters on the model outcome

When plot cluster (Table 2.7.5 to 2.7.6 and Figure 3.7.3 to 3.7.4 in Appendix 3.7.5) was included as a predictor in the models, there was an increase in the overall GDM deviance and a slight decrease in the variance explained for total beta diversity in each model group (all, edible and inedible species). When attempting to the run the GDMs for individual clusters, the models for cluster one, two and three did not run due to too few data points. In cluster four, there was a significant increase in variable importance of human influence variables (DCHP and DNAE) as predictors of the total beta diversity of inedible species, while they were less important for edible species (Figure 3.7.5 to 3.7.6 in Appendix 3.7.5).

3.5. DISCUSSION

3.5.1. Drivers of West African tropical forest tree beta diversity

The turnover component of total beta diversity accounted for most of the tree species dissimilarity observed in the region, meaning that richness was relatively similar across plots and that most of the differences in composition were due to the replacement of species across space. This could be attributed to processes such as dispersal limitation, competition, and environmental filtering along environment gradients (He et al., 2020; Jiang et al., 2021; Verrico et al., 2020). The pool of important variables driving total beta diversity across the region were geographical distance, plot elevation, stem density, distance of plots to human presence (DCHP), and forest species composition.

The unique proportion of variance explained in the models by environmental variables alone was higher than that explained uniquely by geographical distance, thus highlighting the importance of environmental filtering in the tree species community composition of the region. Similar studies in the Cuitzeo basin, Mexico, revealed that environmental heterogeneity has greater impact on beta-diversity due to niche-based processes than geographical distance (Vega et al., 2020). Another study, conducted in Hainan, China, demonstrated that environmental variables including temperature, precipitation and evapotranspiration had far more significant effects on tree species compositional dissimilarity than geographical distance, due to niche-based processes rather than dispersal limitation (He et al., 2020). However, He et al. (2020) did not include the partitioning of geographical distance from environmental variables, as done in this chapter, to control for the possibility of shared effects of both (Mokany et al., 2022). The effects of individual groups of variables will now be discussed in turn.

3.5.2. The impact of human influence on regional beta-diversity

Human influence, as indicated by DCHP (distance to closest human presence), was found to be one of the important indicators of total and turnover resultant beta diversity across all the species categories in the study area, while DNAE was only a significant indicator of turnover in edible species (although low compared to other variables). This suggests that the proxy for high impact human activities were driving the turnover resultant beta diversity of edible species but not inedible species.

The type and intensity of human activities can have diverse impacts on the abundance and distribution of forest tree species, depending on how the species are utilised by humans (Asuk et al., 2023; Ellis et al., 2010, 2021). For example, as pointed out by Socolar et al. (2016), some human activities such as logging, agriculture, hunting, and foraging for food could have varied degrees of direct and indirect impact on the species distribution and abundance dynamics of a forest ecosystem (Jara-Guerrero et al., 2021). Humans typically cover relatively shorter distances for intense forest utilization activities, such as harvesting timber and converting the forest into arable land (Asuk et al., 2023). In contrast, studies have shown that humans can cover wider ground distances when foraging for fruits, seeds, and nuts (Asuk et al., 2023; Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022). However, the level and intensity of these impacts from anthropogenic activities could be dependent on the region (rural or semi-rural or urban), duration of exposure to these activities, level of forest dependence on the forest and type of biome (Asuk et al., 2023; Fotang et al., 2021; Williams et al., 2020; Yuan et al., 2022). It is worth noting that that there is an interaction between human influence on the forest and elevation: human influence tends to be more intense at lower elevations, with a transition to low-intensity activities as elevation increases (Asuk et al., 2023; Malizia et al., 2020; Yano et al., 2021). This interactive elevation-human impact on the forest could imprint varied effects on elevational patterns of the beta diversity of edible and inedible species alike (Asuk et al., 2023; Malizia et al., 2020; Yano et al., 2021).

It is important to note that there are some limitations to consider with regards to using this dataset for assessing the impact of human influence on tree species dissimilarity in the Nigeria-Cameroon forest region. These include the lack of historical data on the forest, which makes it difficult to assess the extent of past human impact on the forest. In addition, the dataset is limited in terms of the number of plots and the size of the study area, which may not be very representative of the entire region. Despite these limitations, and based on what is currently possible with the data available, our findings suggest that human influence is an important driver of beta diversity in the Nigeria-Cameroon forest region. As pointed out, the type of intensity and duration of the different human activities can exert a different response on the beta diversity of different species. Taking the results of this chapter with those from Chapter 2 indicates that these processes are apparent at both local and regional scales in West African tropical forests. More broadly, findings from other studies, e.g. those undertaken in the Amazon, have suggested that the selection and stewardship of desired tree species by indigenous populations over time might leave strong imprints on patterns of forest composition (Asuk et al., 2023; Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022).

3.5.3. Effect of forest composition and tree density on regional beta diversity

The forest in the studied region cuts across two composition types: mixed forest and monodominant forest characterized by one single species making up more than 60% of the tree canopy (ter Steege et al., 2019). According to ter Steege et al. (2019), the main identified reason for monodominance in tropical forest was coppicing and edaphic factors. Coppicing, which can be natural or harvest-induced, occurs when a sprout or regrowth is formed at the tree's base or on its root (ter Steege et al., 2019). Forest composition was driving the dissimilarity due to the total beta diversity of edible tree species, an effect not seen in inedible species. This indicates that the composition and diversity of edible species might differ between monodominant and mixed forests. Multiple factors can influence these differences, including the history and frequency of forest disturbance, successional processes, varying distances of plots from high-intensity and low-intensity human activities, differences in topography, climate and soil conditions (Williams et al., 2020; Fotang et al., 2021; Yuan et al., 2022; Asuk et al., 2023).

Stem density was one of the important variables in the edible tree species models, but not in the inedible species models. In theory, high stem density in tropical forests can create more complex and heterogeneous microhabitats, such as gaps, understory, and canopy layers, supporting different tree species with unique environmental requirements. This could increase beta diversity by promoting the coexistence of a greater number of species with different ecological niches. For edible species that produce food for humans, the observed effect of stem density on total beta may be more pronounced due to the way they are typically managed and cultivated. Low tree stem density can translate to a reduction in abundance and diversity, and limit dispersal and colonization, leading to a decrease in total beta diversity of edible trees species in tropical forests. The intensity of human activities can also exacerbate these effects. Conversely, inedible species may have a lower susceptibility to alterations in tree stem density and habitat fragmentation since they might have greater adaptability to survive in smaller and isolated habitats (Bailey et al., 2010; Fahrig, 2003; de Lima Filho et al., 2021).

There is a known positive relationship between alpha diversity and stand structural heterogeneity (either tree DBH inequality, height inequality, or stand density) (Abbasi et al., 2023; Godlee et al., 2021; Yano et al., 2021). For example, studies in the Amazon Forest have shown that alpha diversity increases with an increase in stem density (ter Steege et al., 2003). However, nestedness was not a significant driver of beta diversity in this study and the stem density of trees in the edible species category is markedly lower than those in the inedible category. Thus, the relationship between tropical forest tree stem density and beta diversity is complex and dependent on various factors (such as intensity of human activities, elevation, distance between plots, soil and others), and therefore further in-depth empirical studies might be necessary to fully understand the underlying mechanisms linking stem density to beta-diversity in tropical forests.

3.5.4. Effects of spatial distance and elevation on the beta diversity of tree species in the region

Although the combined effect of the environmental variables (see model 3 in Table 1) was greater than geographical distance (see model 2 in Table 1), in the overall model (model 1), the geographical distance between sites exerted a stronger individual effect on the pairwise dissimilarity between plots than any other single environmental variable (except for the turnover of inedible species, where elevation had the strongest effect). This evidence suggests that large geographical distance between plots could act as a biogeographical barrier, inducing some level of dispersal limitation in species, driving turnover (Abiem et al., 2022; He et al., 2020; Wayman et al., 2021; Yang et al., 2015; Zahawi et al., 2021). Spatial distance between plots was generally also the most important individual variable driving the pairwise dissimilarity of species in plots for edible and inedible species alike (Asuk et al., 2023; Jimoh et al., 2012; Socolar et al., 2016).

Elevation is known to play a crucial part in the composition and spatial distribution of tree species in forest ecosystems (Asuk et al., 2023; Malizia et al., 2020; Yano et al., 2021).

Elevation was a significant variable in many of the models, which makes sense given the study area is generally characterized as having rough terrain with strong elevational gradients. Elevation exerts varying niche-based effects on species, due to changes in climate, soil, the identity of seed dispersers, and the activities of humans along the elevational gradient (Adnan et al., 2015; Asuk et al., 2023; Verrico et al., 2020). These changes result in strong environmental filtering and the replacement of species along the gradient (Adeyemi, 2016; Aigbe and Omokhua, 2015; Asuk et al., 2023). Although these forests are believed to be intact at the point of the census, any past timber harvesting would likely have been restricted to lower elevations (Adnan et al., 2015; Asuk et al., 2023; Socolar et al., 2016; Verrico et al., 2020), which will have increased the effect of elevation on dissimilarity (Asuk et al., 2023; Ellis et al., 2010)In addition, the aforementioned elevation-human activities interaction (Asuk et al., 2023; Yano et al., 2021; Malizia et al., 2020) could also result in an uneven distribution of other activities along elevational gradients, such as nomadic resettlement of human communities and farming, all of which could potentially affect the pairwise turnover between plots (Asuk et al., 2023; Verrico et al., 2020; Adnan et al., 2015; Aigbe and Omokhua, 2015). However, low intensity activities (e.g., foraging for food) may occur across the elevational gradient, leading to more similar species composition across the gradient (due to humans spreading the seeds of edible species; (Jansen et al., 2020; Williams et al., 2020; Guo et al., 2022; Scerri et al., 2022; Asuk et al., 2023) and explaining why elevation was not a significant predictor in the edible species models.

3.6. CONCLUSION

This study explored the determinants of the beta diversity of tree species in the Nigeria-Cameroon forest region, with a particular focus on the impact of human influence. This chapter builds on findings from chapter two to test the impact of humans on beta diversity patterns at a regional scale. The results revealed that the turnover component of total beta diversity accounted for most of the tree species dissimilarity observed in the Nigeria-Cameroon forest region, likely driven by processes such as dispersal limitation, competition, and environmental filtering. The pool of variables important for driving total beta diversity across the region included geographical distance, plot elevation, stem density, distance of plots to human presence, and forest species composition, with the proportion of variance explained by environmental variables alone being higher than that explained by geographical distance. This points to the importance of environmental filtering in the tree species community composition of the region.

Forest composition was driving the total beta diversity of edible tree species but not inedible species. Although the combined effect of environmental variables was greater than geographical distance, in the overall model, the geographical distance between sites exerted a stronger individual effect on the pairwise dissimilarity between plots than any other single environmental variable. A difference was also seen in the effect of elevation, which was absent in the edible species model, but a significant driver of the dissimilarity of inedible species, consistent with the findings of a previous, more geographically limited study in Nigeria (Chapter 2; Asuk et al., 2023). The impact of elevation and distance was attributed to niche-filtering along elevational gradients as well as the confinement of differential impacts of human activities along the elevational gradient.

This study provides valuable insights into the drivers of tree species dissimilarity in the Nigeria-Cameroon forest region, highlighting the importance of environmental filtering, forest composition, spatial distance, and human influence. We had expected that humans might decrease tree species dissimilarity of edible species locally within plots close to human settlements by spreading edible species, and this could then increase the dissimilarity between plots, particularly those far away from human settlements. However, if this was the case, we would expect to see higher dissimilarity for edible than for non-edible species, which was not observed, thus pointing to the contribution of other variables to the regional species assemblage dynamics.

However, further research is needed to assess the extent and nature of this impact more definitively, such as establishing a link between dissimilarity in species assemblages with tree species traits related to early and late successional species (such as wood density or individual maximum growth rate) (Donoso et al., 2017; García-Navas et al., 2020; Yang et al., 2015; Zambrano et al., 2020). Also, a comparison between logging disturbance and foraging disturbance could be very helpful in understanding this relationship. A long-term evaluation of the socio-economic importance of harvesting and foraging to the forest dependent human communities combined with a measure of the number of trees removed, number and duration of foraging visits made to the forest and an assessment of the forest ecosystem would provide a more in-depth understanding of human impacts on forest composition.

Further research should also consider the use of more comprehensive datasets and advanced remote sensing technologies, such as LiDAR and high-resolution satellite imagery (which the region currently lacks), to assess forest structure, and the impact of human influence more accurately. This would provide a more comprehensive understanding of the relationship between human activities and tree species dissimilarity, as well as enable the assessment of the impact of other factors such as climate change, and natural disturbances. Additionally, this study can inform the development of effective conservation and management strategies focused on the sustainable use of resources for forest-dependent livelihoods.

3.7. APPENDICES

Appendix 3.7.1. Information on the dimension, size, census year of plots establishment and plots located in different forest compositions

Table 3.7.1. Information on tree data from plots used for the study including location of plot code, country of location, dimension, and year censused.

Plot Code	Country	Minimum Dimension (m)	Maximum Dimension (m)	Ground Area (sq. m)	Year Censused
AKG-01	Nigeria	40	120	4800	2019
AKG-02	Nigeria	40	120	4800	2019
BIS-01	Cameroon	100	100	10000	2013
BIS-02	Cameroon	100	100	10000	2013
BIS-03	Cameroon	100	100	10000	2013
BIS-04	Cameroon	100	100	10000	2013
BIS-05	Cameroon	100	100	10000	2013
BIS-06	Cameroon	100	100	10000	2013
CAM-01	Cameroon	100	100	10000	2012
CAM-02	Cameroon	100	100	10000	2012
CAM-03	Cameroon	100	100	10000	2002
DJK-01	Cameroon	100	100	10000	2019
DJK-02	Cameroon	100	100	10000	2019
DJK-03	Cameroon	100	100	10000	2019
DJK-04	Cameroon	100	100	10000	2019
DJK-05	Cameroon	100	100	10000	2019
DJK-06	Cameroon	100	100	10000	2019
DJL-01	Cameroon	100	100	10000	2016
DJL-02	Cameroon	100	100	10000	2016
DJL-03	Cameroon	100	100	10000	2016
DJL-04	Cameroon	100	100	10000	2016
DJL-05	Cameroon	100	100	10000	2016
DJL-06	Cameroon	100	100	10000	2016
DNG-01	Cameroon	100	100	10000	2016
DNG-02	Cameroon	100	100	10000	2016
EJA-04	Cameroon	100	100	10000	2011
EJA-05	Cameroon	100	100	10000	2011
ERK-01	Nigeria	40	120	4800	2019
MDJ-01	Cameroon	100	100	10000	2019
MDJ-03	Cameroon	100	100	10000	2019
MDJ-05	Cameroon	100	100	10000	2019
MDJ-07	Cameroon	100	100	10000	2019

Table 3.7.1 (cont.). Information on tree data from plots used for the study including location of plot code, country of location, dimension, and year censused.

Plot Code	Country	Minimum Dimension (m)	Maximum Dimension (m)	Ground Area (sq. m)	Year Censused
MDJ-10	Cameroon	40	100	4000	2019
MIT-01	Cameroon	100	100	10000	2011
NGI-01	Cameroon	100	100	10000	2011
NGI-02	Cameroon	100	100	10000	2011
NGI-03	Cameroon	100	100	10000	2013
NGI-04	Cameroon	100	100	10000	2013
NGI-05	Cameroon	100	100	10000	2013
NGI-06	Cameroon	100	100	10000	2013
NGI-07	Cameroon	100	100	10000	2013
NGI-08	Cameroon	100	100	10000	2013
NGI-09	Cameroon	100	100	10000	2013
NGI-10	Cameroon	100	100	10000	2013
NGI-11	Cameroon	100	100	10000	2013
NGI-12	Cameroon	100	100	10000	2013
NGO-01	Cameroon	100	100	10000	2012
NGO-02	Cameroon	100	100	10000	2012
NGO-03	Cameroon	100	100	10000	2012
NGO-04	Cameroon	100	100	10000	2013
NGO-05	Cameroon	100	100	10000	2013
NGO-06	Cameroon	100	100	10000	2013
OBE-83	Nigeria	100	100	10000	2002
OBE-84	Nigeria	100	100	10000	2002
OSB-01	Nigeria	40	120	4800	2019
OSB-02	Nigeria	40	120	4800	2019
TNP-06	Cameroon	100	100	10000	2012
TNP-07	Cameroon	100	100	10000	2012
TNP-08	Cameroon	100	100	10000	2012
TNP-09	Cameroon	100	100	10000	2012
TNP-10	Cameroon	100	100	10000	2012
TNP-11	Cameroon	100	100	10000	2012
TNP-12	Cameroon	100	100	10000	2012
TNP-13	Cameroon	100	100	10000	2012
TNP-14	Cameroon	100	100	10000	2012
TNP-15	Cameroon	100	100	10000	2012

Table 3.7.2. Distribution of edible and inedible tree species belonging found in mixed and monodominant forest plots

Plots	Mixed forest		Monodominant forest	
	edible	inedible	edible	inedible
AKG-01	111	107	-	-
AKG-02	118	109	-	-
BIS-01	-	-	87	260
BIS-02	208	261	-	-
BIS-03	-	-	36	293
BIS-04	155	284	-	-
BIS-05	-	-	41	286
BIS-06	206	240	-	-
CAM-01	95	299	-	-
CAM-02	119	226	-	-
CAM-03	112	279	-	-
DJK-01	-	-	43	264
DJK-02	185	179	-	-
DJK-03	-	-	39	301
DJK-04	244	222	-	-
DJK-05	-	-	28	332
DJK-06	192	254	-	-
DJL-01	-	-	27	322
DJL-02	159	245	-	-
DJL-03	-	-	31	401
DJL-04	202	378	-	-
DJL-05	-	-	50	259
DJL-06	189	273	-	-
DNG-01	328	250	-	-
DNG-02	255	273	-	-
EJA-04	385	153	-	-
EJA-05	330	200	-	-
ERK-01	131	88	-	-
MDJ-01	214	348	-	-
MDJ-03	187	247	-	-
MDJ-05	221	527	-	-
MDJ-07	314	146	-	-
MDJ-10	118	47	-	-
MIT-01	82	277	-	-
NGI-01	165	255	-	-
NGI-02	191	276	-	-
NGI-03	147	245	-	-
NGI-04	243	232	-	-

Table 3.7.2 (cont.). Distribution of edible and inedible tree species belonging found in mixed and monodominant forest plots

Plots	Mixed forest		Monodominant forest	
	edible	inedible	edible	inedible
NGI-05	252	241	-	-
NGI-06	229	311	-	-
NGI-07	219	282	-	-
NGI-08	192	257	-	-
NGI-09	286	254	-	-
NGI-10	237	307	-	-
NGI-11	301	274	-	-
NGI-12	228	290	-	-
NGO-01	75	367	-	-
NGO-02	158	355	-	-
NGO-03	152	210	-	-
NGO-04	-	-	75	333
NGO-05	-	-	29	373
NGO-06	-	-	19	354
OBE-83	45	85	-	-
OBE-84	43	80	-	-
OSB-01	138	110	-	-
OSB-02	98	136	-	-
TNP-06	225	236	-	-
TNP-07	268	201	-	-
TNP-08	199	333	-	-
TNP-09	243	269	-	-
TNP-10	174	280	-	-
TNP-11	195	213	-	-
TNP-12	172	249	-	-
TNP-13	220	261	-	-
TNP-14	231	182	-	-
TNP-15	217	200	-	-
Grand Total	10403	12903	505	3778

Table 3.7.3. Distribution and descriptive statistics of predictor variables included in the GDMs models

Variables	Elements within Variables	Count	Min	Max	Mean
Plots		66	-	-	-
Clusters (number of plots)	Cluster 1	3			
	Cluster 2	25			
	Cluster 3	7			
	Cluster 4	31			
Total tree stems		28299	-	-	-
Edible stems		11097	-	-	-
Inedible stems		17202	-	-	-
Forest composition	*Mixed forest plots*	54	-	-	-
	Mixed forest stems	23975	-	-	-
	Monodominant forest plots	12	-	-	-
	Monodominant forest stems	4324	-	-	-
Slope (number of plots)	*Almost Flat*	33	-	-	-
	Flat	17	-	-	-
	Moderately Sloping	8	-	-	-
	Slightly Sloping	5	-	-	-
	Steep	3	-	-	-
Elevation (masl)			38	1314	510.8
Stem density (stems/ha)	*All species*		126	751	452
	Edible species		19	385	181
	Inedible species		83	530	271
DNAE (m)			217	13840	4825.5
DCHP (m)			22.5	2782	306.5

Appendix 3.7.2. Qualitative data collection and structured questionnaire used for collection of data on forest tree species utilization in Oban Division, Cross River National Park

Structured questionnaire (see below) on utilization of fruit/seed/nuts from tree species for food were purposively administered to ten percent of the 39 forest-dependent enclave/buffer zone communities around Oban Division of the Cross River National Park, Nigeria, where all seven Nigerian plots are located. The purposive administration of questionnaires was done using a mixed method interview (Friant et al., 2019) based on the following criteria:

5. Individuals involved in the gathering of fruit/seeds/nuts and farmers
6. Individuals who are at least 30 years and likely to be knowledgeable about forest tree species utilization in the area
7. Individuals who had lived in the area for at least 15 years to give valid information on the study
8. The council of chiefs were interviewed as a group.
9. All gender who met criteria 1 to 4 above.

QUESTIONNAIRE USED FOR THE STUDY

Community Code: _______ Date of interview_________ Interviewers Name: ___________

Demographic data

Q1. Type of interview

Individual [ ] Group [ ] Number of Respondent in Group: ________

Q2. Age group?

25-34 [ ] 35-44 [ ] Above 45 [ ]

Tree species utilization

Q3. What forest tree species and parts are utilized for food in your community?

Species name	Species part utilized for food					
	Fruit	Seed	Nut	Leaf	Flower	Others (specify)

Appendix 3.7.3. Methodology for assessing human impact on tree species composition using proximity measures

To evaluate the human influence on tree species composition within the study region, two distinct variables were employed as proxy measures. The categorisation and quantification of these variables are detailed as follows:

Distance to the Nearest Anthropogenic Edge (DNAE)

DNAE was computed as the Euclidean distance from the geographic coordinates of a given forest plot to the closest discernible anthropogenic edge at the time of the respective census (Figure 3.7.1 and 3.7.2). Anthropogenic edges often manifested as man-made alterations such as farms, settlements, or other types of human disturbance.

For forest plots within the Oban Division dataset, data on the nearest anthropogenic edge was readily available (Asuk et al, 2023). In cases where forest plots from the forestplots.net dataset did not contain this information, Open Street Map and Google Earth were consulted to measure the Euclidean distance from the plot's GPS coordinates to the closest identified anthropogenic edge. This metric acted as a gauge for potential high-impact human activities in areas surrounding the forest plots.

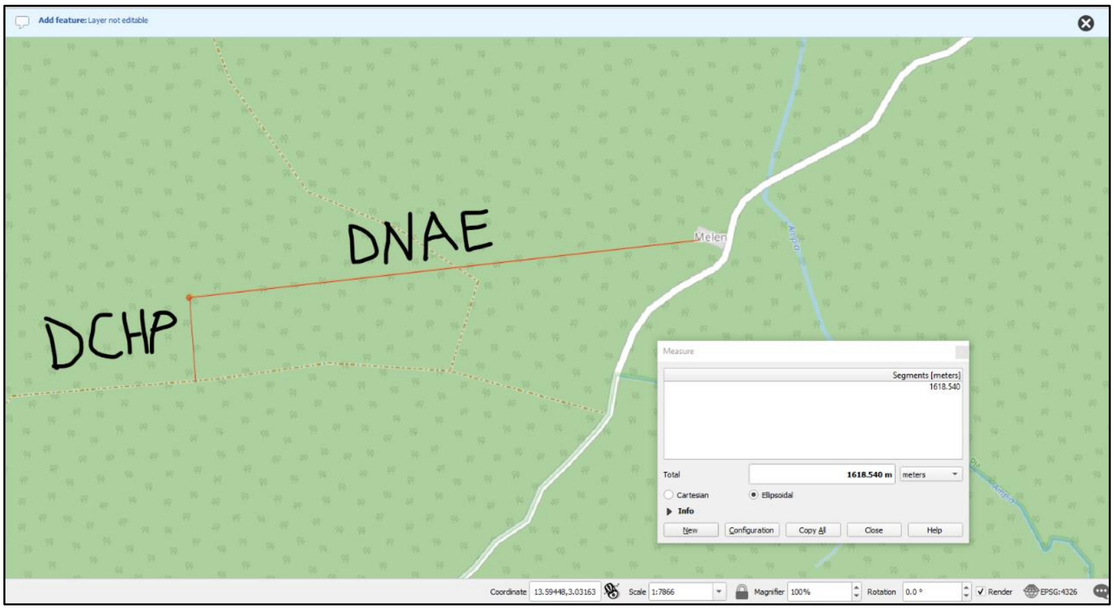
Distance to the Closest Human Presence (DCHP)

DCHP involved measuring the straight-line distance from the GPS centre point of each forest plot to the nearest identified human footpaths (Figure 3.7.1 and 3.7.2). These footpaths are often used for low-impact activities like foraging and hunting.

Spatial data for this variable was initially obtained from Open Street Map and subsequently validated on Google Earth. To accommodate for censuses conducted in different years, the satellite images on Google Earth were adjusted to match the year of each respective census.

DCHP typically exhibited shorter distances in comparison to DNAE, making it a potentially more precise indicator of low-impact human presence in the vicinity of the forest plots. Historical images were used on google earth engine to coincide with the year of plot census (Figure 3.7.2).

By utilizing these two proximity measures, this study offered an insight of the varying degrees of human impact on the tree species composition in the investigated region.



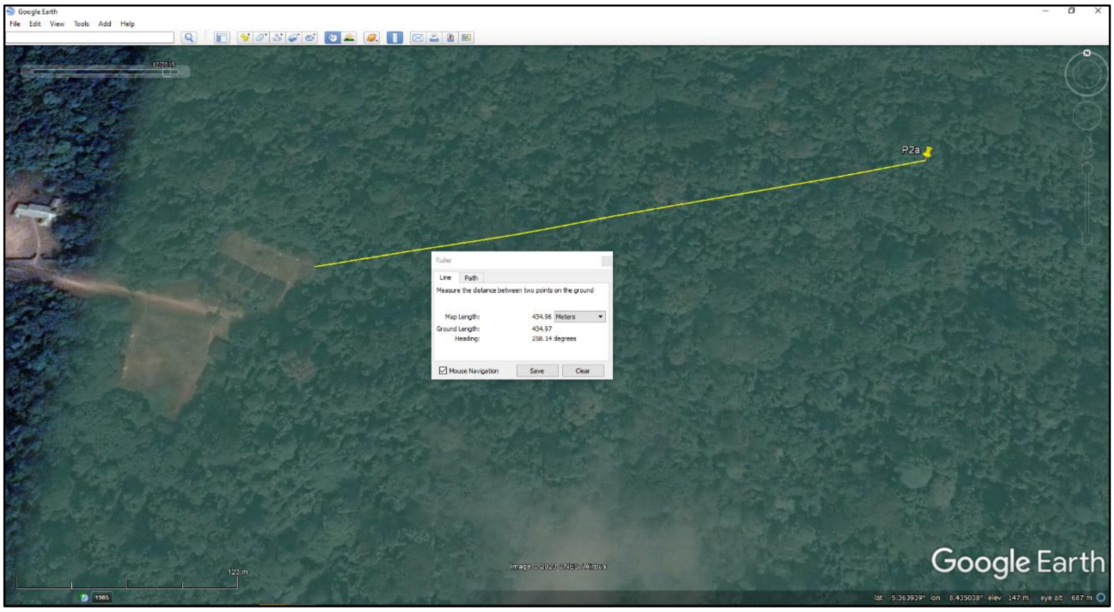
Segments [meters]: 1618.540

Total: 1618.540 m meters

○ Cartesian ● Ellipsoidal

Coordinate 13.59448,3.03163 Scale 1:7866 Magnifier 100% Rotation 0.0 ° ✓ Render EPSG:4326

Figure 3.7.1. Open street map showing distance from plot to closes path representing distance to closest human presence (DCHP) and distance from plot to human settlement representing distance to nearest anthropogenic edge (DNAE).



Measure the distance between two points on the ground

Map Length: 434.96 Meters

Ground Length: 434.97

Heading: 258.14 degrees

☑ Mouse Navigation

lat 5.363939° lon 8.435038° elev 147 m eye alt 687 m

Figure 3.7.2. Map from Google Earth showing how distance from plot was measured based on historical images that coincided with date of plot census (see top left bar).

Appendix 3.7.4. Summary of alpha diversity and total tree stem count

Table 3.7.4. Alpha diversity of plots forest categorised as mix and mono dominant forests

Forest composition	Plots	Alpha diversity		
		edible	inedible	Total
Mixed forest	AKG-01	43	44	87
Mixed forest	AKG-02	43	37	80
Mixed forest	BIS-02	47	63	110
Mixed forest	BIS-04	50	67	117
Mixed forest	BIS-06	50	57	107
Mixed forest	CAM-01	31	51	82
Mixed forest	CAM-02	27	56	83
Mixed forest	CAM-03	30	44	74
Mixed forest	DJK-02	41	62	103
Mixed forest	DJK-04	55	70	125
Mixed forest	DJK-06	50	58	108
Mixed forest	DJL-02	35	54	89
Mixed forest	DJL-04	55	58	113
Mixed forest	DJL-06	44	58	102
Mixed forest	DNG-01	41	53	94
Mixed forest	DNG-02	48	50	98
Mixed forest	EJA-04	40	43	83
Mixed forest	EJA-05	37	52	89
Mixed forest	ERK-01	49	37	86
Mixed forest	MDJ-01	22	30	52
Mixed forest	MDJ-03	31	44	75
Mixed forest	MDJ-05	15	28	43
Mixed forest	MDJ-07	39	43	82
Mixed forest	MDJ-10	22	15	37
Mixed forest	MIT-01	21	52	73
Mixed forest	NGI-01	28	55	83
Mixed forest	NGI-02	27	49	76
Mixed forest	NGI-03	27	61	88
Mixed forest	NGI-04	34	64	98
Mixed forest	NGI-05	33	70	103
Mixed forest	NGI-06	42	60	102
Mixed forest	NGI-07	32	48	80
Mixed forest	NGI-08	37	42	79
Mixed forest	NGI-09	37	48	85
Mixed forest	NGI-10	31	37	68
Mixed forest	NGI-11	34	41	75
Mixed forest	NGI-12	32	38	70
Mixed forest	NGO-01	22	43	65
Mixed forest	NGO-02	38	53	91

Mixed forest	NGO-03	36	42	78
Mixed forest	OBE-83	23	30	53
Mixed forest	OBE-84	20	29	49
Mixed forest	OSB-01	40	42	82
Mixed forest	OSB-02	36	37	73
Mixed forest	TNP-06	43	57	100
Mixed forest	TNP-07	43	60	103
Mixed forest	TNP-08	17	50	67
Mixed forest	TNP-09	22	52	74
Mixed forest	TNP-10	36	65	101
Mixed forest	TNP-11	45	68	113
Mixed forest	TNP-12	37	55	92
Mixed forest	TNP-13	45	69	114
Mixed forest	TNP-14	31	53	84
Mixed forest	TNP-15	33	55	88
Total Alpha diversity in Mixed		232	469	701
Monodominant	BIS-01	28	46	74
Monodominant	BIS-03	20	33	53
Monodominant	BIS-05	23	20	43
Monodominant	DJK-01	18	19	37
Monodominant	DJK-03	16	17	33
Monodominant	DJK-05	12	26	38
Monodominant	DJL-01	15	27	42
Monodominant	DJL-03	9	17	26
Monodominant	DJL-05	25	32	57
Monodominant	NGO-04	17	16	33
Monodominant	NGO-05	10	13	23
Monodominant	NGO-06	8	15	23
Total Alpha diversity in Monodominant		76	96	172
Total Alpha Diversity		236	472	708

The alpha diversity of edible and inedible species was higher in mix forest than in monodominant forest. Also, the difference in alpha diversity of edible and inedible trees in all plots was widder in mixed forest than in monodominant forest. Gilbertiodendron dewevrei, belonging to the inedible species category, was the most dominant species across all plots in the monodominant forest. A presence/absence metrics was used for computing the beta diversity thus reducing the effect of species dominance, however, stem density of each species as well as forest composition were added as variables within the model.

Appendix 3.7.5. List of all models run

Table 3.7.5. Complete summary showing GDM model deviance, variance explained, model intercept, and variable importance for spatial taxonomic beta-diversity

Group	Response	GDM_dev	Null_dev	var_exp	Intercept	Geographic	Elevation	Stem Density	Nearest Anthropogenic Edge	Human Presence	Forest Composition	Ratio
All	Total_all	104.19	176.2	40.87	0.66	24.375	19.831	0	0	18.354	18.248	-
All	Total_geo	144.03	176.2	18.26	0.87	0	0	0	0	0	0	-
All	Total_env	121.76	176.2	30.89	0.94	0	0	0	0	0	0	-
All	Turn_all	127.37	218.03	41.58	0.5	27.511	25.228	0	0	24.339	0	-
All	Turn_geo	180.32	218.03	17.3	0.67	0	0	0	0	0	0	-
All	Turn_env	152.34	218.03	30.13	0.78	0	0	0	0	0	0	-
Edible	Total_all	157.09	230.25	31.77	0.66	27.176	0	19.312	0	14.071	26.86	-
Edible	Total_geo	199.8	230.25	13.22	0.85	0	0	0	0	0	0	-
Edible	Total_env	177.01	230.25	23.12	0.98	0	0	0	0	0	0	-
Edible	Turn_all	208.1	287.99	27.74	0.42	32.361	0	15.036	15.236	24.005	0	-

Table 3.7.5 (cont.). Complete summary showing GDM model deviance, variance explained, model intercept, and variable importance for spatial taxonomic beta-diversity

Group	Response	GDM_dev	Null_dev	var_exp	Intercept	Geographic	Elevation	Stem Density	Nearest Anthropogenic Edge	Human Presence	Forest Composition	Ratio
Edible	Turn_geo	249.99	287.99	13.19	0.63	0	0	0	0	0	0	-
Edible	Turn_env	233.99	287.99	18.75	0.7	0	0	0	0	0	0	-
Inedible	Total_all	120.16	190.19	36.82	0.71	32.535	19.989	0	0	21.543	0	-
Inedible	Total_geo	157.14	190.19	17.38	0.89	0	0	0	0	0	0	-
Inedible	Total_env	142.98	190.19	24.83	1.04	0	0	0	0	0	0	-
Inedible	Turn_all	142.2	251.47	43.45	0.48	22.417	26.975	0	0	26.645	0	-
Inedible	Turn_geo	212.38	251.47	15.54	0.67	0	0	0	0	0	0	-
Inedible	Turn_env	166.74	251.47	33.7	0.76	0	0	0	0	0	0	-

Table 3.7.6. Complete summary showing results from GDM run with clusters as a variable. The results shown include GDM model deviance, variance explained, model intercept, and variable importance for spatial taxonomic beta-diversity

Group	Response	GDM_dev	Null_dev	var_exp	Intercept	Geographic	Elevation	Stem Density	Human Presence	Forest Composition
All	Total_all	127.37	218.03	41.58	0.50	27.52	25.57	0.00	24.42	0.00
All	Total_geo	180.32	218.03	17.30	0.67	0.00	0.00	0.00	0.00	0.00
All	Total_env	152.34	218.03	30.13	0.78	0.00	0.00	0.00	0.00	0.00
All	Turn_all	93.86	176.20	46.73	0.62	19.90	17.30	12.02	16.24	14.82
All	Turn_geo	144.03	176.20	18.26	0.87	0.00	0.00	0.00	0.00	0.00
All	Turn_env	110.25	176.20	37.43	0.87	0.00	0.00	0.00	0.00	0.00
Edible	Total_all	127.37	218.03	41.58	0.50	27.53	25.14	0.00	24.28	0.00
Edible	Total_geo	180.32	218.03	17.30	0.67	0.00	0.00	0.00	0.00	0.00
Edible	Total_env	152.34	218.03	30.13	0.78	0.00	0.00	0.00	0.00	0.00
Edible	Turn_all	93.86	176.20	46.73	0.62	19.90	17.42	12.31	16.33	14.82
Edible	Turn_geo	144.03	176.20	18.26	0.87	0.00	0.00	0.00	0.00	0.00

Table 3.7.6 (cont.). Complete summary showing results from GDM run with clusters as a variable. The results shown include GDM model deviance, variance explained, model intercept, and variable importance for spatial taxonomic beta-diversity

Group	Response	GDM_dev	Null_dev	var_exp	Intercept	Geographic	Elevation	Stem Density	Human Presence	Forest Composition
Edible	Turn_env	110.25	176.20	37.43	0.87	0.00	0.00	0.00	0.00	0.00
Inedible	Total_all	220.80	287.99	23.33	0.49	49.91	0.00	15.62	26.72	0.00
Inedible	Total_geo	249.99	287.99	13.19	0.63	0.00	0.00	0.00	0.00	0.00
Inedible	Total_env	254.36	287.99	11.68	0.85	0.00	0.00	0.00	0.00	0.00
Inedible	Turn_all	182.01	230.25	20.95	0.81	47.88	0.00	0.00	0.00	36.89
Inedible	Turn_geo	199.80	230.25	13.22	0.85	0.00	0.00	0.00	0.00	0.00
Inedible	Turn_env	205.13	230.25	10.91	1.20	0.00	0.00	0.00	0.00	0.00

Except for the edible species group, model 3 recorded 37.43 to 10.91% variance explained while model 1 had the least variable explained of 18.26% to 13.19% (see Table 3.7.4 in Appendix 3.7.5). There was a reduction in the number of significant variables with the addition of clusters from a total of seven to six variables; however, there was a general increase in variable importance values, especially for the edible species group. The five variables identified by the GDMs model to be significant predictors of beta-diversity in the region were geographic distance, elevation, stem density, DCHP, and forest composition (Table 3.7.6 in Appendix 3.7.4). However, like in the main analysis, except for turnover in inedible species where elevation was the predictor with highest variable importance, the predictor with highest variable importance in all other models was geographic distance (Table 3.7.7). The only two generated predictors of total beta-diversity in the edible species group (see Table 3.7.7 and Figure 3.7.3 in Appendix 3.7.5) were geographic distance with the highest variable importance (47.88), and forest composition (36.89). In order of importance, the three predictors of turnover resultant beta-diversity in edible species group (see Figure 3.7.3 in Appendix 3.7.5) were geographic distance (49.91), DCHP (26.72) and stem density (15.62). There was no change in the significant variables and variable importance values results for inedible species, with the inclusion of clusters as an additional variable (see Figure 3.7.3 and 3.7.4 in Appendix 3.7.5). Although the models for cluster one, two and three did not run due to few data points, in cluster four, there was a significant increase in human influence variables as predictors of total beta diversity in inedible species category and less important in edible category (Figure 3.7.5 and Figure 3.7.6).

Table 3.7.7. The GDM result summary shows model deviance, variance explained, model intercept, and variable importance for the spatial taxonomic beta-diversity of the region. Figures bold italics indicate overall model with highest variance explained, and other figures in bold have highest, second highest, third most important variable. "Total" refers to total Sorenson's beta diversity while "Turn" refers to the Simpson's turnover partition of beta diversity.

Groups	All		Edible		Inedible	
	Total	Turn	Total	Turn	Total	Turn
GDM Deviance	93.86	127.37	182.01	220.80	120.16	142.20
Null Deviance	176.20	218.03	230.25	287.99	190.19	251.47
Intercept	0.62	0.50	0.81	0.49	0.71	0.48
Model 1	***46.73***	***41.58***	***20.95***	***23.33***	***36.82***	***43.45***
Model 2	18.26	17.30	***13.22***	***13.19***	17.38	15.54
Model 3	***37.43***	***30.13***	10.91	11.68	***24.83***	***33.70***
Shared Variance (%)	8.96	5.85	3.18	1.54	5.39	5.79
Variable importance						
Geographic distance (m)	**19.90**	**27.53**	**47.88**	**49.91**	**32.54**	**22.44**
Elevation (masl)	**17.42**	**25.14**	NA	NA	**19.67**	**26.72**
Stem Density (stems/ha)	12.31	NA	NA	**15.62**	NA	NA
DCHP (m)	**16.33**	**24.28**	NA	**26.72**	**21.32**	**26.51**
Forest Composition	14.82	NA	**36.89**	NA	NA	NA

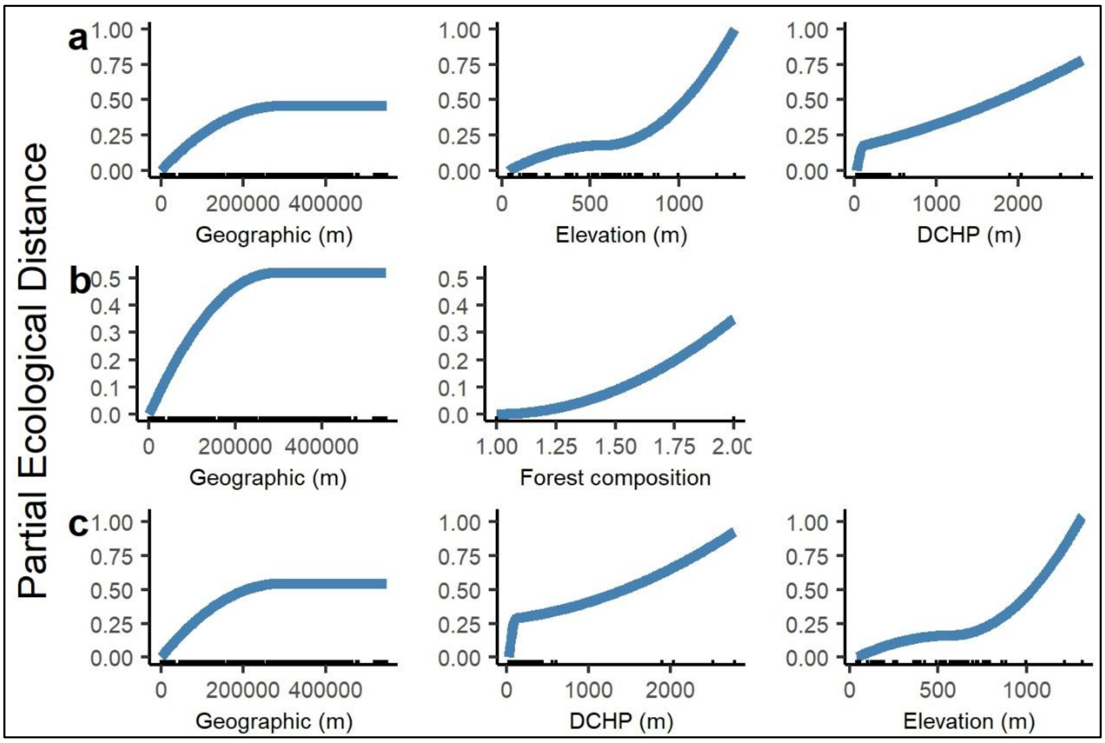


Figure 3.7.3. Plotted I-splines of the three variables with highest importance scores from the GDM analyzing the spatial relationship between geographic gradients, environmental variables, and tree species composition. Plots on row (a) are the Total Sorensen's beta-diversity for the entire region, (b) are the Total Sorensen's beta-diversity *for the edible species category, and (c) Total Sorensen's beta*-diversity *for the inedible species. Plots are organized from left to right in order of increasing variable importance.*

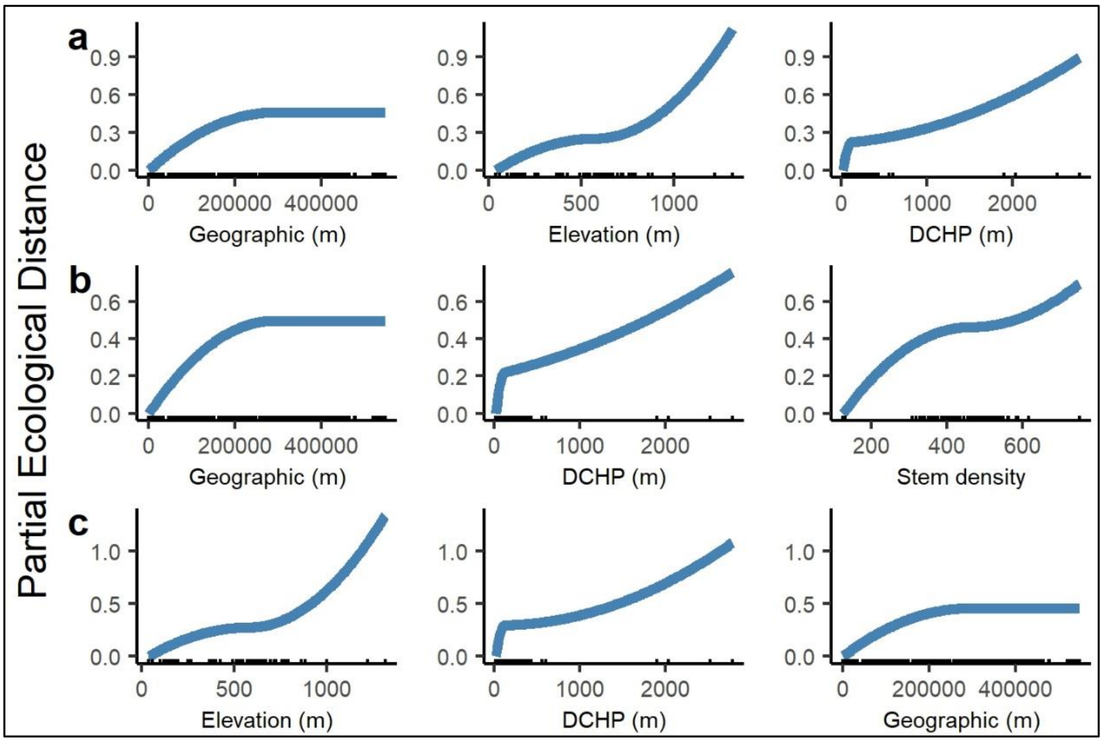


Figure 3.7.4. Plotted I-splines of the variables with highest importance scores from the GDM analysing the spatial relationship between geographic gradients, environmental variables, and tree species composition. Plots on row (a) are the Total Simpson's turnover for the entire region, (b) are the Total Simpson's turnover for the edible species category, and (c) Total Simpson's turnover for the inedible species. Plots are organized from left to right in order of increasing importance.

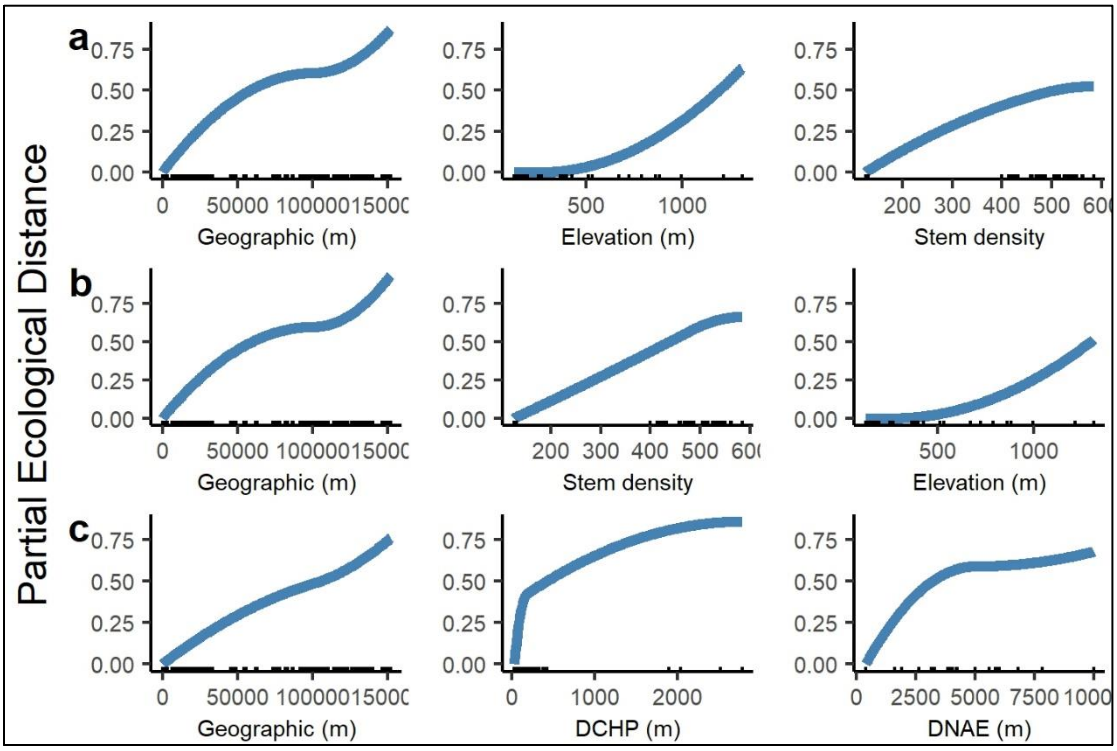


Figure 3.7.5. Plotted I-splines of the three variables with highest importance scores from the GDM analyzing the spatial relationship predictors of total beta diversity in cluster four. Plots on row (a) are the Total Sorensen's beta-diversity for the entire region, (b) are the Total Sorensen's beta-diversity for the edible species category, and (c) Total Sorensen's beta-diversity for the inedible species. Plots are organized from left to right in order of increasing importance.

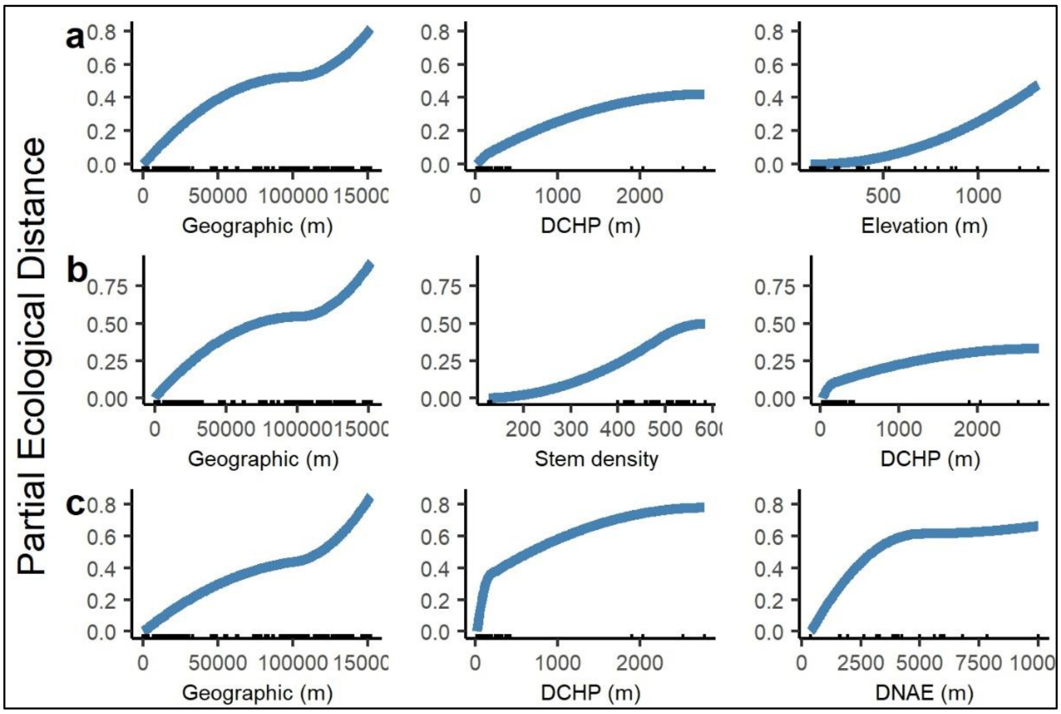


Figure 3.7.6. Plotted I-splines of the variables with highest importance scores from the GDM analysing the spatial relationship predictors of total beta diversity in cluster four. Plots on row (a) are the Total Simpson's turnover for the entire region, (b) are the Total Simpson's turnover for the edible species category, and (c) Total Simpson's turnover for the inedible species. Plots are organized from left to right in order of increasing importance.

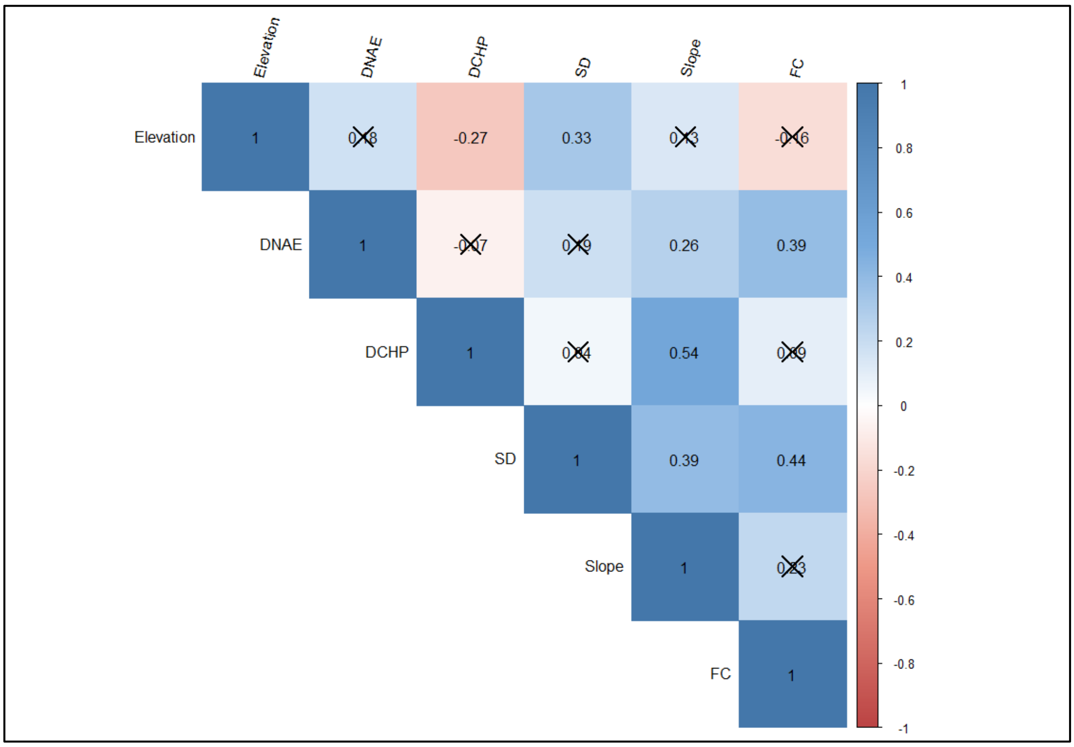


Figure 3.7.7. Plots showing correlation coefficient and non-significant correlations (at p < 0.05) of variables included in the model

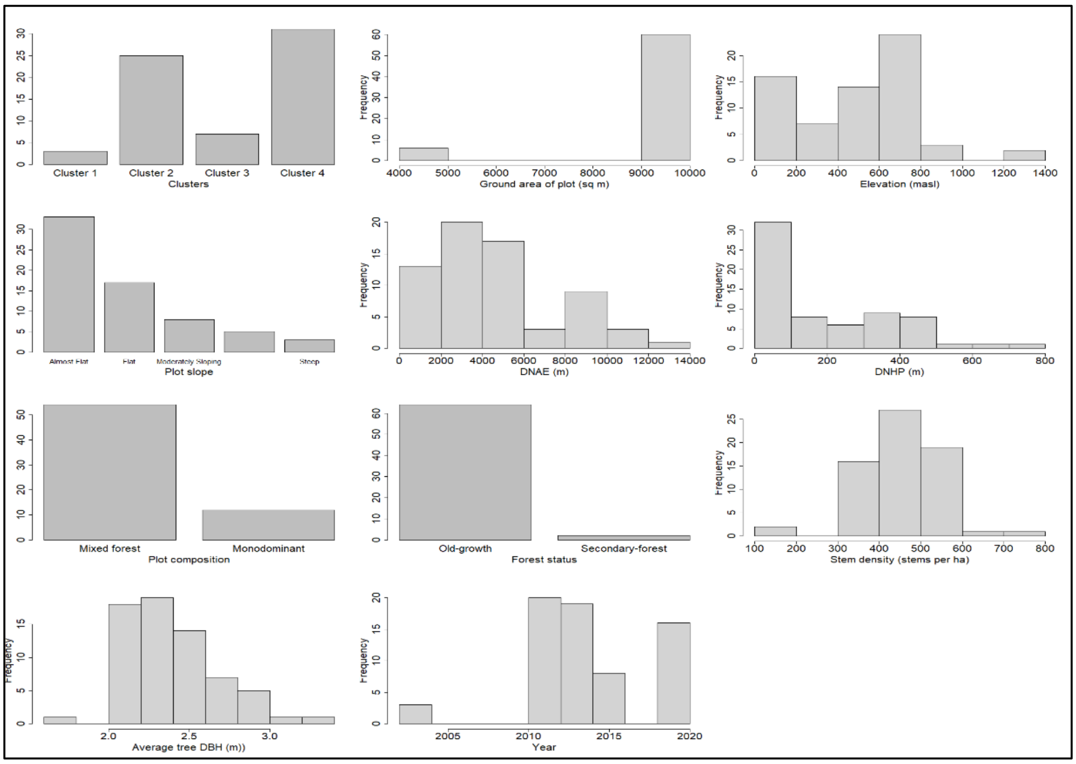


Figure 3.7.8. Distribution of predictor variables used in the study

Table 3.7.8. Mantel's correlation of geographical distance matrix generated from plot longitude and latitude and other environmental variables.

Variable	Mantel's correlation
Elevation	0.23
Slope	-0.02
Stem Density	0.07
DNAE	0.14
DCHP	-0.10
Forest Composition	0.20
Forest Structure	0.05

CHAPTER FOUR: THE EFFECT OF AIR TEMPERATURE AND PRECIPITATION ON LEAF PHENOLOGY IN AN AFRO-TROPICAL RAINFOREST

4.1. ABSTRACT

Tropical rainforests provide valuable ecological services that are dependent on the phenological responses of forest vegetation, which are expected to be influenced by climate change. Understanding the temporal dynamics of these responses in the Oban Forest, south-eastern Nigeria is crucial for preserving the ecological integrity of this important ecosystem and sustaining its economic and cultural importance to the 39 forest-dependent/support zone human communities that depend on it. This study investigated the annual and monthly seasonal variations in the Enhanced Vegetation Index (EVI) due to precipitation and air temperature fluctuations in Oban Forest between 2002 to 2022. EVI was used as an indicator for leaf phenology because it is sensitive to changes in leaf chlorophyll, which is linked to flowering and fruiting events. The data were subjected to correlation, autocorrelation and generalized additive regression Model (GAM) analysis. The results reveal a clear seasonal cycle in EVI, with the highest values recorded between March and October. Precipitation was identified as the most important climatic factor driving the changes in EVI observed in Oban Forest. The EVI cycle identified here provides an important context for the provision of forest services to the local communities, many of which are also expected to follow a seasonal cycle. Changes in the seasonality and timing of precipitation could be expected to bring about changes in the timing of these services, with significant implications for the economic and livelihood sustenance of forest-dependent local communities. Accurate models of how forest services respond to such climate changes will help support forest-dependent communities in adapting to their impacts.

4.2. INTRODUCTION

Tropical rainforest ecosystems play an essential role in the provision of valued ecological services, including a wide range of tangible (such as food and other materials) and intangible (such as environmental regulation) services that contribute significantly to the well-being of humans (Hong & Saizen, 2019; Vauhkonen, 2018). African tropical rainforests are amongst the world's most ecologically valuable and biologically diverse ecosystems (Kothandaraman et al., 2020; Alamgir et al., 2016). They provide regulating, cultural, supporting and provisioning ecosystem services, including providing habitat for numerous species of plants and animals, climate regulation, and carbon sequestration. Many of these services are at least partially dependent on responses of the forest leaf phenology, which itself is expected to be influenced by a warming climate (Englund, Berndes and Cederberg, 2017; Hong and Saizen, 2019; Mengist and Soromessa, 2019).

Many African communities rely on tropical forests for their livelihoods, such as harvesting non-timber forest products (including foraging for food) or engaging in ecotourism. Modification of the physiology, composition and diversity of species in forest ecosystems can directly or indirectly affect tropical forests, thus, altering the service provisioning capacity of forest ecosystems (Morin et al., 2018; Pau et al., 2018a; Santos, Disney and Chave, 2018; Vauhkonen, 2018; Ding, Liang and Peng, 2019; Hong and Saizen, 2019; Bera, Saha and Bhattacharjee, 2020; Montgomery et al., 2020; Naif, Mahmood and Al-Jiboori, 2020; Zambrano et al., 2020; Ellis et al., 2021). The production of flower buds and flowers have been linked to the onset of rainfall and photoperiod in African forest (Dunham et al., 2018; Venter and Witkowski, 2019; Adole et al., 2019).

The Oban Forest, which has 39 forest-dependent/support zone communities within and around the forest, is a fundamental source of cultural dietary needs for these communities (Asuk et al., 2023; Friant et al., 2019). Leaf phenology of trees in the tropical forest are synchronized with seasonal changes as well as the shifts in time and duration of rainfall, temperature, and light intensity which have been reported to range from sub-annual to perennial cycles (Bush et al., 2017; Adamescu et al., 2018; Richardson et al., 2013; Gray and Ewers, 2021; Cleland et al., 2007). This change in the leaf phenological cycles due to the seasonality in climate variables makes it difficult to predict the availability of these food resources thus ultimately impacting the cultural dietary needs of these communities (Friant et al., 2019; Cleland et al., 2007; Adamescu et al., 2018). Thus, understanding temporal dynamics in phenological responses of the tropical rainforest to temperature and precipitation can help in better comprehending the relationships between the forest leaf phenology and how they are affected by environmental changes such as climate change and inform sustainable management practices that can maintain the health and productivity of these forests while also supporting local communities (Hong & Saizen, 2019).

Satellite-derived indices of forest greenness and productivity have shown excellent prospects in the assessment of forest leaf phenology to climatic drivers such as precipitation and temperature at regional and global scales (Camps-Valls et al., 2021; Ding et al., 2019; Medlyn et al., 2011; Morin et al., 2018). Enhanced vegetation index (EVI) is one of the most researched indices used in monitoring, measuring, or assessing the vegetation health forests (Camps-Valls et al., 2021; Chaves et al., 2019; Lim et al., 2020; Samasse et al., 2020; Zheng et al., 2019). Most vegetation indices have some degree of limitations in compensating for the non-linear issues associated with reacting to the presence of green leaves rather than photosynthesis, which could result in a misleading estimation of vegetation growth and productivity (Camps-Valls et al., 2021). EVI is used as an indicator in this study because it has been found to minimise these non-linearities. EVI is closely linked to vegetation chlorophyll content because it is sensitive to changes in chlorophyll which are driven by climatic changes and displays a proportionate response of forest vegetation across different ecozones (Abera et al., 2018; Camps-Valls et al., 2021; Cho et al., 2015; He et al., 2021; Li et al., 2023; Lim et al., 2020). In addition, changes in leaf phenology, such as the timing and duration of leaf growth and maturation, can also be used as indicators for predicting the subsequent onset of flowering buds and fruiting cycles (Bucher and Römermann, 2021).

Plant leaf phenology in the tropical rainforest can be significantly influenced by the fluctuation, intensity, and duration of precipitation, because of its impacts on moisture and nutrient availability, which might either promote increased or reduced photosynthesis, growth, and productivity (Gou et al., 2022). The degree and duration of extreme and average temperature events also provide a first-order control of forest growth and productivity. In some Afrotropical forests, it has been hypothesised that phenological events (such as flowering) might not be triggered until the temperature drops below a certain threshold value (Bush et al., 2020) - known as the critical minimum temperature hypothesis. In tropical rainforests, which are characterised by generally high and stable temperatures, the temperature has been found to have minimal impact on EVI. However, extreme temperature events such as droughts or heat waves like the El Nino events can significantly impact the response of EVI from the vegetation (Samanta et al., 2010).

The effect of temperature and precipitation in triggering significant seasonal phenological cycles has shown promise for understanding spatiotemporal trends in vegetation patterns (Yan et al., 2019; Szabó et al., 2019). The onset of the rainy season is crucial in determining the timing of flowering and fruiting. Higher temperatures during the dry season lead to early leaf fall and shorter fruiting periods (Muller-Landau et al., 2021). The phenology of the tropical forest, specifically in tropical forests located in the Amazon, Panama and Costa Rica Forest and other seasonally dry tropical forests, has shown some relationship with temperature and precipitation, suggesting that the forest was susceptible to climate variability (Smith et al., 2020; Wagner et al., 2016).

There is still much uncertainty in studying the vegetation greenness-climate relationship in tropical forests, especially those in Africa where few studies have been carried out (Brown, 2014; Zhou et al., 2014; Adamescu et al., 2018; Jiang et al., 2019; Bush, Whytock, Bahaa-El-din, et al., 2020). Most forest greenness and productivity studies focus extensively on global and continental forest trends, leaving regional patterns largely understudied (Nakamura et al., 2017). Climate change is likely to affect the timing of phenological events (green-up and senescence) at a local scale, with potentially substantial impacts on the ecosystem and its biodiversity. This study focuses on the Oban Forest, in the Oban division of Cross River National Park in South-eastern Nigeria. Oban Forest has a total of 39 forest dependent/support zone human communities within the National Park, making the ecosystem both economically and ecologically important (Adesoye and Akinwunmi, 2016; Agaldo, Gwom and Apeverga, 2016; Asuk et al., 2023). As a biodiversity hotspot with high levels of precipitation and temperature, Oban Forest is ideal for investigating the climate-EVI relationship. Therefore, there is an urgent need for further research to understand these dynamics better and develop strategies to mitigate the impacts of climate change on Afrotropical rainforests. This could be a helpful management tool for guiding conservation strategies and sustainable utilisation of the forest ecosystem. The study objective is to evaluate the response of forest leaf phenology (EVI) to changes in air temperature and precipitation between 2002 and 2022. The study seeks to answer three research questions: 1) What is the phenological cycle present in Oban Forest? 2)

What is the relationship of this cycle with air temperature and precipitation? 3) Is there a multiannual trend in EVI, air temperature and precipitation?

4.3. MATERIAL AND METHODS

4.3.1. Study Area

Oban Division of Cross River National Park is between longitude 8^o 17.487’ to 8^o 54.677’ East and latitude 5^o 5.607’ and 5^o 49.265’ North in Cross River State, Southern Nigeria (Figure 4.1). The Division covers an estimated area of ~251,345 ha, has a total of 39 forest dependent/support zone human communities within the National Park and is continuous with the Korup National Park and Ejagham Forest Reserve of Cameroon (Adeyemi, 2016; Enuoh & Ogogo, 2018). The forest is a lowland and submontane moist tropical rainforest with 3,000 mm to 3,500 mm average precipitation per annum, 23 °C to 37 °C average monthly temperature, rugged terrain, and varying elevation of ~100 m to over 1000 m above sea level (Agaldo et al., 2016; Asuk et al., 2023).

4.3.2. Data collection and processing

The extensive data on EVI, temperature and precipitation used for the study were collected by NASA EOSDIS Land Processes Distributed Active Archive Centre (LP DAAC) (available for download at https://lpdaac.usgs.gov) (USGS, 2021; Gorelick et al., 2017). Data were compiled and pre-processed using google earth engine (GEE) (USGS, 2021; Gorelick et al., 2017) and then exported in .tiff format using the batch export GEE task with tampermonk (Kong, 2017). Images from EVI, precipitation and temperature were masked using the forest outline polygon of Oban Forest. All daily (CHIRPS) and 16-days (EVI) images were aggregated into monthly mean collections. Yearly means were also computed for all variables to assess the possible differences in annual EVI, air temperature and precipitation trends.

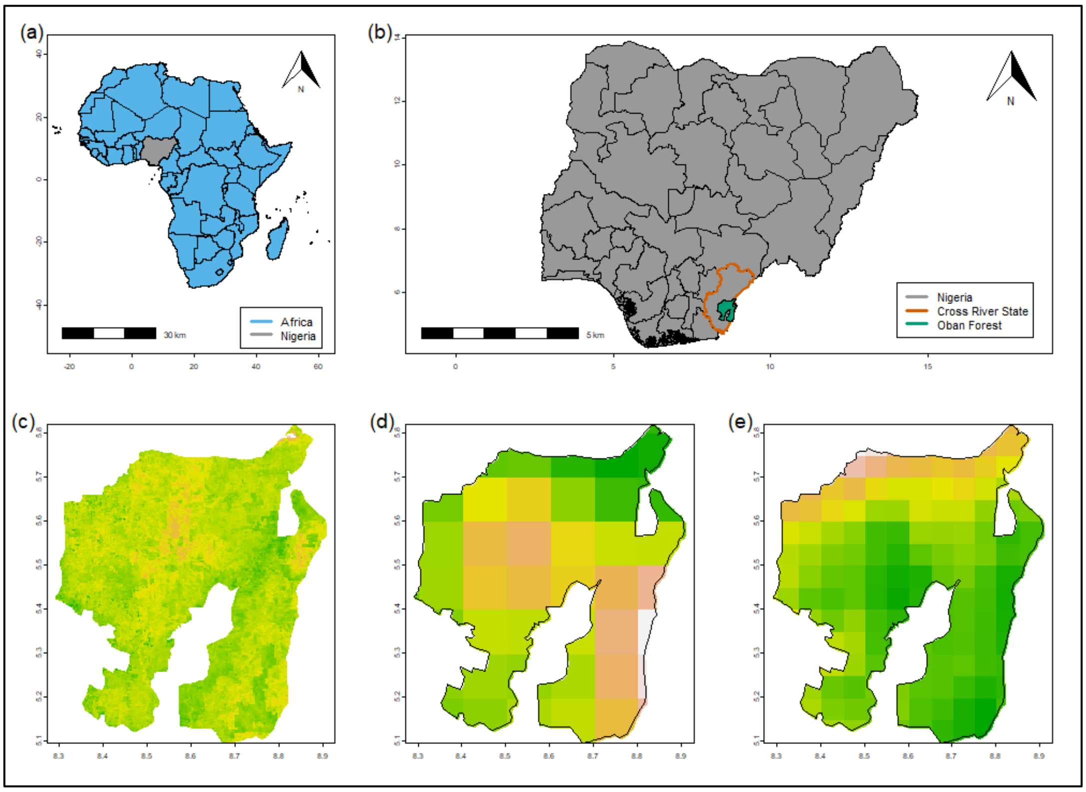


Figure 4.1. Map describing the location of Oban Forest within Nigeria and Africa. (a) Map of Africa showing the location of Nigeria. (b) Map of Nigeria showing Oban Forest. Grid cells images for EVI at 250 m resolution (c), air temperature at 11 km resolution (d) and precipitation at 5 km resolution (e)

4.3.2.1. Vegetation (EVI) data collection

EVI data used as a proxy for forest leaf phenology were from the terra (MOD13Q1) and aqua (MYD13Q1) moderate resolution imaging spectroradiometer (MODIS) Version 6.1 vegetation indices collected at 16 days intervals with 250 m resolution (USGS, 2021; Didan, 2021). The high spatial resolution, long time series, availability of multiple vegetation indices, and free and open access of MOD13Q1 make it an excellent dataset for leaf phenology studies at a local scale (Chakraborty et al., 2018; Szabó et al., 2019; Ghebrezgabher et al., 2020; Lim et al., 2020; Norris and Walker, 2020; Seong et al., 2020; Stan et al., 2020). Studies have also successfully combined EVI bands from terra and aqua MODIS products to improve image quality (Muhammad and Thapa, 2020; Zhao et al., 2020; Hall et al., 2019; Weiss et al., 2014). In addition, MODIS Land Cover Dynamics (MCD12Q2) version 6.1 was used to generate data on EVI amplitude, duration of active EVI event, which is the number of days between Greenup (days from 01-01-1970 when EVI first crossed 15% of the segment EVI amplitude) and date dormancy (days from 01-01-1970 when EVI last crossed 15% of the segment EVI amplitude) (Gray et al., 2022). EVI data were parsed in GEE for quality assurance (see Table 4.7.1 in Appendix 4.7.1) using the bits from VI quality, VI usefulness, aerosol quantity, adjacent cloud detected, atmosphere BRDF correction, mixed clouds, land/water mask, possible snow/ice, and possible shadow as described in the user guide (Didan, Munoz, & Huete, 2015).

Because of the cloud in the EVI images for the area, after parsing for pixel quality, some months had no pixels left. To improve the quality of EVI data, we computed the mean of EVI images from MODIS terra (passes over each point on the Earth's surface at approximately 10:30 am local time) and MODIS aqua (passes over each point on the Earth's surface at approximately 1:30 pm local time) products, as done in some studies (Muhammad and Thapa, 2020; Zhao et al., 2020; Hall et al., 2019; Weiss et al., 2014) which reduced the number of months with no data (see Figure 4.2). However, missing values were still present after computing the mean pixel values. The ‘na_kalman’ function in the “imputeTS” R package provides a powerful and flexible tool for filling in missing values in a time series. This is based on state-space modelling and Kalman filtering principles, a statistical model that can estimate missing values in time series by describing how the time series would evolve (Moritz and Bartz-Beielstein, 2017; Kalman, 1960). The Kalman filter and smoother can efficiently calculate the likelihood of hidden variables in a linear state space model based on observed data. These formulas assume that the model's parameters are already known and aim to determine the likelihood of the hidden (missing) variables (Kalman, 1960).

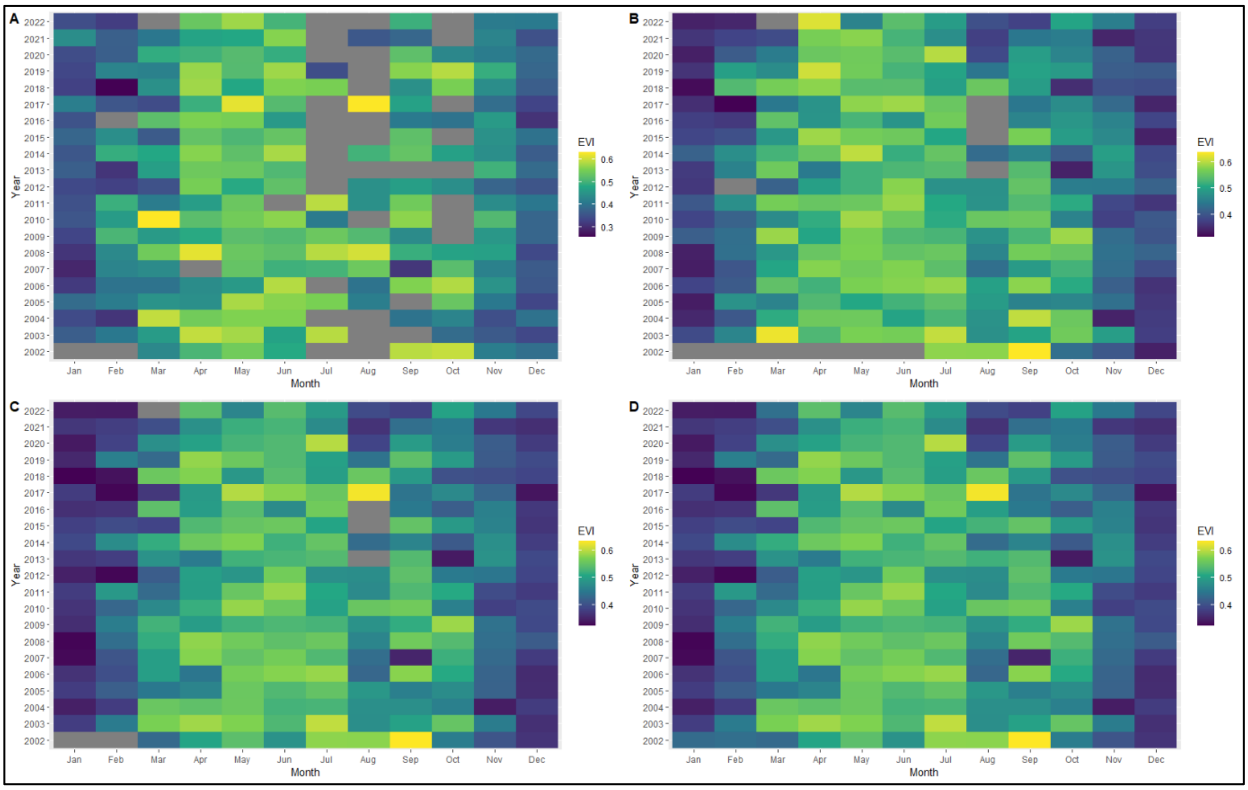


Figure 4.2. Heat map plot showing mean pixels for terra EVI from MOD13Q1 (A), aqua EVI from MYD131 (B), mean value from combining the terra and aqua EVI images (C) and the mean value from combining the terra and aqua EVI images with missing values filled using Kalman smoothing (D).

4.3.2.2. Precipitation and air Temperature data collection

The study utilised 5 km resolution Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) daily precipitation version 2.0 data to generate monthly precipitation data (Funk et al., 2015). CHIRPS precipitation has been found to be reliable for studying precipitation trends in tropical Africa (Didi Sacré Regis et al., 2020; Dinku et al., 2018; Gou et al., 2022; Ocampo-Marulanda et al., 2022; Paredes-Trejo et al., 2020). Air temperature generated in the ERA5-

Land Monthly Aggregated generated by ECMWF Climate Reanalysis data available at ca. 11 km resolution (Muñoz-Sabater et al., 2021) was used for the study. This is a monthly average air temperature at 2 m above ground (Food and Agriculture Organization (FAO) of the United Nations, 2022). No aggregation was done for the monthly temperature data.

4.3.3. Data Analysis

Pre-processed data from GEE were analysed in RStudio. The ‘rast’ function in the “terra” package (Hijmans et al., 2009) was used to upload all images into RStudio. Then, the ‘global’ function was used to calculate the mean, minimum and maximum monthly pixel value from the raster images. A combination of packages, including “tibble” (Wickham, Francois, et al., 2023a), “tidyr” (Hadley et al., 2023) and “ggplot2” (Wickham, 2016), were used to modify and generate mat plots from minimum, mean and maximum monthly value for the three studied variables.

4.3.3.1. Normality in the distribution of variables

The Shapiro-Wilk normality test was applied to assess normality in the distributions of EVI, air temperature and precipitation data, with a statistical significance ($p\text{-value} < 0.05$) indicating a deviation from normality and a non-significant ($p\text{-value} > 0.05$) indicating that the data tested were normally distributed. Q-Q plots were also used to observe the distance between the data distribution points and the normality reference line. Shapiro-Wilk normality test was performed using the ‘shapiro.test’ function, and the Q-Q plots were generated with ‘qqnorm’ and ‘qqline’ functions in R. This informed our choice of using a non-parametric regression analysis for the study.

Based on central limit theory (CLT) assumptions, sample sizes of 30 and above are considered to have a population that approaches normality (Sawada, 2021; Dunn and Shultis, 2023). Although the sample size for this study (n = 252) meets the CLT assumptions, the results from the Shapiro-Wilk normality test suggested some caution would then be needed in the interpretation of parametric model results. To avoid misinterpretation of the relationship between response and predictor variables, a nonparametric regression, the GAM model was used for the analysis.

4.3.3.2. Correlation analysis to assess the relationship between EVI, temperature and precipitation

Spearman rank-order correlation was used to test the relationship between mean EVI, mean air temperature and mean precipitation values. The analysis used the 'chart.Correlation' function in the R package "PerformanceAnalytics" (Brian et al., 2022). The results generated an inter-comparison between all three variables with a combination of fitted scatter plots, histograms, and correlation coefficients. Using the 'kendall' function in the "Kendall" package (McLeod, 2022), the Kendall rank correlation (see equations 1 – 3) was used to confirm further the dependence/independence of EVI on temperature and precipitation (McLeod, 2022). This was done for monthly and annual aggregates of the studied variables.

$$\tau = S/D \qquad \text{Equation 1}$$

$$S = \sum_{i<j}(\mathrm{sign}(\mathrm{x[j]} - x[i]) \times sign(y[j] - y[i])) \qquad \text{Equation 2}$$

$$D = n(n-1)/2 \qquad \text{Equation 3}$$

Where: τ = Kendall's rank correlation coefficient, tau

S = Score

D = denominator

x and y are vectors or variables to be tested.

4.3.3.3. Times series trend, trend direction and seasonality analysis

The Mann-Kendall trend test in R package “Kendall” (Brossart et al., 2018; McLeod, 2022) was used to calculate the monthly and annual trend and trend direction observed in EVI, temperature and precipitation from 2002 to 2022. The function ‘MannKendall’ (with null hypothesis stating that there is no trend in the time series) yields a Kendall tau value (either a negative or positive) indicating the direction of the trend and a *p-value* indicating if there is a significant observed trend in the time series (*p-value* < 0.05) or that there is no trend in the times series (*p-value* > 0.05). Furthermore, a seasonally adjusted Mann-Kendall trend test with the ‘SeasonalMannKendall’ function was used to detect cumulative monotonic trends in the data across the years, producing Kendall’s tau and p-value (McLeod, 2022). A monotonic trend is a significant cumulative change (increase or decrease) in the values of variables over time without any reversals enough to compensate for the change (Helsel et al., 2020). This gives information on the general direction of the time series for the duration of the period considered.

4.3.3.4. Regression analysis to test the response of EVI to monthly variation in air temperature and precipitation

The generalised additive regression model (GAM) in the “gam” R package (Hastie, 2023) was used to assess the relationship between the EVI cycle and predictor variables (annual, monthly, and lagged air temperature and precipitation). The ‘gam.check’ function in “mgcv” R package (Wood, 2017) was used to validate the model by checking the model’s residuals for signs of heteroskedasticity or autocorrelation; and whether the smooth terms in the model are overly or insufficiently wiggly (this is tested formally using a p-value for each smooth). In addition, a multiple linear regression model (MLRM) was also conducted and compared with the GAM using the ‘anova’ function. A parametric and nonparametric test were compared because although the data was not normally distributed and based on central limit theory (CLT) assumptions, sample sizes of 30 and above are considered to have a population that approaches normality (Sawada, 2021; Dunn and Shultis, 2023). Although the sample size for this study (n = 252) met the CLT assumptions, the results from the Shapiro-Wilk normality test suggested some caution would then be needed in the interpretation of parametric model results. To avoid misinterpretation of the relationship between response and predictor variables, a nonparametric regression, the GAM model was used for the analysis. The GAM results outperformed the MLRM; thus, the GAM was adopted for the study (see results in Table 4.6.2 and Figure 4.7.1 in Appendix 4.7.2).

$$g(E(y_i)) = \beta_0 + f_1(x_{i1}) + \cdots + f(x_{i2}) + \mathcal{E}_i, \qquad \text{Equation 4}$$

Where: some exponential family distribution

i = 1, …, N

g = link function (identical, logarithmic, or inverse)

y = model response variable (EVI)

$x_1, \ldots, x_p$ = the independent variables (air temperature and precipitation)

β_0 = model intercept

$f_1, \ldots, f_p$ = are unknown smooth functions

$\mathcal{E}$ = is an i.i.d. random error

Multiple linear regression model was used to test the effect of temperature and precipitation on EVI, EVI amplitude and duration of EVI event. This was done to assess the difference in annual and monthly response of EVI to air temperature and precipitation.

4.3.3.5. Detection of lags in the effect of air temperature and precipitation in EVI

A combination of autocorrelation (ACF) and partial autocorrelation (PACF) was used to assess the correlation between variables and their lagged derivates from month one (lag0) to month thirteen (lag12). In addition, lag cross-correlation (CCF) was used to find the lagged correlation between EVI and pairs of predictor variables (air temperature and precipitation). ACF and PACF analysis and generation of plots were done using a combination of three R packages; “tidyverse” (Wickham & RStudio, 2023) and “lubridate” (Wickham, Vaughan, et al., 2023b) were used for modifying the data to format, while the “timetk” package (Matt et al., 2023) was used to generate plots for ACF, PACF, and CCF using the ‘plot_acf_diagnostics”.

4.4. RESULTS

4.4.1. Seasonal cycles of EVI, temperature and precipitation

Average, minimum, and maximum precipitation patterns were similar but differed in the value ranges (see Figure 4.3 G, H, I and Figure 4.4). The range of values for average, minimum and maximum EVI for Oban Forest were not similar, as also observed in air temperature and precipitation (see Figure 4.3 A, B, C and Figure 4.7.2 in Appendix 3.7.3). Peak EVI values were observed from March to October for average EVI values and to November for maximum EVI values, while minimum EVI values didn’t differ much. The pattern in EVI values suggests a combined effect of increased precipitation and reduced temperature on the increase in EVI in Oban Forest in the period January to April.

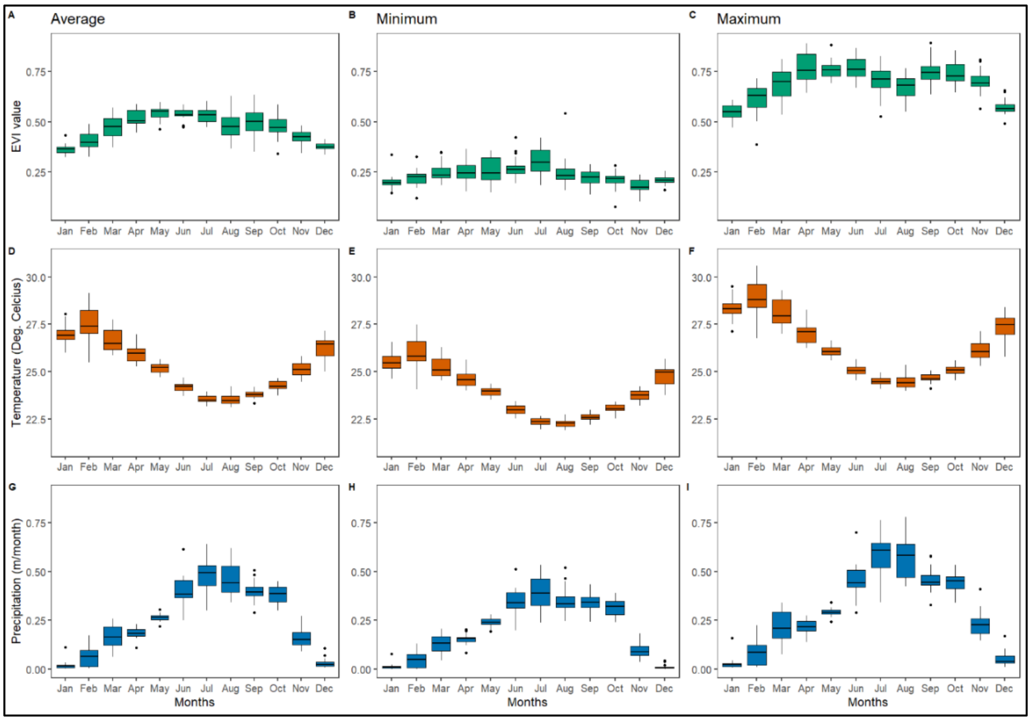


Figure 4.3. Boxplots showing annual variability in EVI (A, B, C), air temperature (D, E, F), and precipitation (G, H, I) values within each month. Organized left to right, the plots display average (A, D, G), minimum (B, E, H), and maximum (C, F, I) values, respectively, assessed across year.

4.4.2. Trend detection in EVI, air temperature and precipitation at monthly and annual scales

A Kendall monthly seasonality test further revealed that EVI had a significant (p-value = 0.0009) negative trend (tau = -0.151). Air temperature also had a significant (p-value < 0.001) positive trend (tau = 0.305), and precipitation had a significant (p-value = 0.007) negative trend (tau = -0.123). A significant negative monotonic trend (tau = -0.098, p-value = 0.021, n=252) was observed in EVI (Figure 4.4a). A negative non-significant trend was observed in precipitation (Figure 4.4c), while a positive non-significant monotonic trend was observed in air temperature (Figure 4.4b). In addition, a significant negative trend was seen in the yearly EVI amplitude. As seen in Figure 4.5, there was a negative non-significant (p-value > 0.05) annual trend in EVI (tau = -0.053) and precipitation (tau = -0.274), air temperature exhibited a positive significant annual trend (tau = 0.411, p-value = 0.012, 20) while there was a non-significant (p-value > 0.05) annual trend in the duration of EVI events (tau = -0.316).

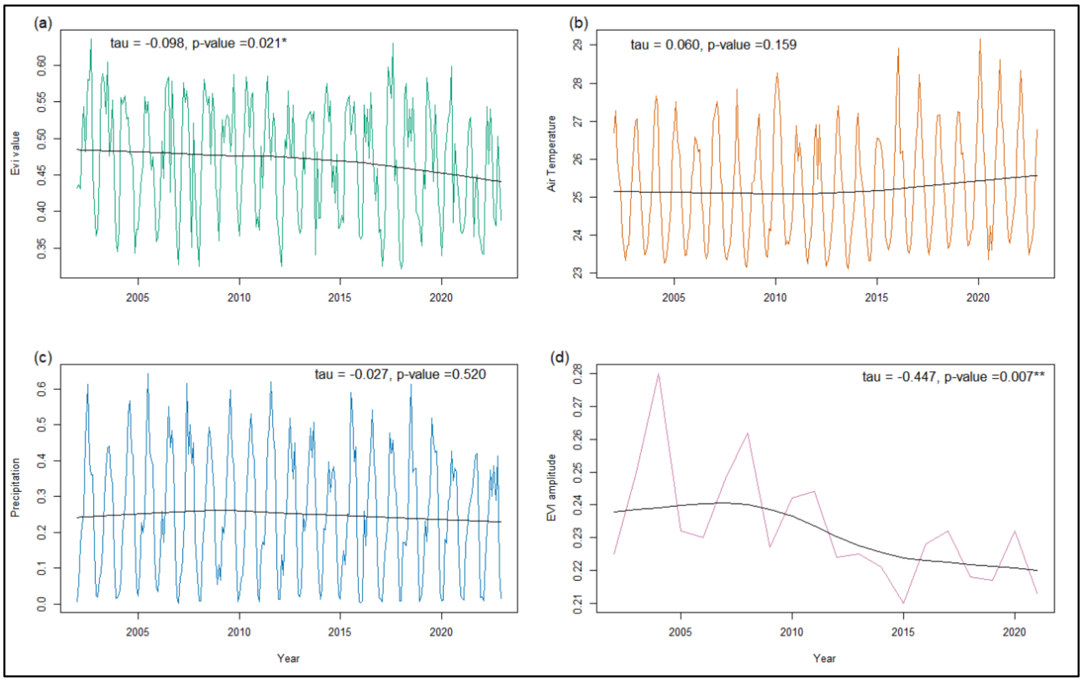


Figure 4.4. Times series showing extent of monotonic monthly trend observed in EVI (a), air temperature (b), precipitation (c), and EVI amplitude (d) across the 21 years in Oban Forest.

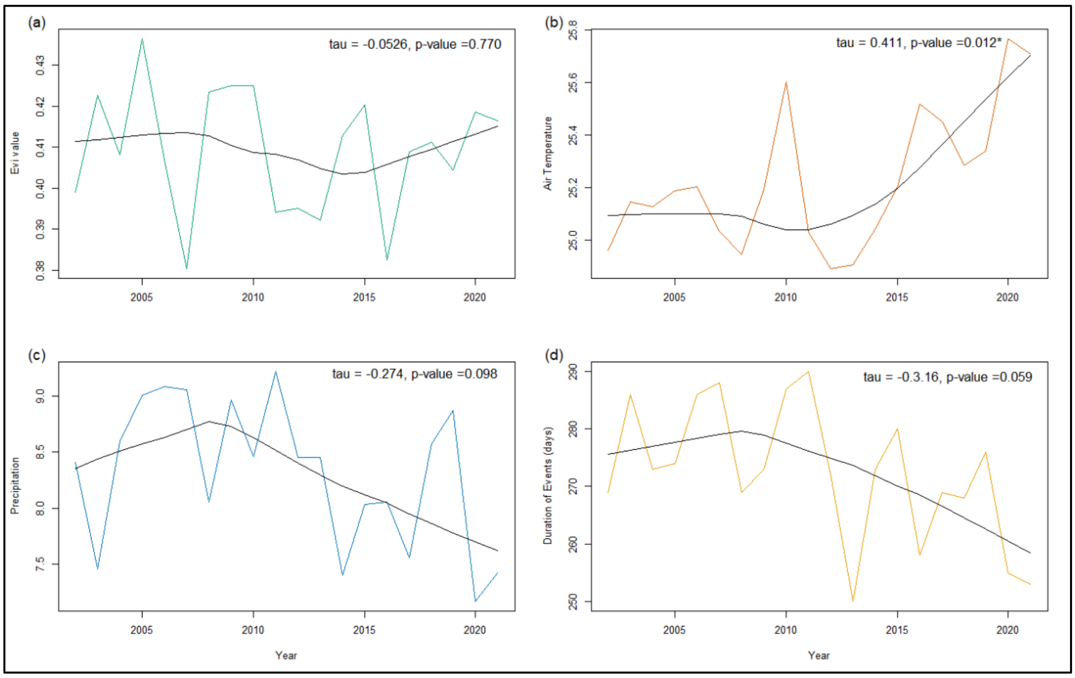


Figure 4.5. Mean annual trend in EVI values (a), air temperature in degrees Celsius (b), precipitation in mm per day (c) and number of durations of annual EVI event in days (d). The tua value highlights the degree and direction of the observed trend with p-value to indicate the statistical significance of the observed trend.

4.4.3. Normal distribution of EVI, air temperature and precipitation

Normal distribution results showed that values for EVI, air temperature and precipitation were significantly different ($p\text{-value} < 0.05$) from a normal distribution (Table 4.1). The Q-Q plots showed that all variable points were not perfectly aligned to the normality reference line, thus suggesting some deviation from normality (see Figure 4.6a,b,c).

Table 4.1. Result from the Shapiro-Wilk normality test. Weight(w) measures how well the data fit the standard normal quantiles with values of 0 and 1, where 1 is a perfect match.

Variable tested	Weight (w)	*p-value*
EVI	0.96304	0.000
Air Temperature	0.94869	0.000
Precipitation	0.95039	0.000

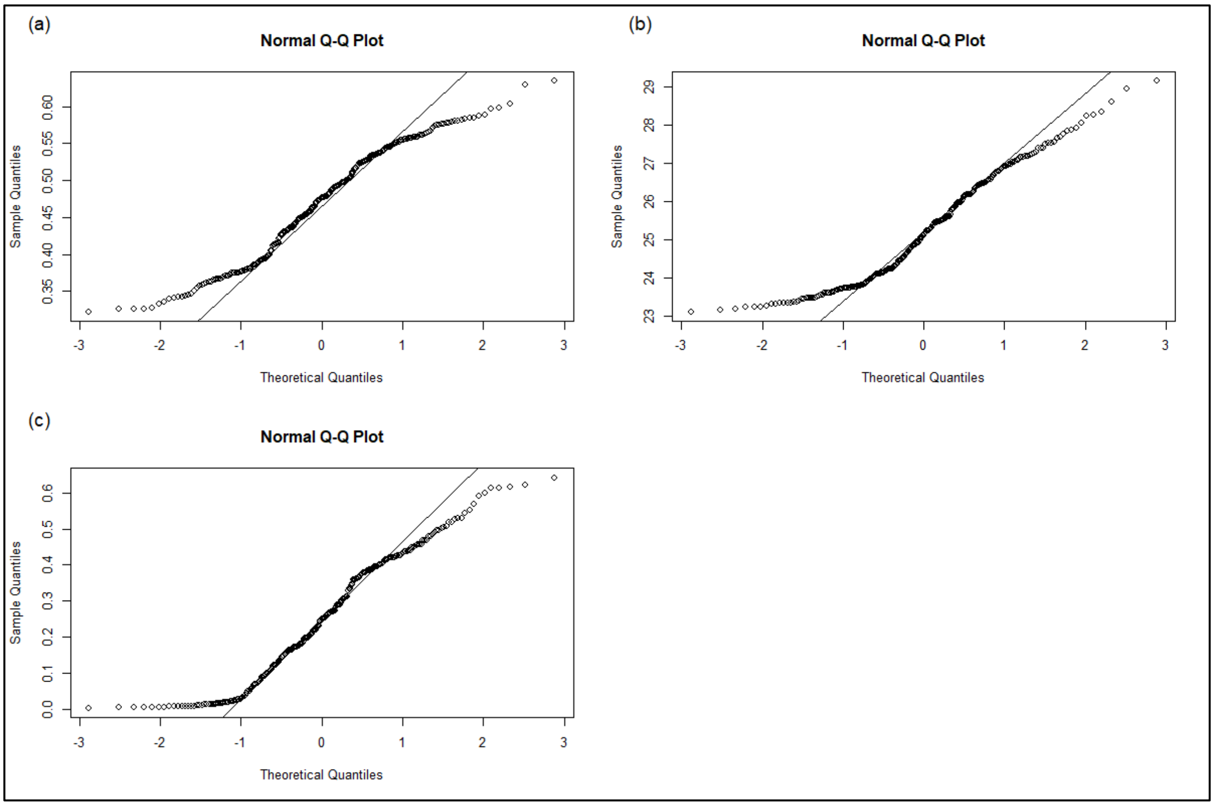


Figure 4.6. Quantile-Quantile plot showing the similarity between the distribution of EVI (a), air temperature (b) and precipitation (c). The solid lines show the expected values of a normal distribution.

4.4.4. Assessment of correlation relationship between response-predictor variable pairs

Kendall rank correlation results (Table 4.2) between variable pairs revealed that all variable pairs (EVI – air temperature, EVI – precipitation, and air temperature – precipitation) tested were significantly (p-value < 0.001) dependent on one another. Negative and positive signs observed in the Kendall score were identical to Spearman's correlation results (see Figure 4.7). Spearman's correlation (Figure 4.7) further revealed that there was a significant correlation between the predictor variables (air temperature and precipitation) and the response variable (EVI). EVI has a significant positive (p-value < 0.001) correlation with precipitation (0.62) and a significant (p-value < 0.001) negative and slightly lower correlation with air temperature (-0.49) while the air temperature was significantly (p-value < 0.001) negatively correlated to precipitation (-0.89). The correlation between annual EVI, air temperature and precipitation were non-significant (see Figure 4.7.6 in Appendix 4.7.4). However, the duration of EVI days had significant positive correlation with precipitation and maximum EVI while amplitude was significantly correlated with maximum EVI and minimum EVI. In addition, the correlation between mean, minimum and maximum monthly values of EVI, temperature and precipitation were also tested with mean EVI recorded highest correlation relationship (see Figure 4.7.7 in Appendix 4.7.4).

Table 4.2. Results from Kendall rank correlation between EVI – air temperature, EVI – precipitation, and precipitation – air temperature pairs. Tau value (either a negative or positive) indicates the direction of the trend, and the p-value indicates if the time series trend is significant.

Variable combinations in the Kendall model	Tau	*p-value*
EVI and Air Temperature	-0.33	0.000
EVI and Precipitation	0.437	0.000
Precipitation and Air Temperature	-0.692	0.000

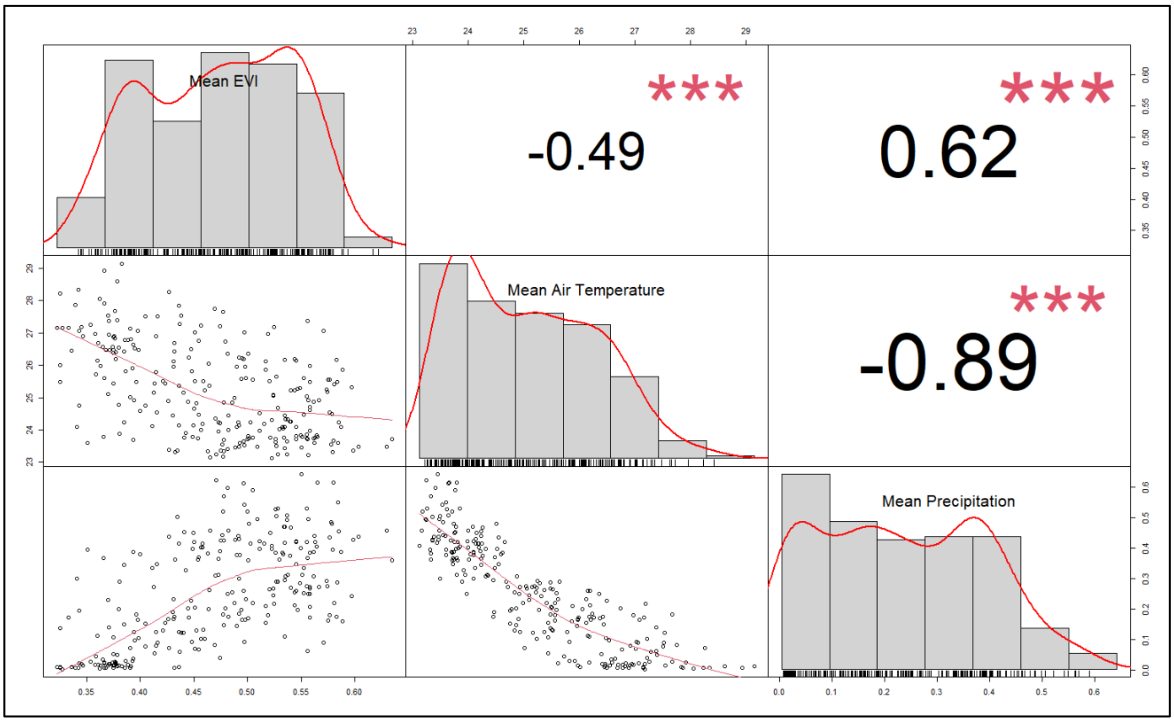


Figure 4.7. Multiple correlation plots showing the distribution of variable values, spearman correlation coefficient and scatter plots showing the relationship between mean EVI, air temperature and precipitation

4.4.5. Effect of changes in temperature and precipitation on the overall leaf phenology (EVI) of the forest

The results from GAM analysis (Table 4.3) revealed significant combined effects of precipitation and air temperature on the EVI of Oban Forest. The analysis yielded an adjusted R-squared value of 0.49; the model explained 50.2% of the deviance and a low GCV value (0.0031). The model validation results in Table 4.4 yielded a non-significant p-value, thus indicating that the residuals generated from both predictor variables in the model were randomly distributed enough to describe the relationship. From the diagnostic plots (Figure 4.8), it was observed that the data were close to the reference line (top left), the residuals were randomly distributed (top right plot), the histogram of residuals exhibited normality (bottom left), and points on the response vs fitted plot had a straight-line trend as well as were between 0.35 and 0.55 (further supported validation statistics from MLRM which revealed that air temperature and precipitation did not have a significant impact on (p-value >0.05) on annual EVI, duration of EVI event days and EVI amplitude is shown in Table 4.7.3, Appendix 4.7.4).

Table 4.3. Results from GAM showing a summary of the model outcome for predicting the response of EVI to temperature and precipitation

Sources	Effective Degrees of Freedom	Reference Degrees of Freedom	F-statistics	*P - value*
EVI ~ s(Temperature) + s(Precipitation)				
Air temperature	4.014	5.002	2.739	0.020
Precipitation	2.713	3.402	29.892	0.000
Adjusted R-squared = 0.49, Deviance explained = 50.2%				
Generalized Cross Validation = 0.0031, Scale est. = 0.00297, n = 252				

Table 4.4. Results from validation of GAM showing the predictive performance of the model for EVI response to temperature and precipitation

	Expected value (K)	Effective Degrees of Freedom	Predictive performance (k-index)	p-value
EVI ~ s(Temperature) + s(Precipitation)				
Air temperature	9.00	4.01	1.05	0.77
Precipitation	9.00	2.71	1.03	0.69
Root Mean Squared Generalized Cross Validation score = 1.23 x 10^6				

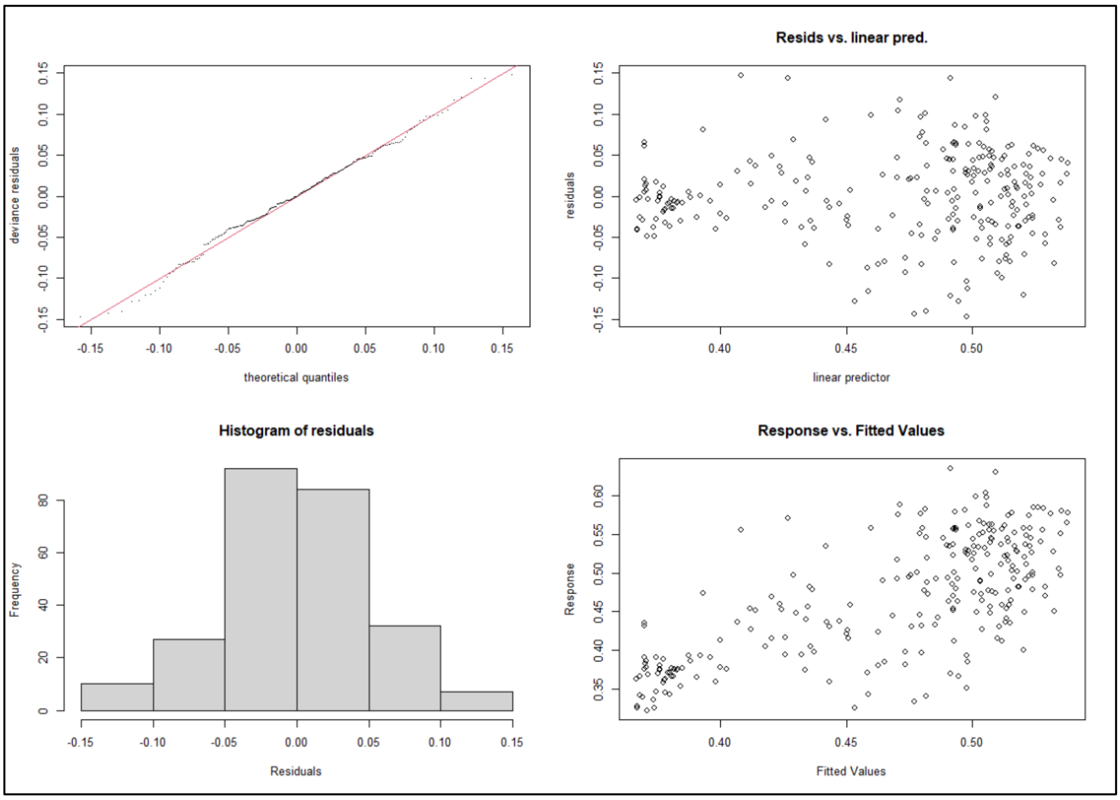


Figure 4.8. Residual diagnostic plot from the GAM results for EVI response to temperature and precipitation. The distribution of residuals compared to a normal distribution is shown in the Q-Q plot (top left) and histogram of residuals (bottom left). The residual vs linear predictor plot shows the patterns in residual plotted against the model's predictor values (top right). The Response vs Fitted Values Plot shows the observed response values plotted against the predicted values from the model (bottom right).

4.4.6. Assessment of monthly lags between changes in temperature and precipitation and the corresponding change in EVI

According to the ACF and PACF plot (see Figure 4.9), EVI displayed a significant positive correlation with a lag of one month and ten to twelve months while exhibiting a significant negative correlation with a lag of three to seven months. Air temperature also exhibited a significant positive lagged correlation one month after as well as an eight to twelve months lag. In addition, air temperature also showed a negative lagged correlation with a two to five-month lag. Furthermore, precipitation showed a positive one-month and an eleven to twelve months lagged correlation, and a significant two to nine-month negative lagged correlation.

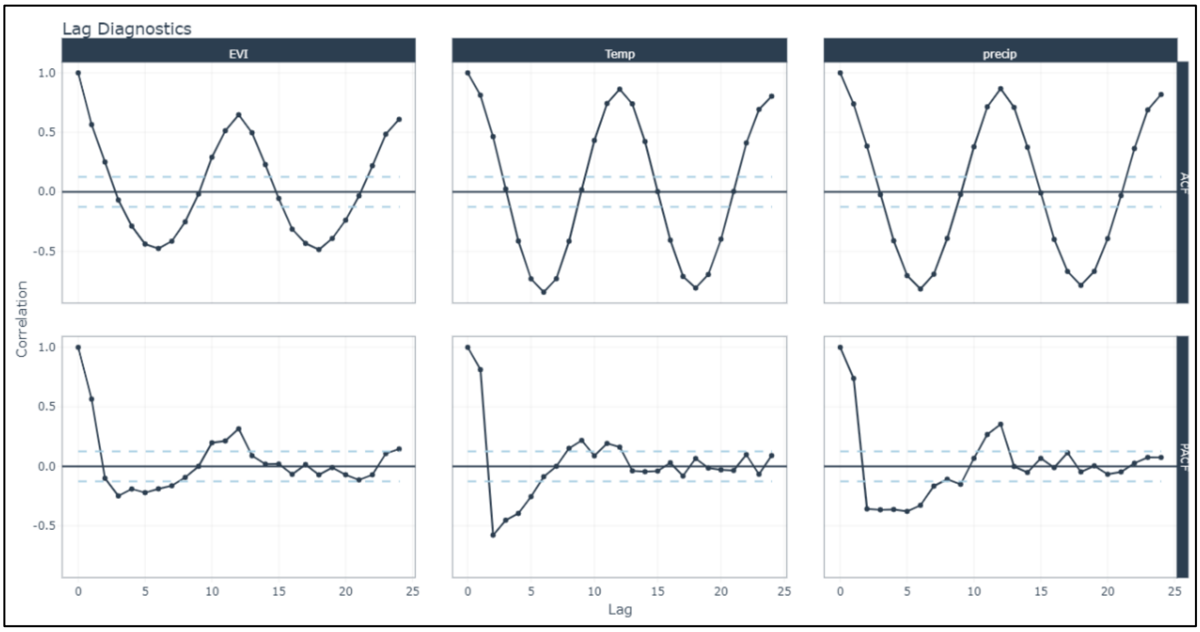


Figure 4.9. Autocorrelation (ACF) plots showing seasonal cycles in monthly lagged correlation in EVI, air temperature and precipitation (above) and partial autocorrelation (PACF) showing significant monthly lagged correlation in within EVI, air temperature and precipitation (below)

The EVI – air temperature cross-correlation (see Figure 4.10) further showed that air temperature was significantly negatively correlated with EVI at zero months and at one month, eight and twelve months (correlations with greater than twelve-month lag showed a seasonal cycle similar to the first twelve months). In contrast, there was a two to six months positive lagged correlation with EVI. Conversely, precipitation had a one-month, nine to twelve months lagged positive correlation with EVI and a three to seven months lagged negative correlation with EVI.

Results from the GAM regression (Table 4.5) between EVI and lagged predictor variables (temperature and precipitation) yielded a significant increase in the adjusted R^2 value observed in the original model from 0.49 to 0.736 and an increase in deviance explained from 50.2% to 79.6%. Out of the 11 significant lags in air temperature and ten significant lags in precipitation generated from the cross-correlation results, the air temperature was only significant at nine months lag. In contrast, precipitation was significant at zero-month lag, three months lag, and seven months lag (Table 4.5). The lagged GAM model validation revealed that the residuals generated by each variable were randomly distributed (see Table 4.6).

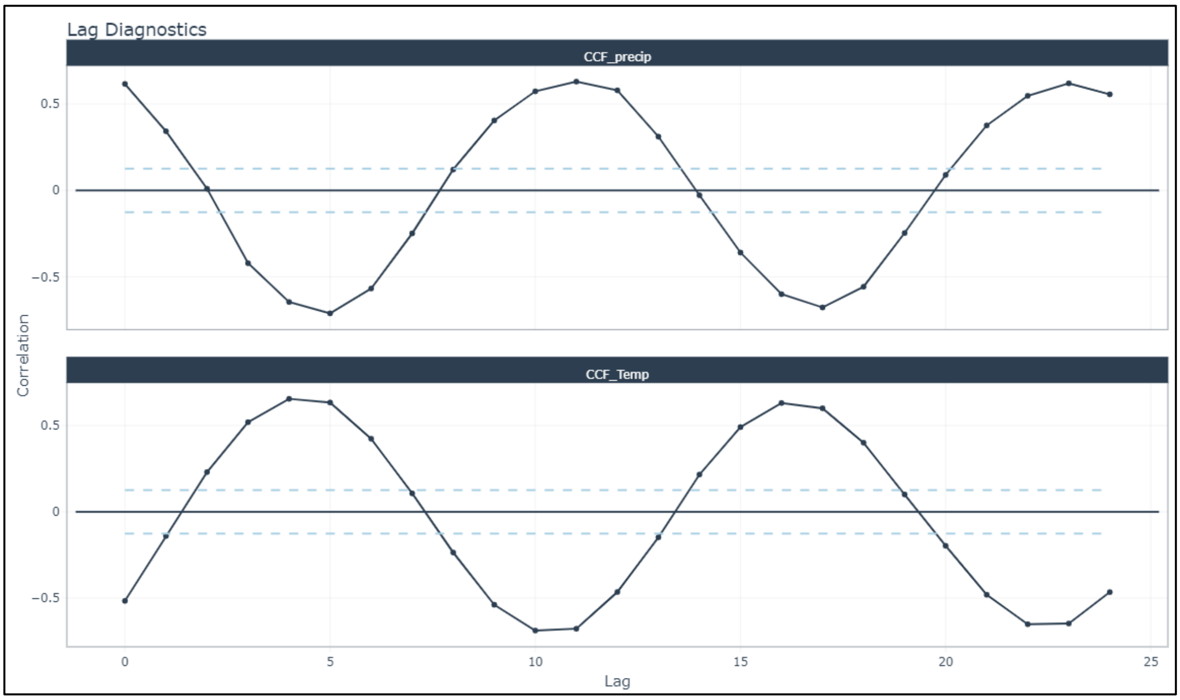


Figure 4.10. Plot from lagged cross-correlation analysis between precipitation and EVI (top) and air temperature and EVI (bottom) pair. This plot shows seasonal cycles in the aged relationship between EVI and each of the response variables (air temperature and precipitation)

Table 4.5. Results from GAM regression with main and significant lagged effects of temperature and precipitation on EVI

Sources	Effective Degrees of Freedom	Reference Degrees of Freedom	F-statistics	*P - value*
EVI ~ s(lag(Air Temp, 1,2,3,4,5,6,8,9,10,11,12)) + s(lag(Precip, 1,3,4,5,6,7,9,10,11,12))				
Air temperature (lag = 0)	1.000	1.000	1.512	0.2204
Air temperature (lag = 9)	1.000	1.000	7.818	0.0057**
Precipitation (lag = 0)	5.304	6.410	2.612	0.0141*
Precipitation (lag = 3)	6.890	7.906	3.285	0.0018**
Precipitation (lag = 7)	4.364	5.369	2.336	0.0383*
Adjusted R-squared = 0.736, Deviance explained = 79.6%				
Generalized Cross Validation = 0.0020, Scale est. = 0.0015, n = 240				

Table 4.6. Results from validation of GAM for EVI response to temperature, precipitation, and their significant lags

	Expected value (K)	Effective Degrees of Freedom	Predictive performance (k-index)	p-value
EVI ~ s(lag(Air Temp, 1,2,3,4,5,6,8,9,10,11,12)) + s(lag(Precip, 1, 3,4,5,6,7,9,10,11,12))				
Air temperature (lag = 0)	9.00	1.00	1.06	0.760
Air temperature (lag = 9)	9.00	1.0	1.09	0.890
Precipitation (lag = 0)	9.00	5.30	1.07	0.820
Precipitation (lag = 3)	9.99	6.89	0.98	0.375
Precipitation (lag = 7)	9.00	4.36	1.08	0.870
Root Mean Squared Generalized Cross Validation score = 6.2 x 10^9				

4.5. DISCUSSIONS

4.5.1. EVI, temperature and precipitation seasonality in Oban Forest

A clear seasonal cycle in EVI in was identified in Oban Forest, with the highest average monthly values recorded between March and October (up to November for maximum values recorded) and low values between December and February, (Figures 4.3, 4.4). The seasonal cycle of EVI was offset from the seasonal cycles in temperature and precipitation, which suggested a combined effect of increased precipitation and reduced temperature on peak EVI values and the reverse for lower EVI values in Oban Forest. The positive correlation between monthly EVI values and precipitation and the negative correlation between EVI and air temperature statistically supported this finding. The anomaly in monthly and annual precipitation was more pronounced than seen in temperature. The area is also characterised by a robust seasonal precipitation cycle and rainy season of up to eight months (Yan et al., 2019) as seen in Oban Forest.

Seasonal annual phenological cycles have been found to be the most common in similar tropical rainforest in in as similar African rainforest in Lope National Park, Gabon (Bush et al., 2017). Bush (2017) further submitted new leaf formation were seen to be produced during the dry season while peaks in fruiting phenological cycles were mostly reported during the rainy season. Precipitation pattern (duration and intensity) has been identified as the major driver of tropical rainforest phenology in the second largest rainforest in the Congo Basin (Jiang et al., 2019). Higher rainfall in tropical forest in Madagascar was seen to significantly influence a higher monthly measure of fruiting richness and intensity in a twelve-year dataset with 69 tree species which usually precedes the onset of leaves (Dunham et al., 2018). According to Dunham et al. (2018) reduced rainfall during dry season and not during the wet season resulted in a significant shift in the timing of EVI peaks. Another study in Kibale National Park, Uganda revealed that high temperature significantly constraints the fruiting in trees (Potts et al., 2020), which could have been linked to the El Niño Southern Oscillation events (Potts et al., 2020; Gray and Ewers, 2021; Bush et al., 2017). In addition, seasonal cycles in forest phenology have also been linked to a significant influence of plants functional types and the potential of these species to adapt to different climatic scenarios (Ibrahim et al., 2021; Cleland et al., 2007).

4.5.2. Trends in EVI

Oban Forest showed a significant (p-value = 0.021) long-term consistent decrease in mean monthly EVI values without any reversals in the changing pattern over the studied period as well as a significant (p-value = 0.0009) seasonal cyclical trend in mean monthly EVI values (Figure 4.4a). Annual mean EVI did not show a significant trend (Figure 4.5a) however, there was a significant negative trend in EVI amplitude (Figure 4.4d). Mean EVI in Oban Forest had a higher minimum and lower maximum than that which was reported in a similar study in the tropical rainforest region of Borneo (Vijith & Dodge-Wan, 2020). Tropical forests are generally characterised by a high and sometimes stable temperature, so there might be little need for trees to adapt their phenological cycles to it. However, extreme rises in temperature associated with droughts and heat stress has been reported to disrupt tree metabolism, leading to decreased EVI (Abera et al., 2018; Dunham et al., 2018; Pau et al., 2018a; Potts et al., 2020).

Oban forest was seen to have a high and somewhat constant temperature (23.12 °C to 29.15 °C) with a difference of about 6 °C between the minimum and maximum mean values recorded across the 20-year period. Air temperature exhibited a significant seasonal monthly trend (p-value < 0.0000) and a non-significant monotonic trend (p-value > 0.05) distinct from zero (see Figure 4.6). Precipitation had a significant seasonal monthly trend and a non-significant negative monotonic trend in Oban Forest (see Figure 4.6). Despite observing a non-significant but positive monotonic trend in precipitation in this study, it agreed with reports from a study that investigated the long-term changes in precipitation from the CHIRPS dataset, pointing out that there has been an increase in the intensity and reduction in duration of precipitation in West Africa (Dinku et al., 2018; Paredes-Trejo et al., 2020; Didi Sacré Regis et al., 2020).

Although, monthly and annual scale data can provide useful insights into long-term trends and patterns in the relationship between phenology and climatic variables, they may mask the effects of extreme weather events. This could limit the ability to capture the complexities and variability that occur daily that could have significant impact on the forest. Thus, in a study of this nature, daily scale EVI and climate data have potential to provide a more detailed and accurate understanding of the variability in the response of forest phenological cycles to climate change. However, the absence of ground truth data and the limited amount of remotely-sensed data, due to a high percentage of cloud cover, make it hard to compare study variables on a daily scale.

In a study assessing how rainfall-vegetation interaction regulates temperature anomalies in the Horn of Africa, Abera et al. (2018) pointed out that precipitation trends substantially affected EVI more than temperature. This could be attributed to the variation in temperature not being enough to cause a significant change in EVI, except in extreme temperatures where trees become heat-stressed due to droughts. Results from Oban Forest supports a robust seasonal precipitation cycle reported by Yan et al., (2019) with a more pronounced variable anomaly in monthly and annual precipitation (between positive 440% and negative 80%) compared to air temperature (positive 6% to negative 7%).

4.5.3. The effect of changes in air temperature and precipitation on overall EVI in Oban Forest

With the increase in precipitation, a decrease in temperature is naturally expected due to the inverse relationship between precipitation and air temperature, as proven by several studies (Ham et al., 2018). The results from the study revealed that temperature and precipitation had a highly negative Spearman correlation coefficient (Figure 4.7). While EVI was negatively correlated with the temperature at a lower degree (compared to the air temperature – precipitation correlation), a significant (p-value < 0.001) positive correlation with precipitation was also observed. However, the EVI – precipitation correlation observed was higher than the EVI – air temperature correlation. Results from the Kendall rank correlation test also supported that there was a significant (p-value < 0.001) correlation between all three pairs (EVI – air temperature, EVI – precipitation, and air temperature - precipitation).

The lower temperature promoted photosynthesis and the production of new leaves of tree species in tropical forests in Central Africa (Bush et al., 2020). This would explain the inverse relationship between precipitation and EVI, which could be a proxy for phenological phase of leaf green-up and senescence. Some studies suggest that precipitation seems to be the significant climate factor driving changes in forest greenness in tropical forests (Abera et al., 2018; Yan et al., 2019). A finding from a precipitation exclusion study in Africa suggested that the amount, frequency, and timing of rainfall strongly affect the structure and functioning of the forest greenness (Yan et al., 2019). In addition, Naif, Mahmood and Al-Jiboori (2020) further reported in another study that forest greenness was negatively correlated with air temperature and positively correlated with precipitation.

The results from GAM regression analysis (adjusted R^2 = 0.49 and 50.2% of deviance explained) revealed that there was a significant (p-values < 0.001) impact of precipitation and air temperature on the overall EVI of Oban Forest. However, precipitation had a higher effect on EVI with a lower significance (p-value < 0.001) than temperature (p-value <0.05). This supports the finding that precipitation is the most important climatic factor that drives the changes in EVI observed in tropical rainforests. According to Gustafson et al. (2017), an increase in precipitation will generally increase photosynthetic activity. Normalized difference vegetation index (NDVI) and precipitation has shown significant relationships in a range of biomes in Africa. In the humid Sudano-Guinean zone in the south, a significant NDVI-precipitation relationship was observed (Georganos et al., 2017), a negative significant trend in normalized difference vegetation index (NDVI) due to precipitation deficit caused by strong El Nino was reported in South Africa (Xulu et al., 2018) and in the Horn of Africa results showed that vegetation seasonality followed precipitation modality patterns in 81% of the region (Abera et al., 2018). In addition to other studies, this explains why precipitation has been characterised as the major climatic factor that influences forest greenness compared to temperature (Abera et al., 2018; Bush, Whytock, Bahaa-El-din, et al., 2020; Didi Sacré Regis et al., 2020; Georganos et al., 2017; Gou et al., 2022; Naif et al., 2020; Paredes-Trejo et al., 2020; Yan et al., 2019).

4.5.4. Lags in the response of EVI to changes in air temperature and precipitation

EVI, air temperature and precipitation exhibited a twelve-month self-correlation in the first cycle (while EVI up to 24 months, i.e., second cycle as seen in the PACF). The correlation coefficient gradually decreased with successive years towards zero (see Figure 4.7.8 in Appendix 4.7.5). With the inclusion of lagged months, the air temperature had a nine-month lag effect on EVI, while precipitation exhibited a zero-month, three months, and seven months lag effect on EVI. The observed delayed response in the phenology of Oban Forest to climatic changes could be due to the functional type of the tree species as well as their growth stage at the time of the change (Ibrahim et al., 2021; Cleland et al., 2007). The soil type, topography, and drainage conditions could cause an immediate or delayed impact on the soil moisture content thus affecting the onset or duration of photosynthesis necessary for forest green-up, growth and productivity (O'Connell et al., 2018). In addition, other environmental factors, such as light intensity, nutrient availability, and atmospheric CO_2 concentrations, may interact with each other, further complicating the response of vegetation to environmental changes (Esmaili et al., 2020; Gray and Ewers, 2021; Xulu et al., 2018; Di Lucchio et al., 2018). Furthermore, the timing and duration of rainfall and dry season could also occur at a dormant period thus causing a delay in the onset of forest green-up.

In a study conducted in a similar African rainforest using monthly CHIRPS precipitation data, it was reported by Gou et al. (2022) found that precipitation had the highest correlation with vegetation at zero-time lag or at a one-month time lag. In a vegetation study conducted in a forest in Namibia, Wingate, Phinn and Kuhn (2019) it was also reported that precipitation had the most significant effect on vegetation and zero lag. Another study in the Amazon revealed that in dense tropical forests, precipitation could have about 2 to 4 months lag effect on photosynthesis from stored with stored rainfall memory (Green et al., 2020). An increase in insolation without water limitation has been seen to drive leaf growth (Wagner et al., 2016, 2017), while other finding has shown that an increase in dry-season length was shown to impact the vegetation in the Amazonian Forest negatively (Marengo et al., 2018). Furthermore, in four Panamanian forests, CO2 fluxes declined in dry season and peaked in the early wet season ahead of peak soil moisture (Cusack et al., 2023). These findings stress the importance of precipitation and, to some extent, daylight intensity in influencing phenology in tropical forests, as seen in Oban Forest.

4.5.5. Implication for the livelihood of forest-dependent communities

The link observed in EVI and climate cycles in Oban Forest has the potential to impact the availability and quality of forest products, particularly those that are important sources of nutrition and income for forest-dependent communities. Oban Forest houses 36 forest-dependent/support zone communities that rely heavily on the forest for their livelihoods, including food that might be eaten directly or solely for income and other non-timber forest products (Asuk et al., 2023; Friant et al., 2019). Climate change in Nigeria was reported to cause a 5 to 20% reduction in agricultural produce (Paeth et al., 2008). While Bush et al. (2020) reported that over 32 years, there was an 81% decline in fruit production in a tropical forest in Gabon. Changes in the phenological cycle of Oban Forest could directly impact or determine the availability and quality of forest resources needed to sustain the livelihoods of forest-dependent communities. The observed shift in the timing of peak EVI values and the correlation with precipitation and air temperature could affect the availability of food resources, such as fruits and nuts, which are important sources of nutrition for these communities. There is also a potential for these changes in the phenology of the forest to impact the availability and quality of plants of ethnobotanical importance used extensively in traditional medicine by these communities (Ebu et al., 2021). These could generally impact the collective income of forest-dependent communities, particularly those involved in collecting and selling non-timber forest products or those specialized in ethnobotany as a trade.

4.6. CONCLUSION

The study the Oban Forest in South-eastern Nigeria identified an association between seasonal EVI patterns—sensitive to leaf chlorophyll fluctuations during phenological cycles—and climatic variables like air temperature and precipitation. Notably, the forest showcases a distinct seasonal EVI pattern, with peak values seemingly influenced by a combination of increased precipitation and reduced temperature. While the observed correlations between EVI, temperature, and precipitation are consistent with patterns seen in other tropical rainforests in regions such as the Congo Basin, Madagascar, and other parts of West Africa, it remains essential to appreciate the unique attributes of each ecosystem when making broad generalizations.

For the 36 forest-dependent local communities surrounding the Oban Forest, this research underscores the critical implications of shifts in the forest's phenological cycle. As these communities derive both sustenance and economic value from the forest, alterations in the phenological patterns could potentially impact their access to vital resources, like food and medicinal plants, and thus their overall well-being. Particularly, changes in the timing of peak EVI values, which correlate with climate variables, could disrupt the availability of nutrition sources and other non-timber forest products that are integral to these communities.

However, this study is not without limitations. The lack of ground truth data and challenges posed by frequent cloud coverage in remote sensing data necessitate a more rigorous, ground-based monitoring approach. Such an approach would facilitate the development of accurate predictive models correlating EVI with climate variables and tying leaf phenological cycles to fruiting patterns. Additionally, addressing variables like light intensity, soil nutrients, atmospheric CO_2 concentrations, and tree species traits would offer a more nuanced understanding of the forest's response to environmental shifts.

Future research endeavours would be focused on holistically addressing the complex interplay of environmental, social, and economic factors, enabling adaptive strategies for forest-dependent communities. As the implications of climatic changes on forest phenology become more pronounced, fostering collaboration among researchers, local inhabitants, and policymakers will be crucial to ensure the sustained health of both the Oban Forest ecosystem and its dependent communities.

4.7. APPENDICES

Appendix 4.7.1. Parsing MODIS data for quality assurance

Table 4.7.1. Detailed image collection criteria used for parsing MODIS data for quality assurance. Values in red were excluded from the MODIS images (Didan, Munoz, Solano, et al., 2015).

Bits	Parameter Name	Value	Description	Used
0-1	VI Quality (MODLAND QA Bits)	00 01 10 11	VI produced with good quality VI produced, but check other QA Pixel produced, but most probably cloudy Pixel not produced due to other reasons than clouds	00 01
2-5	VI Usefulness	0000 0001 0010 0100 1000 1001 1010 1100 1101 1110 1111	Highest quality Lower quality Decreasing quality Decreasing quality Decreasing quality Decreasing quality Decreasing quality Lowest quality Quality so low that it is not useful L1B data faulty Not useful for any other reason/not processed	0000 0001 0010 0100 1000 1001 1010 1100
6-7	Aerosol Quantity	00	Climatology	00

Table 4.7.1 (cont.). Detailed image collection criteria used for parsing MODIS data for quality assurance. Values in red were excluded from the MODIS images (Didan, Munoz, Solano, et al., 2015). (continued)

		01 10 11	Low Intermediate High	01 10
8	Adjacent cloud detected	0 1	No Yes	0
9	Atmosphere BRDF Correction	0 1	No Yes	0
10	Mixed Clouds	0 1	No Yes	0 -
11-13	Land/Water Mask	000 001 010 011 100 101 110 111	Shallow ocean Land (Nothing else but land) Ocean coastlines and lake shorelines Shallow inland water Ephemeral water Deep inland water Moderate or continental ocean Deep ocean	- 1 - - - - - -
14	Possible snow/ice	0 1	No Yes	0 -
15	Possible shadow	0 1	No Yes	0 -

Appendix 4.7.2. Multiple regression analysis

Table 4.7.2. Multiple linear regression result with EVI as the response variable and temperature and precipitation and predictor variables

Sources	Coefficients Estimate	Std. Error	t value	*P - value*
Intercept	0.256385	0.149578	1.714	0.0878
Air temperature	0.005317	0.005520	0.963	0.3364
Precipitation	0.313445	0.045953	6.821	0.0000^{***}

The residual standard error (249 DF): 0.06017

Multiple R-squared: 0.3819

Adjusted R-squared: 0.377

F-statistic: 76.93 (2 and 249 DF)

p-value: < 2.2e-16

Difference between expected DV values from a regression on a training set and the actual DV values within the training set = 0.04705242

Correlation between the expected value and actual values = 0.5981798

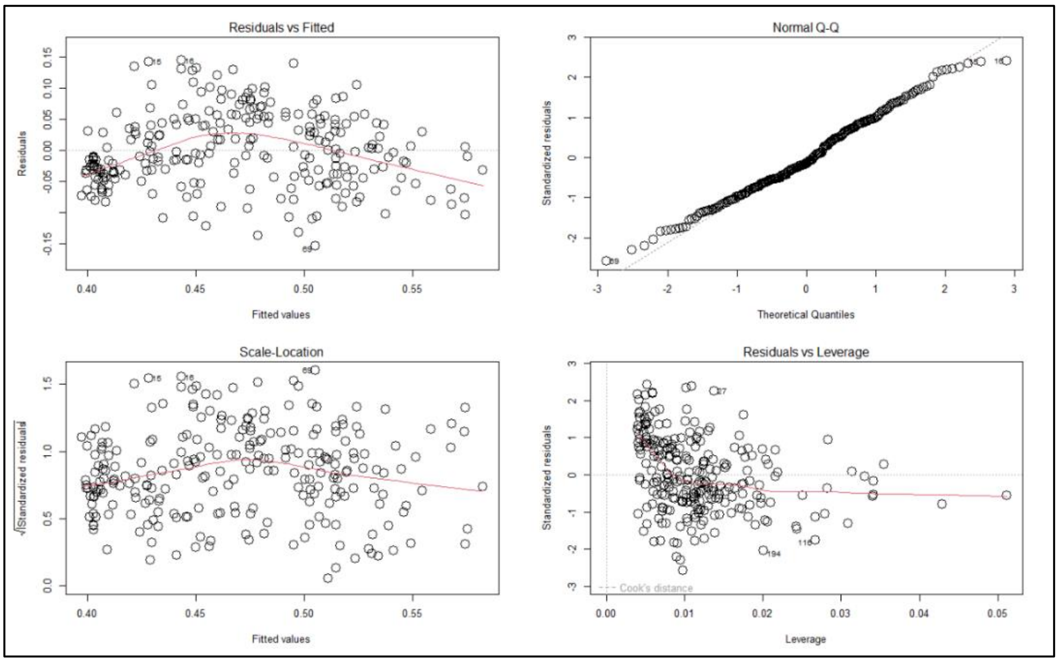


Figure 4.7.1. Diagnostic plot for the effect of precipitation and air temperature on EVI

Appendix 4.7.3. Results from Seasonal cycles, anomaly, and trend detection in EVI, air temperature and precipitation at monthly and annual scales

The percentage EVI anomaly shown in Figure 4.7.3 (Appendix 3.7.3) revealed variability in the monthly vegetation growth of Oban Forest which was also reflected in the overall annual anomaly trend. The largest positive monthly anomaly (exceeding +25%) was observed in September 2002 and August 2017, while 2009 and 2011 were at about +20%. Also, the largest negative monthly anomaly was observed in August of 2007 and October 2013. In addition, the least positive EVI anomaly was observed in 2005, 2021 and 2022.

The annual and monthly anomaly in air temperature ranged between 6% on the positive side to -7% on the negative side (Figure 4.7.4). There was only a little positive-negative monthly anomaly variability in air temperature within years. However, the highest positive temperature anomaly was observed in 2016 and 2020 then 2010, 2021 and 2022 also exhibited high level of positive anomaly. Conversely, the highest negative temperature anomaly was observed in 2012 and 2011, respectively.

The monthly and annual anomaly in precipitation (Figure 4.7.5) was exceedingly varied, ranging from 440% positive to -80% negative. January of 2009 recorded positive anomaly of about 440% making 2009 the year with highest positive anomaly. In addition, other months in 2007, 2011, 2012, 2013 and 2018 also recorded positive anomalies above 100%. On the negative side, the months in 2007, 2008, 2016, 2017, 2020, 2021 and 2022 had the highest anomaly of above -80%.

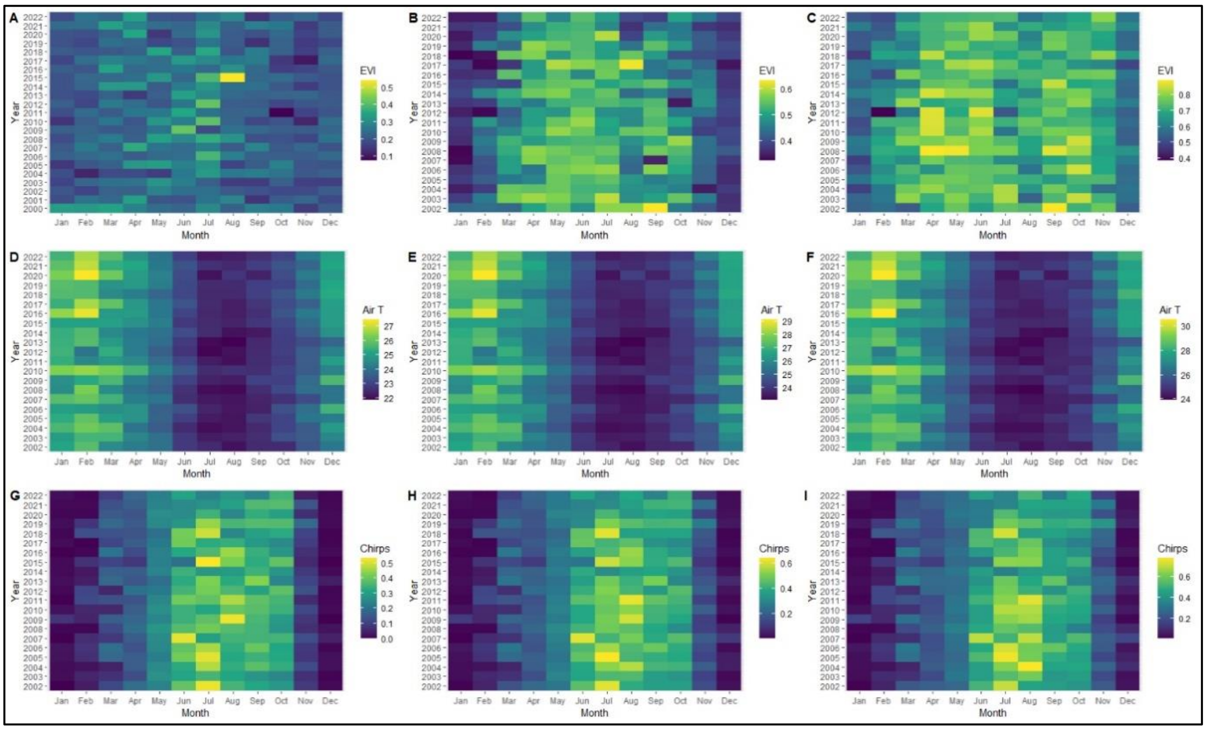


Figure 4.7.2. Heat map plot of the statistical minimum pixel values from images for EVI (A) Air temperature (D) and precipitation (G). The average pixel values from satellite images for EVI (B), air temperature (E) and precipitation (H) and maximum image pixel values for EVI (C), air temperature (F) and precipitation (I). Note: Colour scale in each plot may differ based on the legend range.

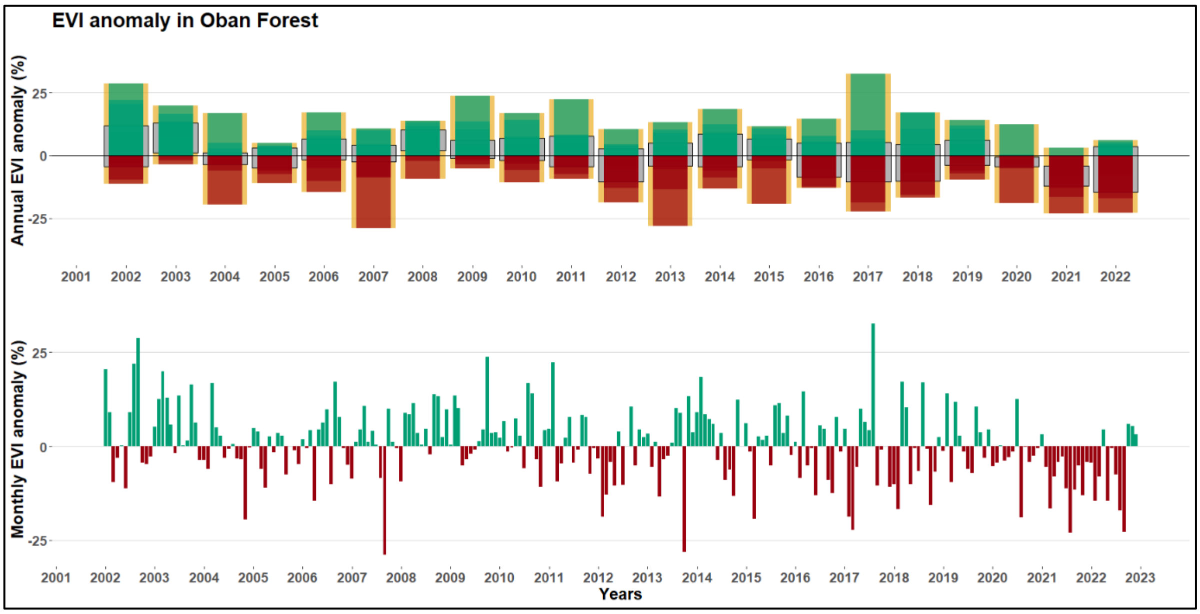


Figure 4.7.3. Plot showing annual (above) and monthly (below) percentage anomaly in EVI values for Oban Forest. Green colour denotes positive anomaly, red colour indicates the negative anomaly while the grey bar represents the 75th and 25th percent quantile range.

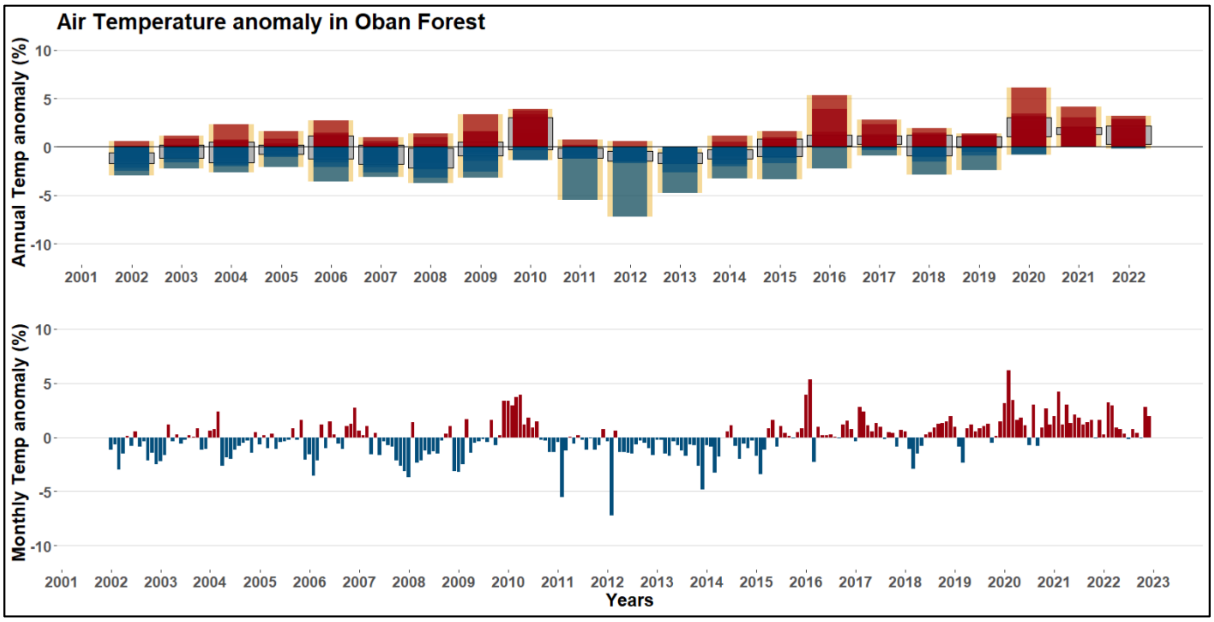


Figure 4.7.4. Plot showing annual and monthly percentage anomaly in ait temperature values for Oban Forest. Red colour denotes positive anomaly, blue colour indicates the negative anomaly while the grey bar represents the 75th and 25th percent quantile range.

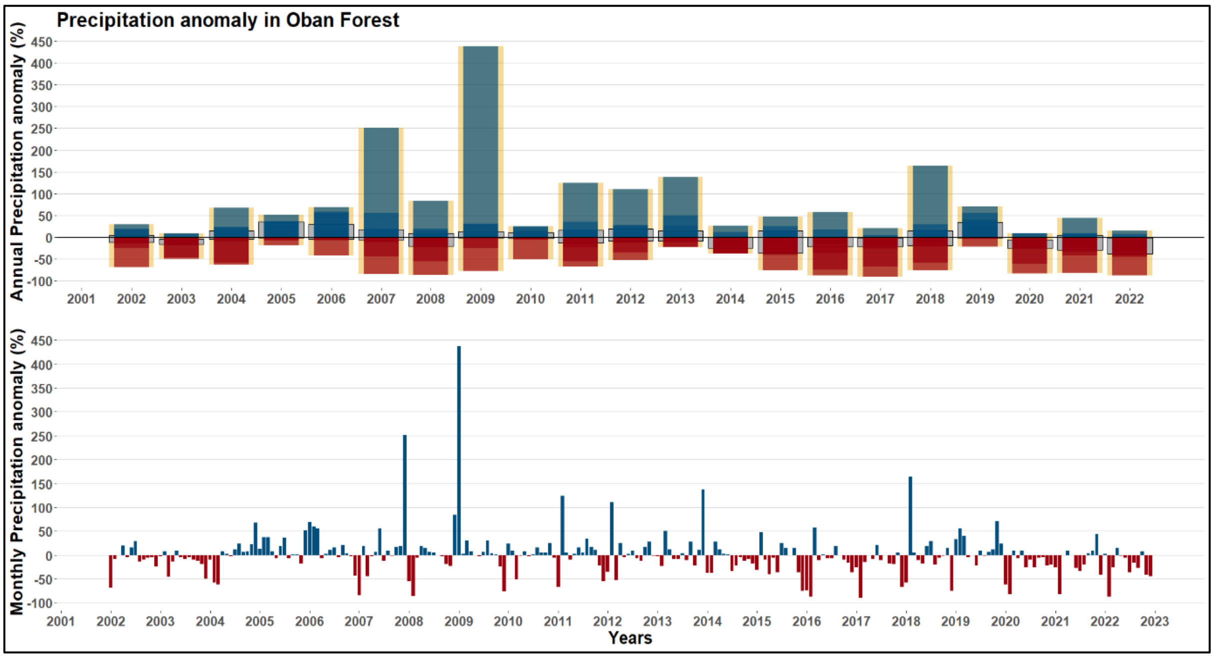


Figure 4.7.5. Plot showing annual and monthly percentage anomaly in precipitation values for Oban Forest. Blue colour denotes positive anomaly, red colour indicates the negative anomaly while the grey bar represents the 75th and 25th percent quantile range.

Appendix 4.7.4. Results from annual data aggregate analysis

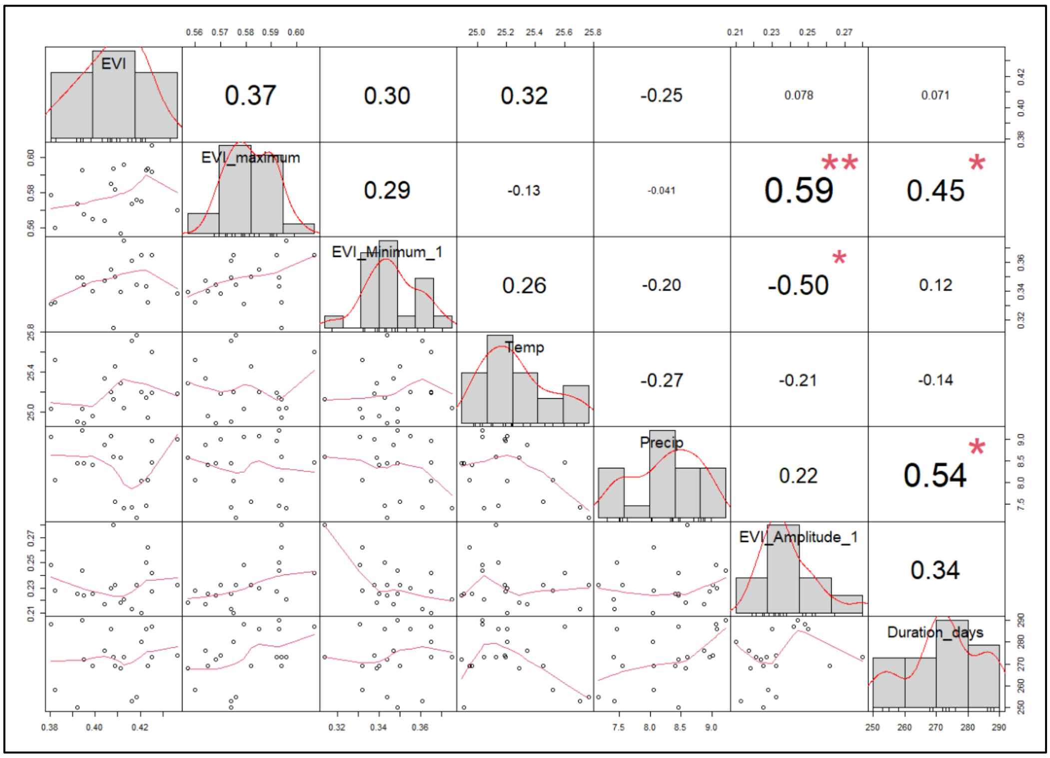


Figure 4.7.6. Correlation results from testing relationship annual aggregates of variables

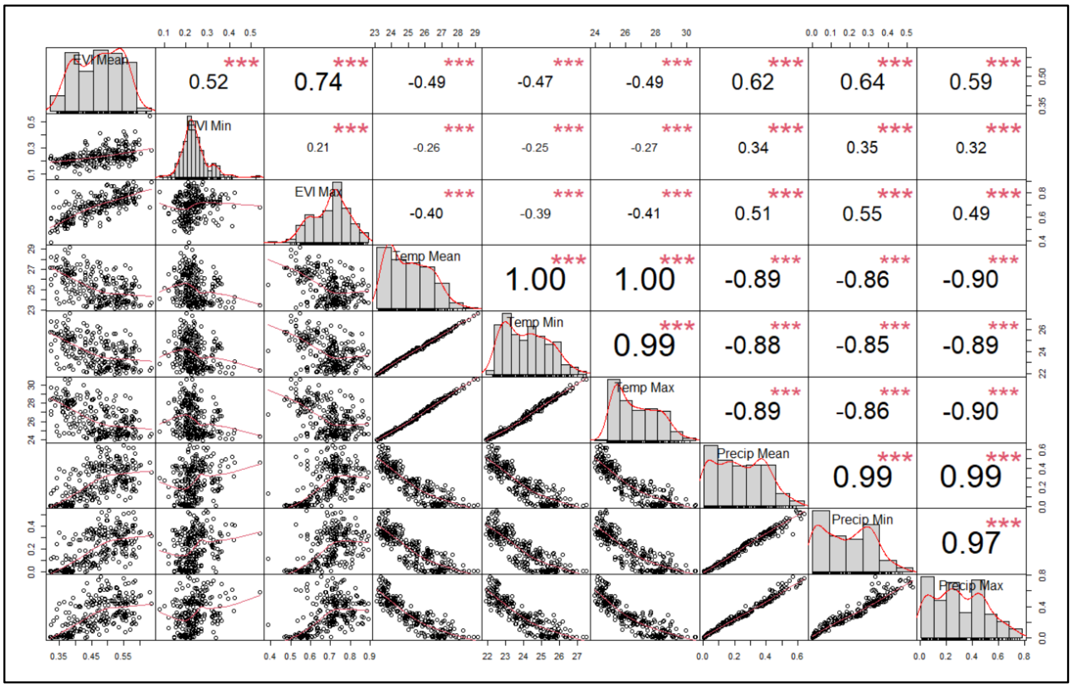


Figure 4.7.7. Correlation results from testing relationship in mean, minimum and maximum values of all variables

Table 4.7.3. Result from MLRM for the impact of air temperature and precipitation on annual EVI generated variables

Sources	**Coefficients Estimate**	**Std. Error**	**t value**	***P - value***	**Adj. R^2**
EVI ~ Air Temperature + Precipitation					
Intercept	0.149	0.394	0.379	0.710	-0.02
Air temperature	0.012	0.015	0.785	0.443	
Precipitation	-0.004	0.006	-0.611	0.549	
EVI Amplitude ~ Air Temperature + Precipitation					
Intercept	0.563	0.459	1.228	0.236	-0.06
Air temperature	-0.013	0.017	-0.793	0.439	
Precipitation	0.001	0.007	0.193	0.849	
EVI maximum ~ Air Temperature + Precipitation					
Intercept	0.759	0.378	2.007	0.061	-0.10
Air temperature	-0.006	0.014	-0.450	0.658	
Precipitation	-0.002	0.006	-0.401	0.694	
EVI_Minimum_~ Air Temperature + Precipitation					
Intercept	0.196	0.389	0.503	0.621	-0.05
Air temperature	0.007	0.014	0.497	0.625	
Precipitation	-0.004	0.006	-0.618	0.545	
Duration days ~ Air Temperature + Precipitation					
Intercept	323.628	282.895	1.144	0.269	0.15
Air temperature	-4.671	10.532	-0.444	0.663	
Precipitation	8.019	4.303	1.864	0.080	

Appendix 4.7.5. Lags in EVI, air temperature and precipitation from ACF and PACF

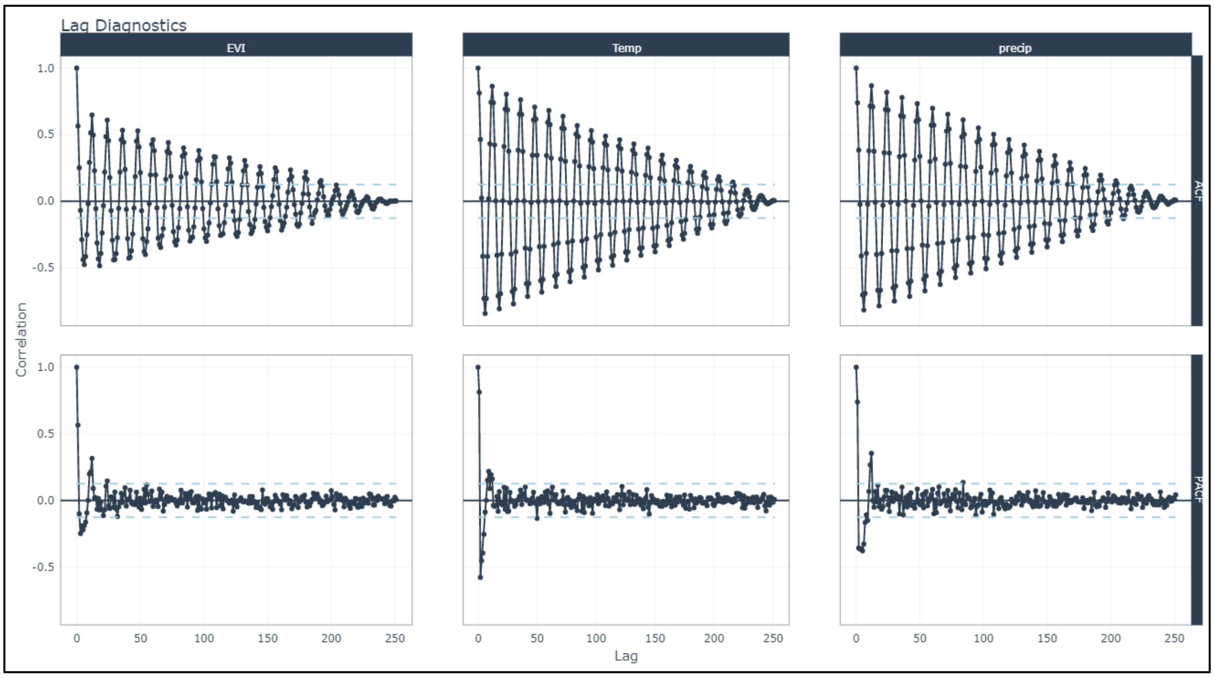


Figure 4.7.8. ACF and PACF plots for all EVI, air temperature and precipitation

CHAPTER FIVE: MONITORING REPRODUCTIVE PHENOLOGY OF FOOD-PRODUCING TREES IN A NIGERIAN RAINFOREST

5.1. Abstract

Nigeria's Oban Forest, the most considerable remaining portion of the country's tropical rainforest, plays a crucial role in the socio-economic development of forest-dependent communities. Reproductive phenology, the timing of flowering and fruiting events in plants, is a fundamental aspect of the life cycle of plants and plays a crucial role in plant reproduction, seed dispersal, ecosystem functioning, and people's engagement with these forests for food. This study aimed to provide two years of baseline monitoring data on the reproductive phenology of food-producing tree species in Oban Forest for two growing seasons (May 2020 to April 2022). The timing of budding, flowering, and fruiting events in all tree species in fifteen 40 by 40 meters plots was monitored and recorded environmental variables such as rainfall, and temperature. We show that the proportion of tree stems (31.10%) with phenological events in the study area compared to the number of tree species (72.72%) represented suggests a variation of phenological cycles within species. The peak timing of flower bud and flower production was consistent with the onset of the rainy season between March and April, indicating the link between the seasonality of climatic variables and phenological events in the forest. However, flowering buds and flowers are shown to be produced continually throughout the year with their onset at the start of the rainy season suggests that there is a continuous supply of fruits through the year, providing the opportunity to support communities in Oban Forest. Long-term monitoring of the reproductive phenology of food-producing tree species is essential to understand their response to environmental factors. This study provides valuable baseline data that can act as a foundation for future research, contributing to a better understanding of the reproductive phenology of tree species in Oban Forest and other Afrotropical Forest at large and their response to environmental factors. It will also provide critical information to help

develop sustainable food systems for forest-dependent communities and aid in forest conservation efforts.

5.2. INTRODUCTION

Reproductive phenology, which is the timing of flowering and fruiting events in plants, is a fundamental aspect of the life cycle of plants. It plays a crucial role in plant reproduction, seed dispersal, and ecosystem functioning. In tropical rainforests, where most tree species range from sub-annual (Adamescu et al., 2018) to continuous (Franklin et al., 1987), reproductive phenology is often synchronised with seasonal changes in environmental factors such as rainfall, temperature, and light intensity (Adamescu et al., 2018; Richardson et al., 2013; Bush et al., 2017; Gray and Ewers, 2021; Cleland et al., 2007). However, the timing and duration of these events can vary widely among species, making it challenging to predict how environmental changes will impact rainforest ecosystems (Cleland et al., 2007; Yu et al., 2017; Visser and Both, 2005).

Tropical rainforests are among the most biodiverse ecosystems on the planet. Although covering less than 10% of the Earth's surface area, tropical forests are estimated to contain about 50% of the world's plant and animal species, some of which are either endemic or at risk of extinction (Pillay et al., 2022; Rajpar, 2018). Tropical rainforests provide climate regulatory services, habitat for millions of species, and livelihood sustenance through providing food for livelihood sustenance amongst forest-dependent human communities, especially during agricultural crop failure. However, tropical rainforests are changing due to the variation in duration and intensity of impact from anthropogenic activities such as deforestation, logging, and climate change (Alamgir et al., 2016; Abbasi et al., 2023; Jara-Guerrero et al., 2021; He et al., 2020). These activities can have far-reaching effects on these ecosystems’ functioning by modifying the composition and life cycles of the species (Abbasi et al., 2023; Jara-Guerrero et al., 2021; Lim et al., 2020; Li et al., 2023; Dunham et al., 2018; Gray and Ewers, 2021).

Nigeria's forests cover approximately 7.7% of the country's land area and are home to a diverse array of tree species, many of which are economically important (Olajuyigbe, 2019; Friant et al., 2019). Oban Forest, in Southwestern Nigeria, is the largest remaining portion of Nigeria’s tropical rainforest (Nigerian National Park Service, 2019). The forest has been described as one of Africa's most biologically diverse hotspots, with over 4,000 plant species, including many endemic species, and numerous fauna such as primates, elephants, and birds (Agaldo et al., 2016; Nigerian National Park Service, 2019; Aladesanmi, 2022; Olajuyigbe, 2019). Oban Forest plays a crucial role in the socio-economic development of forest-dependent communities by providing timber and non-timber forest products, regulating climate, water, and nutrient cycles, and supporting livelihoods. Like other tropical forests, anthropogenic activities and changes in the timing and intensity of climate variables such as precipitation and temperature can impact the abundance, composition, and timing of reproductive phenology of tree species within the forest (Agaldo et al., 2016; Bush et al., 2017; Gray and Ewers, 2021; Cleland et al., 2007; Dunham et al., 2018; Pezzini et al., 2014).

Many forest-dependent human communities in Africa rely on forest livelihood sustenance, including income generation and food provision (Jansen et al., 2020; Mayes et al., 2017; Benítez-López et al., 2019; Friant et al., 2019). Oban Forest has 39 forest-dependent/support zone communities that rely on the forest for dietary needs (Friant et al., 2019; Asuk et al., 2023; Ogogo et al., 2014). Thus, the provision of food by the forest will depend on the time and duration of production/availability of these products. As earlier established, changes in climatic drivers can alter the timing, quantity, and availability of food in Oban Forest, altering the cultural livelihood of these communities (Cleland et al., 2007; Richardson et al., 2013; Gray and Ewers, 2021).

There have been limited studies on the reproductive phenology of some African forest tree species (Adamescu et al., 2018; Di Lucchio et al., 2018; Adole et al., 2019; Bush et al., 2020; Angoboy et al., 2021; Fitchett and Raik, 2021; Ibrahim et al., 2021). Some of these studies have focused on single species (Di Lucchio et al., 2018), leaf phenology (Angoboy Ilondea et al., 2021) or have been on a different kind of forest (Fitchett and Raik, 2021; Ibrahim et al., 2021) therefore, these studies might not be applicable to all tropical forests, which are known for their rich species diversity with distinct characteristics. A notable study on fruiting phenology with long-term data spanning over 32 years was done in Lopé National Park, Gabon (Bush et al., 2020), 19 years of monitoring of 20 tree species in Ngogo in Kibale National Park, Uganda (Potts et al., 2020) and some parts of Central Africa (Adamescu et al., 2018). While these studies are in Africa, they represent Central and East African regions, respectively thus, the availability of data in North, South and West Africa can aid a better understanding of African forest tree phenology. There has been no study on fruiting phenology of tree species found in Oban Forest. Forest-dependent communities thus rely on their historical knowledge of the forest to aid the predictions of food availability in the forest. The responses of tropical forest phenology to different factors, including climate change, are not fully studied. Understanding the dynamics of the change would be beneficial to sustaining the food security of forest-dependent communities who rely on the forest for their cultural diets.

The data that could aid a reliable understanding of the timing and availability of flowering and fruiting events is needed across different species in the habitats. The study aims to provide two years of baseline monitoring data on the reproductive phenology (time of budding, flowering and fruiting) of food-producing tree species in Oban Forest for two growing seasons (May 2020 to May April 2022). This will provide data for future research to build on, thus, contributing to knowledge gaps geared towards a better understanding of the reproductive phenology of Oban Forest tree species.

5.3. MATERIALS AND METHODS

5.3.1. Study location

Oban Forest is located within the Oban Division of Cross River National Park (CRNP) in Nigeria between longitude 8°10´ and 8°55´ East and latitude 5°00´ and 5°50´ North (Figure 5.1b). Covering an estimated area of ~251,345 ha, the forest is bounded by 39 forest-dependent/support zone and small-holder agricultural communities to the North, South, and West and connected to the Korup National Park and Ejagham Forest Reserve of Cameroon to the East(Adeyemi, 2016; Agaldo et al., 2016). The forest vegetation combines the lowland and submontane moist tropical rainforest with rugged terrain and elevation ranging from ~ 100 m to over 1000 m above mean sea level. The mean annual precipitation ranges between 3,000 mm and 3,500 mm, while the mean monthly temperature ranges from 23°C to 37°C (Agaldo et al., 2016; Aigbe and Omokhua, 2015).

5.3.2. Plot establishment

Five plot clusters were selected using consistent plot location the RAINFOR protocol outlined by African Tropical Rainforest Observation Network (AfriTRON) (Phillips et al., 2018) and based on previous studies (Jimoh et al., 2012; Aigbe and Omokhua, 2015; Agaldo, Gwom and Apeverga, 2016). Five clusters were selected in three forest areas, one in Erukut and two in Aking and Osomba, respectively (Figure 5.1a, c, d, e). Within each cluster, three 40 by 40 m plots were established with the aid of a handheld compass (see Figure 5.2a), resulting in 15 sample plots with a combined area of 2.4 hectares (Figure 5.1c, d, e).

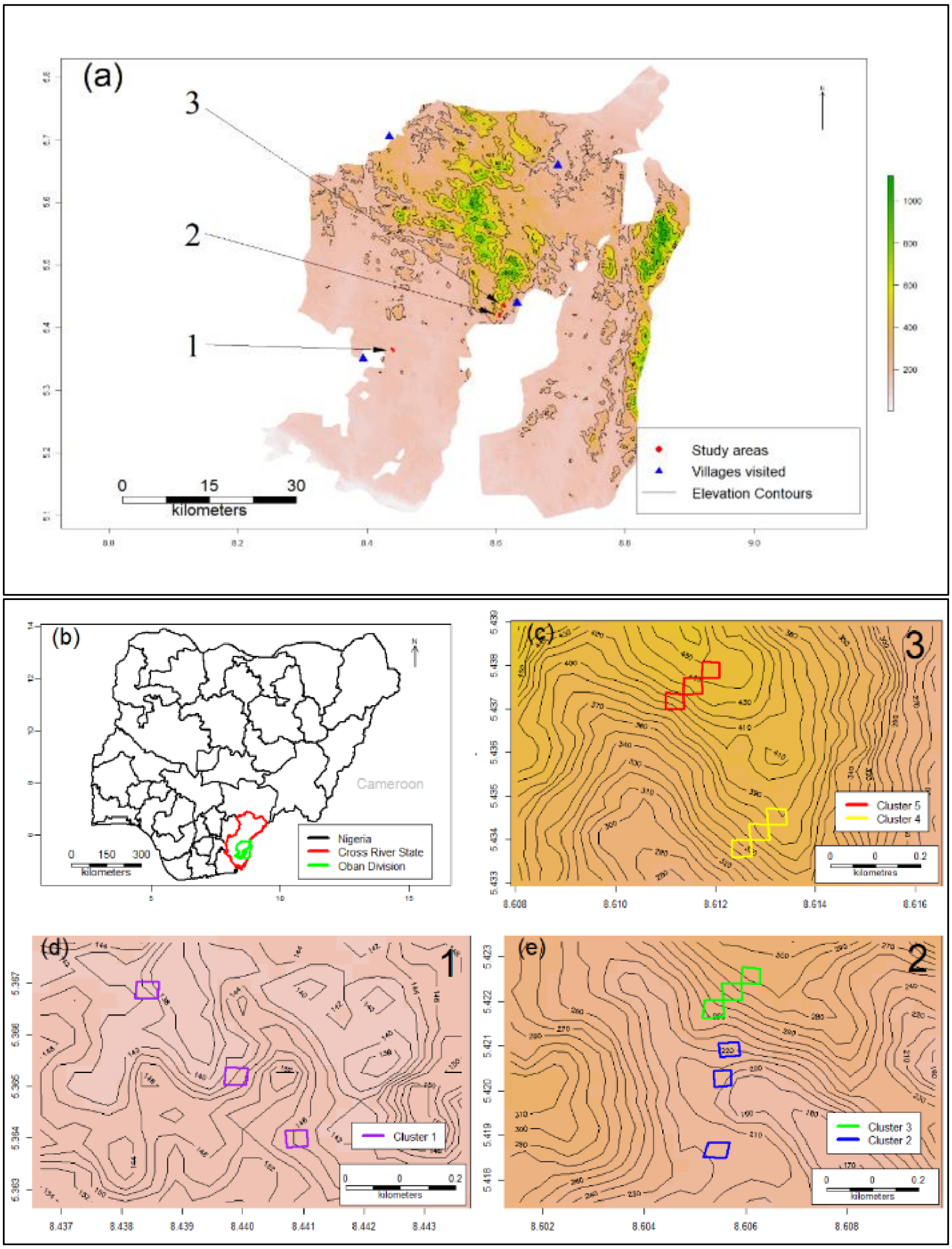


Figure 5.1. Topographic map of Oban Division showing the three areas selected for the location of permanent sample plots and forest-dependent communities used for the study (a). Map of Nigeria showing the Oban Division of Cross River National Park (b). Clusters of plot clusters along elevational bands within the three study areas (c, d, e).

All trees with a minimum diameter at breast height (dbh) of 10 cm within the 15 plots were tagged with a unique number, identified to species level by a field taxonomist and categorised as edible or inedible. All trees were marked with amber oil paint, while tree species identified as producing edible seeds, nuts, or fruits for humans (edible) were marked with additional orange paint (see Figure 5.2b). GPS coordinate of each plot was recorded using a Garmin eTrex 10 Outdoor Handheld GPS Unit. In cases where species identification was uncertain, tree locations were noted, and specimens collected and stored in herbarium presses for further taxonomic work.

Figure 5.2. Image of researcher aligning ranging poles with the aid of a compass during plot establishment (a) and a tree in the study area with a tag, yellow and orange paint marks (b)

The information used for the categorisation of tree species as producing edible fruits, nuts, and seeds for humans (edible category) was obtained from the administration of structured questionnaires to four out of 39 forest-dependent/support zone communities within the Oban Division of Cross River National Park (Ewah, 2013; Enuoh and Ogogo, 2018). Two villages, Nsan and Aking, were selected based on their proximity to the plots, while Obutong and Mkpot were chosen to ensure a spread around the National Park (Figure 4.1c,d,e). Respondents, aged 25 years or older, who had lived in the area long enough to provide information on forest tree species used, were interviewed using mixed method interviews, comprising group interviews with the council of chiefs, farming/gathering household heads, and individual interviews (Asuk et al., 2023; Friant et al., 2019). The collected information was compiled into a comprehensive list to categorise tree species into those producing edible products and those only producing inedible ones (see Chapter Two).

5.3.3. Phenological monitoring and data collection

Phenological monitoring of food-producing tree species was carried out on all fifteen permanent sample plots from May 2020 to April 2022, assisted by a team of three field research assistants at the University of Calabar – Nigeria. With the aid of binoculars, all trees (marked with both yellow and orange paint) in the fifteen plots with 10 cm *dbh* and above were assessed monthly for the seasonal onset of budding, flowering and fruiting for two annual cycles (two-year period) as recommended by Morellato *et al*. (2010). The decision to assess all tree species with 10 cm *dbh* and above was because phenological events (budding, flowering and fruiting) do not commence until a certain level of maturity and reproductive age (usually determined using girth size) is attained. The presence of phenological events, the percentage of the tree canopy covered by the event (based on the viewer's assessment) and additional comments such as fallen, dried or dead bud; fallen, dried or dead flowers; ripe (see Figure 5.3), fallen, dried, dead, or germinating fruits were noted and recorded. The presence of an event was marked with a yes or no, while the percentage of the canopy covered by the event was recorded in percentage.

5.3.4. Data quality control measures

Data collection for phenological monitoring began during the COVID-19 lockdown, which posed challenges due to travel restrictions to the study area. To address this, we constituted a research team comprising a staff member from the University of Calabar (serving as the team leader), a volunteer postgraduate student, and two residents from a forest-dependent community.

The team underwent training on the data collection protocol and I oversaw their activities to ensure adherence to standards. To maintain the quality of the data, during each monthly visit to the plots, a digital camera was used to capture two images for every tree exhibiting phenological events. The first photograph highlighted the phenological event on the tree, while the second focused on the tree tag. The digital camera's functionality, which automatically assigns unique numbers to each photograph, proved invaluable. These numbers were meticulously recorded against the tree tags on the data collection sheets.

After data collection for each month, the field team leader cross-referenced the information on the sheets for accuracy. The compiled data collection sheets and the associated images were subsequently uploaded to Google Drive. This procedure was followed consistently for the 24-month duration of the phenological monitoring.

5.3.5. Data presentation

The data collected on tree reproductive phenology monitoring were presented using line graphs and boxplots to get an insight into the seasonality of tree phenology in the forest. R (version 4.2.2) was used for data processing (R Core Team, 2022).

Figure 5.3. Image showing trees species with ripe fruits found in Oban Forest

5.4. RESULTS

Phenological events were observed in a total of 104 species, with a total of 367 tree stems representing 73% of total species and 31% of total tree stems enumerated for the two years (Table 5.1). Out of the total species and stems with phenological events, 28 species with 104 stems were of the edible species category, while 76 species with 263 stems were of the inedible species category. The list of edible and inedible species with phenological events are shown in Table 5.2.

Table 5.1. Stem density and species count between edible and inedible species found during initial plot establishment and two years of phenological monitoring of trees

	All species (Number (%))	Edible (Number (%))	Inedible (Number (%))
Initial enumeration for the entire forest			
Total tree stands	1180	306	874
Species count	143	32	111
Phenological monitoring			
Tree stands encountered	367 (31.10)	104 (33.99)	263 (30.09)
Species count	104 (72.72)	28 (87.50)	76 (68.47)

Table 5.2. List of edible and inedible species observed during the two-year monitoring period

SN	Inedible	SN	Inedible	SN	Edible
1	Anonidium mannii	39	Microdesmis puberula	1	Allanblackia floribunda
2	Antiaris toxicaria	40	Milicia excelsa	2	Angylocalyx oligophyllus
3	Antidesma vogelianum	41	Millettia grifforniana	3	Baillonella toxisperma
4	Baphia nitida	42	Millettia zechiana	4	Brachystegia eurycoma
5	Bridelia ferruginea	43	Musanga cecropioides	5	Caula edulis
6	Bridelia micrantha	44	Myrianthus arboreus	6	Chrysophyllum albidum
7	Calpocalyx brevibracteatus	45	Nauclea diderrichii	7	Chrysophyllum dumbeya
8	Calpocalyx cauliflorus	46	Neoboutonia glabrescens	8	Cola digitata
9	Carapa procera	47	Octoknema affinis	9	Cola hispida
10	Cleistopholis patens	48	Omphalocarpum elatum	10	Cola lepidota
11	Coelocaryon botryoides	49	Ouratea calophylla	11	Cola verticillate
12	Coelocaryon preussii	50	Panda oleosa	12	Dacryoides edulis
13	Corynanthe pachyceras	51	Pentadesma butyracea	13	Dialium guineense
14	Craterispermum cerinanthum	52	Petersianthus macrocarpus	14	Garcinia mannii
15	Diospyros mespiliformis	53	Piptadeniastrum africanum	15	Irvingia gabonensis
16	Diospyros suaveolens	54	Pterocarpus osun	16	Maesobotrya barteri
17	Diospyros zenkeri	55	Pterocarpus soyauxii	17	Maesobotrya dusenii
18	Distimonanthus benthamianus	56	Pterygota bequaertii	18	Parkia bicolor
19	Drypetes gossweileri	57	Pterygota macrocarpa	19	Pentaclethra macrophylla
20	Drypetes staudtii	58	Rauvolfia mannii	20	Poga oleosa
21	Duboscia macrocarpa	59	Rauvolfia vomitoria	21	Pycnanthus angolensis
22	Enantia chlorantha	60	Ricinodendron heudelotii	22	Tetrapleura tetraptera
23	Entandrophragma cylindricum	61	Rothmannia hispida	23	Uapaca heudelotii
24	Eribroma oblonga	62	Staudtia stipitate	24	Uapaca staudtii
25	Ficus capensis	63	Sterculia rhinopetala	25	Vitex doniana
26	Funtumia elastica	64	Sterculia tragacantha	26	Xylopia aethiopica
27	Garcinia pachycarpa	65	Strombosia grandifolia	27	Xylopia quintasii
28	Garcinia smeathmannii	66	Strombosia pustulata	28	Zanthoxylum zanthoxyloides
29	Guarea thompsonii	67	Strombosia schefflera		
30	Hannoa klaineana	68	Strombosia zenkeri		
31	Hildegardia barteri	69	Tabernaemontana pachysiphon		
32	Hylodendron gabunense	70	Terminalia ivorensis		
33	Hypodaphnis zenkeri	71	Trichilia obovoidea		
34	Isolona hexaloba	72	Trilepisium madagascariense		
35	Khaya senegalensis	73	Uapaca togoensis		
36	Klainedoxa gabonensis	74	Uvariopsis dioica		
37	Lophira alata	75	Uvariopsis gigas		
38	Lovoa trichilioides	76	Uvariopsis memfinis		

Continuous production of flowering buds and flowers was observed throughout the year (Figure 5.4), with peaks around April and May. Production of fruits peaked in June during the first cycle and between July and August in the second cycle. The fruiting peak was seen to occur just after the peak in budding and flowering.

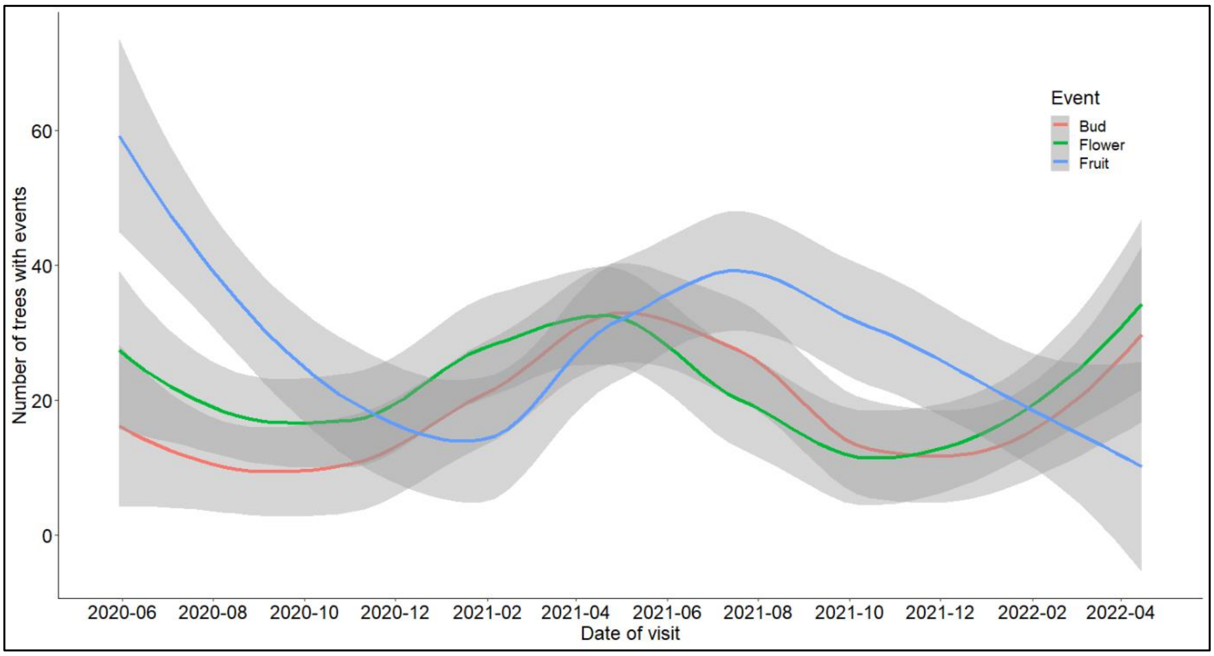


Figure 5.4. The count of tree stems seen in the flower bud production, flowering, and fruiting stages of reproductive phenology during the two years monitored period. The bold lines (red, green and blue) are the trend line, while the grey part represents the confidence interval at 0.95.

Results on the quantity of bud, flowers and fruits produced in Oban Forest in Figure 5.5 showed a seasonal trend in fruit production (Figure 5.5c). Highest mean quantity of fruit production was seen to occur in July and august in the first cycle and in July in the second growing season. Continuous production of flowering buds and flowers was observed throughout the year with no clear indication of a seasonal cycle.

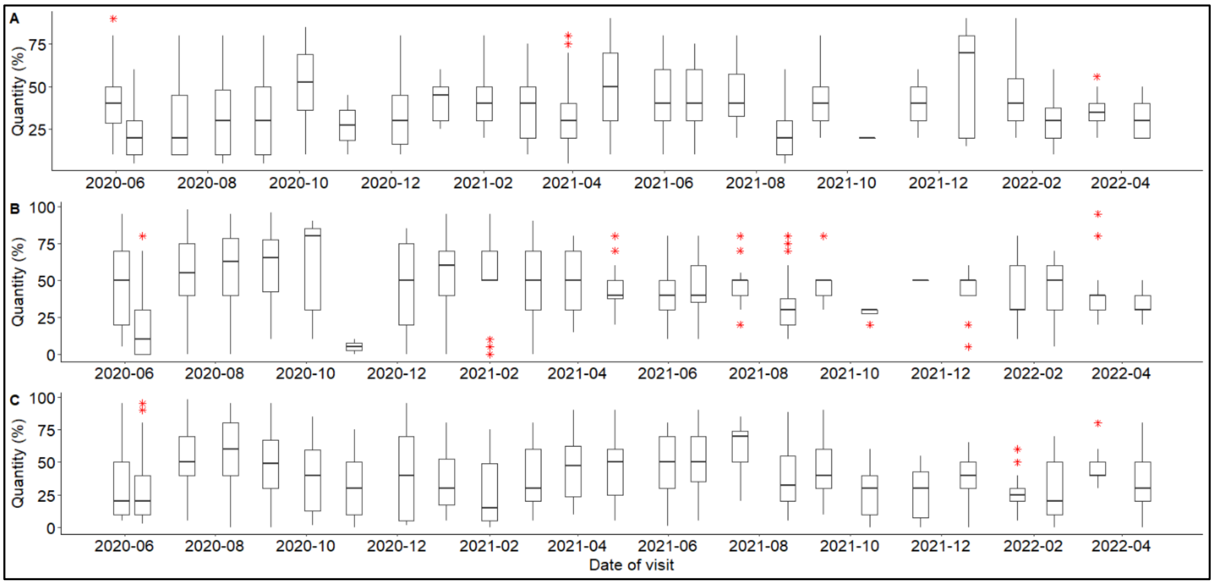


Figure 5.5. The quantity of occurrence of each phenological event. The plot shows the percentage of tree canopy area covered by each phenological event encountered in the study area. The percentage of canopy covered by flower bud encountered during the monitored period (A), the percentage of flowers (B) and the percentage of fruits (C). The variance expressed within each time period as drawn across the fifteen plots.

5.5. DISCUSSION AND IMPLICATIONS

Long-term monitoring of the reproductive phenology of food-producing tree species is essential to understand their response to environmental factors. The continuous production of flowers and fruits/seed throughout the year with a seasonal fruit production cycle, as seen in the data, could indicate that flowering and fruiting in the forest vary based on tree species. The flowering and fruiting of trees in African tropical forests are reported to occur throughout the year, and this has been linked to Phylogeny (Bawa et al., 2003). In a more recent study conducted in Gabon, the continuous production of flowers and fruits throughout the year was attributed to the difference in tree species and their varied adaptation to changes in climate variables (Bush et al., 2017). Most species in the tropical forest exhibit an annual phenological cycle, while some exhibit other trends range from sub-annual or super-annual cycles (Adamescu *et al.*, 2018; Potts *et al.*, 2020) and other trees produce perennial fruits (Franklin et al., 1987).

It was found that 31.10 % of the total tree stems enumerated and 72.72 % of the constituent tree species in the study area were seen to have phenological events. The disparity in the number of tree species with phenological activities compared to the number of stems could be attributed to several factors. These factors might vary based on climate (Polansky and Boesch, 2013; Pau et al., 2018b; Chapman et al., 2018; Parmesan and Yohe, 2003; Bush et al., 2020), the environmental niche, including the dominance of a certain species. Despite being of the same species, individual trees may occupy different environmental niches within the forest, such as differences in soil type, topography, or light availability. These differences can result in variations in the timing and intensity of phenological events among trees of the same species, leading to a disparity in the number of stems with phenological activities compared to the number of tree species. Also, certain tree species may dominate the forest, occupying a larger proportion of the total stem count. These dominant species may exhibit distinct phenological patterns that differ from other tree species in the forest, leading to a disparity in the number of tree species with phenological activities compared to the number of stems (Shirima et al., 2015; de Quesada and Kuuluvainen, 2020). The number of stands belonging to edible tree species with phenological events offers food production potential to the 39 rural forest-dependent communities in and around Oban Forest.

The cycle in the count of tree species and the percentage of tree canopy covered with flowering buds and flowers indicates that the peak of flower buds and flower production is consistent with the onset of the rainy season between March and April (Omogbai, 2017). It has been reported from previous studies that environmental factors with annual cycles strongly drive fruiting phenology in Afrotropical forests (Bush et al., 2017; Adamescu et al., 2018; Dunham et al., 2018). It is crucial to note that changes in climatic drivers can alter the timing, quantity, and availability of food in Oban Forest, affecting the cultural livelihood of these communities, as pointed out in other studies (Polansky and Boesch, 2013; Pau et al., 2018b; Chapman et al., 2018; Parmesan and Yohe, 2003; Bush et al., 2020). Although Adamescu et al. (2018) suggested that triggers from climatic factors are not annually constant, it would be a key contribution to understanding the extent to which these changes might affect fruiting phenology in the forest.

Fruit production heavily relies on environmental cues, and there is extensive proof that climate change has caused alterations in the timing of plant reproduction in temperate regions (Walther et al., 2002; Parmesan and Yohe, 2003). This phenomenon is characteristic of fruiting phenology in Afrotropical forests owing to the variation in flowering and fruiting time in different tree species (Adamescu et al., 2018; Dunham et al., 2018; Bush et al., 2020). There needs to be more data on the reproductive patterns of tropical plants or their changes over time. The specific causes of these changes are not universal and still need to be studied. Therefore, monitoring the phenological cycle of trees in Oban Forest is a critical step towards building a dataset that could aid in determining the dynamics of phenological events and understanding the climate-phenology relationship in Oban Forest.

However, in the Oban Forest and tropical Africa at large, there has been a persistent issue stemming from the lack of comprehensive long-term phenological data on trees. This void has imposed significant constraints on researchers keen on conducting phenological studies in this region. While the study of tree phenology is still an emerging and evolving area of research in tropical Africa, there are additional challenges that exacerbate the problem. Firstly, for those researchers who do possess data on tree phenology, it is often either stored in hard copy formats or has not been shared as open-source information. This has inevitably made the accessibility of this data cumbersome for other researchers, further hindering collaborative and comparative studies.

Secondly, there exists no standardized protocol for collecting data in phenological studies within the region. This lack of uniformity not only complicates the process for newcomers but also poses challenges in ensuring the consistency and reliability of data gathered across different studies. Lastly, the overarching problem compounding these challenges is the difficulty in procuring funding for long-term phenological studies in Africa. Financial constraints severely limit the potential for initiating and sustaining research projects, thereby stalling advancements in this field.

In essence, while the importance of phenological research is unquestionable, a combination of data accessibility issues, lack of standardized methodologies, and funding challenges are significant impediments for researchers in the Oban Forest and the broader African region. There is also a need to adapt the indigenous knowledge held dearly by forest-dependent communities to the potential changing trend and adopt necessary conservation and management strategies to accommodate these changes. This study adds to the limited information available on the reproductive phenology of African forest tree species. It provides valuable baseline data that would act as a foundation for future research to build on, contributing to a better understanding of the reproductive phenology of Oban Forest tree species and their response to environmental factors. It will also provide critical information to help develop sustainable food systems for forest-dependent communities and aid in forest conservation efforts.

CHAPTER SIX: KEY RESEARCH FINDINGS, SYNTHESIS AND FUTURE DIRECTIONS

6.1. INTRODUCTION

The research provides valuable insights into the impact of human activities and environmental factors on the species distribution and structure of Oban Forest in Nigeria. The aim of this research was ‘to investigate the factors affecting the biodiversity and phenology of trees in Oban Forest, Nigeria, including the impact of low-intensity anthropogenic activities such as human foraging, climate variables such as air temperature and precipitation, and to provide two years of baseline monitoring data on the tree reproductive phenology in Oban Forest’. Four main research gaps were focused on: Chapter Two examined the impact of low-intensity anthropogenic activities, such as foraging, on the ecological dynamics of the forest trees along an elevational gradient. Chapter Two also evaluated how low-intensity impacts can vary depending on the usefulness of the tree species in terms of usage for food or not. Chapter Three investigated the magnitude and dynamics of impacts from human-presence indicators on beta diversity in a regional forest between Nigeria and Cameroon, and how these indicators interact with other geographic and environmental drivers. Chapter Four assessed the temporal dynamics in the phenological responses to changes in temperature and precipitation cycle in an Afrotropical rainforest and highlighted the impact on the livelihood of many forest-dependent communities. Chapter Five provided two years of baseline monitoring data on the reproductive phenology of food-producing (edible) and non-food producing (inedible) tree species in Oban Forest. This chapter (Chapter 6) presents key research findings, an analysis of the principal research discoveries, and a projection of possible future research directions. This research has potential implications to affect the availability and quality of forest products, including those crucial for the nutrition and livelihood of the 36 forest-dependent communities in Oban Forest.

6.2. KEY RESEARCH FINDINGS

The research presented here is original and distinct in (1) employing the utilization of forest tree species for food by forest-dependent communities to assess the impact of low-intensity human activities on the composition, abundance, and distribution of tree species. (2) utilizing the interaction between human influence indicators with other geographic and environmental drivers to investigate the beta diversity of tree species in Nigeria and Cameroon. (3) presenting the first evaluation of the impact of climate variables on the phenology (EVI) of the Oban Forest. (4) generating the first phenological monitoring data in Oban Forest with the potential for continuous monitoring. The primary research findings were as follows:

1. Low-intensity human activities, such as foraging, may influence the forest species distribution and structure, leaving observable footprints. The findings suggest that even low-intensity foraging has the potential to change the Oban Forest dynamics. Different intensities of human activities along the studied gradient maybe having varying impacts on the abundance and evenness of edible and inedible tree species. During foraging for food by forest-dependent communities, the dispersal of seeds, in addition to tree management, deliberate planting, and conservation for food production, could have contributed to this pattern. In contrast, inedible species exhibited increasing pairwise spatial beta-diversity with an increase in elevation, suggesting the constant turnover of species due to niche filtering and/or dispersal limitation.
2. Turnover was the primary driver of tree species dissimilarity in the Nigeria-Cameroon forest region, with environmental filtering exerting a stronger effect than geographical distance. Human activities, as indicated by DCHP, were found to be an important driver of beta diversity for edible species but not for inedible species. Forest composition and stem density were also found to be important drivers of dissimilarity, with stem density

having a greater effect on edible species. Spatial distance between plots and elevation were important individual drivers of dissimilarity, with elevation having a stronger effect on the turnover of inedible species. From the findings, it was hypothesised that the impact of human activities on the beta diversity of tropical forests is complex and could depend on various factors, including the type and intensity of activities, elevation, the distance between plots, and soil.

3. Oban Forest showed a clear seasonal cycle in EVI, with the highest average monthly values recorded between March and October, and low values between December and February. This cycle was offset from the seasonal cycles in temperature and precipitation, which suggested a combined effect of increased precipitation and reduced temperature on peak EVI values and the reverse for lower EVI values. The seasonal cycle of EVI was found to be linked to precipitation patterns, with higher rainfall promoting increased photosynthetic activity and leading to higher EVI values with a lagged response of up to seven months. Temperature was negatively correlated with EVI however the impact on EVI was non-significant. Changes in the phenological cycle of Oban Forest could impact the availability and quality of forest resources needed to sustain the livelihoods of forest-dependent communities, particularly those involved in collecting and selling non-timber forest products or those specialized in ethnobotany as a trade.
4. During the two years of baseline phenological monitoring, phenological events were observed in 104 tree species with 367 tree stems, representing 72.72% of the total tree species and 31.10% of the tree stems enumerated in Oban Forest. Continuous production of flowering buds and flowers was observed throughout the year, with peaks around April and May, while fruit production peaked in June during the first cycle and

between July and August in the second cycle. The proportion of tree stems (31.10%) seen to have phenological events compared to the number of tree species (72.72%) represented suggests a variation of phenological cycles within species. The continuous production of flowering buds and flowers throughout the year with seasonal fruit production trends suggests there are opportunities for food production and consumption in Oban Forest.

6.3. SYNTHESIS

6.3.1. Low-intensity human impact on species composition

The impact of human activities on tree species composition and diversity can be determined by factors such as taxa and geographical location. Human activities such as harvesting of timber, farming, nomadic nature of some indigenous settlements, foraging, and conservation efforts by indigenous people can affect the distribution of tree stand density along the elevational gradient (Otu et al., 2012; Jimoh et al., 2012; Asuk et al., 2023; Adeyemi, 2016; Aigbe and Omokhua, 2015). The results suggest that low-intensity human activities, such as foraging for edible species, have the potential to modify the forest and leave visible footprints in the dbh abundance-size distribution and composition of tree species. Several studies have hypothesised that different intensities of human activities can potentially leave footprints in the forest that are visible in the composition and distribution of tree species (Jansen et al., 2020; Jacobson et al., 2019; Asuk et al., 2023; Benítez-López et al., 2019; Waring et al., 2020). The disparity in the trends observed in edible and inedible species could be due to the selective dispersal of propagules during foraging, deliberate conservation, and management of desired species by humans for food production. It has been reported that in populations of a species with limited seed dispersal, human disturbances enhance the impact of founder effects, thus agreeing with the finding that humans influence the dispersal of propagule in a forest (Silvestrini et al., 2015; Waddell et al., 2020; Asuk et al., 2023). Also, humans can cover a wider ground distance when foraging for fruits, seeds, and nuts than for other high-intensity activities like logging (Asuk et al., 2023; Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022). Furthermore, large-scale forest disturbance due to timber harvesting, clear-cutting for agriculture, or agroforestry practices are other factors that can induce large-scale modification of the forest (Seidl et al., 2017; Belote et al., 2009; Sagar et al., 2003; Jaeger et al., 2022; Jara-Guerrero et al., 2021).

In combination with geographical distance, elevation and stem density, low-intensity human activities were one of the main drivers of beta diversity in the regional study involving forests of Nigeria and Cameroon. The impact of human activities on tree species dissimilarity at a regional scale was more significant for inedible species than edible species. The disparity in the effects of human activities at a local and regional scale is consistent with the findings of other studies that have suggested that selection and stewardship of desired tree species by indigenous populations over time might indeed exert different impacts on different species used(Asuk et al., 2023; Levis et al., 2017; Roberts et al., 2021; Scerri et al., 2022). Furthermore, the impact of elevation at the local-scale studies was attributed to the niche-filtering along elevational gradients and the confinement of different intensity human activities to lower or higher elevational gradients. However, some studies have pointed out that tree species traits, dispersal mechanisms, and climate parameters could also significantly influence the species community assemblage (Horbach et al., 2023; Kirk et al., 2021; Buzatti et al., 2019; Fauset et al., 2019). Further studies are needed to understand the potential impacts of these factors on forest tree community assemblage in the region.

6.3.2. Drivers of phenological cycle in Oban Forest

It was observed that the forest is characterized by high and somewhat constant air temperature, with a strongly variable seasonal precipitation cycle. It was found that precipitation was the primary and most important climatic factor that drives the changes observed in EVI. In the tropical rainforest, precipitation could affect EVI from zero-month to seven months past the rainfall event. Conversely, the effect of air temperature was negatively correlated with precipitation and had little effect on the forest vegetation in the tropical rainforest. These findings are consistent with other African studies that have shown the importance of precipitation in driving forest vegetation dynamics (Gou et al., 2022; He et al., 2021; Li et al., 2023; Naif et al., 2020; Wingate et al., 2019).

Research in African rainforests has shown that precipitation is indeed a critical factor in shaping vegetation dynamics (Abera et al., 2018; Wingate, Phinn and Kuhn, 2019; Yan et al., 2019; Gou et al., 2022), with periods of drought leading to decreased growth and increased mortality of trees and other plant species (Abera et al., 2018; Dunham et al., 2018; Pau, Detto, et al., 2018; Naif, Mahmood and Al-Jiboori, 2020; Potts et al., 2020). In Lope National Park in Gabon, annual phenological cycle was the most common cycle observed in the African rainforest (Bush et al., 2017). Bush et al. (2017) further found that new leaf formation was produced during the dry season, while peaks in fruiting phenological cycles were mostly reported during the rainy season. Preciin fruiting phenological cycles were mostote, Sanders and Jones, 2009; Seidl et al., 2017; Jara-Guerrero et al., 2021; Jaeger et al., 2022).

In addition, studies in some African Forests have found that temperature, light availability and other variables (Esmaili et al., 2020; Gray and Ewers, 2021; Xulu et al., 2018; Di Lucchio et al., 2018) can influence vegetation growth, although these factors are generally considered secondary to precipitation (Jiang et al., 2019; Dunham et al., 2018). Similarly, research on Amazonian rainforests has also highlighted the importance of precipitation in driving forest vegetation dynamics (Fauset et al., 2019; Jiang et al., 2019). However, studies have found that the timing and intensity of precipitation can be more important than total rainfall in determining vegetation responses (Esmaili et al., 2020; Bucher and Römermann, 2021).

While the phenology-climate relationship study was limited due to a dearth of ground-truthed data and remotely sensed images with a high percentage of cloud cover, the findings have important implications for conservation and management strategies for Oban Forest and other tropical rainforests in the region. It is crucial to understand the factors that influence forest greenness to protect and manage these ecosystems properly, especially for forest-dependent human communities who rely on the forest for their livelihood. Further research studies that could benefit from better sampling, quality data collection, and improved analytical methods are needed. By improving our understanding of the complex interactions between humans, the environment, and forest ecosystems, we can develop more effective conservation and management strategies to help preserve the ecological integrity of tropical rainforests and biodiversity for future generations.

Additionally, it is essential to note that climate change poses a significant threat to tropical rainforests worldwide. According to recent studies, deforestation and other human activities account for varying major impacts on the forest (Williams et al., 2020; Ite, 2018; McMichael, 2021; Santos et al., 2018; Jacobson et al., 2019; Zheng et al., 2019). Climate change is expected to increase the frequency and intensity of extreme weather events, such as droughts and floods, which can significantly impact the health and productivity of tropical rainforests (Samanta et al., 2010; Rowland et al., 2018; Qie et al., 2017; Abera et al., 2018; Didi Sacré Regis et al., 2020; Chen et al., 2020). Therefore, effective climate change mitigation and adaptation strategies must be implemented to ensure the long-term survival of these ecosystems.

6.3.3. Implications for forest-dependent communities

Human activities such as foraging and deliberate conservation of certain species have potentially modified the forest over time, leaving observable footprints. Past disturbances in the forest caused by large-scale human activities like timber harvesting and clear-cutting for agriculture are also likely to have influenced the species composition and structure of the forest. These findings have broader implications, as studies in other tropical forests have shown evidence of low-intensity human impact on forest ecosystems (Scerri et al., 2022; Guo et al., 2022; Williams et al., 2020; Santos et al., 2018; Asuk et al., 2023; Popradit et al., 2015; Jacobson et al., 2019; Ellis et al., 2021, 2010).

The results have significant implications for the 39 forest-dependent local communities living in and around Oban Forest (Asuk et al., 2023), who rely heavily on the forest for their livelihoods (Friant et al., 2019). The phenological cycle of the forest plays a crucial role in determining the availability and quality of forest products, such as fruits, nuts, and plants of ethnobotanical importance, which are important sources of nutrition and income for these communities (Ebu et al., 2021). Changes in the phenological cycle caused by climate change and other factors could impact the availability and quality of these resources, thereby affecting the income-generating potential of forest-dependent communities (Paeth et al., 2008; Bush et al., 2020).

The increase in mean annual air temperature and decrease in mean annual precipitation observed in the study was in light with the data reported for the Nigeria area by Oderinde (2022). Although the scope of the study did not include climate variables as factors influencing beta-diversity in the Nigeria-Cameroon region, factors like geographic distance and elevation that are highlighted can have strong ties to climate-related shifts (Swenson, Anglada-Cordero and Barone, 2011; Nascimbene and Spitale, 2017; Fontana et al., 2020; Asuk et al., 2023). Determination of the likely changes in forest phenology based on climate change would require the integration of this beta-diversity information with climatic data over a significant period. This would allow for the discernment of patterns that are directly attributable to climate change versus those that are due to other environmental or human factors.

6.3.4. Conclusion

This thesis provided new insight to the drivers of change to the tree species composition, distribution, and phenology. It has shed light on the complex relationships between humans, the environment, and tropical rainforests in Oban Forest in the Oban division of Cross River National Park – Nigeria. The study is the first of its kind conducted in Oban Forest. It presents the interactions between human temperature, and precipitation that could impact the forest while highlighting the implications to the food security of forest-dependent communities. inform decision-making. The findings also highlight the need for continued research to understand these interactions better, which have important implications for conservation and management strategies and climate change mitigation and adaptation policies.

6.4. FUTURE RESEARCH

The research showed that humans and climate influence the composition, distribution and phenology of Oban Forest tree species in the forest. Thus, actions must be taken to protect and preserve tropical rainforests, like Oban Forest, for the sake of biodiversity and ecological integrity and for the benefit of the people who depend on these forests for their livelihoods. Thus, further research projects would focus on

1. The impact of human activities on tropical forest dynamics and species distribution: This would involve plot-based data and interview visits to forest-dependent communities to investigate the potential impact of historical and current human activities. The research would include a comparison between forest exposed to low-intensity activities, such as foraging and seed dispersal, and those known to be exposed to higher-intensity activities such as logging, farming, and agroforestry practices. This research would help to determine the extent to which human activities are altering the structure and composition of tropical forests, and how these impacts may vary across different forest types and regions.
2. The role of trait-environment interactions in species distribution: This would involve exploring the impact of trait-environment interactions on species distribution, particularly in edible and inedible species. This research would require collecting data on species traits and interaction networks in tropical forest ecosystems and would help to better understand how environmental factors and species traits interact to shape species distribution and abundance.
3. Extend monitoring of phenological cycle in the area along with the collection of ground-based data on air temperature, and precipitation in Oban Forest to track changes in the variables over time and identify any emerging trends or patterns. Ground-based

monitoring would allow the development and evaluation of more accurate predictive models for the relationships between EVI and climate variables, as well as to link leaf phenological cycles to fruiting phenology.

4. Collaborating with modellers to explore how factors such as light intensity, soil nutrients, atmospheric CO_2 concentrations, and functional type and traits of the tree species could interact with each other and further complicate the response of vegetation to environmental changes.
5. Research on the social and economic impacts of climate change on forest-dependent communities to explore ways to support their adaptation and resilience to changes in the phenological cycle. This would also explore ways to support forest-dependent communities in adapting to the impacts of climate change, including through sustainable land use practices, alternative livelihoods, and community-based conservation initiatives.

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