COMPARING TREE FUNCTIONAL TRAITS AND SPECIES DIVERSITY ALONG AN INCREASING RAINFALL GRADIENT IN NORTHERN NAMIBIA

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Abstract

Changes in precipitation patterns have the ability to affect the composition and the variety of species within a plant community by altering their functional traits. However, there has been a tendency to underestimate the importance of functional diversity. This is particularly common in Namibia, despite a clear, gradient in precipitation and where forecasts have predicted changes in precipitation regimes in the future. This study examined how tree species diversity and functional traits changed along an increasing rainfall gradient in northern Namibia. It employed a quantitative approach with systematic sampling at 13 points along an approximately 1200 km transect. Tree species diversity fluctuated along the gradient and average annual rainfall did not appear to have a significant effect, yet species diversity was highest at sites with high rainfall. There was no statistical difference in the species diversity among sites, but the estimated beta diversity was high. Plant functional diversity indices and plant functional traits varied along the gradient. All three functional diversity indices revealed weak relationships with species diversity. Among the three functional diversity indices, only functional richness was significantly affected by annual average rainfall. While the current study presents some contrasting results, it remains relevant by providing an understanding of the dynamics between plant species diversity and functional diversity. The results of the current study support the conclusion that plant species diversity and plant functional diversity are both vital components of ecosystem functioning, and that future research should incorporate a wider array of functional traits and use more comprehensive data collection methods that can build on the findings to further elucidate these complex interactions.

Key words: Climate change, plant ecology, precipitation, species composition, functional indices, species evenness, species richness, functional traits

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List of Abbreviations and/or Acronyms

CBD – Convention on Biological Diversity

CWM - Community-Weighted Mean

DBH – Diameter at Breast Height

DS – Deep: Shallow ratio

EIF – Environmental Investment Fund

FDiv – Functional Divergence

FEve – Functional Evenness

FRic – Functional Richness

MBI – Multiple-site Biodiversity Indices Calculator

MEFT – Ministry of Environment, Forestry and Tourism

MET – Ministry of Environment and Tourism

NILALEG - Namibia Integrated Landscape Approach for Enhancing Livelihoods and Environmental Governance to Eradicate Poverty

PCA – Principal Component Analysis

PC – Principal Component

SLA – Specific Leaf Area

SWAFR – Southwest Australian Floristic Region

UNAM – University of Namibia

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Dedication

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Declarations

I, Albertina Shikongo, hereby declare that this study is my own work and is a true reflection of my research, and that this work, or any part thereof, has not been submitted for a degree at any other institution.

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Albertina Shikongo	A. Shikongo	**April 2025**
Name of Student	Signature	Date

CHAPTER ONE

1. Introduction

1.1. Background

Understanding the functional diversity of plants is important to understanding how environmental change, community composition, and ecological processes are related (Lavorel & Garnier, 2002). Community assemblages and resilience are also highly dependent on the diversity of functions of the species inhabiting a given area (Gomes et al., 2023). Despite this recognition, the association between functional diversity and species diversity in most ecosystems is still inadequately identified. It is important to establish this relationship to develop a comprehensive insight into the processes of community formation and suitable strategies for safeguarding and restoring biological communities (Bu et al., 2014).

Historically, studies on the characterization of plant communities were largely based on the concept of species diversity, which is defined as species richness and species evenness within a geographical area of interest, while other aspects of diversity were typically undervalued (Dong et al., 2017). One of such aspects is functional diversity, the diversity and spatial arrangement of plant life-history traits within a community, landscape, or broader geographical regions are functionally significant to the growth, reproduction, and survival of plants. (Ma et al., 2019). These traits are inherited morphological, physiological, or phenological features that affect an organism's performance, fitness, and ultimately the species' ability to adapt to environmental changes (Price, 1994; Violle et al., 2007; Kühn et al., 2021). A range of leaf traits, root traits, bark traits etc. exists and plants in different biomes or those exposed to different evolutionary drivers exhibit different traits. Some community-level traits, Community

Weighted Trait Means (CWM), can anticipate how a plant community would react to large-scale precipitation changes (Le Bagousse-Pinguet et al., 2017). CWM are frequently used to describe communities by merging information on species traits and distribution (Duarte et al., 2018).

Research increasingly demonstrates the direct relationship between functional diversity and the behaviour and interactions of species within an ecosystem (McGill et al., 2006). The composition of functional traits in communities is predicted to be impacted by variations in species richness caused by species turnover and localized extinction, with significant implications for ecosystem function (Gallagher et al., 2013). Therefore, understanding plant functional trait distribution within and among communities is of critical relevance to explain community assembly, dynamics and resilience to disturbance in an era of deep global changes (Gomes et al., 2023).

Climate variability is anticipated to have an effect on the organization, function, and makeup of plant communities (Paz-Kagan et al., 2021)). Therefore, high functional diversity should be desirable, as diversity reflects aspects of ecosystem productivity, dynamics, stability, and nutrient availability (Li et al., 2015). Furthermore, some degree of redundancy in functional traits should be key in the resilience of the ecosystem (Gomes et al., 2023).

The occurrence of plant communities are shaped by changes in the plant traits and their abundance while being mediated by environmental gradients such as changes in the precipitation regime, soil and by other microclimatic (light, windspeed etc.) variables (Griffin-Nolan et al., 2018). Several hypotheses account for the difference in plant species diversity along rainfall gradients. Annual rainfall correlates positively with local plant species richness throughout long rainfall gradients, from continental to global scales. In the Neotropics, woody plant species diversity appears to increase with higher annual precipitation levels (Tuomisto et al., 2014). In addition, in a neotropical environment, species richness increased with increasing rainfall, till rainfall reached 4000 mm.

With climate variability along natural gradients affecting plant functional traits differently and with the threat of climate change on plant communities, Kühn et al. (2021) identified eight essential traits that most accurately forecast positive plant responses to climate changes across different biomes, which include specific leaf area (SLA), plant height, greater water-use efficiency, greater re-sprouting ability, lower relative growth rate, greater below-ground storage, higher wood density, and greater rooting depth. The current study assessed three of these traits that respond positively to climate changes, namely: SLA, plant height, and rooting depth. The study chose to study these three traits since they form the fundamental aspects of a plant's life cycle and are also correlated to each other (Cornelissen et al., 2003). In addition, the nature of assessing the other traits is quite complex and requires sophisticated materials and methods that could not be accommodated in this study (Pérez-Harguindeguy et al., 2013). Additionally, these three traits were assessed on the dominant species (with the most individuals) in a plot. A few indices were established to capture various aspects of the distribution of trait values within and between communities situated along gradients. Commonly applied indices are functional richness, functional evenness, and functional divergence (Legras et al., 2018).

Studying SLA, plant height, and rooting depth along a strong precipitation gradient; would fill some geographical gaps in better understanding the importance of functional diversity and climate variability (Vasilevich, 2009). These geographical gaps refer to regions or ecosystems where there is limited data on how functional traits respond to environmental factors like precipitation gradients. In addition, assessments of biodiversity are essential for identifying changes in environmental conditions and ecosystem functioning brought on by humans or natural processes and plant functional diversity can, therefore, be utilized to forecast how a plant community could react to future environmental shifts (Zuo et al., 2021).

This study is supported by the Namibia Integrated Landscape Approach for Enhancing Livelihoods and Environmental Governance to Eradicate Poverty (NILALEG) Project, which seeks to advance an integrated approach to landscape management in crucial agricultural and forest areas, aiming to alleviate poverty through sustainable livelihoods based on nature, safeguard and restore forests to serve as carbon sinks, and advocate for achieving Land Degradation Neutrality (EIF, 2020).

1.2. Statement of the problem

Presently, there is limited scientific knowledge concerning plant functional diversity, its relationships to plant species diversity, and how these metrics change over rainfall gradients in Namibia. This may hinder the designing of well-informed adaptation measures to climate variability. In other words, the management decisions may be mismatched, and this may result in poor allocation of limited resources and affect ecosystems and livelihoods negatively. In addition to this, there are limited data on local plant species on international databases (TRY Database) of plant functional traits for the northern part of Namibia that support wildlife of extreme relevance to the economy of Namibia and human wellbeing, i.e., ecotourism.

1.3. General and specific objectives of the study

The overall objective of this study is to compare plant functional traits and species diversity along a rainfall gradient from northwest to northeast regions of Namibia.

Specific objectives are:

a. To determine and compare tree species diversity along an increasing rainfall gradient,
b. To determine and compare tree functional diversity (richness, evenness, and divergence) along a rainfall gradient, and
c. To determine the relationship between tree species diversity and functional diversity along a rainfall gradient.

1.4. Study hypotheses

a. Tree species diversity increases along an increasing rainfall gradient,
b. Tree functional diversity (richness, evenness and divergence) varies along the rainfall gradient, and
c. There is a relationship between tree species diversity and functional diversity along the gradient.

1.5. Significance of the study

Knowledge about plant species traits that are more adaptable to climate change can improve climate change strategies and ecosystem service provision. Thus, knowledge about functional traits can inform the sustainable utilization of our plant resources amidst climate change, it can also inform ecological restoration for sustainably resilient ecosystems. Potential beneficiaries of such knowledge are government organs such as the Ministries of Environment, Forestry and Tourism (MEFT) and Agriculture, Water and Land Reform (MAWLR), as well as the private sector and local communities. Furthermore, such knowledge can support ongoing national and global biodiversity monitoring initiatives (e.g., the post-2020 CBD biodiversity framework) which require baseline datasets for monitoring vegetation in relation to climate change and habitat quality (Hughes et al., 2022). Data that have been collected on plant functional traits during this study will be added to global plant functional traits datasets, which will be of value as there is very limited data on species from Namibia on some of these databases. The sets of functional traits that plants in a certain ecosystem possess define how these plant species compete for resources, how they tolerate stress and how they survive destructive events such as fires (Pierce et al., 2017). Possessing knowledge on functional traits and biodiversity patterns is important for the management of biodiversity.

1.6. Limitations

This study, due to resource and time constraints, focused on only three out of the eight plant functional traits of the dominant plant species at each sampling sites for objective 2. The nature of assessing the other traits is complex and requires sophisticated materials and methods that were not available for this study (Pérez-Harguindeguy et al., 2013).

1.7. Delimitations of the study

The study focused on only three out of the eight climate traits identified by Kühn et al. (2021) that most accurately forecast favourable plant responses to climate changes across different biomes. Despite this reduction, the selected traits, namely, SLA, plant height, and rooting depth, are widely regarded as universally relevant because they are fundamental to the plant’s life cycle (Pérez-Harguindeguy et al., 2013). Before the computation of the three functional diversity indices, 45 missing data values for rooting depth and SLA were imputed using the Random Forest Imputation method (Joswig et al., 2023). The study only focused on tree species.

1.8. Research Ethics

Ethical clearance for this study was obtained from the Decentralized Ethics Committee, Centre for Research Services of the University of Namibia (UNAM) and research permission from the National Commission on Research, Science and Technology (RCIV00022018).

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CHAPTER TWO

1. Literature Review

1.1. Biodiversity along climatic gradients

Natural gradients influence species occurrences and distributions due to variations in climate and available resources. Bio-climatic variables such as total annual precipitation and mean monthly temperature are significant as they determine major climatic shifts over a long period (Chapungu et al., 2020). Similarly, species richness and composition fluctuate as one moves from lower to higher latitudes and altitudes due to variations in climatic factors, especially those relating to temperature and precipitation (Rosenfield & Müller, 2020). Geographical distributions of species, species responses to environmental change, community structure, and ecosystem functioning can all be influenced by levels of intraspecific diversity, whether they are defined as functional diversity, phylogenetic divergence, population richness, or genetic diversity within and among populations (Cadotte et al., 2011). A study by Wieczynski et al. (2019) found that functional diversity generally decreases with increasing latitude and elevation. Furthermore, authors indicated that the strongest causes of geographic changes in functional composition and ecological strategies are temperature variability and vapor pressure, and that functional composition might change eventually as due to rapid climate variation.

Species richness tends to increase along a latitudinal gradient towards the equator, both within locally defined areas (alpha diversity) or over a gradient (gamma diversity). Several theories have been proposed to explain these relationships, including the tropics' higher production, greater complexity in species relationships, lower extinction rates, and longer evolutionary timeframes (Painka, 1966; Willig et al., 2003; Nishizawa et al., 2022). Cofactors such as soil type, topography, soil type and texture, nutrients, and substrate stability can also affect the distribution of plant species within a given elevation zone (Silva Mota et al., 2018). Organisms including plants in general organize themselves in space(Dray et al., 2014). This means that plant species organize themselves spatially to occupy distinct ecological niches, reducing competition and maximizing resource use. Work by Lavorel and Garnier (2002) emphasized that plant species traits vary along nutrient gradients, with species from nutrient-rich environments exhibiting inherently rapid growth, efficient resource acquisition, and quick organ turnover. This in turn, leads to poor internal resource conservation, whereas species from nutrient-deficient environments experienced the opposite. This trade-off in plant traits has been linked to several quantitative features. For example, plants in nutrient-rich environments typically combine high SLA with high tissue nutrient concentration (particularly nitrogen), low tissue density and cell wall content, fast rates of carbon and nutrient intake, and short-lived leaves (Pierce et al., 2017; Weemstra et al., 2023). Out of all the traits considered, SLA was found to have the best capacity to describe how species are distributed over Spain's aridity gradient (Costa-saura et al., 2016). Given that SLA has been linked to numerous significant aspects of plant drought tolerance, it is perhaps not unexpected that SLA plays a major role in determining the species niche in arid conditions (Costa-saura et al., 2016).

Even though leaves are present in most species, in arid and semi-arid habitats, root traits such as root depth may be a more accurate predictor of responses than leaf traits (Padilla & Pugnaire, 2007; Laughlin et al., 2021). Depending on the environment, species traits that are most closely associated with plant performance may change. For instance, a study of the annual plant *Polygonum persicaria* showed that, in environments with low water resources, plant fitness was correlated with leaf-level water-use efficiency, whereas root biomass allocation was more closely related with fitness in wet conditions (Funk et al., 2017).

Functional traits are predicted to influence the mechanisms by which communities adapt to environmental changes (Lavorel & Garnier, 2002). Additionally, numerous factors can interact to affect community relationships. For instance, Maire et al. (2013) showed that qualities linked to competitive ability (e.g., height) were stronger displays of abundance across grazing and nutrient treatments in a grassland ecosystem, despite differences in feeding strategy among species (a.k.a. niche differences). Gross et al. (2015) indicated that while the traits (SLA and height) of native and invasive plants varied, their responses to grazing and competition were comparable because diverse trait combinations produced equal success with these parameters.

Variation in trait values between communities has been used to foresee how an ecosystem would evolve under environmental changes (Klumpp & Soussana, 2009) while community-level variation can forecast how resilient an ecosystem's functioning would be to disturbances (Mori et al., 2013). In agreement with expectations based on species trait-environment patterns across much of the Western Hemisphere, Wieczynski et al. (2019) argued that CWM values of leaf traits, height, seed mass, and wood density based on species occurrences were relatively strongly correlated with annual mean and seasonality of temperature and precipitation. However, because of interactions among different environmental factors and assembly processes that might not favour species with intermediate trait values, trait-environment connections did not necessarily scale linearly from the species to community levels (Rosbakh et al., 2015).

1.2. Plant species diversity and plant functional diversity

The association between species diversity and functional diversity has been a subject of considerable investigation within ecological literature (Mayfield et al., 2010). A positive correlation between functional diversity and species diversity suggests that each species encompasses distinctive functional traits. For instance, Biswas and Mallik (2011) examined the relationship between species diversity and functional diversity of riparian and upland vegetation and tried to determine if the slopes of their relationship would vary with disturbance intensity. Their results revealed that for all disturbance intensities, the connections between species richness and functional richness and species evenness and functional evenness were positive and non-zero.

A logarithmic functional diversity-species diversity relationship implies that functional diversity might rise quickly at low levels of diversity and then declines as functional redundancy rises. To illustrate, it was discovered that there is often a weak and trait-dependent link between species and trait relationships. Asymptotic species/trait state relationships are positive for all traits, and their intercept values are almost zero. Few species/trait state regressions, although consistently positive relationships, had curvature parameters that deviated significantly from zero, suggesting weakly saturating relationships (Mayfield et al., 2005). For both types of habitat, the pollination mechanism was the sole trait with statistically significant saturation values, suggesting a rapid accumulation of trait states per additional species (Mayfield et al., 2005). Lastly, a sigmoid logistic functional diversity-species diversity relationship illustrates two-phase functional redundancy, with functional redundancy at low levels of species diversity followed by a swift increase at high levels of diversity (Sasaki et al., 2009).

Functional diversity, although relatively understudied in comparison to taxonomic species richness or diversity, is gaining recognition for its pivotal role in shaping ecosystem processes. Some scholars argue that due to its presumed mechanical link between diversity and ecological processes, functional diversity exerts a more profound influence on ecosystem functioning (S. Diaz & Cabido, 1997). There is a rising accord that the influences of diversity on ecosystem processes should be credited to the functional traits of individual species and their interactions rather than mere species count (Cadotte et al., 2011). Both empirical evidence and theoretical frameworks increasingly support the notion that functional diversity may influence short-term ecosystem resource dynamics and long-term stability (Díaz & Cabido, 2001). Furthermore, mounting evidence suggests that functional diversity significantly regulates ecosystem functioning, stability, and the provision of essential ecosystem services critical for human well-being (Ruiz-Benito et al., 2014).

Petchey and Gaston (2002) stated that functional diversity is a notion that connects species and ecosystems through mechanisms like resource use complementarity and facilitation and can additionally address problems concerning deterministic processes at the ecosystem level. There is therefore a developing view that by assessing and understanding trait diversity, we can make more informed conservation and restoration decisions, especially amidst a changing climate and the Anthropocene era. When making decisions about conservation and restoration, traits are used to inform management methods by considering the functional attributes of ecosystems and species, e.g. in restoration initiatives that need the recovery of degraded ecosystems, restoration efforts can be more successful if plant species are chosen that have traits that are appropriate for the target habitat. Enhancing ecosystem restoration can involve, for instance, selecting plants that can fix nitrogen in soils deficient in nutrients or that can withstand drought in desert ecosystems soil. Trait diversity can also be useful in dynamic environments where conditions may change over time because using traits allows for adaptive management by selecting species with traits that can cope with changing environmental conditions. This flexibility is crucial for long-term conservation success (Nock et al., 2016). Furthermore, through their influence on essential processes such as nutrient cycling and carbon uptake, functional traits provide an important link between biodiversity and ecosystem function.

Trait-based methods are arising swiftly in plant ecology, underlying community assembly and structure, species relations and interlinkages between vegetation and biogeochemical cycles (Schneider et al., 2017). The findings of a study by Soudzilovskaia et al. (2013) shows that the concept of plant functional traits is very helpful in predicting how plant communities and the ecosystem services they provide will change in response to climate change. The effects of plant traits on ecosystems, landscapes and global-scale processes are highly dependent on a combination of traits from species that occur together in an area and are highly likely to be driven by the traits of the species that is most dominant (Funk et al., 2017). Due to these insights, aggregated trait qualities of the community—such as the Community-Weighted Mean (CWM) and indices of community diversity have been quantified and used to shed light on broad trends and account for more variety in trait-environment relationships (Funk et al., 2017). The Mass Ratio Hypothesis is a concept in ecology that explores the importance of the relative abundance and contributions of different species or functional groups to ecosystem processes. The Mass Ratio Hypothesis builds on the idea that the influence of a species on ecosystem processes is proportional to its contribution to the total biomass of the community (Grime, 1998).

1.3. The three plant functional traits and their significance

The wide array of leaf investment strategies observed globally can be effectively captured through leaf traits, which, owing to their strong associations with climate and other abiotic conditions, serve as pertinent indicators for studying plant community responses to their environment (Lavorel & Garnier, 2002). Among these leaf traits, Specific Leaf Area (SLA) stands out. SLA, denoting the ratio of a leaf's light-capturing surface per unit investment of dry mass, is commonly expressed as mm2/mg. Species characterized by low SLA tend to possess longer leaf lifespans, often associated with low relative growth rates and net rates of photosynthesis (Shipley et al., 2005). Conversely, high-SLA plants adopt a more resource-efficient strategy, investing less dry matter per leaf, thereby exhibiting rapid development and shorter leaf lifespans. Notably, evergreen perennial species, particularly in arid climates and on nutrient-poor soils, typically exhibit lower SLA values, prioritizing leaf function sustainability under adverse conditions for leaf formation (Ordoñez et al., 2009). Interestingly, significant SLA variation can exist between species even within annual plant ecosystems, reflecting localized spectra of leaf investment strategies, which may assume organized forms at small scales, influenced by local environmental conditions. Moreover, intraspecific variability in SLA is more prominently driven by local environmental factors compared to other leaf traits (Dwyer et al., 2019).

Plant height plays a pivotal role in shaping the vertical structure of ecosystems, influencing light distribution, temperature regimes, and humidity gradients within the vegetation canopy. This vertical stratification, in turn, impacts the diversity of organisms inhabiting different canopy layers. Defined as the shortest distance between a plant's major photosynthetic tissues and the ground, plant height correlates with competitive vigour, total plant reproduction, and the interval available for growth between disturbances such as fire, storms, ploughing, and grazing (Cornelissen et al., 2003). Generally, plant height exhibits proportional relationships with aboveground biomass, rooting depth, lateral spread, and leaf size (Cornelissen et al., 2003) .

Rooting depth is a critical determinant of a plant's ability to access water and nutrients in the soil, thereby influencing its survival across various soil conditions and climatic regimes. Maximum rooting depth refers to the deepest soil depth reached by a plant root system (Schenk & Jackson, 2002). Diverse root systems, such as taproot and lateral root systems, contribute to a plant's adaptive capacity to varying soil conditions. Taproot systems feature a dominant taproot with faster growth rates compared to branch roots, while lateral root systems comprise outward-growing roots beneath the soil surface (Schenk & Jackson, 2002). Understanding maximum rooting depths and lateral root spreads is crucial for projecting functional variations between plant growth forms under current conditions and potential forthcoming climate change circumstances. Despite their paramount importance for plant functioning and biogeochemical cycles, roots remain relatively understudied compared to aboveground traits, primarily due to methodological challenges associated with belowground trait assessments (Weemstra et al., 2023). In this study, rooting depth was estimated using a validated proxy known as the deep: shallow ratio (DS ratio), calculated by measuring the diameter of a tree's taproot at 10 and 30 cm depths (Zhou et al., 2020). A larger DS ratio (<0.96) indicates deeper rooting, while a smaller ratio (>0.92) suggests shallower roots (Zhou et al., 2020).

1.4. Functional Diversity Indices

Functional diversity indices serve as valuable tools for elucidating systematic variations along environmental gradients and the distribution of trait values within ecological communities. According to Leps and de Bello (2008), functional diversity can be divided into three orthogonal components: richness, evenness, and divergence. Each of these components is represented differently by a different index. Functional richness is the amount of niche space occupied by the species within a community (Mason et al., 2005). Functional evenness measures the regularity of the distribution of species abundances and dissimilarities in functional space and functional divergence quantifies the proportion of the total abundance supported by the species with the most extreme trait values (Villéger et al., 2008).

1.5. Plant species and functional diversity in Namibia

Namibia, one of the largest and driest nations in sub-Saharan Africa, grapples with pronounced climatic uncertainty characterized by prolonged droughts, erratic rainfall patterns, fluctuating temperatures, and water scarcity (World Bank Group, 2021). Its climate, typically hot and arid, features sporadic and irregular rainfall, predominantly shaping its savanna biome, including the study area under current investigation (Maggs et al., 1998). Savannas, spanning approximately two-fifths of Africa's landmass, constitute a substantial portion of the world's terrestrial net primary production (30%) (Guo et al., 2018a). These ecosystems, characterized by little and inconstant rainfall alongside the coexistence of trees and grasses, are particularly prevalent in regions with limited water supply and highly erratic annual precipitation(Hassler et al., 2010).

The distinctive environmental conditions of Namibian savannas foster a remarkable functional diversity in plant communities, driven primarily by significant temporal and spatial variability (Cianciaruso et al., 2012). This variability enables the coexistence of plants employing diverse strategies to cope with prevailing conditions. For instance, intense precipitation events facilitate deep soil infiltration, benefiting woody plants with deeper root systems, whereas species with shallow roots thrive under less intense precipitation regimes (Guo et al., 2018). The heterogeneity in soil conditions, water retention capacities, and topographical features of savanna landscapes significantly influences plant species abundance and distribution, ultimately contributing to the functional diversity of vegetation (Guo et al., 2018).

Studies examining vegetation diversity in northern Namibia reveal varying trends in species richness. For instance, Inman et al. (2020) documented higher woody plant species diversity in less degraded areas of the Kunene region, recording a total of 1,662 individuals representing 56 species across 26 plant families in an area of 14 000m^2. Similarly, Revermann et al. (2017) found higher plant species diversity in less degraded dry tropical woodlands of the Okavango region, identifying a total of 2,775 individuals from 240 species, comprising woody, herbaceous, and grass species. However, the relationship between plant species diversity and functional diversity remains largely unexplored in this specific region of northern Namibia.

The intra-annual seasonality of precipitation, spatial gradients in savanna vegetation, and precipitation patterns pose challenges in adapting land use strategies to the natural dynamics of semi-arid ecosystems, underscoring the need for informed science-based policy interventions in Namibia (Hassler et al., 2010).

Projected climatic changes in Namibia are anticipated to induce significant changes in species diversity, vegetation structure, and ecosystem function (Midgley et al., 2005). Despite the global surge in studies focusing on functional traits, research on functional traits in the Namibian context remains scarce. Therefore, this study aims to investigate plant species diversity and functional trait diversity across northern Namibia along an increasing rainfall gradient, providing critical insights into ecosystem dynamics and resilience in the face of environmental change.

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CHAPTER THREE

COMPARING TREE FUNCTIONAL TRAITS AND SPECIES DIVERSITY ALONG A RAINFALL GRADIENT IN NORTHERN NAMIBIA

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Abstract

Changes in precipitation patterns have the ability to affect the composition and the variety of species within a plant community by altering their functional traits. However, there has been a tendency to underestimate the importance of functional diversity. This is particularly common for Namibia, despite a clear, gradient in precipitation and where forecasts have predicted changes in precipitation regimes in the future. This study examined how tree species diversity and functional traits changed along an increasing rainfall gradient in northern Namibia. It employed a quantitative approach with systematic sampling at 13 points along an approximately 1200 km transect. Tree species diversity fluctuated along the gradient and average annual rainfall did not appear to have a significant effect, yet species diversity was highest at sites with high rainfall. There was no statistical difference in the species diversity among sites, but the estimated beta diversity was high. Plant functional *diversity indices and plant functional traits varied along the gradient. All three functional diversity indices revealed weak relationships with species diversity. Among the three functional diversity indices, only functional richness was significantly affected by annual average rainfall. While this study presents some contrasting results with other studies, it remains relevant by providing an understanding of the dynamics between plant species diversity and functional trait diversity. The results of this study support the conclusion that plant species diversity and plant functional trait diversity are both vital components of ecosystem functioning, and that future research should incorporate a wider array of functional traits and employ more comprehensive data collection methods that can build on the current study findings to further elucidate these complex interactions.*

Key words: Climate change, plant ecology, precipitation, species composition, functional indices, species evenness, species richness, functional traits

3.1. Introduction

Understanding the functional diversity of vegetation is important to better comprehending how environmental change, community composition, and ecological processes are related (Lavorel & Garnier, 2002). Even though for almost all ecosystem types the association between functional diversity and species diversity is still poorly understood, it is important to establish this relationship to develop a mechanistic understanding of community assembly and suitable strategies for safeguarding and restoring biological communities (Bu et al., 2014). A growing body of research suggests that functional traits of individual species and their interactions, not just the number of species, are what really determine how diversity affects ecosystem processes (Cadotte et al., 2011). Plant functional diversity is the range and distribution of plant traits within a community, landscape, or even more extensive geographical scales that are functionally relevant for growth, reproduction, and other aspects of plant life and survival (Ma et al., 2019). The composition of plants in a given community is influenced by changes in plant traits and species abundance while being mediated by changes in the precipitation regime (Griffin-Nolan et al., 2018). Therefore, understanding plant functional trait distribution within and among communities is of enormous relevance to explaining community assembly, dynamics, and resilience to disturbance (Gomes et al., 2023). It is against this background that a high functional diversity should be desirable, as diversity reflects aspects of ecosystem productivity, dynamics, stability, and nutrient availability (Li et al., 2015).

Changing climate is a threat to biodiversity because climatic variables largely determine species geographical distribution ranges (Pearson & Dawson, 2003), and influences plant productivity and performance (Maia et al., 2023; Oyebanji et al., 2021). Changes in climate directly impact the biology and ecology of individual species, consequently influencing the structure and function of ecosystems. This, in turn, affects the goods and services that natural systems offer to society (Diaz et al., 2019). Considering that the trait arsenal of a plant represents its potential to respond to climate variability and changes, the frequency and types of plant traits could serve as reliable predictors of climate change (Madani et al., 2018).

The first step in creating an enhanced mechanistic knowledge of how climate influences ecosystem structure and function is defining how the functional structure of communities varies along ecological gradients (Wieczynski et al., 2019). Natural gradients influence species occurrences and distributions due to variations in climate and available resources (Rosenfield & Müller, 2020). Species richness and composition changes directionally as one moves from lower to higher latitudes and altitudes due to variations in climatic factors, especially those relating to temperature and precipitation (Whittaker & Niering, 1965; Fernandes, 1992; Rosenfield & Müller, 2020). Kühn et al. (2021) identified eight key traits that best predict positive plant responses to climate changes across biomes, which include Specific Leaf Area (SLA), plant height, greater water-use efficiency, greater re-sprouting ability, lower relative growth rate, greater below-ground storage, higher wood density, and greater rooting depth. The current study assessed three of these traits namely, SLA, plant height, and rooting depth using three different functional diversity indices. These three traits were selected because they are fundamental in understanding plant adaptations to precipitation (Kühn et al., 2021). These are integral to a plant life cycle and can be feasibly assessed even under challenging field conditions, making data collecting efficient. Several measures can be used to describe the niche space of plants within a community. Three commonly applied indices are functional richness, evenness and divergence (Mason et al., 2010). Functional richness is the amount of the niche space (i.e., the role and position a species has in its environment, encompassing all the physical, chemical, and biological conditions that a species needs to survive, reproduce, and maintain a stable population.) occupied by the species within a community (Mason et al., 2005). Functional evenness measures the regularity of the distribution of species abundances and dissimilarities in functional space, while functional divergence quantifies the proportion of the total abundance supported by the species with the most extreme trait values (Villéger et al., 2008).

The northern part of Namibia is characterized by a 1,400 km strip of land, that penetrates the African continent, in which a clear pattern of rainfall is present (World Bank Group, 2021). Precipitation increases strongly from the northwest region of the strip which is desertic (shorelines of the Atlantic Ocean, Kunene) into the northeast region (Zambezi). This region covers the tropical forest portion of the gradient bordering Zimbabwe, Botswana, and Zambia. This scenario presents an ideal system to test the hypotheses of the association of SLA, plant height, and rooting depth along a rainfall gradient (Fonseca et al., 2000; Cheng et al., 2016). Hence, filling some geographical gaps in better understanding how functional diversity may vary along natural gradients (Vasilevich, 2009). These gaps refer to ecosystems where there is limited data on how functional traits respond to environmental factors like precipitation gradients. Several hypotheses account for the difference in plant species diversity along rainfall gradients. Plant species richness correlates positively with annual rainfall throughout rainfall gradients, from continental to global scales. In the Neotropics, woody plant species diversity increases with higher annual precipitation levels reaching 4,000 mm (Tuomisto et al., 2014).

Presently, there is very limited scientific knowledge concerning plant functional diversity, functional diversity relationships with plant species diversity, and how these metrics change over rainfall gradients in Namibia (Hauwanga et al., 2018; Schwarz et al., 2023). Additionally, there is limited data on plant functional traits for Namibian plant species in international databases, particularly for this region, which supports wildlife of importance to the economy and human well-being, such as ecotourism. In Namibia, climatic changes are predicted to result in significant shifts in species diversity, vegetation structure, and function (Midgley et al., 2005). While studies focused on functional traits have increased globally over recent decades (Kühn et al., 2021), very few have focused on functional traits in a Namibian context. Therefore, this study aimed to assess plant species diversity and functional traits in Namibia with a focus along the northern regions, along a rainfall gradient. The present study tested the hypotheses i) plant species diversity increases along an increasing rainfall gradient (Tuomisto et al., 2014), ii) that plant functional diversity varies along the rainfall gradient (Zuo et al., 2021), and iii) that there is a relationship between plant species diversity and functional diversity along the rainfall gradient (Díaz & Cabido, 2001). This study focused on a macro scale or landscape level, it covers six political regions and one major biome (tree and shrub savanna), which is further divided into different vegetation types.

3.2. Materials and Methods

3.2.1. Study area

The northern part of Namibia is characterized by a long strip of land, extending approximately 1,400 km from west to east. The range in average annual rainfall over a 30-year period is between 238 mm in the Kunene region and an almost three-fold increase in rainfall of 610 mm in the Zambezi region (World Bank Group, 2021). Thus, the northwest side of the gradient (Atlantic Ocean) is desert, while precipitation increases strongly into the northeast tropical forest portion of the gradient bordering Zimbabwe, Botswana, and Zambia. This scenario presents an ideal system to test the hypothesis linked to the association of functional plant traits in relation to an environmental gradient knowledge that is currently lacking.

The study was conducted in six political regions in northern Namibia in a west-to-east direction, namely the Kunene, Omusati, Ohangwena, Kavango West, Kavango East and Zambezi regions (Figure 1). Field data were collected from 13 sites located approximately 100 km apart along an increasing rainfall gradient from west to east (Table 1). The average annual temperature ranges from approximately 18°C in the Kunene to about 23°C in the Zambezi region (World Bank Group, 2021). The vegetation along this strip falls in the tree and shrub savanna biome and the vegetation diversity and structure changes across the rainfall gradient (Atlas of Namibia Team, 2022a).

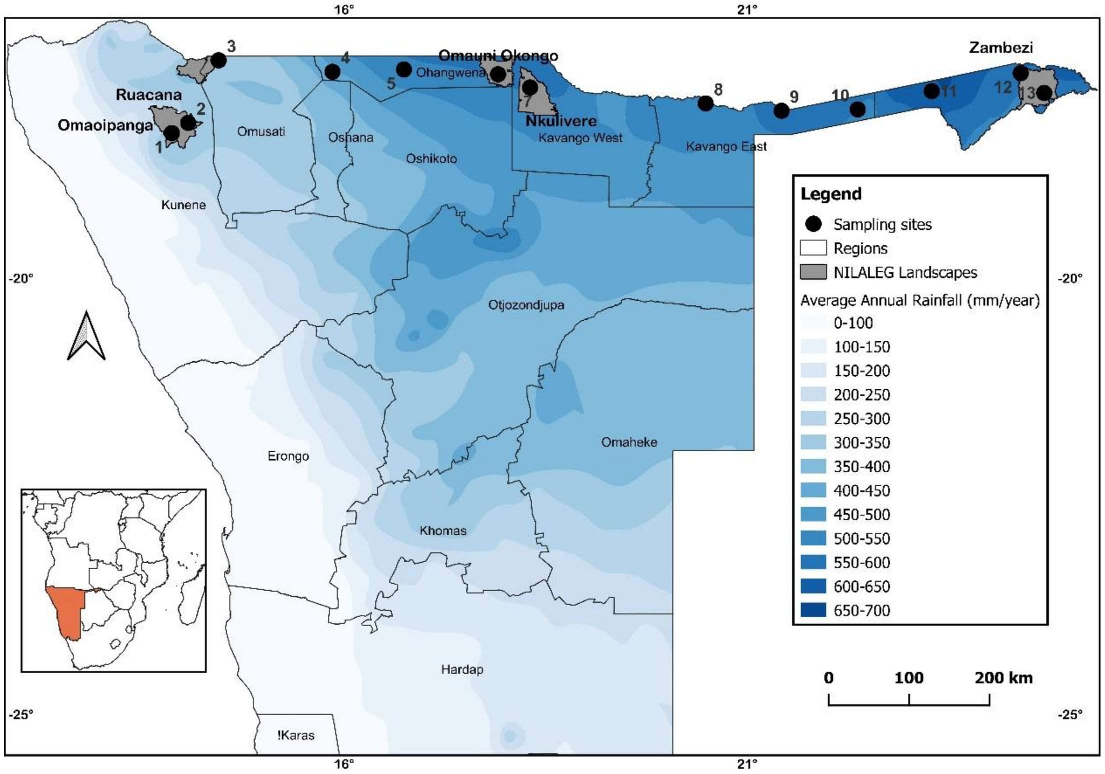

Figure 1: Map with the location of the study area and the 13 sampling sites distributed along an increasing rainfall gradient, in northern Namibia.

The Kunene region is the most western region of the study area and is characterized dominantly by *Colophospermum mopane*, *Terminalia prunioides*, and other species such as *Vachelia erioloba*, *Faidherbia. albida*, and *Commiphora* species(Atlas of Namibia Team, 2022b). The Omusati region is predominantly characterized by *C. mopane* and other species such as *Sclerocarya birrea* and *Hyphaene petersiana*. The Ohangwena region is dominated by *Baikiaea plurijuga*, *Pterocarpus angolensis*, *Guibourtia coleosperma*, *Burkea africana* and Schinziophyton rautanenii. The Kavango west and east regions are dominated by *B. plurijuga*, *P. angolensis*, *G.*

coleosperma, B. africana, *S.* rautanenii*, Combretum collinum*, *T. sericea* and *Strychnos cocculoides*. The Zambezi region is the most east region of the study area and it is mostly dominated by *C. mopane*, *B. africana,* and *T. sericea*(Atlas of Namibia Team, 2022b). Most of the study area is dominated by arenosols, fluvisols, and cambisols soil (Atlas of Namibia Team, 2022a).

Table 1: Biophysical factors of the 13 sample sites across the study area.

Sites	**Annual average rainfall**	**Annual average temperature**	**Land type**	**Land use**	**Geology**	**Soil texture**
Site1	325	19	Watercourse & Tree savannah	Naturally vegetated land (including farmland used for grazing)	Sandstone	Silt loam
Site2	325	21	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy loam & silt
Site3	325	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Quartzite	Loamy sand
Site4	425	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Dolomite/ marble	Loam
Site5	525	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy
Site6	575	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy

Site7	575	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy
Site8	525	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy
Site9	575	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy
Site10	525	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone	Sandy
Site11	625	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Sandstone & Aeolian sand	Sandy
Site12	575	23	Watercourse & Tree savannah	Naturally vegetated land (including farmland used for grazing)	Shale/mud stone	Clay & sandy loam
Site13	575	23	Tree savanna	Naturally vegetated land (including farmland used for grazing)	Shale/mud stone	Sandy clay

3.2.2. Assessed plant functional traits

Three plant functional traits were assessed in this study, plant height, SLA, and rooting depth. Plant height is the shortest distance between the upper boundary of the major photosynthetic tissue of a plant and the ground (Pérez-Harguindeguy et al., 2013). It is related to competitive vigour, total plant reproduction, and the amount of time given for growth between disturbances such as fires, storms, ploughing, and grazing. In general, plant height tends to correlate proportionally with aboveground biomass, rooting depth, lateral spread, and leaf size (Cornelissen et al., 2003).

SLA is the ratio of a leaf light-capturing surface per unit investment of dry mass and is frequently represented as mm^2/mg (Dwyer et al., 2019). SLA, like other leaf traits, is normally linked with the life history, distribution and resource requirements of a species (Hoffmann et al., 2005). There can be significant variation in SLA within the same species and across different species even within annual plant ecosystems, reflecting local scale ranges of leaf investment strategies. Depending on local circumstances, such SLA variation may take on an organized form at small scales. Intraspecific variation in SLA appears to be driven primarily by local environmental variation than other leaf traits (e.g., leaf dry matter) (Dwyer et al., 2019).

Rooting depth or maximum rooting depth is the deepest soil depth that a plant root reaches (Schenk & Jackson, 2002). Data on maximum rooting depths and lateral root spreads may help forecast functional variations between plant growth forms under present-day conditions and those resulting from potential future climate change scenarios (Schenk & Jackson, 2002). Plant roots are crucial for acquiring essential nutrients and water uptake for the plant (Fan et al., 2017). Despite the enormous significance of root features for the functioning of plants and plant communities as well as biogeochemical cycles, there is limited knowledge about the ecology of these roots, especially in comparison to the amount of knowledge that has been gained for leaves and stems (Weemstra et al., 2023). This is mainly due to the difficult nature of studying below-ground traits in comparison to studying above-ground traits.

3.2.3. Data collection

Data were collected from two nested plots at each of the 13 sampling sites (n = 26). Each plot had three nests, which were small (10 m radius (314.2 m^2)), medium (20 m radius (1256.64 m^2)), and large (30 m radius (2,827.4 m^2)) (Figure 2) (MET, 1998). The selected sites were approximately 100 km apart to capture the rainfall variation along the rainfall gradient. This sampling scale reduced the risk of sampling autocorrelation. Seven sites overlapped with the NILALEG landscapes. These landscapes are areas that were targeted for the implementation of integrated landscape management activities in order to improve livelihoods (EIF, 2020).

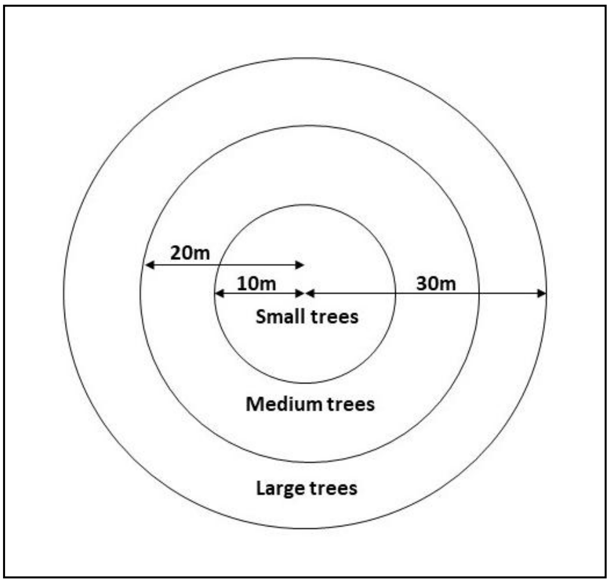

Figure 2: Sampling plot design used for data collection

A tree was defined as a woody plant with a diameter at breast height (DBH, 1.3 m above the ground) larger than 5 cm. In this study, small trees for any species (5 < DBH < 20 cm) were sampled within plots with a radius of 10 m, medium-sized trees (20 < DBH <45 cm) in plots with a radius of 20 m, and large trees (DBH > 45 cm) on plots with a radius of 30 m to determine the species diversity (Figure 2) (MET, 1998). Data on functional traits were gathered from 5 to 15 individual trees of the dominant species (making up more than 50% of trees in the plot), the sampling of the traits was conducted according to the protocols published by Pérez-Harguindeguy et al. (2013) and Wigley et al. (2020). For every tree inside the plot, species name, DBH (cm), and height (m) were recorded. Plant identification was aided through the use of the Trees of Southern Africa field guide (Van Wyk, 2013). DBH was determined using a diameter tape and plant height by using a combination of Measure Tree Heights software from Jelmer Verhoog (Jelmer Verhoog, 2020) and a tower ruler. Five leaves were collected from each of the five individuals of the dominant species in a plot, resulting in 25 leaves being collected per plot, SLA was then determined as the area of each fresh leaf divided by its oven-dry mass (Pérez-Harguindeguy et al., 2013). Leaf area (cm^2) was measured using the Petiole Pro software v.23.9.2 from Petiole (Seleznov & Kuzmenko, 2023). Before the software was used, it was first calibrated by a calibration pad. Rooting depth data was estimated through a proxy that uses the ratio of the diameter of the taproot at 30 cm over the one at 10 cm (deep: shallow, hereafter DS) (Wigley et al., 2020). The DS ratio (rooting depth) was computed by dividing the diameter of the taproot at 30 cm by the diameter of the taproot at 10 cm (DS ratio = D30/D10).

Figure 3: An illustration of how the DS ratio was measured on the tap roots of trees

The regular values of the DS ratio range between 0 and 1. Lower DS ratio values (DS < 0.5) would suggest shallow rooting and higher (DS ≥ 0.5) would suggest deeper rooting. (Zhou et al., 2020). This proxy has been validated by the excavation of taproots of 57 different savanna tree species to a depth of 50–100 cm, in the Kruger National Park, South Africa (Zhou et al., 2020). The proxy was found to be suitable to be applied in this study due to the overlap of seven tree species in this study with those in the validation study. Such species included T. *sericea, B. plurijuga*, *C. mopane*, *C. collinum*, *G. coleosperma*, *T. prunioides,* and *V. tortilis*. In this study, taproot diameter measurements were collected using a diameter tape at depths of 10 and 30 cm from five trees per plot. For trees that had multiple roots, the diameter was measured on the largest root.

Figure 4: Illustrations showing the different vegetation in some of the plots that were sampled.

3.2.4. Data analysis

The study used two datasets. The first dataset was used to assess plant species diversity and the second, assessed plant functional diversity. In the second dataset, only the dominant species in the plots were recorded. Data analysis was performed in RStudio version 4.2.1 (R Core Team, 2023). Before analysis, a normality test was conducted using the Shapiro-Wilk test (Mishra et al., 2019). Results were considered significant at $p < 0.05$. To determine species diversity per site, the Simpson Diversity Index (D) was determined through the function *diversity* in the *vegan* R package (Dixon, 2003; Oksanen et al., 2022) as $D = 1 - (\sum n(n-1))/N(N-1)$ where n = the number of individuals per species and N = the total number of individuals across all the species

(Shah, 2013). The Kruskal-Wallis test was used to determine if there were any statistical differences among sites in the Simpson Diversity indices. The Baselga's Full Index method was used to calculate the beta diversity among the different sites, using the *cfull* function from the MBI R package (Chen, 2013). A multi-linear regression analysis was run to determine the influence of average annual rainfall, average temperature, land type, land use, geology, and soil texture on the Simpson Diversity Index and species richness (i.e., number of species detected per site). Functional diversity was determined using three indices: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) for each site using the functions *fd_fric (), fd_feve(),* and fd*_fdiv(),* in the *fundiversity R* package (Grenié & Gruson, 2023). These indices range between 0 and 1, with 0 indicating a minimal value, 0.1 to 0.5 indicating moderate values, and 0.6 to 1 indicating high to maximal values (Grenié & Gruson, 2023). Before the computation of these indices, 45 missing data values for rooting depth and SLA were imputed using the Random Forest Imputation method (Joswig et al., 2023). A Spearman correlation analysis was conducted to explore the relationships among site Simpson Diversity Index estimates, with FRic, FEve, and FDiv. Additionally, a simple-linear regression was run to determine the effect of rainfall on the three indices. Subsequently, a Principal Component Analysis (PCA) was conducted to elucidate the interrelationships among the three plant functional traits, thereby facilitating their representation within a trait space. This analytical approach employed the *PCA ()* function from the *FactoMine* R package. Additionally, a separate PCA analysis was performed to discern the distribution patterns of distinct species across the trait gradient.

3.3. Results

3.3.1. Plant species diversity

A total of 287 trees belonging to 20 species from seven families was recorded in the 26 sampling plots (Appendix 1). The most frequently sampled woody species was *Colophospermum mopane* (23.6%) followed by *Terminalia prunioides* (13.9%), while the least sampled were Adansonia *digitata* (0.3%), *Diospyros mespiliformis* (0.3%), and *Philenoptera violacea* (0.3%). Over half of the detected species (55%) belonged to the *Fabaceae* family, while the least sampled species belonged to the *Malvaceae* and *Ebenaceae* families (0.3%). (Appendix 1). The number of species detected per site varied from one to 11 species (Figure 3). Rainfall was categorized into three groups: low rainfall sites, receiving 300–450 mm, medium rainfall sites, receiving 451–550 mm and high rainfall sites, receiving 551 mm and above. Site 12, which receives over 550 mm of annual rainfall, exhibited the lowest species richness, whereas Sites 1 and

2, with about 300 mm annual rainfall, had slightly higher richness, suggesting that rainfall alone does not directly predict species richness across these sites. The highest species richness in this study was observed at sites 5, 6, and 7, located in areas receiving high rainfall, approximately ranging from 500-600 mm annually.

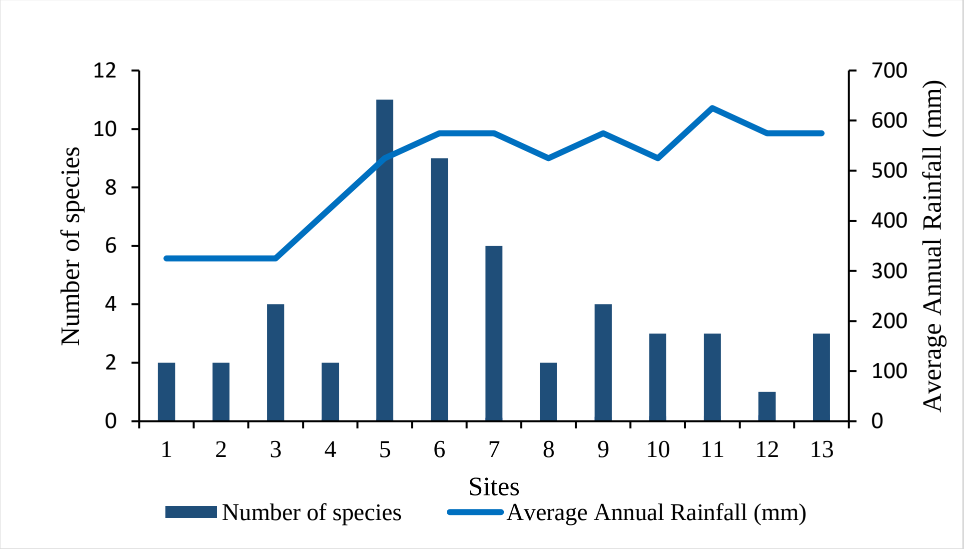

Figure 5: Number of species recorded per site across the 13 sampling sites along an increasing rainfall gradient from Kunene to Zambezi region in northern Namibia.

Results revealed that species richness and the Simpson Diversity Index were strongly positively correlated (rho = 0.787, p = 0.001), therefore all analyses for species diversity were based on the Simpson Diversity Index as it incorporates both richness and evenness. The Simpson Diversity Index ranged from 0 at site 12 to 0.82 at site 6 (Figure 4). Despite this variation in the Simpson Diversity Indices across the sites, there was no statistically significant difference found between sites (p = 0.445). On the other hand, beta diversity was significantly high (0.906), indicating a relatively high species turnover among the sites. A simple linear regression of the Simpson Diversity Index as a function of average annual rainfall, resulted in a non-significant model

($F_{1,11}$= 1.704, R^2 = 0.134; **p = 0.218**). This result suggest that rainfall did not have a statistically significant effect ($p > 0.05$) on the diversity index along the gradient.

The multiple linear regression analysis performed to predict the Simpson Diversity Index from six predictors (average annual rainfall, average temperature, land type, land use, geology, and soil texture) showed the model to be non-significant ($F_{5,7}$ = 3.694; **p = 0.058**, R^2 = 0.725). From these predictors, only soil texture had a significant effect on the plant species diversity index (p = **0.023**; Table 1).

Table 2. Multiple linear regression model for Simpson Diversity Index and five environmental variables. The Simpson Diversity Index had a standard deviation value of 0.26.

Variables	Estimate	Std. error	p-value
Intercept	-12.216	5.174	0.050
Average annual rainfall	0.009	0.005	0.117
Average temperature	0.749	0.335	0.060
Land type	0.141	0.190	0.481
Geology	-0.006	0.108	0.951
Soil texture	0.157	0.054	**0.023**

3.3.2. Plant functional diversity along the rainfall gradient

The three functional diversity indices varied along the rainfall gradient where functional divergence (FDiv) and evenness (FEve) values were high *per se* in comparison, to estimates for functional richness (FRic) (Figure 5). Functional divergence ranged from 0.69 to 0.87, indicating a greater divergence or dissimilarity in the functional traits present along the rainfall gradient. Functional evenness ranged from 0.72 to 0.86, signifying a more even distribution of functional traits among the species or individuals present in the ecosystem. Functional richness ranged from 0 to 0.19, indicating very low functional richness. Functional divergence slightly increased along the rainfall gradient, while FEve and FRic both decreased (Figure 5).

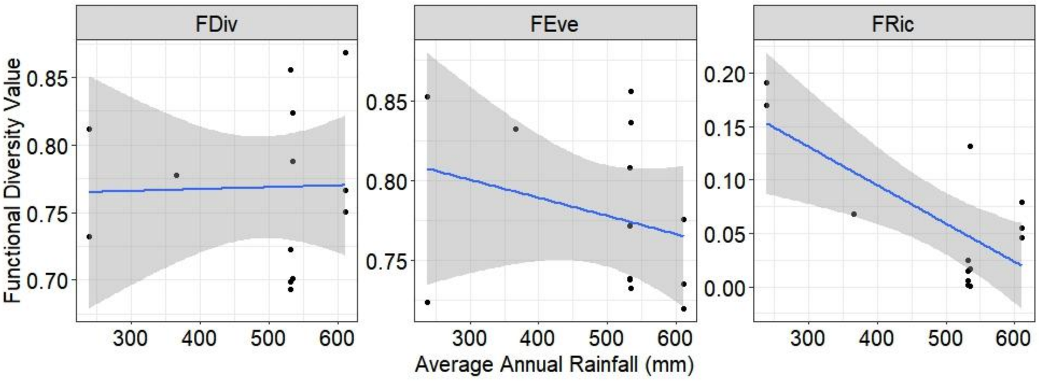

Figure 6: Functional divergence (FDiv), functional evenness (FEve), and functional richness (FRic) values along an increasing rainfall gradient, west to east Namibia.

Results of a simple linear regression of the three functional diversity indices with average annual rainfall as the predictor variable indicated that rainfall only had a statistically significant effect on FRic (F1,11=11.39, R ^{2} =0.509, p = 0.006) but not on FDiv and FEve (Table 2). This result suggests that rainfall correlates negatively with shifts in FRic values.

Table 3. Simple linear regression model for functional divergence (FDiv), functional evenness (FEve), and functional richness (FRic) and annual average rainfall.

Variables	Estimate	Std. error	p-value
Intercept	0.238	0.059	0.001
FRic	-0	0	**0.006**
Intercept	0.761	0.070	0
FDiv	-0	-0	0.923
Intercept	0.834	0.059	0
FEve	-0	0	0.351

A linear regression was used to establish if there is a relationship between rainfall, rooting depth and tree height. The results indicated that there are no significant relationships between height and rainfall (coefficient = 0.001, p = 0.548) or between DS ratio and rainfall (coefficient = -0.003, p = 0.098). Conversely, rainfall was a significant predictor of SLA, suggesting that as rainfall increases, SLA decreases (coefficient = -0.003, p = 0.023) (Fig. 6). For SLA, the model explains 38.4% of the variance, whereas the models for height and DS ratio have low explanatory power and non-significant predictors.

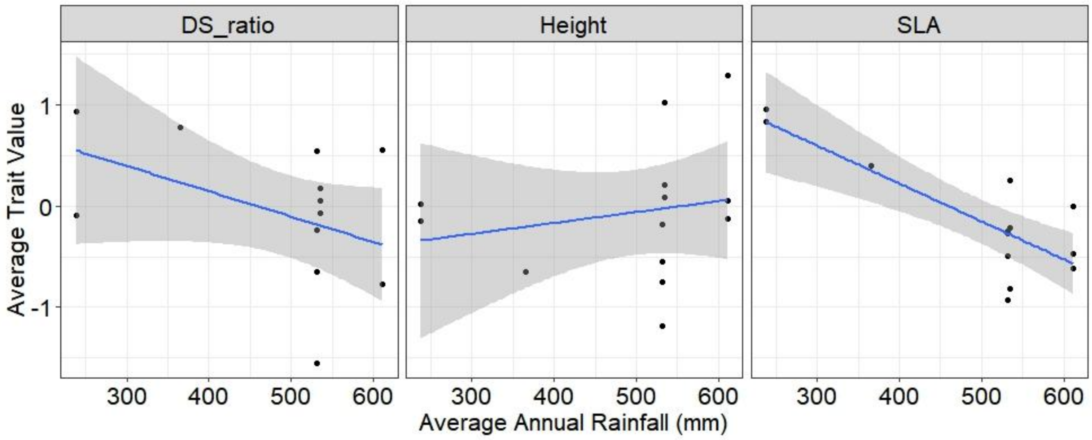

Figure 7: Deep:shallow (DS ratio), height, and SLA along an increasing rainfall gradient from west east, northern Namibia.

Pairwise correlations among the three functional traits revealed that plant height and SLA were not correlated (rho = 0.159, p = 0.604), DS ratio and SLA were moderately positively correlated (rho = 0.5, p = 0.085), and that height and DS ratio were weakly positively correlated (rho = 0.357, p = 0.232). These values suggest that there is a moderate tendency for plants with higher SLA to also have higher DS-ratio and that there is a weak tendency for taller plants to have a higher DS ratio. These relationships are further supported by the results of the PCA analysis (Figure 7). In our PCA analysis, the first principal component (PC1) explained 39% of the variance, and the second component 34%, totalling 73%. This indicates that most of the variability in the dataset was captured by these two principal components (Figure 7).

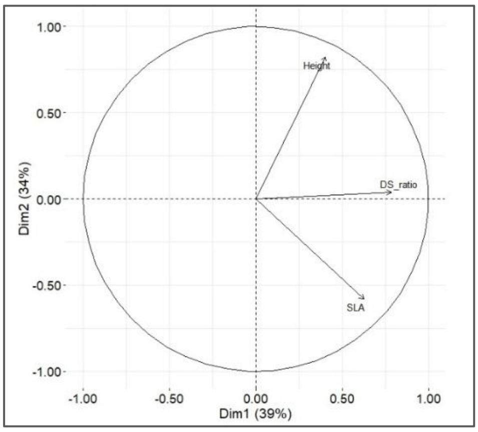

Figure 8: Principal Component Analysis for the three plant functional traits assessed in the study.

Species occupied a distinct portion of the trait space with some species covering a wide range of trait values while others covered a limited range of trait values. Figure 8 presents the dominant species functional diversity analysis along their trait space. *Colophospermum mopane*, *C. collinum,* and *T. prunioides* occurred in all four quadrants of the PCA, suggesting that they have a broad range of trait values. These species may thrive across a wide range of environmental conditions and could well-adapted to multiple conditions. In turn *B. plurijuga* and *V. tortilis* occurred in two quadrants of the PCA and *Strychnos cocculoides* in a single quadrant, indicating a unique combination of trait values and restricted trait space.

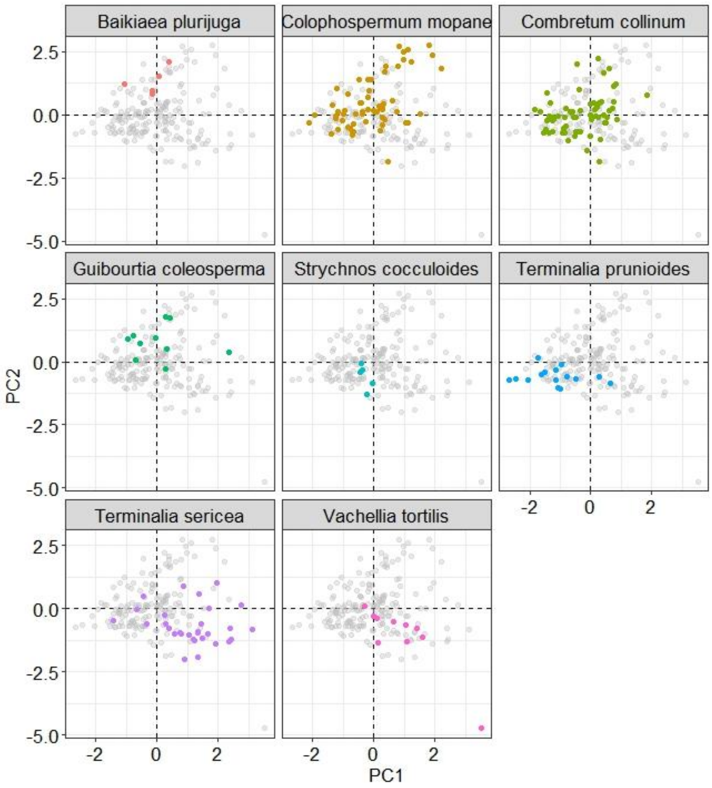

Figure 9: Principal Component Analysis of the distribution of eight tree species across the trait space along an increasing rainfall gradient in northern Namibia. Grey points represent the presence of all other species.

3.3.3. Relationship between plant species diversity and functional diversity along an increasing rainfall gradient

The Spearman pairwise correlations between plant species diversity and three functional diversity indices (Fric, FDiv, and FEve) were found to be weak and negative, and not statistically significant. Specifically, the correlation between plant species diversity and Fric was (rho = -0.286, p = 0.342), and for FDiv, (rho = -0.413, p = 0.160). There was no statistically significant correlation between plant species diversity and FEve (rho =−0.093, p = 0.760). Therefore, the three functional diversity indices did not show a statistically significant correlation with plant species diversity in this study.

3.4. Discussion

The study, assessed woody plant functional traits, species diversity and compared how these change along an increasing rainfall gradient. From the three functional diversity indices, only functional richness showed a significantly decreasing trend along the gradient. The functional diversity indices showed no correlation with plant species diversity. These results indicate that spatial patterns in plant species diversity and functional diversity and their association are modulated by various processes operating at local to regional scale.

3.4.1. Trends in plant species diversity

One of this study's hypotheses was that tree species diversity would increase with increasing annual rainfall. This hypothesis was rejected as the Simpson Diversity Index values did not increase statistically with increasing rainfall but rather remained similar among sites. These findings diverge from existing literature, as previous studies have reported the Simpson Diversity Index to be positively correlated with average annual rainfall For instance, a study by O'Brien (1993), conducted in southern Africa reported a positive correlation between woody species richness and mean annual rainfall. Rudolph (1991) showed that species richness of neotropical plants increased with precipitation up to about 4,000 mm, at which point it plateaued. The distribution of plant species is affected by several environmental factors, and how these factors interact, including the interaction between alpha and beta diversity (Pausas & Austin, 2001).

First, the study's finding of a lack of linearity can be attributed to differences in environmental variables including water availability, edaphic variables, plant functional traits, and their interaction along this gradient. Water availability is one of the critical factors influencing plant species dispersal (Renne et al., 2019). Its availability to plants is a function of the amount of rainfall, soil drainage index, topography, and evapotranspiration. It is a critical resource for plant survival, growth, and distribution.

Over time, plants have developed various adaptation strategies to cope with differing water conditions, leading to diverse water regulation mechanisms. These adaptive strategies, including water transport, mechanical support, and defence mechanisms, collectively influence plant survival and distribution in their environments (Zhang et al., 2022). These varied adaptation strategies of different plant species to fit varying water availability levels then lead to the distribution of plant species in different areas. The rainfall gradient (the main factor of investigation in this study) present here is strong, but despite it, it was not sufficient to influence the diversity patterns. The fluctuation of species diversity along the decreasing rainfall gradient reflects a more complex level of interaction involving multiple environmental factors and ecological processes. Furthermore, there may be strong filters along the gradient such as human disturbances or other factors responsible for this.

Soil texture was the only variable among five covariates found to significantly influence plant species diversity in this study. Soil texture is an important determinant of nutrient availability and water retention. The study findings agrees with that of Whisler et al (2016), where the investigation into the correlation among species diversity, productivity, and soil texture in relation to soil carbon and nitrogen revealed that soil texture emerged as the most influential predictor. Conversely, our conclusion differs from Mensah et al. (2023), who revealed that in regions with lower average annual rainfall (precipitation range was 700 to 1300mm), none of the soil physical properties, including soil texture, showed significant associations with woody plant species diversity. On the other hand, in areas with higher average annual rainfall, soil physical properties tend to play a regulatory role in plant species diversity (Mensah et al., 2023). Water availability and soil texture are somewhat linked, hence, different plant species in different areas thrive based on whether the soil contains the necessary nutrients and how efficiently these species can make use of the water available in the soil (Renne et al., 2019).

The variation in the plant species distribution can be attributed to the sampling scale employed in this study. The macro scale sampling of this study resulted in two average rainfall extremes, low and high annual rainfall. Hence, the lack of linearity.

A second explanation for this divergence in findings can be explained by the landscape species pool hypothesis (Tscharntke et al., 2012). According to Cornell and Lawton (1992), regional or historical processes (dispersal and speciation), as well as local biotic interactions (competition and predation) are strong predictors of the diversity of species. Implicitly, it is hypothesized that biotic and dispersion mechanisms alone account for a species' presence in each area. However, dispersal methods would vary according to changes in the temperature or soils (Pausas & Austin, 2001). Although the size of the local species pool may have a role in some of the variations in local species richness, high regional species richness may simply be a result of high environmental heterogeneity within a region (Cornell & Lawton, 1992).

The beta diversity estimate suggests a relatively high level of species composition dissimilarity among the sites along the rainfall gradient. While diversity levels are maintained across the gradient, species composition change from one site to another. This is an important aspect that indicates some degree of specificity of the plant community along the gradient with systematic replacement of species as rainfall changes (Barwell et al., 2015).

Yet, another possible explanation for the lack of the expected trend in plant species diversity along the rainfall gradient may be the variation in methods used for field data collection, sampling methods, data analysis techniques, spatial scale and diversity indices. These can all influence the detection of relationships between species diversity and environmental factors (Lavorel et al., 2008; Mart et al., 2018). Other studies that found positive relationships between plant species diversity and rainfall have used a variety of sampling techniques such as plots, transects or quadrats for sampling (Hassler et al., 2010).

Khaine et al. (2017) found that a rainfall difference of approximately 600 mm among sites did not significantly impact species diversity, but a difference of around 1000 mm did. In the current study, the rainfall difference between the extreme ends of the study area is about 370 mm. Comparing the rainfall difference in the current study with that of Khaine et al. (2017),these results are supported by their study because this study found no significant difference in the species diversity among sites as a function of rainfall (325 to 625 mm per year).

Altogether, differences among studies that look at the relationship between mean annual rainfall and species diversity, measured using the Simpson Diversity Index highlight that the degree to which rainfall influences vegetation distribution depends on multiple factors, and the ability of the plant to efficiently absorb the water (Renne et al., 2019).

3.4.2. Functional diversity

The second study hypothesis predicted that functional diversity would increase with increasing rainfall. The hypothesis was partially supported as the three functional diversity indices varied along the gradient, with FRic significantly decreasing with increasing rainfall, unlike functional evenness and divergence. The combination of low functional richness, and high functional divergence and evenness in the current study suggests that while the plant community may have a limited set of functional trait values, these trait values are utilized in diverse ways by the different species, resulting in a balanced distribution of ecological functions (Mason et al., 2005; Tilman et al., 1997).

The functional diversity results may be supported by a study that looked at factors influencing plant functional traits in a tropical forest. In that study they reported that a variety of mechanisms and factors, such as topo-edaphic factors, biotic interactions, and climate, contribute to diversity and trends in plant functional traits (Hofhansl et al., 2021). Furthermore, studies of trait-environment relationships at the global scale have found that trade-offs at the species level were only weakly correlated with climate and soil conditions. This is because local-scale factors like disturbance, fine-scale soil conditions, niche partitioning, and biotic interactions largely filtered trait combinations and therefore plant functional diversity (Philip, 2006). However, since biotic and abiotic factors both influence trait variation in different ways and typically change in their relative dominance over trait expression across spatial gradients in response to various environmental factors, it is ideal to consider all of these factors when analysing the variation of functional traits in plants (Hofhansl et al., 2021), as the case of this study.

At the trait level, SLA decreased with an increase in rainfall in the current study. These results contrast with global patterns (Dong et al., 2017), as well as with results of a study by Costa-saura et al. (2016) that found that species from hot and dry environments tend to have lower SLA. In contrast, the current study results suggest that the shrublands in the western part of the study area have higher SLA than the woodlands towards the eastern part of the study area. As such, species appear to have shifted from more acquisitive strategies to more conservative strategies with increase in rainfall. The study results are supported by a study of Amissah et al. (2022) that also found a negative relationship between SLA and rainfall. The study found that their species from the drier area had higher SLA then their species from the wetter area. In contrast with this study, modelling and plot data suggest that species with a lower SLA may be better able to withstand drought conditions and establish themselves as dominant in Costa Rica's moist forests because smaller exposed leaf surfaces minimize water loss through evapotranspiration (Kühn et al., 2021). The same pattern was also observed in the Bolivian dry forests, the Ecuadorian savannas, the Australian deserts, and the Brazilian savannas (Kühn et al., 2022). In these regions, plants with lower SLA showed greater persistence under decreased precipitation. Species with acquisitive ecological strategies are usually linked with higher SLA while the opposite is true for species with conservative strategies (Pérez-Harguindeguy et al., 2013; Wondimu et al., 2023)

The current study unveiled differences in the direction of average trait values of species that occur at multiple sites, with some increasing along the gradient while others fluctuated. This indicates that plant traits are influenced by several factors, such as environmental, behavioural, geographical or can even be influenced by phenotypic plasticity. The four species found in more than one site are *C. mopane, C. collinum, T.*

sericea, and T. *prunioides* (Figure 8). The average height of *C. mopane* was higher in the areas where more rainfall was recorded, while the pattern for SLA and DS ratio fluctuated along the gradient, suggesting that the same species presented different rooting depths and SLA at different sites, independent of rainfall. On the PCA for multiple species, high values on PC1 and PC2 suggest that these species exhibit important combinations of traits that are influential in the ecosystem. Additionally, positive contributions to both axes might indicate synergistic traits that work well together.

One of the current study limitations was that the study could only study three plant functional traits; the number of traits may also have influenced the results of the study, as other studies usually consider three traits or more (Andrew et al., 2021; Zuo et al., 2021).

3.4.3. Plant species diversity and plant functional diversity

The final hypothesis of the study hypothesized a relationship between plant species diversity and plant functional diversity. The current study found different responses of plant species diversity and plant functional diversity to the rainfall gradient, indicating the importance of using both these metrics as ecological indicators to understand the effects of rainfall changes on the plant community. The results were that as plant species diversity increased across the landscape, there was a tendency for functional richness, functional divergence, and functional evenness to decrease, indicating a negative relationship between plant species diversity and plant functional diversity in this study. These results suggest a narrow range of functional traits among the plant species present. A study by Andrew et al. (2021) that investigated functional diversity of the Australian flora found that functional diversity was strongly positively related to species diversity. Nonetheless, authors noted differences in functional diversity at intermediate levels of species diversity. In the same study, but at a smaller spatial scale in a biodiversity hotspot region called the SWAFR, functional diversity and species diversity were not positively correlated; hence supporting the current study results at a smaller scale.

The weak negative lack correlation between plant species diversity and functional richness may suggest that other factors may modulate the influence of functional richness within the community. This is supported by the deterministic process theory (niche-based process) that states that the composition of species in a community is very closely related to the biotic and abiotic environment and that the composition may change along environmental gradients (Cornwell & Ackerly, 2010). The negative correlation might imply that as more species are introduced into the community, there could be increased competition for resources, leading to a reduction in the range of functional traits represented (i.e., functional richness). This may be explained by the fact that the fundamental processes influencing the diversity of traits in the tropical regions are linked to various environmental influences that serve as determinants in the formation of species composition (Hofhansl et al., 2021). Consequently, the plant functional traits associated with these determinants have been observed to change along latitudinal and altitudinal scales (Ackerly & Cornwell, 2007). However, other biotic factors that affect ecosystem structure and functioning at smaller spatial scales include competition between coexisting tree species, which has a significant impact on the makeup of the local species pool (Fauset et al., 2012). A study by Mason et al. (2010) found that despite functional richness's reliance on species richness, it was extremely sensitive to environmental filtering in simulated communities. In addition, research has demonstrated that competition can affect trait expression just as strongly as the main abiotic driver (Valencia et al., 2015), which emphasizes even more how important it is to take into consideration various factors influencing the variation in plant functional traits (Hofhansl et al., 2021). In a study that looked at fertilization effects on species diversity and functional diversity, it was found that species diversity and functional diversity were independent of each other (Li et al., 2015). Wondimu et al. (2023) found evidence for environmental filtering and how it is linked to environmental heterogeneity in their study.

3.5. Conclusion and recommendations

Some of our findings diverge from the common patterns reported in the literature, but they underscore the variability and context-dependence of ecological relationships. One key limitation of our study is that we examined only three out of the eight plant functional traits identified as important for coping with climate change and that we only had two plots per site. This narrower focus may have influenced the observed patterns. Our study contributes to the broader ecological discourse by highlighting the potential for variability in trait-environment and trait-diversity relationships.

Future research incorporating a wider array of functional traits and employing more comprehensive data collection methods can build on our findings to further elucidate these complex interactions. Conservation and biodiversity management efforts should consider both plant species diversity and plant functional diversity because they are both vital components of ecosystem functioning and they may be linked, based on the context, it is likely that we are not yet able to detect the right patterns!

3.6. References

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CHAPTER FOUR

4.1. Conclusion

The results of this study offer insights into the complex relationships between plant species diversity and functional trait diversity. While some of the findings diverge from the common patterns reported in the literature, they underscore the variability and context-dependence of ecological relationships. Several factors may explain these differences. A limitation of this study is that it examined only three out of the eight plant functional traits identified as important for coping with climate change. This narrower focus may have influenced the observed patterns. Our study contributes to the broader ecological discourse by highlighting the potential for variability in trait-environment and trait-diversity relationships. This variability can be influenced by local conditions, species composition, spatial scale and methodological differences. This study has outlined the status of plant species and plant functional trait diversity along an increasing rainfall gradient in northern Namibia, while acknowledging areas for future study enhancements.

In conclusion, while our study presents some contrasting results, it remains relevant by providing an understanding of the dynamics between plant species diversity and functional trait diversity.

4.2. Recommendations

Future research incorporating a wider array of functional traits and employing more comprehensive data collection methods can build on our findings to further elucidate these complex interactions. The study calls for continued investigation and consideration of local and methodological factors when interpreting ecological patterns. Conservation and biodiversity management efforts should therefore consider both plant species diversity and plant functional diversity because they are both vital components of ecosystem functioning and they may be independent or linked, based on the context.

4.3. Author contributions

A.M.N. Shikongo, E.C. Fabiano and G.W Fernandes were all involved in the conceptualization of the study. A.M.N. Shikongo was involved in the development of the methods under the guidance of E.C. Fabiano and G.W. Fernandes. A.M.N. Shikongo was involved in the data collection as well as data management and formal analysis. A.M.N. Shikongo was involved in the original draft preparation. E.C. Fabiano and G.W. Fernandes were involved in the review and supervision while A.M.N. Shikongo was involved in the editing of the work.

4.4. Acknowledgements

We would like to generously thank the NILALEG project for funding this study. We would also like to thank everyone who has contributed to this work, either through data collection, academic advice, or any other form of assistance.

Appendices

Appendix 1: List of tree species sampled throughout the study area and their respective families

Tree species name	**Family**
Adansonia digitata	*Malvaceae*
Baikiaea plurijuga	*Fabaceae*
Burkea africana	*Fabaceae*
Colophospermum mopane	*Fabaceae*
Combretum collinum	*Combretaceae*
Combretum zeyheri	*Combretaceae*
Commiphora africana	*Burseraceae*
Croton menyhartii	*Euphorbiaceae*
Diospyros mespiliformis	*Ebenaceae*
Guibourtia coleosperma	*Fabaceae*
Philenoptera nelsii	*Fabaceae*
Philenoptera violacea	*Fabaceae*
Pterocarpus angolensis	*Fabaceae*
Schinziophyton rautanenii	*Euphorbiaceae*
Senegalia fleckii	*Fabaceae*
Strychnos cocculoides	*Loganiaceae*
Terminalia prunioides	*Combretaceae*
Terminalia sericea	*Combretaceae*
Vachellia erioloba	*Fabaceae*
Vachellia tortilis	*Fabaceae*

Appendix 2: Average and standard error values of functional traits of plant species that occurred at multiple sampling sites in northern Namibia.

Species name	**Site number**	**Average Height (m)**	**Average SLA (cm^2mg^{-1})**	**Average DS ratio**
Colophospermum mopane	1	5.3 ± 0.44	188 ± 8.70	0.9 ± 0.10
	3	4.1 ± 0.19	191.1 ± 21.96	1 ± 0.10
	4	6 ± 0.51	124.1 ± 9.97	1 ± 0.03

	12	5.5 ± 0.61	142.1 ± 12.73	0.7 ± 0.04
	13	9.3 ± 0.86	154.5 ± 8.76	1.1 ± 0.04
Combretum collinum	5	8.8 ± 0.59	165.9± 15.76	1 ± 0.09
	6	6.4 ± 0.69	220.4± 40.47	0.9 ± 0.04
	7	5.3 ± 0.33	175 ± 10.64	1.1 ± 0.04
	8	3.8 ± 0.13	173 ± 14.51	0.7 ± 0.03
	9	4.8 ± 0.48	106.5 ± 7.26	0.8 ± 0.10
Terminalia prunioides	2	5.8 ± 0.46	284.6± 17.68	1.2 ± 0.09
	3	4 ± 0.28	276.2± 25.71	1.2 ± 0.09
Terminalia sericea	10	2.6 ± 0.25	113.5± 16.70	0.5 ± 0.10
	11	4 ± 0.21	207.7± 11.89	0.7 ± 0.07

Appendix 3: Plant species diversity data collection sheet

PLANT DIVERSITY FIELD DATA COLLECTION SHEET

Date: __________________

Collector's name: ______________________ Region: ____________________

Collection site: ____________________ Plot no.:

____

Coordinates at centre of plot: ____

Land type: ___________________ Geology:

____

Land use: __________________ Soil type: ______________

Tree number	Species Name	Diameter at Breast Height	Plant height	Status	Distance from centre of plot	Bearing

Appendix 4: Plant functional diversity data collection sheet

PLANT FUNCTIONAL DIVERSITY FIELD DATA COLLECTION SHEET

Date: ___________________

Collector’s name: _______________________ Region: _____________________

Collection site: _____________________ Plot: _______________________

Coordinates: ____

Land type: ____________________ Geology:

____

Land use: ___________________ Soil type: _______________

Species Name	Plant height (m)				Diameter at Breast Height (mm)	Specific Leaf Area		Rooting depth		
								Single-stemmed trees		Multi-stemmed trees
	d	Tan(α)	Tan(β)	Height (m)		Leaf area	Oven dry mass	Diameter at 10cm	Diameter at 30cm	

Appendix 5: Ethical Clearance Certificate

ETHICAL CLEARANCE CERTIFICATE

Ethical Clearance Reference Number: KMC0007 **Date: 16 /02/2023**

This Ethical Clearance Certificate is issued by the University of Namibia Ethics Committee (REC) in accordance with the University of Namibia's Research Ethics Policy and Guidelines. Ethical approval is given in respect of undertakings contained in the Research Project outlined below. This Certificate is issued on the recommendations of the ethical evaluation done by the ethics committee.

Title of Project: Comparing Plant Functional Traits and Species Diversity Along a Rainfall Gradient in Northern Namibia

Principal researchers: ALBERTINA M.N. SHIKONGO

Staff Number/ Student number: 201610564

Remarks: This ethical clearance is granted with the condition that the student include under research ethics, issues like anonymity, confidentiality, explain respondents right to withdraw from participation etc.

Centre for Research Services

Take note of the following:

1. Any significant changes in the conditions or undertakings outlined in the approved Proposal must be communicated to the ethics committee. An application to make amendments may be necessary.
2. Any breaches of ethical undertakings or practices that have an impact on ethical conduct of the research must be reported to the ethics committee
3. The Principal Researcher must report issues of ethical compliance to the ethics committee (through the Chairperson) at the end of the Project or as may be requested by the ethics committee
4. The ethics committee retains the right to:

i) Withdraw or amend this Ethical Clearance if any unethical practices (as outlined in the Research Ethics Policy) have been detected or suspected,

ii) Request for an ethical compliance report at any point during the course of the research.

The ethics committee wishes you the best in your research.

Dr David Nkengbeza

(Chairperson Decentralized Ethics Committee)

Prof. Davis Mumbengegwi (Head, Multidisciplinary Research)

Appendix 6: NCRST Research Permission letter

NCRST
National Commission
on Research Science & Technology

AUTHORIZATION OF RESEARCH PROJECTS

Authorization is hereby granted in terms of Section 21 of the RST Act No. 23 of 2004, to:

Name: Albertina Megameno Nalukale Shikongo

Address: P.O.Box 1527, Keetmanshoop,
Namibia

Coworkers: Simon Tuhafeni Angombe, Ezequiel Chimbioputo Fabiano

Certificate Number (if applicable): RCIV00022018 **Authorization No:** 202201115

Type of Research:
Non- Commercial research and the use of resources be limited to what is in the proposal.

Title of Research Authorized:
Comparing plant functional traits and species diversity along a rainfall gradient in northern Namibia

Locality:
Northern regions of Namibia, Kunene, Omusati, Ohangwena, Kavango West, Kavango East and Zambezi, along the road

Duration: 21 November 2022 - 30 November 2023

Research / Sample Collection Conditions:
Five leaves will be collected from five individuals per tree species at each collection site.
Refer to research conditions on the next page.

Yours sincerely,

2 2 NOV 2022
P / Bag 13253
Windhoek, Namibia

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RESEARCH/SAMPLE COLLECTION CONDITIONS

1. You must report to the Park Chief warden and / or Regional Office of the Ministry of Environment and Tourism prior to arrival in fieldwork area, and must present your permit.
2. This permit does NOT entitle the holder to free entry to the protected areas or state land outside protected areas.
3. For Field work in National Parks you have to make arrangement with park management in advance prior to arrival in fieldwork area.
4. Voucher specimens should be deposited with National Museum of Namibia.
5. If you would like to export samples of specimens you must loan them from the National Museum of Namibia.
6. To conduct research work in the rhinos and elephants range all persons listed on the permit must be in possession of a police clearance certificate.
7. The permission of the land owner is required to work/collect on private lands.
8. The permission of the concession holder is required to work/collect in concession areas.
9. The permission of the communal authority is required to work/collect in communal areas.
10. No commercial filming will be permitted without prior approval by the Ministry of Environment and Tourism under this permit.
11. Duplicates of publications and / or final report should be made available to the Ministry of Environment and Tourism and also the final report.
12. The specimens and their derivatives may be used for the purposes of this study only and may not be patented, commercialised, donated or sold to a third party without the written consent of the Ministry of Environment and Tourism.
13. All results (raw materials) or technology derived directly or indirectly from this research must be made available free of charge without reservations to the Ministry of Environment and Tourism.
14. A report on the work conducted under this permit must be submitted to the Ministry of Environment and Tourism not later than one month after the expiry of this permit as well as to regional office in whose area research was conducted.
15. Applications for renewal of this permit must reach this office at least three months prior to the expiry of this permit.
16. Habitat destructive collecting methods must not to be used.
17. Veterinary restriction may apply in the case of movement of samples and it is the applicants' responsibility to obtain such permits.
18. Foreign (or destination) wildlife import, and veterinary import permits may be required.
19. CITES import permit from the country of the destination is required for the application of export permit for CITES –listed species.
20. All field teams must be in possession of the permit and permit copy must accompany the transport of specimens.
21. You are subject to all conditions listed on the entry permit to any of the protected areas, unless specifically exempted.
22. Failure to adhere to the conditions will lead to cancellation of the research permit.
23. It is your responsibility to make the necessary contacts and arrangements as specified above.
24. The applicant should submit the final research finding with the National Botanic Research Institute library.