Plant diversity on inselbergs along the aridity gradient of the central Namib Desert

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PREFACE AND ACKNOWLEDGMENTS

This research aimed to investigate plant diversity on inselbergs along an aridity gradient in the central Namib Desert, contributing to the currently fragmented biodiversity data of inselbergs in this region. It was guided by the following objectives: (i) to compile an inventory of species richness and composition on inselbergs and in the surrounding matrix; (ii) to compare species richness and composition between topographical positions, aspects, and geological types of inselbergs; and (iii) to determine the relationship between species richness and composition with inselberg size, spatial isolation, and aridity. This study contributes to our understanding of plant diversity patterns and biogeography on inselbergs in the central Namib Desert.

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ABSTRACT

Inselbergs are isolated, rocky outcrops that rise above the surrounding plain landscape. They are globally recognised as important biodiversity hotspots, and support a variety of plant communities because of their ability to create microclimatic conditions and stable microhabitats, often with higher moisture availability than the surrounding matrix in arid or semi-arid environments. Studies on plant diversity and the ecological factors that influence diversity on inselbergs have largely focused on tropical regions, with comparatively few studies conducted in arid environments, where inselberg refugia may contribute considerably to overall diversity. In particular, limited knowledge exists regarding the influence of large-scale aridity gradients on plant diversity patterns of inselbergs in the central Namib Desert.

This study aimed to document and compare plant diversity patterns on inselbergs of varying sizes and different geological substrates (marble, schist, and granite) along an east-west transect that represented an aridity gradient in the central Namib Desert. Transect-based field surveys were conducted at 25 sites to assess plant diversity patterns. Vascular plant species including trees, shrubs, and forbs, were recorded on inselbergs and the surrounding matrix. Data were analysed using univariate (diversity indices, one-way ANOVA and Kruskal-Wallis ANOVA) and multivariate techniques to evaluate compositional differences, and Similarity Percentage (SIMPER) and Indicator Species Analysis (IndVal%) to identify species contributing most to group dissimilarities and habitat associations.

Species richness and composition differed significantly between inselbergs and the surrounding matrix. Inselbergs supported a significantly higher species richness per plot compared to the surrounding matrix. Topography influenced species richness and composition only between inselbergs and the matrix; however, no significant differences were detected among topographical positions on the inselbergs themselves. Geology influenced species richness between the inselbergs and matrix, but no significant differences were observerd among the geological types (marble, schist and granite), although species composition was significantly affected by geology. *Euphorbia virosa* and *Pogonospermum cleomoides* were strongly associated with schist inselbergs, whereas *Ceropegia pedicellata*, *Euphorbia giessii* and *Arthraerua leubnitziae* were associated with marble inselbergs. Slope aspect had no significant effect on species richness or composition. Contrary to island biogeography predictions, species richness showed no relationship with inselberg size, precipitation (aridity gradient proxy) or spatial isolation, but species composition was significantly influenced by precipitation and isolation, while inselberg size had little effect on species composition. An important finding was that species richness remained invariant along the aridity gradient, whereas species composition shifted significantly with precipitation. Environmental variables explained 7.7% of the total variation in species

composition (total inertia = 12.22%), suggesting that other variables not explored in this study also shape the species assemblages on inselbergs in the central Namib Desert and require further investigation.

These findings demonstrate that, in hyper-arid environments, inselbergs function as compositional refugia, rather than following classical island biogeography predictions, with species richness decoupled from spatial variables and community assembly primarily structured by environmental filtering. The results highlight their importance as ecological refugia and conservation value as biodiversity hotspots in the central Namib Desert.

Key words: Phytogeography, species composition, species richness, geoecology, island biogeography

ABBREVIATION AND ACRONYMS

Ai	Aridity Index
ANOSIM	Analysis of Similarities
ANOVA	Analysis of Variance
CANOCO 5	Canonical Community Ordination
CCA	Canonical Correspondence Analysis
FNASREC	Faculty of Natural and Agricultural Sciences Ethics Committee
GBB	Gobabeb Herbarium
Gobabeb	Gobabeb-Namib Research Institute
IBM SPSS	Statistical Package for Social Sciences
IndVal	Indicator Species Analysis
IPCC	Intergovernmental Panel on Climate Change
MoU	Memorandum of Understanding
MEA	Millenium Ecosystem Assessment
NE	Northeast
NMDS	Non-Metric Multidimensional Scaling
PAST	Palaeontological Statistics
PERMANOVA	Permutational Multivariate Analysis of Variance
pCCA	Partial Canonical Correspondence Analysis
PRIMER 6	Plymouth Routines in Multivariate Ecological Research 6
SIMPER	Similarity Percentage analysis
SW	Southwest
Tukey HSD Test:	Tukey Honestly Significant Difference Test
UESM	Unit of Environmental Sciences and Management

KEY DEFINITIONS

For the purpose of this dissertation, the words or phrases set below have the following meanings:

Crest	summit of an inselberg
Footslope	base of an inselberg
Inselberg	isolated rocky outcrops that rise above the surrounding plain landscape
Matrix	gravel plains/landscape that surround the inselbergs
Midslope	position between the footslope and the crest of an inselberg
Slope aspect	compass direction of inselberg slope faces, indicating how much sun and wind it receives
Species composition	identity and assemblage of species in a given area
Species diversity	the number of different species and their relative abundance in a given area
Species richness	number of different species in an area
Togopraphical position	position of sampling plot along the vertical gradient of inselbergs from the surrounding matrix to the crest

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CHAPTER 1 INTRODUCTION

1.1 Background

Biodiversity encompasses the variety of life on Earth, including genetic, species, and ecosystem diversity (Wu, 2025; Secretariat of the Convention on Biological Diversity, 2005). It is a fundamental component of ecosystem structure and function (Jayaramaiah *et al.*, 2024), plays a crucial role in maintaining ecosystem stability (Wu, 2025), and enhancing ecosystem resilience. Species diversity has been identified as a key driver of ecosystem functioning and resilience to environmental change (Wang *et al.*, 2024). Diverse ecosystems provide a wide range of essential ecosystem services, including supporting, provisioning, regulating, and cultural services (Corlett, 2016). These services underpin human well-being by supplying oxygen, sequestering carbon dioxide, regulating the water cycle, and maintaining healthy soils (Corlett, 2016; Millennium Ecosystem Assessment, 2005). Consequently, the conservation of biodiversity is vital, as it is fundamental to human well-being and long-term survival (MEA, 2005), a principle emphasised by the Convention on Biological Diversity (CBD).

Arid environments, including deserts, occupy approximately 35% of the Earth's terrestrial surface (Tchakerian & Pease, 2015). These regions are characterised by high temperatures, low and highly variable precipitation, and generally support fewer species than more humid biomes (McNeely, 2003). Deserts are often perceived as simple ecosystems with low species diversity; however, they can be highly diverse and structurally complex (Polis *et al.*, 2004). Plant communities in arid regions are frequently characterised by high levels of endemism and specialised adaptations to extreme environmental conditions (Aili *et al.*, 2024). As such, desert biodiversity plays an important role in enhancing resilience to climate change (Conkey *et al.*, 2023), by maintaining ecosystem functions, nutrient cycling, and productivity (Wu, 2025). According to Maestre et al. 2012, species richness in drylands is positively correlated to ecosystem multifunctionality, highlighting the importance of biodiversity in sustaining ecosystem stability under environmental stress. In addition, inselbergs may function as important refugia by providing heterogeneous microhabitats that can buffer climatic extremes and locally enhance moisture availability, thereby allowing the persistence of species that may not survive in the drier matrix under future climate change (Vanschoenwinkel et al., 2025).

The central Namib Desert is characterised by a pronounced east–west climatic gradient, with rainfall increasing inland from the coast and fog occurrence decreasing in the same direction (Lancaster *et al.*, 1984). Species diversity within the region is strongly influenced by this climatic gradient (Hachfeld and Jürgens, 2000, cited by Rhodhe *et al.*, 2019). The gravel plains of the central Namib Desert are punctuated by inselbergs (Jürgens & Burke, 2000) of varying size,

morphological type, and geological origin. Inselbergs create distinct microhabitats that differ markedly from the surrounding lowlands (Glime & Da Silva, 2019), often providing more mesic conditions than the surrounding matrix in arid environments (Jürgens & Burke, 2000). These features typically have sparse soil cover (Bremer & Sander, 2000), shallow depressions, drainage channels, and crevices that can temporarily retain water (Glime & Da Silva, 2019), resulting in ephemeral micro-wetlands during rainy periods (Johnson & Roger, 2003, cited by Kulkami, 2023). Moreover, inselbergs are often regarded as terrestrial islands (Parmentier *et al.*, 2005). Thus, Island Biogeography Theory has been applied as a conceptual framework to explain patterns of species richness and composition in relation to inselberg size and spatial isolation, although the strength of these relationships may vary across ecosystems (Porembski & Barthlott, 2000; Vanschoenwinkel et al., 2025).

This study aims to document the plant diversity of inselbergs along an aridity gradient in the central Namib Desert, and to identify the environmental factors influencing species richness and composition. In doing so, the study seeks to contribute to the limited understanding of arid-zone inselberg biogeography and to address gaps in existing plant biodiversity data. Ultimately, the research may highlight the importance of inselbergs as key reservoirs of plant diversity within Namibia's unique desert ecosystems.

1.2 Problem statement and rationale for the study

Inselbergs, which are characterised by extreme environmental conditions, are recognised as important biodiversity hotspots worldwide (Yang *et al.*, 2016). These isolated formations function as ecological refugia for species with restricted distributions (Fitzsimons & Michael, 2017; Barthlott *et al.*, 1993, cited in Pinto-Junior *et al.*, 2020). Inselbergs may also act as critical seed reservoirs, providing propagules that could be used in the ecological restoration of disturbed landscapes, such as post-mining sites in arid environments (Burke, 2003). Despite their ecological significance, inselbergs are increasingly subjected to anthropogenic threats, including the collection and trade of ornamental rocks (Campello, 2000, cited by Pinto *et al.*, 2020), poaching of plant species for horticultural and ornamental purposes. Moreover, habitat disturbance associated with tourism activities such as rock crawling (Fitzsimons & Michael, 2017), and landscape modification from mining activities and infrastructure development, including the installation of cellular communication towers is another threat to inselberg's biodiversity.

Notwithstanding their perceived importance, inselberg floras remain poorly documented and insufficiently understood. Global studies on inselberg vegetation have predominantly focused on tropical regions (Safford & Martinelli, 2000, cited by Pinto-Junior *et al.*, 2020), resulting in a substantial knowledge gap regarding the biogeography, ecology and conservation status of

inselberg biota in arid environments. In Namibia, in particular, there is limited information on how large-scale aridity gradients influence plant species richness and composition on inselbergs. While previous studies in Namibia have focused mainly on the Nama-Karoo biome (Burke, 2002a, 2002b, 2003), they have not explicitly considered the pronounced east-west aridity gradient characteristic of the country's desert region. Additionally, inselberg vegetation studies in the central Namib Desert have been largely restricted to the Spitzkoppe (Burke, 2003), limiting the extent to which findings can be generalised to the broader central Namib Desert, which comprises numerous inselbergs differing in size, geology, and spatial context.

Although Burke (2002a) reported high species richness and greater floristic diversity on Spitzkoppe inselbergs compared to the surrounding matrix, the spatial distribution of this diversity across the central Namib Desert remains unclear. Similarly, Burke (2003) demonstrated that inselbergs contribute significantly to both local and regional plant species richness, thereby enhancing overall biodiversity within the Namib Desert. However, the extent to which these patterns vary along the steep aridity gradient of the central Namib Desert, and among inselbergs of different sizes and lithological types, has not been systematically investigated.

Addressing this knowledge gap is essential for improving our understanding of the geoecology of inselberg vegetation in arid environments. The lack of comprehensive data on plant diversity patterns across aridity gradients may hinder effective conservation planning and biodiversity management of these unique landforms. Furthermore, understanding how plant diversity responds to intense aridity gradients is increasingly important in the context of projected future climate change, which is expected to exacerbate aridification and drying trends in desert landscapes (Huang *et al.*, 2015).

1.3 Research aim and objectives

The main aim of this study was to document and compare patterns of plant species richness and composition on inselbergs along an aridity gradient in the central Namib Desert.

The specific objectives of the study were to:

i. Compile an inventory of plant species richness and composition on inselbergs and in the surrounding matrix.

ii. Compare species richness and composition across different topographical positions, slope aspects, and geological types of inselbergs.

iii. Examine the relationships between species richness and composition and inselberg size, spatial isolation, and aridity.

1.4 Research questions

The following questions were addressed in this study:

i. How do plant species richness and composition differ between inselbergs and the surrounding matrix?
ii. How do species richness and composition vary within inselbergs across topographical positions, slope aspects, and geological substrates?
iii. What are the relationships between species richness and composition and inselberg size, spatial isolation, and aridity?

1.5 Hypotheses

This study tests predictions derived from island biogeography theory, environmental filtering, and substrate-mediated habitat heterogeneity in arid systems. Hypotheses are structured around three ecological domains: (1) habitat differentiation (inselbergs vs. matrix), (2) internal inselberg environmental gradients (topography, aspect, geology), and (3) landscape-scale spatial and climatic gradients (size, isolation, aridity).

1.5.1 Habitat differentiation: inselbergs vs. matrix

H1(i) (Species richness)

Plant species richness and alpha diversity will be significantly higher on inselbergs than in the surrounding matrix.

Inselbergs function as habitat islands characterised by enhanced microhabitat heterogeneity, edaphic variability, and moisture retention relative to the surrounding plains. According to habitat heterogeneity theory and inselberg ecology, structurally complex substrates should support greater niche partitioning and thus higher richness.

It is expected that Shannon diversity, Margalef richness, and total species counts will be significantly greater on inselbergs than in matrix habitats.

H1(ii) (Species composition)

Species composition will differ significantly between inselbergs and the surrounding matrix.

Environmental filtering driven by lithology, soil development, and microclimatic buffering should result in distinct species assemblages. Inselbergs are expected to harbour habitat specialists not prevalent in the matrix.

It is expected that NMDS ordination will show discrete clustering of inselberg and matrix plots, and PERMANOVA will detect significant compositional differences.

1.5.2 Internal inselberg environmental gradients

H2(i) (Topographical position)

Lower topographical strata (footslopes) will support higher species richness and differ compositionally from midslopes and crests.

Footslopes are predicted to accumulate deeper soils, organic matter, and moisture via downslope transport processes. Vertical gradients is therefore anticipated to drive patterns of species richness and community structure.

It is expected that diversity indices will decline from footslope to crest, and PERMANOVA will detect compositional differentiation among strata.

H2(ii) (Slope aspect)

Southwest-facing slopes will support higher species richness and distinct species composition compared to northeast-facing slopes.

In the central Namib Desert, southwest slopes are expected to intercept greater fog input, lower solar radiation, and consequently experience lower temperatures and reduced evaporative stress. These microclimates increase moisture availability, which is likely favour greater richness and shape community structure.

It is expected that diversity will be significantly higher on southwest slopes, and ordination analyses will reveal aspect-related clustering.

H2(iii) (Geological substrate)

Species composition and richness will differ among granite, marble, and schist inselbergs.

Lithological differences generate contrasting soil chemistries and nutrient availability. Granite-derived substrates are expected to favour oligotrophic specialists; marble-derived soils should support calcicolous assemblages; schist is predicted to exhibit intermediate characteristics.

It is expected that PERMANOVA and indicator species analysis will detect significant compositional differences among geological types. Richness patterns will reflect substrate-driven environmental filtering.

1.5.3 Landscape-scale environmental gradients

H3(i) (Inselberg size — species–area relationship)

Species richness will be positively correlated with inselberg area.

Classical island biogeography predicts increasing richness with area due to greater habitat heterogeneity and reduced extinction probability.

It is expected that Pearson correlation and Spearman correlation analyses will show a significant positive relationship between diversity indices and inselberg size.

H3(ii) (Spatial isolation)

Species richness will be negatively correlated with spatial isolation.

Increased isolation is predicted to reduce immigration rates, thereby limiting colonisation and lowering species richness.

It is expected that diversity indices will decline with increasing inter-inselberg distance, and composition will shift along the isolation gradient in CCA ordination.

H3(iii) (Aridity gradient)

Species richness and evenness will decline with increasing aridity (lower precipitation), while species composition will shift along the precipitation gradient.

Increasing aridity intensifies environmental filtering, favouring stress-tolerant taxa and reducing competitive diversity.

It is expected that diversity indices will show significant relationships with precipitation, and CCA will reveal compositional structuring along the climatic gradient.

1.6 Scope of the research

This study was conducted in the central Namib Desert, Namibia, across 25 inselbergs distributed along an east-west gradient extending from the coastal zone to approximately 112 km inland. The

inselbergs varied in size, ranging from small (0–19 ha) to medium (20–50 ha) and large (≥50 ha), and comprised different geological substrates, including marble, granite, and schist.

The research focused on patterns of plant species richness and composition on inselbergs and in the surrounding matrix. Variation was examined across topographical positions (matrix, footslope/baseslope, midslope, and crest), slope aspects (northeast and southwest), and geological types. Additionally, the study explored the relationships between species richness and composition and inselberg size, spatial isolation, and aridity index.

Each inselberg was stratified into four zones (strata). Vegetation sampling was conducted using 400m^2 quadrats placed along transects extending from the surrounding matrix across the highest point of each inselberg to the opposite surrounding matrix. A total of seven quadrats were sampled per inselberg, resulting in 175 quadrats across the study area.

The scope of the study was limited to vascular plant species recorded during field surveys. Other components of biodiversity, including fauna, soil micro-organisms, and cryptogams, fell outside the scope of this research and were not considered. Only the presence and total number of vascular plant species were recorded within each quadrat. To minimise edge effects, the surrounding matrix was sampled at least 100 m from the footslope of each inselberg, and drainage channels/washes within the matrix were not sampled. The study did not assess temporal changes in vegetation, but instead provides a spatial comparison at a single point in time. Consequently, the findings should be interpreted within the ecological context of the central Namib Desert and similar arid systems, and broader generalisations should be made with caution.

1.7 Assumptions and limitations

According to the long-term climatic averages for the study site, it was anticipated that bulk of the rainfall will occur between October 2023 and March 2024, thereby facilitating the emergence of cryptic, annual, and opportunistic plant species. However, no rainfall was recorded during the hydrological year prior to or during the study period. Consequently, many annual and opportunistic species were absent from the vegetation sampled (Burke, find reference). The dataset, therefore, largely reflects perennial plant species adapted to the unpredictable, low-intensity rainfall regime of the central Namib Desert. While this limited the representation of annuals, it nonetheless provides a realistic reflection of the typical vegetation in the central Namib Desert, where perennial species dominate with 73% of the flora (Jürgens *et al*., 2013), and exhibit relative stability across seasons. However, these estimates represent the flora of the central Namib Desert as has not been quantified for inselbergs or the matrix. Furthermore, no study quantified the influence of geology, slope, aspect and aridity gradient on annuals species on the central Namib Desert inselbergs; thus, the proportion of unsampled flora remains unknown.

Several additional limitations were encountered during the study. Access to some inselbergs was restricted due to their location on privately owned land, and permission to conduct sampling was not granted in all cases. Consequently, certain inselberg size categories were underrepresented in the final dataset. Furthermore, the absence of rainfall during the study period constrained the detection of cryptic, annual, and opportunistic species, thereby reducing their contribution to the overall plant species inventory.

1.8 Potential contribution of the research

Inselbergs remain among the most poorly studied terrestrial ecosystems globally (Larson et al., 2000, cited in Ayeko et al., 2003). The documentation and dissemination of country-specific data on inselberg biodiversity are therefore essential. On the absence of reliable baseline data, the development of targeted conservation strategies and the effective monitoring of these unique landforms remain challenging (Ayeko et al., 2003).

In the context of increasing anthropogenic pressures, such as mining and infrastructure development, inselbergs may function as important refugia for plant species. Their relative isolation and generally low levels of disturbance allow them to act as reservoirs of native flora, with potential value for the rehabilitation of degraded surrounding landscapes (Burke, 2003). Furthermore, inselbergs are ancient and geomorphologically stable landforms (Bremer & Sander, 2000) that often retain higher moisture levels than adjacent habitats (Jürgens & Burke, 2000), suggesting they may play an important role in conserving plant biodiversity under changing climatic scenarios.

This study contributes to addressing the existing gaps in plant biodiversity data for inselbergs in the central Namib Desert and advances understanding of biogeographical patterns shaping plant communities across aridity gradients in this region. The findings provide a scientific basis for future ecological research and conservation planning aimed at safeguarding inselberg ecosystems within Namibia’s arid landscapes.

1.9 Structure and outline of the dissertation

This dissertation comprises seven chapters, structured in accordance with North-West University guidelines. Chapters 4, 5 and 6 are presented as separate results and discussion chapters aligned to each of the objectives of the study.

Chapter 1 introduces the research by providing the background, problem statement, research aim and objectives, research questions and hypotheses, scope of the study, as well as the assumptions and limitations encountered.

Chapter 2 presents a review of the relevant literature, focusing on inselbergs, the theory of island biogeography and its applicability to inselberg systems, and key environmental factors shaping plant communities on inselbergs, including slope aspect, topographical position, geology and aridity gradients. The chapter concludes by discussing methodological considerations associated with sampling plant diversity in arid environments.

Chapter 3 describes the methodology, including the study area, climatic context, research design, data collection procedures (vegetation and climatic data), statistical analysis, software used, ethical clearance, and study limitations and assumptions.

Chapter 4 examines patterns of species richness and composition on inselbergs and in the surrounding matrix of the central Namib Desert and is written in a format that will allow for easy construction of a manuscript to submit to a peer-reviewed scientific journal.

Chapter 5 compares species richness and composition across topographical positions (strata), slope aspects (northeast and southwest), and geological types (schist, marble, and granite). This is written in a format that will allow for easy construction of a manuscript to submit to a peer-reviewed scientific journal.

Chapter 6 examines the relationship between species richness and species composition and sizes, spatial isolation, and aridity index of the inselbergs in the central Namib Desert. This chapter is written in a format that will allow for easy construction of a manuscript to submit to a peer-reviewed scientific journal.

Chapter 7 synthesises the main findings of this study and provides recommendations for future research and for the conservation of inselbergs in the central Namib Desert.

Each chapter includes its own reference list, and the dissertation concludes with an appendix containing supplementary information relevant to the study.

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CHAPTER 2 LITERATURE REVIEW

2.1 Introduction

The term inselberg (*insel* = *island*, and *berg* = *mountain*) was first defined in 1900 by Walt Bornhardt, a German naturalist and traveler, who described the isolated hills in East Africa as resembling islands rising from the sea (Bremer & Sander, 2000; Migon, 2013). Inselbergs are isolated rocky outcrops that emerge abruptly from a flat plain and consist of massive granite, or quartz-rich gneiss and schist intruded by granite (Willis, 1934). They are an example of geomorphological equifinality (Migon, 2013); their origin varies depending on the underlying lithology and regional geomorphological processes. Inselbergs occur all over the world and represent independent ecosystems with distinct microclimatic and edaphic conditions because of their isolation and heterogeneity (Kluge & Büdel, 2009). They are regarded as terrestrial islands because they create stable microclimatic conditions and heterogeneous habitats such as crevices, depression, and fractures with higher moisture content compared to the surrounding areas (Burke, 2003; Yates *et al.*, 2019). Thus, they are habitats for specialised species that may not be present in the surrounding area (Bremer & Sander, 2000). Consequently, the flora of inselbergs differs almost completely compared to their surrounding areas (Barthlott *et al.*, 1993, cited by Glime & da Silva, 2009), as a function of differences in microhabitats between rock habitats and the surrounding areas with deeper soils (Anderson *et al.*, 1999). In many regions, inselbergs belong to the least disturbed ecosystems and are therefore of special interest and have a crucial role as biodiversity hotspots (Kluge & Büdel, 2009). Additionally, they have the potential to serve as a reservoir of plant species that can recolonise the surrounding areas (Burke, 2003b).

In the central Namib Desert, there are numerous outcrops of Precambrian dolomitic marbles, composed of marbles (Hamilton Range), granite (Mirabib), and schist (Goudie & Viles, 2015). Namib inselbergs are of both extrusive (basaltic) and intrusive (granite) igneous origins, and they have been in their current positional and configuration since the Miocene (Ward & Corbert, 1990, cited by Burke, 2019). In contrast to the tropical inselbergs that create xeric islands and hotter microclimates due to thermal uplifting (Szarzynski, 2000, cited by Yates *et al.*, 2019), inselbergs in arid regions create wetter islands with higher moisture content than the surrounding areas due to cooler air formed by higher elevation (Shakdofa *et al.*, 2024; Jürgens & Burke, 2000). These conditions may support species with greater moisture requirements, typically found in more mesic zones (Burke, 2003a). Namibia's mountain ranges and rock outcrops are therefore recognised as vital ecological refuges for many species (fauna and flora) with limited geographical range, and they are impractical to restore once they are degraded (Barnard, 1998).

Namibia's inselbergs may be essential in preserving biodiversity and providing refuges for species that are no longer able to grow in the surrounding plains, as well as providing a species pool that can recolonise the surrounding plains (Burke, 2002a). The results from Burke (2002a) revealed that inselbergs and their surrounding matrix shared 50% of species in three out of four study areas. Furthermore, desert inselbergs can act as a refuge for species from higher rainfall areas, as highlighted by Burke (2000a, 2000b) who noted that many species were typically associated with the escarpment zone and highland savanna, such as *Commiphora* species, *Euphorbia guerichiana,* and *Euclea undulata.* However, this study was conducted at the interface between the Nama Karoo and the Namib Desert biomes, and close to the higher rainfall areas. These results cannot be generalised for all central Namib Desert inselbergs; hence, more research is needed to assess and compare the extent to which inselbergs across the aridity gradient function as biodiversity refugia. Inselbergs could supply nutrients to the surrounding lowlands, which is essential in maintaining the functioning of ecosystems and landscape (Burke, 2002).

The importance of inselbergs for conservation and maintenance of biodiversity has been recognised in arid regions (Bond & Richardson, 1990, cited by Burke, 2001). Conversely, inselbergs are threatened by tourism pressure (rock crawling), as well as increasing demand for granite and gneiss for construction purposes (Esson *et al.,* 2015). There is little knowledge of the inhabitants of inselbergs and the biogeography and ecology of Namibia's inselbergs (Barnard, 1998). Empirical research comparing vegetation on inselbergs with the surrounding matrix are rare (Buschke, 2020). Therefore, this study aims to assess plant diversity on inselbergs along the aridity gradient in the central Namib Desert to fill a critical gap in knowledge about the region's biodiversity and biogeography. Focusing on three objectives: (i) Assessing species richness and species composition on inselbergs and the surrounding matrix. (ii) Comparing species richness and species composition across topographical positions, slope aspects, and geological types. (iii) Determining the relationships between species richness and species composition with the size, spatial isolation, and aridity index.

2.2 Theory of Island Biogeography and its applicability to inselbergs

The theory of island biogeography, originally developed for true islands (Matthews, 2021), has long been applied to a broader spectrum of island-like ecosystems called habitat islands (Matthews & Triantis, 2021). Such habitat islands, or rather, terrestrial islands, are defined as areas of natural habitat surrounded by a less hostile matrix (Matthews & Triantis, 2021; Whittaker & Fernadez, 2007). Inselbergs, in that context, are regarded as terrestrial islands because of their ecological and isolation contrast with the surrounding matrix (Barthlott & Porembski, 2000). They generate a range of microhabitats where ecological conditions contrast moderately to extremely with the surrounding landscape (Parmentier *et al.*, 2005). Although they differ in origin and

geological nature from oceanic islands, inselbergs share key biogeographical characteristics, notably the effects of area and isolation on species diversity (Kluge & Büdel, 2000). Inselbergs vary widely in both size and degree of isolation (Barthlott & Porembski, 2000). Subsequently, the theory of island biogeography can be applied to inselbergs, treating them as terrestrial islands.

Isolation and the size of the island are key factors in the Theory of Island Biogeography (MacArthur & Wilson, 1967), which are known to shape plant communities. The relationship between area and the number of species is well known as the species-area relationship (Lomolino, 2001), a well-established ecological pattern. Species-area relationships on islands focus primarily on two explanations: habitat heterogeneity & island size (Matthews & Triantis, 2021). Larger islands support larger populations, which are less vulnerable to extinction; second, larger islands encompass a broader range of habitat types, including those needed by specialist species (Kohn & Walsh, 1994). This supports the notion that species diversity will increase with the number of habitats and indirectly with the size of an inselberg (Kluge & Büdel, 2009). Traditionally, the species-area relationship describes a general trend in which species numbers increase with island area, though the slope of this relationship tends to decline (but remain positive) as area increases (Lomolino, 2001).

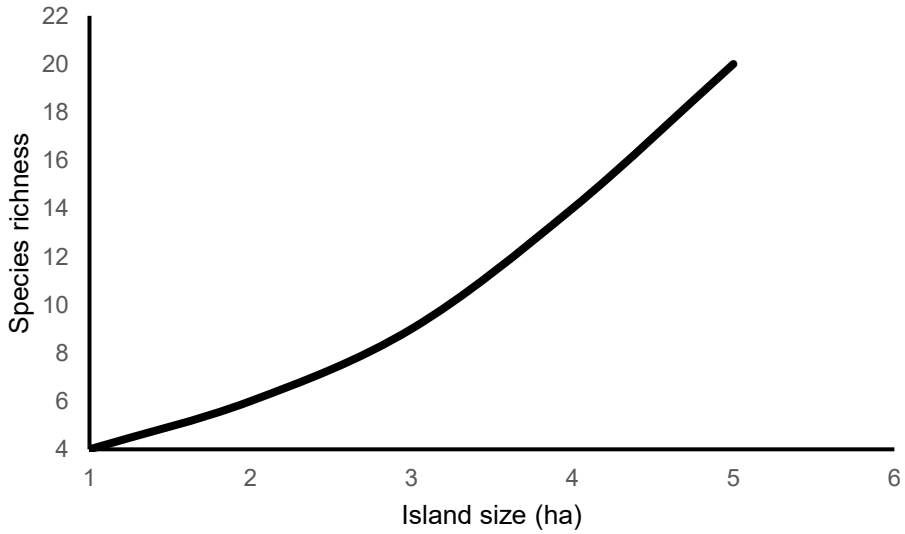


Figure 2.1. Species-area relationship showing species richness increasing with the increase in the island size.

It has been hypothesised that species richness decreases with increased isolation (Whittaker & Fernandez, 2007). More isolated islands have lower colonisation rates as they are harder for prospective colonists to reach (Angela & Lei, 1998). Islands that are closer to the mainland are hypothesised to have more species because of the higher potential colonisation rates (MacArthur & Wilson 1963, 1967, cited by Matthews, 2021). Traditionally, isolation is defined as the distance

between an island and the mainland (Whittaker & Fernandez, 2007). However, this definition does not take into account the distance to the nearest island or the configuration of islands within an archipelago (Itescu *et al.*, 2020; Matthews & Triantis, 2021). In this study, isolation is defined as the distance from one inselberg to the nearest neighbouring inselberg (island). In addition, not all inselbergs are entirely isolated; some form an archipelago, while others form at the end of spurs and ridges.

The inselbergs of the central Namib Desert provide an ideal natural setting for testing the applicability of island biogeography theory in a hyper-arid environment (with aridity index of < 0.05 and a <25 mm annually (Meslier and DiRuggiero, 2019)). Examining these principles in such an extreme climatic context allows for the evaluation of whether inselbergs conform to classical island biogeography predictions. Furthermore, this approach enhances our understanding of the ecological and environmental factors that shape patterns of species diversity in isolated terrestrial systems.

2.3 Species Indices and Environmental variables

Identifying the factors that influence species diversity and distribution is a central theme in ecology (Fayolle *et al.*, 2012). However, plant diversity on inselbergs remains understudied, partly because these rocky outcrops are discontinuously distributed across landscapes, and standardised sampling methods remain limited (Buschke, 2020; Clegg *et al.*, 2025). Understanding environmental drivers of diversity, therefore, requires careful consideration of both landscape context and methodological constraints. Diversity is often quantified through metrics such as species richness, evenness, and community composition (Heip *et al*., 1998; Peet, 1974).

Species richness, defined as the total number of species in an area, remains the most used metric of species diversity (Millennium Ecosystem Assessment, 2005). While it provides a valuable and accessible measure of biodiversity, it is only one component of diversity (Aggemyr *et al.*, 2018; Magurran, 1983). Despite species richness being popularly used as the easiest measure of species diversity, it does not account for species' relative abundance or species evenness/equitability of the species abundance distribution (Gotelli & Chao, 2013). Species richness cannot reveal how similar or different two communities are, as it weighs each species as an equal contributor to species diversity regardless of its abundance (Latimer, 2014; Wilsey *et al.*, 2005). Communities with the same species richness may differ substantially in species composition and relative abundance (Kadmon & Pulliam, 1993). Therefore, reliance on species richness alone can underestimate plant diversity and obscure ecological differences between communities (Latimer, 2014; Wilsey *et al.*, 2005).

On the other hand, species composition is defined as the number of species in an area and their relative abundance (Behera *et al.*, 2023). Species frequency distribution is more informative and a representation of the community diversity than just species number (richness). Hence, integrating other species diversity measures to account for both species richness and relative abundance of species that are present is crucial in assessing plant diversity and capturing the full complexity of diversity. Recognising that species richness and species composition are interlinked dimensions of diversity (Latimer, 2014; Roswell *et al.*,2021), this study integrates both metrics to capture the full complexity of plant diversity across the aridity gradient. Specifically, we assess not only how many species are present, but also their composition to better capture the community structure.

The distribution of plant diversity is shaped by multiple environmental factors, which influence their distribution across space (Phil-Eze, 2012). These factors are critical for understanding diversity patterns at local and regional scales. Plant diversity changes along environmental gradients such as aridity and salinity, which is interpreted as a result of habitat filtering, which eliminates species that lack physiological tolerance and competitive capacity from the species pool (Keddy, 1992; Zobel, 1997, cited by Dwyer & Laughlin, 2017). In Namibia, factors like climate, topography, geology, and human activities influence biodiversity patterns (MEFT, 2014). Topographic features such as elevation, slope aspect, and position significantly influence vegetation distribution by modifying local microclimates, particularly in mountainous ecosystems (Yang *et al.*, 2020; Wani *et al.*, 2023). By evaluating the drivers of plant communities on inselbergs, we will be able to understand their distribution patterns. In this study, we examine how species richness and species composition on inselbergs are shaped by different environmental factors, such as geology, topographical positions, slope aspects, and aridity index (precipitation).

2.3.1 Geology

The study of the relationship between floristic composition and different rock types has intrigued naturalists since at least the 16th century (Mota *et al.*, 2008, cited by Cantero *et al.*, 2021). However, it was only until the 19th century that Unger (1836) presented perhaps the first scientific survey that established the relationship between geology and plants (Kruckerberg, 1984, cited by Cantero *et al.*, 2021). Geology is recognised as an important determinant of species composition (Ertsgaard *et al.*, 2025). Different geological types create unique microenvironments that support distinct plant communities on each outcrop (Clegg *et al.*, 2025).

As inselbergs vary in lithologies (Migon, 2022), they consequently weather at different rates (Clegg *et al.*, 2025). These variations generate different surface heterogeneity and microhabitats with different soil depths that influence species communities (Anderson *et al.*, 1999). The

influence of geological types can be split into two basic areas: the direct influence of the rock type and, indirectly, via its role in soil formation by influencing the geochemical composition of the soil (Cottle, 2004), as well as water retention and runoff, some of the key factors in shaping species composition (Vanegas *et al.*, 2006). Geological variation among inselbergs plays an important role in shaping plant and animal communities (Cottle, 2004), but it is not an ultimate shaper of the community. The local variations on inselbergs, such as a variety of microhabitats, crevices, and soil pockets, may be more important determinants of plant communities than the variations in rock chemistry alone (Cottle, 2004). Inselbergs differ in rock type composition, and this can promote the growth of diverse plant communities that can establish themselves in that specific soil composition present on the inselberg (Glime & Da Silva, 2019).

In the central Namib Desert, granite, schist, marble, and gneiss are the most common lithologies (Selby, 1981). Moreover, the central Namib Desert holds a wide range of granite landforms, including domes, boulders, and pediments (Migon & Goudie, 2003). Granite outcrops have been shown to support high species richness and endemism in regions such as southeastern Brazil, Madagascar, and southwestern Australia (Porembski, 2007), making them recognised as biodiversity hotspots globally (Glime & Da Silva, 2019). However, floristic studies of arid inselbergs often reveal lower species richness and endemism (Hopper *et al.*, 2020). Given the climatic conditions, arid inselbergs may serve as local, rather than global biodiversity hotspots.

Marble outcrops are associated with high carbonate solubility, which creates diverse microhabitats such as soil pockets, caves, and gullies (Goudie, 2004, cited by Azevedo *et al.*, 2024; Jiang *et al.*, 2020). The high concentration of carbonate/bicarbonate ions produces high pH, which may be essential in the absorption of nutrients (Tyler, 1992, cited by Cantero *et al.*, 2021), which can restrict or promote plant growth. Faster chemical weathering in limestone leads to the formation of soil pockets that allow the development of deeper soils that can retain more moisture (Estrada-Medina *et al.*, 2012, cited by Clegg *et al.*, 2025).

Schist is characterised by pronounced foliation, comprising platy minerals such as mica, chlorite, or talc, which allows it to split into thin sheets (Burbank & James, 2024). Weathering of schist often produces anisotropic microfractures and cleavage planes, which can facilitate infiltration of water into the rock more readily along these planes than across them (Park *et al.*, 2024). Soils formed on schist are often shallow and poorly developed, with coarse texture and limited horizonation (Allen *et al.*, 2002). The interplay of rock structure, microtopography, and soil depth heterogeneity makes schist a potentially influential substrate in shaping species composition.

This study aims to compare species composition and species richness associated with different lithologies in the central Namib Desert.

2.3.2 Topography

Topographic features such as elevation, slope aspect, and position significantly influence vegetation distribution by modifying local microclimates, particularly in mountainous ecosystems (Yang *et al.*, 2020; Wami *et al.*, 2023). Topography creates different physical and environmental conditions over elevational ranges, resulting in different microhabitats (Moeslund *et al.*, 2013). Consequently, species with specific adaptation traits establish in those microhabitats, so the more microhabitats present, the more species will be present (Hortal *et al.*, 2009). Although topography is recognised as an important driver of vascular plant diversity at the local scale, the impact of topography is poorly understood at a finer spatial scale where the elevation does not fluctuate enough to cause temperature variation (Moeslund *et al.*, 2013). In this study, the topographical variables included were topographical positions (strata as a proxy) and aspect (the direction of the belt transect (northeast and southwest)).

Latitudinal and elevational gradients in diversity are widespread patterns across taxa and geographical regions (Chakravarty *et al.*, 2023). Elevation or altitudinal gradients influence the distribution of hydrothermal resources (Xu *et al.*, 2021), indirectly affecting the species composition, richness, and distribution (Di Musciano *et al.*, 2024; Xu *et al.*, 2021).

Slope aspect is a key environmental factor influencing vegetation patterns in arid areas (Yang *et al.*, 2020). Generally, aspect influences mountainous environments by regulating insolation (Yangan *et al.*, 2017). Unique, localised microclimates are created by solar radiation exposure received on different aspects (Holland & Steyn 1975, cited by Måren *et al.*, 2015). According to Cantlon (1953), north-facing slopes can differ significantly from adjacent south-facing slopes in terms of soil and air temperature, atmospheric moisture, light intensity, and wind speed. These variations influence plant community composition, species diversity and distribution, and nutrient dynamics (Qin *et al.*, 2019; Yanyan *et al.*, 2017), often resulting in distinct vegetation types on contrasting slopes. Understanding these relationships provides crucial insights into the mechanisms structuring plant communities, particularly within heterogeneous systems such as inselbergs.

2.2.3 Aridity Index

Aridity gradients are significant for understanding how species diversity responds to water availability (Sánchez-Bermejo *et al.*, 2022), which is crucial for sustaining life. Natural ecosystems

in arid and semi-arid regions rely heavily on water availability, making them highly vulnerable to changes in precipitation and potential evapotranspiration (Mirzabaev *et al.*, 2022). In Namibia, aridity is primarily influenced by two factors: limited rainfall and high rates of evapotranspiration (Mendelsohn *et al.*, 2022). Moreover, water availability in the Namib Desert is already a critical issue and has long been acknowledged as a key constraint on biological processes (Scola *et al.*, 2017). Furthermore, climate change is predicted to decrease precipitation and increase precipitation variability events across arid and semi-arid regions (Mirzabaev *et al.*, 2022). Consequently, the predicted effects of global climate change will have profound effects on the structure of plant diversity (Huang *et al.*, 2015).

Aridity serves as a primary filter in drylands (Berdugo *et al.*, 2001). As aridity increases, typically along a gradient from high to low precipitation, ecosystems shift in species composition, structure, and functioning (Mirzabaev *et al.*, 2022). Numerous studies have established a negative correlation between species richness and aridity, with richness declining as aridity intensifies. Hopper *et al.* (2020) demonstrated a decline in species richness and local endemism as aridity increased, reaching a stage where there was minimal distinction in species composition between the northern Kimberley and northwestern Pilbara outcrops and their surrounding landscape. Similarly, the same trend of a decrease in species numbers from coastal rock outcrops toward the arid interior was observed in a few case studies (Hopper *et al.*, 1997, cited by Hopper *et al.*, 2020).

In the Namib Desert, the aridity gradient follows an east-to-west transect, primarily reflected by precipitation patterns and fog inputs from the Atlantic Ocean (Scola *et al.*, 2017). Coastal fog, generated by the Benguela Current, can penetrate up to 60 km inland: however, the intensity and frequency decline with increasing distance from the coast (Eckard *et al.*, 2013). This has led to a well-defined gradient of xeric stress across the Namib Desert (Scola *et al.*, 2017). This provides an excellent basis to evaluate the relationships between species composition and richness on inselbergs along an aridity gradient at a regional scale.

2.4 Methodological issues

Inselbergs have attracted strong interest from scientists; however, only since the 1980s have botanical and ecological inselberg studies emerged (Kruge & Büdel, 2009). In recent years, studies of inselbergs have rapidly increased. However, the studies were mainly restricted to individual countries, biomes, or single disciplines, limiting their generality (Clegg *et al.*, 2025). Designing standardised vegetation monitoring protocols remains a key challenge, largely due to the uneven distribution of plant species across landscapes (Stohlgren, 2006). This is more challenging for larger and heterogeneous landscapes because of high spatial and temporal

heterogeneity, which occurs at multiple spatial scales (Stohlgren, 2006). For inselbergs, comparative studies face an additional methodological hurdle: the lack of standardised or repeatable sampling methods. This limits direct comparison, and should therefore be interpreted with caution, even when similar metrics are used. Moreover, methods have not been consistently applied across inselberg studies. This may be attributed to the difficulty of establishing replicable sampling units across diverse topographies, habitat heterogeneity, and regionally variable climatic conditions (Caiafa & Silva, 2007, cited by Couto *et al.*, 2021). The inconsistency in methods across inselberg studies is primarily driven by geographical and climate variability in regional precipitation between study areas. The distinct microhabitats and spatial variability in plant communities on inselbergs may require a more flexible and adaptive sampling approach to accurately capture plant diversity. On central Namib Desert inselbergs, plants are very sparse and sometimes localised in specific microhabitats. Employing a random sampling method will underestimate the diversity on inselbergs as the quadrats may fall on bare, barren surfaces. The sampling method in this study is explained in detail in Chapter 3.

2.5 Chapter summary

This chapter reviewed literature relevant to the study, beginning with an introduction to inselbergs as isolated rocky outcrops that rise from otherwise homogeneous landscapes. Inselbergs are often considered terrestrial islands due to their ecological isolation and distinct size, making them suitable systems for testing the principles of island biogeography. To understand the species distribution patterns, it is important to understand the environmental variables that may influence plant diversity on inselbergs. For instance, topographical features are well known to influence local microclimates on inselbergs that may in turn influence plant communities. Similarly, geology influences the edaphic conditions on inselbergs, consequently shaping plant communities. The aridity index may influence plant communities by filtering out species that lack the physiological strategies to persist under dry conditions.

This chapter also discussed how habitat heterogeneity and climatic variability contribute to differences in species richness and composition. Finally, it highlighted methodological challenges in vegetation studies on inselbergs, particularly the lack of standardised sampling protocols due to spatial heterogeneity and climatic variability. The next chapter presents the methodology employed in this study.

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CHAPTER 3 METHODOLOGY

3.1 Introduction

This chapter outlines the methodological approach used to assess plant diversity, species richness, and species composition on inselbergs along the aridity gradient in the central Namib Desert. It provides a detailed description of the study area, research design, sampling approach, criteria used in the selection of inselbergs, data collection techniques, statistical analyses, and the software used for data analysis. Each component is discussed in detail to illustrate how the research objectives were addressed. Additionally, the chapter considers the ethical aspects of the study, along with methodological assumptions and limitations.

3.2 Study area

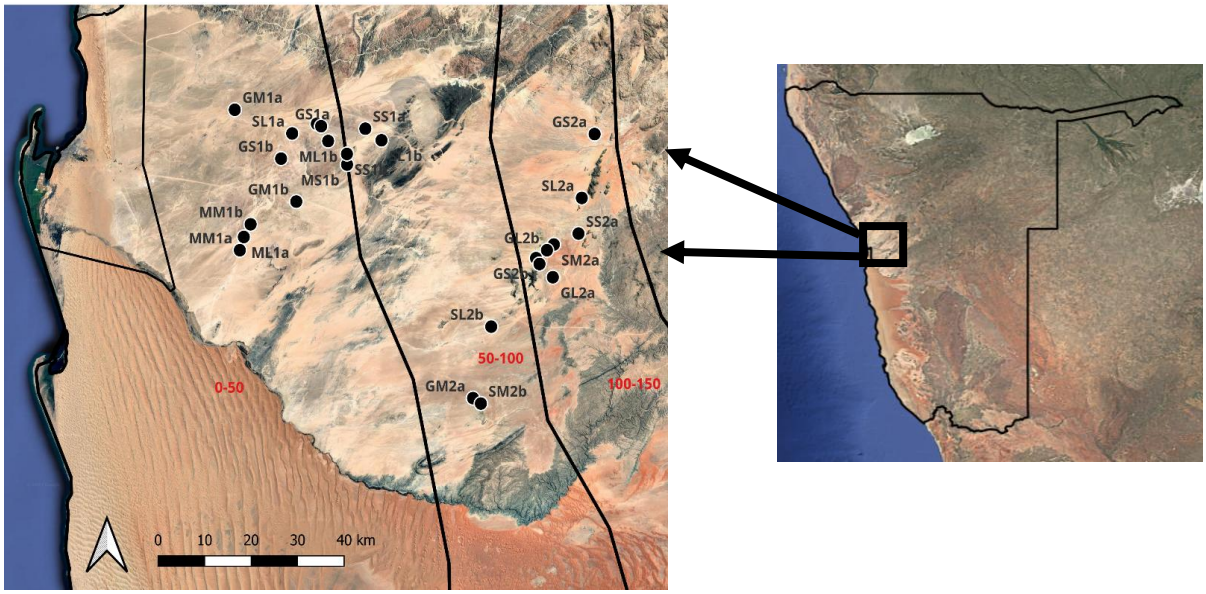


Figure 3. 1. Map of the study sites in the central Namib region of the Namib Desert with an insert map indicating their position in Namibia. The red text indicates the annual average rainfall.

3.2.1 Namib Desert

The study was conducted in the central Namib region of the Namib Desert (Figure 3.1). The Namib is a hyper-arid desert located along the Atlantic coast of southern Africa (Goudie & Viles, 2013). Its extreme aridity results from several interacting climatic factors, including the South Atlantic anticyclone, the cold Benguela Current, and the dry descending air associated with the Global Hadley Circulation (Eckardt *et al.*, 2013; Van Zinderen, 1975).

A defining feature of the Namib Desert is characterised by its east-to-west precipitation gradient (Goudie & Eckardt, 1999; Scola *et al.*, 2017). Rainfall is both spatially and temporally highly variable, typically low in intensity, and highly localised (Eckardt *et al.*, 2013; Lancaster *et al.*, 1984). Annual rainfall increases progressively from the coast towards inland areas with the mean annual rainfall ranging from 15 mm to 90 mm for western and eastern desert margins respectively (Viles & Goudie, 2013).

In addition to limited rainfall, the coastal zone frequently experiences fog due to the influence of the cold Benguela Current (Li *et al.*, 2016; Viles & Goudie, 2013). Fog can extend up to 60 km inland (Lancaster *et al.*, 1984), although its intensity and frequency decrease with increasing distance from the coast to the inland (Eckard *et al.*, 2013; Lancaster *et al.*, 1984). The spatial variation in the amount and frequency of rainfall and fog has produced a distinct gradient of xeric stress across the Namib Desert (Scola *et al.*, 2017).

3.2.2 Central Namib Desert

The central Namib is one of the driest parts of the Namib desert (Lancaster *et al.*, 1984), extending approximately 140 km inland from the coast. It is situated on the southwestern edge of the summer rainfall zone (Lancaster *et al.*, 1984), with most precipitation occurring from January to March (Schulze, 1969). However, rain may occur in any month and may be entirely absent in some years (Viles & Goudie, 2013). The vegetation in the central Namib Desert is sparsely distributed (Jürgens *et al*., 2013). However, the unique climate has contributed to a high level of endemism in the Namib Desert (Scola *et al.*, 2017). The central Namib hosts to approximately 806 taxa, of which 13% are endemic, and 3.3% are nearly endemic to Namibia. Two percent of the taxa found is endemic to central Namib plains; which most are perennial species (Jürgens *et al*., 2013).

Despite the notable level of endemism, species typically occur in low population densities compared to more humid biomes, limiting both their resistance and resilience to environmental change and disturbance (McNeely, 2003). Consequently, desert ecosystems, such as the central Namib, may be particularly vulnerable to disturbances associated with global climate change such as increased frequency and intensity of droughts, and warmer temperatures (Mirzabaev *et al*., 2022). Species of arid regions are not uniformly distributed; rather, they tend to concentrate in favourable microhabitats such as ephemeral rivers, dunes, washes, and outcrops.

Among these microhabitats, outcrops play a particularly important role in shaping biodiversity patterns by providing unique and relatively stable ecological niches (Glime & Da Silva, 2019). In the central Namib, numerous outcrops of the Precambrian Damara Orogenic System occur and are composed primarily of marble, granite, schist, gneiss and quartzite (Goudie & Eckardt, 1999;

Logan, 1961; Selby, 1982). The three dominant lithologies of the central Namib inselbergs (granite, schist, and marble) differ markedly in their geochemical composition and nutrient availability, which influence soil development and plant establishment. Granite, an acidic igneous rock composed largely of quartz and feldspar, weathers into coarse-textured, nutrient-poor soils that favour oligotrophic plant species. In contrast, marble, a metamorphic derivative of limestone, is rich in calcium and magnesium carbonates, producing alkaline soils with high base saturation that support calcicolous vegetation. Schist, formed through metamorphism of shale or mudstone, contains micas and feldspars that contribute to moderate nutrient levels and intermediate soil fertility. These substrates possess distinct physical and chemical properties, creating a variety of microenvironments capable of supporting diverse plant communities (Bojorquez-Quintal *et al.*, 2017, cited by Clegg *et al.*, 2025).

This combination of prolonged aridity, geological heterogeneity, and a strong west-east climatic gradient makes the central Namib Desert an ideal natural laboratory for studying plant diversity on inselbergs across an aridity gradient. The region has remained arid for much of the past 130 million years (Goudie & Eckardt, 1999, cited by Viles & Goudie, 2013) and features a variety of outcrops occurring along a west-east transect defined by a pronounced climatic gradient (Migon & Goudie, 2003).

3.3 Research design

Dannels (2018) defines research design as a structured plan that integrates all elements of a study to ensure credible, unbiased, repeatable, and widely applicable results. It functions as the framework that guides the research process and ensures alignment between the study's objectives, methods, and outcomes (Leavy, 2017). As Trochim (2006) aptly explains, “research design provides the glue that holds the research project together.”

There are various research design approaches, including quantitative, qualitative, mixed methods, and arts-based, each with distinct characteristics and applications (Leavy, 2017). While these approaches may sometimes overlap, they differ in underlying assumptions, data collection strategies, and modes of analysis (Dulock, 1993). The choice of research design depends on the research questions, objectives, and the nature of the data required.

This study's research design was selected to provide a coherent framework for assessing plant diversity on inselbergs across an aridity gradient in the central Namib Desert. The following section outlines the specific research approach adopted to meet the study’s objectives.

3.3.1 Quantitative approach

This study adopted a quantitative process, incorporating both descriptive and correlation research approaches. Quantitative research design deals with the numerical measurement of variables and the statistical testing of relationships between variables to identify patterns, correlations, or casual links (Leavy, 2017). It is typically used when objective, factual data are required to answer specific research questions and is considered free from personal opinions or subjective interpretations (Hammarberg *et al.*, 2016). Moreover, quantitative research enables formulation and testing hypotheses through statistical analyses (Lee & McKinney, 2013; Schilderman, 2011).

Quantitative research is typically categorised into four groups: descriptive, correlation, quasi-experimental and experimental (Dulock, 1993). This study followed a descriptive design to document and compile inventory of plant diversity along the aridity gradient, and to compare species richness and composition between inselbergs and their surrounding matrix habitats. Descriptive analysis was also used to explore variation in species richness and composition in relation to topographic position, aspect, and geological substrate of inselbergs.

In addition, a correlation approach was incorporated to identify and quantify the relationships between species richness and composition, and environmental variables such as inselberg size, spatial isolation and position along the aridity gradient.

3.4 Sampling

Sampling is the process of systematically selecting a subset from a defined population to serve as a data source for observational or experimental research, as per study objectives (Sharma, 2017). Ideally data would be collected from the entire population to ensure reliable, valid, and accurate results; this is rarely possible in practice due to logistical constraints. Consequently, sampling techniques to select representative subsets, offering a more practical solution in terms of cost, time, and convenience are advocated (Taherdoost, 2016). A well-selected sample allows for meaningful conclusions to be drawn about the broader population (Rai & Thapa, 2015).

This study used a combination of purposive and stratified sampling techniques. Purposive sampling involves the deliberate selection of sampling units based on specific, pre-defined characteristics relevant to the research objectives (Campell *et al.*, 2022). In this study, purposive sampling was used to select inselbergs based on geological type (granite, schist, and marble), size (ranging from 0.5 ha-250 ha), and accessibility.

On the other hand, stratified sampling involves dividing the population into homogeneous subgroups or strata, based on shared characteristics, and then independently sampling from each

stratum (Singh & Mangat, 1996; Sharma, 2017). This technique is particularly useful when dealing with a heterogeneous population, as it ensures that each subgroup is adequately represented (Singh & Masuku, 2014).

Stratified sampling was applied to individual inselbergs. Sampling was then conducted in each stratum to account for the heterogeneity and complex nature of inselbergs (Kluge & Büdel, 2009). To ensure comparability among inselbergs of different sizes, the sampling effort was standardised across sites. Each inselberg was sampled using an identical number of plots per topographic stratum: matrix, footslope, midslope, crest. Plot dimensions were kept constant throughout the study and consequently, the total sampled area per inselberg was equal irrespective of overall inselberg size.

This standardisation ensured that observed differences in species richness among inselbergs reflect ecological patterns rather than variation in sampling intensity. Species–area relationships were therefore interpreted in the context of fixed sampling effort, reducing the likelihood that larger inselbergs exhibited higher richness simply due to greater survey coverage.

3.4.1 Identification of geology

The geological types of inselbergs were initially identified by extracting coordinates from Google Earth Pro and manually cross-referencing them with the 1: 250 000 Geological map of Namibia (Geological Survey of Namibia, 1995). Geological information was verified through comparison between the printed geological map and the digital map of the EDN Geological and Mineral Information System Namibia (Geological Survey of Namibia and Beak Consultants, 2024). This was also accompanied by geological hand samples collected from each inselberg during fieldwork to confirm the lithology.

3.4.2 Accessibility

Inselbergs were selected based on accessibility, with preference given to those located near roads or accessed through mining tracks. This was done to minimise off-road driving and minimise damage to the environment, as the study was conducted in a national park. Accessibility considerations were also aligned with the broader aim of supporting biodiversity conservation by reducing anthropogenic impacts during sampling.

3.4.3 Size allocation and sample size

Inselbergs were categorised for selection based on their sizes. Inselberg size was based on surface area, as measured using polygon tools in Google Earth Pro. The following sizes classes were applied: small, ranging from 0.5 to 20 ha; medium, ranging from 21 to 40 ha; and large, 41

to 254.92 ha. Inselbergs smaller than 0.5 ha were excluded from the study due to their limited spatial extent, which was considered insufficient for reliable sampling.

Table 3. 1. The total number of inselbergs of varying sizes sampled on different geological types in coastal (30-70 km) and inland (71-123 km) zones. Marble inselbergs occurred only in the coastal zone and were therefore not represented in the inland zone.

Size	Coastal			Inland		Total
	Marble	Granite	Schist	Granite	Schist	
Small	2	2	2	2	2	10
Medium	2	2	0	1	2	7
Large	2	0	2	2	2	8
Total	6	4	4	5	6	

A total of 25 inselbergs (Table 3.1) were sampled across three geological types: marble, schist, and granite, and within two distance zones (coastal and inland). For the inland zone, 12 inselbergs were initially selected; however, only 11 were sampled in the Namib-Naukluft National Park, due to access limitations. Moreover, marble inselbergs were not available, hence only two geologies were sampled in the inland zone. In the coastal zone, in the Namib-Naukluft and Dorob National Parks, all 14 selected inselbergs were successfully sampled.

3.4.4 Vegetation of the central Namib Desert

The western part of the central Namib Desert is dominated by halophytic dwarf shrubs, *Arthraerua leubnitziae, Tetraena stapffii*, and *Calicorema capitata*, particularly (Jürgens et al., 2013; Jürgens et al., 1997). *Arthraerua leubnitziae* is commonly associated with saline habitats across a range of topographical positions in the western zone, while further inland it is largely restricted to drainage channels. *Tetraena stapffii* has a broader habitat spectrum than *A. leubnitziae*, occurring not only in saline flats but also on rocky outcrops (Robinson, 1976, cited in Jürgens et al., 1997). These species are generally accompanied by *Salsola tuberculata* throughout their distribution ranges.

With increasing distance inland, and corresponding increases in rainfall, woody species such as *Vachellia erioloba*, *Boscia* spp., *Commiphora* spp., and *Combretum* spp. become more prominent, particularly along drainage lines and on rocky outcrops, reflecting more reliable moisture availability (Jürgens et al., 2013).

3.5 Data collection

Vegetation data was collected over a period of approximately three weeks (16 days) between July and September 2024. Sampling time ranged from two to five hours per inselberg depending on its size, with smaller inselbergs requiring less time than larger ones.

3.5.1 Vegetation sampling

An uninterrupted belt transect was laid out at each inselberg, extending from matrix to matrix and across the highest peak of the inselberg along a northeast-southwest (NE-SW) orientation. The matrix was sampled atleast 100m from inselberg footslope to reduce the stepping stone effect. Each inselberg was stratified in which quadrats wereplaced as follows: two matrix, two footslope, two midslope, and one crest, resulting in seven quadrats per inselberg. A 400 m^2 quadrat was placed in each stratum. The shape of each quadrat (rectangular or square) was adjusted based on the vegetation cover and geomorphology. Within each quadrant, all vascular plants were identified to species level, and counted, and all life forms were recorded.

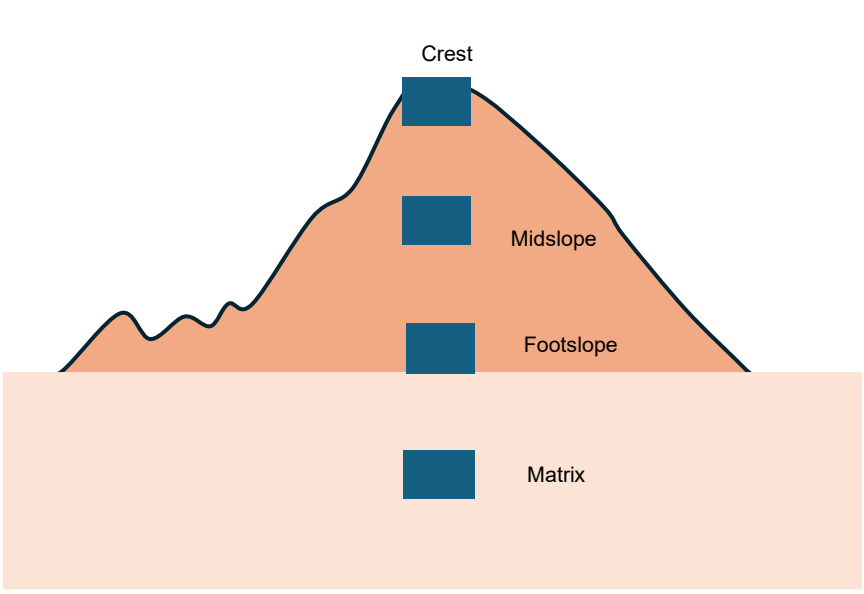




Figure 3. 2. Plot measurement of a 400 m^2 quadrat in each stratum for vegetation sampling.

3.5.2 Climatic data

3.5.2.1 Precipitation

Precipitation data for each inselberg was downloaded from the WorldClim 2.0 database, covering a five-year period from 2020 to 2024, at a spatial resolution of 2.5 arcminutes. These datasets

are downscaled from CRU-TS-4.09 by the Climatic Research Unit, University of East Anglia, and corrected for bias using WorldClim 2.1. Precipitation values were extracted using QGIS 3.40.3, as WorldClim 2.0 provides data in raster format only.

3.5.2.2 Aridity Index

The aridity index (AI) is defined as the ratio of mean annual precipitation to mean annual potential evapotranspiration (Greve *et al.*, 2019). Aridity index data were obtained from the Global Aridity Index (Global-Aridity_ET0) and Global Reference Evapo-Transpiration (Global-ET0) database, which provide high-resolution (30 arc-seconds) global raster climate data for the 1970–2000 period (Trabucco & Zomer, 2018). These datasets are based on the Penman–Monteith reference evapotranspiration (ET_0) equation and represent rainfall deficits relevant to potential vegetative growth.

The aridity index was extracted using QGIS 3.40.3, and the values were multiplied by 0.0001 to retrieve the correct units, as the geodatasets are distributed as integers multiplied by 10,000 to retain four-decimal accuracy (Trabucco & Zomer, 2018).

3.5.3 Species identification

Species were identified using various plant identification guides such as the *Wildflowers of the Central Highlands of Namibia* (Mannheimer, 2012), *Wildflowers of the Southern Namib* (Mannheimer *et al.*, 2002), *Field Guide to Trees and Shrubs of Namibia* (Muller & Le Roux, 2008), and the online platform *iNaturalist*. Information on endemicity and IUCN Red List status was obtained from the *Checklist of the Namibian Indigenous and Naturalised Plants* (Klaassen and Kwembeya, 2013) and the online *Namibia Biodiversity Database*.

3.5.4 Herbarium specimens

Voucher specimens were collected during fieldwork; each assigned a unique collection number and photo number for reference. Specimens were processed according to the standard techniques for vascular plants and will be deposited in the National Herbarium of Namibia (WIND), with duplicates deposited in the Gobabeb Herbarium (GBB) at the Gobabeb - Namib Research Institute.

3.6 Data analysis

Vegetation data from 25 inselbergs, comprising 175 sample plots, were analysed to assess the influence of topographical position, rock type, slope aspect, inselberg size, precipitation/aridity index, and spatial isolation on species richness, complimentary diversity indices (Shannon

diversity index, Margalef's richness, Simpson's diversity index, and species evenness), and composition. Both descriptive (e.g. box and whisker plots, NMDS scatter plots) and inferential statistical methods (e.g. one-way ANOVA, Kruskal Wallis tests) were used, with a significance level of α = 0.05.

3.6.1 Data preparation

Prior to analysis, the dataset was checked for missing values. A species accumulation curve was compiled in PRIMER 6 (Clarke & Gorley, 2006) to assess sampling sufficiency.

For multivariate analysis (Anderson, 2024), species abundance data were fourth root transformed to reduce the influence of dominant species. Diversity indices (species richness, abundance, and complementary diversity indices—Shannon diversity index, Margalef's richness, Simpson's diversity index, and species evenness) were calculated in PRIMER 6.

Species richness – The total number of species in a community.

Pielou's species evenness (Pielou, 1975) measures how evenly individual species are distributed among species. This determines whether the values from species richness, Margalef's richness index, represent a stable, well-distributed community, or a community dominated by a few abundant species with many rare ones.

$$\mathrm{E} = \frac{\mathrm{H}'}{\ln(\mathrm{S})}$$

Simpson's index (Simpson, 1949) is a measure of dominance. It indicates the dominance of species in a habitat. This is the probability that two randomly chosen individuals belong to the same species (Pielou, 1975).

$$D = \sum_{i=1}^{S} pi2$$

Shannon index (Shannon, 1948) is a measure of diversity. It incorporates both species richness and species evenness and provides insight into how equitably individuals are distributed among species (Peet,1974).

$$H' = -\sum_{i=1}^{S} pi * \ln pi$$

Margalef's index (Clifford & Stephenson, 1975, cited by Maurer & McGill, 2011) is a measure of richness. It incorporates both the number of species and the total number of individuals observed, while accounting for the sample size.

$$Dmg = \frac{S-1}{\ln(\mathrm{N})}$$

Total individuals show the total number of individual species in a habitat

$$N = \sum_{i=1}^{S} n\mathrm{i}$$

Where: **S** = number of species (species richness), **N** total number of individuals, ***ni*** = number of individuals of species *i*, ***pi*** = proportion (relative abundance) of species *i*, and **ln** is the natural logarithm.

Normality of data was tested using the Shapiro–Wilk test in Statistica. Where data was not normally distributed ($p < 0.05$), values were log(x+1) transformed in PRIMER 6 and retested for normality. Depending on the distribution, either parametric test (one-way ANOVA) was used for normal distributions and non-parametric tests (Kruskal Wallis) were data was not normally distributed.

3.6.2 Comparing species richness across factors

A stepwise approach was followed to evaluate differences in diversity indices across inselbergs vs. matrix habitats, topographical positions, slope aspects, and geological types.

One-way ANOVA was used for Shannon diversity index, total number of individuals and Margalef's richness. Where ANOVA results were significant ($p < 0.05$), Tukey's HSD post hoc tests were conducted to identify which groups differed significantly.

Kruskal–Wallis ANOVA by ranks was used for Simpson's index, evenness and species richness when data were non-normally distributed. If significant ($p < 0.05$), post-hoc multiple comparisons (2-tailed) were used to identify significant differences between topographical positions and geological types. All analysis were performed in Statistica version 14.0.1.25.

3.6.3 Comparing species composition across factors

Species composition was analysed using non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity to visualise differences across inselbergs and matrix, topographical positions, slope aspects, and geological types. To test the significance of group differences, PERMANOVA was used, with pairwise PERMANOVA applied when results were significant ($p < 0.05$), particularly for topographical positions and geological types.

One–way ANOSIM (Analysis of Similarity) was used to test for statistically significant differences in species composition among groups. Similarity percentages (SIMPER) analysis was conducted

to identify species contributing most to observed dissimilarities. Indicator species analysis (IndVal%) with Bonferroni-corrected p-values was used to identify species significantly associated with specific conditions (e.g. inselbergs, matrixes, geological types, and slope aspects).

These analyses were conducted using PRIMER 6, PERMANOVA+, and PAST.

3.6.4 Relationship between diversity indices and environmental variables

To evaluate the relationship between diversity indices and environmental variables (inselberg size, spatial isolation, and precipitation), Pearson correlation coefficients (r) were calculated for normally distributed indices (e.g., Margalef's richness, Shannon diversity index, total individuals). Spearman's rank correlation was used for non-normally distributed indices, such as species richness, evenness, and Simpson's diversity index. These tests were performed using IBM SPSS Statistics.

3.6.5 Relationship between species composition and environmental variables

To determine the relationship between species composition and environmental variables (inselberg size, spatial isolation, and precipitation), Canonical Correspondence Analysis (CCA) was used. A gradient length of 6.0 SD, calculated via Detrended Correspondence Analysis (DCA), indicated that a unimodal method would be appropriate, justifying the use of CCA (Canoco 5).

One geological type, marble, was restricted to the coastal zone and did not occur across the whole precipitation gradient. To disentangle the relative influence of geology and precipitation on community composition, partial canonical correspondence analysis (pCCA) was performed. In this approach, precipitation was treated as a covariate while testing geological effects, and conversely geology was conditioned upon when testing precipitation effects. This allowed partitioning of explained variance into (i) pure geological effects, (ii) pure climatic effects, and (iii) shared explained variation attributable to their covariance. This procedure enabled a more conservative interpretation of substrate effects, reducing the risk of attributing climatically structured variation solely to lithological differences.

3.6.6 Data analysis software

All data were entered and pre-processed in Microsoft Excel and analysed using Statistica (for diversity index testing and significance analyses), PRIMER (for multivariate analyses, diversity indices, NMDS, PERMANOVA), PAST (for SIMPER, one-way ANOSIM and indicator species analysis), IBM SPSS Statistics (for correlation analyses), and Canoco 5 (for Canonical Correspondence Analysis (CCA)).

3.7 Ethical considerations

This study was conducted in collaboration with Namib specialists based at the Gobabeb - Namib Research Institute (Gobabeb). The Unit for Environmental Sciences and Management (UESM) at North-West University has a formal Memorandum of Understanding with Gobabeb to collaborate and conduct research.

All necessary research and sampling permits were obtained through Gobabeb, in accordance with Namibian environmental regulations and park authority guidelines. Park entry permissions for working within the Namib-Naukluft and Dorob National Parks were obtained from the Ministry of Environment, Forestry and Tourism. Gobabeb is a registered Namibian-based research institution with the National Commission on Research, Science and Technology - NCRST (# RCIV00062018). This research was conducted under NCRST Research Authorisation for the Namib Green Genome Project (# 202201119), granted in terms of Section 21 of the Research, Science and Technology Act No. 23 of 2004.

Ethical approval for this research was granted by the Faculty of Natural and Agricultural Sciences Ethics Committee (FNASREC) at North-West University. The project was approved under the ethics number NWU-01350-24-A9.

3.8 Methodological assumptions and limitations

The overlap between Namib-Naukluft National Park borders and adjacent private farms was not clear from satellite imagery (Google Earth Pro). Hence, some inselbergs were located on private-owned farms.

One assumption during project planning was that inselbergs representing all size classes and geological categories would be available for sampling across the aridity gradient. While schist and granite occurred throughout the study area, marbles were exclusively found in the coastal zone, and this assumption could not be fully met for the overall study design. This led to an uneven representation of geological types across the aridity gradient.

A third study zone was originally identified and delineated (referred to as the central zone). However, due to its limited variation of geological types and inselberg sizes, and its proximity to the inland zone, it was subsequently merged with the inland zone to maintain consistency and avoid redundancy in sampling.

Certain variables, such as height, stem circumference and crown diameter of woody species taller than 1 m, were excluded from data collection. This decision was made due to practical field

constraints, as many of these taller species formed dense thickets with multiple stems at the base, making accurate and consistent measurements difficult to obtain in the field.

Despite these constraints, care was taken to ensure that the resulting dataset remained representative and sufficient to address the study's core research questions.

3.9 Chapter Summary

This chapter outlined the methodology used to assess plant diversity on inselbergs across an aridity gradient in the central Namib Desert. A quantitative research design was adopted, combining descriptive and correlational approaches. Twenty-five inselbergs, representing three geological types (granite, schist, marble) in two aridity zones (inland and coastal) (Table 3.2), were selected using purposive and stratified sampling. Vegetation data were collected using uninterrupted belt transects, with seven 400 m² quadrats placed across five topographic strata per inselberg. Climatic data were sourced from WorldClim 2.0, and plant species were identified using field guides and expert consultation. Diversity indices and species composition were analysed using PRIMER, Statistica, SPSS, and Canoco 5, employing ANOVA, NMDS, PERMANOVA, and CCA, among others (Table 3.3). Ethical clearance was obtained, and permits were secured through Gobabeb Namib Research Institute. Limitations included restricted access to some inselbergs, uneven geological representation across zones, and exclusion of certain woody species measurements due to field constraints.

Table 3. 2. Summary of the total number of inselbergs sampled according to their size, geological type, and distance zone in the central Namib Desert.

Sites	Coordinates		Aridity Index	Precipitation (mm)	Geology	Size	Zone
	Longitude	Latitude					
GS2b	15.48979	-23.1718	0.0445	9.76	Granite	Small	Inland
GL2a	15.52509	-23.2103	0.0484	9.76	Granite	Large	Inland
SL2a	15.58593	-23.0501	0.0543	11.9	Schist	Large	Inland
MM1b	14.8897	-23.1033	0.0134	2.55	Marble	Medium	Coastal
GM1a	14.85641	-22.8719	0.011	2.51	Granite	Medium	Coastal
GM1b	14.98577	-23.0575	0.0171	3.45	Granite	Medium	Coastal
MS1b	15.09244	-22.9826	0.0201	4.31	Marble	Small	Coastal
GS1b	14.9538	-23.9706	0.0151	2.98	Granite	Small	Coastal
SL1a	14.97711	-22.9198	0.0138	3.05	Schist	Large	Coastal
SS1b	15.0922	-22.9612	0.0201	4.34	Schist	Small	Coastal
ML1a	14.87542	-23.1289	0.0178	3.6	Marble	Large	Coastal
MM1a	14.86707	-23.1557	0.0108	2.23	Marble	Medium	Coastal

GM2a	15.35727	-23.4546	0.0263	5.94	Granite	Medium	Inland
SM2b	15.37378	-23.4656	0.028	5.77	Schist	Medium	Inland
GS2a	15.61286	-22.921	0.0574	12.74	Granite	Small	Inland
SS2a	15.57909	-23.1221	0.0499	10.83	Schist	Small	Inland
SM2a	15.52722	-23.1442	0.0489	10.49	Schist	Small	Inland
MS1a	15.02887	-22.9003	0.0151	3.25	Marble	Small	Coastal
SL2b	15.39554	-23.3102	0.0329	6.89	Schist	Large	Inland
GL2b	15.51272	-23.1557	0.05	10.49	Granite	Large	Inland
ML1b	15.05271	-22.9351	0.0151	3.25	Marble	Large	Coastal
GS1a	15.03798	-22.9051	0.0154	3.26	Granite	Small	Coastal
SS1a	15.13092	-22.9101	0.0211	4.67	Schist	Small	Coastal
SL1b	15.1649	-22.9335	0.045	4.7	Schist	Large	Coastal
SS2b	15.49703	-23.1835	0.0543	9.77	Schist	Small	Inland

Table 3. 3. Summary of data analysis methods, variables, and software used.

Objective / Analysis Type	**Variables / Indices**	**Statistical Test / Method**	**Software Used**
Check for data completeness and sufficiency	Presence/absence, species accumulation	Species accumulation curve	PRIMER 6 & PERMANOVA+
Transform abundance data	Species abundances	Fourth-root transformation	PRIMER 6
Calculate diversity indices	Species richness, Shannon index, Simpson's index, evenness, Margalef's richness, total individuals	Index computation	PRIMER 6
Test for normality	Diversity indices	Shapiro–Wilk test	Statistica
Compare diversity across groups	Shannon, Margalef, total individuals (normal); Simpson, evenness, richness (non-normal)	One-way ANOVA; Kruskal–Wallis ANOVA	Statistica

Objective / Analysis Type	Variables / Indices	Statistical Test / Method	Software Used
Post-hoc comparisons	Topographical positions, geological types	Tukey HSD (ANOVA); Multiple comparisons (Kruskal–Wallis)	Statistica
Visualise species composition	Species presence/abundance	NMDS (Bray–Curtis similarity)	PRIMER 6
Test species composition differences	Topography, geology, aspect, habitat	PERMANOVA; Pairwise PERMANOVA	PRIMER 6 & PERMANOVA+
		One-way ANOSIM	PAST
Identify species driving differences	Species contributing to dissimilarity	SIMPER	PAST
Identify indicator species	Species linked to groups (e.g., geology, slope, habitat)	Indicator Species Analysis (IndVal%)	PAST
Test relationship between diversity and environmental variables	Inselberg size, isolation, precipitation; diversity indices	Pearson (parametric); Spearman (non-parametric)	IBM SPSS Statistics
Assess species composition–environment relationship	Species composition; size, isolation, precipitation	Canonical Correspondence Analysis (CCA)	Canoco 5

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CHAPTER 4: SPECIES RICHNESS AND COMPOSITION PATTERNS OF NAMIB INSELBERGS AND MATRICES.

4.1 Introduction

Biodiversity encompasses the variety of life on Earth, including genetic, species, and ecosystem diversity (Secretariat of the Convention on Biological Diversity, 2005). Among these, species diversity represents a fundamental component of biodiversity and remains the most straightforward and effective means of assessing diversity at both community and regional scales (Xu *et al.*, 2021). Importantly, species diversity underpins ecosystem functioning, stability, and resilience to environmental change, and is widely recognised as a primary driver of ecosystem resilience (Staudhammer *et al.*, 2018). However, plant diversity is increasingly threatened by anthropogenic pressures such as habitat loss and fragmentation driven by rapid human population growth, contributing to the ongoing global decline in biodiversity (Ayeko *et al.*, 2023).

Species diversity continues to be a central focus in community ecology (Begon *et al.*, 1996 cited in Pelissier *et al.*, 2002; Krebs, 1994; Ricklefs, 1990). Despite being one of the most frequently measured ecological attributes, its inherently multidimensional nature makes it challenging to quantify (Millennium Ecosystem Assessment, 2005; Roswell *et al.*, 2021). Diversity is often quantified using metrics such as species richness, evenness, and community composition (Staudhammer *et al.*, 2018). Species richness, defined as the total number of species in a given area, remains the most widely applied metric of species diversity (Millennium Ecosystem Assessment, 2005). However, it fails to account for the relative abundance of species or the evenness of their distribution (Gotelli & Chao, 2013). Consequently, species richness alone cannot reveal how similar or different two communities are, as it treats each species as an equal contributor to species diversity regardless of abundance (Latimer, 2014; Wilsey *et al.*, 2005).

By contrast, species composition incorporates not only the number of species present, but also their identities and the relative abundances (Behera *et al.*, 2023). This approach provides a more comprehensive representation of community structure (Kempton, 1979), and can reveal ecological differences between sites that species richness alone may obscure (Wilsey *et al.*, 2005; Latimer, 2014). Integrating measures of richness and composition is therefore crucial for assessing plant diversity and capturing the full complexity of ecological communities.

Arid environments, such as the Namib Desert, cover approximately 35% of the Earth's terrestrial surface (Tchakerian & Pease, 2015). Arid environments are regions or areas that are characterised by water scarcity due to low precipitation and high evapotranspiration, with a maximum precipitation ranging from 100-300 mm annually and aridity index <= 0.03 (Steven, 2017). These ecosystems are characterised by high temperatures, low and erratic precipitation,

and typically support fewer species than mesic biomes (McNeely, 2003). Nevertheless, they harbour numerous rare and endemic species, and provide vital ecosystem services, including foraging resources for wildlife (Timis-Gansac *et al.*, 2025). In the Namib Desert, plant species are not evenly distributed, but tend to concentrate in microhabitats such as ephemeral rivers, dunes, washes, and isolated mountains.

Inselbergs are isolated rock outcrops that rise abruptly from the surrounding plains and represent distinct geomorphological and ecological features (Da Silva & Glime, 2019; Kluge & Büdel, 2009; Porembski *et al.*, 2016; Tindano *et al.*, 2023). They function as independent ecosystems, characterised by unique edaphic and microclimatic conditions that differ markedly from the surrounding matrix (Sander & Bremer, 2000). In arid regions, inselbergs act as comparatively wetter “islands” within otherwise dry landscapes (Da Silva & Glime, 2019). Their microenvironments support diverse and well-developed soil and vegetation assemblages, forming plant communities distinct from those of the adjacent plains (Da Silva & Glime, 2019; Jurgens & Burke, 2000). Consequently, inselbergs are recognised as biodiversity hotspots in Madagascar, Southeastern Brazil and Southwestern Australia (Porembski, 2000), and are rated among the least disturbed ecosystems (Fitzsimons & Michael, 2017; Kluge & Büdel, 2009) owing to their inaccessibility because of their steep slope (Tindano *et al.*, 2023).



Figure 4. 1. Typical inselbergs of the central Namib Desert rising above the adjacent plains. These landforms differ markedly from the surrounding matrix physical structure and surface characteristics from the surrounding matrix.

Inselbergs contribute to the structural diversity of the Namib Desert (Jürgens & Burke, 2000). However, previous studies in Namibia have focused primarily on the arid Nama Karoo and a

limited number of inselbergs in the central Namib Desert, constraining broader generalisations of plant communities in the central Namib Desert (Burke, 2002). The central Namib is an area of considerable ecological and tourism value, yet its biodiversity and landscapes face multiple threats, including mining, off-road driving, and tourism pressures (Wassernaar *et al.*, 2013). Inselbergs are particularly difficult to restore once degraded (Barnard,1998). Despite these pressures, biodiversity data for inselbergs in the region remain sparse (Burke, 2005). This is problematic because biodiversity loss in arid regions can have disproportionate ecological consequences as the loss of a single species may have a far greater impact than in more species-rich ecosystems (McNeely, 2003) and should therefore be given substantial conservation priority. Moreover, empirical studies directly comparing the vegetation of inselbergs with that of the surrounding matrix remain limited (Buschke, 2020).

Biodiversity inventories provide essential biodiversity data for understanding species distributions and community structure at both local and regional levels. Assessing the richness and composition of inselberg vegetation in the central Namib Desert can improve ecological knowledge and inform habitat restoration and conservation planning. Furthermore, because of their heterogeneous habitats with stable microclimate, inselbergs may serve as refugia under climate change, buffering species from surrounding arid plains and preserving regional biodiversity (Burke, 2000b; Cowling *et al.*, 1999).

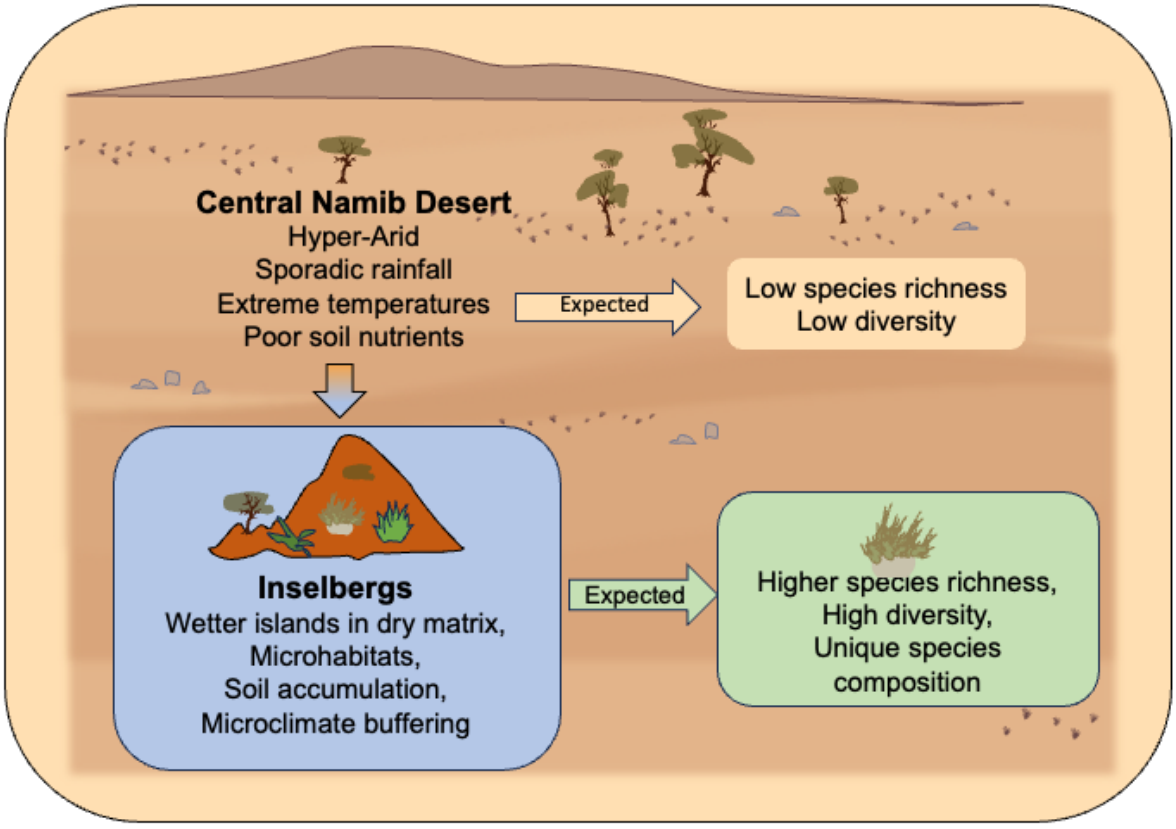


Figure 4. 2. Conceptual framework of concepts, variables, and theories guiding the study design to compare species richness and species composition on inselbergs and the surrounding matrix in the central Namib Desert.

Overall, the chapter aims to conduct an inventory of species richness and composition on inselbergs in the central Namib Desert. Specifically, it addresses how species richness and composition differ between inselbergs and the surrounding matrix. To achieve this, the chapter tests two hypotheses. Firstly, it is proposed that plant species richness and alpha diversity will be significantly higher on inselbergs than in the surrounding matrix. Inselbergs function as habitat islands characterised by enhanced microhabitat heterogeneity, edaphic variability, and moisture retention relative to the surrounding plains. According to habitat heterogeneity theory and inselberg ecology, structurally complex substrates should support greater niche partitioning and thus higher richness. It is, therefore, expected that Shannon diversity, Margalef's richness, and total species counts will be significantly greater on inselbergs than in matrix habitats.

Secondly, it is predicted that species composition will differ significantly between inselbergs and the surrounding matrix. Environmental filtering driven by lithology, soil development, and microclimatic buffering should result in distinct species assemblages. Inselbergs are expected to harbour habitat specialists not prevalent in the matrix. It is expected that NMDS ordination will show discrete clustering of inselberg and matrix plots, and PERMANOVA will detect significant compositional differences.

For data analyses, refer to the Methodology Chapter.

4.2 Results

To compile an inventory of species richness on inselbergs and their surrounding matrix, and to address how species richness differs on inselbergs and the surrounding matrix, several diversity indices were calculated as complementary diversity indices. These included Shannon diversity index (H′), Simpson's diversity index (D), Pielou's evenness (J′), Margalef's richness index (d), and total number of individuals. The alternative hypothesis tested was that species richness would be greater on inselbergs compared to the surrounding matrix.

4.2.1 Species richness on inselbergs and the surrounding matrix

A non-parametric Kruskal-Wallis ANOVA results demonstrated overall significant difference in species richness between inselbergs and the surrounding matrix ($p < 0.001$). Inselbergs exhibited significantly higher species richness, with a mean of six species per plot, compared to three

species in the matrix (Figure 4-3a). Similarly, Margalef's richness index was significantly higher (one-way ANOVA; $p < 0.001$) on inselbergs than in the matrix (Figure 4-3b).

Inselbergs in the central Namib Desert also supported a significantly higher (one-way ANOVA; $p < 0.001$; Figure 4-3c) total number of individuals per plot (mean of 46) compared to the surrounding matrix (mean of nine). Shannon diversity index followed the same pattern, with higher mean diversity on inselbergs (one-way ANOVA; $p < 0.001$; Figure 4-2d) of H′ = 1.24 than in the surrounding matrix (H′ = 0.85). Overall, inselbergs displayed greater species richness and diversity when compared to the surrounding matrix habitats.

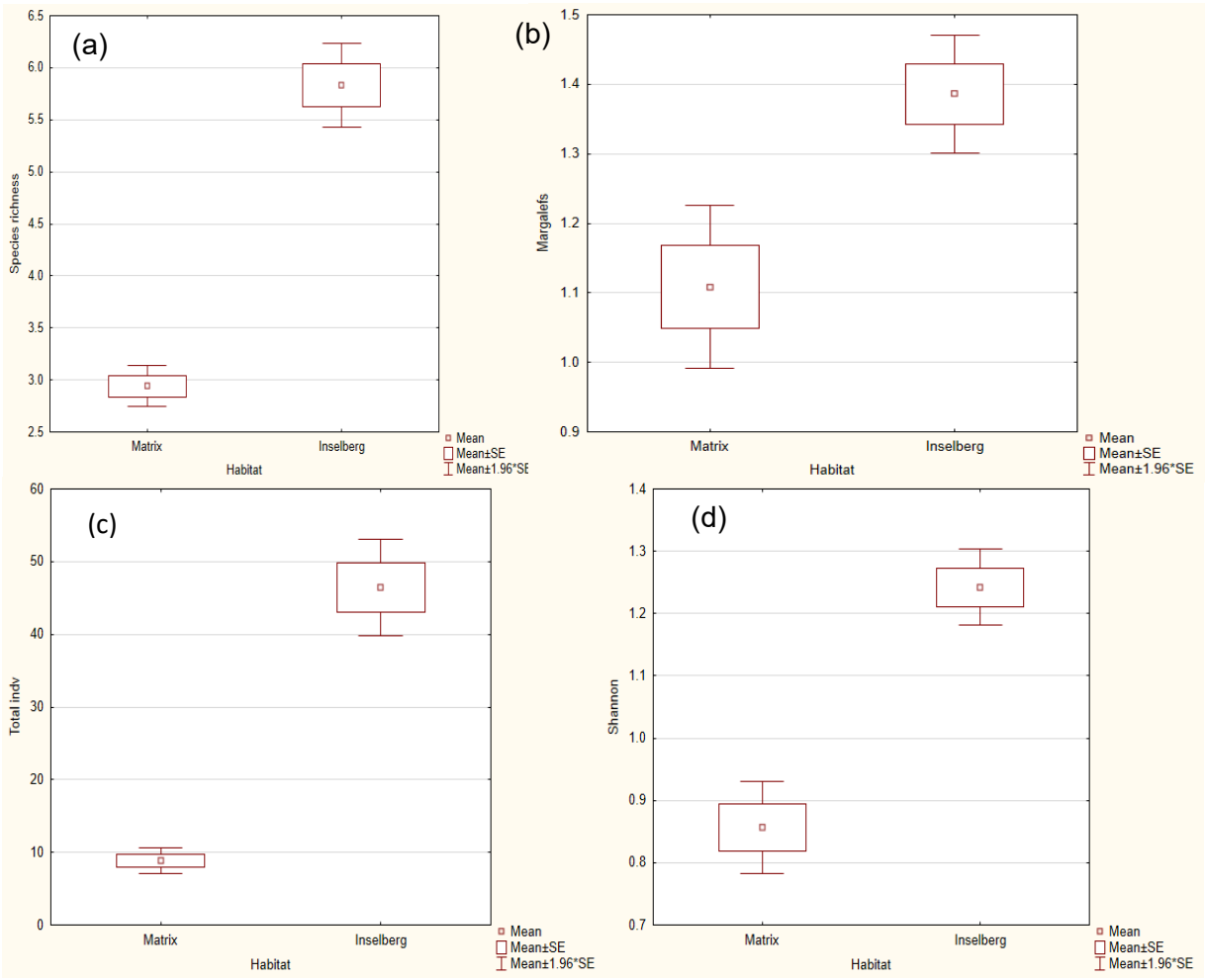


Figure 4. 3. Diversity indices comparing inselbergs from the surrounding matrix in the central Namib Desert: (a) mean species richness, (b) Margalef's richness index, (c) total number of individuals, and (d) Shannon diversity index. All diversity indices were significantly higher on inselbergs than in the surrounding matrix ($p < 0.001$).

In contrast, species evenness was significantly higher in the surrounding matrix than on the inselbergs (Kruskal–Wallis; $p = 0.011$). The matrix had a mean evenness of 0.81, while species evennes on inselbergs had a significantly lower mean of 0.75 (Figure 4-4a). Species were thus

more evenly distributed in the matrix, whereas certain dominant or rare species on the inselbergs reduced overall evenness.

According to the Kruskal-Wallis ANOVA, Simpson's diversity index did not differ significantly between habitats (p = 0.647), with mean values of 0.66 on inselbergs and 0.65 in the surrounding matrix (Figure 4-4b).

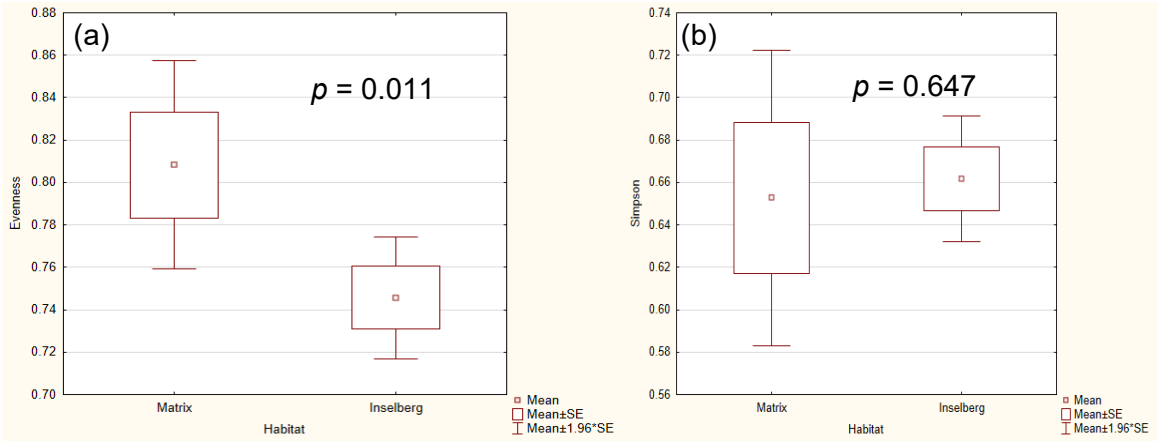


Figure 4. 4. Diversity indices on inselbergs and in the surrounding matrix of the central Namib Desert: (a) mean species evenness and (b) Simpson's diversity index. Evenness was significantly higher in the matrix (p = 0.011), whereas Simpson's index showed no significant difference between habitats (p = 0.647).

4.2.2 Species composition on inselbergs and the surrounding matrix

Species composition differed significantly between the two habitats (*p(perm) = 0.001*; Figure 4.5). The ordination plot showed distinct clustering of species composition on inselbergs and the surrounding matrix. One-way Analysis of Similarity (ANOSIM) detected significant compositional differences (R = 0.205, p < 0.001; Table 4-1) between inselbergs and the matrix, the relatively low R value indicates partial overlap in species composition between the two habitats. This suggests that while inselbergs and matrices share several species, the relative abundance and community structure differ substantially. The NMDS yield a 2D stress value of 0.15, which falls within acceptable threshold <0.2 for ecological community data.

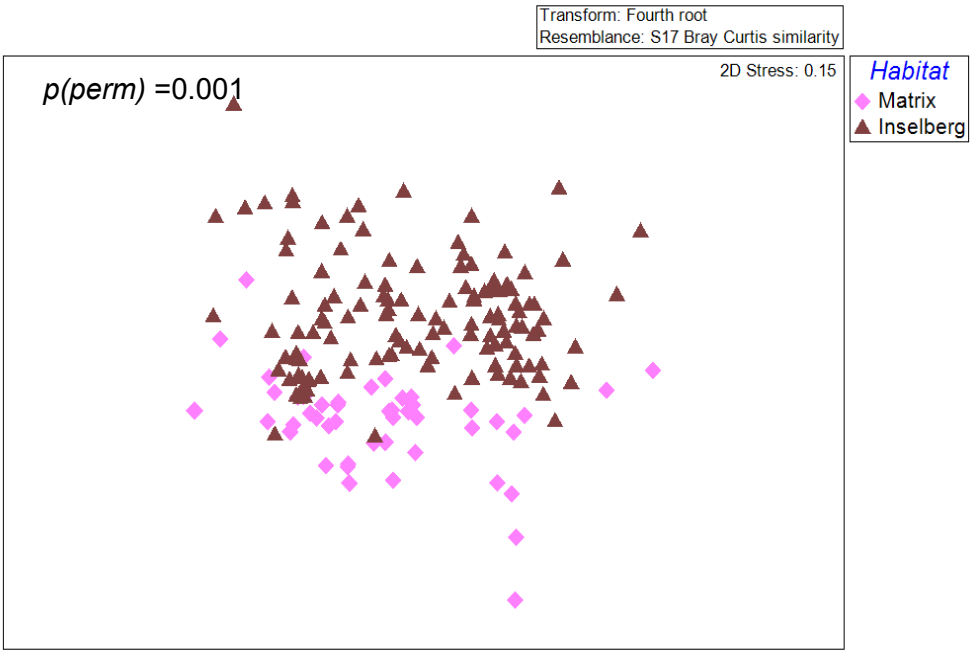


Figure 4. 5. Non-metric multidimensional scaling (NMDS) ordination of species composition on inselbergs and in the surrounding matrix of the central Namib Desert. The ordination indicates a clear separation between inselbergs and the matrix plots, reflecting differences in species assemblages.

Table 4. 1. One-way analysis of similarities (ANOSIM) comparing species composition between inselbergs and the surrounding matrix in the central Namib Desert. Species composition differed significantly between the two habitats.

Item	**Value**
R-statistic	0.2048
p-value	<0.001
Mean rank within	6973
Mean rank between	8532
Number of permutations	9999

4.2.2.1 Similarity in species composition

SIMPER analysis (Table 4-2) indicated an overall average dissimilarity of 91.58% in species composition between inselbergs and the surrounding matrix. The key species driving these compositional differences were *Pogonospermum cleomoides* (subshrub, 22.43%), *Caroxylon*

species (shrub, 11.31%), *Tetraena stapffii* (dwarf shrub, 7.9%), *Aloe asperifolia* (succulent, 7.1%), *Petalidium setosum* (shrub, 5.7%), *Tetraena cylindrifolia* (subshrub, 5%), *Arthraerua leubnitziae* (shrub, 4.5%), *Sesamum* species (herb, 3.7%), *Kleinia longiflora* (succulent shrub,1.8%), and *Commiphora saxicola* (shrub,1.5 %). Although most species were shared between the inselbergs and the surrounding matrix, they occurred in different abundances, with inselbergs generally hosting higher abundances than the matrix.

Table 4. 2. Similarity percentage analysis (SIMPER) showing species that contribute more than 1% to the overall dissimilarity between inselbergs and the surrounding matrix in the central Namib Desert. The results highlight the species most responsible for compositional differences between the two habitats.

Taxon	**Contrib. %**	**Cumulative %**	**Mean Matrix**	**Mean Inselberg**
Pogonospermum cleomoides	22.43	22.43	1.04	12.4
Caroxylon spp.	11.31	33.74	2.88	2.82
Tetraena stapffii	7.859	41.6	0.58	3.78
Aloe asperifolia	7.081	48.68	0.2	4.46
Petalidium setosum	5.675	54.36	0.26	2.3
Tetraena cylindrifolia	5.215	59.57	0.44	2.66
Arthraerua leubnitziae	4.547	64.12	0.82	0.68
Sesamum spp.	3.733	67.85	0.44	1.14
Kleinia longiflora	1.784	69.63	0	1.08
Commiphora saxicola	1.463	71.1	0.06	0.576
Overall average dissimilarities = 91.58%				

4.2.2.2 Indicator species

Indicator species Analysis (IndVal) (Table 4-3) revealed six species as significant indicators of either inselbergs or the matrix based on Bonferroni-corrected p-values (Table 4-4). *Pogonospermum cleomoides* (subshrub) was the strongest inselberg indicator (IndVal = 52.4%, p = 0.016), while *Commiphora saxicola* (shrub) (IndVal = 30%, p = 0.016), *Petalidium setosum* (subshrub) (IndVal = 27%, p = 0.047), *Aloe asperifolia* (succulent) (IndVal =26%, p = 0.032), and *Commiphora glaucescens* (shrub) (IndVal = 18.4%, p =0.016) showed moderate but significant associations with inselbergs. In contrast, only one species, *Vachellia (Acacia) erioloba* (tree), was associated with the matrix (IndVal = 14%, p = 0.047). The low IndVal percentages indicate that these species were not exclusively restricted to either inselbergs or matrix habitats, but also

occurred in the other habitat, albeit at different abundances. Nonetheless, they remain characteristic of the inselbergs or the matrix, respectively.

Table 4. 3. Percentages of indicator species associated with inselbergs and the surrounding matrix in the central Namib Desert. Most indicator species were associated with inselbergs, while fewer were characteristic of the matrix, reflecting differences in species composition between the two habitats.

Species	**IndVal%**	
	Matrix	**Inselberg**
Aloe asperifolia	0.2573	26.03
Commiphora saxicola	0.3774	29.71
Pogonospermum cleomoides	2.323	52.4
Petalidium setosum	0.8138	26.59
Commiphora glaucescens	0	18.4
Vachellia erioloba	14	9.652

Table 4. 4. Bonferroni-corrected p-values for indicator species of inselbergs and the surrounding matrix in the central Namib Desert. These results identify the species significantly associated with each habitat.

Species	**Bonferroni p-values**	
	Matrix	**Inselberg**
Aloe asperifolia	1	0.0316
Commiphora saxicola	1	0.0158
Pogonospermum cleomoides	1	0.0158
Petalidium setosum	1	0.0474
Commiphora glaucescens	1	0.0158
Vachellia erioloba	0.0474	1

These results supported our first hypothesis that plant species richness and alpha diversity will be significantly higher on inselbergs than in the surrounding matrix. Inselbergs had significantly higher species richness and diversity than the matrix. Meeting the expectation that Shannon diversity index, Margalef richness, and total species counts will be significantly greater on inselbergs than in matrix habitats. Therefore, the null hypothesis was rejected.

The second hypothesis that predicted species composition to differ significantly between inselbergs and the surrounding matrix was also supported. Inselbergs and the matrix had significantly different species composition, and discrete clustering of the two habitats were shown by NMDS. These results rejected the null hypothesis.

4.3 Discussion

The focus of this section is on species richness and composition on inselbergs and in the surrounding matrix of the central Namib Desert. Specifically, it addresses how species richness and composition differ between inselbergs and the surrounding matrix. The study hypothesised that inselbergs would have greater species richness and distinct species composition compared to the surrounding matrix. The chapter attempts to highlight that although inselbergs and the matrix are part of the same arid ecosystem, they are unique in terms of plant richness and composition.

4.3.1 Species richness on inselbergs and the surrounding matrix

The first research question explored how species richness/community structure differs between inselbergs and the surrounding matrix. Inselbergs in the central Namib Desert supported significantly higher species richness, Margalef's index, and species abundance per plot compared to the matrix plots. Additionally, inselbergs exhibited higher species diversity than the matrix according to the Shannon index. These findings support the hypothesis that inselbergs possess greater species richness than the surrounding matrix.

In the central Namib Desert, inselbergs harbour higher species richness than the surrounding matrix vegetation. This aligns with the general link between species richness and habitat heterogeneity (Hortal *et al.*, 2009), where heterogeneous habitats host more species than homogeneous ones. Although inselbergs may initially appear inhospitable due to the dominance of boulders and bare rocks, closer inspection reveals that they provide a range of ecological niches occupied by specialised species (Kluge & Büdel, 2009). Species like *Commiphora saxicola* and *Commiphora glaucescens* are petrophytes species, which specialised roots that can penetrates rocks and rock cracks, allowing them to establish on inselbergs. The unique ecological characteristics of inselbergs allow them to function as independent ecosystems with distinct microclimatic and edaphic conditions (Burke, 2003; Yates *et al.*, 2019).

In arid regions, inselbergs often act as "wetter islands" due to the cooler air created by their higher elevation relative to the surrounding lowlands (Jürgens & Burke, 2000; Shakdofa *et al.*, 2024). Jürgens and Burke (2000) highlight that the combination of enhanced moisture predictability and increased habitat heterogeneity enable inselbergs to support a richer biodiversity than adjacent

lowland habitats. Furthermore, their geological and topographical complexity also creates a mosaic of microhabitats capable of supporting more diverse and specialised plant communities than the relatively uniform matrix (Burke, 2002; Bremer & Sander, 2000). Inselbergs additionally buffer extreme diurnal temperature fluctuations typical of deserts, and their soils derived from different rock types contrast markedly with those of the surrounding matrix (Porembski *et al.*, 1996). Similar patterns have been reported, Jürgens and Burke (2000) found greater species richness on inselbergs than on surrounding plains on the arid western part of the central Namib Desert, while Shakdofa *et al*. (2024) reported that species numbers on granite inselbergs of the Arabian Shield exceeded those in the adjacent matrix by 29.2%. Similarly, Burke (2000) reported higher species diversity on inselbergs, except at Brukkaros in the Nama Karoo, where the opposite trend occurred.

Although the central Namib Desert inselbergs support more species than the surrounding matrix, the total species richness recorded was lower than that of inselbergs in more humid regions. For instance, Yates *et al.* (2019) recorded a mean species richness of 7.8 to18 herbaceous species and 13.5-26.3 woody species per plot on Australian inselbergs. In contrast, central Namib Desert inselbergs averaged only six species per plot. It is important to note that this study took place in a year with below-average rainfall, which likely excluded many opportunistic and annual species that respond to the region's highly patchy and localised rainfall (Eckardt *et al.*, 2013; Lancaster *et al.*, 1984). Nevertheless, as Burke (2000) observed, long-lived perennials tend to persist regardless of seasonal fluctuations, therefore, these results still reflect the typical plant community composition and species richness in the central Namib Desert.

Interestingly, while inselbergs had substantially higher species diversity, the matrix displayed higher species evenness where individuals were more equitably distributed. Species evenness measures how evenly individuals are distributed among species in a community (Alatalo, 1981). Higher evenness in the matrix indicates that individuals were more equitably distributed among species and not dominated by a single taxon (Pielou, 1966), despite lower overall diversity. In contrast, inselbergs may have been dominated by a few well-adapted species, or the presence of rare species could have reduced evenness (Peet, 1974). Evenness typically decreases with increasing abundance or the addition of rare species (Dalton, 1920, cited by Tuomisto, 2012), and communities with many rare species can exhibit low evenness despite high richness (Peet, 1974). As Ricotta (2003) noted, an ecologically consistent evenness index should decline when the rarest species become rarer or when less dominating species are added to a community.

In this study, the matrix likely had fewer species that occurred consistently throughout a plot, preventing local dominance and therefore higher evenness despite the overall low richness. The relative homogeneity and lack of distinct microhabitats allow species to occur across broad areas

in more or less equal numbers (Jürgens & Burke, 2000). The uniform distribution of resources in the matrix may reduce the likelihood of any single species dominating available niches. In contrast, the more complex microhabitats on inselbergs may favour certain species, promote dominance and reducing evenness. As environmental conditions on inselbergs vary markedly over short distances (Vanschoenwinkel *et al.*, 2024), these fine-scale heterogeneities influence species distribution patterns. Overall, this demonstrates that high species richness does not necessarily equate to high evenness when a few species disproportionately shape community composition.

4.3.2 Species composition on inselbergs and the surrounding matrix

Species composition differed markedly between inselbergs and the surrounding matrix. Furthermore, this study shows that there was a low but significant separation in terms of species composition between the matrices and the inselbergs with substantial overlap. It is also possible that nestedness may influence this pattern, where the species composition of the matrix could represent a subset of the inselbergs (Baselga, 2010). However, this is not the case as the low ANOSIM indicates that nestedness alone cannot fully explain the observed patterns.This suggests that inselbergs do not function as entirely isolated ecological islands but rather form a compositional continuum with the surrounding matrix (Burke, 2000). This challenges the classical view of inselbergs as discrete islands of biodiversity and supports the notion that they are centres of diversity with ecological linkages to adjacent habitats.

The clear compositional separation between inselberg and matrix communities supports the hypothesis that inselbergs host distinct plant assemblages. The SIMPER analysis showed a 91.58% dissimilarity in species composition between the two habitats, meaning 8.4% of species were shared. Species such as *Aloe asperifolia*, *Commiphora saxicola*, *Kleinia longiflora*, and *Tetraena cylindrifolia* have been shown by Jürgens and Burke (2000) as inselbergs specialists. *Arthraerua leubnitziae* and C*aroxylon spp* were more abundant in the matrix and this has also been documented by Jürgens *et al*. (1997) to be more associated with the matrix. These patterns confirm that inselbergs support a more complex and diverse community structure than the surrounding matrix.

This difference can be attributed to the heterogeneous and complex physical environments of inselbergs. As Pianka (1966) suggested, structurally complex environments support greater species diversity. Inselbergs create stable microclimatic conditions with soils that retain moisture and allow root penetration (Burke, 2003; Yates *et al.*, 2019), thereby favoring species absent from the surrounding plains (Bremer & Sander, 2000). Consequently, the inselberg flora often differs markedly from that of surrounding areas (Barthlott *et al.*, 1993, cited by Glime & da Silva, 2009).

Indicator species analysis revealed that *Aloe asperifolia*, *Commiphora glaucescens, Commiphora saxicola*, *Petalidium setosum, and Pogonospermum cleomoides* were strongly associated with inselbergs, whereas *Vachellia erioloba* was associated with the matrix. This supports the observed pattern of higher compositional distinctiveness on inselbergs. Notably, *Aloe asperifolia* (protected under the Nature Conservation Ordinance and CITES Appendix II) and *Commiphora saxicola* are Namibian endemics, while others are near-endemic (Checklist, 2014). Although none of these species are exclusive to inselbergs, families such as *Burseraceae* (*Commiphora*) and *Asphodelaceae* (*Aloe*) have previously been identified as inselberg specialists (Barthlott & Porembski, 2000). However, floristic data on inselberg communities remain sparse.

These findings highlight the role of inselbergs as potential refugia under changing climate conditions (Burke, 2003; Buschke *et al.*, 2020). Given that nestedness implies that conserving species-rich subsets can safeguard much of the regional biodiversity (Baselga, 2010), the protection of inselbergs could indirectly conserve large proportions of a region's biodiversity. Particularly in dryland landscapes where inselbergs function as important biodiversity refugia. Further studies should quantify the relative contributions of turnover and nestedness in structuring these communities to better guide conservation strategies.

4.4 Chapter summary

This study investigated how species richness and composition differ between inselbergs and the surrounding matrix in the central Namib Desert, testing the two hypotheses that inselbergs support greater species richness and distinct community composition. The first hypothesis proposed that plant species richness and alpha diversity will be significantly higher on inselbergs than in the surrounding matrix. Inselbergs function as habitat islands characterised by enhanced microhabitat heterogeneity, edaphic variability, and moisture retention relative to the surrounding plains. According to habitat heterogeneity theory and inselberg ecology, structurally complex substrates should support greater niche partitioning and thus higher richness. It is, therefore, expected that Shannon diversity, Margalef's richness, and total species counts will be significantly greater on inselbergs than in matrix habitats. The findings of this study supported this hypothesis, with the results revealing significant differences in community structure between the two habitats. Inselbergs had higher species richness, Shannon diversity, Margalef's richness, and total species counts with low species evenness. Conversely, the matrix had a high species evenness, with species being distributed more evenly, compared to inselbergs where certain specialist species may have dominated.

The second hypothesis predicted that species composition will differ significantly between inselbergs and the surrounding matrix. Environmental filtering driven by lithology, soil

development, and microclimatic buffering should result in distinct species assemblages. Inselbergs were expected to harbour habitat specialists not prevalent in the matrix. It was expected that NMDS ordination will show discrete clustering of inselberg and matrix plots, and PERMANOVA will detect significant compositional differences. The second hypothesis was also supported by the results presented in this chapter, suggesting that inselbergs do not function as completely isolated islands, but form part of a compositional continuum connected by a partially permeable matrix. This connectivity results in interwoven ecological systems rather isolated patches, with inselbergs acting as centres of floristic diversity within the surrounding landscape.

Overall, these findings emphasise the importance of inselbergs as biodiversity hotspots and potential refugia in arid landscapes, highlighting their conservation value in the central Namib Desert. Conserving inselbergs could indirectly preserve a large portion of the region's matrix biodiversity. However, future research should quantify the relative contributions of nestedness and turnover to better inform conservation management in desert ecosystems.

Table 4. 5. Evaluation of study hypotheses in relation to observed patterns.

Hypothesis	**Expectation**	**Findings**	**Support**
(i) Inselbergs support more species richness, abundance and diversity due to habitat heterogeneity, microclimatic buffering than the matrix	Inselbergs > matrix	Significant differences between inselbergs and matrix. Inselbergs had higher richness, diversity and abundance than matrix.	**Supported**. Species richness, abundance and diversity differ among strata.
(ii) Inselbergs and the matrix support distinct species composition because of environmental filtering driven by lithology, soil development	Inselbergs host unique species composition	Significant differences in species composition between inselbergs and matrix. 92% variations	**Supported.** Inselbergs hosted distinct species composition than the matrix.

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CHAPTER 5: SPECIES RICHNESS AND COMPOSITION ACROSS GEOMORPHOLOGICAL GRADIENTS OF INSELBERGS IN THE CENTRAL NAMIB DESERT

5.1 Introduction

Identifying the factors that influence species diversity and distribution remains a central theme in ecology (Fayolle *et al.*, 2012). The distribution of plant diversity is shaped by multiple environmental factors that influence species distribution and abundance across the land (Phil-Eze, 2012; Tindano *et al.*, 2023). Abiotic factors such as topographical position, slope aspect, and geological type affect community patterns and species distribution by modifying local microclimates, particularly in mountainous and rocky ecosystems (Yang *et al.*, 2020; Zhang *et al.*, 2021; Wani *et al.*, 2023). Elevation, for example, has been shown to significantly influence species richness and distribution (Di Musciano *et al.*, 2024), although findings vary among regions (Xi *et al.*, 2021).

Slope aspect shapes mountainainous environments by regulating insolation (Yangan *et al.*, 2017), which alters the microclimate due to differences in solar radiation received on contrasting aspects (Holland & Steyn, 1975, cited by Maren *et al.*, 2015). This leads to variations in soil and air temperature, atmospheric moisture, light intensity, and wind speed between slope orientations (Cantlon, 1953). Such microclimatic differences often affect plant community composition, species diversity, and nutrient dynamics (Qin *et al.*, 2019; Yanyan *et al.*, 2017), resulting in distinct vegetation patterns on contrasting slopes. These effects are generally more pronounced in semi-arid regions, where water availability is a limiting factor for vegetation development (Yang *et al.*, 2020).

Geology is another key determinant of species diversity. Different geological types create unique microenvironments that support distinct plant communities (Clegg *et al.*, 2025). Substrate type influences soil formation, water retention, and runoff—all key factors in shaping species composition (Cottle, 2004; Gröger & Huber, 2007, cited by Clegg *et al.*, 2025). In the central Namib Desert, the most common lithologies include granite, schist, marble, and gneiss (Selby, 1981).

Inselbergs, isolated rocky mountain outcrops that emerge abruptly from a flat plain (Willis, 1934), naturally integrate abiotic factors such as topography, slope aspect, and geology. This makes them ideal natural laboratories for exploring how these variables influence plant communities in the central Namib Desert. Inselbergs occur worldwide and function as independent ecosystems with distinct microclimatic and edaphic conditions due to their isolation and heterogeneity (Kluge

& Büdel, 2009). The importance of biodiversity conservation of inselbergs in arid regions has long been acknowledged (Bond & Richardson, 1990, cited by Burke, 2001), yet vegetation dynamics on rocky outcrops remain poorly studied (Clegg *et al.*, 2025). This highlights the need to better understand the factors that shape plant community patterns on inselbergs.

Understanding these drivers is essential for interpreting the diversity patterns of inselbergs in the central Namib Desert. This study, therefore, investigated how species richness or community structure and composition differ among topographical positions (strata), slope aspects (northeast- and southwest-facing), and geological types (granite, schist, and marble) of inselbergs in the central Namib Desert. Based on ecological theory and prior observations, the following three hypotheses were posed:

(i) Lower topographical strata (footslopes) will support higher species richness and differ compositionally from midslopes and crests. Footslopes are predicted to accumulate deeper soils, enhanced organic matter, and moisture via downslope transport processes. Environmental filtering along vertical gradients should therefore drive species richness and vegetation structure. It is expected that diversity indices will decline from footslopes to crest, and PERMANOVA will detect compositional differentiation among strata.

(ii) Southwest-facing slopes will support higher species richness and distinct species composition compared to northeast-facing slopes. In the central Namib Desert, southwest slopes are expected to intercept greater fog input and experience reduced evaporative stress. Increased moisture exposure should favour greater richness, and altered community structure. It is expected that diversity indices will be significantly higher on southwest slopes, and ordination analyses will reveal aspect-related clustering.

(iii) Species composition and richness will differ among granite, marble, and schist inselbergs. Lithological differences generate contrasting soil chemistries and nutrient availability. Granite-derived substrates are expected to favour oligotrophic specialists; marble-derived soils should support calcicolous assemblages; schist is predicted to exhibit intermediate characteristics. It is expected that PERMANOVA and indicator species analysis will detect significant compositional differences among geological types. Richness patterns will reflect substrate-driven environmental filtering.

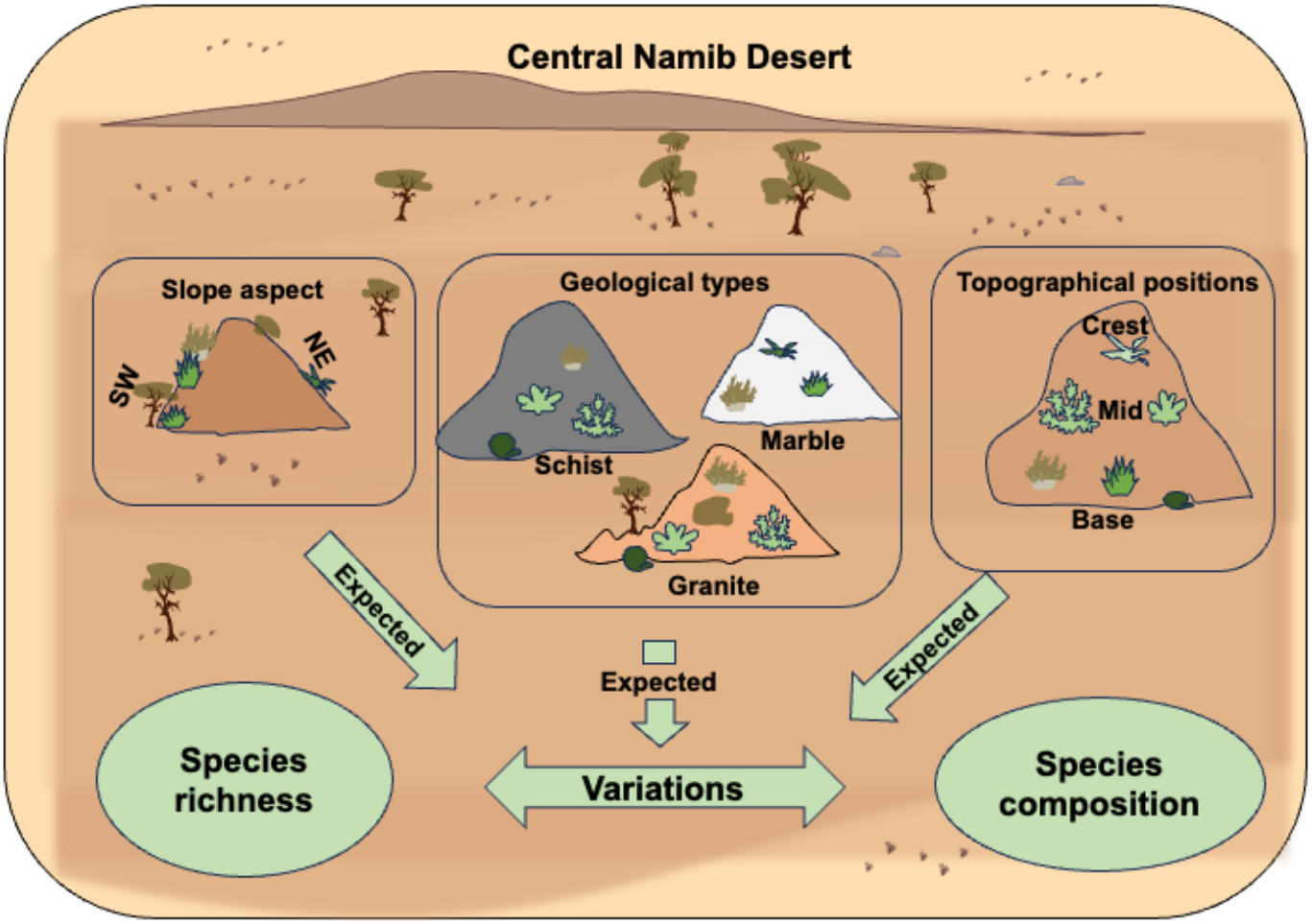


Figure 5. 1. Conceptual framework illustrating the hypothesised influence of slope aspect, geological types, and topographical position on species richness and species composition of inselbergs in the central Namib Desert.

For data analyses, refer to the Methodology Chapter.

5.2 Results

5.2.1 Topographical positions

5.2.1.1 Species richness and abundance

Overall, inselberg strata had higher species richness (mean = 6 species) than the surrounding matrix (mean = 3 species). Species richness differed significantly among topographical positions (strata) and the matrix according to the Kruskal-Wallis ANOVA ($p < 0.001$; Figure 5.2a). Pairwise multiple comparisons (2-tailed) indicated that the significant difference occurred only between the matrix and all three inselberg strata (footslope, midslope and crest), with all $p < 0.001$ (Table 5.1). No significant differences in species richness were observed across the three inselberg strata

(footslope, midslope and crest) themselves (p > 0.05; Table 5.1). Topographical strata of inselbergs therefore do not differ in species richness.

Similarly, there was a significant difference in the total number of individuals between topographical positions (one-way ANOVA, p < 0.001; Figure 5.1b). Tukey HSD test (Table 5.1b) showed significant differences between the matrix and all inselberg strata (footslope, midslope, crest; p = 0.001).

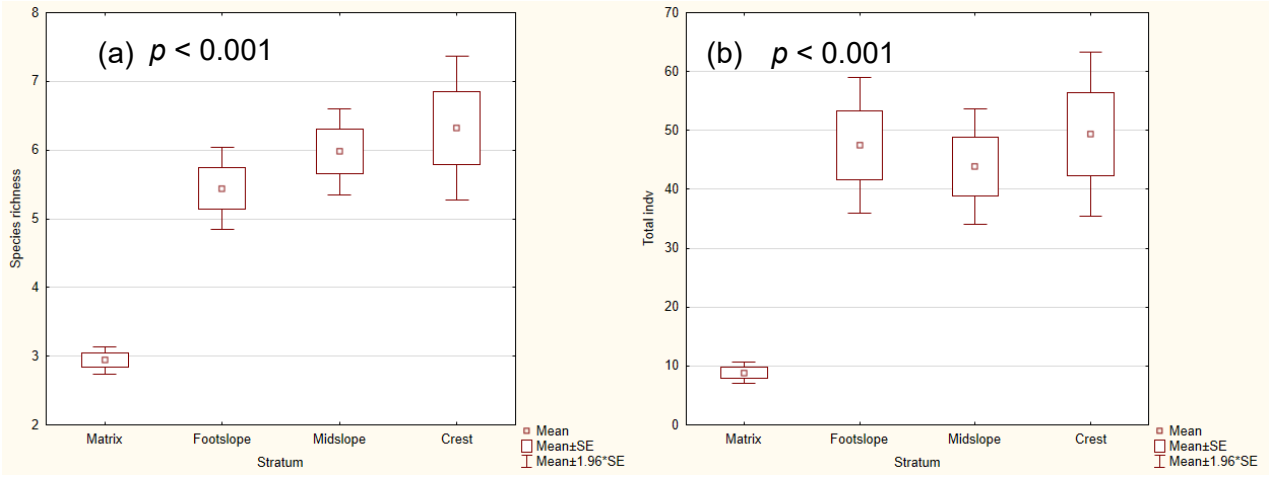


Figure 5. 2. Species richness and the total number of individuals across topographical positions of inselbergs in the central Namib Desert: (a) mean species richness of the matrix was significantly lower than the strata found on inselbergs; And (b) a mean number of total individuals was significantly lower for the matrix.

Table 5. 1. Pairwise multiple comparisons (2-tailed) for species richness across topographical positions (strata). * Denotes significant difference (p < 0.001).

Topographical positions	**Matrix**	**Footslope**	**Midslope**
Footslope	<0.001*		
Midslope	<0.001*	1.0	
Crest	<0.001*	1.0	1.0

Table 5. 2. Tukey HSD test of differences in total individuals between topographical positions. * Denotes significant difference (p < 0.001).

Topographical Positions	**Matrix**	**Footslope**	**Midslope**
Footslope	<0.001*		

Midslope	<0.001*	0.87	
Crest	<0.001*	0.985	0.76

5.2.1.2 Species diversity

Simpson's diversity index did not differ significantly among topographical positions (p = 0.072; Kruskal-Wallis ANOVA by ranks). The footslope exhibited the lowest mean Simpson's diversity index, indicating dominance by certain species (Figure 5.2a). This pattern was supported by Pielou's evenness, which showed a similar trend (Figure 5-3a).

Similarly, Kruskal-Wallis ANOVA by ranks (p = 0.011) revealed a significant difference in Pielou's evenness between strata (Figure 5.3b). Pairwise comparisons showed that only the matrix and footslope differed significantly (p = 0.010), while no significant differences were detected between the matrix, midslope or crest, or among footslope, midslope, or crest (p > 0.05; Table 5.3).

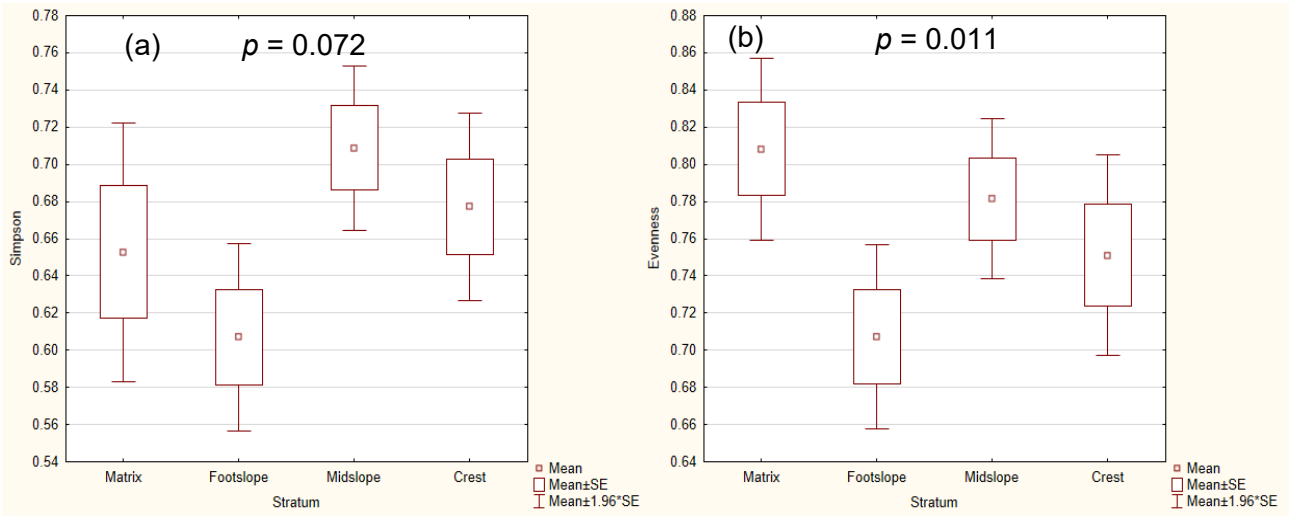


Figure 5. 3. Mean Simpson's diversity and Pielou's evenness across topographical positions of inselbergs: (a) mean Simpson's diversity index did not differ significantly among positions; and (b) mean evenness had a significant difference between footslope and matrix.

Table 5. 3. Pairwise multiple comparisons of Pielou's evenness between topographical positions (strata). * Denotes significant difference (p < 0.001).

Topographical Positions	**Matrix**	**Footslope**	**Midslope**
Footslope	0.009*		
Midslope	1.0	0.207	
Crest	0.359	1.0	1.0

One-way ANOVA revealed a significant difference in Margalef's richness among the topographical positions ($p < 0.001$; 5.4a). Tukey HSD test indicated significant differences between the matrix and midslope ($p < 0.001$), and matrix and crest ($p = 0.001$; Table 5.4). Midslope and footslope were marginally non-significant ($p = 0.055$), whereas comparisons between all strata were non-significant ($p > 0.05$; Table 5.4).

Shannon diversity index differed significantly among topographical positions ($p < 0.001$; Figure 5-4b). The matrix sites revealed significantly lower diversity compared to footslopes, midslopes, and crests (Figure 5.4b). The Tukey HSD test (Table 5.5) revealed significant differences between the matrix and footslope, midslope, and crest ($p < 0.001$). No significant differences were observed among inselbergs strata. ($p > 0.05$), but between midslope and footslope was a marginal difference ($p = 0.0514$).

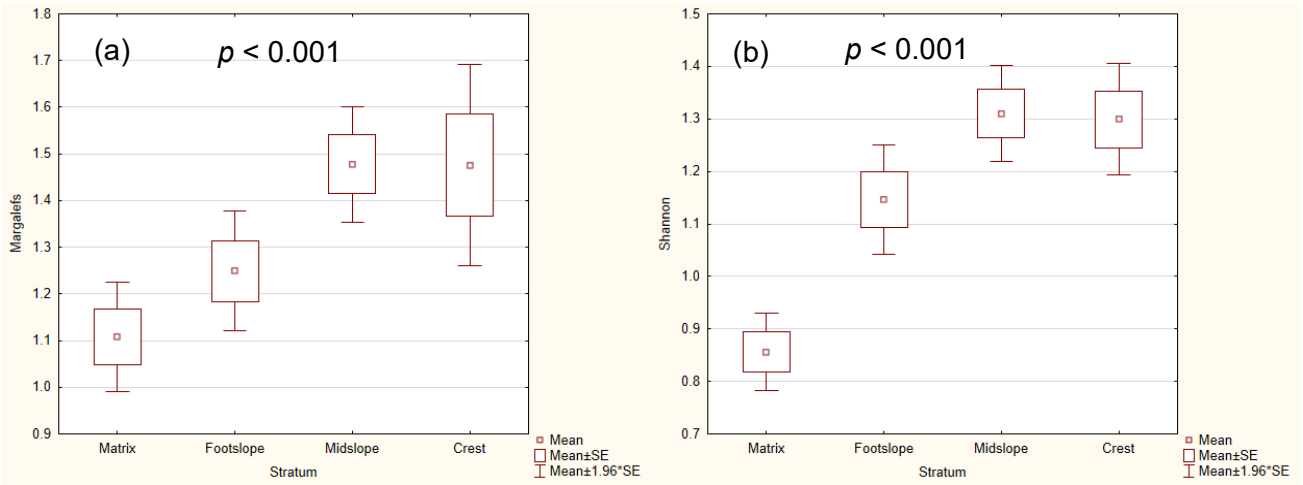


Figure 5. 4. Margalef's richness and Shannon diversity across topographical positions: (a) mean Margalef's richness with matrix showing significantly lower richness than inselberg strata; and (b) mean Shannon index indicating significantly lower diversity for the matrix.

Table 5. 4. Tukey HSD test results for Margalef's richness across topographical positions (strata). * Denotes significant difference ($p < 0.01$).

Topographical Positions	**Matrix**	**Footslope**	**Midslope**
Footslope	0.369		
Midslope	<0.001*	0.056	
Crest	0.006*	0.217	0.910

Table 5. 5. Tukey HSD test of differences in Shannon diversity between topographical positions. * Denotes significant difference ($p < 0.001$).

Topographical Positions	Matrix	Footslope	Midslope
Footslope	<0.001*		
Midslope	<0.001*	0.051	
Crest	<0.001*	0.208	0.999

5.2.1.3 Species composition

Topographical positions and the matrix sites revealed distinct species composition. Results from the NMDS revealed clustering according to topographical positions, and matrix sites separated clearly from inselberg strata (Figure 5.5). PERMANOVA confirmed a significant difference in species composition between topographical positions (p = 0.001, *pseudo-F* = 4.85). Pairwise PERMANOVA revealed that differences were only between the matrix and the inselberg strata (matrix vs. footslope, midslope, crest; p = 0.001), with no significant differences between the strata themselves (p > 0.05). Footslope, midslope, and crest formed a single distinct group from the matrix. PERMANOVA results were corroborated by ANOSIM showing, showing a weak but significant difference in species composition between strata (R = 0.13, p < 0.001). The 2D Stress: 0.15 indicates an acceptable ordination, suggesting that the 2- dimensional provides a reasonable representation of dissimilarity in species composition among topographical positions.

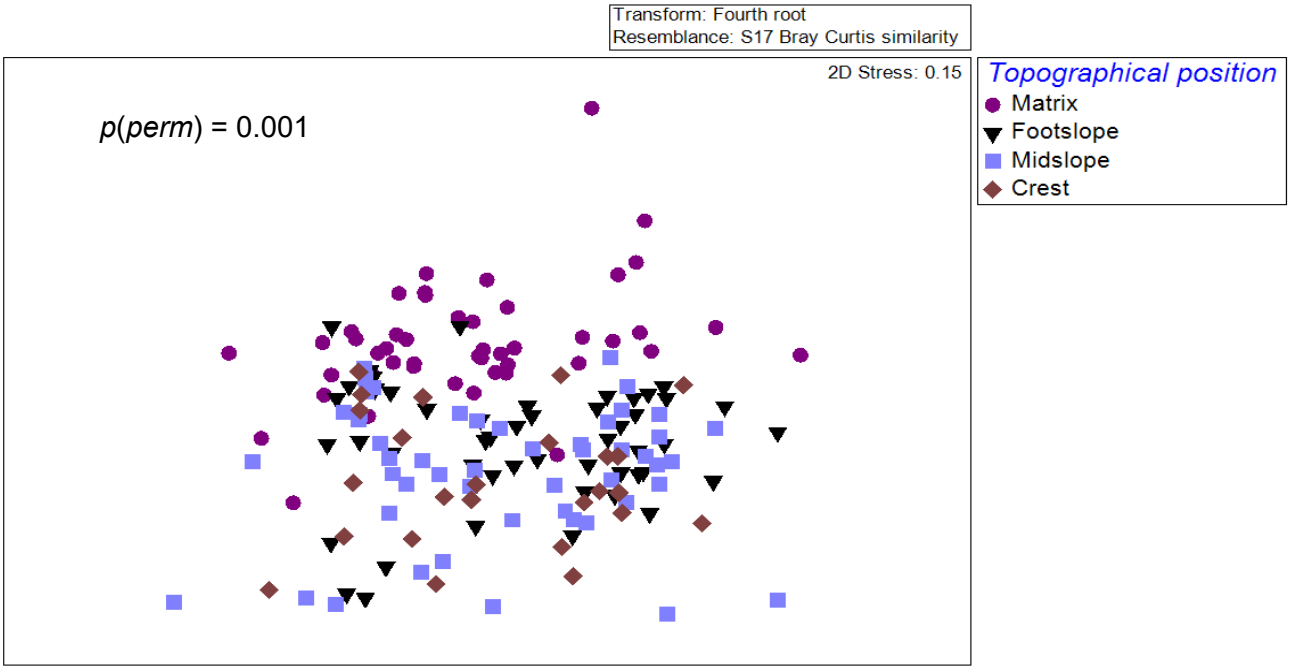


Figure 5. 5. NMDS ordination of species assemblages across topographical positions.

Table 5. 6. Analysis of similarity (ANOSIM) between topographical positions.

Item	Value
R-statistic	0.1335
p-value	<0.001
Mean rank within	6862
Mean rank between	7878
Number of permutations	9999

SIMPER analysis indicated an overall dissimilarity of 88.88% in species composition between topographical positions. Species contributing most to this difference included *Pogonospermum cleomoides* (subshrub), *Caroxylon* spp. (dwarf shrub), *Tetraena stapffii* (shrub), *Aloe asperifolia* (succulent), *Petalidium setosum* (shrub), *Tetraena cylindrifolia* (succulent subshrub), *Sesamum* spp. (herb), *Tetragonia reduplicata* (shrub) and *Kleinia longiflora* (succulent shrub). These species were more abundant on the footslope, midslope, and crest compared to the matrix (Table 5-7).

Table 5. 7. SIMPER analysis of species contributions to compositional dissimilarity among topographical positions. Inclusion in the table was dependent on a 1% minimum.

Taxon	Contrib. %	Cumulative %	Mean Matrix	Mean Footslope	Mean Midslope	Mean Crest
Pogonospermum cleomoides	22.49	22.49	1.04	14.3	10.5	12.4
Caroxylon spp.	9.589	32.08	2.88	2.34	3.12	3.16
Tetraena stapffii	7.859	39.94	0.58	4.52	3.6	2.64
Aloe asperifolia	7.784	47.72	0.2	4.7	4.88	3.16
Petalidium setosum	5.781	53.5	0.26	2.6	2.12	2.04
Tetraena cylindrifolia	5.576	59.08	0.44	1.54	2.92	4.4
Arthraerua leubnitziae	3.756	62.83	0.82	0.64	0.68	0.76
Sesamum spp.	3.599	66.43	0.44	1.14	0.66	2.12
Kleinia longiflora	2.019	68.45	0	0.2	1.46	2.08
Dyerophytum africanum	1.593	70.05	0	1.04	0.3	0.88
Commiphora saxicola	1.422	71.47	0.06	0.32	0.74	0.76
Tetragonia reduplicata	1.377	72.84	0	0.1	1.16	4.04
Calicorema capitata	1.313	74.16	0.24	0.3	0.44	0.6
Monsonia marlothii	1.269	75.43	0	0.3	0.42	1.08
Blepharis obmitrata	1.184	76.61	0	1.64	0.3	0.24
Euphorbia giessii	1.17	77.78	0	0.7	0.54	0.68
Overall average dissimilarity = 88.88%						

These results did not support the first hypothesis, which predicted (i), Lower topographical strata (footslopes) will support higher species richness and have distinct flora compared to the matrix, midslopes, and crests. Furthermore, we expected that diversity will decline from footslopes to crests, and PERMANOVA will detect compositional differentiation among strata. However, there were no significant differences between the lower topographical strata, midslopes and crests in terms of species richness, diversity and abundance. Moreover, species composition did not differ among the topographical strata. Thus, the null hypothesis was accepted.

5.2.2 Slope aspects

5.2.2.1 Species richness and abundance

Species richness did not differ significantly between slopes (Kruskal-Wallis, p = 0.096; Figure 5.6a) between southwest (SW) and northeast (NE) slope aspects. Similarly, the total number of individuals did not differ between slope aspects (one-way ANOVA , p = 0.077; Figure 5.5b) of inselbergs in the central Namib Desert.

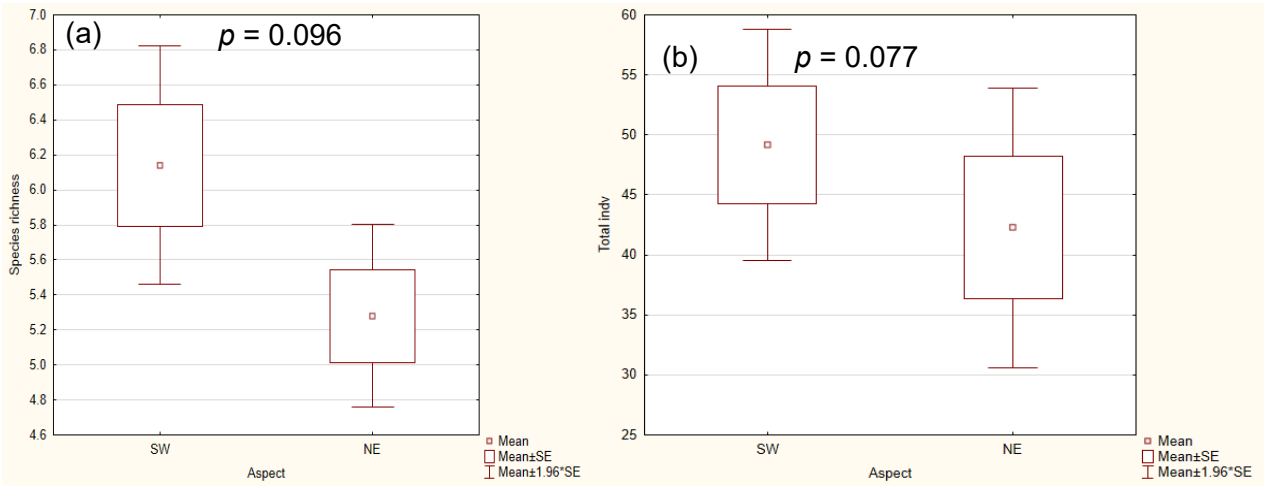


Figure 5. 6. (a) Mean species richness and (b) mean total number of individuals between southwest (SW) and northeast (NE) aspects of the central Namib Desert inselbergs.

5.2.2.2 Species diversity

Kruskal-Wallis tests indicated no significant differences in Simpson index (p = 0.251) and Pielou evenness (p = 0.178) between SW and NE slope aspects (Figure 5.7). Margalef's richness (p = 0.680) and Shannon diversity (p = 0.478) did not differ significantly between slope aspect according to one-way ANOVA (Figure 5.7).

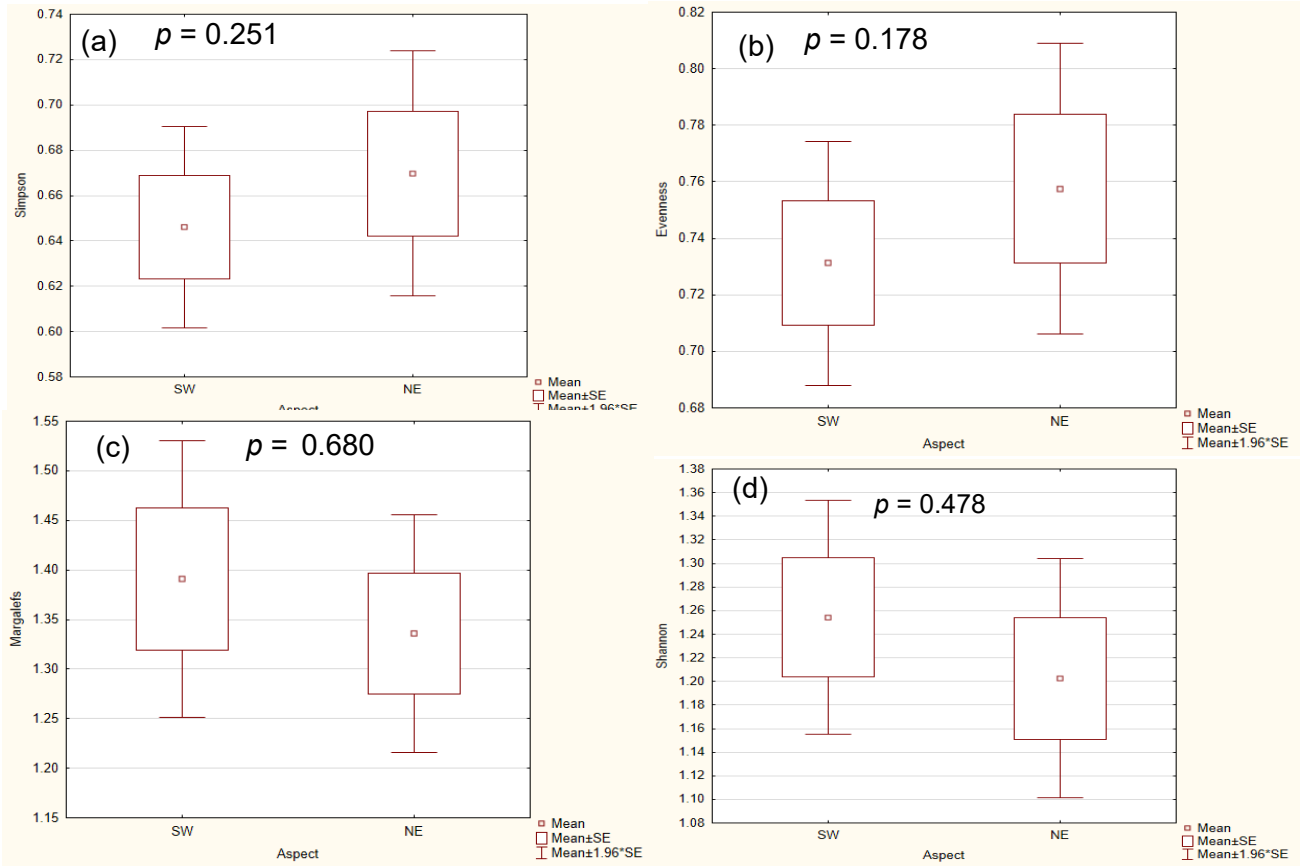


Figure 5. 7. Diversity metrics between slope aspects of inselbergs in the central Namib Desert (a) mean Simpson's diversity index, (b) mean Pielou's evenness, (c) mean Margalef's richness, and (d) mean Shannon diversity. None of the indices differed significantly between aspects.

5.2.2.3 Species composition

Like species diversity and richness, species composition was not affected by slope aspect (Figure 5.8), NMDS showed no distinct clustering. These observed patterns were corroborated by PERMANOVA results indicating no significant difference in species composition between NE and SW slope aspects (p = 0.445; *pseudo-F* = 0.958).

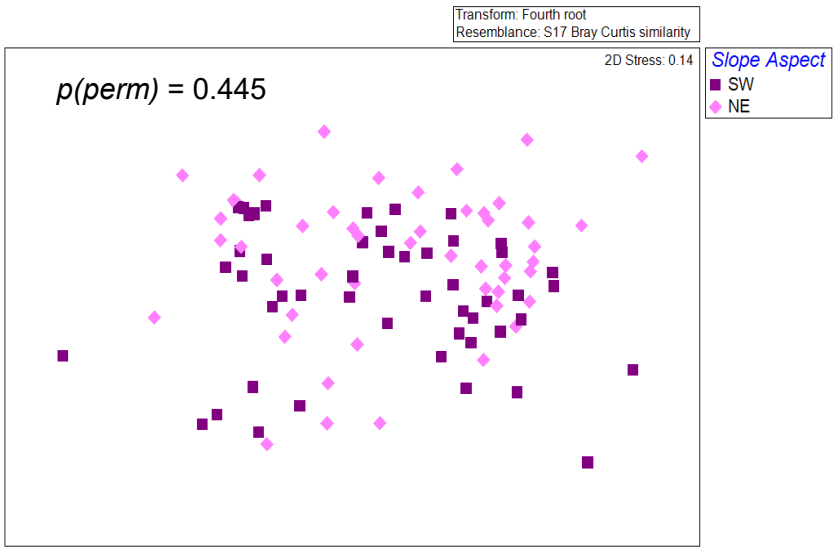


Figure 5. 8. NMDS ordination of species composition between slope aspects of inselbergs in the central Namib Desert.

These results supported the null hypothesis that slope aspects had no influence on species richness, diversity, and composition; hence the null hypothesis was accepted. The alternative hypothesis of southwest-facing slopes supporting higher species richness, abundance, diversity indices and distinct species composition compared to northeast-facing slopes, and ordination analyses revealing aspect-related clustering was not supported, thus the alternative hypothesis was rejected.

5.2.3 Geological types

5.2.3.1 Species richness and abundance

Species richness differed significantly among geological types (Kruskal-Wallis ANOVA, $p < 0.001$; Figure 5.9a). Pairwise comparisons revealed significant differences between the matrix versus marble, granite, and schist ($p < 0.001$; Table 5.8), but not among the geological types themselves ($p > 0.05$ for all). Mean species richness of the matrix (3 spp. per plot) was lower than the inselberg geological types (6 spp.; Figure 5.9a). The total number of individuals also differed significantly among geological types (Kruskal-Wallis ANOVA; $p < 0.001$; Figure 5.9b), with Tukey HSD tests indicating significant differences between the matrix and geological types ($p < 0.001$; Table 5.9).

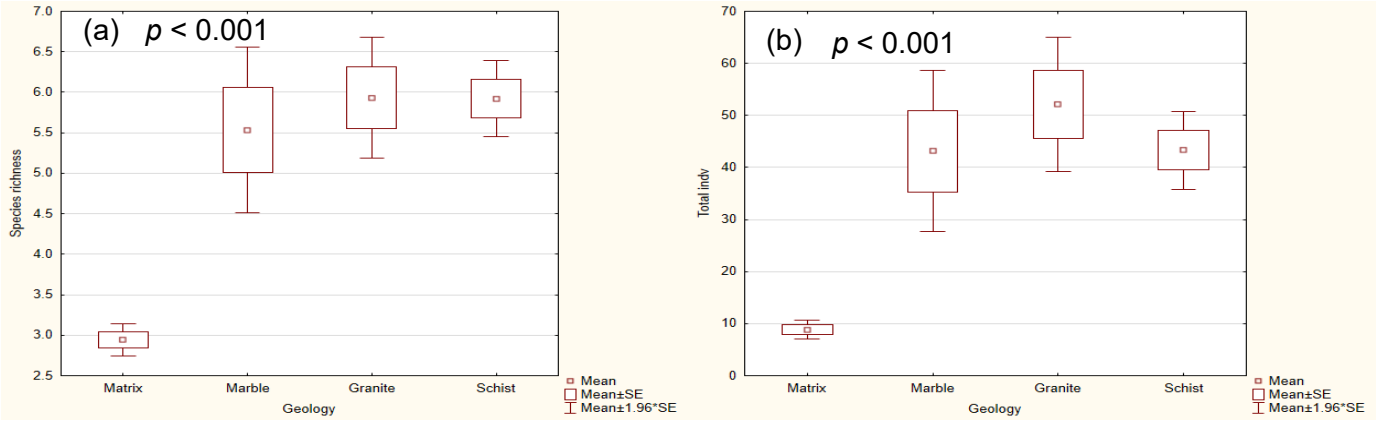


Figure 5. 9. (a) Mean species richness and (b) mean total number of individuals across geological types of inselbergs in the central Namib Desert. Both indices were significantly different across the geological types.

Table 5. 8. Multiple comparisons (2-tailed) of species richness across geological types. * Denotes significant difference at $p < 0.001$.

Geological types	Matrix	Marble	Granite
Marble	<0.001*		
Granite	<0.001*	1.0	
Schist	<0.001*	0.576	1.0

Table 5. 9. Tukey HSD of differences in the total number of individuals across geological types. * Denotes significant difference at $p < 0.001$.

Geological types	Matrix	Marble	Granite
Marble	<0.001*		
Granite	<0.001*	0.689	
Schist	<0.001*	0.504	0.990

5.2.3.2 Species diversity

Simpson's diversity did not differ significantly among geological types and the matrix sites (Kruskal-Wallis ANOVA, $p = 0.969$; Figure 5.10a). Species evenness was marginally significant among geological types (Kruskal-Wallis ANOVA; $p = 0.044$; Figure 5.9b) but not confirmed with Tukey HSD (Table 5.10). Margalef's richness differed significantly (one-way ANOVA; $p = 0.004$; Figure 5.10c). Tukey HSD showed significant differences in species evenness between the matrix versus granite ($p = 0.005$) and schist ($p = 0.008$), but not between any other pairs ($p > 0.05$; Table 5.11).

Shannon diversity index also differed significantly among geological types (one-way ANOVA; $p < 0.001$; Figure 5.10d), with Tukey HSD test indicating significant differences between the matrix and geological types ($p < 0.001$; Table 5.12).

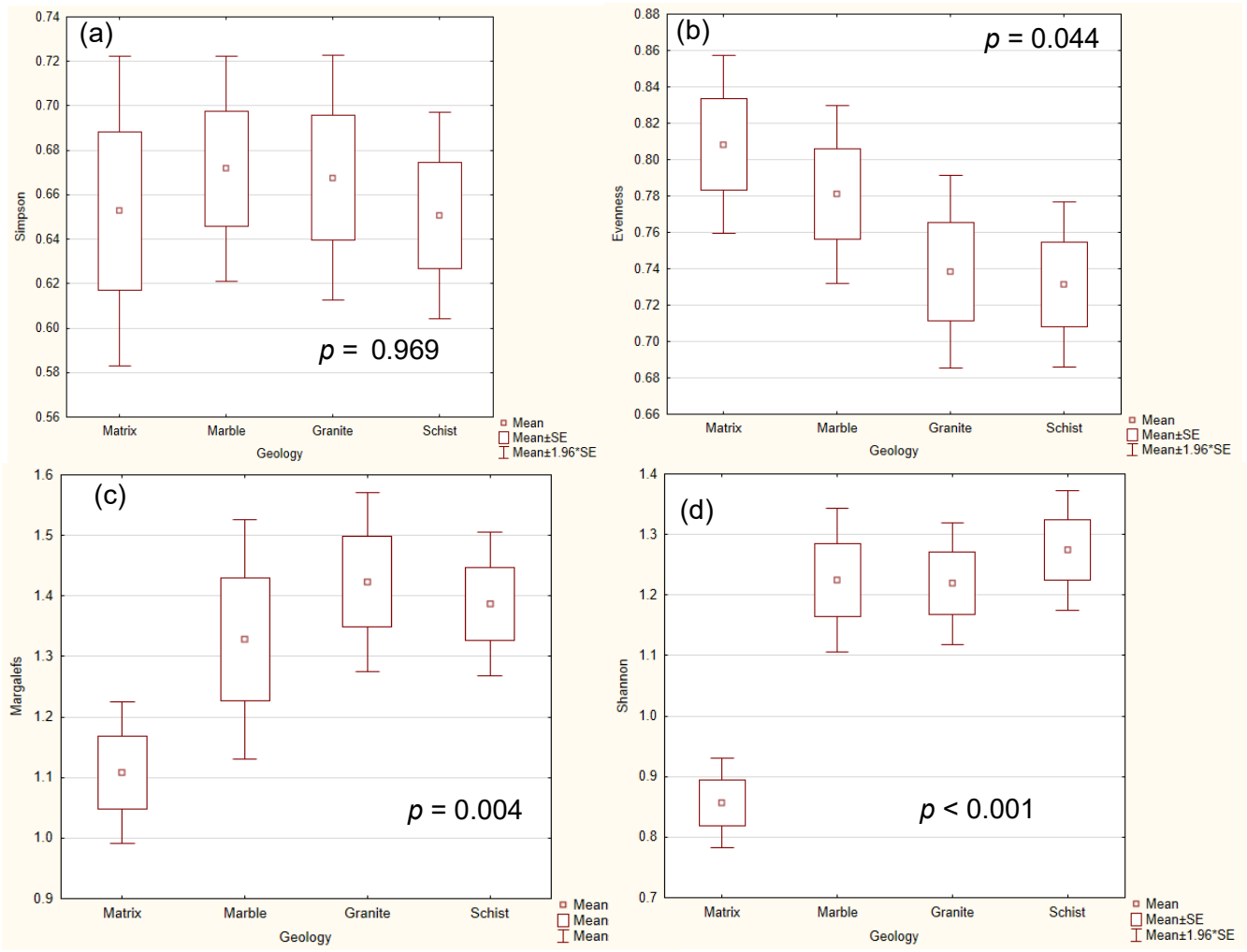


Figure 5. 10. Diversity metrics across geological types of inselbergs in the central Namib Desert: (a) mean Simpson's diversity, (b) mean Pielou's evenness, (c) mean Margalef's richness, and (d) mean Shannon index. All metrics differed significantly between geological types ($p < 0.001$), except for the Simpson diversity index ($p = 0.969$).

Table 5. 10. Multiple comparisons (2-tailed) of Pielou's evenness across geological types.

Geological types	Matrix	Marble	Granite
Marble	1.0		
Granite	0.148	1.0	
Schist	0.061	1.0	1.0

Table 5. 11. Tukey HSD of differences in Margalef index across geological types. * Denotes significant difference at $p < 0.01$.

Geological types	Matrix	Marble	Granite
Marble	0.182		
Granite	0.005*	0.801	
Schist	0.008*	0.891	0.995

Table 5. 12. Tukey HSD of differences in Shannon index across geological types. * Denotes significant difference at $p < 0.001$.

Geological types	Matrix	Marble	Granite
Marble	<0.001*		
Granite	<0.001*	0.999	
Schist	<0.001*	0.914	0.840

5.2.3.3 Species composition

Species composition differed between geological types (PERMANOVA, $p = 0.001$, *pseudo-F* = 12.213), with pairwise tests indicating significant differences between the matrix versus granite, marble, and schist ($p = 0.001$). Similarly, there were significant differences between marble versus granite, marble versus schist, and granite versus schist ($p = 0.001$). NMDS ordination (Figure 5-10) depicts clustering by geological type, with some species shared. There is a trend that schist shares some species with granite (Figure 5-11). ANOSIM confirmed significant differences in species composition ($p < 0.001$) and supporting the PERMANOVA. However, the separation was weak ($R = 0.27$; Table 5-13).

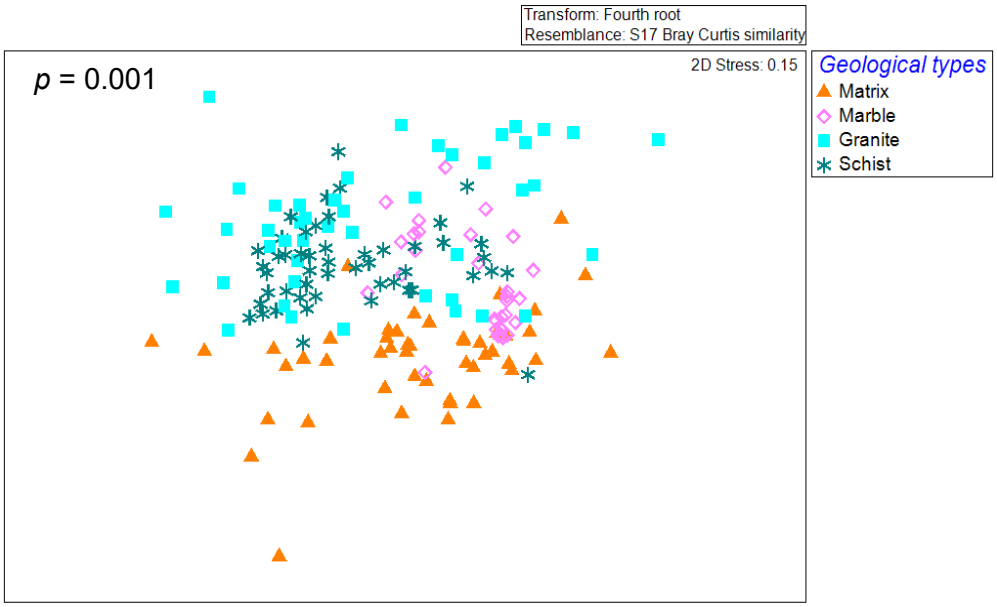


Figure 5. 11. NMDS ordination of species composition between geological types of inselbergs in the central Namib Desert.

Table 5. 13. Analysis of similarity (ANOSIM) between different geological types of inselbergs in the central Namib Desert. Species composition differed across the geological types ($p < 0.001$; R = 0.27).

Item	Value
R-statistic	0.2682
p-value	<0.001
Mean rank within	6091
Mean rank between	8133
Number of permutations	9999

SIMPER analysis indicated an overall dissimilarity of 89.93% (Table 5.14), with *Pogonospermum cleomoides*, *Caroxylon spp.*, *Tetraena stapffii*, and *Aloe asperifolia* contributing most to the differences in species composition.

Table 5. 14. Similarity analysis of species contributions to composition dissimilarity among topographical positions. Inclusion in the table was dependent on a 1% minimum.

Taxon	Contrib. %	Cumulative %	Mean Matrix	Mean Marble	Mean Granite	Mean Schist
Pogonospermum cleomoides	22.53	22.53	1.04	5.07	12.4	16.8
Caroxylon spp.	9.662	32.19	2.88	4.43	1.18	3.32

Tetraena stapffii	7.978	40.17	0.58	4.8	3.22	3.66
Aloe asperifolia	7.887	48.06	0.2	6.77	6	1.7
Petalidium setosum	5.704	53.76	0.26	0	3.2	2.86
Tetraena cylindrifolia	5.437	59.2	0.44	2.87	2.11	3.04
Arthraerua leubnitziae	3.933	63.13	0.82	2.2	0.178	0.22
Sesamum spp.	3.515	66.65	0.44	0	0.4	2.5
Kleinia longiflora	2.007	68.65	0	3.07	0.667	0.26
Dyerophytum africanum	1.541	70.19	0	0	1.27	0.64
Commiphora saxicola	1.421	71.62	0.06	0.367	0.422	0.84
Overall average dissimilarity = 89.93%						

Indicator species analysis revealed a strong association between *Arthraerua leubnitziae* (39%), *Ceropegia pedicellata* (20%), and *Euphorbia giessii* (19%) associated and marble inselbergs, whilst *Pogonospermum cleomoides* (39%) and *Euphorbia virosa* (21%) were associated with schist (Table 5.15). However, no species were strictly confined to a single geological type.

Table 5. 15. Indicator species significantly associated with specific geological types in the central Namib Desert. * Denotes significant Bonferroni test ($p < 0.05$).

Geological types	***Arthraerua leubnitziae***	***Ceropegia pedicellata***	***Euphorbia giessii***	***Pogonospermum cleomoides***	***Euphorbia virosa***
Matrix	6.718	0.0181	0	0.8841	0
Marble	38.62*	19.62*	18.78*	3.829	0
Granite	0.4624	0.0224	0.1353	17.21	6.615
Schist	0.6437	0	0	38.94*	21.35*

These results partially supported the 3rd hypothesis, while species composition significantly differed among the geological types (marble, schist, granite) and the matrix sites,and formed distinct clusters. Species richness and diversity indices did not show significant differences among the geological types.

5.3 Discussion

5.3.1 Species richness, diversity and composition across topographical positions

Species richness and diversity differ significantly between strata except for the Simpson index on inselbergs in the central Namib Desert. Pairwise multiple comparisons indicated that the matrix was poor in diversity measures compared to the other strata. Similarly, species composition differed between the topographical positions, with PERMANOVA indicating the matrix is distinct from the other strata.

Although species richness and species composition differed among strata, these differences were confined to contrasts between the matrix and the inselbergs strata. These findings are similar to what was reported in Chapter 4, which indicated a clear distinction between the matrix species richness and composition and the inselberg. Therefore, the footslope, midslope, and crest did not form distinct clusters, but are a more-or-less single ecosystems distinct from the matrix. Topography has been documented to influence vascular plant diversity (He *et al.*, 2023; Moeslund, 2013; Tenaw *et al.*, 2024) by creating microclimatic conditions and influencing the degree of insularity (Cleggs *et al.*, 2025). Changes in topographical position can modify abiotic factors, such as water, temperature, and soil composition, which in turn influence species distribution and diversity along the gradient (Abd El-Ghani & Al Borki, 2024; Tenaw *et al.*, 2024). For instance, on arid mountains, a common pattern (hump shaped) has been observed, with species richness peaking at the intermediate elevation and declining towards both upper and lower elevations (Abd El-Ghani & Al Borki, 2024; He *et al.*, 2023), though other patterns exist (Ahmad *et al.*, 2020). However, in the central Namib Desert, topographical positions on inselbergs did not influence species richness or species composition.

The results imply that plant communities on inselbergs of the central Namib Desert differ from those in the surrounding matrix in terms of species richness and composition. However, the patterns did not align with the 1st hypothesis predicting a decrease in species richness, abundance, diversity and dissimilarity in species composition from footslopes, midslopes and crests, therefore the hypothesis was not supported. Instead, the significant difference only exists between the matrix and all inselberg strata (footslope, midslope, and crest). The contrast, therefore, lies firmly between the inselberg environment as a whole and the surrounding matrix, rather than between different topographical positions on the inselberg itself.

This pattern could be attributed to the terrain difference between inselbergs and the surrounding matrix (Kluge & Büdel, 2009). Inselbergs create distinct microclimatic conditions (Bremer & Sander, 2000). Burke (2002a) similarly observed that inselbergs form unique plant communities that are more similar to one other than the surrounding matrix. This separation suggests that,

regardless of the topographical positions, inselbergs support distinct species assemblages compared to the matrix. Geological and topographical complexity likely contribute to this pattern, as these features create heterogeneous environments with a variety of microhabitats that support diverse and specialised plant communities (Burke, 2002b; Bremer & Sander, 2000; Hulshof & Spasojevic, 2020).

Moreover, the topographical position did not significantly influence species richness or composition within inselbergs (footslopes, midslopes, and crests). Other environmental factors may play a more important role such as soil depth, the availability of rock crevices, and soil-filled depressions (Jürgens and Burke, 2000; Kluge & Büdel, 2009). These microhabitats can occur across all positions on an inselberg, leading to the same species occupying the same microhabitats in different strata. Moreover, inselbergs in the central Namib Desert may not be high enough to exhibit fluctuations in temperature which cause variations in microhabitats, soil moisture and other abiotic factors.

Overall, these results do not support the hypothesis that topographical position significantly structures species richness, diversity or composition on inselbergs.

5.3.2 Species richness, diversity and species composition between slope aspects

This section addressed the question whether species richness and composition differ between slope aspects (northeast and southwest) on inselbergs of the central Namib Desert. It was hypothesised that species richness and diversity would be greater on southwest slopes and compositionally different, as it receives more fog which is a more reliable source of moisture than rainfall in the Namib Desert. Eventhough the frequency and intensity decreases as you move inland. The absence of significant differences among aspects does not support this hypothesis that aspect acts as a primary driver of plant community structure in this system.

Kruskal-Wallis ANOVA and one-way ANOVA showed no significant differences in species richness or diversity. Species composition also did not differ between aspects, as supported by the NMDS ordination, which displayed no distinct clustering. PERMANOVA confirmed the absence of significant differences in species composition between aspects. These results did not support the 2nd hypothesis that the southwest aspect hosts greater species richness, species abundance and distinct species composition than the northeastern slope. In the central Namib Desert, southwest slopes are expected to intercept greater fog input and experience reduced evaporative stress. Increased moisture reliability should favour greater richness and altered community structure. The expectation that diversity indices will be significantly higher on southwest slopes, and ordination analyses will reveal aspect-related clustering was not supported.

Results from this study suggests that slope aspect does not significantly influence species richness, diversity or composition on the inselbergs of the central Namib Desert. This pattern is consistent with Parmentier (2003), who reported a similar lack of correlation on rainforest inselbergs in Equatorial Guinea. Despite contrasting environments between hyper-arid desert and humid tropical rainforest, both cases suggest that slope orientation may play a secondary role in shaping the inselberg vegetation.

Several factors may explain this phenomenon. In both extreme arid and very humid tropical environments, differences in solar radiation between slope aspects tend to be minimal, reducing the influence of aspect on biotic and abiotic conditions (Kutiel & Lavee, 1999; Phil-Eze, 2012). In regions receiving less than 600 mm of annual precipitation, moisture availability rather than slope orientation largely determines plant community structure and composition (Kutiel and Lavee, 1999) rather than slope aspects. Similarly, Burke (2002) demonstrated that solar radiation varies little between slope orientations in the Namib, while fog deposition plays a more critical role in shaping vegetation patterns.

Comparable results have been reported in other mountainous systems. For instance, in the Manang Valley, Panthi *et al.* (2007) and Maren *et al.* (2015) found that moisture availability, rather than slope aspect, primarily governed species composition and richness. Collectively, these findings imply that in hyper-arid environments, slope aspect may exert a limited influence on plant community structure compared to overriding factors such as soil properties and moisture inputs (Burbanck & Platt, 1964).

5.3.3 Species richness, diversity and species composition between geological types

Species richness and diversity on central Namib Desert inselbergs did not differ significantly among geological types. However, pairwise multiple comparisons and Post hoc Tukey HSD showed that the surrounding matrix was different from marble, granite and schist in all cases, while no significant differences occurred among the three inselberg geological types themselves. From this, it is clear that the effect of geology on richness and diversity is not as pronounced as the plains-inselbergs divide.

Species composition varied significantly among geological types, as indicated by PERMANOVA. Pairwise tests revealed distinct compositional differences between the matrix and each inselberg geology (granite, marble, and schist) and among the three inselberg geological types themselves. NMDS ordination showed distinct clustering by geological type, with some overlap between schist and granite. SIMPER analysis supported this, showing 89.93% overall dissimilarity in species composition among geological types.

Findings from this chapter demonstrate that geology exerts a strong influence on species composition of the central Namib Desert inselbergs and this was expected as geological composition has been identified as a key driver of plant community variation (Burke, 2002, Porembski *et al.*, 1996) and diversity (Cottle, 2004; Migon, 2022) that promote the development of unique vegetation types (Glime & Da Silva, 2019). The association of *Arthraerua leubnitziae*, *Euphorbia* giessii, and *Ceropegia pedicellata* (formerly *Hoodia pedicellata*) (Figure 5.12) with marble inselbergs, and of *Pogonospermum cleomoides* and *Euphorbia virosa* (Figure 5.13) with schist inselbergs further illustrates this pattern.

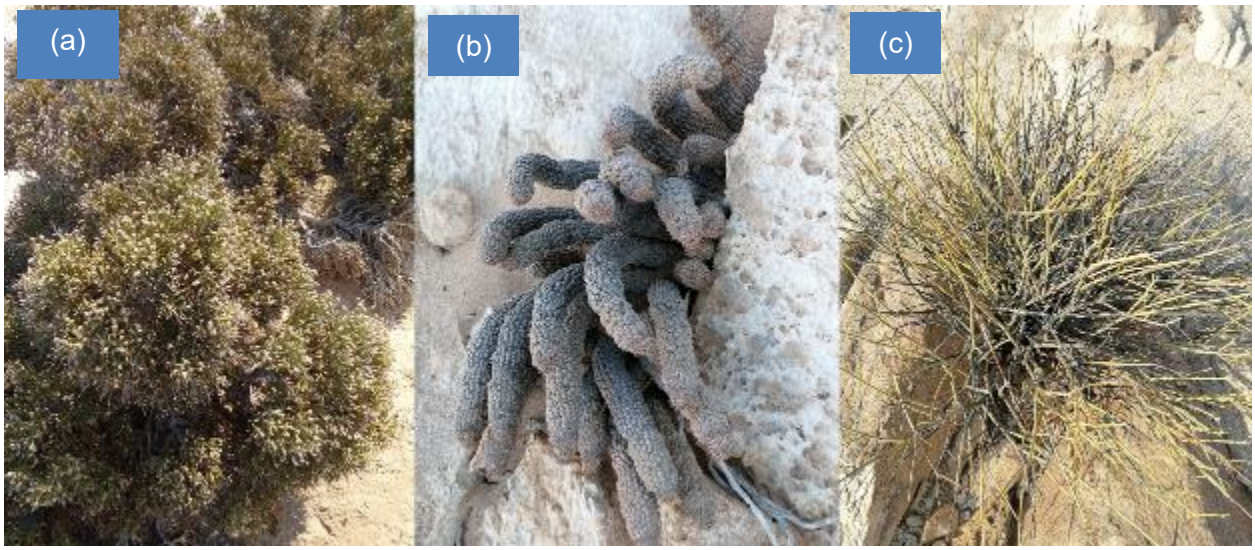


Figure 5. 12. Indicator species associated with marble inselbergs: (a) *A. leubnitziae,* (b) *C. pedicellata,* and (c) *E. giessii*.

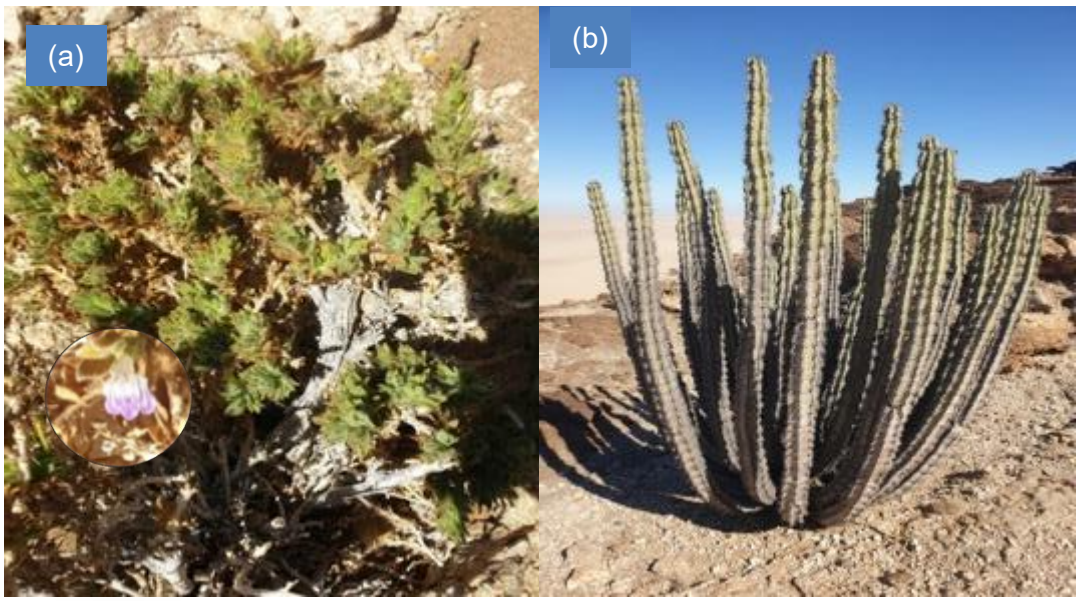


Figure 5. 13. Indicator species associated with schist inselbergs: (a) *P. cleomoides* and (b) *E. virosa*.

Different lithologies influence soil chemistry and texture, including pH, metal content, and nutrient availability, which in turn affect nutrient uptake and plant establishment (Bojorquez-Quintal *et al.*, 2017, cited by Clegg *et al.*, 2025). These results build on existing evidence in literature that geological variation is a major driver of plant diversity on inselbergs (Burke, 2001; Cottle, 2004; Migon, 2022). These substrates thus create a variety of geochemical and physical environments for plant growth (Cottle, 2004). Weathering patterns, influenced by underlying geology, determine regolith development, water retention, and runoff (Gröger & Huber, 2007, cited byClegg *et al.*, 2025; Jing *et al.*, 2020; Vanegas *et al.*, 2006). Such processes shape the amount and type of soil available (Gröger & Huber, 2007, cited by Clegg *et al.*, 2025; Vanegas *et al.*, 2006), producing more diverse soils on inselbergs than in the surrounding matrix (Jürgens & Burke, 2000). These edaphic and hydrological differences may explain the strong compositional turnover observed between geological types, even when species richness remained similar (Duniway *et al.*, 2022; Vanegas *et al.*, 2006).

The distinct separation between the matrix and inselberg geologies underscores the ecological uniqueness of inselbergs in the central Namib Desert. These patterns are consistent with Cantelo *et al.* (2021), where marble outcrops in Argentina supported plant communities distinct from those of the surrounding matrix. Burke (2000c) similarly found that soils derived from different geological substrates on inselbergs varied considerably, leading to differences in edaphic conditions and vegetation composition (Duniway *et al.*, 2022).

In this study, schist and granite shared several species, likely due to similarities in their weathering patterns and resultant soil properties. By contrast, marble hosted unique indicator species, reflecting specialised adaptations to calcareous substrates. These findings partially supported the 3rd hypothesis that species richness and composition would significantly differ among granite, schist and marble inselbergs. Species richness did not differ significantly among geological types, but species composition differed significantly between all, reflecting substrate-driven environmental filtering.

The findings indicate that while species richness remains relatively constant across geological types, species composition differs substantially. This underscores geology as a key driver of plant community structure on inselbergs in the central Namib Desert.

5.4 Chapter summary

This study set out to investigate how species richness and composition vary with topographical position, slope aspect, and geology on inselbergs in the central Namib Desert. Although significant differences in species richness and composition were found across topographical positions, these were confined to contrasts between inselbergs and the surrounding matrix. The

footslope, midslope, and crest strata did not differ significantly from one another, indicating that inselbergs function as relatively homogeneous ecological systems distinct from the surrounding plains. This study did not support the 1st hypothesis that predicted lower topographical strata (footslopes) to support higher species richness and differ compositionally from midslopes and crests (Table 5-16). Footslopes were predicted to accumulate deeper soils, organic matter, and moisture via downslope transport processes. Environmental filtering along vertical gradients should therefore structure both richness and composition. It was expected that diversity indices will decline from footslopes to crests, and PERMANOVA will detect compositional differentiation among strata. Instead, it highlighted the strong ecological contrast between inselbergs and the matrix, likely reflecting the inselbergs' heterogeneous terrain, microclimatic variation, and specialised habitats.

Slope aspect had no significant effect on either species richness or composition, contrary to expectations that southwest-facing slopes would host greater plant diversity due to enhanced fog interception (Table 5-16). This suggests that in the hyper-arid central Namib Desert, factors such as soil depth, rock crevices, and moisture availability may outweigh the influence of aspect on plant community patterns. This study accepted the null hypothesis as ordination analyses did not reveal aspect-related clustering. The alternative hypothesis was therefore not supported that southwest-facing slopes would be characterised by higher species richness, abundance, diversity indices and distinct species composition compared to northeast-facing slopes.

In contrast, geology exerted a pronounced influence on species composition, but not on species richness. While the total number of species was similar across granite, marble, and schist inselbergs, indicator species and relative abundance varied significantly among them. Each geological substrate supported distinct assemblages, reflecting differences in soil chemistry, nutrient availability, and weathering processes. These results demonstrate that, regardless of geological type, inselbergs consistently support richer plant communities than the surrounding matrix. The distinct species assemblages across schist, marble, and granite inselbergs underscore the importance of geology in structuring plant communities within the central Namib Desert inselbergs. These findings partially support the hypothesis that nutrient-poor granite inselbergs host more distinct species assemblages, though species richness remained comparable among all rock types (Table 5-16). This study partially supported the 3rd hypothesis, while species composition significantly differed among the geological types (marble, schist, granite) and formed distinct clusters. Species richness did not show significant differences among the geological types.

Overall, the study demonstrates that inselbergs in the central Namib Desert consistently support richer and compositionally distinct plant communities compared to the surrounding matrix. Among

the factors examined, geology emerges as the strongest driver of species composition, while topography and slope aspect exert unmeasurable effects. The results underscore the ecological uniqueness of inselbergs as islands of diversity within the desert landscape, structured more by their geological and microhabitat heterogeneity than by broad-scale topographical or orientation gradients.

Table 5. 16. Evaluation of study hypotheses in relation to observed patterns.

Hypothesis	**Expectation**	**Findings**	**Support**
(i) Lower strata (footslopes) support greater species richness and composition than higher strata (midslopes and crests).	Footslopes > midslopes/crests	No significant differences among footslope, midslope, and crest. All strata had higher richness than matrix.	**Not supported** — richness did not differ among strata. Inselbergs as a whole differed from matrix only.
(ii) Southwest-facing slopes host more diverse plant communities than northeast-facing slopes due to fog interception.	SW > NE	No significant differences in richness, diversity indices, or composition.	**Not supported.** Slope aspect had no measurable effect.
(iii) Species composition and richness will differ among granite, marble, and schist inselbergs. Lithological differences generate contrasting soil chemistries and nutrient availability.	Richness and composition patterns will reflect substrate-driven environmental filtering.	Species richness did not differ among granite, marble, and schist. Composition differed significantly among all three, but with overlapping species.	**Partially supported.** Composition differs, but richness pattern does not match prediction.

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CHAPTER 6: THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND COMPOSITION WITH INSELBERG SIZE, SPATIAL ISOLATION AND ARIDITY OF THE CENTRAL NAMIB DESERT

6.1 Introduction

Island biogeography and environmental filtering are two key ecological frameworks that emphasise the role of island size, isolation, and abiotic conditions as drivers of species richness and community structure (Henneron *et al.*, 2019). For decades, it has been hypothesised that island size strongly influences diversity through several mechanisms. Larger islands tend to support larger populations, which reduces extinction risk, and they typically contain a greater diversity of habitats (Matthews & Triantis, 2021; Kohn & Walsh, 1994), thereby promoting higher levels of coexistence and diversification (Angela & Lei, 1998).

Isolation has traditionally been measured as the distance between an island and the nearest mainland (Whittaker & Fernandez, 2007). However, recent studies show that additional metrics, such as distance to the nearest island and the spatial configuration of islands within an archipelago, also influence colonisation dynamics (Itescu *et al.*, 2020; Matthews & Triantis, 2021). In this study, isolation was quantified as the distance to the nearest island. Species richness is generally expected to decline with increasing isolation (Whittaker & Fernandez, 2007), as isolated islands receive fewer colonists (Angela & Lei, 1998; Matthews *et al.*, 2005, cited in Al-Namazi & Bonser, 2022).

While the Theory of Island Biogeography provides a strong conceptual foundation for understanding spatial drivers of diversity (Angela & Lei, 1998; MacArthur & Wilson, 2001; Whittaker & Fernández-Palacios, 2007), it does not fully account for other ecological processes that influence community assembly (Al-Namazi & Bonser, 2022). In contrast, environmental filtering theory emphasises how species are differentially sorted along abiotic gradients, such as moisture, temperature, and nutrient availability, allowing only those capable of tolerating specific conditions to persist (Keddy, 1992; Weiher & Keddy, 1999). Testing island biogeography principles using only species richness may therefore overlook the influence of environmental filters and biotic interactions (Al-Namazi & Bonser, 2022).

Aridity is a particularly strong environmental filter in dryland ecosystems (Berdugo *et al.*, 2019, cited by Castro Sánchez-Bermejo *et al.*, 2022). It shapes plant community structure by constraining species diversity, distribution, and adaptive capacity (Rafiq *et al.*,2025). Increasing aridity, often reflected by decreasing precipitation along inland-coastal gradients, leads to marked shifts in species composition, ecosystem functioning and community resilience (Hurlbert *et al.*, 2019, cited in Mirzabaev *et al.*, 2022). In hyper-arid systems such as the central Namib Desert,

water availability governs plant establishment and survival (Scola *et al.*, 2017). Understanding how climate stress interacts with spatial processes is therefore essential for explaining biodiversity patterns in such environments. Aridity gradients are significant for understanding how species diversity responds to water availability and water stress (Castro Sánchez-Bermejo *et al.*, 2022; Moreira *et al.*, 2025), both of which are crucial in sustaining life in drylands.

However, island biogeography theory primarily seeks to explain broad-scale patterns of species richness and distribution and therefore does not explicitly account for species-level differences or trait-based processes that influence community assembly (McGill *et al.*, 2006, cited by Al-Namazi & Bonser, 2022). Species richness alone cannot fully describe the ecological processes structuring communities (Aggemyr *et al.*, 2018). Two islands may host the same number of species, yet differ markedly in their species composition, and thus in assembly processes and function (Kadmon & Pulliam, 1993). Integrating both species richness and composition therefore provides deeper insight into the ecological dynamics in fragmented or insular environments (Aggemyr *et al.*, 2018). Hence, it is important to integrate both diversity measures to understand the biodiversity patterns in an area.

Island biogeography is not limited to water-bounded landmasses (Al-Namazi & Bonser, 2022; Barthlott & Porembski, 2000). Terrestrial habitat islands, areas of favourable habitat surrounded by inhospitable matrices, function similarly (Al-Namazi & Bonser, 2022). Inselbergs are defined as rocky outcrops rising abruptly from a homogeneous landscape (Bremer & Sander, 2000; Willis, 1934). They serve as terrestrial islands (Barthlott & Porembski, 2000) with distinct microhabitats and sharp environmental contrasts relative to their surroundings (Matthews & Triantis, 2021; Parmentier *et al.*, 2005). Inselbergs vary greatly in both size and isolation (Barthlott & Porembski, 2000), some inselbergs stand completely isolated (Porembski, 2007), others occur as archipelagos (Jürgens & Burke, 2000), and some form detached remnants of spurs or ridges (Romer, 2005). Importantly, inselbergs in the central Namib Desert occur along a pronounced aridity gradient (Migon & Goudie, 2003), with inland inselbergs receiving more rainfall than coastal ones (Scola *et al.*, 2017). These spatial and climatic differences may act as environmental filters that influence plant communities. Consequently, inselbergs have proven valuable natural laboratories for studying biogeographical patterns (Barthlott & Porembski, 2000, cited by Hopper *et al.*, 2020).

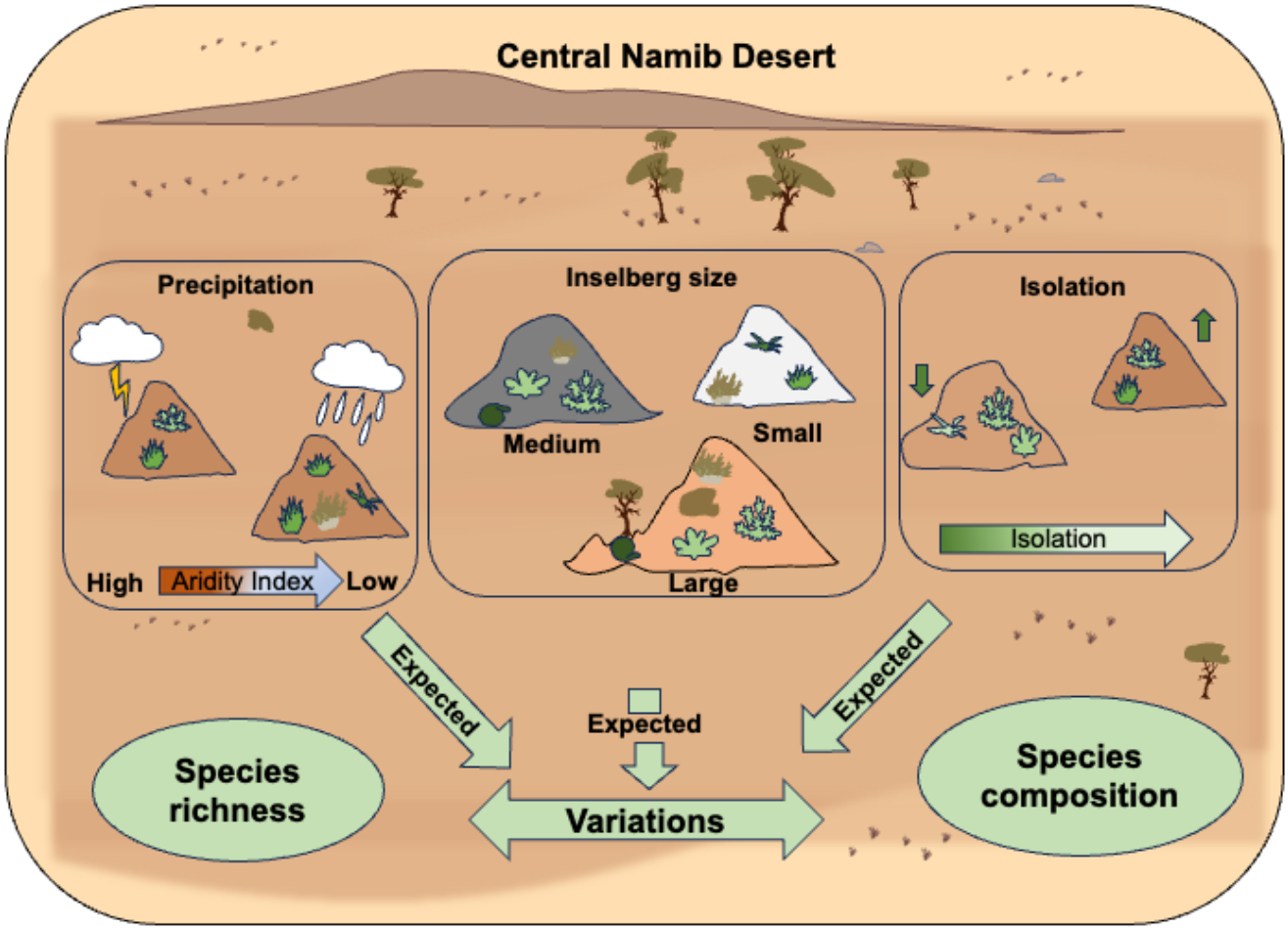


Figure 6. 1. Conceptual framework illustrating the influence of spatial isolation, size and precipitation on species richness and species composition on inselbergs in the central Namib Desert. This study examined how spatial factors (inselberg size and spatial isolation) and environmental filters (aridity index based on precipitation) influence species richness and species composition of vascular plants on inselbergs in the central Namib Desert.

The chapter postulates that:

(i) Species richness will be positively correlated with inselberg area. Classical island biogeography predicts increasing richness with area due to greater habitat heterogeneity and reduced extinction probability. It is expected that Pearson correlation and Spearman correlation analyses will show a significant positive relationship between diversity indices and inselberg size, and species composition will change with inselberg size

(ii) Species richness will be negatively correlated with spatial isolation. Increased isolation is predicted to reduce immigration rates, thereby limiting colonisation and lowering species richness. It is expected that diversity indices will decline with increasing inter-inselberg distance, and composition will shift along the isolation gradient in CCA ordination.

(iii) Species richness and evenness will decline with increasing aridity (lower precipitation), while species composition will shift along the precipitation gradient. Increasing aridity intensifies environmental filtering, favouring stress-tolerant taxa and reducing competitive diversity. It is expected that diversity indices will show significant relationships with precipitation, and CCA will reveal compositional structuring along the climatic gradient.

To test these hypotheses, the objectives of the study were to assess the relationship between inselberg size and both species richness and species composition, determine how spatial isolation (distance to the nearest inselberg) affects species richness and species composition, evaluate the influence of aridity (aridity index/precipitation) on species richness and species composition, and compare the relative importance of spatial processes (size and isolation) and environmental filtering (aridity) in shaping biodiversity patterns across inselbergs.

6.2 Results

6.2.1 Relationship between species richness, inselberg sizes, spatial isolation, and aridity index

Species richness showed no significant relationships with inselberg size (r_s = 0.026, p = 0.731; Table 6-1), precipitation (r_s = 0.111, p = 0.145), or spatial isolation (r_s = -0.031, p = 0.685) in the central Namib Desert. Pielou's evenness showed a significant negative relationship with precipitation (r_s = –0.243, p = 0.001; Table 6-1), indicating that evenness decreased as precipitation increased. However, evenness showed no correlation with inselberg's size (r_s = 0.048, p = 0.531) or spatial isolation (r_s = 0.032, p = 0.674).

Simpson's diversity index was not significantly correlated with any predictor, although it showed non-significant decrease with increasing precipitation (r_s = –0.142, p = 0.061; Table 6-1). Pearson's correlation coefficients further indicated that the total number of individuals, Margalef's richness, and Shannon diversity index were not significantly related to inselberg size, precipitation (aridity), or spatial isolation (Table 6-2; Figure 6-2).

Table 6. 1. Spearman's correlation coefficients between species richness, Pielou's evenness and Simpson's index in relation to environmental variables of inselbergs in the central Namib Desert. *Correlation is significant at the 0.01 level (2-tailed).

Spearman's rho		Size (ha)	Precipitation	Isolation
Species richness	Correlation Coefficient	0.026	0.111	-0.031
	Sig. (2-tailed)	0.731	0.145	0.685
Pielou's evenness	Correlation Coefficient	0.048	-0.243*	0.032

	Sig. (2-tailed)	0.531	0.001	0.674
Simpson's index	Correlation Coefficient	0.048	-0.142	0.016
	Sig. (2-tailed)	0.524	0.061	0.838
N		175	175	175

Table 6. 2. Pearson's correlation coefficients for the total number of individuals, Margalef's richness and Shannon diversity index in relation to environmental variables of inselbergs in the central Namib Desert.

Pearson's Correlation		**Size (ha)**	**Precipitation**	**Isolation**
Total individuals	Correlation Coefficient	-0.059	0.051	0.006
	Sig. (2-tailed)	0.436	0.5	0.938
Margalef' richness	Correlation Coefficient	0.092	0.098	0.075
	Sig. (2-tailed)	0.227	0.197	0.324
Shannon Index	Correlation Coefficient	0.031	-0.021	0.077
	Sig. (2-tailed)	0.683	0.783	0.313
N		175	175	175

6.2.2 Relationship between species composition and inselberg size, spatial isolation, and aridity

Canonical Correspondence Analysis (CCA) was performed to examine how species composition varied in response to inselberg size, spatial isolation, and precipitation (as a proxy for aridity). Unlike the richness results, the CCA ordination revealed clear compositional responses to environmental gradients.

The CCA biplot showed that isolation and precipitation were the most influential environmental variables shaping species composition as shown by their long arrows on the first two axes (Figure 6-2). The first two canonical axes captured 86.2% of the constrained variation, representing approximately 6.6% of total community variation. Species (eg. *Sesamum spp., Commiphora virgata and Vachellia erioloba)* clustering in the direction of the precipitation arrow were associated with high moisture availability, whereas species (eg. *Aloe asperifolia*, *Ceropegia pedicellata* and *Arthraerua leubnitziae*) positioned on the opposite side of the biplot occurred on more arid inselbergs.

Isolation also structured species composition with species (such *as Leptodenia albida* (formerly *Orthanthera albida*), *Pogonospermum cleomoides*, *Boscia foetida*, *Sesamum spp.*) clustering in

the direction of the isolation vector were associated with highly isolated inselbergs, whereas species (such as *Caroxylon* spp., *Tetraena cylindrifolia*, *Adenia pechuelii*, *Vachellia erioloba* and *Petalidium setosum*) occurring opposite the vector were associated with less isolated inselbergs. In contrast, inselberg size also contributed to compositional differences, although to a lesser extent, with species oriented toward the size vector associated with larger inselbergs.

Canonical correspondence analysis revealed a total inertia of 12.22. Environmental variables collectively explained 7.7% of the total variation in species composition (constrained inertia ≈ 0.94). Although environmental gradients structured species composition, a substantial amount of variation likely reflects microhabitat heterogeneity and unmeasured environmental or ecological processes. The overall model was statistically significant (*pseudo-F* = 4.8, *p* = 0.002; permutation test, Table 6.3). Eigenvalues for axes 1 and 2 were 0.5704 and 0.2402, respectively, indicating that most of the environmentally structured variation was concentrated along the primary gradient. These results suggest that precipitation and inselberg isolation are more important than inselberg size in structuring species assemblages across inselbergs of the central Namib Desert.

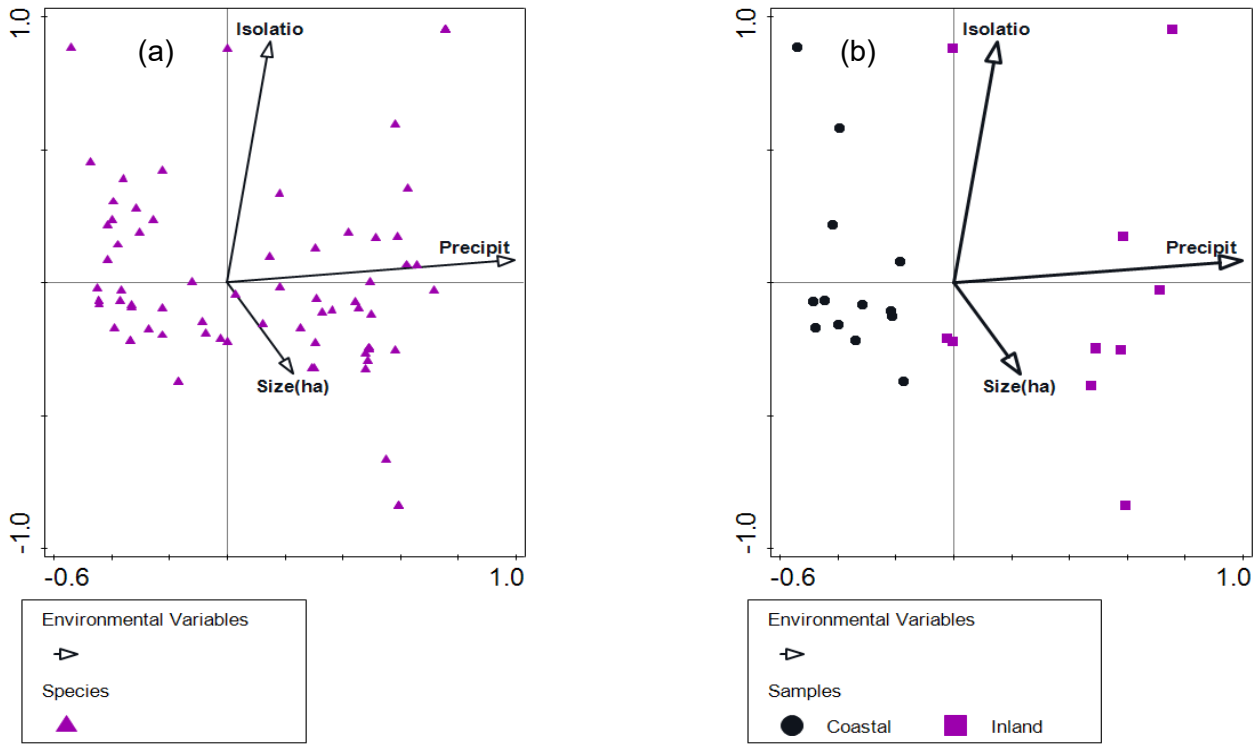


Figure 6. 2. CCA ordination showing the relationship between (a) species composition, (b) Sample sites and environmental variables (precipitation, inselberg size, and spatial isolation) in the central Namib Desert.

Table 6. 3. CCA summary.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5704	0.2402	0.1298	0.5427
Explained variation (cumulative)	4.67	6.63	7.69	12.13
Pseudo-canonical correlation	0.8965	0.7811	0.6771	0
Explained fitted variation (cumulative)	60.65	86.2	100	
Permutation Test Results:	*pseudo-F*=4.8, *p* =0.002			
Total variation is 12.22487, explanatory variables account for 7.7%				

The first hypothesis was partially supported as species richness and diversity indices showed no significant relationship with inselberg area. However, species composition was influenced by the size of inselbergs. The second hypothesis was also partially supported by the results - species richness, abundance and diversity indices showed no significant relationships with spatial isolation, however, species composition did. Finally, the last hypothesis was also partially supported as species richness and diversity indices showed no significant relationship with precipitation. Species evenness decreased with increasing precipitation, whereas it was predicted to decline with decreased precipitation. However, species composition differed significantly along the climatic gradient.

To disentangle the relative influence of geology and precipitation on community composition, partial canonical correspondence analysis (pCCA) was performed. This was done because one geological type (marble) was restricted to the coastal zone and did not occur along the whole precipitation gradient. Canonical correspondence analysis revealed that precipitation and geology both influenced species composition (Figure 6.3), collectively explaining 5.9% variation in species composition (Table 6.4). pCCA showed that geology independently explained 1.3% variation, whereas precipitation accounted for 4% (Table 6.4). Both variations explained only a small portion of differences in species composition (0.6%). Although these percentages seem low, the relationships were still statistically significant (rain and geology $p = 0.002$; just rain $p = 0.002$; just geology $p = 0.002$) indicating that these variables nevertheless contributed measurably to community structuring. These results indicated that precipitation was the dominant driver of species composition patterns, although geological substrates also contributed independently.

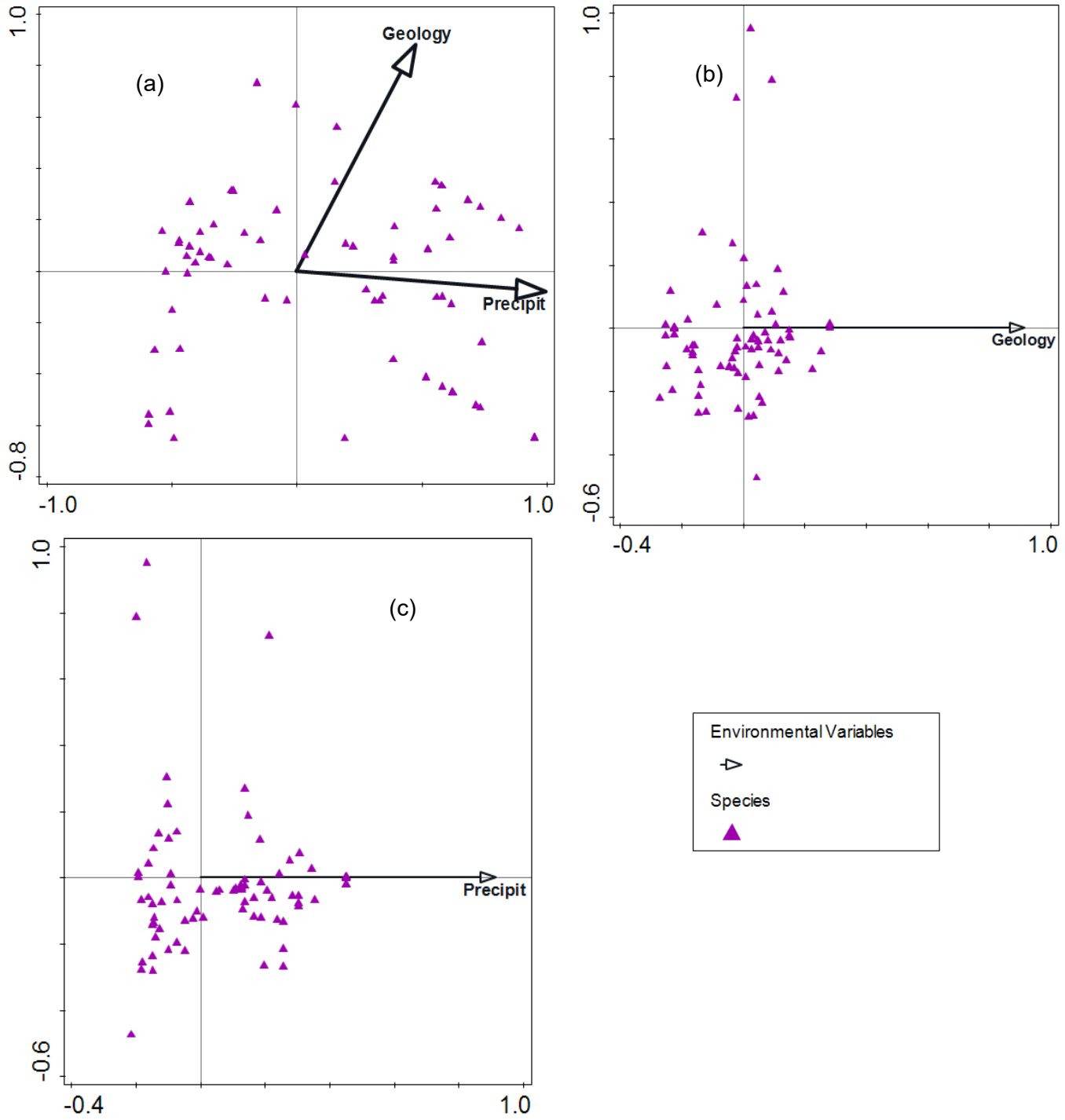


Figure 6. 3. Ordination showing the relationship between geology, precipitation and species composition in the central Namib Desert: (a) CCA including both geology and precipitation as explanatory variables, (b) pCCA ordination of species composition with geology as explanatory variable and precipitation as a covariate variable, (c) pCCA with precipitation as an explanatory variable and geology as a covariate variable.

Table 6. 4. Summary statistic table for CCA and pCCA.

Statistic (CCA **precipitation and geology**)	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5705	0.1533	0.5399	0.4932
Explained variation (cumulative)	4.67	5.92	10.34	14.37
Pseudo-canonical correlation	0.8969	0.6789	0	0
Explained fitted variation (cumulative)	78.82	100		
Permutation Test Results:	*pseudo-F* = 5.4, *p* = 0.002			
Total variation is 12.22487, explanatory variables account for 5.9%, adjusted explained variation is 4.8%				

Summary Table: **Geology**				
Statistic (pCCA)	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.156	0.5399	0.4932	0.4551
Explained variation (cumulative)	1.34	5.97	10.2	14.11
Pseudo-canonical correlation	0.6746	0	0	0
Explained fitted variation (cumulative)	100			
Permutation Test Results:	*pseudo-F* = 2.3, *p* = 0.002			
Partial variation is 11.65708, explanatory variables account for 1.3%, adjusted explained variation is 0.8%				

Summary Table: **Precipitation**				
Statistic (pCCA)	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4763	0.5399	0.4932	0.4551
Explained variation (cumulative)	3.98	8.48	12.6	16.4
Pseudo-canonical correlation	0.8883	0	0	0
Explained fitted variation (cumulative)	100			
Permutation Test Results:	*pseudo-F* = 7.1, *p* =0.002			
Partial variation is 11.97735, explanatory variables account for 4.0%, adjusted explained variation 3.4%				

6.3 Discussion

6.3.1 Relationships between diversity indices and inselberg size and spatial isolation

Pearson's correlation analysis showed no significant relationships between Shannon index, Margalef's richness, or total number of individuals with inselberg size or spatial isolation in the central Namib Desert. Similarly, Spearman rank correlations indicated no significant relationships between species richness or Simpson index with inselberg sizes or spatial isolation in the central Namib Desert.

These findings contrast with the classic island biogeography theory, which predicts increasing species richness with island area and decreasing richness with isolation. Several studies have supported the species-area relationship, (Aggemyr *et al.*, 2018; Couto *et al.*, 202; Kallimanis *et al.*, 2010; Porembski *et al.*, 1996), yet our results did not follow this pattern. Likewise, our findings did not support the commonly observed negative relationship between species richness and isolation. Several studies have similarly reported weak or absent isolation effects on species richness (Henneron *et al.*, 2019; Krauss *et al.*, 2004; Liu *et al.*, 2020a), suggesting this deviation may not be unusual, especially in terrestrial archipelagos.

A likely explanation is that many inselbergs in the central Namib Desert form archipelagos rather than isolated "islands" (Jürgens & Burke, 2000). Shared floras across neighbouring inselbergs may reduce the isolating effect of distance. Furthermore, environmental variables not measured here, especially substrate and microhabitat heterogeneity, may influence species richness more strongly than size or isolation. Burke (2019) reported that patch area and isolation explained little variation in inselberg specialists, whereas edaphic factors were highly influential. Similarly, Yates *et al.* (2019) showed species richness to be associated more strongly with bioclimatic variables than area or isolation. These results highlight the importance of effective habitat availability and heterogeneity over spatial metrics, which may drive species richness patterns on inselbergs.

The field observations support this interpretation. Inselbergs of similar size differed markedly in microhabitat diversity (Figure 6-3). A medium-sized inselberg with extensive smooth surfaces provided few microhabitats, whereas a smaller inselberg with rougher surfaces that accumulate soil supported more potential niches. This illustrates the concept of effective habitat area, where microhabitat diversity and the availability of colonisable substrates may outweigh total area as predictors of richness. This pattern is consistent with the Small Island Effect (Lomolino, 2000; Schrader *et al.*, 2020), where species richness becomes independent of area below a threshold due to limited habitat heterogeneity. Earlier studies (Hortal *et al.*, 2009; Ornduff, 1987; Pianka, 1966) similarly emphasised the importance of microhabitat diversity in structuring inselberg floras.

Together, these findings suggest that species richness on central Namib Desert inselbergs is rather shaped by habitat heterogeneity than by inselberg size or isolation. This is supported by Liu *et al.* (2023b), who observed habitat heterogeneity to be the most important predictor of vascular plants. This addresses objectives 1 and 2 of the chapter by indicating that area and spatial distance have limited explanatory power for richness in this hyper-arid context.

It is evident that these results do not support the hypothesis that species richness increases with inselberg size, contrary to classical species–area relationship expectations. There is also lack of a relationship between isolation and species richness that does not support the hypothesis that more isolated inselbergs would support fewer species. In contrast to species richness, species composition showed clear relationships with environmental variables, partially supporting the hypothesis that isolation structures community composition.

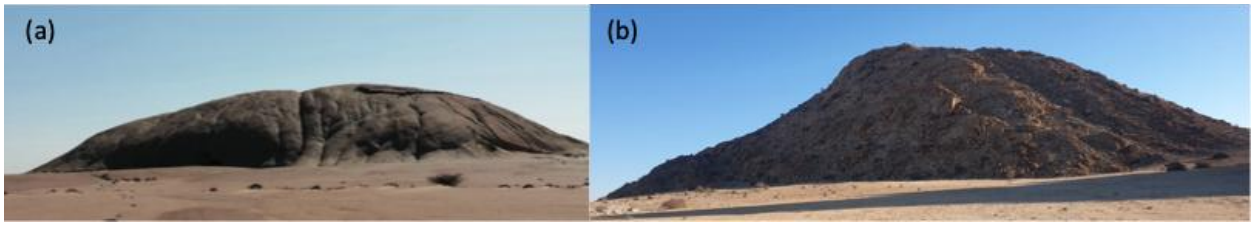


Figure 6. 4. Different morphological types of inselbergs in the central Namib Desert: (a) smooth surface with less soil accumulation and (b) rough surface with more soil accumulation.

6.3.2 Relationship between diversity indices and aridity of inselbergs

Species richness showed no significant relationship with precipitation, suggesting that richness is largely insensitive to rainfall variation in this hyper-arid system. This finding aligns with Luzuriaga *et al.* (2020), reporting that species richness in gypsum dryland was unresponsive to precipitation. Communities on nutrient-poor, stress-dominated soils may be buffered against short-term climatic fluctuations due to the dominance of long-lived, slow-growing, stress-tolerant species (Grime *et al.*, 2008). The hyper-arid conditions of the study region (aridity index < 0.10; UNEP, 1997) likely further constrain species turnover. While richness was unaffected, evenness showed a weak but significant negative relationship with precipitation, indicating that species abundances became more uneven with increasing precipitation. This likely reflects the episodic emergence of opportunistic, fast-growing species following rainfall events (Grime, 1977), which temporarily outcompete long-lived stress-tolerant species. Similar decreases in evenness with increasing resources have been reported across ecosystems (Engel *et al.*, 2009; Lewandowska *et al.*, 2016; Smith *et al.*, 2022) as competitive interactions intensify, allowing a few opportunistic species to dominate and reducing evenness across inselbergs.

These findings are consistent with Grime's (1988) Competitors, Stress-tolerators, and Ruderals (CSR) theory, which predicts competitive dominance under high-resource conditions and Tilman's (1982) resource-ratio theory, which suggests that increases in limiting resources, such as water, shift competitive dynamics in favour of species best able to exploit those resources. Thus, even though overall richness remains stable due to the persistence of stress-tolerant perennials, evenness is more responsive to rainfall, reflecting short-lived competitive dynamics.

These results address Objective 3 by demonstrating that aridity shapes community structure (evenness), but not richness. The absence of a clear relationship between species richness and precipitation does not support the hypothesis that richness declines with increasing aridity. However, in contrast to species richness, species composition showed clear relationships with environmental variables, partially supporting the hypothesis that aridity structures community composition.

6.3.3 Relationship between species composition and environmental variables

Unlike richness, species composition exhibited clear responses to environmental gradients. CCA revealed that precipitation (as a proxy for aridity index) and spatial isolation were stronger predictors than inselberg size. This suggests that while precipitation and isolation did not affect richness, they did affect which species occurred on different inselbergs. This follows the notion that two islands can have the same number of species, yet differ markedly in their composition (Kadmon & Pulliam, 1993).

The observed turnover may be strongly linked to differences in substrate among inselbergs. Geological types such as granite, schist, and marble vary in soil depth, nutrient availability, and microhabitat structure, which may act as environmental filters determining which species will colonise (Burke, 2001; Porembski, 2007). In Chapter 5, species richness did not differ significantly among geological types on inselbergs, while species composition did. This suggested that although the total number of species remained similar, the identities of the species present were influenced by substrate differences. The present analysis extends this pattern by showing that composition also responds to broader environmental gradients, specifically precipitation and spatial isolation, while richness remains largely unaffected. Together, these findings reinforce the idea that environmental filtering and habitat heterogeneity determine species presence, whereas richness is controlled by broader regional dynamics or long-term persistence of stress-tolerant species.

In other arid systems, precipitation has been shown to shape community composition by determining which species can persist in wetter versus drier microhabitats (Uhlmann *et al.*, 2004). Some of the species, like *Arthraerua leubnitziae*, *Aloe asperifolia* and *Ceropegia pedicellata*, were

mainly associated with drier inselbergs in the coastal sites. These species have xeromorphic features, they all possess succulence that specialised in water storage enabling them to survive in harsh conditions (Von Willert, 1992).

Isolation had a strong influence on species composition on inselbergs of the central Namib Desert. This pattern aligned with Kadmon and Pulliam, (1993), who found isolation to influence species composition in the absence of corresponding effect on species richness. The differences in environmental conditions may have led to the differences in species composition, influencing the effect of isolation (Field *et al.*, 2009).

Island area has been identified as a predictor of species composition on true islands (Aggermyr *et al.*, 2018). Size of Inselbergs in the central Namib Desert also influenced species composition, althought to a lesser extend in comparison to precipitation and isolation.

Total variation in species composition was 12.22%, of which the measured environmental variables explained 7.7% (constrained inertia ≈ 0.94). Although this represents a relatively small proportion, the model was highly significant, suggesting that precipitation and spatial isolation exert meaningful effects on community turnover. The large amount of unexplained variation is typical of ecological community datasets, which often reflect the influence of unmeasured abiotic or biotic factors (Borcard *et al.*, 1992; Økland, 1999). Since this study did not include all potentially relevant variables, it is likely that additional factors, such as soil depth, pH, moisture, shading, rock weathering features, and biotic interactions may also shape species composition. These results address Objective 4 and suggest that while precipitation and spatial isolation influence floristic patterns on Namib Desert inselbergs, unexplained finer-scale habitat conditions and ecological interactions may play a more decisive role in determining species composition.

This study also showed that geology influenced species composition independently of precipitation, although its contribution was relatively small, accounting for only 1.3% of the total inertia (11.7%) in the partial CCA. In contrast, precipitation emerged as the stronger driver of species composition independent of geology, explaining 4% of the total inertia (12%). This highlights the role of climatic gradients in structuring vegetation patterns on the inselbergs of the central Namib Desert.

The importance of substrate and microhabitat heterogeneity is widely recognised in inselberg ecology (Burke, 2001; Porembski, 2007). Differences in soil depth, fissure density, moisture retention, and nutrient availability among substrate types can strongly influence which species are able to persist. The present findings suggest that composition is shaped by both environmental filtering (precipitation, microhabitats & geology) and spatial processes (isolation).

Although some inselbergs form archipelagos, reducing complete isolation (Jürgens & Burke, 2000), the strong isolation gradient in the CCA indicates that dispersal processes still structure species turnover. Matrix permeability may moderate isolation effects (Burke, 2002; Martin-Queller *et al.*,2017; Zhang *et al.*, 2023), but it does not eliminate them. Further research is needed to quantify functional connectivity and confirm the role of the matrix in dispersal pathways.

6.4 Chapter summary

This chapter investigated how the patterns of species diversity and composition are influenced by environmental variables (size, isolation, and aridity) on inselbergs in the central Namib Desert. The main hypotheses postulated that species richness will be positively correlated with inselberg area. It was expected that Pearson correlation and Spearman correlation analyses would show a significant positive relationship between diversity indices and inselberg size, and species composition to change with inselberg size. This hypothesis was partially supported, species richness, abundance and diversity indices showed no significant relationships with inselberg size. However, species composition was significantly influenced by size of inselbergs, although to a lesser extent.

The second hypothesis predicted species richness to be negatively correlated with spatial isolation. It was expected that diversity indices will decline with increasing inter-inselberg distance, and composition to shift along the isolation gradient in CCA ordination. This hypothesis was also not supported as species richness, abundance and diversity indices was not significantly affected by distance. However, species composition was strongly shaped by spatial isolation. This study did not support the classic theory of island biogeography that predicts species richness to increase with area due to greater habitat heterogeneity and reduced extinction probability, nor did it support the prediction that increased isolation will reduce immigration rates, thereby limiting colonisation and lowering species richness.

The third hypothesis predicted species richness and evenness to decline with increasing aridity (lower precipitation) and species composition to shift along the precipitation gradient. However, species richness, abundance and diversity measures were not significantly correlated with precipitation, although species evenness was negatively correlated with precipitation (aridity index) and species composition was strongly shaped by precipitation/aridity index.

Although species composition was significantly influenced by the measured variables, these findings should be applied with caution when explaining the results. Most of the variation, 92.3%, is ascribed to unmeasured abiotic factors, biotic interactions, and stochastic processes, a pattern commonly observed in ecological community studies (Økland, 1999).

Overall, these results indicate that while the total number of species remains constant, the identity of species changes across environmental gradients. This turnover reflects environmental filtering and substrate-mediated microhabitat differences. This chapter demonstrates that species richness on Namib Desert inselbergs is resilient to variations in size, isolation, and precipitation, whereas species composition is more sensitive to environmental gradients and microhabitat differences. These findings highlight the importance of considering both richness and composition, as well as substrate heterogeneity and environmental filtering, when assessing biodiversity patterns in terrestrial island-like systems such as inselbergs. Collectively, these findings indicate that, in this system, classical island biogeography predictions are not supported for species richness, while community composition is primarily structured by environmental filtering along climatic and spatial gradients. However, isolation in this study was quantified as the distance to the nearest neighbouring inselberg rather than the distance to a mainland source area, as originally proposed by MacArthur and Wilson (1967). Future research should evaluate alternative measures of isolation, including distance to a potential mainland source, to determine which metric better explains vegetation patterns in the central Namib Desert.

Table 6. 5. Evaluation of study hypotheses in relation to observed patterns.

Hypothesis	**Expectation**	**Findings**	**Support**
(i) Species richness, diversity and abundance will be positively correlated with inselberg area. Classical island biogeography predicts increasing richness with area due to greater habitat heterogeneity and reduced extinction probability. Species composition will change will inselbergs size	Pearson correlation and Spearman correlation analyses will show a significant positive relationship between diversity indices and inselberg size. CCA will reveal compositional structuring with inselbergs size	No significant relationships between species richness, abundance, diversity indices inselbergs size. Species composition was significantly influenced by the size of inselbergs.	**Partially supported.** Species richness, abundance, diversity was not positively correlated with inselbergs sizes. However, CCA reveal a compositional structuring.
(ii) Species richness, diversity, and abundance will	Diversity indices will decline with increasing	No significant relationships	**Partially supported.**

be negatively correlated with spatial isolation, while species composition will shift along. Increased isolation is predicted to reduce immigration rates, thereby limiting colonisation and lowering species richness.	inter-inselberg distance, and composition will shift along the isolation gradient in CCA ordination.	between richness, diversity indices and spatial isolation. Spatial isolation strongly structured species composition in CCA.	Species richness, diversity indices had no significant relationship. Species composition was strongly structured by spatial isolation.
(iii) Species richness, diversity, and abundance will decline with increasing aridity (lower precipitation), while species composition will shift along the precipitation gradient. Increasing aridity intensifies environmental filtering, favouring stress-tolerant taxa and reducing competitive diversity.	Diversity indices will show significant relationships with precipitation, and CCA will reveal compositional structuring along the climatic gradient.	Species richness, diversity indices showed no significant relationships with precipitation. Species evenness declined with increasing precipitation. However, species composition was strongly shaped by precipitation in CCA.	**Partially supported.** Composition differed, but richness patterns does not match predictions.

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CHAPTER 7: CONCLUSIONS AND RECOMMENDATIONS

7.1 Revisiting the hypotheses

Inselbergs are defined as isolated rocky outcrops that rise above a plain landscape (Barthlott & Porembski, 2000). While inselbergs are recognised as being important for conservation in arid regions, as they may potentially provide a buffer in the face of a changing climate (Bond & Richardson, 1990, cited in Burke, 2001). To understand the biodiversity of inselbergs in the central Namib Desert to inform conservation planning, this study examined the patterns of plant diversity on inselbergs along the aridity gradient in the central Namib Desert. The study had three objectives with associated hypotheses (Table 7.1). The first was to compile an inventory of species richness and species composition on inselbergs and the surrounding matrix, focusing on the question “How does species richness differ between inselbergs and the surrounding matrix?” To address the research question, chapter 4 tested two hypotheses. The first hypothesis proposed that plant species richness and alpha diversity will be significantly higher on inselbergs than in the surrounding matrix. It was therefore expected that Shannon diversity, Margalef’s richness, and total species counts will be significantly greater on inselbergs than in matrix habitats. The second hypothesis was that species composition will differ significantly between inselbergs and the surrounding matrix. It was expected that NMDS ordination will show discrete clustering of inselberg and matrix plots, and PERMANOVA will detect significant compositional differences.

The second objective of the dissertation was to compare species richness and species composition across topographical positions, slope aspects, and geological types. The research question asked how do species richness and species composition vary across environmental variables? Several hypotheses were tested: (i) Lower topographical strata (footslopes) will support higher species richness and differ compositionally from midslopes and crests. It is expected that diversity indices will decline from footslope to crest, and PERMANOVA will detect compositional differentiation among strata. (ii) Southwest-facing slopes will support higher species richness and distinct species composition compared to northeast-facing slopes. It was expected that diversity indices will be significantly higher on southwest slopes, and ordination analyses will reveal aspect-related clustering.; (iii) Species composition and richness will differ among granite, marble, and schist inselbergs. Granite-derived substrates were expected to favour oligotrophic specialists; marble-derived soils should support calcicolous assemblages; schist was predicted to exhibit intermediate characteristics. It was expected that PERMANOVA and indicator species analysis will detect significant compositional differences among geological types. Richness patterns would reflect substrate-driven environmental filtering.

The final dissertation objective was to determine the relationship between species richness and species composition with respect to size, isolation, and aridity index (precipitation). This involved answering the questions what are the relationships between species richness and species composition, and the size, isolation, and aridity index? We hypothesised that species richness will be positively correlated with inselberg area. It was expected that Pearson correlation and Spearman correlation analyses would show a significant positive relationship between diversity indices and inselberg size, and species composition will be unique with inselberg sizes. The second hypothesis postulated that species richness would be negatively correlated with spatial isolation. It was expected that diversity indices would decline with increasing inter-inselberg distance, and composition would shift along the isolation gradient in CCA ordination. According to the third hypothesis, species richness and evenness would decline with increasing aridity (lower precipitation), while species composition would shift along the precipitation gradient. It was expected that diversity indices would show significant relationships with precipitation, and CCA would reveal compositional structuring along the climatic gradient.

Table 7. 1. Evaluation of study hypotheses in relation to observed patterns.

Hypothesis	**Tested in chapter**	**Supported**	**Evidence**
Inselbergs will support more species richness, abundance and diversity due to habitat heterogeneity, microclimatic buffering than the matrix	Chapter 4	**Supported**. Species richness, abundance and diversity differ among strata.	Significant differences between inselbergs and matrix. Inselbergs had higher richness, diversity and abundance than matrix.
Inselbergs and the matrix will support distinct species composition because of environmental filtering driven by lithology, soil development	Chapter 4	**Supported.** Inselbergs hosted distinct species composition than the matrix.	Significant differences in species composition between inselbergs and matrix. 92% variations
Lower strata (footslopes) will support greater species richness and composition than higher	Chapter 5	**Not supported.** Species richness did not differ among strata. Inselbergs as	No significant differences among footslope, midslope, and crest. All strata had higher richness than matrix.

strata (midslopes and crests).		a whole differed from matrix only.	
Southwest-facing slopes will host more diverse plant communities than northeast-facing slopes due to fog interception.	Chapter 5	**Not supported.** Slope aspect had no measurable effect.	No significant differences in richness, diversity indices, or composition.
Species composition and richness will differ among granite, marble, and schist inselbergs. Lithological differences generate contrasting soil chemistries and nutrient availability.	Chapter 5	**Partially supported.** Composition differed, but richness pattern does not match predictions.	Species richness did not differ among granite, marble, and schist. Composition differed significantly among all three, but with overlapping species.
Species richness, diversity and abundance will be positively correlated with inselberg area. Classical island biogeography predicts increasing richness with area due to greater habitat heterogeneity and reduced extinction probability. Species will change will inselbergs size	Chapter 6	**Partially supported.** richness, abundance, diversity was not positively correlated with inselbergs sizes. However, CCA reveal a compositional structuring.	No significant relationships between species richness, abundance, diversity indices inselbergs size. Species composition was significantly influenced by the size of inselbergs.
Species richness, diversity and abundance will be negatively correlated with spatial isolation, while species composition will shift along. Increased isolation is predicted to reduce immigration rates, thereby limiting	Chapter 6	**Partially supported.** Species richness, diversity indices had no significant relationship. Species composition was strongly structured by spatial isolation.	No significant relationships between richness, diversity indices and spatial isolation. Spatial isolation strongly structured species composition in CCA

colonisation and lowering species richness.			
Species richness and diversity indices will decline with increasing aridity (lower precipitation), while species composition will shift along the precipitation gradient. Increasing aridity intensifies environmental filtering, favouring stress-tolerant taxa and reducing competitive diversity.	Chapter 6	**Partially supported.** Composition differed, but richness pattern does not match prediction.	Species richness, diversity indices showed no significant relationships with precipitation. Species evenness declined with increasing precipitation. However, species composition was strongly shaped by precipitation in CCA.

7.2 Major findings

This study revealed that inselbergs host greater species richness and unique species composition compared to the surrounding matrix. This supported the hypotheses that plant species richness and alpha diversity will be significantly higher on inselbergs and differ compositionally from the surrounding matrix (Figure 7.1; Table 7.1). This study failed to accept the null hypotheses.

Topographical positions hosted unique flora and high levels of species richness, whilst species richness on matrix sites were low. The specific position on inselbergs (i.e. footslopes, midslopes, and crests) did not affect either species richness, or floristic composition, they separated the matrix from the inselberg strata. This partially supported the hypothesis that lower topographical strata (footslopes) will support higher species richness and differ compositionally from midslopes and crests (Figure 7.1; Table 7.1).

Similar to inselberg strata, slope aspect did not have a significant effect on the richness and composition of flora on inselbergs. These findings did not support the hypothesis that southwest-facing slopes will support higher species richness and distinct species composition compared to northeast-facing slopes (Figure 7.1; Table 7.1). Diversity indices were not significantly higher on southwest slopes, and ordination analyses did not reveal aspect-related clustering.

Geological types influenced species richness and species composition significantly, with species richness only separating the matrix from inselbergs' geology (marble, granite, and schist). Geological types had higher species richness compared to the surrounding matrix, however,

species richness did not differ among the geological types. On the other hand, species composition significantly differed among inselbergs' geology as well as the surrounding matrix. These findings partially supported the hypothesis that species composition and richness will differ among granite, marble, and schist inselbergs (Figure 7.1; Table 7.1).

Moreover, there were no relationships between diversity indices and the size, isolation, and aridity index of inselbergs, except for evenness that decreased with increasing precipitation (Figure 7.1; Table 7.1). The size and precipitation (aridity index) influenced species composition, while isolation had little influence. The lack of correlation with isolation may reflect the semi-permeable nature of the surrounding matrix, enabling species dispersal despite geographic separation. There were no significant relationships between species richness and diversity indices with inselberg size. However, species composition was significantly influenced by the size of inselbergs. Diversity indices did not decline with increasing inter-inselberg distance, indicating a no significant relationship. However, species composition shifted along the isolation gradient in CCA ordination. Species richness and diversity showed no significant relationships with precipitation. Species richness or evenness did not decline with lower precipitation. Species evenness increased with increasing precipitation. However, species composition was strongly influenced by precipitation and CCA revealed compositional structuring along the climatic gradient.

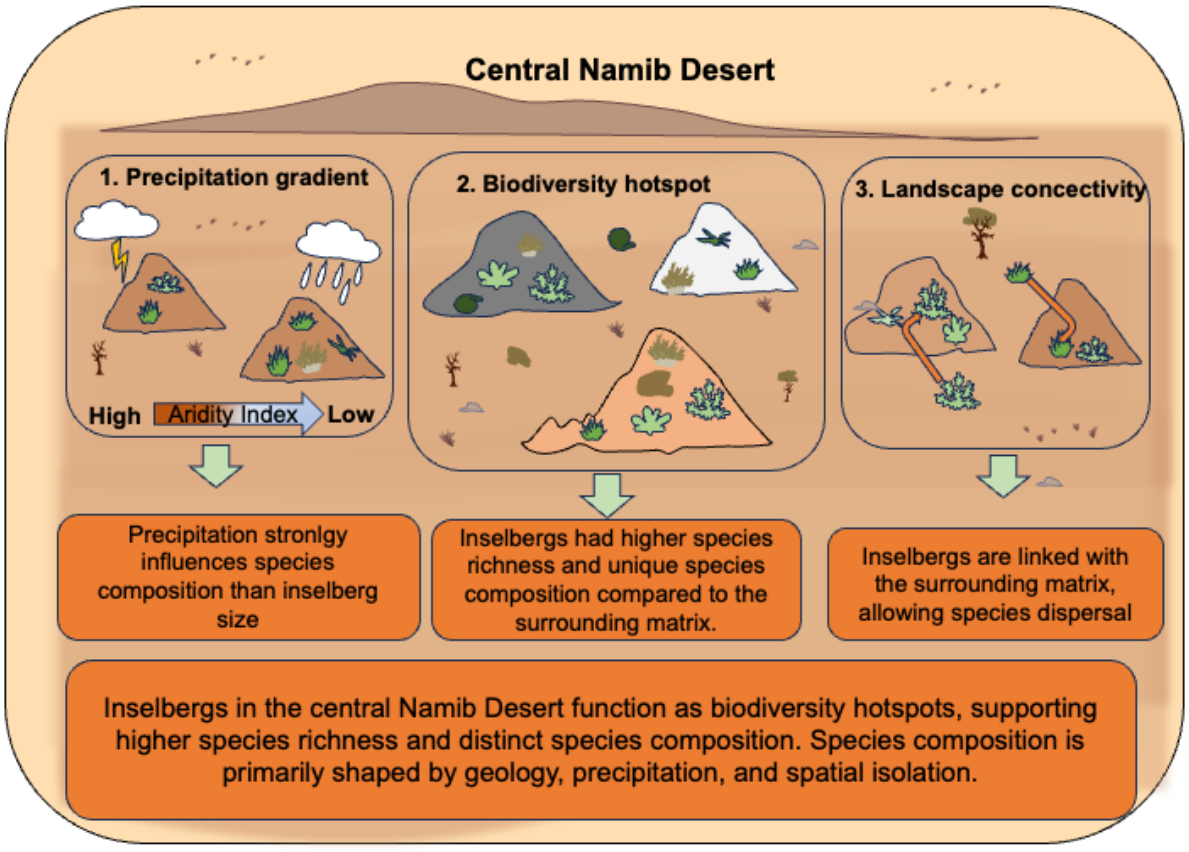


Figure 7. 1. Conceptual framework illustrating the major findings of the study.

The consistent pattern observed from this study was that inselbergs host more species compared to the surrounding matrix. It does not matter the geology or topographical position; it will still have more species than the surrounding matrix. This can be attributed to the heterogeneity of inselbergs, microclimate, and microhabitats which contrasts with the surrounding matrix. Supported by previous studies such as Kluge & Büdel, 2009. The availability of microhabitats and edaphic conditions on inselbergs that are different from the surrounding matrix supports plant communities that differ from the surrounding matrix. The other important pattern is that geological type influences the species composition on inselbergs of the central Namib Desert. Different rock types may influence the edaphic conditions, and this may promote different species on inselbergs (Glime & da Silva, 2009).

There are three main findings from this study. Firstly, inselbergs increase plant compositional heterogeneity and richness in the central Namib Desert. This pattern is consistent with previous studies showing that inselbergs often support higher species richness and distinct plant communities compared to the surrounding matrix. In hyper-arid environments such as the central Namib Desert, plant diversity is generally expected to be low due to extreme temperatures, nutrient-poor soils, and highly sporadic rainfall. However, inselbergs create localised environmental conditions that differ from the surrounding matrix. Their topographic complexity can enhance water accumulation, reduce evapotranspiration in certain microhabitats, and create small-scale refugia for plant establishment. As a result, inselbergs function as “wetter islands” within the desert landscape, supporting higher species richness and unique plant composition. This highlights the ecological importance of inselbergs as biodiversity hotspots within the Namib Desert, which may be critical for maintaining regional plant diversity, particularly in hyper-arid environments where suitable habitats are limited. Conservation efforts should prioritise minimising disturbances such as mining and driving on inselbergs as they may support species that are absent in the surrounding desert matrix.

Secondly, precipitation structures plant composition more strongly than inselberg size in the hyper-arid central Namib Desert. A common expectation for habitat islands is that larger islands support more diverse and compositionally complex communities because they provide a greater variety of microhabitats for species establishment. Consequently, inselberg size would be expected to play a key role in shaping plant community composition. However, the results of this study indicated that precipitation gradients exert a stronger influence on plant composition than inselberg size. The central Namib Desert is adjacent to two floristically distinct biomes, the Nama-Karoo and the Succulent Karoo, and the influence of these biomes may have shaped plant communities on inselbergs along the west–east aridity gradient. From field observation, more arid

inselbergs on the western side were dominated by succulent species and drought-tolerant plants that require minimal and irregular moisture inputs, reflecting the potential floristic influence of the Succulent Karoo biome. In contrast, inselbergs located in relatively wetter eastern areas support a greater proportion of non-succulent species, although these plants still exhibit adaptations to dry conditions. The composition of these eastern inselbergs may be more strongly influenced by species associated with the Nama-Karoo biome.

These findings suggest that regional climatic gradients and biogeographic influences may override the effects of inselberg size in determining plant community composition in hyper-arid regions. This highlights the importance of inselbergs across the full west–east precipitation gradient of the central Namib Desert as species composition changes along climatic gradients. Inselbergs should therefore be considered as part of a broader landscape-scale network of habitat islands shaped by regional climate and potentially surrounding biomes.

Lastly, inselbergs (desert “islands”) function along a connectivity continuum rather than as isolated entities only. True islands are typically separated by an inhospitable matrix that restricts species dispersal, resulting in distinct and clearly bounded biological communities. Thus, island communities are expected to be strongly isolated from their surrounding environment. However, the results of this study suggest that inselbergs in the central Namib Desert are not ecologically isolated in the same way as true oceanic islands. Instead, they are embedded within a semi-permeable matrix that allows some degree of species movement through dispersal. Plant communities on inselbergs and the surrounding matrix do not exhibit a sharp boundary, but rather a gradual transition in species composition. Several plant species occur both on inselbergs and in the surrounding matrix, although often in different abundances. This indicates that inselbergs function as part of a connected landscape mosaic rather than as completely discrete ecological units. The matrix may facilitate species dispersal and contribute to maintaining plant populations on inselbergs and vice versa, as they operate as interconnected components of the broader desert landscape.

These findings highlight the ecological importance of inselbergs in biodiversity conservation in the Namib Desert and as a potential refuge under changing climate conditions (Burke, 2003; Buschke *et al.*, 2020). The results highlight inselbergs as biodiversity hotspots with distinct plant communities relative to the surrounding matrix, indicating their importance as conservation priority habitats within the central Namib Desert. The study further shows that species composition is primarily structured by precipitation, geology, and spatial isolation rather than inselberg size, suggesting that conservation prioritisation should not rely solely on island size as a proxy for biodiversity value. These findings support the conservation of multiple inselbergs across different geological types and environmental gradients to capture regional plant diversity and maintain

landscape-scale heterogeneity. This supports Burke's (2002) conclusion that conservation should prioritise representative networks of inselbergs to maximise regional biodiversity and maintain ecological connectivity. Given that turnover due to nestedness implies that conservation strategies can prioritise species-rich subsets (Baselga, 2010), conserving inselbergs could indirectly preserve a significant proportion of the matrices' biodiversity as well.

7.3 Rethinking inselbergs as ecological islands in arid landscapes

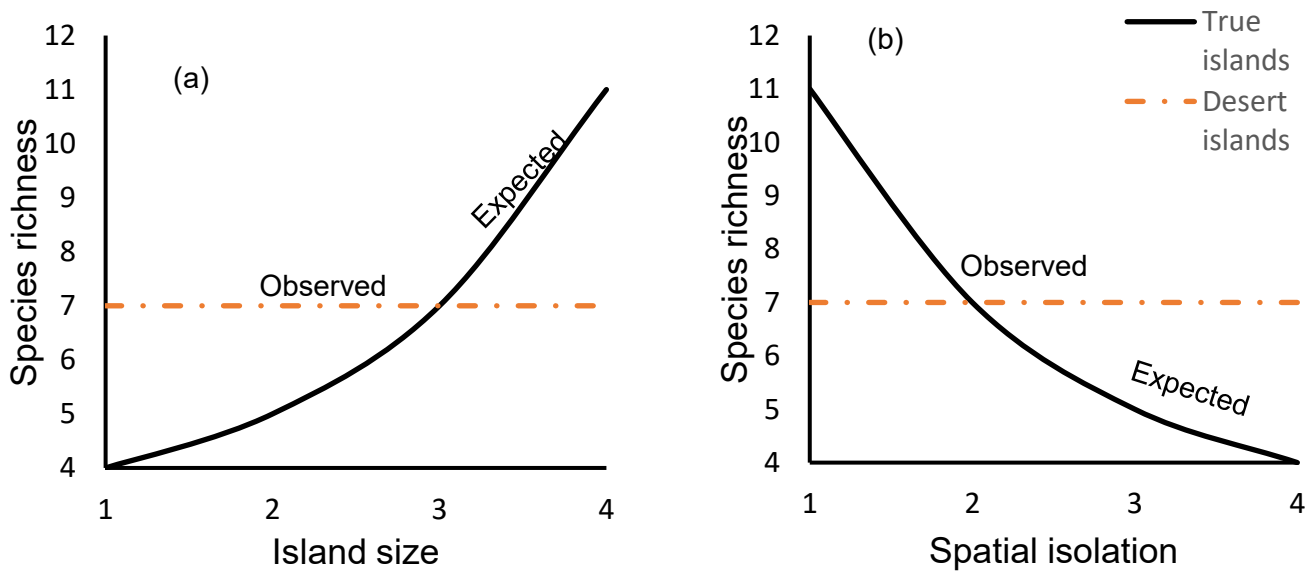


Figure 7. 2. Comparison of species richness patterns predicted by the classic Theory of Island Biogeography in relation to observed patterns in a hyper-arid desert. (a). Species richness is predicted to increase with island size in traditional islands (solid black line). (b). Species richness is predicted to decrease with increasing isolation in traditional islands (solid black line). However, inselbergs showed no significant relationships with either size or isolation (orange dashed lines, observed).

The most fundamental premise of island biogeography theory states that species richness increases with island area. This is ascribed to larger islands having lower extinction rates and contain greater habitat heterogeneity. In this study, it was found that larger inselbergs did not support more species than smaller inselbergs and area was not positively correlated with alpha diversity.

Further theory suggests that species richness increases not only with area but with environmental heterogeneity. This was expected for the inselbergs in this study, due to geological complexity, topographic variation and microclimatic gradients. However, no differences were detected for any such variables.

In Island Biogeography Theory, more isolated islands show greater compositional distinctness. This is because reduced immigration leads to divergence and stochastic colonisation events shape communities. This study supports this theory, as inselberg species composition increased with distance (isolation) and the ordinations showed such spatial structuring, especially for the most isolated inselbergs. However, isolation had no effect on species richness.

Species assemblages on small islands are considered as subsets of those on large islands (nestedness) according to island biogeography theory. There is selective extinction of rare species on small islands. This was not supported by this study, the Simper analysis showed that most species occurred on all inselbergs of varying sizes, just in different mean abundance. In fact, small inselbergs had more species that contributed to the overall dissimilarity than large or medium-sized inselbergs. This again supported the conclusion that effective habitat availability influences species community more than the mere size of an island.

Table 7. 2. Evaluation of true islands in relation to observed patterns on terrestrial islands (inselbergs) in the central Namib Desert.

	True islands	Habitat islands (inselbergs)	Supported
Island size	Species richness increases with island area.	Larger inselbergs did not support more species than smaller inselbergs and area was not positively correlated with alpha diversity.	Not supported.
Habitat heterogeneity	Species richness increases with environmental heterogeneity.	No differences were detected for any such variables (geology, topography).	Not supported.
Isolation	More isolated islands show greater compositional distinctness.	This study supports this theory, as inselberg species composition increased with distance (isolation) and the ordinations showed such spatial structuring, especially for most isolated inselbergs. However, isolation had no effect on species richness. Furthermore, isolation in this study was quantified as the distance to the nearest inselbergs. Future should use other metric such as distance to the mainland for comparison.	Partially supported

From the above, central Namib inselbergs function not as discrete oceanic analogues, but as semi-connected habitat features embedded within a dispersal-permeable desert matrix. As a terrestrial system, this study also explores beyond classical island biogeography theory. It investigated how environmental gradients (e.g., aridity, substrate) modify colonisation success. The study clearly showed that not all species can colonise all inselbergs and that substrate and precipitation constrain community assembly.

7.4 Recommendations and future research

To better understand the influence of environmental factors on species composition and species richness on the inselbergs in the central Namib Desert, more environmental variables and species functional traits should be included. Further research should incorporate additional abiotic variables such as microhabitat data (soil nutrient content, pH, organic matter) and microtopography, as these factors likely influence plant distribution and diversity on inselbergs. The environmental variables measured in this study only explained 7.7% of the variation in species composition, meaning 93.4% remained unexplained. Moreover, additional research is needed to quantify how the surrounding matrix facilitates or restricts species movement to clarify whether it acts as a dispersal corridor or barrier. Further studies are needed to quantify the relative contributions of turnover and nestedness in structuring these communities on inselbergs and the surrounding matrix.

Geological substrate and precipitation regime were partially confounded in this study because marble inselbergs only occurred within the coastal zone. Consequently, lithological effects cannot be interpreted as fully independent of climatic gradients. It is therefore possible that some compositional differences attributed to geology reflect underlying aridity or fog-related moisture inputs. Although CCA identified significant substrate associations, the shared variance between geological and climatic predictors limits definitive causal inference. Future studies employing balanced sampling across geological types within similar precipitation regimes, or variance partitioning approaches, would allow clearer separation of these effects.

Moreover, future studies should consider alternative isolation metrics such as distance to the mainland to compare it to the classical Theory of Island Biogeography to see if they will get the same patterns as this study.

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ANNEXURE A

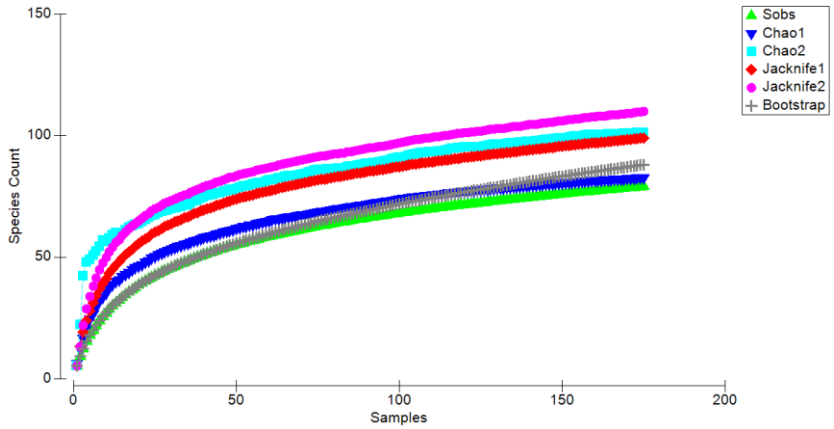


Figure A- 1. Species accumulation curve of inselbergs in the central Namib Desert.

Table A- 1. SIMPER analysis of species composition between inselbergs and their surrounding matrices in the central Namib Desert.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Matrix	Mean Inselberg
Pogo cle	20.54	22.43	22.43	1.04	12.4
Caro sp	10.36	11.31	33.74	2.88	2.82
Tetr stap	7.197	7.859	41.6	0.58	3.78
Aloe asp	6.485	7.081	48.68	0.2	4.46
Peta set	5.197	5.675	54.36	0.26	2.3
Tetr cyl	4.775	5.215	59.57	0.44	2.66
Arth leu	4.164	4.547	64.12	0.82	0.68
Sesa sp	3.418	3.733	67.85	0.44	1.14
Klei lon	1.634	1.784	69.63	0	1.08
Comm sax	1.34	1.463	71.1	0.06	0.576
Cali cap	1.31	1.43	72.53	0.24	0.416
Dyer afr	1.282	1.4	73.93	0	0.712
Mons mar	1.003	1.095	75.02	0	0.504
Comm vir	0.9917	1.083	76.1	0.12	0.368
Euph gla	0.9676	1.057	77.16	0.22	0.296
Tetr red	0.9252	1.01	78.17	0	1.31
Blep obm	0.9245	1.01	79.18	0	0.824
Orth alb	0.9117	0.9955	80.18	0.1	0.2
Euph gie	0.9035	0.9866	81.16	0	0.632
Euph vir	0.8329	0.9095	82.07	0	0.368
Heli tom	0.8265	0.9025	82.98	0	0.4
Hood ped	0.8131	0.8879	83.86	0.02	0.528
Blep gro	0.7837	0.8558	84.72	0	1.56
Peta var	0.7713	0.8423	85.56	0	0.52
Comm gla	0.7191	0.7852	86.35	0	0.36
Tric afr	0.7111	0.7765	87.12	0	0.544
Sear mar	0.6761	0.7383	87.86	0.3	0.032
Chas gar	0.6653	0.7265	88.59	0.18	0.12
Pech leu	0.663	0.7239	89.31	0.16	0.144
Myro fla	0.6508	0.7106	90.02	0	0.696
Cryp dec	0.6276	0.6854	90.71	0	0.216
Cyna vim	0.5985	0.6535	91.36	0	0.6
Barl mer	0.5966	0.6515	92.01	0.04	0.24
Hood cur	0.5391	0.5887	92.6	0	0.184
Aizo afr	0.5268	0.5752	93.18	0.14	0.016
Acac eri	0.5222	0.5702	93.75	0.14	0
Aden pec	0.4588	0.501	94.25	0.14	0.016
Jame max	0.3824	0.4176	94.67	0.06	0.136
Amph div	0.3744	0.4088	95.07	0	0.304
Euph lig	0.3729	0.4072	95.48	0	0.2
Unid 11	0.3397	0.3709	95.85	0	0.256
Aden pec	0.3378	0.3688	96.22	0	0.184
Cada aph	0.3357	0.3666	96.59	0	0.152
Aspa pea	0.285	0.3112	96.9	0.06	0.112
Unid 4	0.2542	0.2776	97.18	0	0.12
Unid 6	0.2436	0.266	97.44	0	0.08
Bosc foe	0.2344	0.256	97.7	0.04	0.088
Mont car	0.2121	0.2316	97.93	0	0.2
Unid 1	0.1914	0.209	98.14	0.08	0
Vach ref	0.1776	0.1939	98.33	0.04	0.104
Pela ota	0.1643	0.1794	98.51	0	0.168
Maer sch	0.1576	0.1721	98.68	0	0.048
Cucu mee	0.1134	0.1238	98.81	0	0.048
Codo sp	0.09975	0.1089	98.92	0	0.048
Grew sp	0.09222	0.1007	99.02	0	0.016
Gorm fil	0.08851	0.09666	99.11	0.02	0.008
Ster afr	0.08756	0.09561	99.21	0	0.024
Park afr	0.08735	0.09538	99.31	0.04	0
Unid 2	0.07336	0.08011	99.39	0	0.032
Abut pyc	0.06529	0.0713	99.46	0	0.04
Geig orn	0.06338	0.06921	99.53	0	0.032
Teph dre	0.05408	0.05906	99.59	0	0.056
Comm squ	0.04955	0.05411	99.64	0	0.056
Unid 3	0.04725	0.05159	99.69	0	0.016
Unid 8	0.0362	0.03953	99.73	0	0.04
Lyci cin	0.03595	0.03925	99.77	0	0.024
Euph phy	0.02599	0.02838	99.8	0	0.008
Bosc alb	0.02436	0.0266	99.82	0	0.008
Sola hum	0.0203	0.02217	99.85	0	0.016
Comm ter	0.01816	0.01983	99.87	0	0.008
Crot gra	0.01769	0.01932	99.89	0	0.016
Unid 9	0.01712	0.0187	99.9	0	0.016
Fors sp	0.01504	0.01643	99.92	0	0.008
Dico tom	0.01448	0.01581	99.94	0	0.016
Unid 7	0.01448	0.01581	99.95	0	0.016
Eucl und	0.01423	0.01554	99.97	0	0.008
Aloe dic	0.01121	0.01225	99.98	0	0.008
Unid 5	0.009047	0.009879	99.99	0	0.008
Unid 10	0.008561	0.009348	100	0	0.008
Overall average dissimilarity = 91.58%					

Table A- 2. Pairwise PERMANOVA of species composition between the topographical positions.

Pairwise PERMANOVA				
	Matrix	Footslope	Midslope	Crest
Matrix		0.0006	0.0006	0.0006
Footslope	0.0006		1	1
Midslope	0.0006	1		1
Crest	0.0006	1	1	

Table A- 3. Pairwise PERMANOVA of species composition between the geological types of inselbergs in the central Namib Desert.

Pairwise permanova				
	Matrix	Marble	Granite	Schist
Matrix		0.0762	0.0006	0.0006
Marble	0.0762		0.0006	0.0006
Granite	0.0006	0.0006		0.0018
Schist	0.0006	0.0006	0.0018	

Table A- 4. SIMPER analysis of species composition between topographical positions and geological types of inselbergs in the central Namib Desert.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Matrix	Mean Footslope	Mean Midslope	Mean Crest	
Pogo cle	19.99	22.49	22.49	1.04	14.3	10.5	12.4	
Caro sp	8.523	9.589	32.08	2.88	2.34	3.12	3.16	
Tetr stap	6.985	7.859	39.94	0.58	4.52	3.6	2.64	
Aloe asp	6.918	7.784	47.72	0.2	4.7	4.88	3.16	
Peta set	5.138	5.781	53.5	0.26	2.6	2.12	2.04	
Tetr cyl	4.956	5.576	59.08	0.44	1.54	2.92	4.4	
Arth leu	3.339	3.756	62.83	0.82	0.64	0.68	0.76	
Sesa sp	3.199	3.599	66.43	0.44	1.14	0.66	2.12	
Klei lon	1.795	2.019	68.45	0	0.2	1.46	2.08	
Dyer afr	1.416	1.593	70.05	0	1.04	0.3	0.88	
Comm sax	1.264	1.422	71.47	0.06	0.32	0.74	0.76	
Tetr red	1.224	1.377	72.84	0	0.1	1.16	4.04	
Cali cap	1.167	1.313	74.16	0.24	0.3	0.44	0.6	
Mons mar	1.128	1.269	75.43	0	0.3	0.42	1.08	
Blep obm	1.053	1.184	76.61	0	1.64	0.3	0.24	
Euph gie	1.04	1.17	77.78	0	0.7	0.54	0.68	
Blep gro	0.9912	1.115	78.9	0	3.8	0.1	0	
Peta var	0.9232	1.039	79.94	0	0.04	0.82	0.88	
Heli tom	0.9051	1.018	80.95	0	0.24	0.6	0.32	
Hood ped	0.896	1.008	81.96	0.02	0	0.88	0.88	
Comm vir	0.8803	0.9904	82.95	0.12	0.32	0.46	0.28	
Euph vir	0.8625	0.9704	83.92	0	0.22	0.4	0.6	
Euph gla	0.8135	0.9152	84.84	0.22	0.62	0.1	0.04	
Tric afr	0.797	0.8967	85.73	0	0.34	0.98	0.08	
Orth alb	0.7902	0.889	86.62	0.1	0.24	0.2	0.12	
Myro fla	0.7748	0.8717	87.5	0	0.64	1.1	0	
Comm gla	0.7654	0.8612	88.36	0	0.22	0.44	0.48	
Cyna vim	0.7333	0.8251	89.18	0	1.16	0.02	0.64	
Cryp dec	0.6117	0.6882	89.87	0	0.3	0.16	0.16	
Barl mer	0.5777	0.65	90.52	0.04	0.12	0.4	0.16	
Hood cur	0.5582	0.628	91.15	0	0.06	0.2	0.4	
Chas gar	0.5298	0.5961	91.74	0.18	0.2	0.1	0	
Pech leu	0.5189	0.5838	92.33	0.16	0.26	0	0.2	
Amph div	0.4836	0.5441	92.87	0	0.04	0.16	1.12	
Euph lig	0.4108	0.4622	93.33	0	0.12	0.24	0.28	
Sear mar	0.4063	0.4571	93.79	0.3	0.06	0.02	0	
Unid 11	0.3912	0.4401	94.23	0	0	0.64	0	
Jame max	0.3692	0.4154	94.65	0.06	0.1	0.02	0.44	
Cada aph	0.3604	0.4055	95.05	0	0.12	0.26	0	
Aden pec	0.3569	0.4016	95.45	0	0.12	0.3	0.08	
Aizo afr	0.3395	0.3819	95.84	0.14	0.04	0	0	
Acac eri	0.2901	0.3264	96.16	0.14	0	0	0	
Aden pec	0.2872	0.3231	96.48	0.14	0.02	0.02	0	
Unid 4	0.2781	0.3129	96.8	0	0.08	0.12	0.2	
Aspa pea	0.2586	0.2909	97.09	0.06	0.2	0.06	0.04	
Unid 6	0.2531	0.2847	97.37	0	0.2	0	0	
Mont car	0.2528	0.2844	97.66	0	0.26	0.18	0.12	
Bosc foe	0.2059	0.2317	97.89	0.04	0.06	0.1	0.12	
Pela ota	0.1967	0.2213	98.11	0	0.02	0.38	0.04	
Maer sch	0.1793	0.2017	98.31	0	0	0	0.24	
Vach ref	0.1484	0.167	98.48	0.04	0.26	0	0	
Cucu mee	0.1184	0.1332	98.61	0	0.06	0.06	0	
Codo sp	0.1081	0.1217	98.73	0	0	0.12	0	
Unid 1	0.1063	0.1196	98.85	0.08	0	0	0	
Ster afr	0.08677	0.09762	98.95	0	0	0.06	0	
Unid 2	0.08607	0.09683	99.05	0	0	0.04	0.08	
Grew sp	0.07853	0.08835	99.14	0	0.02	0.02	0	
Abut pyc	0.07388	0.08312	99.22	0	0.1	0	0	
Geig orn	0.06914	0.07778	99.3	0	0	0.08	0	
Teph dre	0.06665	0.07498	99.37	0	0.08	0.04	0.04	
Comm squ	0.05968	0.06715	99.44	0	0.08	0.06	0	
Gorm fil	0.0586	0.06593	99.51	0.02	0.02	0	0	
Unid 3	0.05723	0.06439	99.57	0	0	0	0.08	
Park afr	0.04853	0.0546	99.62	0.04	0	0	0	
Unid 8	0.04379	0.04927	99.67	0	0.1	0	0	
Lyci cin	0.0403	0.04534	99.72	0	0.02	0.04	0	
Euph phy	0.02675	0.03009	99.75	0	0.02	0	0	
Bosc alb	0.02491	0.02802	99.78	0	0	0.02	0	
Crot gra	0.02476	0.02786	99.81	0	0	0	0.08	
Unid 9	0.02406	0.02707	99.83	0	0	0	0.08	
Sola hum	0.02353	0.02648	99.86	0	0.04	0	0	
Comm ter	0.01943	0.02186	99.88	0	0	0.02	0	
Eucl und	0.01869	0.02102	99.9	0	0	0	0.04	
Dico tom	0.01752	0.01971	99.92	0	0.04	0	0	
Unid 7	0.01752	0.01971	99.94	0	0.04	0	0	
Fors sp	0.01671	0.0188	99.96	0	0.02	0	0	
Aloe dic	0.01293	0.01455	99.97	0	0.02	0	0	
Unid 10	0.01203	0.01353	99.99	0	0	0	0.04	
Unid 5	0.01062	0.01195	100	0	0	0.02	0	
Overall average dissimilarity =88.88%								

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Matrix	Mean Marble	Mean Granite	Mean Schi
Pogo cle	20.26	22.53	22.53	1.04	5.07	12.4	16.8
Caro sp	8.69	9.662	32.19	2.88	4.43	1.18	3.32
Tetr stap	7.175	7.978	40.17	0.58	4.8	3.22	3.66
Aloe asp	7.093	7.887	48.06	0.2	6.77	6	1.7
Peta set	5.13	5.704	53.76	0.26	0	3.2	2.86
Tetr cyl	4.89	5.437	59.2	0.44	2.87	2.11	3.04
Arth leu	3.537	3.933	63.13	0.82	2.2	0.178	0.22
Sesa sp	3.161	3.515	66.65	0.44	0	0.4	2.5
Klei lon	1.805	2.007	68.65	0	3.07	0.667	0.26
Dyer afr	1.386	1.541	70.19	0	0	1.27	0.64
Comm sax	1.278	1.421	71.62	0.06	0.367	0.422	0.84
Tetr red	1.258	1.399	73.01	0	5.47	0	0
Cali cap	1.16	1.29	74.31	0.24	0.0667	0.956	0.14
Euph gie	1.127	1.254	75.56	0	2.4	0.156	0
Mons mar	1.074	1.194	76.75	0	0.233	0.622	0.56
Blep obm	1.061	1.18	77.93	0	0	2.09	0.18
Blep gro	1.022	1.137	79.07	0	0	4.22	0.1
Hood ped	0.9448	1.051	80.12	0.02	2.17	0.0222	0
Heli tom	0.9086	1.01	81.13	0	0	0.644	0.42
Peta var	0.889	0.9886	82.12	0	0.467	0	1.02
Comm vir	0.8866	0.9858	83.1	0.12	0	0.711	0.28
Euph vir	0.8522	0.9476	84.05	0	0	0.356	0.6
Euph gla	0.8211	0.913	84.97	0.22	0	0.556	0.24
Tric afr	0.8188	0.9104	85.88	0	0.633	0.133	0.86
Myro fla	0.8061	0.8964	86.77	0	0	1.93	0
Orth alb	0.797	0.8862	87.66	0.1	0.1	0.289	0.18
Comm gla	0.7562	0.8408	88.5	0	0	0.556	0.4
Cyna vim	0.7201	0.8007	89.3	0	0	1.67	0
Cryp dec	0.6159	0.6848	89.98	0	0	0.311	0.26
Barl mer	0.5897	0.6557	90.64	0.04	0	0.533	0.12
Hood cur	0.5592	0.6218	91.26	0	0.3	0.0444	0.24
Chas gar	0.5392	0.5996	91.86	0.18	0	0.333	0
Pech leu	0.5073	0.5641	92.43	0.16	0.0333	0.378	0
Amph div	0.449	0.4992	92.92	0	0	0.844	0
Euph lig	0.4148	0.4613	93.39	0	0.367	0	0.28
Unid 11	0.4072	0.4527	93.84	0	0	0.711	0
Sear mar	0.4059	0.4513	94.29	0.3	0	0.0889	0
Cada aph	0.3643	0.4051	94.7	0	0	0	0.38
Aden pec	0.3628	0.4034	95.1	0	0.333	0.0222	0.24
Jame max	0.3523	0.3917	95.49	0.06	0.0333	0.356	0
Aizo afr	0.3394	0.3774	95.87	0.14	0	0	0.04
Aden pec	0.2881	0.3203	96.19	0.14	0	0	0.04
Acac eri	0.2875	0.3197	96.51	0.14	0	0	0
Unid 4	0.2737	0.3043	96.81	0	0	0	0.3
Aspa pea	0.2606	0.2898	97.1	0.06	0	0.244	0.06
Mont car	0.2579	0.2867	97.39	0	0	0.556	0
Unid 6	0.2536	0.282	97.67	0	0	0	0.2
Pela ota	0.2201	0.2447	97.92	0	0.7	0	0
Bosc foe	0.2066	0.2298	98.15	0.04	0	0.244	0
Maer sch	0.1581	0.1758	98.32	0	0	0.0667	0.06
Vach ref	0.1509	0.1678	98.49	0.04	0	0.289	0
Cucu mee	0.1202	0.1337	98.62	0	0	0.0444	0.08
Codo sp	0.1126	0.1252	98.75	0	0	0.133	0
Unid 1	0.1054	0.1172	98.86	0.08	0	0	0
Ster afr	0.09019	0.1003	98.96	0	0	0.0667	0
Grew sp	0.08088	0.08993	99.05	0	0	0.0444	0
Unid 2	0.0788	0.08762	99.14	0	0	0	0.08
Abut pyc	0.07622	0.08476	99.23	0	0	0.111	0
Geig orn	0.07199	0.08005	99.31	0	0	0.0889	0
Teph dre	0.06942	0.07719	99.38	0	0.1	0.0889	0
Comm squ	0.06211	0.06906	99.45	0	0	0.156	0
Gorm fil	0.06021	0.06695	99.52	0.02	0.0333	0	0
Unid 3	0.04939	0.05492	99.58	0	0	0	0.04
Park afr	0.0481	0.05348	99.63	0.04	0	0	0
Unid 8	0.04527	0.05034	99.68	0	0	0.111	0
Lyci cin	0.04443	0.04941	99.73	0	0.0667	0.0222	0
Euph phy	0.02909	0.03235	99.76	0	0.0333	0	0
Bosc alb	0.02536	0.0282	99.79	0	0	0	0.02
Sola hum	0.0243	0.02702	99.82	0	0	0.0444	0
Unid 9	0.02104	0.02339	99.84	0	0	0.0444	0
Crot gra	0.0208	0.02312	99.86	0	0	0	0.04
Comm ter	0.01964	0.02184	99.88	0	0	0	0.02
Dico tom	0.01811	0.02013	99.9	0	0	0.0444	0
Unid 7	0.01811	0.02013	99.92	0	0	0.0444	0
Fors sp	0.01665	0.01852	99.94	0	0	0	0.02
Eucl und	0.01642	0.01826	99.96	0	0	0.0222	0
Aloe dic	0.01335	0.01485	99.98	0	0	0.0222	0
Unid 5	0.01061	0.0118	99.99	0	0	0	0.02
Unid 10	0.01052	0.0117	100	0	0	0.0222	0
overall average dissimilarity =89.93%							

Table A- 5. Summary of CCA eigenvalues representing the proportion of variance in species composition explained by measured environmental variables.

Analysis 'Constrained'				
Method: CCA				
Total variation is 12.22487, explanatory variables account for 7.7%				
(adjusted explained variation is 6.1%)				
Summary Table:				
Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.5704	0.2402	0.1298	0.5427
Explained variation (cumulative)	4.67	6.63	7.69	12.13
Pseudo-canonical correlation	0.8965	0.7811	0.6771	0
Explained fitted variation (cumulative)	60.65	86.2	100	
Permutation Test Results:				
On All Axes	pseudo-F=4.8, P=0.002			

Table A- 6. Checklist of plant species recorded on inselbergs in the central Namib Desert.

Species	Family	Life forms	IUCN status	Endemism	Legal status	Marble	Granite	Schist	Matrix
Abutilon pycnodon	*Malvaceae*	Therophyte	LC			0	5	0	0
Adenia pechuelii	*Passifloraceae*	Phanerophyte	LC	E		10	1	12	0
Adenolobus pechuelii	*Fabaceae*	Phanerophyte	LC	NE		0	0	2	7
Aizoon africanum	*Aizoaceae*	Phanerophyte	NE			0	0	2	7
Aloe asperifolia	*Asphodelaceae*	Meso-chamaephyte	LC	E	Protected by Nature	203	270	65	10
Aloidendron dichotomum	*Asphodelaceae*	Phanerophyte	LC	NE	Protected by Nature Conservation Ordinance	0	1	0	0
Amphiasma divaricatum	*Rubiaceae*	Chamaeophyte	NE	E		0	38	0	0
Arthraerua leubnitziae	*Amaranthaceae*	Phanerophyte	LC (Least Concerned)	E (Endemic)		66	8	11	41
Asparagus pearsonii	*Asparagaceae*	Chamaeophyte	LC	NE		0	11	3	3
Barleria merxmuelleri	*Acanthaceae*	Chamaeophyte	LC	E/ NE		0	24	6	2
Blepharis grossa	*Acanthaceae*	Therophyte	LC	NE		0	190	0	0
Blepharis obmitrata	*Acanthaceae*	Meso-chamaephyte	LC			0	94	9	0
Boscia albitrunca	*Capparaceae*	Phanerophyte	LC		Protected under the Forestry Ordinance 37 of 1952 & the Forestry Act no 72 of 1968	0	0	1	0
Boscia foetida	*Capparaceae*	Phanerophyte	LC			0	11	0	2
Cadaba aphylla	*Brassicaceae*	Phanerophyte	LC			0	0	19	0
Calicorema capitata	*Amaranthaceae*	Phanerophyte	LC	NE		2	43	7	12
Caroxylon spp.	*Amaranthaceae*	Phanerophyte	defiecient	endemic)		133	53	166	144
Ceropegia currorii	*Apocynaceae*	Chamaeophyte	LC			9	2	12	0
Ceropegia pedicellata	*Apocynaceae*	Chamaeophyte	LC	NE		65	1	0	1
Chascanum garipense	*Verbenaceae*	Chamaeophyte	LC	NE		0	15	0	9
Codon sp	*Boraginaceae*	Therophyte				0	6	0	0
Commicarpus squarrosus	*Nyctaginaceae*	Chamaeophyte	LC	E		0	7	0	0
Commiphora glaucescens	*Burseraceae*	Phanerophyte	LC	NE		0	25	20	0
Commiphora saxicola	*Burseraceae*	Phanerophyte	LC	E		11	19	42	3
Commiphora tenuipetiola	*Burseraceae*	Phanerophyte	LC			0	0	1	0
Commiphora virgata	*Burseraceae*	Phanerophyte	LC	NE		0	32	14	6
Croton gratissimus	*Euphorbiaceae*	Phanerophyte	LC			0	0	2	0
Cryptolepis decidua	*Apocynaceae*	Phanerophyte	LC	NE		0	14	13	0
Cucumis meeusei	*Cucurbitaceae*	Chamaeophyte	LC			0	2	4	0
Cynanchum viminale	*Apocynaceae*	Phanerophyte	LC			0	75	0	0
Dicoma tomentosa	*Asteraceae*		LC			0	2	0	0
Dyerophytum africanum	*Plumbaginaceae*	Chamaeophyte	LC			0	57	32	0
Ehretia alba	*Boraginaceae*	Phanerophyte	LC			0	0	1	0
Euclea undulata	*Ebenaceae*	Phanerophyte	LC			0	1	0	0
Euphorbia giessii	*Euphorbiaceae*	Phanerophyte	LC	E		239	7	0	0
Euphorbia glanduligera	*Euphorbiaceae*	Chamaeophyte	LC			0	25	12	11
Euphorbia lignosa	*Euphorbiaceae*	meso-chamaephyte	LC	NE		11	0	14	0
Euphorbia phylloclada	*Euphorbiaceae*	Chamaeophyte	LC			1	0	0	0
Euphorbia virosa	*Euphorbiaceae*	Phanerophyte	LC	NE	CITES Appe	0	16	30	0
Forsskaolea sp	*Urticaceae*					0	0	1	0
Geigeria ornativa	*Asteraceae*	Therophyte	DD			0	4	0	0
Gomphocarpus filiformis	*Apocynaceae*	Phanerophyte	LC	E (Southern africa)		1	0	0	1
Grewia sp.	*Malvaceae*	Phanerophyte				0	2	0	0
Helichryum tomentosulum tomentosulum	*Asteraceae*		NE			0	29	21	0
Jamesbrittenia maxii	*Scrophulariaceae*	Chamaeophyte	LC			1	16	0	3
Kleinia longiflora	*Asteraceae*	Phanerophyte	LC			92	30	13	0
Leptodenia albida	*Apocynaceae*	Chamaeophyte	LC	NE		3	13	9	5
Lycium cinereum	*Solanaceae*	Phanerophyte	DD			2	1	0	0
Maerua schinzii	*Brassicaceae*	Phanerophyte	LC		Protected under the Forestry Ordinance 37 of 1952 & the Forestry Act no 72 of 1968	0	3	3	0
Monsonia marlothii	*Geraniaceae*	Phanerophyte	LC	E		7	28	28	0
Montinia caryophyllacea	*Montiniaceae*	Phanerophyte	LC			0	25	0	0
Myrothamnus flabellifolius	*Myrothamnaceae*	Chamaeophyte	DD			0	87	0	0
Parkinsonia africana	*Fabaceae*	Phanerophyte	LC		protected under the Forestry Ordinance 37 of 1952 & the Forestry Act no 72 of 1968	0	0	0	2
Pechuel-loeschea leubnitziae	*Asteraceae*	Phanerophyte	LC	E (Southern africa)		1	17	0	8
Pelargonium otaviense	*Geraniaceae*	Phanerophyte	LC	NE		21	0	0	0
Petalidium setosum	*Acanthaceae*	Nano-phanerophyte	LC	NE		0	144	143	13
Petalidium variabile	*Acanthaceae*	Chamaeophyte	NE (Not Evalu	E		14	0	51	0
Pogonospermum cleomoides	*Acanthaceae*	Chamaeophyte		NE		152	559	838	52
Searsia marlothii	*Anacardiaceae*	Phanerophyte	LC			0	4	0	1
Sesamum sp.	*Petaliaceae*	Therophyte				0	18	125	22
Solanum humile	*Solanaceae*	Chamaeophyte	LC			0	1	0	0
Sterculia africana	*Malvaceae*	Phanerophyte	LC		Protected under the Forestry Ordinance 37 of 1952 & the Forestry Act no 72 of 1968	0	3	0	0
Tephrosia dregeana	*Fabaceae*	Therophyte	LC	NE		3	4	0	0
Tetraena cylindrifolia	*Zygophyllaceae*	Chamaeophyte	LC	NE		86	95	152	22
Tetragonia reduplicatae	*Aizoaceae*	Phanerophyte	LC			4	0	0	0
Tetreaena stapffii	*Zygophyllaceae*	Phanerophyte	LC	E		144	145	183	29
Trichodesma africanum	*Boraginaceae*	Therophyte	LC			19	6	43	0
Unid1						0	4	0	4
Unid10						0	1	0	0
Unid11						0	32	0	0
Unid2						0	0	2	0
Unid3						0	0	2	0
Unid4						0	0	1	0
Unid5						0	0	1	0
Unid6						0	0	10	0
Unid7						0	2	0	0
Unid8						0	5	0	0
Unid9						0	2	0	0
Vachellia erioloba	*Fabaceae*	Phanerophyte	LC		Protected under the Forestry Ordinance 37 of 1952 & the Forestry Act no 72 of 1968	0	0	0	7
Vachellia reficiens	*Fabaceae*	Phanerophyte	LC			0	13	0	2

Table A- 7. SIMPER analysis of species composition between the size of inselbergs.

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean Small	Mean Medium	Mean Large
Pogo cle	19.04	21.61	21.61	8.22	10.6	9.32
Caro sp	8.984	10.2	31.81	3.48	2.07	2.52
Aloe asp	7.285	8.268	40.08	1.21	6.55	3.57
Tetr stap	6.594	7.484	47.56	3.91	0.548	3.16
Peta set	4.89	5.55	53.11	2.16	1.81	1.04
Tetr cyl	4.889	5.549	58.66	1.96	2.62	1.68
Arth leu	3.553	4.033	62.69	0.766	0.524	0.804
Sesa sp	3.14	3.563	66.26	0.818	0.0952	1.75
Klei lon	1.782	2.022	68.28	0.247	2.14	0.464
Dyer afr	1.363	1.547	69.83	0.312	0.952	0.446
Tetr red	1.321	1.499	71.32	0	3.9	0
Comm sa	1.273	1.444	72.77	0.364	0.524	0.446
Cali cap	1.122	1.273	74.04	0.779	0	0.0714
Blep obm	1.052	1.194	75.24	0.506	1.4	0.0893
Blep gro	1.037	1.177	76.41	0.0649	0	3.39
Mons ma	1.014	1.151	77.56	0.312	0.286	0.482
Comm vi	0.9465	1.074	78.64	0.26	0	0.571
Euph gla	0.9404	1.067	79.71	0.325	0.524	0.0179
Hood ped	0.8963	1.017	80.72	0.169	1.26	0.0179
Euph gie	0.89	1.01	81.73	0.883	0.262	0
Orth alb	0.8862	1.006	82.74	0.156	0.31	0.0893
Peta var	0.8239	0.9352	83.67	0.416	0	0.589
Euph vir	0.8222	0.9332	84.61	0.13	0.0952	0.571
Cyna vim	0.8192	0.9298	85.54	0	1.79	0
Heli tom	0.7782	0.8832	86.42	0.545	0	0.143
Tric afr	0.7577	0.86	87.28	0.377	0	0.696
Comm gl	0.7127	0.809	88.09	0.273	0.214	0.268
Myro fla	0.6722	0.7629	88.85	1.13	0	0
Barl mer	0.6337	0.7192	89.57	0.026	0.333	0.286
Cryp dec	0.5726	0.6499	90.22	0.117	0.167	0.196
Pech leu	0.5668	0.6434	90.87	0.208	0.238	0
Chas gar	0.5372	0.6097	91.47	0.169	0.262	0
Hood cur	0.4806	0.5455	92.02	0.143	0	0.214
Aizo afr	0.449	0.5096	92.53	0.039	0.0952	0.0357
Sear mar	0.4449	0.505	93.04	0.234	0.0238	0
Acac eri	0.4179	0.4744	93.51	0.013	0	0.107
Unid 11	0.4074	0.4624	93.97	0	0	0.571
Jame ma	0.4048	0.4595	94.43	0.0779	0.333	0
Euph lig	0.3958	0.4492	94.88	0.0909	0.0476	0.286
Aden pec	0.3853	0.4373	95.32	0.039	0.119	0.0179
Amph div	0.3724	0.4227	95.74	0.494	0	0
Aden pec	0.3694	0.4193	96.16	0.026	0.262	0.179
Cada aph	0.313	0.3552	96.52	0.234	0.0238	0
Mont car	0.2932	0.3328	96.85	0	0.595	0
Aspa pea	0.2804	0.3183	97.17	0.0519	0.214	0.0714
Unid 4	0.2538	0.2881	97.45	0.0779	0	0.161
Unid 6	0.2118	0.2404	97.69	0.13	0	0
Bosc foe	0.2062	0.234	97.93	0.13	0.0476	0.0179
Vach ref	0.1951	0.2215	98.15	0.0519	0.262	0
Pela ota	0.1688	0.1916	98.34	0.273	0	0
Maer sch	0.1682	0.1909	98.53	0.026	0.0952	0
Unid 1	0.1251	0.142	98.67	0.0519	0	0
Cucu me	0.1105	0.1255	98.8	0.0519	0.0238	0.0179
Codo sp	0.09257	0.1051	98.91	0.0779	0	0
Ster afr	0.0866	0.09829	99	0	0	0.0536
Unid 2	0.0793	0.09001	99.09	0	0	0.0714
Park afr	0.07535	0.08553	99.18	0	0.0476	0
Gorm fil	0.06979	0.07921	99.26	0.026	0	0
Grew sp	0.06574	0.07461	99.33	0.026	0	0
Abut pyc	0.06293	0.07143	99.4	0.0649	0	0
Geig orn	0.06163	0.06996	99.47	0.039	0	0.0179
Teph dre	0.0559	0.06344	99.54	0.0909	0	0
Comm sc	0.05186	0.05886	99.6	0.0909	0	0
Unid 3	0.04901	0.05562	99.65	0	0	0.0357
Lyci cin	0.0402	0.04563	99.7	0.013	0	0.0357
Unid 8	0.03778	0.04289	99.74	0.0649	0	0
Euph phy	0.03032	0.03441	99.77	0	0.0238	0
Bosc alb	0.02511	0.0285	99.8	0	0	0.0179
Crot gra	0.02179	0.02474	99.83	0	0	0.0357
Sola hum	0.02014	0.02286	99.85	0.026	0	0
Fors sp	0.01935	0.02197	99.87	0	0.0238	0
Unid 9	0.01751	0.01987	99.89	0.026	0	0
Comm te	0.01661	0.01885	99.91	0.013	0	0
Eucl und	0.01626	0.01846	99.93	0	0	0.0179
Dico tom	0.01511	0.01715	99.95	0.026	0	0
Unid 7	0.01511	0.01715	99.96	0.026	0	0
Aloe dic	0.01333	0.01513	99.98	0	0	0.0179
Unid 5	0.009184	0.01042	99.99	0.013	0	0
Unid 10	0.008753	0.009935	100	0.013	0	0
Overall dissimilarities = 88.1%						