THE BIOGEOGRAPHY OF *BRACHYSTEGIA* WOODLAND RELICTS IN SOUTHERN AFRICA
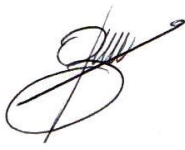
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A dissertation submitted in fulfilment of the academic requirements for the degree of Master of Science in the School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg.

May 2015

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

Brenden Pienaar

Signed on the 25th day of May 2015 in Hoedspruit

"The wonder is that we can see these trees and not wonder more."

Ralph Waldo Emerson

ABSTRACT

In this study I investigated the climate ecology and population biology of *Brachystegia spiciformis* (miombo) woodland at the distributional range edge in southern Africa. The main aim of the study was to exploit miombo relict populations, isolated well beyond contemporary distribution, to establish likely spatial and population dynamic response to future global climate change.

Miombo woodlands have expanded and contracted across the central African plateau over geological time, with palynological evidence supporting an extensive latitudinal range during the Holocene altithermal. It is hypothesised that small shifts in climate may have major impacts on woodland dynamics and distribution. However, miombo relict populations in southern Africa, one in Mozambique and one in South Africa, suggest refugia; physiographic settings that support a once prevalent regional climate that has been lost (or is being lost) due to climatic shifts. Inclusion of relict populations has been shown to improve the performance of model-based projections elsewhere and have value as natural laboratories for investigating how populations react to on-going climatic change. This study aims to contribute to a better understanding of miombo woodland - an ecologically and economically significant savanna community - response to global climate change in southern Africa.

A niche modelling approach was used to produce present-day and select future *B. spiciformis* woodland ecological niche models. Precipitation of the wettest quarter and temperature seasonality were identified as the two most important bioclimatic variables explaining *B. spiciformis* woodland distribution in southern Africa. Both variables displayed a relatively narrow range of optimal suitability for the species; 422 - 576 mm and 2.6 - 3.0 °C, respectively. In addition, significantly high temperature seasonality and maximum temperature of the warmest month were identified as limiting factors at the periphery of the contemporary miombo woodland distribution. Considering future regional climate change projections, it is suggested that the *B. spiciformis* climate niche could retract by between 30.6 - 47.3% in southern Africa by 2050.

In addition, a meta-population analysis of miombo woodland at the southern distributional range edge was carried out to elucidate patterns in population dynamics that could validate theorized climate response. Whilst the continuous miombo woodlands occurring to the north of the southern African range edge are internally relatively homogenous in community composition, relict populations reflected a loss of natural biota and a restructuring of the vegetation unit resulting in clear divergence from the core and range edge communities, and from each other.

Although *B. spiciformis* reproduction, population density and structural dimensions were significantly low at the recently discovered relict population in South Africa relative to populations occurring to the north, we suggest that the medium-term persistence of this population is plausible based on the longevity of genets, their historic resilience, and a traditional management regime. The vicariant *B. spiciformis* relict population located in southern Mozambique is greater in extent than its South African counterpart and data suggest suitable reproduction dynamics for medium-term persistence. However, this population is currently heavily impacted by unsustainable habitat transformation under a lack of formal ecological or conservation protection.

This study uniquely highlights *B. spiciformis* woodland as a climate (precipitation) sensitive component of savanna ecosystems in southern Africa and provides important baseline data for population dynamics at the distributional range edge.

ACKNOWLEDGEMENTS

I would like to thank my post graduate research committee; Barend Erasmus, David Mycock, which includes my supervisors Trevor Hill, Dave Thompson and Ed Witkowski for their continued support and guidance throughout my progression in mastering science. Barend Erasmus provided essential input during the ecological niche modelling (ENM) component of chapter two, while Edward Mwavu assisted with ANalysis Of SIMilarity (ANOSIM) in chapter three. Dr Mervyn Lötter (Mpumalanga Tourism and Parks Authority) and Mr John Burrows (Buffelskloof Herbarium) assisted with *ex situ* identification of voucher species. Furthermore, I am ever appreciative of my tenacious field assistants and friends; Janet and Trevor Kleyn, Laura Panaino, Tamsyn Pienaar and Drew Pollard. Your selfless assistance towards my personal objective is colossal.

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LIST OF ABBREVIATIONS

ACH Abundant Centre Hypothesis

AETFAT Association for the Taxonomical Study of the Flora of tropical Africa

ANOSIM ANalysis Of SIMilarity

ANOVA ANalysis Of VAriance

AOGCMs Atmosphere-Ocean General Circulation Models

AUC Area Under the receiving operating characteristic Curve

BP   Before Present

CDEs Climate Dependant Environments

ENMs Ecological Niche Models

ENSO El Niño Southern Oscillation

FDEs Fire Dependant Environments

GCSRI Global Change and Sustainability Research Institute

HSD Honestly Significant Difference

HWSD Harmonised World Soil Database

LGM Last Glacial Maximum

MCPS Minimum Critical Patch Size

NMDS Non-Metric Multi-Dimensional Scaling

NRF National Research Foundation

OAVs Ocean-Atmosphere-Vegetation Models

OSI   Open Society Institute

PMIP2 Palaeoclimate Modelling Intercomparison Project Phase 2

QDS Quarter degree square

SAAB South African Association of Botanists

SAEON South African Environmental Observation Network

SCD Size Class Distributions

WUF Water Use Efficiency

PREFACE

The motivation behind this research was the need for a more comprehensive understanding of *Brachystegia spiciformis* (miombo) woodland response to global climate change in southern Africa. Miombo woodland is undergoing widespread anthropogenic transformation through burning and conversion to cultivated fields and plantations. With the prospect of increasing pressure from human population growth and global climate change, the possibility of biodiversity loss, shifting resource extraction and more intense and unsustainable land use practices cannot be ruled out. Biodiversity conservation, sustainable resource use and benefit sharing can only be possible under large-scale priority adaptive land use management, based on a comprehensive understanding of *B. spiciformis* response to all facets of change, which currently experiences an information deficient climate component.

There are four chapters in this dissertation; a general introduction, two 'results' chapters and a final concluding chapter. The general introduction chapter provides a literature review and explicates the dissertation aim and objectives. Chapter two focuses on the climate niche of *B. spiciformis* woodland in southern Africa and was presented at the XXth Association for the Taxonomical Study of the Flora of tropical Africa (AETFAT) Congress in Stellenbosch 13 - 17 January 2014, co-hosted by the South African Association of Botanists (SAAB). This work has been accepted for publication in the *South African Journal of Science* (Pienaar, B., Thompson, D.I., Erasmus, B.F.N., Hill T.R., Witkowski, E.T.F. *In press*. Evidence for climate-induced range shift in *Brachystegia* (miombo) woodland). The formatting style of chapter two contrasts with that of the dissertation, which includes a specific reference and appendix section. Chapter three addresses the patterns in community dynamics of *Brachystegia* (miombo) woodland climate relicts at the trailing range edge in southern Africa. Degrees of contextual overlap between the two 'results' chapters were unavoidable due to the intention of multiple publications. The concluding chapter provides a detailed synthesis of the work completed and makes suggestions with regards to further research that extended beyond the scope of this study and arises as a consequence of this work.

CHAPTER ONE

Introduction

Miombo is a colloquial term used to describe the vegetation unit dominated by *Brachystegia, Julbernardia* and *Isoberlinia* - three closely related genera from the legume family Fabaceae, subfamily Caeasalpinioideae (Campbell 1996). It is synonymous with White's (1983) Zambezian Phytochorion, the largest regional centre of endemism in Africa. An estimated 75 million people inhabit the miombo region, with a supplementary 25 million urbanites depending on miombo as an energy resource (Campbell *et al.* 2007). Miombo provides a plethora of ecosystem goods and services, especially in the form of edible species, fuelwood harvesting, charcoal production and extraction of construction material. Large areas of miombo are being modified or transformed by burning and conversion to cultivated fields and plantations under increasing pressure from sustained human population growth (see Desanker *et al.* 1997). As miombo and associated biota form a crucial component of diversity and livelihoods in central and southern Africa, fundamental concern should be with the consequences of change. Although an important task for research has been miombo response to direct anthropogenic activities, a more comprehensive understanding of miombo response to climate, and climate change, is required.

1.1 Miombo ecology

Miombo has variously been classified as savanna (Huntley 1982; Frost *et al.* 1986), woodland (White 1983) and forest (Freson *et al.* 1974; Malaisse 1978); an indication of the time-honoured debate among ecologists in Africa over how best to categorise the wooded formations in areas receiving distinctly seasonal precipitation. In part, the complexity of classification originates from the frequent concurrence of miombo woodland and areas of semi- to evergreen forest in the higher precipitation regions Africa (White 1983). Lowland evergreen forest of the Congo Basin and the East African coastal zone is the only vegetation unit, outside

of miombo, to host a number of *Brachystegia*, *Julbernardia* and *Isoberlinia* species (Campbell 1996). However, across most of its range, mature undisturbed miombo is physiognomically closed deciduous woodland within the continuum of savanna ecosystems (Walker 1981, Huntley 1982). Miombo is the most widespread woodland formation on the continent (Millington *et al.* 1994), covering an estimated 2.7 million km^2 of south-central Africa.

Brachystegia spiciformis is the most abundant component of miombo woodland in southern Africa, only conceding dominance to *Julbernardia globiflora* in drier extents of the range (Timberlake & Chidumayo 2011). Miombo woodland commonly occurs on geologically old, nutrient poor soils in the unimodal summer precipitation zone. The dominance of Caeasalpinioideae is an interesting yet poorly understood phenomenon, although the consistent incidence of ectomycorrhizae in their roots may permit them to exploit porous, nutrient poor soils more resourcefully than asymbiotic groups (Högberg & Nylund 1981). In areas with more alkaline soil and/or lower precipitation zones, miombo woodland gives way to arid, eutrophic savannas dominated by the genera *Senegalia, Vachelia* (both formerly *Acacia*) and *Colophospermum mopane* (White 1983). The distinctive structure of miombo woodland is consequently characteristic of the dominant Caesalpinioid trees. Species have slim stems with sharply vertical branches which spread out to support a light, shallow and often umbrella shaped canopy of pinnately compound leaves at a height of 6 to 20 meters (Campbell 1996). In addition, miombo woodland have the functional attribute of being briefly deciduous and flush prior to the summer rains, the seasonality being related to water stress and/or low temperatures (Timberlake & Chidumayo 2011). Woody plants comprise 95 - 98% of the aboveground biomass in undisturbed miombo stands with grasses and herbs making up the remainder (Martin 1974; Malaisse 1978; Chidumayo 1993). The miombo lower strata is inconsistent in density and composition.

Most miombo woodland trees flower during the warm dry months of September and October prior to the rainy season. Fruit production varies between years

(Malaisse, 1978; Campbell *et al.* 1988; Ernst 1988) and *Brachystegia* species often flower abundantly without producing a correspondingly large seed crop (Campbell 1996). Mast fruiting may reflect interannual variations in pollinator activity, bud predation, flower abortion or resources limitation for pod and seed production rather than physiological constraints (Campbell 1996). Atypical of legumes, seed from the majority of woody miombo species germinate instantly after dispersion (August to November), as long as there is adequate moisture, for example after heavy precipitation (Strang 1966; Ernst 1988; Chidumayo 1991; 1992a). *Ex situ* germinated seeds with an intact outer integument start germinating 4 – 5 days after imbibition, while scarified seeds germinate within 3 days. Success of natural seedling establishment among miombo woodland canopy species is low and there is no dormancy or extensive store of seeds in the soil. By mid-summer any seeds of *B. spiciformis* occurring in the soil are not viable (Ernst 1988; Chidumayo, pers. obs.). Seed dispersal distance is limited; Ernst (1988) recorded seeds of *B. spiciformis* dispersing up to 5.6 m from the parent tree, although most seeds fell within 2 to 4 m.

Seedling roots of many miombo woodland tree species grow faster than the shoots (Chidumayo 1993); with seedlings producing no more than two leaves. The ability of the seedling to grow and survive through the first dry season may be related to their ability to put down deep enough roots to facilitate access to subsoil moisture and nutrients for at least part of the dry season. Initial seedling mortality during the establishment phase is high in miombo, but decreases significantly thereafter, even during the following dry season (Robertson 1984). Under experimental field conditions, tree seedling mortality ranged from 22% in *B. spiciformis* to 67% in *J. globiflora* (Campbell 1996). Significantly larger numbers of *B. spiciformis* seedlings are found underneath the tree canopies than in the open (Grundy *et al.* 1994), either because of greater seedling survival in more mesic and fertile environments under tree canopies (Campbell *et al.* 1988), or because of higher initial seed input (Ernst 1988). However, further development of *B. spiciformis* saplings is suppressed by the woodland canopy. Lees (1962) observed that old, stunted saplings of many miombo woodland trees are heliophytic and require high

light intensities to develop and mature further. In contrast, recruitment of *J. globiflora* appears to be independent of canopy closure (Grundy *et al.* 1994), despite apparent similar limitations to those of *B. spiciformis* for seed dispersal and susceptibility of seedlings to desiccation (Strang 1969). The high seedling mortality in miombo woodland has been attributed to water stress and fire (Trapnell 1959; Strang 1966; Ernst 1988; Chidumayo 1991; 1992a; 1992b). Nevertheless, miombo species regenerate predominantly through coppice regrowth and root suckers rather than through seeds (Trapnell 1959; Boaler & Sciwale 1966; Strang 1974; Robertson 1984).

Tree densities are apparently unrelated to rainfall (Savory 1963; Grundy 1995) and are higher in secondary miombo woodland than in mature woodland (Chidumayo 1993), despite inter-shoot competition limiting stem density with increasing age following prolific coppicing (Chidumayo 1988; 1989). The size-class distribution of mature miombo woodlands commonly show the reverse-J distribution characteristic of self-replacement stands (Chidumayo & Frost 1996), with many smaller individuals (seed and clonal recruitment) and exponentially fewer larger individuals.

The dynamics of miombo woodland is largely determined by the woody component which, apart from climate, is influenced by three interacting factors: people, fire and elephants.

1.2 The 'social woodland'

Miombo woodlands have been utilised by humans since the late Pleistocene (Musonda 1986) and more intensively so since 10 000 years before present (Chidumayo 1997). The principal traditional form of land use in miombo involves cultivation of small fields of sorghum, millet, maize and pulses either under some form of shifting agriculture or in conjunction with rearing livestock (Puzo 1978). The density of domestic livestock supported by miombo is relatively low compared to more grassy savanna systems and reflects, to some extent, inter-

relationships between geology, soils, plant production and quality, wildlife and disease (Bell 1982). To a great extent miombo woodland has been, and continues to be, modified by people, predominantly through removal of woodland cover (Chidumayo 1989) and fire.

Dry-season fires in the understory occur frequently in miombo woodland (Trapnell 1959; Kikula 1986). Many fires originate accidentally from people preparing land for cultivation, collecting honey or making charcoal (Chidumayo 1995). Livestock owners burn areas to provide a green flush for their livestock, and to control pests such as ticks. More commonly, people use fire to clear areas flanking paths between villages. Frequent fire change *i)* vegetation structure by transforming woodland into open, tall grass savanna and *ii)* species composition, resulting in secluded, fire tolerant canopy trees and sparse mid-strata trees and shrubs (Trapnell 1959).

The woodlands are not only a source of material goods, they are also central to the spiritual needs of people, with specific trees and even blocks of woodland being protected by communities for cultural reasons (Morris 1995).

1.3 Miombo and mega-herbivores

Another striking feature of miombo woodland is the apparent paucity of a faunal component (Bell 1982). However, large herbivores such as Sable Antelope and Lichtenstein's Hartebeest are specific to the miombo region. Elephants are notable localised exceptions, and are capable of transforming the nature of woody vegetation by breaking, ring-barking, pollarding and uprooting established woody vegetation (Buechner & Dawkins 1961; Laws 1970; Thomson 1975; Guy 1989; Helm & Witkowski 2013). Damage to trees by elephants has resulted in dramatic changes in miombo woodland cover in several areas. The overall effect in these cases has been to transform relatively dense woodlands into more open grassy systems with scattered tall trees, resprouting tree stumps, and a dense layer of low growing shrub. The changes have occurred both as a direct result of felling and

debarking trees, and as an indirect effect from changes in fire regime brought about by higher grass production under a more open tree canopy (Anderson & Walker 1974; Thomson 1975; Guy 1981; 1989; Jachmann & Bell 1985). Such changes impact the moisture and temperature micro-climate beneath the canopy, which likely impacts regeneration from seed.

1.4 Miombo palaeohistory

The contemporary southern distribution of continuous miombo woodland on the central African plateau is sited in south-central Zimbabwe (~21° S). However, palynological evidence (Scott 1982) tentatively suggests that the central African plateau has undergone significant flux in vegetation, ranging from cool upland grassland during the Last Glacial Maximum (19 000 years BP), to *Brachystegia* dominated savanna during the hotter and wetter conditions of the Mid-Holocene (6000 years BP) interglacial period (Scott 1982; Campbell 1996). Correspondingly, sediment cores containing *Brachystegia* pollen (genus level) from Tate Vondo, Mookgophong and Pretoria in South Africa (Scott 1982; 1983) suggests a widespread historic range during the Mid-Holocene, well south (~26° S) of the present-day distribution limit.

Acocks (1953) hypothesised that extensive (slash-and-burn) woody clearance by Iron Age farmers may have lead to the alteration in distribution range of certain vegetation types. However, charcoal evidence from the historic *Brachystegia* range in South Africa indicates no obvious signs of increased fire frequency associated with the manifestation of farming practice in the last millennium (Scott 2002). A more likely hypothesis is that marginal shifts in climate may result in major impact on woodland dynamics. Bond *et al.* (2003) suggest that summer rainfall areas of South Africa, which receive <650 mm precipitation per annum, can be classified as climate-dependent environments (CDEs). The annual precipitation records at the paleohistoric miombo locations range between 450 to 700 mm (Mucina & Rutherford 2006), suggesting that climate may be the primary

driver responsible for the current distribution and range edge population dynamics.

1.5 Miombo climate relicts

Climate-induced range retractions are frequently incomplete, but instead leave behind fragmented populations that remain as relicts, isolated enclaves of favourable environmental conditions within an inhospitable regional climate (Hampe & Jump 2011). The relatively recent discovery of an isolated *B. spiciformis* woodland in north-eastern South Africa (Hurter & van Wyk 2001) suggests a refugium separated from the continuous miombo woodlands of the central African plateau by ~200 km. A second vicariant *B. spiciformis* woodland in southern Mozambique is located some ~340 km south of the continuous miombo woodland. The presence of communities outside their contemporary range is a source of information from which to infer past climates. However, the strongest evidence for the past occupation of any area by a particular community is provided by fossil or pollen records. We therefore hypothesise that the two miombo woodland populations represent climate relicts (fragments) from the trailing latitudinal range edge in southern Africa. Climate relicts are critical components of local and regional biodiversity (Hampe & Jump 2011), they exert important functions within local communities and ecosystems (Eriksson 2000), serve as models for understanding species' dynamics in past environments (Horsak & Cernohorsky 2008), and help improve the performance of model-based projections (Thuiller *et al*. 2008).

1.6 Rationale

Although climate fluxes and associated biological responses are natural phenomenon that take place over geological time, the present trend of hurriedly increasing global temperatures due to continued combustion of fossil fuels since the mid-nineteenth century has been well established (Le Quere *et al.* 2009; Houghton *et al.* 2001). One major consequence of rising global temperatures is

the reshuffling of species' geographic distributions (Parmesan & Yohe 2003). Numerous studies and meta-analyses have revealed that modern climatic change has already influenced species' geographical distributions and the persistence of populations (Parmesan 1996; Walther *et al*. 2002). There is however a deficient understanding with regards to shifts of miombo spatial and population dynamics in response to global change. The dynamics of populations that inhabit the margins of distribution range are critically important in determining a species' ultimate response to projected climate change (Thomas *et al.* 2001; Iverson *et al.* 2004; Travis & Dytham 2004). Hampe & Petit (2005) identified 300 studies related to latitudinal range margins of which the majority are from terrestrial ecosystems of Europe and North America. The research represents a sturdy bias in favour of high-latitude range margins (86%), which have minimum temperature related constraints. Limited experimental work has focused on low-latitude range margins, where dissimilar climatic constraint may exert distinct biological responses. Furthermore, no theoretical or modelling exercise has to date unequivocally researched the dynamics of rear edge populations, be they 'stable' or 'trailing' (cf. Travis & Dytham 2004 for a related study). Few ecological studies have been designed to assess spatial and population dynamics of a savanna species at the latitudinal trailing range edge, and none have incorporated climate relicts. This research strives to improve our understanding of how *Brachystegia* (miombo) woodland may react in response to on-going global climate change.

1.7 Aim and objectives

The aim of the study was to utilize miombo relict populations, isolated beyond contemporary distribution, to establish likely spatial and population dynamic responses to global climate change.

The model-based objectives (chapter two) were to establish *i)* the bioclimatic niche dimensions of *B. spiciformis* woodland at the trailing range edge in southern Africa, *ii)* whether palaeohistoric distribution sites could have supported *B. spiciformis* during the Mid-Holocene, *iii)* the likely geographic footprint of the *B.*

spiciformis woodland bioclimatic niche under present-day and selected future (2050) global climate change scenarios.

The field study objectives (chapter three) were to elucidate patterns in miombo woodland relict communities at the trailing range edge in southern Africa, with regards to their *i)* floral diversity and representivity, *ii)* rate of recruitment, *iii)* population density, *iv)* structural dimensions and *v*) likely persistence under global change.

CHAPTER TWO

Evidence for climate-induced range shift in *Brachystegia* (miombo) woodland

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B. Pienaar and D.I. Thompson conceived the study; B. Pienaar and B.F.N. Erasmus performed the analyses; B. Pienaar drafted the first complete version of the manuscript. All co-authors read and improved the manuscript.

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2.1 Summary

Brachystegia spiciformis Benth. is a dominant component of miombo, the sub-tropical woodlands which cover 2.7 million km^2 of south-central Africa[9] and which is coincident with the largest regional centre of endemism in Africa.[10,11] However, pollen records from the genus *Brachystegia* suggest that miombo has experienced rapid range retraction (~450 km) from its southern-most distributional limit on the central African plateau over the past 6000 years. This abrupt biological response created an isolated (by ~200 km) and incomparable relict at the trailing population edge in north-east South Africa. These changes in miombo population dynamics may have been triggered by minor natural shifts in temperature and moisture regimes.[6] Should this be correct, it suggests that *B. spiciformis* is likely to be especially responsive to present and future anthropogenic climate change. This rare situation offers a unique opportunity to investigate climatic determinants of range shift at the trailing range edge of a savanna species. A niche modelling approach was used to produce present-day and select future *B. spiciformis* woodland ecological niche models. In keeping with recent historic range shifts, further ecological niche retraction of between 30.6 - 47.3% of the continuous miombo woodland in Zimbabwe and southern Mozambique is predicted by 2050. Persistence of the existing relict under future climate change is plausible, but range expansion to fragmented refugia in north-east South Africa is unlikely. As *Brachystegia* woodland and associated biota form a crucial socio-economic and biodiversity component of savannas in southern Africa, their suggested further range retraction is of concern.

2.2 Keywords

Brachystegia spiciformis, Climate change, Ecological niche model, MaxEnt, Refugia.

2.3   Introduction

At regional and global scales climate broadly limits the distribution of plant taxa,[1,2] and the response of species to changing environments is consequently likely to be largely determined by population responses at range margins.[3] However, few studies have examined climatic determinants of range shift at the trailing margin of a savanna species in the southern hemisphere. Understanding the historic and present-day spatial dynamics of vegetation plays a crucial role in our ability to predict the likely community responses and biodiversity consequences of future global change.[4]

Brachystegia spiciformis Benth. is a dominant component of miombo, the colloquial term used to describe sub-tropical woodlands dominated by *Brachystegia, Julbernardia* and *Isoberlinia* - three closely related genera in the family Fabaceae, subfamily Caesalpinioideae.[5] Miombo encompasses the woodland-dominated savanna ecosystems[6,7] which cover (Fig. 1) an estimated 2.7 million km^2 of south-central Africa[8] and is coincident with White's[9] Zambezian Phytochorion, the largest regional centre of endemism in Africa.[10] The dynamics of miombo woodland are largely determined by the woody component which, apart from climate, is predominantly influenced by people and fire. An estimated 75 million people inhabit areas covered by, or formerly covered by, miombo woodland, with an additional 25 million urban dwellers relying on miombo wood or charcoal as a source of energy.[11] Much of the woodland has been, and continues to be, modified by people. Changes in vegetation structure occur both as a direct result of woodland cover removal, and as an indirect effect from changes in fire regime brought about by higher grass production under a more open tree canopy.[12] Most of the dominant miombo canopy species, including *B. spiciformis*, are considered to be fire-tender species, which decline in abundance under regular burning and increase under complete fire-protection[5].

Mean annual precipitation and mean annual temperature throughout the miombo region range from 650 to 1400 mm and 15 to 25 °C, respectively. The majority (>

95 %) of precipitation falls during the summer season which prevails from October to March.[5] However, sporadic dry periods during the onset of the precipitation season may cause large fluctuations in soil moisture and temperature. Consequential drought and water stress during this concurrent and limited germination phase accounts for high seedling mortality in miombo woodlands.[13] Once established, the influence of climate, and of precipitation in particular, on *B. spiciformis* growth performance is strongest during the core of the precipitation season (December to February).[14]
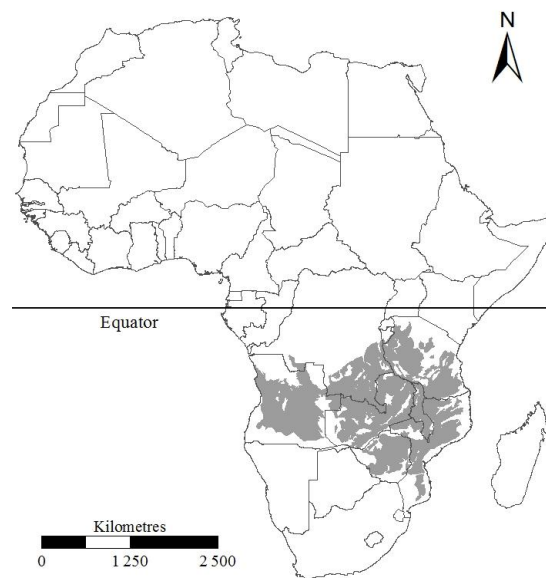
Figure 1.   Distribution of miombo woodland in Africa. Adapted from White's (1983) map of African vegetation.

Brachystegia are likely under-represented in pollen spectra due to the relatively low pollen production typical of entomophily.[5] Nevertheless, sediment cores containing pollen from the genus, dated to 38 000 years BP, have been recovered from the south-central African plateau.[15,5] Evidence suggests that the central plateau vegetation has undergone significant flux over this period, ranging from cool upland grassland during the Last Glacial Maximum (LGM, 19 000 years BP),

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to *Brachystegia* dominated-savanna during the warm interglacial period of the Mid-Holocene (6000 years BP).[5,16] Although literature regarding climate-induced range shifts at the genus level is limited for the subcontinent, Eeley *et al.*[17] concluded that the distribution of the forest biome in KwaZulu-Natal, South Africa, receded during the colder and drier conditions of the LGM, while warmer and wetter conditions during the Mid-Holocene were conducive to forest expansion. Correspondingly, *Brachystegia* woodland likely expanded to occupy a widespread historic range across south-central Africa prior to the LGM and during the warmer and wetter conditions of the Mid-Holocene.[15,18,19] Sediment cores containing pollen from the genus *Brachystegia* have been recovered from Pretoria, Mookgophong and Tate Vondo (Fig. 2) in South Africa,[15] the dates of which stand as evidence of a much more widespread distribution during the recent past (~6000 to less than 1000 years BP). These records support the presence of the genus at least up to 450 km south-west of the present-day distribution limit. This most recent and abrupt range retraction suggests either a sudden change in climate, for which there is no evidence,[19] or that minor shifts in temperature and moisture regimes have triggered marked changes in *Brachystegia* population dynamics.[5]

A change in geographic distribution from the simultaneous migration of populations throughout their range is unlikely. Instead, change is generated by the establishment of new, often discontinuous, populations at the leading edge of a species distribution and the coincident death of individuals and extirpation of populations at the trailing edge.[20] These retractions are often not complete, but instead leave behind fragmented populations that persist as relicts; isolated enclaves of favourable environmental conditions within an inhospitable regional climate.[21] Globally, numerous relict populations resulted from species range shifts experienced after the LGM.[21] For example, the present-day distribution of Neotropical seasonal dry forest formations is considered to comprise fragmentary remnants of the once extensive forests that characterized the dry climatic maxima of the Pleistocene.[22]
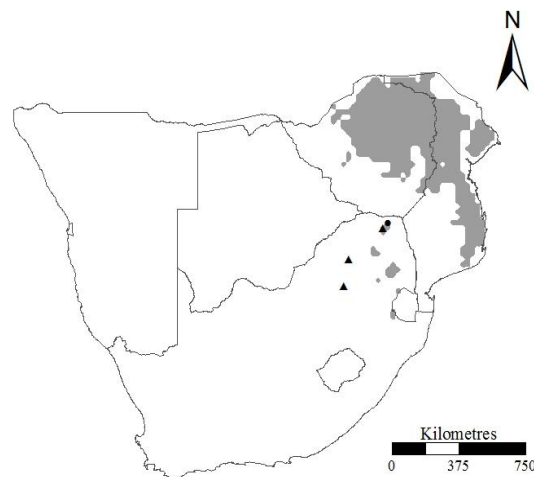
Figure 2.　　　Ecological niche of *Brachystegia spiciformis* woodlands in southern Africa under present-day climate conditions. Location of the Gundani climate relict population (black circle) and three Mid-Holocene pollen records (black triangles) included

Rutherford *et al.*[23] suggested that *B. spiciformis,* which at the time was known only from north of the South African border, could find a suitable ecological niche under future global climate change conditions along the high rainfall savanna-grassland biome interface of north-east South Africa. However, they concluded that range expansion through long-distance dispersal of the species into South Africa, across the Limpopo River Valley, was unlikely to occur unassisted given that seed dispersal distance is limited to less than 6 m[24] and that regeneration takes place predominantly through coppice regrowth and root suckers, rather than seed.[25] Startlingly, the discovery of the isolated *B. spiciformis* woodland (~15 ha, Fig. 2) in the eastern Soutpansberg of South Africa[26] placed the species within the region predicted by Rutherford *et al.*[23] This isolated population, occurring some 200 km south of the continuous miombo woodlands of the subcontinent, suggests a trailing edge refugium persisting from a previously wider historic range dating prior to the LGM or during the Mid-Holocene. This woodland relict (known as Gundani locally) shares characteristics of the extensive *B. spiciformis* woodlands of Zimbabwe and southern Mozambique, including the open structure, medium canopy height, poorly developed lower strata and high dependence on root suckering and coppicing for regeneration.[27] The presence of a second *Brachystegia* species within the Gundani woodland, limited to a single *B. utilis*

individual, further suggests that this is likely a climate relict of a vegetation type from a time when, at least, the genus *Brachystegia* dominated the Soutpansberg massif in north-eastern South Africa.[28]

Trailing range edge studies reflect a bias (86 %) towards high-latitude range margins and temperate vegetation communities,[3] which have minimum temperature related constraints. Conversely, this rare situation provides a unique opportunity to explore climatic constraint at low-latitude range margins for an ecologically significant savanna species.

Using a predictive modelling approach, this climate specific study determined i) the likely geographic footprint of the *B. spiciformis* woodland ecological niche in southern Africa under present-day and selected future (2050) global climate change scenarios, ii) the specific ecological niche dimensions of *B. spiciformis* woodland in southern Africa, and iii) whether bioclimatic variables at palaeohistoric distribution sites for the genus could have supported *B. spiciformis*, the dominant component of present-day miombo woodland in southern Africa, during the Mid-Holocene.

2.4   Methods

2.4.1   Species data

A total of 914 mature *B. spiciformis* specimens, from south of the Zambezi River, were considered (717 *in situ* observations and 197 from regional and online herbaria). These were subsequently converted to Quarter Degree Square (QDS) centroid points to accommodate numerous herbaria records. All duplicates were excluded producing a total of 76 QDS centroid points ($n = 76$). QDS is a commonly used format for general species distribution mapping in South Africa.[29] These species data include the vicariant *B. spiciformis* population from South Africa, as the inclusion of relict populations has been shown to improve the performance of model-based projections.[20]

2.4.2 Predictor modelling

MaxEnt v.3.3.3k[30] was used to project suitable ecological niche models (ENMs) for *B. spiciformis* woodland in southern Africa as it has been found to perform best among many different modelling approaches.[31] Functionality relies on a list of presence-only locations and a set of environmental predictors across a user-defined landscape, which is divided into grid cells, to generate species presence probability.

2.4.3 Predictor variables

Nineteen regional bioclimatic variables and altitude ('BioClim') grid data were downloaded from the 'WorldClim'[32] database. The bioclimatic variables are derived from monthly temperature and rainfall recorded worldwide (period 1950-2000) and are often used in ecological niche modelling (e.g.[33,34]). A soil variable (dominant soil group) was added from the Harmonised World Soil Database (HWSD).[35] ENM Tools v.1.3[36] was used to produce pairwise Pearson correlation coefficients to eliminate spatially correlated variables (>0.85) from the modelling process, with preference given to variables with higher influence on species presence probability. Summer precipitation variables were also prioritised during the elimination process as Trouet *et al.*[14] suggests they have a strong influence on *B. spiciformis* growth performance. The 14 variables used in all models were Bio2-6, Bio8-9, Bio15-19, altitude and soil (Appendix 1).

There are currently at least 24 coupled atmosphere-ocean general circulation models (AOGCMs) being used to project climatic changes for more than ten different greenhouse-gas emission scenarios.[37] We selected three (HadCM3, CGCM2 & CSIRO-MK2) commonly used AOGCMs (see[38,39]) to forecast the impact of climate change on *B. spiciformis* distribution. The A2a emission scenario, an intermediate scenario representing regional development and slow economic growth, was used across all three AOGCMs.

2.4.4   Model settings

The spatial resolution of all variables and landscape grid cells was resampled to QDS resolution. MaxEnt iterations were set to 5000 and accuracy evaluated by constructing the model using 75% of presence records as training points, with the remaining 25% used in validation. The accuracy of the present-day ecological niche model was inferred from the area under the receiving operating characteristic curve (AUC) score that varies from 0 to 1, with 0 being the lowest and 1 being the highest probability of matching the species distribution.[31] Subsequently, the present-day ecological niche model was applied to the three selected future (2050) AOGCMs. The increase in AUC score was used as a test metric to determine the most important bioclimatic variables explaining *B. spiciformis* woodland distribution, when each variable was used in isolation.

2.4.5   Ecological niche comparison

The fundamental niche[40] was represented by a box plot, with the inter-quartile range (box with median present) representing 50% of the total data values and the upper and lower whiskers representing 25% of the values, respectively. The inter-quartile space is interpreted as the 'most suitable' range of climatic or environmental conditions for the species, while the lower and upper whiskers span less suitable conditions, reflecting lower and upper tolerance limits, respectively. Extreme values, beyond the 1.5 coefficient value, were plotted as individual open circles.

Geospatial Modelling Environment v.0.7.2.1[41] was used to intersect *B. spiciformis* distribution records (*n = 76)* from selected (highest AUC scores and limiting factors) bioclimatic layers (Bio4, 5, 6, 15 and 16). The grid value at each point was used to create box plots representing the present-day ecological niche (Fig. 3).
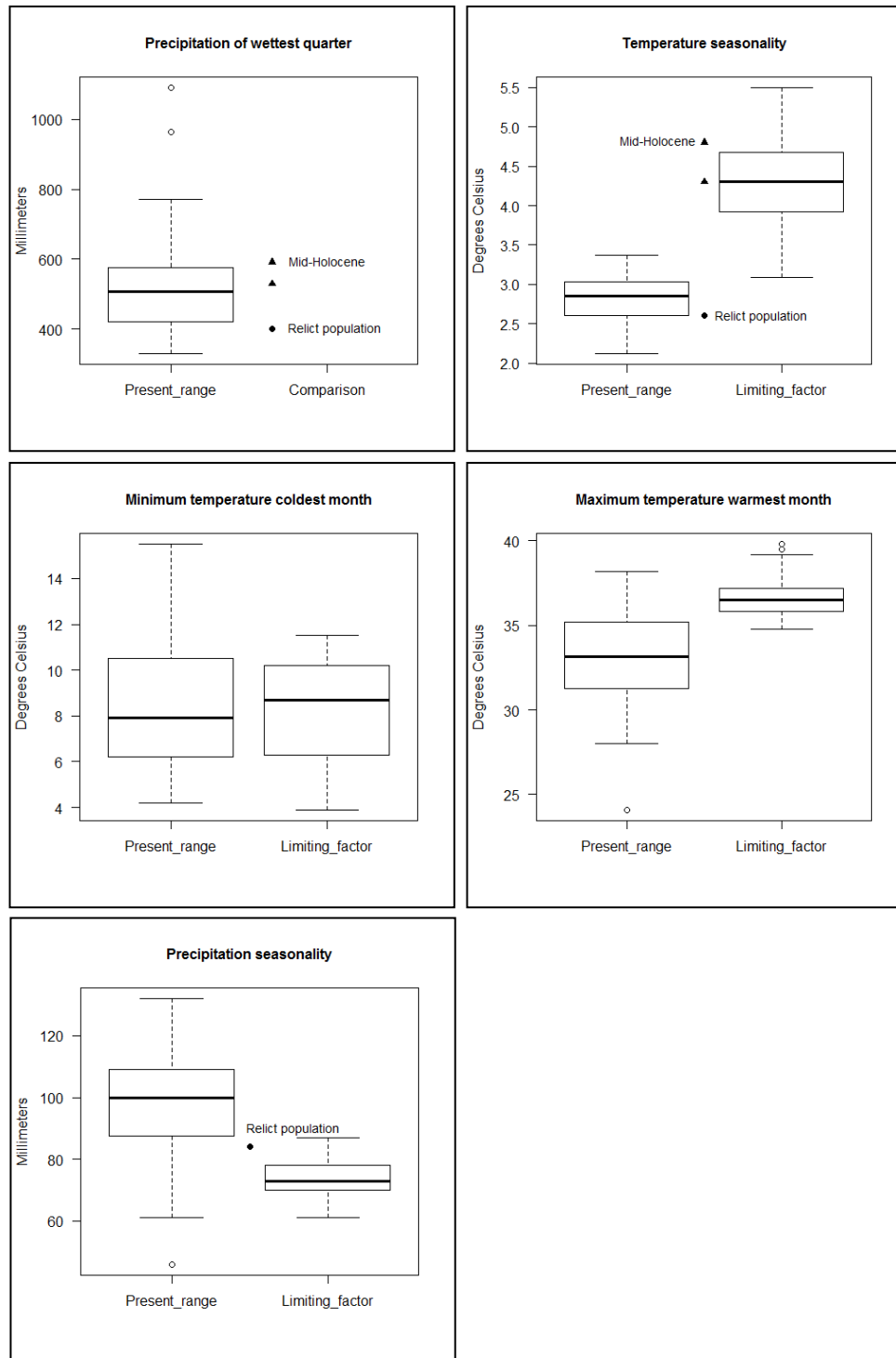
Figure 3. Comparative box plots for the present-day range (76 quarter-degree-square (QDS) centroid points) representing the ecological niche of *Brachystegia spiciformis* woodland in southern Africa vs. a limiting factor (76 adjacent, randomly selected QDS centroid points). Extreme values included as open circles. Palaeohistoric (solid triangle) and relict population (solid circle) values are included for comparison.

Seasonal data (precipitation and temperature) from Mid-Holocene ocean-atmosphere-vegetation models (OAVs) was used to intersect three palaeohistoric *Brachystegia* distribution points with the Geospatial Modelling Environment. These grid values were subsequently used to construct Bio16 (precipitation of the wettest quarter) and Bio4 (temperature seasonality, the standard deviation of mean monthly temperature in degrees Celsius) as per BioClim. These two bioclimatic variables were selected as they achieved the highest increase in AUC score. This was repeated across all available Mid-Holocene OAVs (ECBILTCLIOVECODE, ECHAM53-MPIOM127-LPJ, FOAM, MRI-CGCM2.3.4fa, MRI-CGCM2.3.4nfa and UBRIS-HadCM3M2) from the Palaeoclimate Modelling Intercomparison Project Phase 2 (PMIP2[42]) database (http://www-lscedods.cea.fr/pmip2_dbext/pmip2_6k_oav/atm/se/). Mid-Holocene Bio16 and Bio4 values, averaged across all six models, were evaluated against the present-day ecological niche.

2.4.6 Limiting factors map

A limiting factor map (Fig. 4) was produced as per Elith *et al.*[31] Using Geospatial Modelling Environment and implementing the method described above, box plots were created from randomly selected QDS centroid points (*n = 76)* within the area immediately adjacent to the current distribution of the species where a specific bioclimatic variable was shown as limiting. Box plots and paired sample *t-tests* were used to compare *B. spiciformis* ecological niche and limiting factor dimensions per selected bioclimatic variable (Bio4, 5, 6, and 16). Comparison of means was done using R v.3.0.3.[43]
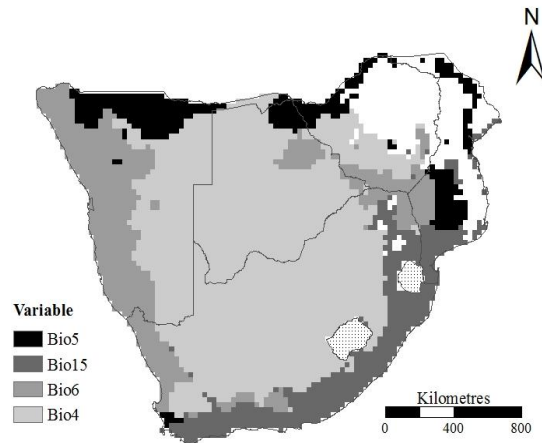
Figure 4.   Limiting factors of the present-day ecological niche of *Brachystegia spiciformis* woodland in southern Africa (excluding Lesotho and Swaziland). Bioclimatic variables: Bio5 = Maximum temperature of the warmest month; Bio15= Precipitation seasonality; Bio6 = Minimum temperature of the coldest month; and Bio4 = Temperature seasonality.

2.5   Results

2.5.1   Model performance and variable contribution

The present-day ecological niche model for *B. spiciformis* achieved an AUC value of 0.923, which is considered very good[44]. The model was subsequently applied to three future AOGCMs. Precipitation of the wettest quarter (Bio16) and temperature seasonality (Bio4) were identified as the two most important bioclimatic variables explaining *B. spiciformis* woodland distribution in southern Africa (Table 1). This was consistent across the present-day and three future models.

Table 1.   Area under the curve (AUC) scores for top-performing bioclimatic variables explaining current and three future distributions for *B. spiciformis* in southern Africa.

	AUC Score			
Bioclimatic variable	Present	HadCM3	CGCM2	CSIRO-MK2
Precipitation of Wettest Quarter (Bio16)	0.916	0.911	0.901	0.913
Temperature Seasonality (Bio4)	0.854	0.856	0.848	0.849

2.5.2   Present-day ecological niche

The ENM (Fig. 2) predicts the presence of isolated *B. spiciformis* populations in South Africa, one of which is coincident with the location of the Gundani relict discovered in 2001. The model further indicates suitable ecological conditions for the species elsewhere at disjunct locations along the high rainfall savanna-grassland interface of north-eastern South Africa. However, the species does not presently occur outside of the relict population.[45] Besides the fact that White's map of African vegetation[9] does not indicate miombo woodland presence in South Africa, it is coincident with the present-day ENM projection for *B. spiciformis* in southern Africa.

Precipitation of the wettest quarter (Fig. 3) suggests a relatively narrow range of optimal suitability of 422 - 576 mm, with a median of 507 mm. Similarly, the 'most suitable' range for temperature seasonality (Fig. 3) is constrained between 2.6 °C and 3.0 °C, with a median of 2.8 °C. The value of the former variable at the Gundani relict population (401 mm) falls within the lower tolerance limit of conditions experienced by the species, whereas the value for the latter variable at the relict population (2.6 °C) falls within the 'most suitable' range for *B. spiciformis* in southern Africa.

2.5.3 Past ecological niche

A crude palaeohistoric distribution of *Brachystegia*, as inferred from three Mid-Holocene sediment core pollen records from South Africa (Fig. 2), supports past average climate values of 529 mm and 591 mm (2 records) for precipitation of the wettest quarter, and temperature seasonality averages of 4.3 °C and 4.8 °C (2 records) for that period. For the former (Fig. 3), these averages fall within (or nearly so) the 'most suitable' range identified under present-day conditions (422 - 576 mm). Alternatively, the historic temperature seasonality values exceed even the upper tolerance limit (a maximum of 3.4 °C) for this species across its present-day southern African distribution (Fig. 3).

2.5.4 Future ecological niche

The future ecological niches for all three models (Fig. 5) are consistent with a predicted decrease in the continuous *B. spiciformis* woodland distribution of Zimbabwe and southern Mozambique (30.6% to 47.3%) and a decrease in the overall ecological niche (including South Africa) of between 16.9 - 32.2% by 2050 (Table 2). These figures reflect net change, with a decreased niche potentially resulting from larger retraction at present-day distributions combined with comparatively smaller range increases at newly favourable distributions elsewhere.
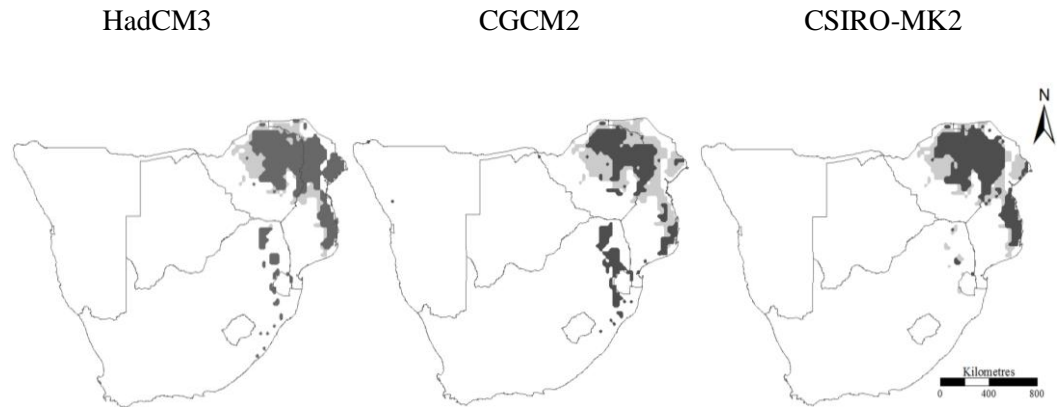
Figure 5. Predicted future (2050) ecological niche for *Brachystegia spiciformis* woodland in southern Africa (dark grey) under the A2a scenario across three general circulation models. Present-day ecological niche (light-grey) is included for comparison

Table 2. Percentage ecological niche change by 2050 for *Brachystegia spiciformis* woodland in Southern Africa according to three different climatic models under the A2a scenario.

Ecological niche change (%)	Scenario A2a		
	HadCM3	CGCM2	CSIRO-MK2
South Africa	+170.6	+376.5	-70.6
Continuous	-31.3	-47.3	-30.6
Overall	-16.9	-32.2	-32.0

Two models (HadCM3 & CGCM2) suggest extensive southward ecological niche expansion in South Africa by approximately 200% and 400%, respectively, at the savanna-grassland biome interface; and into areas south (29 ºS) of the present-day actual (22.5 ºS) and predicted (~27 ºS) ranges. Models HadCM3 and CSIRO-MK2 indicate that a suitable ecological niche at the location of the South African *B. spiciformis* woodland relict will not persist. Under no climatic scenario does the predicted future distribution mirror the south-western range historically occupied by the species during the Mid-Holocene.

2.5.5 Present-day limiting factors

Climate values falling outside of the present-day fundamental niche or suitability range of *B. spiciformis* woodland in southern Africa place climatic constraint on the species, and can therefore be considered as limiting factors to its geographic footprint. Three bioclimatic variables were identified as potential limiting factors for *B. spiciformis*.

Temperature seasonality (Bio4) and maximum temperature of the warmest month (Bio5) are suggested to be responsible for restricting distribution of the continuous *B. spiciformis* woodlands of Zimbabwe and southern Mozambique (Fig. 4). The temperature seasonality range in areas to the south-west of the present-day distribution in Zimbabwe is broad (3.9 – 4.7 °C), but exceeds the maximum 'most suitable' temperature seasonality of 3.0 °C experienced by the species across its present-day range (Fig. 3). Although there is overlap between the lower quartile of the limiting factor range and the upper tolerance limit of the current distribution, the mean (4.2 °C vs. 2.8 °C) of the former is significantly higher ($P < 0.01$).

Maximum temperature of the warmest month in areas to the north and north-west of the Zimbabwean population, and to the south and east of the Mozambican population (Fig. 4), is tightly constrained between 35.9 °C and 37.2 °C (Fig. 3). This exceeds the upper limit of the 'most suitable' range of 35.2 °C for this variable established from the present-day distribution of the species. Despite substantial overlap between the upper tolerance of the current distribution range and the upper- and even the inter- quartiles for the limiting factor range, the means (36.6 °C vs. 33.1 °C) differed significantly ($P < 0.01$), with temperatures being too high to support *B. spiciformis* woodland.

Correspondingly, precipitation seasonality (Bio15) and minimum temperature of the coldest month (Bio6) may restrict present-day distribution of the fragmented *B. spiciformis* ecological niche in South Africa (Fig. 4). However, there is no

significant difference ($P = 0.5499$) between the limiting factor mean of adjacent minimum temperature of the coldest month (8.4 °C) and that of the 'most suitable' range (8.7 °C) for *B. spiciformis* (Fig. 3). Consequently we rejected minimum temperature of the coldest month as a valid limiting factor for this species. Alternatively, precipitation seasonality's range is tightly constrained (70 – 78 mm) and falls short of the minimum precipitation seasonality value of 87.8 mm which bounds the present-day 'most suitable' range of the species (Fig. 3). Although there is overlap between the inter-quartile range of the limiting factor and the lower tolerance limit of the current distribution range, the mean (74.3 mm vs. 98.2 mm) of the former is significantly lower ($P < 0.01$).

2.6   Discussion

2.6.1   Present-day ecological niche

The fragmented ecological niche suggested for *B. spiciformis* in South Africa is a refinement of the Rutherford *et al.*[24] model, which predicted a similar distribution for this species under future global change conditions. Moreover, the presence of a population within one of the modelled ecological niche fragments suggests a refugium. Defined on climatic grounds, refugia are physiographic settings that can support once prevalent regional climates that have been lost (or are being lost) due to climate shifts.[46] The isolated *B. spiciformis* woodland relict at Gundani has therefore likely persisted in a refugium created by the varied topography of the Soutpansberg massif in South Africa. This topography has led to the formation of an isolated pocket of habitat experiencing the suitable climatic conditions (precipitation of the wettest quarter and temperature seasonality) that define the distribution of the species across the remainder of its current southern African range, and which prevailed at sites where *Brachystegia* occurred prior to the LGM and during the warmer and wetter conditions of the Mid-Holocene in the recent past.

Precipitation seasonality values in areas immediately adjacent to this isolated refugium are significantly lower than for the ecological niche dimension of *B. spiciformis* woodland in the rest of southern Africa (Fig. 3). Consequently, this bioclimatic variable reflects climatic constraints on the present-day ecological niche and isolated relict population in South Africa, potentially preventing the distribution of the species outside of the relict population. Similarly, high temperature seasonality and maximum temperature of the warmest month (Fig. 3) place climatic constraints on the extremities (south-west and north-east respectively) of the continuous *B. spiciformis* woodlands of Zimbabwe and southern Mozambique (Fig. 4). Although most savanna plants can tolerate maximum temperature extremes, Chidumayo[47] showed that some savanna trees are sensitive to seasonal highs.

2.6.2   Past ecological niche

According to the precipitation of the wettest quarter bioclimatic variable, conditions were evaluated to be suitable for the presence of *B. spiciformis* at the three *Brachystegia* pollen sites during the Mid-Holocene. However, temperature seasonality 6000 years BP was unfavourably high according to the present-day ecological niche dimensions of *B. spiciformis* woodland in southern Africa, casting doubt as to the value of this climatic metric in controlling the distribution of *B. spiciformis* in its current range (from ENM), and in limiting its distribution north of South Africa's border (from limiting factors). However, two assumptions underlie most analyses of past climate using proxies and models. The first is that climate sets the boundaries to vegetation types, and therefore vegetation types are in equilibrium with climate except during the most rapid periods of climate change. Under this assumption pollen-climate transfer functions can therefore provide reliable estimates of past climate. Second, on long time scales, climate changes are driven by solar insolation changes.[48]

It should therefore be considered that precessional insulation in the southern hemisphere reached a minimum during the Early-Holocene ~ 9000 years BP.[49] Hence, there were reduced seasonal cycles and lower temperature seasonality.

Subsequently, a steady increase in summer insolation, and therefore temperature seasonality, between 9000 and 6000 years BP may already have reached an unfavourable range for *B. spiciformis* as the Mid-Holocene bioclimatic layer would suggest. The presence of pollen at these sites indicates that vegetation type boundaries are not in equilibrium with climate during rapid response phases to climate change. Adult trees may persist in an area of previously suitable climate during extended periods of climatic constraint (the storage effect), particularly if populations are capable of adaptive dynamics such as clonal regeneration. *Brachystegia* may therefore be subject to an extensive period of persistence between vegetation-climate equilibrium and local extirpation.

2.6.3   Future ecological niche

In keeping with the approximate north-eastward retraction of the species distribution over the past 6000 years, a further ecological niche retraction of between 30.6% and 47.3% of the continuous *B. spiciformis* woodland in Zimbabwe and southern Mozambique is predicted by 2050. The decreasing suitability of habitat at the periphery of the continuous miombo population is supported by climate projections for the subcontinent.

Southern Africa is suggested to become hotter (temperature increase of up to 3 °C) and drier (precipitation decrease of ~10%) by 2060 and 2100 respectively.[50,51] The projected increase in heat waves and the number of days above 35 °C[51] over the continuous miombo woodland region will subsequently amplify variability in mean monthly temperatures. This is likely to stress the tolerance of *B. spiciformis* further by pushing maximum temperature of the warmest month and temperature seasonality into the upper tolerance limit of the species, and closer to the limiting factor mean (Fig. 3).

The future predicted decline in rainfall indicates a relatively strong drying signal for Zimbabwe and central Mozambique.[51-53] The associated decrease in precipitation of the wettest quarter over central Zimbabwe[51] may therefore place

climatic constraint on the future ecological niche as this variable, which is considered the most important in determining *B. spiciformis* distribution, will become increasingly unsuitable.

In contrast, the suitable *B. spiciformis* niche in South Africa is modelled to experience very large and inconsistent spatial shifts by 2050, varying between range retractions of 70.6% to range expansion of 376.5% (Table 2). The large discrepancy between models likely relates to the coincidence with a topographical heterogenous area on the north-eastern escarpment, where the central highlands of South Africa abruptly give way to low-lying coastal plains. Fine scale topographical effects on climate, which seem necessary for refugia, are not well captured within downscaled AOGCMs, contributing to model uncertainty.

Nevertheless, future climate change projections for north-east South Africa, which include the *B. spiciformis* woodland relict, suggest hotter (temperature increase of ~0.9 °C) and wetter (precipitation increase of ~11%) conditions by 2100.[54] Although subcontinental projections indicate increases in temperature seasonality[51], we suggest that future change will be buffered by the varied topography of the Soutpansberg massif, as it has occurred historically. We suggest that the subsequent increase in precipitation of the wettest quarter (~8%[54]) will shift local climatic conditions at Gundani, from the present-day lower tolerance limit, into the 'most suitable' range as identified for the species (Fig 3). However, the concurrent regional decrease (~6%[54]) in precipitation seasonality may cause conditions to become less tolerable as it shifts away from the 'most suitable' range of *B. spiciformis* woodland (Fig. 3).

Considering that there may be greater uncertainty with regards to the impact of climate on the ecological niche of *B. spiciformis* at the distribution edge, as compared to the continuous range, all three possible responses of populations to climate change should be considered.

Migration

It is unlikely that *B. spiciformis* woodland is capable of unaided range expansion through long-distance dispersal events, particularly given the very limited dispersal distances reported for the genus. There are limited untransformed or protected areas that could facilitate the establishment of new populations within the suggested ecological niche. In addition, current land use practices have lead to large scale fragmentation which does not allow natural corridors for population expansion through clonal regeneration. Subsequently, any predicted range expansion of *B. spiciformis* woodland in South Africa along the eastern escarpment is considered unlikely due to anthropogenic constraints.

Adaptation

The persistence of populations as relicts may result from pockets of environmental suitability within the landscape, or may be the consequence of some adaptive dynamics by which species manage to overcome the climatic constraints posed by a changing climate. For example, plant ecology studies indicate climatic constraints on seed production.[55] Consequently, rather than relying on pollination and seed production, many climate relicts rely more strongly on vegetative or clonal reproduction. The well-documented reliance of *B. spiciformis* on coppice regrowth and root suckering both at the Gundani relict[28] and in the continuous woodland[6], rather than seed germination, suggest that even in the event of failed recruitment through climatic intolerance, the populations would persist though vegetative reproduction and the longevity of genets. Relict populations can furthermore improve their survival prospects by enlarging their climatic tolerance through phenotypic plasticity or micro-evolutionary adaptation.[56] Once the capacity for phenotypic adjustment is exceeded, genetic adaptation remains the only option.[22]

However, several characteristics of relict populations imply that their potential for micro evolutionary adaptation may be limited. First, strong phenotypic divergence

compared with conspecifics from other parts of the range does not appear to be a common phenomenon despite the presumed long-term exposure of relict populations to relatively strong selective pressures.[57] Second, within-population genetic variation tends to be low in many climate relicts as a consequence of small population size, past bottlenecks[3] and the occurrence of clonality. Third, the small size of many relict populations, in combination with strong selection pressure, is likely to substantially elevate their risk of extinction due to demographic or environmental stochasticity before they can effectively adapt.[57]

Extinction

Although broad-scale changes in species distribution can reasonably be forecast[21], our understanding of the environment and ecology of most climate relicts remains too poor to adequately anticipate their persistence or demise[22]. The historical resilience of such populations demonstrates that we cannot simply assume that they will be extirpated rapidly after climate change[22]. The storage effect suggests that individuals of the species may be present in an area long after the climate has become marginally tolerable, or completely unsuitable, depending on the life stage on which the climate control may act. The isolated *B. spiciformis* woodland plays an important role in the natural heritage of the local people and has been placed under a traditional woodland management regime. The tree is not currently used ethnobotanically and the direct threat of anthropogenic extinction is considered unlikely.

Having ruled out future climate-induced migration and recognising that opportunities for adaptation beyond phenotypic adjustment are limited, what then is the fate of South Africa's only miombo woodland? We suggest that the medium-term persistence of the relict is plausible based on i) future climate change projections (2100), which suggest that local climatic variables will remain within (or nearly so) the 'most suitable' range of *B. spiciformis*, ii) the longevity of genets and the species' ability to regenerate vegetatively, and iii) its historic resilience.

The suggested ecological niche retraction of the continuous *B. spiciformis* woodland in Zimbabwe and southern Mozambique may however be less exaggerated. Bioclimatic models are limited in their ability to determine the full extent of ecological interactions, especially in savannas where the direct impact of climate on species distribution may be variable. One such example is that of future increases in atmospheric CO_2. Species with large below-ground carbon sinks, like miombo, benefit from CO_2 fertilisation[58] which increase tree water use efficiency (WUE).[59] This is consequently likely to contribute towards a greater tolerance of suggested decreased precipitation of the wettest quarter.

2.7   Conclusion

This study identifies the likely climatic determinants responsible for range shift at the trailing distribution margin of *B. spiciformis* in southern Africa. Given the suggested divergent future responses of the continuous woodlands of Zimbabwe and Mozambique relative to that of the South African relict, an understanding of population dynamics and demographics across the subcontinent will prove critical in validating our predictions concerning the climate response phases (migration, adaptation, persistence) of *B. spiciformis* and elucidating the life history stages during which climatic constraints may be imposed. Understanding both historic and contemporary climatic determinants of a species range is the first step towards assessing the vulnerability of extant climate relicts under global climate change. Theoretical responses must then be supported by *in situ* monitoring of the populations.

Climate relicts have value as instructive models and natural laboratories for investigating how populations react to on-going climatic change.[60] Beyond the scope of this study exists an opportunity to explore genetic variation within the *B. spiciformis* relict population and investigate potential micro evolutionary adaptation since isolation. Furthermore, development of long *B. spiciformis* and *B. utilis* tree-ring chronologies from the relict would allow for the investigation of

temporal El Niño Southern Oscillation (ENSO) variability and predictions of future regional effect. Considering that ENSO effects on precipitation variability are strongest in southern Africa during the wettest quarter,[14] the investigation may assist to adequately anticipate persistence or demise of the relict population.

2.8 Acknowledgements

2.9   References

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2.10 Appendices

Appendix 1: Bioclimatic (BioClim) variables used in the ecological niche models of past, present and future *Brachystegia spiciformis* distributions.

Bio1 -   Annual Mean Temperature

Bio2 -   Mean Diurnal Range (Mean of monthly (max temp – min temp))

Bio3 -   Isothermality (Bio2/Bio7) (*100)

Bio4 -   Temperature Seasonality (standard deviation *100)

Bio5 -   Maximum Temperature of Warmest Month

Bio6 -   Minimum Temperature of Coldest Month

Bio7 -   Temperature Annual Range (Bio5-Bio6)

Bio8 -   Mean Temperature of Wettest Quarter

Bio9 -   Mean Temperature of Driest Quarter

Bio10 -   Mean Temperature of Warmest Quarter

Bio11 -   Mean Temperature of Coldest Quarter

Bio12 -   Annual Precipitation

Bio13 -   Precipitation of Wettest Month

Bio14 -   Precipitation of Driest Month

Bio15 -   Precipitation Seasonality (Coefficient of Variation)

Bio16 -   Precipitation of Wettest Quarter

Bio17 -   Precipitation of Driest Quarter

Bio18 -   Precipitation of Warmest Quarter

Bio19 -   Precipitation of Coldest Quarter

CHAPTER THREE

Patterns in community dynamics of *Brachystegia* (miombo) woodland climate relicts at the southern African trailing range edge

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B. Pienaar and D.I. Thompson conceived the study; B. Pienaar performed the analyses; B. Pienaar drafted the first complete version of the manuscript. All co-authors read and improved the manuscript.

3.1 Abstract

Brachystegia spiciformis is the dominant component of miombo, the colloquial term used to describe sub-tropical woodlands dominated by three closely related genera in the family Fabaceae, subfamily Caesalpinioideae (Campbell 1996). Miombo cover an estimated 2.7 million km^2 of south-central Africa (Millington *et al.* 1994) and has a contemporary latitudinal distribution range limit at $\sim 21^o$ S on the central Africa plateau. In particular, the dynamics of populations comprising the margins of the distribution range are important in determining a species ultimate response to anthropogenic climate change (Thomas *et al.* 2001; Iverson *et al.* 2004; Travis & Dytham 2004). This southern African study provides a unique opportunity to explore climate relict and trailing range edge population dynamics of an economically and ecologically significant tropical African savanna species. *Julbernardia globiflora* is more abundant than *B. spiciformis* at the drier periphery and displays weaker recruitment and population density. The woodland also exhibit smaller basal diameter and decreased total basal area. Relict miombo population dynamics were primarily driven by insular biogeography effects with signs of natural biota loss and reduced recruitment. It is suggested that population dynamics of *Brachystegia* (miombo) woodland, which receives < 650 mm precipitation per annum, at the distributional range edge in southern Africa are no longer in equilibrium with their environment.

3.2 Keywords

Brachystegia spiciformis, Climate change, Reproduction, Refugia, Size class distribution, Species composition.

3.3 Introduction

At regional and global scales climate broadly limits the distribution of plant taxa (Woodward 1987; Prentice *et al.* 1992) and the response of species to changing environments is likely to be predominantly determined by population responses at range margins (Hampe & Petit 2005). However, changes in geographic distributions do not simply result from the simultaneous migration of individuals, and populations, throughout their range. Instead, they are generated by the establishment of new, often discontinuous populations at the leading distribution range edge of a species and extinction of individuals and populations at the trailing range edge (Thuiller *et al.* 2008). Range retractions are often not complete, but rather leave behind fragmented populations that remain as relicts within isolated enclaves of favourable environmental conditions surrounded by an inhospitable regional climate (Hampe & Jump 2011).

Brachystegia spiciformis Benth. is a dominant woody component of miombo, the colloquial term used to describe sub-tropical woodlands dominated by *Brachystegia, Julbernardia* and *Isoberlinia*; three closely related genera in the family Fabaceae, subfamily Caesalpinioideae (Campbell 1996). Miombo encompasses the woodland-dominated spectrum of savanna ecosystems (Walker 1981; Huntley 1982) and covers an estimated 2.7 million km^2 of south-central Africa (Millington *et al.* 1994). Further, miombo are coincident with White's (1983) Zambezian Phytochorion, the largest regional centre of endemism in Africa (Chidumayo 1997). The contemporary latitudinal distribution range limit of miombo woodland on the central Africa plateau is ~21° S, sited in central Zimbabwe. However, palynological evidence suggests a more widespread historic range which extended to ~26° S, during the mid-Holocene (Scott 1982, 1983, 1984). The range retraction of miombo woodland during the past ~6000 years has been incomplete and resulted in the formation of two isolated *B. spiciformis* dominated communities located in refugia well beyond the contemporary southern-most latitudinal distribution range limit. The presence of such communities outside of their contemporary range and evidence, provided by fossil or pollen records, of past occupation (Hampe & Jump 2005) allows for the

inference of past climates. It has therefore been suggested (Pienaar *et al.* 2015) that the two out-of-range miombo communities - one in southern Mozambique and one in South Africa, represent climate relicts isolated from the trailing latitudinal range edge of the continuous miombo woodlands of south-central Africa. The biological response of miombo woodland, here being range retraction, propose either a key change in climate, something for which there is no evidence (Scott 1984), or that marginal natural shifts in temperature and moisture regimes triggered marked changes in community dynamics. In keeping with the woodland's distributional range retraction northwards over recent millennia, further ecological niche retraction for *B. spiciformis* is predicted for Zimbabwe and southern Mozambique by 2050 under plausible future climates (Pienaar *et al.* 2015).

The dynamics of those populations that inhabit the margins of the distribution range are important in determining a species' ultimate response to anthropogenic climate change (Thomas *et al.* 2001; Iverson *et al.* 2004; Travis & Dytham 2004). In the case of *B. spiciformis*, understanding population reproduction and resilience will prove critical in validating predictions concerning the possible climate response phases (migration, adaptation, persistence) of the woodland and elucidating the life history stages during which climatic constraints may be imposed.

Investigating the population dynamics of *B. spiciformis* at the retreating range limit will contribute towards the understanding of woodland response to predicted future anthropogenic climate change. Trailing range edge studies reflect a bias (86%) towards high-latitude range margins and temperate vegetation communities (Hampe & Petit 2005). This southern African study provides a unique opportunity to explore climate relict and trailing range edge population dynamics of an economically and ecologically significant tropical African savanna species. We elucidate patterns in miombo woodland relict communities, with regards to their *i)* floral diversity and representivity, *ii)* rate of reproduction, *iii)* population density, *iv)* structural dimensions and *v)* likely persistence under global change.

3.4 Methods

3.4.1 Study area

Miombo woodland extends across the African sub-humid tropical zone from Tanzania and the Democratic Republic of Congo in the north, through Zambia, Malawi and Angola, to Mozambique and Zimbabwe in the south. Although disjunct in distribution, the majority of southern miombo woodland occurs on the central African plateau of Zimbabwe, where granite and gneiss inselbergs recurrently augment the flat to undulating terrain. This, the largest section of unfragmented miombo woodland (Figure 1) dominated by *B. spiciformis*, extends further east beyond the Chimanimani mountain range of Zimbabwe into Mozambique, where it dominates sandstone formations at lower elevations (Barnes 1998) and is henceforth referred to as the continuous miombo woodland. The miombo woodlands of southern Africa are coincident with geologically old, nutrient-poor soils and a savanna climate of moderate temperature seasonality and uni-modal summer rainfall from November through March. Mean annual temperatures range from 16 to 24 °C, while mean annual precipitation ranges from 600 to 950 mm. The plant community is dominated by *B. spiciformis* and *Julbernardia globiflora* (Benth.) Troupin, which produce the characteristic 'woodland' physiognomy and have the functional characteristic of being only briefly deciduous during winter.

Two relict communities exist to the south of the continuous contemporary miombo distribution range limit. Panda (S 24°00' E 34°40') is the only locality in Mozambique where miombo woodland occurs south of the Save River (Parker 1999). This community comprises ~32 000 ha of *B. spiciformis* dominated woodland, which is isolated by ~340 km from the continuous miombo of east-central Africa and is hereafter referred to as the *Mozambique relict*. The second relict, Gundani (S 22°52' E 31°25') is South Africa's only miombo woodland and was only discovered by the scientific community in 2001 (Hurter & van Wyk 2001). It is restricted to only ~15 ha of *B. spiciformis* woodland on the eastern

Soutpansberg and is isolated from the woodlands of Zimbabwe by ~240 km. It is henceforth referred to as the *South African relict*.
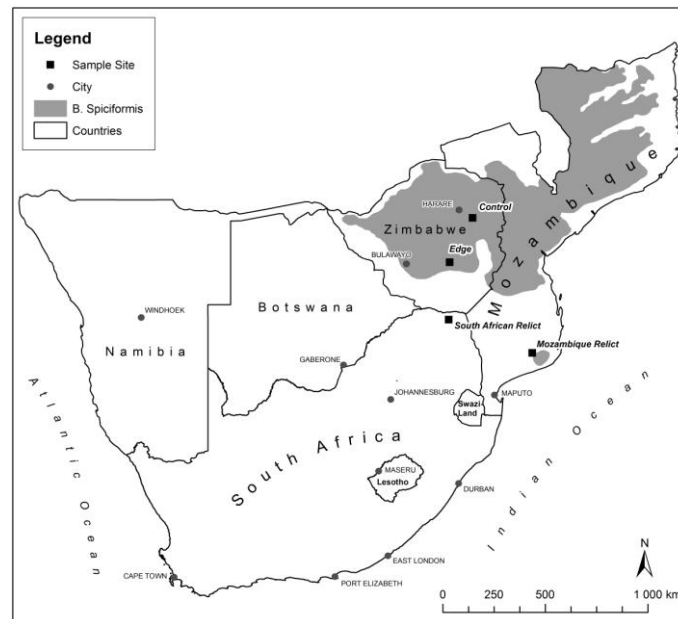
Figure 1. Distribution of *Brachystegia spiciformis* (miombo) woodland and the four sample sites in southern Africa.

In addition to these two geographically isolated communities, a further two study sites were selected to best elucidate patterns in floral diversity, composition and structure of miombo woodland at its southern-most distributional range limit in Africa. Gosho Park (S 18°10' E 31°37') on the Mashonaland plateau in central Zimbabwe was established in 1984 to protect ~340 ha of undisturbed miombo woodland. This mature and relatively pristine community is located well within the continuous miombo distribution range of southern Africa and was selected as the ecological *Control*. The Masvingo region (S 22°52' E 30°25') of Zimbabwe is the southern-most distributional limit of the continuous miombo woodland of the central African plateau. This site selection was based on the assumption that climate determines the boundaries of vegetation units, with vegetation being in equilibrium with climate except during periods of rapid flux. This location is hereafter referred to as the population *Edge*.

3.4.2 Sampling design

Field data were collected between December 2012 and February 2013, from 72 Modified-Whittaker plots (Stohlgren *et al.* 1995). This sampling design has been widely used for the assessment of plant communities at multiple scales (Beater *et al.* 2008; Mwavu & Witkowski 2009; Kalema & Witkowski 2012) and has been used successfully in assessing miombo woodland (Luoga *et al.* 2004). Plots were randomly established within each of the defined sites (*viz.* Control, Edge, Mozambique and South Africa relict) at a minimum distance of 300 m apart and placed parallel to major environmental gradients to encompass landscape heterogeneity. Plots were not evenly allocated and vary from 14 to 21 per site. Within each 0.1 ha plot, understory cover comprising percent un-vegetated soil, rock, grass and forb cover was estimated, and woody plant species, the number of individuals thereof, their height, basal diameter, canopy length and perpendicular width were measured. Only woody species were recorded as they comprise 95 to 98 % of the aboveground biomass in undisturbed miombo stands and largely determine the community dynamics (Chidumayo 1993). Seedlings were defined as the *i)* current season's recruits (neonatal) with *ii)* non-woody root collars. Juveniles were defined as *i)* the previous season's growth with *ii)* woody root collars and *iii)* having attained sub-canopy height (< 6 m; Campbell 1996). Mature trees were considered established individuals at canopy height ($\geq$ 6 m). Evidence for recruitment by means of flowering and seed pod production was noted across both juvenile and mature classifications. All free-standing stems were treated as individual plants as it was not possible to distinguish the origin of plants (seed, coppice or root sucker) beyond the seedling stage. In instances of obvious connection between stems, the sum of the cross-sectional area of total stems were aggregated to determine a single composite stem diameter (cm) and basal area (m^2/ha) for that multi-stemmed individual. Voucher specimens of species that could not be definitively identified *in situ* were collected, pressed and subsequently identified at Buffelskloof Nature Reserve Herbarium, Mpumalanga Province, South Africa. Evidence and level of browsing, fire and harvesting were

recorded in each plot as potential explanatory factors of diversity and community density.

3.4.3 Data and statistical analysis

Species richness is the least problematic way to describe community and regional diversity (Magurran 1988), and forms the basis of many ecological models of community structure (MacArthur & Wilson 1967; Connell 1978; Stevens 1989). Colwell & Coddington (1995) and Gotelli & Colwell (2001) advocate the measurement and comparison of species richness through taxon sampling or accumulation curves. Therefore, species accumulation functions were used to quantify richness at the 0.1 ha scale across the four sample sites, while rarefaction was used to estimate the number of species expected ($E(Sn)$) to be present in a random sample and provides confidence limits of species richness (Magurran 2004). Plotting rarefaction curves facilitates improved interpretation of species richness from sample plots of varying number and from different communities (Gotelli & Colwell 2001; Williams *et al.* 2005). Sample plots were randomized 100 times to compute the mean estimator, expected species richness and sufficient sampling effort for each study site. Species accumulation curves were constructed for both the number of samples (n) and the number of individuals (N). Variations in community species composition were tested by employing ANalysis Of SIMilarity (ANOSIM), which computes a test statistic (R_{ANOSIM}) reflecting the observed differences among replicates (plots) between the study sites, contrasted with differences among replicates within a study site. A zero (0) R statistic occurs if the high and low similarities are perfectly mixed and bears no relationship to group (plots within a particular study site). An R-value of negative one (-1) indicates that the most similar sample plots are all outside of a group and conversely, a value of positive one (+1) indicates that the most similar sample plots occur within the same group (Seaby *et al.* 2007). Non-Metric Multidimensional Scaling (NMDS) was used to display the Bray-Curtis measure of similarity between sample plots. This method operates at the species level and therefore the mean similarity between theoretical groups 1 and 2 can be obtained

for each species, and is performed in multivariate analyses of assemblage data to reflect the differences between two sites due to differing community composition and/or differing total abundance (Seaby *et al.* 2007).

Species richness (*S*), Shannon-Wiener diversity (*H'*) and evenness (*J'*) indices were calculated per sample site. Differences in species richness and diversity between sites were compared using one-way ANalysis Of VAriance (ANOVA) and Tukey's Honest Significant Difference (HSD) for unequal sample sizes (i.e. different number of plots per sample site).

All biological populations have age, size, spatial and genetic dimensions and understanding the dynamics thereof provides insight into the functioning of populations (Hara 1988). A feasible way to investigate population dynamics is to use snapshot population assessments distributed over space as opposed to time (Perez Farrera & Vovides 2004). However, it is important not to make demographic characterisations of species based on a single population if a snapshot study is used. Rather, demographic studies should be carried out at a meta-population level to understand the variation and behaviour of the species within and between populations in the range of habitats in which it occurs (Perez Farrera & Vovides 2004).

Population size structure and information on the distribution of its abundance in both time and space helps elucidate the relationship between the species and its environment (Brown *et al.* 1995). Both height and basal diameter structures are important when interpreting size class distributions (SCD), as the combined metric provides greater insight into population structure than either metric in isolation (Helm & Witkowski 2012). The basal diameter and height dimensions of *i*) all miombo species (those species belonging to miombo-definitive genera *viz. Brachystegia*, *Julbernardia* and *Isoberlinia*, $n=3390$) and *ii*) *B. spiciformis* ($n=2496$) individuals were subject to a linear regression (Fig. 2) to establish their numerical relationship and synchronise size classes (e.g. Cousins *et al*. 2013). Size class bins were delimited to accommodate more individuals with increasing

size, as advised by Condit *et al.* (1998). Size class distributions were subsequently delimited for basal diameter ($\leq$0.25, 0.26-1, 1.1-2.5, 2.6-5, 5.1-10, 10.1-15, 15.1-20, 20.1-25, 25.1-30, 30.1-40, 40.1-50, 50.1-65, $\geq$65.1 cm) and synchronized height ($\leq$0.25, 0.26-1, 1.1-2, 2.1-3, 3.1-4, 4.1-5, 5.1-6, 6.1-7, 7.1-8, 8.1-10, 10.1-12, 12.1-15, $\geq$15.1 m), respectively. Population density estimates take cognisance of multi-stemming and were calculated from counts of individuals and not the number of stems.

Basal diameter SCD slopes were used as indicators of population trends following the calculation of Condit *et al.* (1998). A regression was performed using corrected abundance per size class ($\ln(N_i+1)$) as the dependent variable and the size class midpoint (d_i) as the independent variable. The corrected abundance (N_i+1) was calculated by dividing the number of individuals in each size class by the range of that size class (see Helm & Witkowski 2012). Following Everard *et al.* (1995), negative slopes indicate ongoing reproduction or growth suppression, with more individuals in smaller size classes than in larger ones. Flat slopes indicate equal numbers of plants in small and large size classes, suggesting either limited reproduction or relatively high numbers of large plants, possibly from earlier reproduction events. Positive slopes imply limited recent reproduction, but possibly prior episodic reproduction or accelerated growth across intermediate size classes. Steepness of the basal diameter SCD slope was used, as shown by Cousins *et al.* (2014), to further describe reproduction trends: for example steeper negative slopes indicate better reproduction than shallower ones, given the greater number of individuals in the smaller size classes. In addition, basal diameter SCDs were compared between sample sites using the Kolmogorov-Smirnov distribution test.
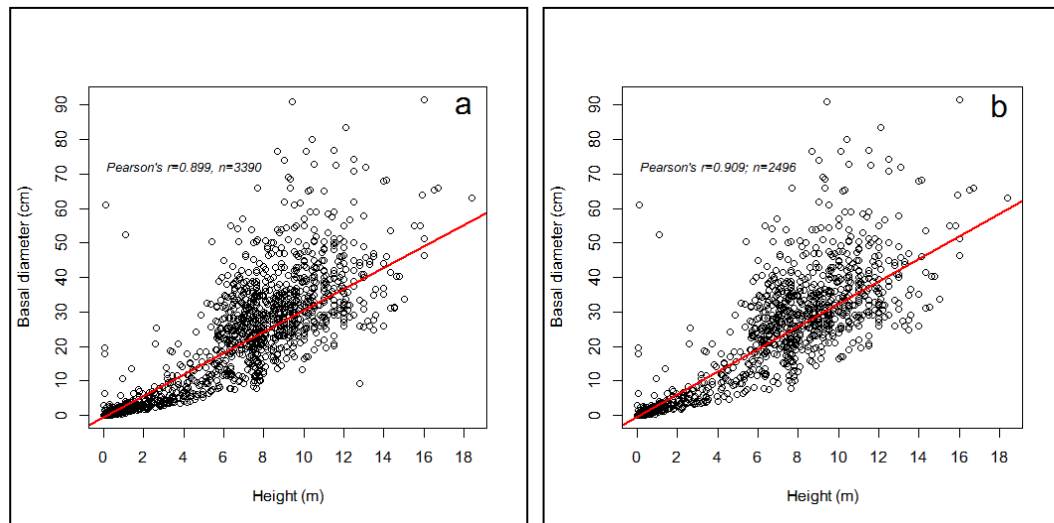
Figure 2. The regression relationship between height and basal diameter of a) pooled miombo species and b) *Brachystegia spiciformis* alone, across four miombo woodland study sites in southern Africa. The linear fit (solid line) was used to synchronise basal diameter size class distributions with height size class distributions.

Life stage (juvenile and mature) class bins were delineated to make size classes biologically meaningful (Helm & Witkowski 2012). To ascertain which size and life stage class correspond, it was necessary to define the approximate height and basal diameters at which juveniles become mature, with the onset of reproduction providing a relatively clear distinction (Donovan & Ehleringer 1991). However, there is little consensus regarding the point at which a seedling becomes a juvenile (Hanley *et al.* 2004) and seedlings were therefore not classified separately, but were included in the juvenile life stage class. Miombo reproduction predominantly takes place vegetatively (Luoga *et al.* 2004) and species, such as *J. globiflora*, can start recruiting from approximately 1.5 m in height when vegetative in origin (Campbell 1996). In contrast, species from the genus *Brachystegia* only produce seed when the plant emerges in the woodland canopy (Campbell 1996). Mature *Brachystegia* trees were previously defined as being ≥ 20 cm in basal stem diameter, as per Luoga *et al.* (2000a, 2000b, 2002) and in excess of 70% of reproductive activity observed during the current study occurred in individuals with basal stem diameters beyond this point (B. Pienaar pers. obs.). The life stage classes were therefore defined as juvenile (basal diameter < 20 cm,

height < 6 m) and mature (basal diameter ≥ 20 cm, height ≥ 6 m). Life stage class distributions were analysed and presented in terms of tree density (trees/ha).

R version 3.0.3 (R Development Core Team 2014) was used for all statistical analyses, with the exception of the ANOSIM pairwise comparisons, for which Community Assessment Package version 5.0 was used (Henderson & Seaby 2014).

3.5 Results

Species accumulation asymptotes were reached at each of the four study sites and across the combined miombo woodland sample area in southern Africa (Fig. 3 & 4). The observed species accumulation curves were situated below the rarefaction curves in all cases, suggesting heterogeneity among samples (Magurran 2004).

3.5.1 Species composition

A total of 146 woody species from 99 genera within 35 families were recorded across the study sites in southern Africa. The most species rich families were Fabaceae (24 species), Rubiaceae (18), Anacardiaceae (13), Euphorbiaceae (8) and Combretaceae (7), with a further 21 families comprising 2-6 species and 9 families comprising only one species each (Appendix 1). The most species rich genera were *Searsia* (8 species), *Albizia* (5), *Combretum* (5) and *Ochna* (4). Community species composition was significantly different (ANOSIM, Global $R_{ANOSIM} = 0.42$, P=0.001) between sites. Pairwise comparisons indicated that the compositions of the two relict communities were significantly different from the Control and Edge communities, and from each other, while the Control and Edge communities were not significantly different from each other (Table 1).
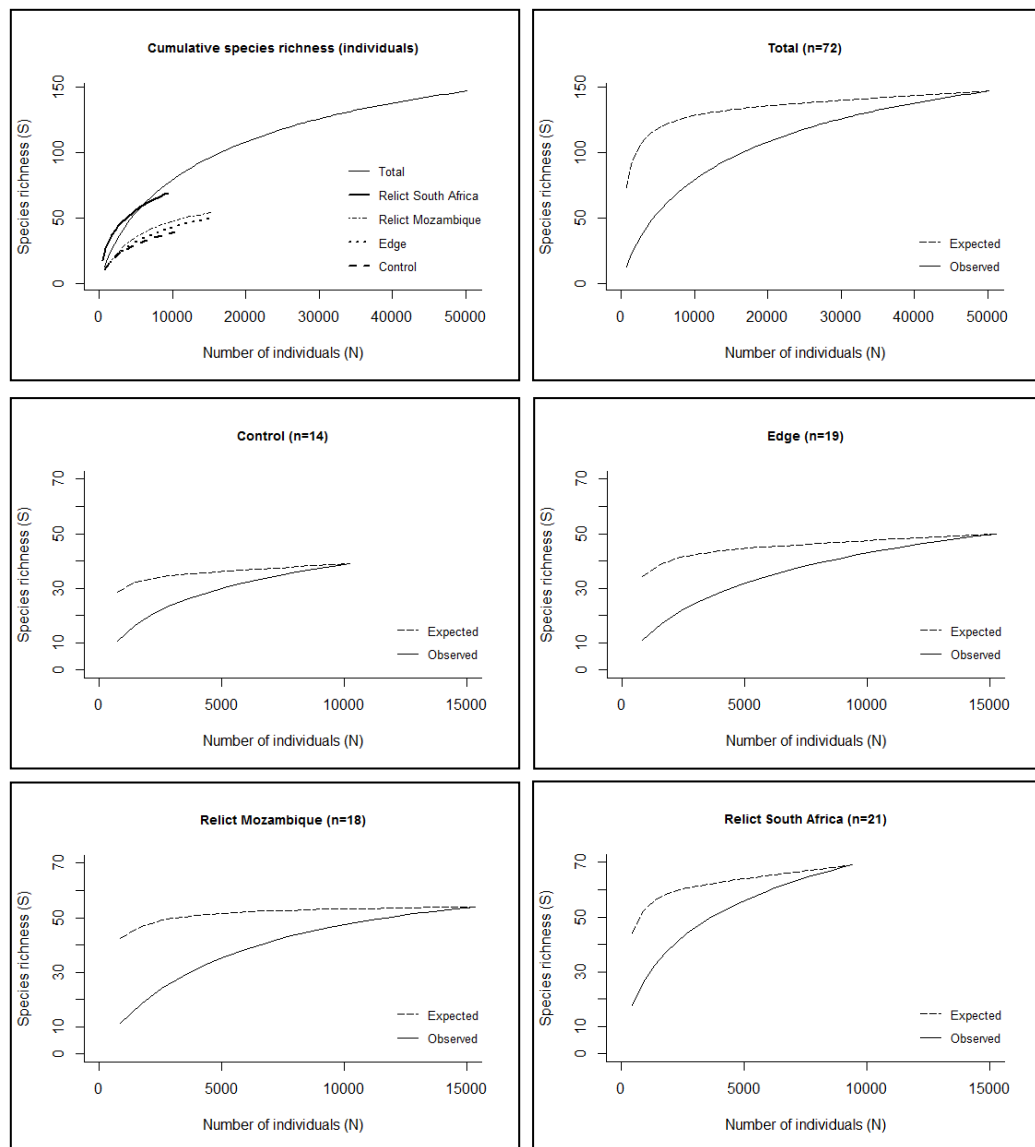
Figure 3.　　　Rarefaction (expected) and woody species accumulation (observed) curves for successively pooled and randomly ordered number for individuals (*N*) at four miombo woodland sites in southern Africa. Note the different y-axis scales, due to variation in species richness (*S*) and number of individuals (*N*) between the two summary curves (top) and the four sample sites.
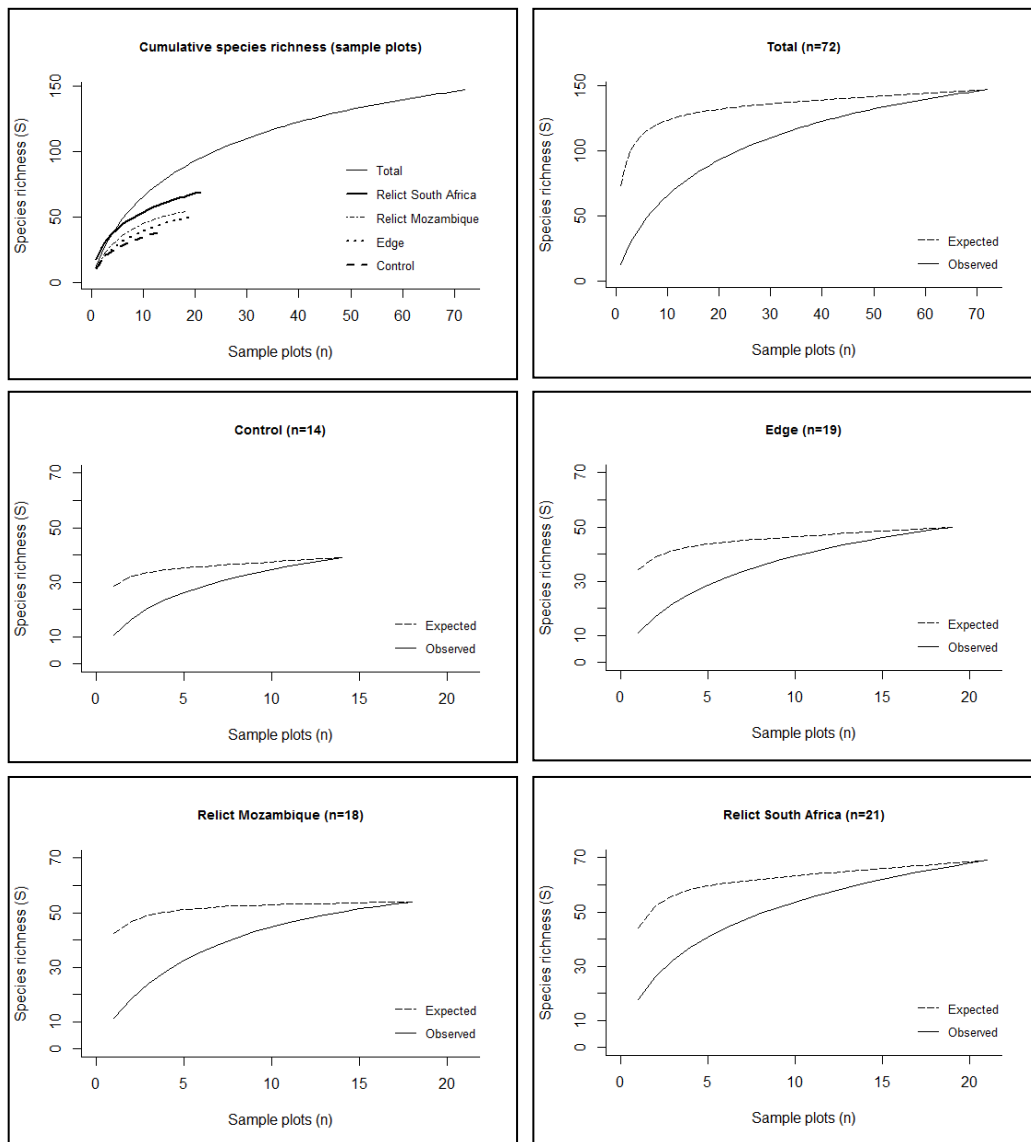
Figure 4. Rarefaction (expected) and woody species accumulation (observed) curves for successively pooled and randomly ordered sample plots (*n*) at four miombo woodland sites in southern Africa. Note the different y-axis scales, due to variation in species richness (*S*) and number of plots (*n*) between the two summary curves (top) and the four sample sites.

Table 1. Comparison of community species composition of four miombo sample sites: Control, Edge, Mozambique Relict and South Africa Relict. The ANOSIM sample statistic (R_{ANOSIM}) is reported, with significance level (P value) in parentheses.

Site	Control	Edge	Mozambique Relict
Edge	0.03 (0.236)		
Mozambique Relict	0.23 (**0.001**)	0.32 (**0.001**)	
South Africa Relict	0.71 (**0.001**)	0.66 (**0.001**)	0.47 (**0.001**)

Non-metric Multi-Dimensional Scaling (Fig. 5) depicts broad divergent species richness and abundance between the two relict communities relative to the Control and Edge communities. At the plot level, the Mozambique and South Africa relict communities represent a greater spread, which was driven by high levels of species diversity and low miombo species abundance. Site level species dissimilarities were greatest between the Control and Mozambique relict communities (88.1%). Correspondingly abundance dissimilarities, which were dominated by miombo species, were greatest between the Control and South African relict communities (88.9%), followed by the Mozambique and South Africa relict communities (88.0%).
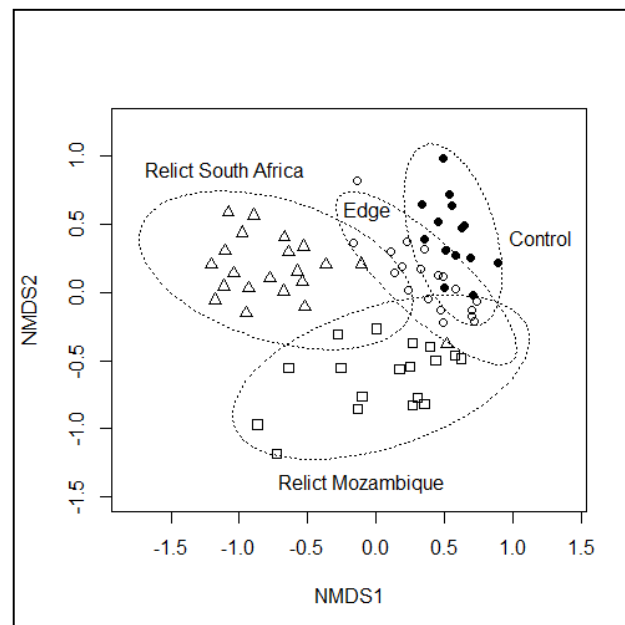
Figure 5. Non-Metric Multi-Dimensional scaling (NMDS) of miombo sample plots in southern Africa.

Plant diversity indices (S, H' and J') were consistently highest for the South African relict communities followed by the Mozambique relict communities, Edge community and Control community, respectively. Woody species richness (S) ranged from 3 to 29 per plot in the South African relict community (mean±SE = 16.62±1.35) being significantly higher than the Control (9.64±0.93), Edge (9.84±0.83) and Mozambique relict (10.17±1.40) communities (Table 2). Cumulative species richness, based on either *i)* individual plants (Fig. 3) or *ii)* plots (Fig. 4), was highest in the South African relict community.

Table 2.   Woody diversity indices of four miombo sample sites in southern Africa. Number of sample plots (Plots), total species recorded (Species), mean and standard error (in parentheses) of species richness (S), Shannon-Weiner (H') and evenness (J') are shown. Different letters denote significant differences between sites (Tukey, $P<0.05$).

Site	Cumulative (site level)		Diversity indices (plot level)		
	Plots	Species	S	H'	J'
Control	14	37	9.64 (±0.93)[b]	1.18 (±0.10)[b]	0.54 (±0.04)[b]
Edge	19	49	9.84 (±0.83)[b]	1.26 (±0.09)[b]	0.57 (±0.03)[b]
Mozambique Relict	18	53	10.17 (±1.40)[b]	1.55 (±0.12)[b]	0.71 (±0.03)[a]
South Africa Relict	21	68	16.62 (±1.35)[a]	1.99 (±0.11)[a]	0.73 (±0.03)[a]
F, P value			(3,68) 8.68, **<0.001**	(3,68) 12.00, **<0.001**	(3,68) 9.36, **<0.001**

According to the Shannon-Weiner (H') index, diversity of the South African relict community (1.99±0.11) was significantly higher than the Control (1.18±0.10), Edge (1.26±0.09) and Mozambique relict (1.55±0.12) communities, respectively. The South African (0.73±0.03) and Mozambique (0.71±0.03) relict communities were significantly more even (J') than both the Control (0.54±0.04) and Edge (0.57±0.03) communities.

Four miombo species were recorded across the study sites in southern Africa; *viz.* *B. boehmii*, *B. glaucescens*, *B. spiciformis* and *J. globiflora* and are henceforth referred to as the combined miombo species. However, a single large *B. utilis* exists within the South African relict (not sampled, but see Burrows *et al.* 2003). This is likely the only specimen of this species in South Africa and supports the notion that this is a climate relict community, as long distance dispersal events are unlikely for the genus, given their short dispersal distance and seed dormancy.

Combined miombo species comprised 55.4% proportional community abundance across the sample range. *B. spiciformis* was the most abundant species overall contributing 39.1% of encounters, followed by *J. globiflora* with 15.1% (Appendix 1). The Edge community was the only site where *B. spiciformis* was not most abundant, but ranked a relatively close second after *J. globiflora* (Fig. 6). There was little similarity between sites regarding the relative abundance of non-miombo species. Apart from *Burkea africana*, which was found in relatively high abundances in both the Control (rank 3) and Edge communities (rank 4), sites were dominated by unique species assemblages.
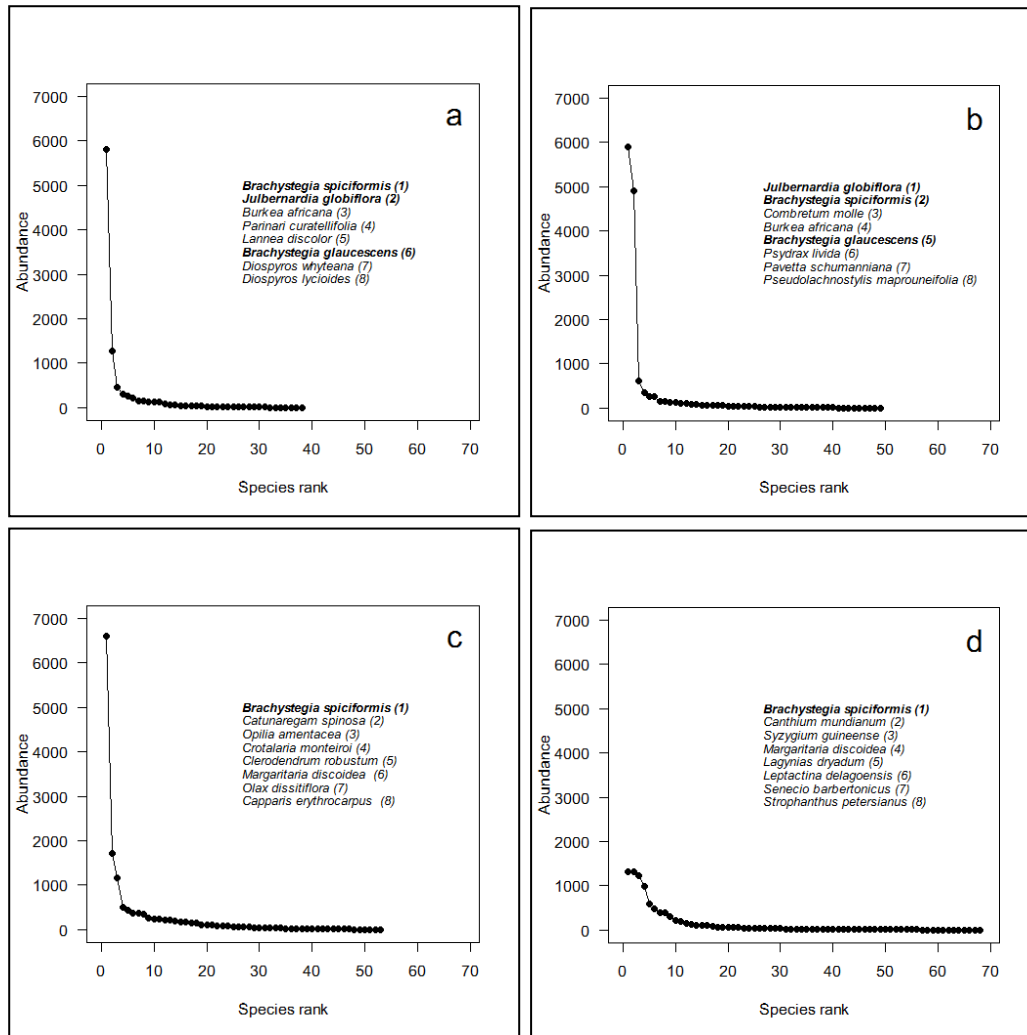
Figure 6. Abundance for all woody plant species encountered at study sites a) Control, b) Edge, c) the Mozambique relict and d) the South African relict. *Brachystegia spiciformis* was most abundant at all sites, with the exception of b) the Edge community, where *Julbernardia globiflora* was dominant. Although a) Control and b) Edge communities contained four miombo species each, only *B. spiciformis* was present in the c) Mozambique and d) South African relicts. The eight most abundant species, with rank in parenthesis and miombo species indicated in bold, are listed.

3.5.2 Size Class Distributions (SCDs) and slope

Basal diameter distributions for the combined miombo species (Fig. 7) and exclusively for *B. spiciformis* (Fig. 8) demonstrates typical inverse J-shaped curves for Control, Edge and Mozambique relict communities, which is indicative of reproductive communities. High levels of recent reproduction were evident, with large numbers of juveniles and fewer mature individuals present. This pattern was moreover reflected in negative basal diameter SCD slopes (Table 3). Slope steepness suggested decreasing reproduction of combined miombo species, and *B. spiciformis*, from Control, Edge and Mozambique relict communities, respectively. However, the South African relict community showed a very different flat to unimodal curve 'peaking' among mid-spectrum juveniles (Fig. 7 & 8) and with a much gentler slope than that of the other three communities.

Similarly, height distributions for combined miombo species (Fig. 9) and *B. spiciformis* (Fig. 10) showed inverse J-shaped curves in Control, Edge and Mozambique relict communities. The South African relict community was again anomalous, with fewer trees in the first two size classes when compared to the other sites. As with basal diameter SCD there is a reduction in slope, which suggests decreasing recruitment from Control, Edge, Mozambique relict and, in particular the South African relict, which shows only weak recruitment (Table 3).

Table 3.   Regression slope of basal diameter size class midpoint against the number of trees per size class for combined miombo species and *Brachystegia spiciformis* at all sample sites in southern Africa.

Diameter SCD Miombo				Diameter SCD *Brachystegia spiciformis*			
Site	Slope (°)	t	P	Site	Slope (°)	t	P
Control	-1.46	-14.3	**<0.001**	Control	-1.46	-14.3	**<0.001**
Edge	-1.38	-24.7	**<0.001**	Edge	-1.31	-13.9	**<0.001**
Mozambique Relict	-1.28	-13.1	**<0.001**	Mozambique Relict	-1.28	-13.1	**<0.001**
South Africa Relict	-0.84	-17.4	**<0.001**	South Africa Relict	-0.84	-17.4	**<0.001**

Kolmogorov-Smirnov tests showed significant differences (P <0.001) between the basal diameter SCDs of the four communities (Table 4).

Table 4.   Kolmogorov-Smirnov test for differences in basal diameter distribution for combined miombo species (top) and *Brachystegia spiciformis* (bottom) at all sample sites in southern Africa. The sample statistic (D) is reported with significance level (P value) in parentheses.

Diameter Miombo

Site	Control	Edge	Mozambique Relict
Edge	0.12 (**<0.001**)		
Mozambique Relict	0.23 (**<0.001**)	0.22 (**<0.001**)	
South Africa Relict	0.58 (**<0.001**)	0.55 (**<0.001**)	0.58 (**<0.001**)

Diameter *Brachystegia spiciformis*

Site	Control	Edge	Mozambique Relict
Edge	0.13 (**<0.001**)		
Mozambique Relict	0.10 (**<0.001**)	0.13 (**<0.001**)	
South Africa Relict	0.57 (**<0.001**)	0.61 (**<0.001**)	0.58 (**<0.001**)
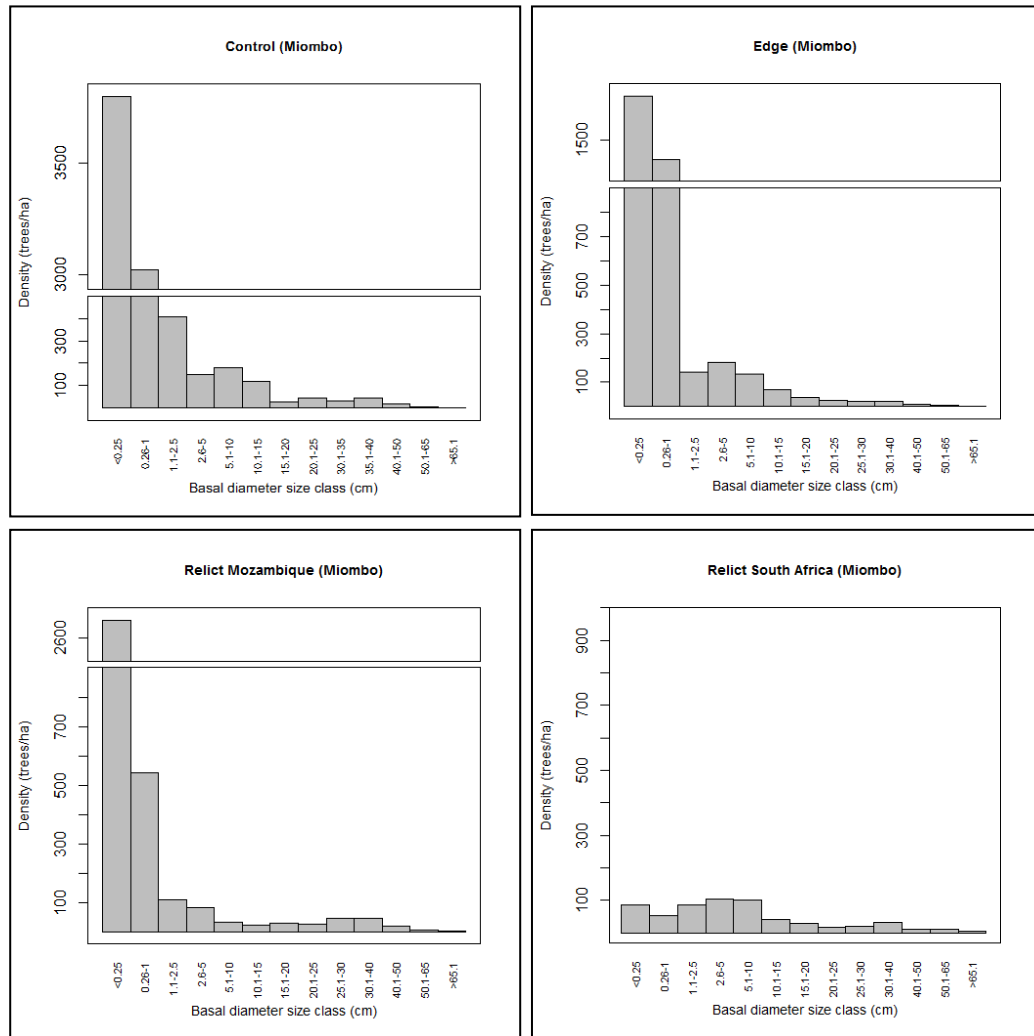
Figure 7. Basal diameter size class distributions (trees/ha) of combined miombo species at the four sample sites in southern Africa. Note the different y-axis scales due to the large variation in densities across sites.
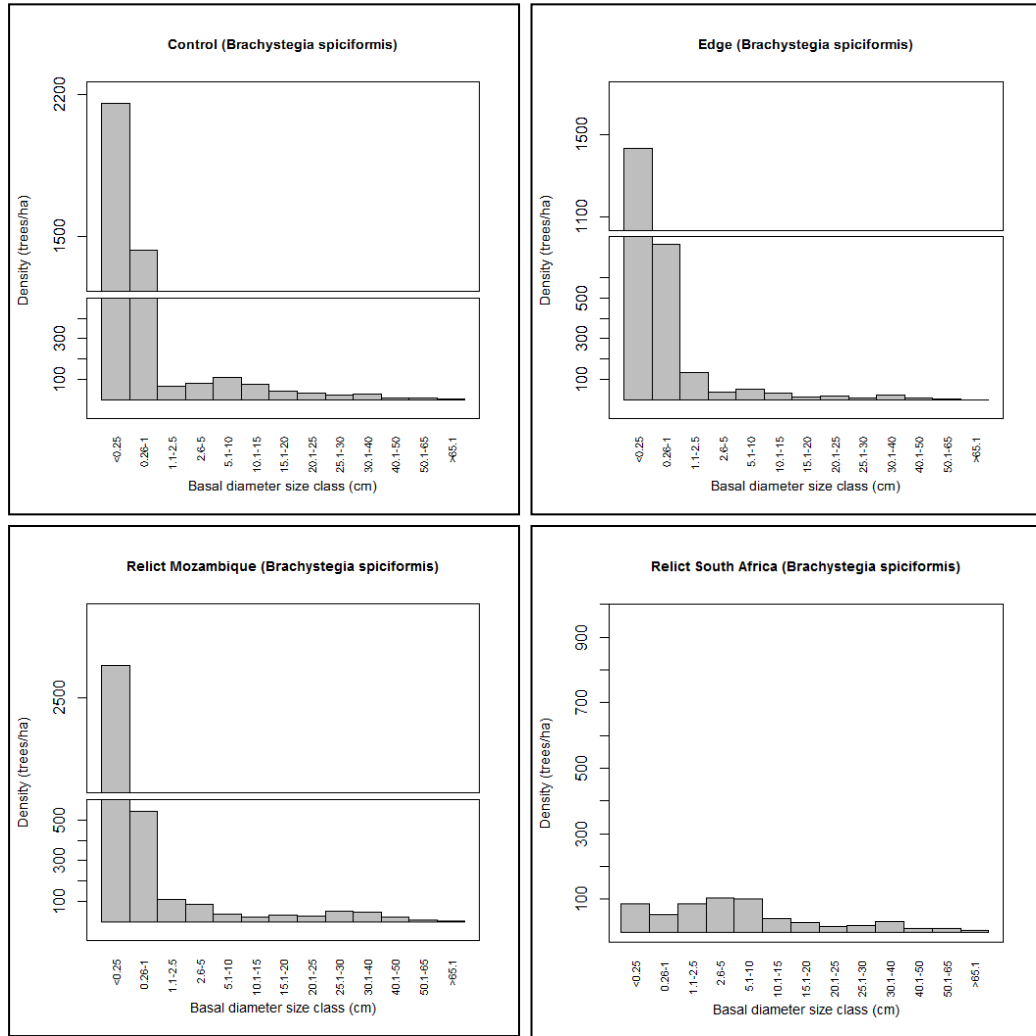
Figure 8.　　　Basal diameter size class distributions (trees/ha) of *Brachystegia spiciformis* at the four sample sites in southern Africa. Note the different y-axis scales due to the larger variation in densities across sites.
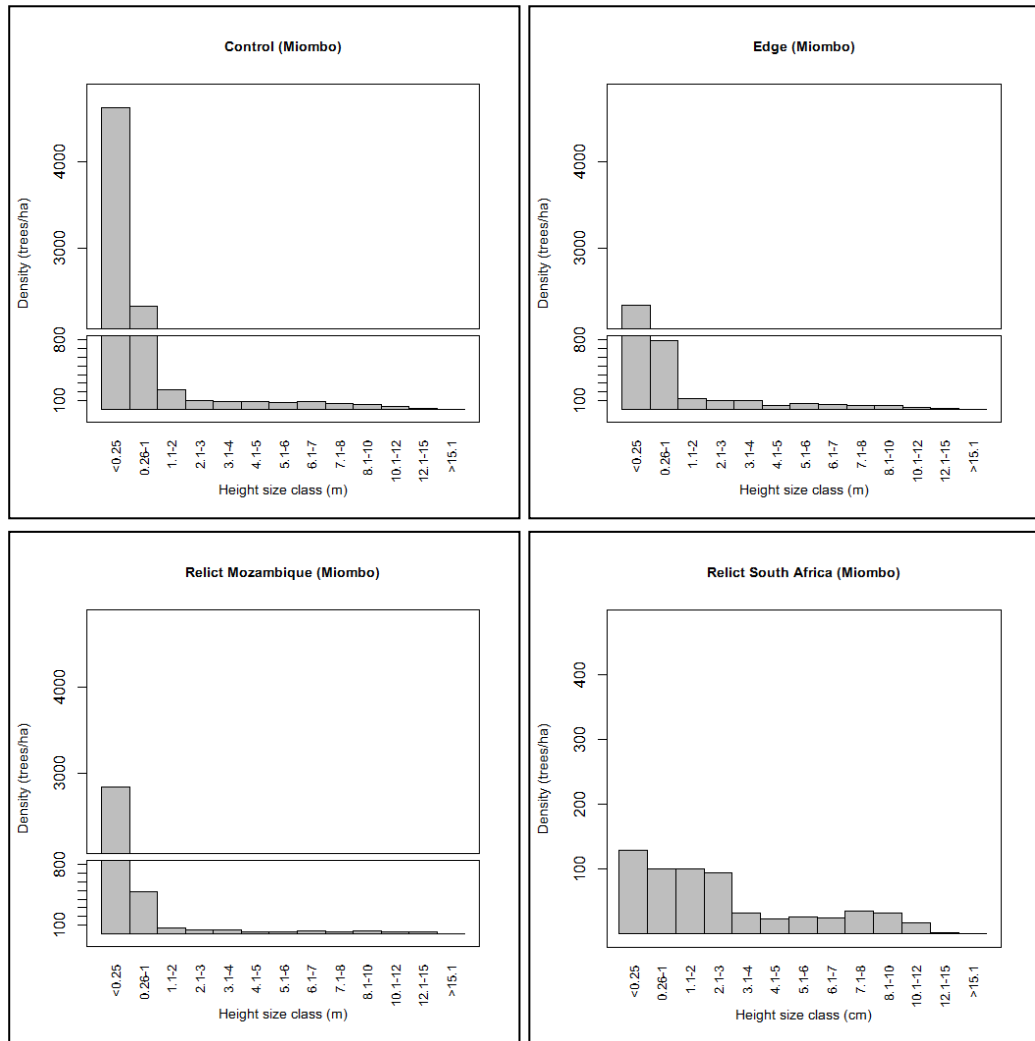
Figure 9.   Height size class distributions (trees/ha) of combined miombo species at the four sample sites in southern Africa. Note the different y-axis scales due to the large variation in densities across sites.
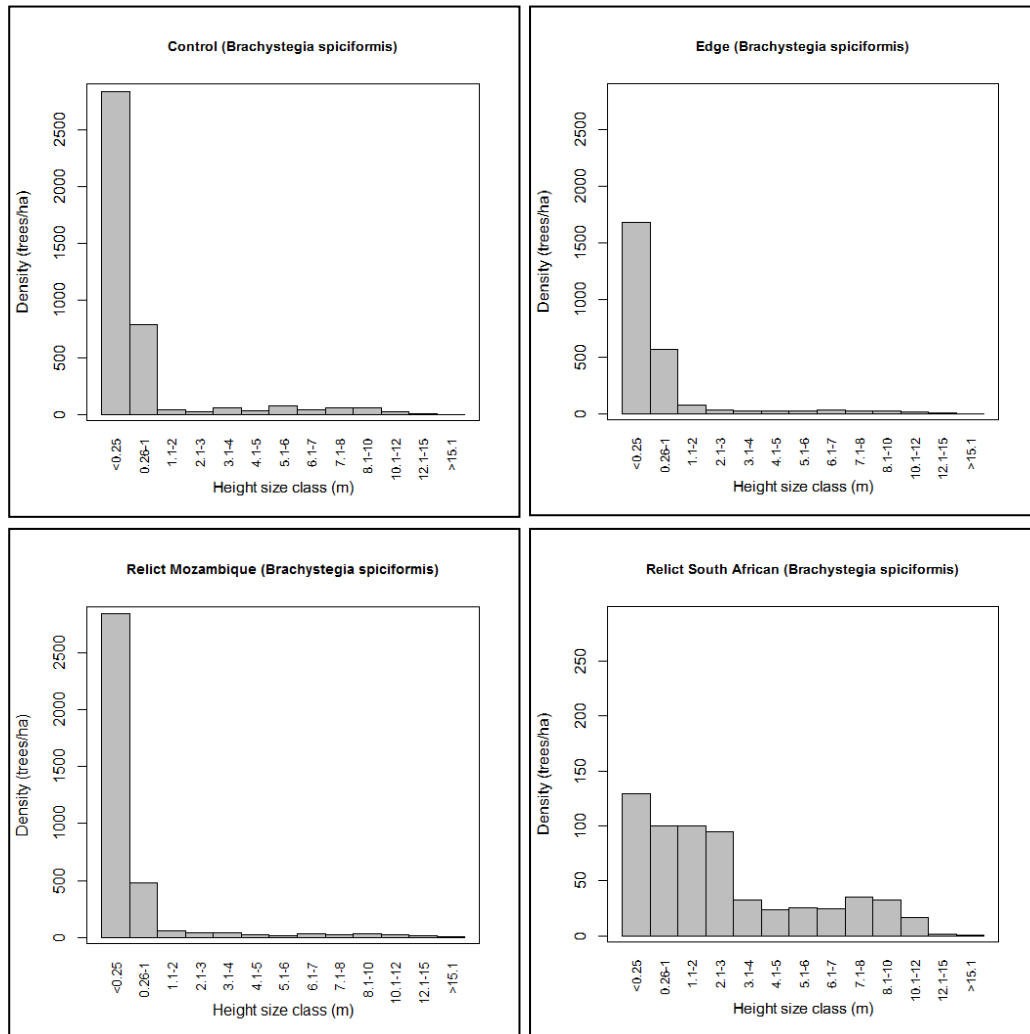
Figure 10.   Height size class distributions (trees/ha) of *Brachystegia spiciformis* at the four sample sites in southern Africa. Note the different y-axis scales due to the large variation in densities across sites

3.5.3 Population Density and Structure

Combined miombo species proportions at the Mozambique and South African relict communities were significantly different from Control and Edge communities as they comprise exclusively *B. spiciformis* (Table 5). The two relict communities displayed significantly low combined miombo densities under a decreasing trend from the Control, Edge, Mozambique relict and South African relict communities (Fig. 11), respectively. The Edge community, which unlike the other three sites was dominated by *J. globiflora* and not *B. spiciformis*, had significantly lower *B. spiciformis* densities than both Control and Mozambique relict communities (Fig. 11). However, in both combined miombo and *B. spiciformis*, the South African relict had the lowest per hectare tree density. Furthermore, the combined miombo and *B. spiciformis* density per life stage class indicates that the two relict communities were significantly different from the Control and Edge communities (Fig. 12). Proportionally, these relict communities comprised significantly fewer juveniles and correspondingly more mature trees.
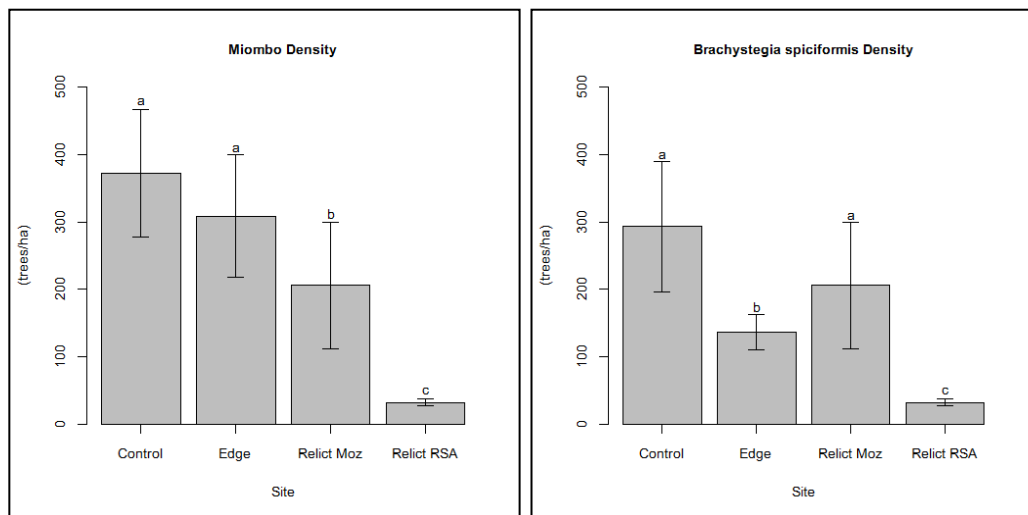
Figure 11. Density (mean±S.E., trees/ha) for combined miombo and *Brachystegia spiciformis* at all sample sites in southern Africa. Different letters denote significant differences between sites (Tukey, P<0.05). Note: Relict Moz refers to Mozambique relict and Relict RSA refers to the South African relict.
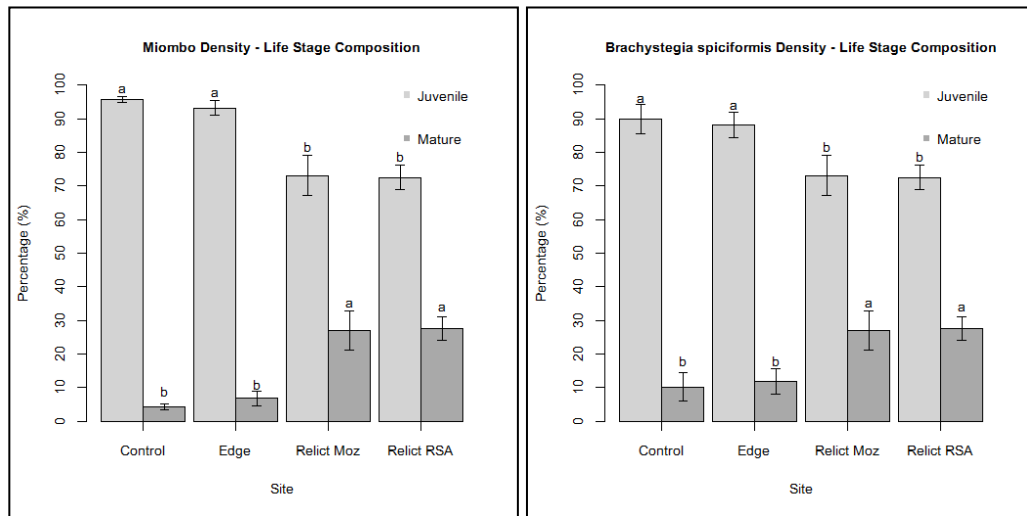
Figure 12. Density (mean±S.E.; trees/ha) for combined miombo and *Brachystegia spiciformis* life stage classes at all sample sites in southern Africa. Different letters denote significant differences between sites for juvenile and mature separately (Tukey, P<0.05). Note: Relict Moz refers to Mozambique relict and Relict RSA refers to the South African relict.

Herbaceous aerial cover was significantly different ($F_{3,68} = 68.1$; $P<0.001$) between all miombo woodland communities sampled, with a decreasing trend in total herbaceous, grass ($F_{3,68} = 57.5$; $P<0.001$) and forb ($F_{3,68} = 17.1$; $P<0.001$) aerial cover from Control, Edge, Mozambique relict to the South African relict, respectively. Combined miombo ($F_{3,847} = 10.2$; $P<0.001$) and *B. spiciformis* ($F_{3,847} = 13$; $P<0.001$) tree heights showed a similar trend, with the tallest trees (on average) being present in the Control community (9.7±1.6 m) and the shortest tree community confined to the South African relict (8.4±1.2 m). The Edge community showed a significantly narrow cumulative miombo basal diameter (28.5±0.7 cm) and a low proportion *B. spiciformis* basal area (43.9±6.9 %), the latter being defined as the percentage basal area (Table 5). Total species canopy area of the lower stratum (< 6 m in height) displayed an increasing trend from Control, Edge, Mozambique relict to the South African relict.

Table 5. Structural and disturbance characteristics of four miombo communities in southern Africa (mean±S.E.) for variables at each location followed by F statistic (*F*), degrees of freedom (shown in parentheses) and significance (*P*) of each model are shown. Different letters denote significant differences between sites (Tukey, P<0.05).

	Control	Edge	Mozambique Relict	South Africa Relict	F	P
Surface Cover - Soil (%)	94.0 (±2.7)[a]	95.3 (±1.9)[a]	100 (±0.0)[a]	72.2 (±4.2)[b]	$_{(3,68)}$ 18.6	**<0.001**
Surface Cover - Rock (%)	6.0 (±2.7)[b]	4.7 (±1.9)[b]	0.0 (±0.0)[c]	27.8 (±4.2)[a]	$_{(3,68)}$ 34.0	**<0.001**
Aerial Cover - Herbaceous (%)	36.9 (±2.9)[a]	20.9 (±1.3)[b]	11.0 (±1.9)[c]	3.6 (±0.5)[d]	$_{(3,68)}$ 68.1	**<0.001**
Aerial Cover - Grass (%)	27.1 (±2.3)[a]	14.8 (±1.2)[b]	8.0 (±1.6)[c]	1.7 (±0.4)[d]	$_{(3,68)}$ 57.5	**<0.001**
Aerial Cover - Forb (%)	9.8 (±1.5)[a]	6.1 (±0.9)[b]	3.0 (±0.6)[bc]	1.9 (±0.2)[c]	$_{(3,68)}$ 17.1	**<0.001**
Total Basal Area (m²/ha)	17.9	14.2	19.2	17.6		
Total Canopy Area ≥6m (m²/ha)	10 321.9	7 112.1	10 378.5	8 090.7		
Total Canopy Area <6m (m²/ha)	3 022.9	3 127.9	4 112.2	4 742.4		
Proportion Miombo Species present (%)	44.6 (±4.7)[a]	46.1 (±3.5)[a]	25.0 (±0.0)[b]	25.0 (±0.0)[b]	$_{(3,68)}$ 22.6	**<0.001**
Mean Miombo Basal Diameter (cm)*	34.0 (±1.1)[a]	28.5 (±0.7)[b]	33.2 (±0.8)[a]	34.4 (±0.9)[a]	$_{(3,847)}$ 10.5	**<0.001**
Total Miombo Basal Area (m²/ha)	16.0	11.8	16.8	14.1		
Mean Miombo Proportion Basal Area (%)	88.2 (±3.0)[a]	84.16 (±1.9)[a]	87.9 (±2.7)[a]	80.4 (±2.5)[a]	$_{(3,68)}$ 2.9	0.039
Mean Miombo Tree Height (m)**	9.6 (±1.5)[a]	9.1 (±1.2)[ab]	8.9 (±1.8)[b]	8.4 (±1.2)[c]	$_{(3,847)}$ 10.2	**<0.001**
Total Miombo Canopy Area ≥6m (m²/ha)	9 757.9	6 647.3	9 526.5	7 768.1		
Total Miombo Canopy Area <6m (m²/ha)	2 426.9	1 942.3	2 311.5	2 062.3		
Miombo Proportion Canopy Area ≥6m (%)	92.8 (±2.3)[a]	94.2 (±1.3)[a]	92.1 (±2.2)[a]	96.2 (±1.0)[a]	$_{(3,68)}$ 1.2	0.321
Miombo Proportion Canopy Area <6m (%)	64.3 (±8.6)[a]	54.4 (±7.0)[a]	49.9 (±7.9)[a]	41.6 (±5.4)[a]	$_{(3,68)}$ 2.1	0.115
Mean *B. spiciformis* Basal Diameter (cm)*	34.0 (±1.2)[a]	31.1 (±0.8)[a]	33.2 (±0.8)[a]	34.4 (±0.9)[a]	$_{(3,713)}$ 1.9	0.14
Total *B. spiciformis* Basal Area (m²/ha)	13.5	6.4	16.8	14.1		
B. spiciformis Proportion Basal Area (%)	73.2 (±7.6)[a]	43.9 (±6.9)[b]	87.9 (±2.7)[a]	80.4 (±2.5)[a]	$_{(3,68)}$ 15.2	**<0.001**
Mean *B. spiciformis* Tree Height (m)**	9.7 (±1.6)[a]	9.5 (±1.7)[ab]	8.9 (±1.8)[b]	8.4 (±1.2)[c]	$_{(3,847)}$ 13.0	**<0.001**
Total *B. spiciformis* Canopy Area ≥6m (m²/ha)	8 343.9	3 459.5	9 526.5	7 768.1		
Total *B. spiciformis* Canopy Area <6m (m²/ha)	1 603.0	777.4	2 311.5	2 062.3		
B. spiciformis Proportion Canopy Area ≥6m (%)	78.9 (±8.1)[b]	54.1 (±8.4)[c]	92.1 (±2.2)[ab]	96.2 (±1.0)[a]	$_{(3,68)}$ 13.9	**<0.001**
B. spiciformis Proportion Canopy Area <6m (%)	43.9 (±9.8)[a]	24.1 (±7.2)[a]	49.9 (±7.9)[a]	41.6 (±5.4)[a]	$_{(3,68)}$ 2.0	1.22
Browsing (%)	0.3 (±0.1)[b]	1.1 (±0.6)[b]	0.9 (±0.4)[b]	14.7 (±3.0)[a]	$_{(3,68)}$ 28.4	**<0.001**
Fire (%)	4.7 (±3.4)[ab]	2.2 (±1.1)[b]	13.7 (±5.7)[a]	0.0 (±0.0)[b]	$_{(3,68)}$ 6.5	**<0.001**
Harvesting (%)	0.0 (±0.0)[b]	0.8 (±0.3)[a]	0.1 (±0.1)[b]	0.2 (±0.1)[b]	$_{(3,68)}$ 3.7	**0.015**

* Mature trees (≥20 cm basal diameter)

** Mature trees (≥6 m in height)

3.5.4 Explanatory variables

Higher levels of browsing were correlated with higher species richness (S: $F_{4,9}=26.45$; $P=0.001$) and Shannon-Weiner indices (H': $F_{5,13}=7.55$; $P=0.017$) at the Control community, and decreased *B. spiciformis* juvenile density ($F_{5,13}=27.76$; $P<0.001$) at the Edge community (Appendix 6). Browsing was significantly more prevalent in the South African relict community (14.7±3.0 %) than any other community (Appendix 6), where it positively influenced species evenness (J': $F_{3,17}=7.97$; $P=0.012$). Despite having significant influence at local levels, browsing did not impact significantly on any diversity index between sample sites.

Fire occurrence was significantly higher (Appendix. 6) at the Mozambique relict community (13.7±5.7 %), tended to be less at the Control community (4.7±3.4 %), and significantly less frequent in the Edge community (2.2±1.1 %). There was however no evidence of fire at the South African relict community. The Control community experienced decreasing miombo ($F_{4,9}=6.54$; $P=0.031$) and *B. spiciformis* juvenile densities ($F_{4,9}=6.93$; $P=0.027$) with increasing fire disturbance. Despite the significantly lower occurrence of fire in the Edge community, it nevertheless correlated with lower *B spiciformis* juvenile density ($F_{5,13}=14.09$; $P=0.002$). Ultimately, fire disturbance significantly negatively influenced *B. spiciformis* juvenile density ($F_{24,47}=4.40$; $P=0.017$) between sample sites.

The percentage of a site comprising bare rock or 'site rockiness' was significantly the highest at the South African relict (Appendix 6), where it positively influenced both diversity and evenness (H'; $F_{20,51}=14.45$; $P<0.001$ and J'; $F_{20,51}=8.99$; $P=0.004$). Moreover, site rockiness significantly influenced combined miombo ($F_{24,47}=15.44$; $P<0.001$) and *B. spiciformis* ($F_{24,47}=8.17$; $P<0.001$) juvenile densities negatively at the Control community. However, the level of rockiness did not have a significant influence on any diversity or density measure between locations.

Harvesting had significant impact on differences in H' ($F_{20,51}$=3.35; P=0.042) between locations, with increasing harvesting leading to higher diversity between sites (Appendix 6).

3.6 Discussion

3.6.1 Species composition

The divergence seen in species composition between the miombo woodland communities - especially between the relicts and the continuous woodland sites was driven by *i*) declining miombo species, and *ii*) increasing non-miombo species diversity.

The two relict communities were characterised by lower miombo species richness, comprising exclusively (at least in the South African relict sample plots) of *B. spiciformis*. It is suggested that the nested pattern of miombo species in the relict communities relative to the continuous woodlands of Zimbabwe is a result of insular biogeography effects. It has been well established that fragmented landscapes have a reduced capacity to conserve their natural biota (Blake 1991; McIntyre 1995; Warburton 1997). Associated disturbance effects often dominate the ecology of such landscapes and may cause highly deterministic species extinction within a patch, resulting in characteristic community composition (Cutler 1994; Lomolino 1996). Communities therefore respond to changes in spatial patterns and, in turn, ecological patterns and processes are affected (Templeton *et al.* 1990; Simberloff 1994; Forman & Collinge 1996). Climate relicts therefore tend to have low within-population genetic variation as a consequence of extended isolation, past reproductive bottlenecks (Hampe & Petit 2005) and the occurrence of clonality. The small size of many relict communities, in combination with strong selection pressure, substantially elevates the risk of species extinction due to demographic or environmental stochasticity before they can effectively adapt (Pfenning *et al.* 2010). As a consequence, community composition is altered as specific species are lost in sequence of their extinction risks (Bierregaard *et al.* 1992; Wiens 1994).

Within the spectrum of vegetation communities which constitute the savanna ecosystem, a wide range of species composition, diversity and richness values exists. For example, Shackleton (2000) established a woody species richness of 24.9±2.58 per 0.1 ha (Modified-Whittaker plot) within Granite Lowveld savanna (Mucina & Rutherford 2006). Comparatively, the woody species richness of miombo woodland across all sample sites was much lower at 11.9±0.69, despite an overlap in mean annual precipitation (600 to 950 mm). Miombo woodland is relatively homogenous and species poor due to the proportional abundance of *B. spiciformis* and *J. globiflora* (54.2 %) within the southern African community. The trailing range edge of miombo woodland in southern Africa is delimited by a more heterogenous spectrum of savanna ecosystems and it is therefore suggested that this has lead to the unexpected increase in the species diversity of the insular relicts. The miombo range Edge and relict communities showed an increase in diversity indices (*S'* and *H'*) relative to the Control community, which correspond to isolation and decreased habitat area. Harvesting may have contributed to increased diversity at the Edge and Mozambique relict communities (see Shackleton 2000). Nevertheless, it is suggested that permeation of species from the comparatively heterogenous and diverse surrounding habitat has taken place according to decreasing interior-to-edge ratios of the two relict populations. The high level of evenness (*J'*) in the relict community is suggested to be a direct result of high non-miombo species richness and lower miombo species proportional abundance. Two explanatory variables are likely to have contributed towards increased diversity at the South African relict. First, elevated levels of site rockiness may have provided a more heterogenous environment, which was suitable for a different suite of woody species. Second, high browsing incidence may have increased evenness, a notion supported by Bakker *et al*. (2006) and Jacobs & Naiman (2008).

Species composition of the two relict communities was most similar to the Edge community, while the Edge was, in turn, most similar to the Control community. It would therefore seem that divergence in species composition of the miombo

woodland relicts in southern Africa conform to a typical insular biogeography effects.

3.6.2 SCDs and slope

The size-class distributions of undisturbed, continuous *Brachystegia* woodland generally illustrate the reverse-J distribution characteristic of self-replacement stands (Chidumayo & Frost 1996), with numerous small individuals and exponentially fewer larger individuals. However, slope steepness suggested a decrease in combined miombo and *B. spiciformis* recruitment between the Control and Edge communities. The decreased recruitment broadly supports the 'abundant centre' hypothesis (ACH; Sagarin *et al.* 2006), which assumes that population per-capita reproductive output (and density) should peak at the centre of a species' geographic range and decline towards the periphery. ACH states that species should be most abundant at its distributional centre, because environmental conditions are there expected to be most favourable (Brown 1984).

Relict populations are excluded from ACH relationships, as they persist in refugia. Refugia are physiographic settings that support a once prevalent regional climate that has been lost (or is being lost) due to climate shifts (Dobrowski 2011). The populations that occupy these refugia may therefore be buffered against the climatic constraint that is experienced at the contemporary retreating range margin, particularly under climate change. Hence, environmental conditions experienced in refugia are likely to more closely resemble those of the continuous range, rather than those experienced at the range edge. Nevertheless, measures of reproduction within the *B. spiciformis* relict communities were much weaker than the Edge community, suggesting that these may be influenced by alternative, non-environmental factors. Insular biogeography effects are again suggested to be influential in limiting relict reproduction. Fragmentation and loss of suitable habitat may reduce a population to a size where stochastic events could cause demographic collapse (Rolstad 1991; Simberloff 1994; Meffe & Carroll 1997). The SCD slopes of the *B. spiciformis* woodland relicts are likely correlated with

area, with slope decreasing from Control, Edge, Mozambique relict to South African relict communities. The extent of the Mozambique relict may therefore offer a buffer to insular biogeography effects on reproduction compared to the smaller South African relict, which displayed a comparatively flat size class distribution and reproduced weakly. This is likely attributed to ensuing demographic stochasticity and/or abiotic influence. Browsing was significantly more prevalent in the South African relict community than any other community and it is suggested that high livestock numbers, in combination with reduced area, could likely be contributing towards a recruitment bottleneck (see Venter & Witkowski 2013).

However, the population demography trends of long-lived species in relict communities cannot plainly be inferred from only their reproduction rates (e.g. Eriksson 1996; Clark *et al.* 1999). Rather, it has been suggested that changes in adult mortalities may be more efficient indicator (Hampe & Petit 2005) of persistence.

3.6.3 Population Density and Structure

According to Grundy (1995), miombo woodland population density (trees/ha) is unconnected to precipitation or any other solitary factor. Nevertheless, there was an evident decrease in combined miombo community and *B. spiciformis* population densities between the Control and distributional range Edge. According to ACH, the low population density of *B. spiciformis* at the distributional range Edge suggests less favourable environmental conditions for the species at the southern distribution boundary relative to conditions further northwards.

A relationship between rainfall and miombo woodland production and physiognomy is evident in structural variation along the precipitation gradient that exists from the wetter core area to the drier fringes (Desanker *et al.* 1997). For example, miombo stand basal area (m^2/ha) increases linearly with increasing

mean annual precipitation (Chidumayo 1987b). The recorded basal areas of miombo trees in undisturbed woodland range from 7 m2/ha at about 650 mm (Lowore et al. 1994a) to 22 m2/ha at 1270 mm mean annual precipitation (Freson *et al*. 1974). Most miombo stands have basal areas of 7-19 m^2/ha (Boaler & Sciwale 1966; Allen 1986; Chidumayo 1987a). Furthermore, miombo canopy height has been related to increasing precipitation and soil depth (Savory 1963; Grundy 1995). Canopy dominants, such as *B. spiciformis*, that grow on deep (> 3 m), porous soils can reach heights of ≤ 27 m in areas that receives high annual rainfall (> 1000 mm), although the canopy height is generally between 15-20 m (Campbell 1996).

In this study there was a steep gradient in mean annual precipitation between the wetter Control (894 mm) and drier Edge (603 mm) communities. Combined miombo basal diameters (cm) and basal areas (m^2/ha) were significantly smaller under drier conditions, while *B. spiciformis* population density, and consequently, basal area (m^2/ha) and canopy area ≥ 6m (m^2/ha) decreased at the Edge relative to the Control. It is therefore suggested that *B. spiciformis*, a species with minimum precipitation constraints (Pienaar *et al.* 2015), experiences selective climatic pressure under the drier conditions of the distributional range Edge. Consequently, the Edge community was the only site where *B. spiciformis* was not dominant, but ranked a relatively close second after *J. globiflora*. Timberlake & Chidumayo (2011) echo the dominance of *J. globiflora* over *B. spiciformis* across drier extents of southern miombo range.

Relict communities are excluded from the precipitation gradient relationships, as they persist in refugia. Accordingly, both the Mozambique (676 mm) and South African relict (936 mm) communities experience higher annual precipitation than the Edge (603 mm) community at the drier distribution periphery. Although *B. spiciformis* relict communities experience less climatic constraint than the Edge community, they may be more vulnerable to other factors such as fragmentation and/or increased disturbance severity.

Fire in miombo woodland is fuelled predominantly by grass, with woody material contributing only marginally to the main fire front (Campbell 1996). Fire frequency, and the intensity thereof, is therefore linked through grass above-ground primary production to the previous season's rainfall, the intensity of grazing, and the extent of woody plant cover; all of which control standing grass biomass.

B. spiciformis is considered to be a fire-tender species, which declines in density under frequent burning and increases under complete fire protection (Trapnell 1959). In accordance, fire decreased *B. spiciformis* juvenile density between the sample sites. Bond *et al.* (2003) distinguished between fire-dependent ecosystems (FDEs) and climate-dependent ecosystems (CDEs). In FDEs regular fires restrict succession to closed forest or thicket that is too shady to support a grassy understorey. Members of the Caesalpinioideae dominate in FDEs in the tropics (White 1983). Bond *et al.* (2003) suggests that summer rainfall areas of South Africa that receive > 650 mm of precipitation per annum can be considered FDEs, while areas below this precipitation threshold are CDEs. Hence, the Edge community may be considered a CDE, as it is the only sample community that receives < 600 mm annual precipitation.

The Mozambique relict displayed slightly lower, but similar *B. spiciformis* population density compared to the Control population, with reduced levels of reproduction and proportionally fewer juveniles (Figure 13). Fire contributed towards decreased *B. spiciformis* juvenile density at this population, it is however suggested that the population dynamics primarily reflect fragmentation and insular biogeography effects. Nevertheless, *B. spiciformis* basal area (16.8 m^2/ha) was representative of the typical miombo range. So too was the average tree height (8.9 m) when compared to miombo canopy heights (8-15 m) reported in southern Africa (Fors 2002). Tree heights were however at the shorter end of the spectrum and most likely a direct result of lower annual precipitation.

Basal area (14.1 m^2/ha) and tree height (8.4m) of the *B. spiciformis* relict in South Africa were within the range recorded previously for miombo woodland. The

average tree height was shortest at this sample site relative to other sites studied here, likely due to shallow soils and increased rockiness. Furthermore, the high percentage of area covered by rock could be responsible for a 'fire refugia' as no evidence of fire was observed at this site. The exclusion of fire may be the reason that the South African relict displayed the largest proportion of canopy area, a notion supported by Bond *et al.* (2003). Accordingly, increased canopy cover could be correlated with the relict's sparse herbaceous layer. Alternatively, high herbivory and/or increased rockiness recorded for the South African community has led to decreased *B. spiciformis* recruitment and low herbaceous cover.
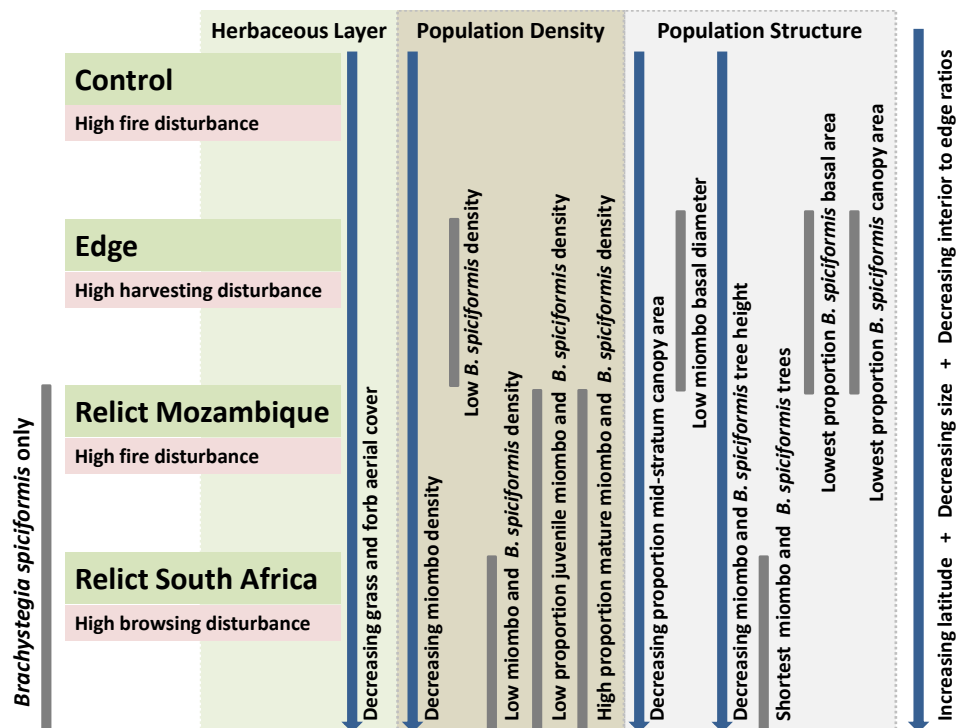
Figure 13. Herbaceous layer, population density and structure comparisons (bars) and trends (arrows) between all miombo woodland sites in southern Africa.

3.7 Conclusion

The investigation of *Brachystegia* (miombo) woodland community dynamics at the trailing range edge in southern Africa supports ACH from the continuous range to the distributional range edge, whilst relict community dynamics are primarily driven by insular biogeography effects.

Jansson & Dynesius (2002) suggest that climate relicts have likely been exposed to stronger and longer lasting climate related selection than their conspecifics from the main distribution range. Due to their persistence under such selection pressure, climate relicts have been identified as instructive models and natural laboratories for investigating how populations will react (and potentially adapt) to ongoing climatic change (Davis *et al.* 2005, Hampe & Petit 2005). However, this study suggests that refugial *Brachystegia* community dynamics and diversity can be ascribed to fragmentation disturbance effects rather than exclusive climatic constraints. Rather, unfragmented trailing range edge margins, where populations show the effects of a marginal climate, are better used to investigate how populations of this significant savanna species will react to on-going climate change.

Population dynamics of *B. spiciformis* woodland at the distributional range edge in southern Africa, which receives < 650 mm precipitation per annum, are seemingly climate driven as the population is not in equilibrium with the environment. The life stage of miombo woodland was negatively influenced at a recruitment level, while height and basal diameter also show signs of phenotypic divergence.

The medium-term survival of the two *B. spiciformis* relict populations is plausible, when considering strictly climatic factors and storage effect. It is however likely that the two populations will succumb to insularisation effects in the long-term.

CHAPTER FOUR

Synthesis

African savannas and associated woodlands are generally believed to be undergoing extensive degradation primarily through human population growth and associated land use impacts such as settlement, grazing and resource extraction, with increasing pressure on their ecology and conservation. Given the socio-economic and ecological significance of miombo woodland in Africa, the conservation and sustainable utilisation of these woodlands constitute an important theme of adaptive natural resource management, particularly under supplementary climate-induced range retraction. This chapter provides a synthesis of the dissertation outcomes, with discussions and suggestions regarding conservation management and further research opportunities.

Precipitation of the wettest quarter and temperature seasonality were identified as the two most important bioclimatic variables explaining *B. spiciformis* woodland distribution in southern Africa. Both variables displayed a relatively narrow range of optimal suitability for the species, stressing their sensitivity to minor climatic shifts. Maximum temperature of the warmest month and high temperature seasonality were suggested to place climatic constraint on the continuous *B. spiciformis* woodland extremities. Considering future global change projections, it is suggested that the *B. spiciformis* climate niche could retract between 30.6 - 47.3% in southern Africa by 2050. However, bioclimatic models are restricted in their capacity to determine the full extent of ecological interactions, particularly in savannas where the direct impact of climate on species distribution may be variable. For example, species with large below-ground carbon sinks, such as miombo, benefit from CO_2 fertilisation (Hoffmann 2002) which increases tree water use efficiency (WUE; Polley *et al*. 1999). Future increases in atmospheric CO_2 are likely to contribute towards a greater tolerance of suggested decreased precipitation of the wettest quarter. In addition, there is a paucity of literature to support savanna plant species being intolerant of maximum temperature extremes.

Adult trees may persist in an area of previously suitable climate during extended periods of climatic constraint (the storage effect), particularly if populations are capable of adaptive dynamics such as clonal regeneration. *B. spiciformis* may therefore be subject to an extensive period of persistence between vegetation-climate equilibrium and local extirpation. Therefore, the suggested ecological niche retraction of *B. spiciformis* woodland in southern Africa may be less extreme than the model projections suggest. Realistic predictions of future trailing edge population performance requires the development of models that can integrate population dynamics, ecosystem processes and climate trends at landscape to regional scales (Hannah *et al*. 2002).

Nevertheless, as opposed to high latitude studies, where temperature constraint shift plants to higher latitudes (polewards) or to higher elevations (Parmesan 2006), the Ecological Niche Models (ENMs) from this study imply that precipitation constraint on low latitude plants, in the case of *B. spiciformis*, may shift to *i*) lower latitudes (equatorwards), *ii*) higher rainfall areas such as escarpments or *iii*) persist in isolated refugia created by heterogenous landscapes. This study has shown that the minimum moisture requirements of *B. spiciformis* woodland are a mean annual precipitation of > 650 mm and a minimum precipitation of the wettest quarter of 420 mm.

White (1983) distinguished between the floristically rich miombo woodland at low latitudes (high rainfall > 1000 mm) and the floristically impoverished miombo woodland at higher latitudes (lower rainfall < 1000 mm), nearer the edge of the distributional range in southern Africa. This would suggest a correlation of decreasing miombo species richness with increasing latitude (lower precipitation stability). Whilst the miombo woodland community composition of the continuous woodlands is relatively homogenous in southern Africa, the relict communities located beyond contemporary latitudinal distribution reflected further loss of miombo biota, with only *B. spiciformis* being present. There were clear divergence in the patterns of non-miombo diversity, with an increase from the Core and range Edge communities to the relict communities, and also between

the two relict communities. These miombo relict populations displayed significantly lower *B. spiciformis* reproduction and population density relative to the continuous woodlands. However, it should be considered that refugial population dynamics could, to some extent, be better ascribed to fragmentation disturbance rather than climatic constraint, although this was not directly quantified in this study.

Apart from biological range shift, direct loss of habitat is the most obvious and immediate form of habitat alteration and is the major cause of fragmentation of continuous, natural landscapes in southern Africa (for example see Coetzer *et al.* 2010, 2013). The *B. spiciformis* woodland relict in South Africa plays an important role in the natural heritage of the local people from Gundani and has been placed under a traditional woodland management regime. The Venda common name for the plant "*mussiwa*", meaning the one that is left behind, suggesting an understanding by the indigenous people of a species displaced within human time-frames. The significant diversity of woody plant species associated with *B. spiciformis* in this particular woodland establishes it of high ecological and conservation value (Saidi & Tshipala-Ramatshimbila 2006). Although the woodland is not directly used ethnobotanically, indirect impact from browsing by livestock is severe. It is hypothesised that high livestock density could be causing the observed recruitment bottleneck (see for example Venter & Witkowski 2013). In contrast, slash-and-burn type agriculture poses the greatest threat to the more extensive *B. spiciformis* woodland relict population in southern Mozambique. The site is heavily impacted by woodland transformation to subsistence farmland and is afforded no cultural or formal protection. Critically, associated biota includes the only population (∼100 pairs) of the globally near-threatened Olive-headed Weaver in southern Africa. The nearest populations are patchily distributed in the miombo woodlands of Tanzania, Zambia, Malawi and northern Mozambique (Hockey, Dean & Ryan 2005).

The miombo relict communities of southern Africa seem to depend on the storage effect for their persistence. We suggest that their medium-term survival is

plausible when strictly considering climatic factors. However, the most immediate threat to these regionally unique vegetation types and associated biota are land-use practices. It is hereby suggested that the *B. spiciformis* woodland relict populations be considered for more formal protection status. Given the inability of *B. spiciformis* to exercise long distance dispersal, biodiversity conservation strategies for the woodland at a local to regional scale should consider improvement of landscape connectivity and the incorporation of heterogenous landscapes to allow range shift under climate change.

Beyond the scope of this research exists opportunities for long-term experimental studies to elucidate climate effects from other factors, such as habitat fragmentation and biotic interactions. For example, simple herbivory exclusion experiments in climate relicts could determine if recruitment is seed or establishment limited, and to what extent external factors such as high livestock numbers influence reproduction success. Furthermore, short-term reproduction studies should be synergised with alternative approaches such as studies of adult tree health and growth to infer long-term population trends and their relationship with climate (Hampe & Jump 2011). One approach could be the development of extended tree-ring chronologies that would allow for the investigation of temporal El Niño Southern Oscillation (ENSO) variability and predictions of future regional effect. Considering that ENSO effects on precipitation variability are strongest in southern Africa during the wettest quarter (Trouet 2010), such an investigation would assist in anticipating the persistence or demise of the relict populations. Alternative opportunities exist to explore genetic variation at a meta-population level to investigate potential micro evolutionary adaptation since relict isolation, and possible inbreeding depression.

This study provides important baseline data for *B. spiciformis* woodland population dynamics at the trailing range edge and supports future climate change detection monitoring for this ecological and economic keystone species in southern Africa. It is suggested that unfragmented range margins, rather than climate relict populations, be used to investigate on-going climatic constraints on

population processes at the trailing range edge of this precipitation-sensitive African savannas species.

In conclusion, the study achieved the aim of utilizing miombo relict communities to establish likely spatial and population dynamic responses to global climate change very well. Furthermore, the model-based objectives (chapter two) were satisfied comprehensively contributing towards the advancement of knowledge with regards to the biogeography of *B. spiciformis* in southern Africa. The field study objectives (chapter three) were fulfilled fairly efficiently contributing towards the ecological knowledge of a climate sensitive vegetation community, especially in the mid-latitudes.

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APPENDICES

Appendix 1   Combined sample site species inventory

Families	Species	Rank	Abundance	Proportion (%)	Plot (frequency)	Site (frequency)
Anacardiaceae	*Lannea antiscorbutica* (Hiern) Engl.	128	3	0.01	3	1
	Lannea discolor (Sond.) Engl.	15	459	1.00	15	3
	Ozoroa obovata (Oliv.) R.& A.Fern.	83	31	0.10	3	2
	Ozoroa reticulata (Baker f.) R.& A.Fern.	124	5	0.00	5	2
	Sclerocarya birrea (A.Rich) Hochst.	87	30	0.10	3	2
	Searsia chirindensis (Baker f.) Moffet	118	10	0.01	1	1
	Searsia harveyi (Moffett) Moffett	100	20	0.01	2	1
	Searsia lancea (L.f.) F.A.Barkley	119	10	0.01	1	1
	Searsia leptodictya (Diels) T.S.Yi, A.J.Mill. & J.Wen	120	10	0.01	1	1
	Searsia lucida (L.) F.A.Barkley	121	10	0.01	1	1
	Searsia magalismontana (Sond.) Moffett	30	216	0.50	15	1
	Searsia pyroides (Burch.) Moffett	40	130	0.30	10	1
	Searsia tenuinervis (Engl.) Moffett	26	275	0.60	5	2
Annonaceae	*Artabotrys brachypetalus* Benth.	18	430	0.90	23	3
	Hexalobus monopetalus (A.Rich) Engl. & Diels	90	28	0.10	8	1
	Monodora junodii Engl. & Diels	32	212	0.40	6	1
	Sphaerocyrne gracilis (Engl. & Diels) Verdc.	34	185	0.40	4	1
	Uvaria lucida Benth.	37	141	0.30	2	1
	Xylopia parviflora (A.Rich.) Benth.	126	4	0.01	3	1
Apocynaceae	*Carissa edulis* (Forssk.) Vahl	36	144	0.30	4	1
	Diplorhynchus condylocarpon Welw. ex Ficalo & Hiern.	61	61	0.10	8	2
	Holarrhena pubescens (Buch.-Ham.) Wall.	71	43	0.10	3	1
	Strophanthus petersianus Klotzsch	19	429	0.90	17	2
	Tabernaemontana elegans Stapf	70	48	0.10	8	2
Araliaceae	*Cussonia arborea* Hochst. Ex A.Rich	77	33	0.10	5	2
Asteraceae	*Brachylaena huillensis* O.Hoffm.	108	10	0.01	1	1
	Brachylaena rotundata S.Moore	132	1	0.01	1	1
	Senecio barbertonicus Klatt	21	398	0.80	15	1
	Vernonia colorata (Willd.) Drake	50	82	0.20	2	1
Balanitaceae	*Balanites maughamii* Sprague	41	114	0.20	4	1
Capparaceae	*Boscia albitrunca* (Burch.) Gilg & Ben.	97	20	0.01	2	1
	Capparis erythrocarpus Isert.	23	340	0.70	1	1
	Maerua parvifolia Pax	116	10	0.01	1	1
	Thilachium africanum Lour.	145	1	0.01	1	1
Celastraceae	*Elaeodendron schlechterianum* (Loes.) Loes.	112	10	0.01	1	1
	Gymnosporia buxifolia (L.) Szyszyl.	114	10	0.01	1	1
	Gymnosporia senegalensis (Lam.) Loes.	82	31	0.10	3	2
	Maytenus undata (Thunb.)	80	32	0.10	2	2
	Pleurostylia opposita (Wall.) Alston	68	51	0.10	4	1
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	16	449	0.90	17	3
Clusiaceae	*Garcinia livingstonei* Anders.	81	31	0.10	3	1
	Psorospermum febrifugum Spach	64	60	0.10	2	1
Combretaceae	*Combretum collinum* Fresen.	39	130	0.30	8	2
	Combretum microphyllum (Klotzsch)	133	1	0.01	1	1
	Combretum molle R.Br. ex G.Don	9	681	1.40	18	3
	Combretum pisoniiflorum (Klotzsch) Engl.	42	110	0.20	3	1
	Combretum zeyheri Sond.	134	1	0.01	1	1
	Pteleopsis myrtifolia (C.Lawson) Eng. & Diels	91	27	0.10	4	1
	Terminalia sericea Burch. ex DC.	65	60	0.10	4	2

Dipterocarpaceae	*Monotes glaber* Sprague	43	108	0.20	9	1
Ebenaceae	*Diospyros inhacaensis* F.White	110	10	0.01	1	1
	Diospyros lycoides Desf.	31	213	0.40	9	2
	Diospyros whyteana (Hiern) F.White	35	156	0.30	7	1
	Euclea crispa (Thunb.) Guerke	74	40	0.10	1	1
	Euclea divinorum Hiern	137	1	0.01	1	1
	Euclea natalensis A.DC.	27	256	0.50	13	2
Erythroxylaceae	*Erythroxylem emarginatum* Thonn.	113	10	0.01	1	1
	Erythroxylum delagoense Schinz	127	3	0.01	2	1
Euphorbiaceae	*Bridelia mollis* Hutch.	69	50	0.10	8	2
	Euphorbia ingens E.Mey. ex Boiss.	78	33	0.10	6	1
	Euphorbia tirucalli L.	93	21	0.01	2	1
	Margaritaria discoidea (Baill.) Webster	4	1483	3.10	31	3
	Pseudolachnostylis maprouneifolia Pax	33	209	0.40	15	2
	Sapium integerrimum (Hochst.) J.Léonard	99	20	0.01	2	1
	Suregada zanzibariensis Baill.	96	21	0.01	2	1
	Uapaca kirkiana Müll.Arg.	123	6	0.01	6	1
Fabaceae	*Albizia adianthifolia* (Schumach.) W.F.Wight	51	80	0.20	3	2
	Albizia amara (Roxb.) Biov.	131	1	0.01	1	1
	Albizia anthelmintica (A.Rich.) Brongn.	44	100	0.20	6	1
	Albizia forbesii Benth.	67	51	0.10	4	1
	Albizia versicolor Welw. ex Oliv.	55	72	0.20	8	2
	Bauhinia galpinii N.E.Br.	103	18	0.01	6	1
	Brachystegia boehmii Taub.	47	93	0.20	2	2
	Brachystegia glaucescens Burtt Davy & Hutch.	14	475	1.00	4	2
	Brachystegia spiciformis Benth.	1	18607	39.10	70	4
	Burkea africana Hook.	8	827	1.70	18	2
	Craibia zimmermannii (Harms) Dunn	45	100	0.20	1	1
	Crotalaria monteiroi Taub. ex Baker.f.	12	526	1.10	11	3
	Dalbergia nitidula Baker	135	1	0.01	1	1
	Dichrostachys cinerea (L.) Wight & Arn.	11	595	1.30	22	3
	Julbernardia globiflora (Benth.) Troupin	2	7166	15.10	23	2
	Mundulea sericea (Willd.) A.Chev.	117	10	0.01	1	1
	Peltophorum africanum Sond.	141	1	0.01	1	1
	Pterocarpus angolensis DC.	105	13	0.01	2	2
	Pterocarpus rotundifolia (Sond.) Druce	52	80	0.20	4	1
	Rhynchosia sublobata (Schumach. & Thonn.) Meikle	62	61	0.10	4	2
	Rhynchosia vendae C.H.Stirt	84	31	0.10	2	1
	Senegalia burkei Benth.	122	6	0.01	2	1
	Senna petersiana (Bolle) Lock	28	242	0.50	5	2
	Vachellia tortilis (Forssk.)	85	30	0.10	2	1
Flacourtiaceae	*Dovyalis caffra* (Hook.f. & Harv.) Hook.f.	136	1	0.01	1	1
	Flacourtia indica (Burm.f.) Merr.	63	60	0.10	3	2
Lamiaceae	*Clerodendrum robustum* (Klotzsch)	17	440	0.90	5	1
	Tetradenia riparia (Hochst) Codd	101	20	0.01	1	1
	Tinnea rhodesiana S.Moore	130	2	0.01	1	1
Malvaceae	*Azanza garckeana*(F.Hoffm.) Exell & Hillc.	129	2	0.01	2	2
	Grewia caffra Meisn.	57	70	0.10	2	1
	Grewia flavescens Juss.	86	30	0.10	3	2
	Grewia microthyrsa K.Schum. ex Burret	66	57	0.10	8	1
Meliaceae	*Ekebergia pterophylla* (C.DC.) Hofmeyr	111	10	0.01	1	1
Moraceae	*Ficus burkei* (Miq.) Miq.	107	11	0.01	2	2
	Ficus glumosa Delile	138	1	0.01	1	1
Myrtaceae	*Syzygium guineense* (Willd.) DC.	6	1225	2.60	10	1
Ochnaceae	*Ochna natalitia* (Meisn.) Walp.	60	63	0.10	6	2
	Ochna pulchra Hook.	38	140	0.30	2	1
	Ochna schweinfurthiana F.Hoffm.	49	91	0.20	6	2
Olacaceae	*Olax dissitiflora* Oliv.	20	419	0.90	12	2
	Ximenia caffra Sond.	58	68	0.10	11	3

Family	Species					
	Schrebera alata (Hochst.) Welw.	143	1	0.01	1	1
Opiliaceae	*Opilia amentacea* Roxb.	7	1160	2.40	5	1
Plumbaginaceae	*Plumbago zeylanica* L.	75	40	0.10	1	1
Proteaceae	*Faurea rochetiana* (A.Rich.) Pic.Serm	92	23	0.01	3	1
	Faurea saligna Harv.	72	42	0.10	3	1
Rubiaceae	*Canthium ciliatum* (Klotzsch) Kuntze	73	41	0.10	2	1
	Canthium mundianum Cham. & Schlechtd.	5	1314	2.80	18	1
	Canthium setiflorum Hiern.	109	10	0.01	1	1
	Catunaregam spinosa (Thunb.) Tirvengadum	3	1742	3.70	10	2
	Coddia rudis (E.Mey. Ex Harv.) Verdc.	98	20	0.00	2	1
	Gardenia volkensii K.Schum.	79	33	0.10	4	2
	Hyperacanthus amoenus (Sims) Bridson	104	18	0.01	1	1
	Lagynias dryadum (S.Moore) Robyns	10	599	1.30	19	1
	Lagynias lasiantha (Sond.) Bullock	115	10	0.01	1	1
	Lagynias monteiroi (Oliv.) Bridson	29	216	0.50	3	1
	Leptactina delagoensis K.Schum.	13	477	1.00	15	1
	Pavetta catophylla K.Schum.	140	1	0.01	1	1
	Pavetta gardeniifolia A.Rich.	59	65	0.10	4	1
	Pavetta schumanniana F.Hoffm. ex K.Schum.	24	324	0.70	20	3
	Psydrax livida (Hiern) Bridson	22	392	0.80	16	2
	Tarenna littoralis (Hiern) Bridson	56	72	0.20	5	2
	Tarenna supra-axillaris (Hemsl.) Bridson	144	1	0.01	1	1
	Vangueria infausta Burch.	25	278	0.60	22	3
Rutaceae	*Vepris lanceolata* (Lam.) G. Don	89	30	0.10	2	1
	Zanthoxylum leprieurii Guill. & Perr.	102	20	0.01	2	1
Sapindaceae	*Allophylus natalensis* (Sond.) De Winter	46	94	0.20	1	1
	Pappea capensis (Eckl. & Zeyh.)	139	1	0.01	1	1
Sapotaceae	*Englerophytum magalismontanum* Krause	106	11	0.01	2	1
	Manilkara concolor (Harv. ex C.H.Wright) Gerstner	125	4	0.01	1	1
	Mimusops zeheri (Sonder)	54	78	0.20	4	1
Strychnaceae	*Strychnos madagascariensis* Poir.	48	93	0.20	6	2
	Strychnos spinosa Lam.	88	30	0.10	3	3
Thymelaeaceae	*Synaptolepis oliveriana* Gilg	53	80	0.20	1	1
Verbenaceae	*Vitex ferruginea* Schumach. & Thonn.	76	39	0.10	7	1
	Vitex payos (Lour.) Merr.	146	1	0.01	1	1
Vitaceae	*Rhoicissus digitata* (L.f.) Gilg & Brandt	94	21	0.01	2	1
	Rhoicissus revoilii Planch.	95	21	0.01	2	2
	Rhoicissus tridentata (L.f.)	142	1	0.01	1	1

Appendix 2   Control species inventory

Families	Species	Rank	Abundance	Proportion (%)	Plot (frequency)
Anacardiaceae	*Lannea discolor* (Sond.) Engl.	5	264	2.90	6
	Ozoroa reticulata (Baker f.) R.& A.Fern.	35	1	0.10	1
	Searsia harveyi (Moffett) Moffett	29	10	0.10	2
	Searsia pyroides (Burch.) Moffett	9	110	1.20	10
Araliaceae	*Cussonia arborea* Hochst. Ex A.Rich	22	13	0.10	4
Celastraceae	*Gymnosporia senegalensis* (Lam.) Loes.	23	11	0.10	2
	Maytenus undata (Thunb.)	16	32	0.40	2
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	4	299	3.30	6
Clusiaceae	*Psorospermum febrifugum* Spach	13	60	0.60	2
Combretaceae	*Combretum molle* R.Br. ex G.Don	14	52	0.60	4
Ebenaceae	*Diospyros lycoides* Desf.	10	102	1.10	8
	Diospyros whyteana (Hiern) F.White	11	95	1.10	7
	Euclea crispa (Thunb.) Guerke	15	40	0.50	1
Euphorbiaceae	*Euphorbia ingens* E.Mey. ex Boiss.	18	23	0.30	6
	Uapaca kirkiana Müll.Arg.	31	5	0.10	6
Fabaceae	*Brachystegia boehmii* Taub.	17	31	0.10	1
	Brachystegia glaucescens Burtt Davy & Hutch.	6	209	2.30	2
	Brachystegia spiciformis Benth.	1	5486	61.30	14
	Burkea africana Hook.	3	440	4.90	6
	Crotalaria monteiroi Taub. ex Baker.f.	24	10	0.10	1
	Dalbergia nitidula Baker	33	1	0.01	1
	Julbernardia globiflora (Benth.) Troupin	2	1250	14.00	8
	Mundulea sericea (Willd.) A.Chev.	26	10	0.30	1
	Pterocarpus angolensis DC.	32	2	0.01	2
	Rhynchosia sublobata (Schumach. & Thonn.) Meikle	28	10	0.10	2
Flacourtiaceae	*Flacourtia indica* (Burm.f.) Merr.	25	10	0.10	2
Lamiaceae	*Tetradenia riparia* (Hochst) Codd	21	20	0.20	1
Malvaceae	*Grewia flavescens* Juss.	20	20	0.20	2
Moraceae	*Ficus burkei* (Miq.) Miq.	34	1	0.01	1
Ochnaceae	*Ochna schweinfurthiana* F.Hoffm.	12	60	0.70	4
Proteaceae	*Faurea rochetiana* (A.Rich.) Pic.Serm	19	23	0.30	3
Rubiaceae	*Pavetta schumanniana* F.Hoffm. ex K.Schum.	8	110	1.20	7
	Vangueria infausta Burch.	7	120	1.30	5
Strychnaceae	*Strychnos spinosa* Lam.	30	10	0.10	1
Verbenaceae	*Vitex payos* (Lour.) Merr.	36	1	0.01	1
Vitaceae	*Rhoicissus revoilii* Planch.	27	10	0.10	2
	Rhoicissus tridentata (L.f.)	36	1	0.01	1

Appendix 3   Edge species inventory

Families	Species	Rank	Abundance	Proportion (%)	Plot (frequency)
Anacardiaceae	*Lannea discolor* (Sond.) Engl.	9	123	0.90	9
	Ozoroa obovata (Oliv.) R.& A.Fern.	34	11	0.10	2
	Ozoroa reticulata (Baker f.) R.& A.Fern.	41	4	0.10	4
	Sclerocarya birrea (A.Rich) Hochst.	32	20	0.10	2
	Searsia chirindensis (Baker f.) Moffet	40	10	0.10	1
	Searsia tenuinervis (Engl.) Moffett	25	32	0.20	3
Annonaceae	*Artabotrys brachypetalus* Benth.	16	70	0.50	4
Apocynaceae	*Diplorhynchus condylocarpon* Welw. ex Ficalo & Hiern.	19	60	0.40	7
Araliaceae	*Cussonia arborea* Hochst. Ex A.Rich	36	10	0.10	1
Asteraceae	*Brachylaena rotundata* S.Moore	45	1	0.01	1
	Vernonia colorata (Willd.) Drake	13	82	0.60	2
Celastraceae	*Gymnosporia senegalensis* (Lam.) Loes.	31	20	0.10	1
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	24	34	0.20	3
Combretaceae	*Combretum collinum* Fresen.	11	117	0.80	5
	Combretum molle R.Br. ex G.Don	3	616	4.40	11
	Terminalia sericea Burch. ex DC.	20	50	0.40	3
Dipterocarpaceae	*Monotes glaber* Sprague	12	108	0.80	9
Ebenaceae	*Diospyros lycoides* Desf.	15	71	0.50	1
	Euclea divinorum Hiern	47	1	0.01	1
Euphorbiaceae	*Bridelia mollis* Hutch.	28	22	0.20	2
	Margaritaria discoidea (Baill.) Webster	10	123	0.90	6
	Pseudolachnostylis maprouneifolia Pax	8	152	1.10	8
Fabaceae	*Albizia amara* (Roxb.) Biov.	43	1	0.01	1
	Brachystegia boehmii Taub.	17	62	0.40	1
	Brachystegia glaucescens Burtt Davy & Hutch.	5	266	1.90	2
	Brachystegia spiciformis Benth.	2	4896	34.90	17
	Burkea africana Hook.	4	357	2.50	12
	Dichrostachys cinerea (L.) Wight & Arn.	22	41	0.30	4
	Julbernardia globiflora (Benth.) Troupin	1	5896	42.00	15
	Pterocarpus angolensis DC.	35	11	0.10	1
	Pterocarpus rotundifolia (Sond.) Druce	14	80	0.60	4
	Rhynchosia sublobata (Schumach. & Thonn.) Meikle	23	41	0.30	2
	Vachellia tortilis (Forssk.)	26	30	0.20	2
Flacourtiaceae	*Dovyalis caffra* (Hook.f. & Harv.) Hook.f.	46	1	0.01	1
	Flacourtia indica (Burm.f.) Merr.	38	10	0.10	1
Lamiaceae	*Tinnea rhodesiana* S.Moore	42	2	0.01	1
Malvaceae	*Azanza garckeana*(F.Hoffm.) Exell & Hillc.	44	1	0.01	1
	Grewia flavescens Juss.	39	10	0.10	1
Moraceae	*Ficus burkei* (Miq.) Miq.	37	10	0.10	1
Ochnaceae	*Ochna schweinfurthiana* F.Hoffm.	33	11	0.10	2
Olacaceae	*Ximenia caffra* Sond.	30	21	0.10	3
Proteaceae	*Faurea saligna* Harv.	21	42	0.30	3
Rubiaceae	*Catunaregam spinosa* (Thunb.) Tirvengadum	27	30	0.20	2
	Gardenia volkensii K.Schum.	29	22	0.20	2
	Pavetta schumanniana F.Hoffm. ex K.Schum.	7	152	1.10	7
	Psydrax livida (Hiern) Bridson	6	251	1.80	7
	Vangueria infausta Burch.	18	61	0.40	6
Sapindaceae	*Pappea capensis* (Eckl. & Zeyh.)	48	1	0.01	1
Vitaceae	*Rhoicissus revoilii* Planch.	49	1	0.01	1

Appendix 4   Mozambique relict species inventory

Families	Species	Rank	Abundance	Proportion (%)	Plot (frequency)
Anacardiaceae	*Lannea antiscorbutica* (Hiern) Engl.	51	3	0.01	3
	Sclerocarya birrea (A.Rich) Hochst.	46	10	0.10	1
	Searsia tenuinervis (Engl.) Moffett	10	243	1.60	2
Annonaceae	*Artabotrys brachypetalus* Benth.	16	173	1.20	6
	Monodora junodii Engl. & Diels	13	212	1.40	6
	Sphaerocyrne gracilis (Engl. & Diels) Verdc.	14	185	1.30	4
	Uvaria lucida Benth.	18	141	1.00	2
Apocynaceae	*Carissa edulis* (Forssk.) Vahl	17	144	1.00	4
	Strophanthus petersianus Klotzsch	32	42	0.30	2
	Tabernaemontana elegans Stapf	53	1	0.01	1
Balanitaceae	*Balanites maughamii* Sprague	19	114	0.80	4
Capparaceae	*Capparis erythrocarpus* Isert.	8	340	2.30	1
	Maerua parvifolia Pax	45	10	0.10	1
Celastraceae	*Elaeodendron schlechterianum* (Loes.) Loes.	43	10	0.10	1
	Pleurostylia opposita (Wall.) Alston	30	51	0.30	4
Clusiaceae	*Garcinia livingstonei* Anders.	34	31	0.20	3
Combretaceae	*Combretum molle* R.Br. ex G.Don	40	12	0.10	3
	Combretum pisoniiflorum (Klotzsch) Engl.	20	110	0.70	3
Ebenaceae	*Diospyros inhacaensis* F.White	42	10	0.10	1
	Euclea natalensis A.DC.	15	176	1.20	8
Erythroxylaceae	*Erythroxylum delagoense* Schinz	50	3	0.01	2
Euphorbiaceae	*Euphorbia tirucalli* L.	36	21	0.10	2
	Margaritaria discoidea (Baill.) Webster	6	373	2.50	7
	Sapium integerrimum (Hochst.) J.Léonard	39	20	0.10	1
	Suregada zanzibariensis Baill.	38	21	0.10	2
Fabaceae	*Albizia adianthifolia* (Schumach.) W.F.Wight	28	60	0.40	1
	Albizia forbesii Benth.	29	51	0.30	4
	Albizia versicolor Welw. ex Oliv.	25	71	0.50	7
	Brachystegia spiciformis Benth.	1	6596	44.60	18
	Craibia zimmermannii (Harms) Dunn	21	100	0.70	1
	Crotalaria monteiroi Taub. ex Baker.f.	4	514	3.50	8
	Dichrostachys cinerea (L.) Wight & Arn.	9	258	1.70	7
	Senegalia burkei Benth.	48	6	0.01	2
	Senna petersiana (Bolle) Lock	11	231	1.60	3
Lamiaceae	*Clerodendrum robustum* (Klotzsch)	5	440	3.00	5
Malvaceae	*Grewia caffra* Meisn.	27	70	0.50	2
Ochnaceae	*Ochna natalitia* (Meisn.) Walp.	35	22	0.10	2
Olacaceae	*Olax dissitiflora* Oliv.	7	366	2.50	7
	Ximenia caffra Sond.	33	36	0.20	6
Opiliaceae	*Opilia amentacea* Roxb.	3	1160	7.80	5
Rubiaceae	*Catunaregam spinosa* (Thunb.) Tirvengadum	2	1712	11.60	8
	Gardenia volkensii K.Schum.	41	11	0.10	2
	Lagynias lasiantha (Sond.) Bullock	44	10	0.10	1
	Lagynias monteiroi (Oliv.) Bridson	12	216	1.50	3
	Pavetta catophylla K.Schum.	52	1	0.01	1
	Tarenna littoralis (Hiern) Bridson	31	51	0.30	2
Sapindaceae	*Allophylus natalensis* (Sond.) De Winter	22	94	0.60	1
Sapotaceae	*Manilkara concolor* (Harv. ex C.H.Wright) Gerstner	49	4	0.01	1
	Mimusops zeheri (Sonder)	24	78	0.50	4
Strychnaceae	*Strychnos madagascariensis* Poir.	26	71	0.50	3
	Strychnos spinosa Lam.	47	10	0.10	1
Thymelaeaceae	*Synaptolepis oliveriana* Gilg	23	80	0.50	1
Vitaceae	*Rhoicissus digitata* (L.f.) Gilg & Brandt	37	21	0.10	2

Appendix 5 South Africa relict species inventory

Families	Species	Rank	Abundance	Proportion (%)	Plot (frequency)
Anacardiaceae	*Lannea discolor* (Sond.) Engl.	18	72	0.80	5
	Ozoroa obovata (Oliv.) R.& A.Fern.	40	20	0.20	1
	Searsia lancea (L.f.) F.A.Barkley	52	10	0.10	1
	Searsia leptodictya (Diels) T.S.Yi, A.J.Mill. & J.Wen	53	10	0.10	1
	Searsia lucida (L.) F.A.Barkley	54	10	0.10	1
	Searsia magalismontana (Sond.) Moffett	10	216	2.40	15
Annonaceae	*Artabotrys brachypetalus* Benth.	11	187	2.00	13
	Hexalobus monopetalus (A.Rich) Engl. & Diels	33	28	0.30	8
	Xylopia parviflora (A.Rich.) Benth.	57	4	0.01	3
Apocynaceae	*Diplorhynchus condylocarpon* Welw. ex Ficalo & Hiern.	63	1	0.01	1
	Holarrhena pubescens (Buch.-Ham.) Wall.	24	43	0.50	3
	Strophanthus petersianus Klotzsch	8	387	4.20	15
	Tabernaemontana elegans Stapf	23	47	0.50	7
Asteraceae	*Brachylaena huillensis* O.Hoffm.	48	10	0.10	1
	Senecio barbertonicus Klatt	7	398	4.40	15
Capparaceae	*Boscia albitrunca* (Burch.) Gilg & Ben.	38	20	0.20	2
	Thilachium africanum Lour.	68	1	0.01	1
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	14	116	1.30	8
Combretaceae	*Combretum collinum* Fresen.	44	13	0.20	3
	Combretum microphyllum (Klotzsch)	61	1	0.01	1
	Combretum zeyheri Sond.	62	1	0.01	1
	Pteleopsis myrtifolia (C.Lawson) Eng. & Diels	34	27	0.30	4
	Terminalia sericea Burch. ex DC.	56	10	0.10	1
Ebenaceae	*Euclea natalensis* A.DC.	17	80	0.90	5
Erythroxylaceae	*Erythroxylem emarginatum* Thonn.	51	10	0.10	1
Euphorbiaceae	*Bridelia mollis* Hutch.	32	28	0.30	6
	Margaritaria discoidea (Baill.) Webster	4	987	10.80	18
	Pseudolachnostylis maprouneifolia Pax	21	57	0.60	7
Fabaceae	*Albizia adianthifolia* (Schumach.) W.F.Wight	37	20	0.20	2
	Albizia anthelmintica (A.Rich.) Brongn.	15	100	1.10	6
	Albizia versicolor Welw. ex Oliv.	59	1	0.01	1
	Bauhinia galpinii N.E.Br.	42	18	0.20	6
	Brachystegia spiciformis Benth.	1	1314	14.40	21
	Crotalaria monteiroi Taub. ex Baker.f.	58	2	0.01	2
	Dichrostachys cinerea (L.) Wight & Arn.	9	296	3.20	11
	Peltophorum africanum Sond.	65	1	0.01	1
	Rhynchosia vendae C.H.Stirt	30	31	0.10	2
	Senna petersiana (Bolle) Lock	46	11	0.10	2
Malvaceae	*Azanza garckeana* (F.Hoffm.) Exell & Hillc.	60	1	0.01	1
	Grewia microthyrsa K.Schum. ex Burret	20	57	0.60	8
Meliaceae	*Ekebergia pterophylla* (C.DC.) Hofmeyr	50	10	0.10	1
Moraceae	*Ficus glumosa* Delile	64	1	0.01	1
Myrtaceae	*Syzygium guineense* (Willd.) DC.	3	1225	13.40	10
Ochnaceae	*Ochna natalitia* (Meisn.) Walp.	27	41	0.40	4
	Ochna pulchra Hook.	13	140	1.50	2
Olacaceae	*Olax dissitiflora* Oliv.	22	53	0.60	5
	Schrebera alata (Hochst.) Welw.	66	1	0.01	1
	Ximenia caffra Sond.	47	11	0.10	2
Plumbaginaceae	*Plumbago zeylanica* L.	28	40	0.40	1
Rubiaceae	*Canthium ciliatum* (Klotzsch) Kuntze	26	41	0.40	2
	Canthium mundianum Cham. & Schlechtd.	2	1314	14.40	18
	Canthium setiflorum Hiern.	49	10	0.10	1

	Coddia rudis (E.Mey. Ex Harv.) Verdc.	39	20	0.20	2
	Hyperacanthus amoenus (Sims) Bridson	43	18	0.20	2
	Lagynias dryadum (S.Moore) Robyns	5	599	6.50	19
	Leptactina delagoensis K.Schum.	6	477	5.20	15
	Pavetta gardeniifolia A.Rich.	19	65	0.70	4
	Pavetta schumanniana F.Hoffm. ex K.Schum.	25	42	0.50	6
	Psydrax livida (Hiern) Bridson	12	141	1.50	9
	Tarenna littoralis (Hiern) Bridson	36	21	0.20	3
	Tarenna supra-axillaris (Hemsl.) Bridson	67	1	0.01	1
	Vangueria infausta Burch.	16	97	1.10	12
Rutaceae	*Vepris lanceolata* (Lam.) G. Don	31	30	0.30	2
	Zanthoxylum leprieurii Guill. & Perr.	41	20	0.20	2
Sapotaceae	*Englerophytum magalismontanum* Krause	45	11	0.20	2
Strychnaceae	*Strychnos madagascariensis* Poir.	35	22	0.20	3
	Strychnos spinosa Lam.	55	10	0.10	1
Verbenaceae	*Vitex ferruginea* Schumach. & Thonn.	29	39	0.40	7

Explanatory variables within and between sample sites

Site and factor	Mean (±SE)	S F	S P	H' F	H' P	J' F	J' P	Miombo juvenile density F	Miombo juvenile density P	*B. spiciformis* juvenile density F	*B. spiciformis* juvenile density P
Control											
Altitude (masl)	1610 (±7.0)	$_{(4,9)}$ 0.01	0.917	$_{(4,9)}$ 2.56	0.144	$_{(4,9)}$ 1.05	0.328	$_{(4,9)}$ 0.13	0.722	$_{(4,9)}$ 0.03	0.869
Browsing (%)	0.3 (±0.1)	$_{(4,9)}$ 26.45	**0.001**	$_{(4,9)}$ 2.71	0.134	$_{(4,9)}$ 0.09	0.770	$_{(4,9)}$ 0.05	0.833	$_{(4,9)}$ 1.04	0.334
Fire (%)	4.7 (±3.3)	$_{(4,9)}$ 0.00	0.943	$_{(4,9)}$ 0.03	0.862	$_{(4,9)}$ 0.02	0.900	$_{(4,9)}$ 6.54	**0.031**	$_{(4,9)}$ 6.93	**0.027**
Rock (%)	6.0 (±2.6)	$_{(4,9)}$ 2.73	0.131	$_{(4,9)}$ 2.55	0.145	$_{(4,9)}$ 1.09	0.320	$_{(4,9)}$ 15.44	**<0.001**	$_{(4,9)}$ 8.17	**<0.001**
Edge											
Altitude (masl)	1004 (±10.0)	$_{(5,13)}$ 6.01	**0.029**	$_{(5,13)}$ 0.17	0.687	$_{(5,13)}$ 1.35	0.267	$_{(5,13)}$ 11.40	**0.005**	$_{(5,13)}$ 0.12	0.734
Browsing (%)	1.1 (±0.6)	$_{(5,13)}$ 1.55	0.235	$_{(5,13)}$ 7.55	**0.017**	$_{(5,13)}$ 4.58	0.052	$_{(5,13)}$ 0.57	0.462	$_{(5,13)}$ 27.76	**<0.001**
Fire (%)	2.2 (±1.1)	$_{(5,13)}$ 3.52	0.083	$_{(5,13)}$ 1.68	0.217	$_{(5,13)}$ 0.08	0.775	$_{(5,13)}$ 3.17	0.098	$_{(5,13)}$ 14.09	**0.002**
Harvesting (%)	0.8 (±0.3)	$_{(5,13)}$ 0.04	0.841	$_{(5,13)}$ 0.08	0.788	$_{(5,13)}$ 0.33	0.577	$_{(5,13)}$ 0.19	0.667	$_{(5,13)}$ 0.12	0.734
Rock (%)	4.7 (±1.9)	$_{(5,13)}$ 0.09	0.769	$_{(5,13)}$ 1.03	0.328	$_{(5,13)}$ 0.81	0.384	$_{(5,13)}$ 1.85	0.197	$_{(5,13)}$ 33.28	**<0.001**
Mozambique Relict											
Altitude (masl)	86 (±3.5)	$_{(4,13)}$ 0.05	0.823	$_{(4,13)}$ 0.46	0.511	$_{(4,13)}$ 0.09	0.770	$_{(4,13)}$ 0.83	0.380	$_{(4,13)}$ 0.83	0.380
Browsing (%)	0.9 (±0.4)	$_{(4,13)}$ 0.32	0.580	$_{(4,13)}$ 0.63	0.440	$_{(4,13)}$ 0.18	0.680	$_{(4,13)}$ 0.01	0.920	$_{(4,13)}$ 0.01	0.920
Fire (%)	13.7 (±5.7)	$_{(4,13)}$ 0.23	0.640	$_{(4,13)}$ 1.66	0.221	$_{(4,13)}$ 1.05	0.320	$_{(4,13)}$ 0.20	0.660	$_{(4,13)}$ 0.20	0.660
Harvesting (%)	0.1 (±0.1)	$_{(4,13)}$ 3.34	0.098	$_{(4,13)}$ 4.10	0.064	$_{(4,13)}$ 0.61	0.450	$_{(4,13)}$ 0.41	0.530	$_{(4,13)}$ 0.41	0.530
South Africa Relict											
Altitude (masl)	806 (±5.0)	$_{(4,16)}$ 0.62	0.440	$_{(4,16)}$ 0.19	0.669	$_{(4,16)}$ 0.40	0.533	$_{(4,16)}$ 0.77	0.390	$_{(4,16)}$ 0.77	0.390
Browsing (%)	14.7 (±3.0)	$_{(4,16)}$ 0.22	0.639	$_{(4,16)}$ 4.31	0.054	$_{(3,17)}$ 7.97	**0.012**	$_{(4,16)}$ 0.00	0.990	$_{(4,16)}$ 0.00	0.990
Harvesting (%)	0.2 (±0.1)	$_{(4,16)}$ 0.67	0.430	$_{(4,16)}$ 0.02	0.895	$_{(4,16)}$ 2.07	0.169	$_{(4,16)}$ 0.77	0.390	$_{(4,16)}$ 0.77	0.390
Rock (%)	27.8 (±4.2)	$_{(4,16)}$ 0.25	0.620	$_{(4,16)}$ 14.45	**<0.001**	$_{(4,16)}$ 8.99	**0.004**	$_{(4,16)}$ 0.40	0.540	$_{(4,16)}$ 0.40	0.540
Between Sites											
Altitude (masl)		$_{(20,51)}$ 0.47	0.704	$_{(20,51)}$ 0.21	0.888	$_{(20,51)}$ 0.95	0.372	$_{(24,47)}$ 1.87	0.146	$_{(24,47)}$ 0.63	0.596
Browsing (%)		$_{(20,51)}$ 1.16	0.336	$_{(20,51)}$ 0.41	0.748	$_{(20,51)}$ 0.30	0.823	$_{(24,47)}$ 0.14	0.933	$_{(24,47)}$ 2.32	0.086
Fire (%)		$_{(20,51)}$ 0.60	0.522	$_{(20,51)}$ 1.23	0.300	$_{(20,51)}$ 0.37	0.694	$_{(24,47)}$ 1.83	0.171	$_{(24,47)}$ 4.40	**0.017**
Harvesting (%)		$_{(20,51)}$ 2.89	0.065	$_{(20,51)}$ 3.35	**0.042**	$_{(20,51)}$ 1.01	0.372	$_{(24,47)}$ 0.80	0.454	$_{(24,47)}$ 1.18	0.315
Rock (%)		$_{(20,51)}$ 0.32	0.725	$_{(20,51)}$ 1.86	0.165	$_{(20,51)}$ 1.29	0.283	$_{(24,47)}$ 0.22	0.804	$_{(24,47)}$ 2.24	0.285