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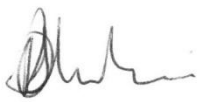
A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science

31 October 2014 in Johannesburg

DECLARATION

I declare that this thesis is my own, unaided work, unless otherwise noted within the text. 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 other degree or examination in any other university.

Odette Suzanne Prinsloo



31st day of October 2014 in Johannesburg

ABSTRACT

Over one-third of South Africa's surface area is covered by savanna woodlands. The structure and dynamics of savannas within communal rangelands have not only been formed by environmental determinants (rainfall and soil) but have also been influenced and manipulated by anthropogenic disturbances (fire, herbivory by livestock, harvesting of resources and cultivation). The aim of this study was to determine the individual and interactive influences of rainfall and catenal position on woody vegetation composition and structure in human-impacted woodlands of Bushbuckridge, Mpumalanga Province, from 2011 to 2013. Three zones were selected that differed in mean annual rainfall: (a) wet west (>700mm), (b) mesic (600-700mm), and semi-dry east (<600m), with three villages per zone. For the rangeland of each village, plots were sampled in 2011, 2012 and 2013 to cover the upland and bottomland variations in catenal position. All trees >6m in height, and their individual stems, were counted and measured within a total of 56 circular plots (only 28 in 2011) each with a radius of 50m. Trees <6m, and their stems, were counted and measured in a circular plot with a radius of 6m, nested centrally within each 50m plot. All analyses were undertaken on (a) total trees and stems and (b) recently harvested (within the last 12 month) trees and stems.

The density of small trees (<6m in height) was significantly higher than that of large trees (>6m in height) from 2011 to 2013. Trees and stems were more abundant in the smaller height and diameter classes, respectively, indicating stable populations. The densities of stems for large trees did not show any change over time, whereas the densities of small trees decreased from 2011 to 2013. When comparing across time between rainfall zones, the densities were higher in the high rainfall zone than in the low and medium rainfall zones for each survey year. On the other hand, densities were similar between uplands and bottomlands for each survey year. The intensity of harvesting increased for large trees over time (between 0% in 2011, 2.3% in 2012 and 10.6% in 2013), whereas small trees did not show any change over time. The most harvested trees were between 0.6-4m in height and 1.1-10cm in stem diameter. There were however some signs that harvesting in the larger size classes (>6m in height and >20cm diameter) were increasing over time. The highest proportion of trees was harvested in the medium rainfall zone compared to the other two rainfall zones, but there was similar harvesting intensity between uplands and bottomlands.

Overall species richness, Shannon and Simpson's (Diversity), and Evenness at the plot level did not change for either large or small trees from 2011 to 2013. The species richness and Shannon's diversity was higher in the high rainfall zone than in the other two rainfall zones, whereas there was no difference in species richness, diversity or evenness between catenal positions for either large or small trees over time. Because there are similar patterns between the species accumulation and rarefaction curves for both the large and small trees, species are distributed at random across the plots, and this is consistent for the three survey years. The most abundance large tree species were *Sclerocarya birrea* > *Philenoptera violacea* > *Pterocarpus angolensis*, which were very different from the most abundant small tree species that were dominated by *Dichrostachys cinerea, Terminalia sericea, Acacia exuvialis, Strychnos madagascariensis* and *Combretum hereroense*. A greater species richness, diversity and evenness of harvested trees were observed in 2013 compared to 2011 and 2012. Species that were most harvested for large trees comprised *Combretum collinum, Acacia gerrardii, T. sericea, Acacia robusta, Combretum zeyheri* and *S. birrea,* whereas harvested small trees comprised *D. cinerea, T. sericea, A. exuvialis* and *C. hereroense*. Even though there were no differences in density, structure, species richness, diversity or harvesting intensity, the species composition did however differ between the uplands and bottomlands. The bottomlands had more abundant fine-leaved species (e.g. *Acacia* spp. and *Dichrostachys cinerea*) and the uplands had more abundant broad-leaved species (particularly *Combretum* spp.). There was a greater difference in species composition in the high rainfall zone relative to the low and medium rainfall zones. This difference in species composition was consistent with the findings that the high rainfall zone had higher density, and a taller, single stemmed tree structure, as well as species richness and diversity when compared to the low and medium rainfall zones. Harvesting intensity was higher in the bottomlands than in the uplands and also higher in the low and medium rainfall zones than in the high rainfall zone. Recent harvesting appeared to have had less influence on species composition than catenal position or rainfall zone.

The harvesting of these resources has an impact on both human livelihoods and the ecosystem and must therefore occur in a sustainable way. When the rate of wood production is less than or equal to the rate of wood harvesting, harvesting can be defined as sustainable. The rate of fuelwood harvesting is driven by the demand for the resource, which in most cases is driven by local human population size. With the increase in human

population size over time, and the scarcity of fuelwood from the surrounding rangelands, the existence of fuelwood markets is fast becoming a part of daily life as it ensures fuelwood for daily usage such as cooking. For this reason, long-term monitoring is needed. Long-term monitoring will not only allow for better future management of natural resources, but it also allows for the communities to get involved in protecting the resources which are so vital to a vast number of people for daily living. Future studies analysing the data from these plots over longer time periods will provide a better understanding of the role that environmental and anthropogenic determinants play in the changes observed over time in the woody vegetation.

DEDICATION

I wish to first dedicate this work to the Glory of God, as He gave me strength to see this though.

Secondly to my mom and dad, Jennie and Francois, respectively.

Thirdly to my fiancé, Robert.

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"When you've done everything you can, that's when God will step in and do what you can't" – 2 Corinthians 12:10

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"For I know the plans I have for you, "declares the Lord, "plans to prosper you and not to harm you, plans to give you hope and a future" – Jeremia 29:11

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LIST OF ABBREVIATIONS

2011_{28}	28 plots in 2011
2012_{28}	28 plots in 2012
2013_{28}	28 plots in 2013
2012_{56}	56 plots in 2012
2013_{56}	56 plots in 2013
$2012_{28\&56}$	28 and 56 plots in 2012
$2013_{28\&56}$	28 and 56 plots in 2013
CA	Correspondence Analysis
CCA	Canonical Correspondence Analysis
GIS	Geographic Information Systems
KS	Kolmogorov-Smirnov Test
LiDAR	Light Detection and Ranging
PCA	Principal Components Analysis
RDA	Redundancy Analysis
SCD_{diam}	Stem diameter size class distribution
SCD_{ht}	Height size class distributions
SUCSES	Sustainability in Communal Socio-Ecological Systems

1 Chapter 1: INTRODUCTION

1.1 RATIONALE

Savannas are globally important because they cover 10-15% of the earth's land surface and provide a range of important ecosystem services (Higgins *et al.* 2007; Kanniah *et al.* 2010). Savannas are also responsible for 13% of net primary production on a global scale (Grace *et al.* 2006). Around 40%-50% of Africa is covered by savannas and forms the most extensive vegetation types (Scholes and Walker 1993; Hassler *et al.* 2010; Hejcmanova *et al.* 2009). Savannas in South Africa add to the rich diversity of plants found in the country overall (Botha *et al.* 2004a; Dovie *et al.* 2002; Shackleton *et al.* 2002).

Savanna vegetation consists of a continuous herbaceous layer and discontinuous woody layer (Colgan *et al.* 2012; Sankaran *et al.* 2005; Scholes and Archer 1997; Wessels *et al.* 2011). The composition and structure of savannas are determined by precipitation, fire regime, soil type and herbivory (Belsky 1990; Fisher *et al.* 2009; Govender *et al.* 2006; Hassler *et al.* 2010; Hejcmanova *et al.* 2009; Le Roux and Bariac 1998; Scholes and Archer 1997; Scholes and Walker 1993; Wessels *et al.* 2011). In addition to these environmental factors, the practice of different land uses is another major determinant of savannas (Fairbanks 2004; Higgins *et al.* 1999; Scholes and Archer 1997). The different uses of land within the communal rangelands are thought to be one of the drivers of change in vegetation structure of savannas (Breshears and Barnes 1999; Fisher *et al.* 2011; Gilson *et al.* 2003; Higgins *et al.* 1999; Kristensen and Lykke 2003).

Communal rangelands cover nearly 6 million hectares and are home to an estimated 2.4 million rural households in South Africa (Shackleton *et al.* 2001). Millions of rural South Africans depend on the ecosystem services that these savannas provide (Higgins *et al.* 1999; Shackleton *et al.* 2001; Twine *et al.* 2003a). The vegetation in the communal rangelands plays a vital role in the livelihoods of the majority of these rural communities throughout South Africa through the resources that they provide (Dovie *et al.* 2004; Giannecchini *et al.* 2007; Pote *et al.* 2006; Shackleton and Shackleton 2004; Shackleton *et al.* 2005; Twine *et al.* 2003b; Twine 2005; Williams and Shackleton 2002). Not only do they support livestock, but they are also used by local communities for harvesting natural resources (Dovie *et al.* 2002; 2004; Twine 2005). The services and

goods provided include wood fuels, timber, fruits, wild herbs, mushrooms, honey, grazing for livestock, building materials, bush meat, shade, protection, and materials for household utensils, to name but a few (Arnold 1987; Higgins *et al.* 1999; Moe and Rackman 1992; Pote *et al.* 2006; Shackleton 1996; Shackleton 2004; Shackleton *et al.* 2002; Twine 2005).

Harvesting of these natural resources is a land-based livelihood strategy which allows for both daily usage and income generation during times of unemployment and financial difficulties (Giannecchini *et al.* 2007; Shackleton *et al.* 2005; Twine 2005). The use of natural resources is not restricted to poor households, as is commonly believed (Madubansi and Shackleton 2007; Shackleton and Shackleton 2006; Twine *et al.* 2003a). The only difference found by Twine *et al.* (2003a) between poor and wealthy households is the level of reliance on the resources. Poor households rely more on fuelwood as their main fuel source whereas wealthier households will rely on both fuelwood and other different types of fuel resources such as paraffin, candles, gas, coal, dry cell batteries, dung, lead acid batteries and some electricity (Arnold 1987; Madubansi and Shackleton 2007). The rural communities rely on the natural resources as it acts as a buffer against poverty as these resources are used either for domestic purposes or to generate an income (Dovie *et al.* 2004; Twine *et al.* 2003a).

There is a need for more detailed information on how woody composition and structure changes across both environmental variables and anthropogenic disturbances across time. With extensive research already done on tree composition and structure in savannas, the background for this project is well established and will allow for comparison of change over time with regards to selected environmental factors and anthropogenic disturbances (Brotherson 1999; Shackleton *et al.* 1994; Vazquez and Givnish 1998; Witkowski and O'Connor 1996). Limited research has been done on both the interactions between anthropogenic disturbance and environmental determinants of woodland composition and structure within communal rangelands (Dahlberg 2000; Shackleton *et al.* 1994).

Bushbuckridge is an excellent study area as there is a large amount of information in the literature on natural resource harvesting, tree coppicing and environmental factors and their role on tree community composition and structure. By increasing the understanding of the role of environmental factors in combination with the human

impacts on woody vegetation, management strategies can be established to ensure that sustainable usage occurs. By determining composition and structure of woody vegetation in these systems over time, the role of environmental factors in combination with human impacts provide insights that will be useful for resource management of these systems. Useful information that this study will be able to provide include identifying key conditions for the provision of tree-based resources, or identifying communities or areas in the landscape that may be less resilient to human impacts than others. This information is also useful for refining resource supply models, which often generalize over a range of local environmental conditions. By managing resource harvesting and ensuring sustainable reproduction of tree communities, their sustainability can be ensured for future generations (Dovie *et al.* 2004; Van Gelder *et al.* 1983).

Another important contribution to science is that it provides detailed data on structure of vegetation of smaller size classes, i.e. trees <2.0 m in height, to the existing Light Detection and Ranging (LiDAR) cover data for the study area (Fisher *et al.* 2012). LiDAR cannot detect the smaller size classes and thus this study will contribute information on the importance of the smaller size classes to vegetation structure within this area. This study will also add valuable knowledge in the science community with regards to the conservation and management of areas that are of vital importance for both humans and nature (Pote *et al.* 2006). The study will also determine if the catenal position and rainfall gradient are important in the trees chosen for harvesting. This might also help future management plans to ensure the sustainability of selected preferred species and selected environmental factors at a landscape scale (Van Gelder *et al.* 1983; Williams and Shackleton 2002). The project will thus be a way to bridge the lack of data available on environmental factors involved with harvesting fuelwood.

This study forms part of a larger long-term livelihoods and environment monitoring project called SUCSES ("Sustainability in Communal Socio-Ecological Systems"). SUCSES in the larger part aims at understanding the complex relationships between rural livelihoods and the surrounding environment. This is mainly achieved through linking household livelihood surveys with monitoring of the surrounding herbaceous and woody vegetation around the study villages. The study reported here focuses on the woody vegetation component around the study villages. By monitoring the woody vegetation on an annual basis, this study was able to determine whether environmental variables or anthropogenic disturbances account more for the change in

structure and composition. This study focused on the individual and interactive influences of rainfall and catenal position on woody vegetation composition and structure across time (2011-2013) in human-impacted woodlands, and will thus contribute to understanding these interactions. This study will also provide status, determinants and changes of woody vegetation composition and structure in these communal lands.

1.2 LITERATURE REVIEW

1.2.1 Environmental determinants of vegetation structure and composition

The main environmental determinants of vegetation structure and composition, of interest for this study, are water and nutrients, which are shaped by rainfall (climate) and soil (geology). Fire and herbivory are also environmental determinants (Colgan *et al.* 2012; Kanniah *et al.* 2010; Shackleton 1999; Witkowski and O'Connor 1996), but are mainly driven by humans within communal rangelands and are thus dealt with in the next section as anthropogenic disturbances. Woody vegetation structure and composition may be driven to a greater extent by a certain environmnmetal factor than by other factors (rainfall, temperature, soil, etc.) in any one place, but all factors have an influence in combination to produce differences in structure and composition (Coughenour and Ellis 1993). The study by Coughenour and Ellis (1993) found that canopy cover was mainly driven by rainfall, tree height mainly by drainage water subsidies, and species composition mainly by substrate and elevation (Coughenour and Ellis 1993). It is thus clear that a combination of all factors is of importance if one is to establish the reason(s) for change within a savanna ecosystem (Belsky 1990; Colgan *et al.* 2012; Coughenour and Ellis 1993; Kanniah *et al.* 2010; Shackleton 1999; Walker 1987 in Colgan *et al.* 2012; Witkowski and O'Connor 1996).

Geology plays a key role in determining savanna vegetation composition and structure (Coughenour and Ellis 1993; Fisher *et al.* 2009; Kanniah *et al.* 2010; Shackleton 1999; Witkowski and O'Connor 1996). The role of geology in savanna composition and structure is of vital importance as different woody vegetation is found on different geology types (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Mathieu *et al.* 2009; Parsons *et al.* 1997; Witkowski and O'Connor 1996). Mathieu *et al.* (2009) also found different geology types to have an influence on the structure of woody vegetation. The two major geological formations in the Lowveld (Mpumalanga Province, South Africa) are basalt and granite (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Scholes and Walker

1993; Helm & Witkowski 2012). Granite gives rise to soils with higher sand content, usually nutrient poor, while soils derived from basalt are usually black or red clay soils which contain higher nutrient contents (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Helm *et al.* 2009; Witkowski and O'Connor 1996).

Savannas consist of catena sequences, which generally have distinct upland and bottomland vegetation (Colgan *et al.* 2012; Parsons *et al.* 1997; Scholes and Walker 1993; Witkowski and O'Connor 1996). A catena can be defined as a topographic sequence of soils, of the same age and usually on the same parent material, which is repeated across larger landscape transects. Individual soil-profile types are related to site conditions and to position on a slope. The term was introduced in East Africa in the 1930s, and is mainly applicable in certain non-glaciated landscapes, particularly those with small, hilly relief (Allaby 2010). More studies have been done on granitic catenal sequences than basaltic catenal sequences (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997; Scholes and Walker 1993; Witkowski and O'Connor 1996). The contrasts in soil type along the catena are greater in granitic landscapes (Colgan *et al.* 2012). In South Africa, the soil composition in granitic landscapes differs and results in two distinguishable vegetation structures (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997). The hill crest area has a species composition that is adapted to the deep sandy soil and that is uniquely different from the bottomland species composition which is adapted to the sodic clay soil (Colgan *et al.* 2012; Dzerefos *et al.* 2003). On the hill crests, the vegetation structure is dominated by broad leaved tree species, such as *Combretum* spp., *Diospyros mespiliformis*, *Peltophorum africanum*, *Terminalia sericea* and *Sclerocarya birrea* (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997; Witkowski and O'Connor 1996). The bottomlands are often dominated by fine leaved trees such as *Acacia* spp., *Dichrostachys cinerea*, *Albizia harveyi*, *Euclea* spp. and *Gymnosporia* spp. (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997; Witkowski and O'Connor 1996). The change in composition and structure can be seen when moving along the catena or gradient as the vegetation structure changes from a predominantly broadleaf species composition to a predominantly fine leaf species composition with a visible seep line in between (Colgan *et al.* 2012) after a fringe of *Terminalia sericea* on the upslope position of the seep line. The catenal sequence of basaltic landscapes in South Africa, are less obvious in structural change due to the small change in the gradient (Colgan *et al.* 2012).

The typical savanna experiences strong seasonal climatic conditions, having wet, hot summer periods and dry, warm winter periods, with rainfall being largely unpredictable and variable in each year (Hester *et al.* 2006). Savannas are limited by water to some extent (Colgan *et al.* 2012; Scholes and Archer 1997). Water limits vegetated growth by 40% on a global scale and thus the availability of water is one of the key environmental determinants, not only in savannas but globally as well (Kanniah *et al.* 2010; Nemani *et al.* 2003). The availability of water is dependent on the annual rainfall, infiltration capacity, soil composition and texture (Kanniah *et al.* 2010). Various studies found that the higher rainfall will result in higher vegetation densities (Buitenwerf *et al.* 2012; Sankaran *et al.* 2005; Shackleton and Scholes 2011; Smith and Goodman 1986). Shackleton and Scholes (2011) also found that the stem diameter, height of trees and number of species were higher with the higher availability of water.. High rainfall and low fire intensity can lead to bush encroachment whereas low rainfall can lead to the mortality of seedlings (Govender *et al.* 2006; Hoffman & Solbrig 2003; Roques *et al.* 2001). In terms of seed recruitment, high rainfall can allow more seedlings to survive, if grazing and fire intensity is low (Govender *et al.* 2006; Hoffman & Solbrig 2003; Roques *et al.* 2001). On a long-term scale, rainfall is important for the co-existence of grasses and trees (Hoffman & Solbrig 2003; Roques *et al.* 2001; Sankaran *et al.* 2005; Scholes and Archer 1997; Shackleton and Scholes 2011).

1.2.2 Anthropogenic disturbance

Anthropogenic disturbance or human disturbance can be divided into direct and indirect human impacts. Direct impacts includes fire and harvesting of natural resources, whereas indirect impacts include grazing of livestock, and invasion by alien species (Arnold 1987; Dovie *et al.* 2004; Foxcroft *et al.* 2010; Giannecchini *et al.* 2007; Higgins *et al.* 1999; Moe and Rackman 1992; Pote et al. 2006; Shackleton 1996; Shackleton 2004; Shackleton *et al.* 2002; Shackleton *et al.* 2005; Rodger and Twine 2002; Twine *et al.* 2003b; Twine 2005; van Wilgen *et al.* 2004; Williams and Shackleton 2002; Vila and Ibanez 2011; Vila *et al.* 2011). The focus for this study in terms of disturbance was on wood harvesting.

1.2.2.1 *Fuelwood harvesting*

The primary energy source in rural households in South Africa is fuelwood (Dovie *et al.* 2004; Giannecchini *et al.* 2007; Kaschula *et al.* 2005; Shackleton *et al.* 2005; Twine 2005; Williams and Shackleton 2002). Fuelwood production is one of the

many important roles of trees within communal rangelands across the globe (Arnold 1987; Madubansi and Shackleton 2007; Sande 2003). Nearly 50% of all wood production is used as fuelwood in the majority of developing countries (Van Gelder *et al.* 1983). In developing countries, fuelwood is the primary energy source within households and is one of the many important resources to rural communities (Arnold 1987; Dovie *et al.* 2004; Madubansi and Shackleton 2007). Households continue to use fuelwood as the primary energy source, even though electricity is available as a substitute (Dovie *et al.* 2004; Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013). This is mainly because fuelwood harvested from surrounding woodlands provides a free or cheap energy source to households that does not require the use of expensive appliances (Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013). Various studies found that even where communities were supplied with electricity, the use of fuelwood is still widespread as the cost of electrical appliances and electrical power is unaffordable (Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013).

All wood collected in South Africa in the past was generally dead wood, with little preference to species but in more recent years live trees are being increasingly harvested as dry wood is scarce or absent from surrounding areas (Kirkland *et al.* 2007; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Wessels *et al.* 2011; Wessels *et al.* 2013; Williams and Shackleton 2002). The preference of the size structure of trees to be harvested is dependent on the use of the harvested wood (Shackleton 2001). The preferred stem sizes are between 1.1-10 cm in diameter that is easy to use for daily cooking and heating needs, and which is easy to transport in bundles on foot (usually headloads) (Dovie *et al.* 2004; Neke *et al.* 2006; Van Gelder *et al.* 1983). Various studies (Giannecchini *et al.* 2007; Shackleton 1993; Twine *et al.* 2003b) state that the lack of harvesting of large fruit-bearing species is due to the local law that forbids it. However, Kirkland *et al.* (2007) found a contradiction in this statement in their study, as people are harvesting fruit-bearing trees despite the local laws due to acute wood shortages in some areas. The demand for fuelwood is often determined by the human population size that uses the resource (Banks *et al.* 1996; Coetzer *et al.* 2010; Fisher *et al.* 2011; Matsika *et al.* 2013a). Harvesting of larger size classes is becoming more apparent in the rangelands. The increase in harvesting of larger trees and fruit bearing trees is possibly be due to the depletion of wood on the village periphery (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.*

2013a; Shackleton 2004). The increase in large trees harvesting is possibly due to the development of rural and urban fuelwood markets (Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton *et al.* 2006). Rural households increasingly buy fuelwood due to the shortage of dead wood within surrounding rangelands (Madubansi and Shackleton 2007; Matsika *et al.* 2013a). Harvesting for these markets are often on a large scale as harvesters have access to motor-vehicles and mechanized equipment (Matsika *et al.* 2013a; Shackleton *et al.* 2006). This type of harvesting allows for larger live trees to be harvested (Matsika *et al.* 2013a; Shackleton *et al.* 2006).

Fuelwood harvesting of live wood has an impact on the ecosystem (Jurisch *et al.* 2012; Pote et al. 2006; Shackleton *et al.* 2007). The most noticeable change at the community level is the change in physiognomy by the removal of certain size classes of trees and the increased production of coppice regrowth (Higgins *et al.* 1999; Twine 2005). The structure of the most utilized species populations has become characterized by a decline in large mature stems and an increased abundance of smaller stems (Jurisch *et al.* 2012; Higgins *et al.* 1999; Kaschula *et al.* 2005; Twine 2005). Harvesting and resprouting results in sexually mature individuals reverting to a functionally juvenile growth phase (Kaschula *et al.* 2005; Twine 2005). The reverting back to a juvenile growth phase reduces the production of seed by mature trees (Kaschula *et al.* 2005; Twine 2005). Most savanna tree species have the ability to produce coppice regrowth if stems are damaged or killed (Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). The removal of stems alleviates some of the impacts of fuelwood harvesting by producing coppice regrowth (Twine 2005). The increased cutting of live stems and widespread coppice regrowth has changed the tree morphology of many woody species (Higgins *et al.* 1999; Twine 2005).

1.2.2.2 Timber harvesting for building

Trees provide resources other than fuelwood (Cousins 1999; Dovie *et al.* 2002; Twine 2005). They also produce poles for building and fencing (Cousins 1999; Dovie *et al.* 2002; Twine 2005). Dovie *et al.* (2002) found 57% of households use indigenous housing poles for building purposes. Poles are used for either roofs or walls or a combination of both (Dovie *et al.* 2002). Traditional structures (huts, granaries, fences, kraals) are mainly built by use of indigenous poles (Makhado *et al.* 2009). Dovie *et al.* (2002) also found that 33% of households, in the village Thorndale, use indigenous wooden poles for livestock kraals whereas Hansen (1998) found that 53% of households

across the whole Bushbuckridge uses poles made from both indigenous and exotic species,for fencing and livestock pens. Live stems are generally cut for the use of poles (Banks *et al.* 1996; Hansen 1998).

1.2.2.3 Harvesting of wood for utensils and crafts

Other important resources provided by trees are household utensils and implements which include spoons, bowls, mortars, pestles, axe handles, hoe and pick handles (Dovie *et al.* 2002; Shackleton and Shackleton 2000, Twine 2003a). These household utensils are used by 29% of communities (Hansen 1998). It was found however that wealthy households used more wooden utensils and poles than poor households (Twine *et al.* 2003a). Some of these utensils have become commercialized, similar to crafts that are carved from wood. This practice of carving has been increasing as it is a tradition that is passed on from father to son within rural communities (Makhado *et al.* 2009). Other than the tradition being passed down over generations, commercialization of utensils and crafts has also increased (Makhado *et al.* 2009; Shackleton and Shackleton 2004). The harvesting of wood for this practice requires a substantial amount of wood (Makhado *et al.* 2009; Shackleton and Shackleton 2004) which can lead to the decrease in species diversity, abundance and existence (Belcher and Schreckenberg 2007; Klooster 2002; Shackleton 2004; Williams *et al.* 2000).

1.2.2.4 Edible fruit harvesting

The majority of African rural communities eat and trade fruits collected in the rangelands (Cousins 1999; Makhado *et al.* 2009; Shackleton 2003; Twine 2005). With a variety of different species, fruits are available during most seasons of the year (Dovie *et al.* 2002; Makhado *et al.* 2009). Twine *et al.* (2003a) and Shackleton (2003) found poor households rely more on the availability of fruit for survival than richer households. With some fruit having the ability to be dried, made into jam or brewed into beer (Shackleton *et al.* 2000; Twine 2005), a number of resources are provided to the community. With 81% of households using fruit (Twine 2005) and with the majority of additional studies finding most households both collect and buy fruits, harvesting of these resources are seen to be of vital importance for the livelihoods of rural communities (Cousins 1999; Dovie *et al.* 2002; Makhado *et al.* 2009; Shackleton and Shackleton 2004; Shackleton *et al.* 2002; Shackleton *et al.* 2000; Twine *et al.* 2003a).

The harvesting of fruit and seed can have both positive and negative impacts on the existence of the selected species (Shackleton *et al.* 2005; Shackleton *et al.* 2000). The positive impact is that seeds are dispersed but the negative impact is the recruitment of seedlings can be reduced or prohibited (Shackleton *et al.* 2005). The recruitment of trees is thus impacted if both fruits and seeds are not harvested sustainably (Shackleton *et al.* 2005). The removal of all fruit and seeds when harvesting could results in the limited or absence of new recruitment of seedlings which could lead to the local extinction of the species (Shackleton *et al.* 2005).

1.2.2.5 Grazing and fire

Grazing (including browsing) and fire are large-scale disturbances within savannas (Archibald *et al.* 2005; Noy-Meir 1995; Scholes 2009; Scholes and Archer 1997; Scholes and Walker 1993). Both fire (Fisher *et al.* 2009; Govender *et al.* 2006; Noy-Meir 1995; Scholes and Archer 1997; Scholes and Walker 1993; Snyman 2003; Snyman 2004; Uys *et al.* 2004; Wessels *et al.* 2011) and grazing (Fisher *et al.* 2009; Govender *et al.* 2006; Hejcmanova *et al.* 2009; Scholes and Archer 1997; Scholes and Walker 1993; Wessels *et al.* 2011; Zedler 2007) are seen as determinants of vegetation structure and composition within the grass and woody communities.

Fire is an important driver of species composition and structure within savannas (Archibald *et al.* 2005; Govender *et al.* 2006; Hoffman & Solbrig 2003; Scholes 2009; Scholes and Archer 1997; Scholes and Walker 1993). In the absence of fire, savannas have the possibility to become closed woodlands (bush encroachment), whereas with to frequent occurrence, savannas have the possibilities to become grasslands (Archibald *et al.* 2005; Hoffman & Solbrig 2003; Govender *et al.* 2006; Roques *et al.* 2001; Scholes 2009; Scholes and Archer 1997). Understanding this co-existence of trees and grasses is important for the management of savannas (Hoffman & Solbrig 2003; Govender *et al.* 2006; Scholes and Walker 1993; Trollope 1974). Fire intensity is an important determinant in the mortality of trees and recruitment of trees into larger size classes (Archibald *et al.* 2005; Chidumayo 2013; Govender *et al.* 2006; Higgins *et al.* 2000; Lehmann *et al.* 2009; Trollope 1974). Recruitment of trees is thus limited by the survival of seedlings (Chidumayo 2013; Govender *et al.* 2006; Higgins *et al.* 2000; Lehmann *et al.* 2009; Trollope 1974). As the seedling stage is the most vulnerable stage in the life cycle of trees, the survival of this stage is important for the existence of trees within savannas (Chidumayo 2013). Trees in savannas are only recruited to large size classes

once they have escaped the zone which is influenced by grass fires, the zone known as the “fire-trap” (Chidumayo 2013; Higgins *et al.* 2000). Seedlings are often killed by fire as they fall within the “fire-trap” zone, which is created by grass and the biomass produced by grass (Chidumayo 2013; Govender *et al.* 2006; Higgins *et al.* 2000; Trollope 1974). The small trees that do survive fires have the possibility to produce coppice regrowth (Higgins *et al.* 2000; Hoffman & Solbrig 2003; Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). This ability to produce coppice regrowth is often the key life-history trait that ensures the persistence of trees within savannas (Chidumayo 2013; Higgins *et al.* 2000; Govender *et al.* 2006). Large trees survive fires due to their thick bark (Chidumayo 2013; Higgins *et al.* 2000; Hoffman & Solbrig 2003).Unless these smaller trees produce thicker bark to withstand fires they will be unable to survive. Similarly,unless smaller trees have faster growth rates, they will be unable to produce seeds due to lack of sexual maturity (Chidumayo 2013; Higgins *et al.* 2000; Hoffman & Solbrig 2003; Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005).

Mature trees have a strong suppressive effect on grasses, while grasses have a weak direct effect on mature trees (Scholes 2009). Grasses are known to have a strong competitive effect on tree seedlings and the establishment of seedlings (Scholes 2009). If the grasses are too vigorous, the seedlings are unable to establish and are thus killed (Scholes 2009). The effects of a vigorous and dense grass component on tree seedlings (and their establishment) is also impostant form competitive balance between trees and grasses.The competitive effect of grasses on trees is mainly indirectly through fire, as more intense fires result in tree seedling/sapling mortality (Hoffman & Solbrig 2003; Govender *et al.* 2006; Scholes 2009; Scholes and Archer 1997; Trollope 1974; Zedler 2007). The occurrence of fire in dry season results in establishing trees being damaged or killed, while the grasses are unharmed as regenerative tissues are stored below ground (Scholes 2009; Scholes and Archer 1997; Zedler 2007). As fire needs grass biomass to occur, grazing can reduce the occurrences and intensity of fire to an extent (Archibald *et al.* 2005; Scholes 2009; Snyman 2003; Snyman 2004; Uys *et al.* 2004; Zedler 2007). Grazing reduces biomass, which in turn leads to a decrease in fuel load for fires, which can result in fire being rare or absent, as in the case of rangelands (Scholes 1990; Scholes 2009; Zedler 2007).

The combination of fire and grazing leads to less tree seedlings being killed as a result of the reduced fuel load. This change in the competitive effect of grasses on trees

allows for bush encroachment to occur (Hester *et al.* 2006; Scholes and Archer 1997; Ward 2005). Grazing reduces not only the grass biomass that is necessary to fuel fire occurrence and intensity but also the competition for resources such as light and water, which suppress the establishing of seedlings (Hester *et al.* 2006; Scholes 2009; Scholes and Archer 1997; Ward 2005; Zedler 2007). As seedlings are not being killed by fire (Chidumayo 2013; Hester *et al.* 2006; Higgins *et al.* 2000; Lehmann *et al.* 2009; Govender *et al.* 2006; Trollope 1974), and the competition for light and water from the herbaceous layer has been decreased due to heavy grazing, bush encroachment occurs resulting in a closed woodland (Hester *et al.* 2006; Scholes and Archer 1997; Ward 2005). Heavy grazing or over grazing does not only change the competition between trees and grasses, but also the competition between palatable and unpalatable grasses (Hester *et al.* 2006; Scholes and Archer 1997; Ward 2005). The reduction in competition caused by the increase of preference from grazers results in the change of dominant species (Hester *et al.* 2006; Scholes 2009; Zedler 2007). Selective feeding results in a change in species composition of palatable and unpalatable grasses (Scholes 2009). The grasses change from dominant perennial grasses which are mostly palatable, to unpalatable perennial and annual grasses (Archibald *et al.* 2005; Scholes 2009; Scholes and Archer 1997; Skarpe 1991; Skarpe 1992; Zedler 2007). The livestock commonly found within communal rangelands include both cattle and goats (Shackleton *et al.* 2001) and cattle tend to be more selective feeders than goats (Carmel and Kadmon 1999). The survival of seedlings and coppice shoots at ground level is reduced due to the presence of goats.

1.2.2.6 *Alien invasives*

Alien plant species are seen as a growing threat on indigenous plant species on both local and global scales (Berry *et al.* 2011; Sahid and Sugua 1993; van Wilgen *et al.* 2004; Vardien *et al.* 2012; Versfeld *et al.* 1998). The invasion of *Lantana camara* L. across South Africa found, based on findings by Vardien *et al.* (2012), that *L. camara* had invaded between 25,000 and 30,000 hectares of land 1962 (Stirton 1977; Wells and Stirton 1988) and a total area of two million hectares by 2000 (Le Maitre *et al.* 2000; Versfeld *et al.* 1998) and is especially abundant in the Lowveld (Versfeld *et al.* 1998; Rodger and Twine 2002). *L. camara* does not only alter ecosystem function but is also detrimental to livestock farming (Berry *et al.* 2011; Ghisalberti 2000; Morton 1971; Pass 1991; Rodger and Twine 2002; Sahid and Sugua 1993). The altering of ecosystems

occurs by changing the fire regime and nutrient cycling of surrounding area (Berry *et al.* 2011; Rodger and Twine 2002; Vila *et al.* 2011). The impacts on this invasive species for livestock include the loss of grazing areas as well as the possible loss of the livestock itself, if grazed on by livestock (Ghisalberti 2000; Morton 1971; Morton 1994; Pass 1991; Rodger and Twine 2002; Sahid and Sugua 1993). This species is known to thrive in disturbed area such as heavy grazing area where disturbance takes place through trampling, biomass removal and fertilisation (Berry *et al.* 2011; Rodger and Twine 2002; Sharma *et al.* 2005a,b; Sharma & Raghubanshi 2007; Vardien *et al.* 2012). It has strong allelopathic properties, which allows it to interrupt the regeneration process of other plant species by decreasing germination, reducing early growth rates and selectively increasing mortality of other plant species (Berry *et al.* 2011; Sahid and Sugua 1993; Sharma *et al.* 2005a,b;Sharma & Raghubanshi 2007). This leads to a reduction of species diversity (Berry *et al.* 2011; Sharma & Raghubanshi 2007).

Within the communal rangelands of Bushbuckridge, *L. camara* occurs mainly in thick clumps under trees (Rodger and Twine 2002). Both birds and mammals are known to disperse the seeds of *L. camara* (Rodger and Twine 2002; Vardien *et al.* 2012). This clumped effect can be due to the lower density of large mature trees within the communal rangelands resulting in the perching and roosting sites being limited to individual trees (Rodger and Twine 2002). The invasion of *L. camara* can also be seen as a form of bush encroachment due to it being avoided for fuelwood and is known to be resistant to herbivores (Rodger and Twine 2002; Sharma & Raghubanshi 2007). This allows the species to become persistent resulting in bush encroachment (Rodger and Twine 2002; Sharma & Raghubanshi 2007). Once encroachment has occurred, the natural fire regime is altered as *L. camara* reduces the grass biomass that is required for the occurrence of fire (Sahid and Sugua 1993; Rodger and Twine 2002; Sharma & Raghubanshi 2007).

1.2.3 Sustainable harvesting

The harvesting of natural resources (fuelwood in particular), has an impact on both human livelihoods and the ecosystem and must therefore occur in a sustainable way (Pote et al. 2006; Shackleton *et al.* 2007; Von Maltitz and Scholes 1995). When the rate of wood production is equal to the rate of wood harvesting, harvesting can be defined as sustainable (Von Maltitz and Scholes 1995). The rate of fuelwood harvesting is often driven by the demand of the resource, which is seen in various cases to be driven by human population size (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and

Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Von Maltitz and Scholes 1995; Williams and Shackleton 2002). Between 1972 and 1994, the Bushbuckridge human population density has doubled from 150 people km^2 to 300 people km^2 (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). With the increase in human population size and the scarcity of fuelwood from surrounding rangelands, the existence of fuelwood markets is fast becoming a part of daily live as it ensures fuelwood for daily usage such as cooking (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Williams and Shackleton 2002). Rural households increasingly buy fuelwood due to the shortage of dead wood within surrounding rangelands (Madubansi and Shackleton 2007; Matsika *et al.* 2013a). Harvesting for these markets are often on a large scale as harvesters have access to motor-vehicles and mechanized equipment (Matsika *et al.* 2013a; Shackleton *et al.* 2006). This type of harvesting allows for larger live trees to be harvested (Matsika *et al.* 2013a; Shackleton *et al.* 2006). The existence of these fuelwood markets on the positive side, provides availability of fuelwood to local communities but on the negative side, they have been found to be driven by harvesting of live, large, fruit-bearing trees which are vitally important in the functioning of ecosystems (Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Von Maltitz and Scholes 1995; Williams and Shackleton 2002).

With the harvesting of large fruit-bearing trees, a change in vegetation structure is occurring (Higgins *et al.* 1999; Kaschula *et al.* 2005; Neke *et al.* 2006; Twine 2005). The most noticeable change in vegetation structure is the increase of coppice regrowth production (Higgins *et al.* 1999; Twine 2005). Savanna tree species have the ability to produce coppice regrowth if stems are damaged or killed (Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). The impacts of the removal of stems are thus alleviated in a sense that the coppice regrowth grows faster than old stems (Twine 2005). The tree morphology of many woody species has changed by the increased cutting of live stems and widespread coppice regrowth (Higgins *et al.* 1999; Twine 2005). The structure of the most utilized species and their populations has become characterized by a lack of large mature stems and an increased abundance of smaller stems (Higgins *et al.* 1999; Kaschula *et al.* 2005; Twine 2005). The coppiced adult trees are increasingly becoming more juvenile in function as there is no production of seeds (Kaschula *et al.* 2005; Twine

2005). This type of harvesting is not only unsustainable in the long term, but will have devastating effects on both local communities and the surrounding ecosystems and their functioning (Von Maltitz and Scholes 1995).

Various techniques are used to attempt the management of sustainable wood harvesting. These techniques vary between pollarding, coppicing and pruning (Arnold 1987). These techniques help to obtain a sustainable yield of wood or fodder for a longer period of time (Arnold 1987). Pollarding is a tree management technique where the top branches of a tree are cut off, which encourages growth of new branches (Musvoto *et al.* 2006; Sande 2003) where as coppicing is a technique where trees with one or more trunks, have stems cut to produce the regrowth of new shoots (Kaschula *et al.* 2005; Sande 2003). Coppicing usually occurs near ground level and pollarding occurs in the top branches (Kaschula *et al.* 2005). Pollarding is a more sustainable way of fuelwood harvesting than coppicing in the rural rangelands because partially-pollarded trees still have the ability to produce fruit and reproduce sexually. Fruits are both an ecological and social importance within rural communities as edible fruits are a part of local diet and nutrition (Shackleton 2004). In cases where the stems of fruit trees are harvested, the harvesting is mutually exclusive between the harvesting of edible fruits and fuelwood (Shackleton 1996). Partially-pollarded trees allow these two uses to be compatible. Trees that were coppiced and felled can take up to ten years to reach a status where production of fruit is reached (Twine 2005). Resprouting shoots produced by coppicing is non-sexual reproduction as all shoots are genetically identical to each other (Bellingham and Sparrow 2000). This means that no new genetic variation is obtained as in the case of sexual reproduction (seed production). Another reason why pollarding is a more sustainable method of harvesting, is because the shoots are out of reach of goats and fire which will normally reduce the survival of the shoots when exposed to these damages. This is thus a more desirable outcome than that produced by coppice, where the shoots are subject to these types of damage (Kaschula *et al.* 2005; Neke *et al.* 2006).

By assessing the sustainability of current harvest levels, Banks *et al.* (1996) predicted that the available woody standing stocks around the Bushbuckridge villages of Athol and Welverdiend, and the supply of wood is insufficient to meet current demands under current population growth rates. This was found to be upheld in the study by Matsika *et al.* (2013) with the only difference being that the complete loss of woodlands in Welverdiend, as predicted by Banks *et al.* (1996) has yet to occur. Both these studies

did however establish that the current available woody standing stock is insufficient and that this will result in harvesting of live trees of larger size classes (Banks *et al.* 1996; Matsika *et al.* 2013). It is clear that the harvesting of these resources have an impacts on human livelihoods and on vegetation structure as well as on the function of ecosystems, and therefore harvesting must occur in a sustainable way to ensure future availability of services and the selected resources (Kusters et al. 2006; Mutenje *et al.* 2011; Pote et al. 2006; Shackleton *et al.* 2007; Shackleton *et al.* 2002; Ticktin 2004; Von Maltitz and Scholes 1995).

1.3 AIM, OBJECTIVES AND KEY QUESTIONS

The aim of this study is to determine the individual and interactive influences of rainfall and catenal position on woody vegetation composition and structure across time (2011-2013), in human-impacted woodlands. The four objectives of the study, with associated research questions, were:

1.3.1 Objective 1: Determine how woody vegetation density and structure differ along a rainfall gradient and between catenal positions in a human-impacted landscape across time (addressed in Chapter 2)

- How does density and structure change over time (2011-2013), ignoring effects of rainfall zone and catenal position?
- How does density and structure differ across rainfall zones over time?
- How does density and structure differ across catenal positions over time?
- How does density and structure differ across a combination of rainfall zones and catenal positions over time?

1.3.2 Objective 2: Determine how the density and structure of woody vegetation differs along rainfall and catenal (environmental) gradients for harvested and unharvested trees from 2011 to 2013 in the woodlands of Bushbuckridge, Mpumalanga Province (addressed in Chapter 3)

- How does woody vegetation density and structure of harvested species differ over time?
- How does woody vegetation density and structure of harvested species differ across rainfall zones over time?

- How does woody vegetation density and structure of harvested species differ across catenal positions over time?
- How does woody vegetation density and structure of harvested species differ across a combination of rainfall zones and catenal positions over time?

1.3.3 Objective 3: Determine how species richness, diversity and evenness of woody vegetation differ over time along rainfall and catenal gradients. Secondly, to assess the species richness, diversity and evenness of tree species that were harvested (addressed in Chapter 4)

1.3.3.1 Determine how species species richness, diversity and evenness differ between rainfall zones and catenal positions

- How do species richness, diversity and evenness change over time in general?
- How does species richness, diversity and evenness differ between rainfall zones while controlling for time by assessing three different time periods?
- How does species richness, diversity and evenness differ between catenal positions while controlling for time by assessing three different time periods?
- How does species richness, diversity and evenness differ between a combination of rainfall zones and catenal positions while controlling for time by assessing three different time periods?

1.3.3.2 Determine how species richness, diversity and evenness differ across rainfall zones and catenal positions when only focusing on the harvested species

- How do species richness, diversity and evenness of harvested species differ over time?
- How do species richness, diversity and evenness of harvested species differ across rainfall zones over time?
- How do species richness, diversity and evenness of harvested species differ across catenal positions over time?
- How do species richness, diversity and evenness of harvested species differ across a combination of rainfall zones and catenal positions over time?

1.3.4 Objective 4: Determine how woody plant species composition changes across a rainfall gradient and with catenal position for harvested and unharvested trees in a human-impacted landscape over time (addressed in Chapter 5)

- How does species composition differ in response to environmental variables (a rainfall gradient and catenal position) and a disturbance gradient (harvesting intensity) in each of the study years (2011, 2012 and 2013)?
- How does species composition change in response to these environmental variables and the disturbance gradient over time (2011-2013)?

1.4 STRUCTURE OF DISSERTATION

The chapters of this dissertation, excluding the introductory and concluding chapters, have been written in a free-standing format for eventual submission to a scientific journal for publication. Chapters 2-5 of the dissertation are thus each structured in the form of papers, and hence there is unavoidable repetition in the introductions and other places. To minimize repetition, much of the methods in chapters 3-5 refer back to sections in chapter 2, similarly for the study site description. The literature review is primarily in context of the study area.

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2 Chapter 2: Change in woody vegetation density and structure in communal rangelands across catenal and rainfall gradients (2011-2013)

2.1 ABSTRACT

The structure and dynamics of savannas within communal rangelands are driven by environmental determinants and anthropogenic disturbances. Most research focuses mainly on the drivers of savanna change in areas where human impacts are largely excluded. The aim of this study was to determine how woody vegetation density and structure change across a rainfall gradient and catenal positions in human-impacted woodlands of Bushbuckridge, Mpumalanga Province. This study also assesses the relative importance of these two environmental factors, and the interactions between them. Three zones were selected that differed in annual rainfall: (a) wet west (>700mm), (b) mesic (600-700mm), and semi-dry east (<600m), with three villages per zone. For the rangeland of each village, plots were sampled in 2011, 2012 and 2013 to cover the upland and bottomland variations in catenal position. All trees >6m in height, and their individual stems, were counted and measured within a total of 56 circular plots (only 28 in 2011) each with a radius of 50m. Trees <6m, and their stems, were counted and measured in a circular plot with a radius of 6m, nested centrally within each 50m plot. Higher abundance of stems occurred in smaller tree height and stem diameter size classes compared to large trees. Small trees (<6m in height) had significantly higher densities than large trees (>6m) from 2011-2013. Small tree densities decreased from 2011 to 2013 whereas large tree densities did not change over time. Across time, woody vegetation density was similar between uplands and bottomlands, but was higher in the high rainfall zone than in the medium and low rainfall zones.

Keywords: Density, rainfall, rangelands, structure, topography

2.2 INTRODUCTION

The savanna regions in Africa are important landscapes, providing valuable services and resources to millions of people who depend on them for a daily way of life (Botha *et al.* 2004a; Dovie *et al.* 2002; Hassler *et al.* 2010; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Higgins *et al.* 2007; Jurisch *et al.* 2012; Scholes and Walker 1993; Shackleton *et al.* 2002; Twine *et al.* 2003a). In South Africa, savanna communal rangelands cover nearly 6 million ha and are home to roughly 2.4 million people (Shackleton *et al.* 2001). Differences in vegetation structure of savannas are driven by environmental determinants such as rainfall and soil but also by different land use practices, as seen in communal rangelands (Breshears and Barnes 1999; Colgan *et al.* 2012; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Shackleton *et al.* 1994; Shackleton 1999; Witkowski and O'Connor 1996).

Soil type plays a key role in determining savanna vegetation structure (Coughenour and Ellis 1993; Fisher *et al.* 2009; Kanniah *et al.* 2010; Shackleton 1999; Witkowski and O'Connor 1996). Savannas consist of catenal sequences which generally have distinct uplands and bottomlands, especially in granitic landscapes (Colgan *et al.* 2012; Parsons *et al.* 1997; Scholes and Walker 1993). A catena is defined as a topographic sequence of soils, of the same age and usually on the same parent material, which is repeated across larger landscape transects. Individual soil-profile types are related to site conditions and to position on a slope. The term was introduced in East Africa in the 1930s, and is mainly applicable in certain non-glaciated landscapes, particularly those with small, hilly relief (Allaby 2010). The granite landscapes have steeper gradients and greater contrasts in soil type along the catena than basalt landscapes (Colgan *et al.* 2012). Topographical locations are characterised by different soils. The different vegetation composition and structure is adapted to the different soils (Colgan *et al.* 2012). For hill crests on granitic soils (deep sandy soil), the vegetation structure is dominated by broad leaved trees whereas the bottom lands (soils with higher clay content and some sodic soils) are often dominated by fine leaved trees (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997; Witkowski and O'Connor 1996).

The typical savanna experiences strong seasonal climatic conditions, with rainfall being largely unpredictable and variable in each year (Colgan *et al.* 2012; Frost *et al.* 1986; Le Roux and Bariac 1998). Savannas are generally considered water-limited

systems. Water availability limits vegetation growth by 40% on a global scale, and the availability of water is thus one of the key environmental determinants, not only in savannas, but globally as well (Archibald and Scholes 2007; Colgan *et al.* 2012; Kanniah *et al.* 2010; Nemani *et al.* 2003; Scholes and Archer 1997; Smith and Goodman 1986). The availability of water is dependent on the annual rainfall, and infiltration and retention capacity of the soil (Kanniah *et al.* 2010). The density of woody vegetation in savannas increases with water availability in lower rainfall areas but this relationship disappears at higher rainfall levels (Sankaran *et al.* 2005; Shackleton and Scholes 2011; Smith and Goodman 1986). Mean stem diameter, tree height, and tree species richness has also been shown to increase with water availability in savannas (Shackleton and Scholes 2011).

Environmental determinants can have a larger influence on savanna ecosystems than anthropogenic disturbances in cases where harvesting is low (Dahlberg 2000; Wessels *et al.* 2011). With the possible interactions between anthropogenic disturbances and environmental determinants, the systems are often difficult to understand. Research on the drivers of savanna change has been done in a variety of landscapes, including many where human impacts were included, and others where human impacts were excluded (Belsky 1990; Colgan *et al.* 2012; Coughenour and Ellis 1993; Kanniah *et al.* 2010; Shackleton 1999; Walker 1987; Witkowski and O'Connor 1996).

This study aimed to determine how woody vegetation density and structure differ along a rainfall gradient and between catenal positions in a human-impacted landscape across time. This study also assessed the relative importance of these two environmental factors, and the interactions between them. This was determined by answering four questions. Firstly, how does woody vegetation density and structure change over time (2011-13), ignoring effects of rainfall zone and catenal position? Secondly, how does woody vegetation density and structure differ across rainfall zones over time? Thirdly, how does woody vegetation density and structure differ across catenal positions over time? Finally, how does woody vegetation density and structure differ across a combination of rainfall zones and catenal positions over time?

2.3 MATERIALS AND METHODS

2.3.1 Study site

The study was carried out in the communal rangelands of Bushbuckridge, a rural region in Mpumalanga Province, South Africa (31°0'-31°35'E; 24°30'-25°0'S). The area

is defined as the region between the Sabie River in the south and the Klaserie-Orpen road in the north, and between the Drakensberg escarpment in the west and the border with the Sabi-Sand Game Reserve and Kruger National Park in the east (Dovie *et al.* 2004; Kaschula *et al.* 2005). The area covers approximately 241 684 ha, the majority of which comprises rangelands (Dovie *et al.* 2004; Kaschula *et al.* 2005).

Bushbuckridge is a single rural local municipality but was part of the former Bantustan districts of Mhala in Gazankulu and Mapulaneng in Lebowa, under the *apartheid* system before democratic change in 1994 (Giannecchini *et al.* 2007). Between 1972 and 1994, the Bushbuckridge human population density has doubled from 150 people km^2 to 300 people km^2 (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). As all former homelands, the land tenure for this region is communal (Giannecchini *et al.* 2007; Madubansi and Shackleton 2007; Shackleton and Shackleton 2000). The local land use patterns are thus determined by the traditional leaders who are in authority over the land (Shackleton and Shackleton 2000)

Rainfall occurs mainly in the summer months (October to April), and mean annual rainfall ranges between 500mm in the east and 800mm in the west (Higgins *et al.* 1999; Kaschula *et al.* 2005; Giannecchini *et al.* 2007). Three rainfall zones, the wet west, the mesic mid and semi-dry east, were selected with three villages per zone. The typical rainfall for the west is more than 700 mm per year. For the mid zone, rainfall ranges between 700-600 mm per year and the dry zone has a rainfall of less than 600 mm per year.

The geology for the area is underlain by granitic gneiss with local intrusions of gabbro (Matsika *et al.* 2013b; Rutherford *et al.* 2006a, 2006b). The area consists of the typical savanna vegetation and characterized as Mixed Lowveld Bushveld with *Combretum* and *Terminalia* genera tree species as main dominating species (Matsika *et al.* 2013b; Rutherford *et al.* 2006a, 2006b).

2.3.2 Study design

2.3.2.1 The placement of sampling plots

In this study, all trees and shrubs were quantified in 56 sampling plots in 2012 and 2013. An initial 28 (spanning rainfall and catenal gradients) of the 56 plots had already been sampled in February and March in 2011, and these data were also used in the study. Sampling occurred in February and March in 2012 and 2013. All plots were

located at least 300m from the edge of a village and are not in cultivated land. All 56 sampling plots were randomly placed in pairs along catenal slopes across the three different rainfall zones, by using Geographic Information Systems (GIS). Stratification of catenal position placed the selected plots on either upslope position or bottom slope position. Distance between plots within pairs varied due to the variation in catenal length within the rangelands. Upslope plots were above the seepline, and bottom slope plots below the seepline (Colgan *et al.* 2012; Levick *et al*. 2010; Scholes and Walker 1993). In the GIS, an elevation of 10m above the nearest drainage line was used as the boundary between upslope and lower slope, as this tended to coincide with the elevation of seeplines. Stratification of rainfall zones placed the selected plot in one of three rainfall zones (low (<600mm), medium (600-700mm) and high (>700mm) rainfall). Geology of the selected area consists predominantly of granite with a gabbro dyke intrusion in the far eastern edge of the site.

Three villages were selected for each rainfall zone. Villages that utilize the rangelands in the high rainfall zone (wet west region) include Xanthia, Cunningmore B and Agincourt. Ireagh A, Ireagh B and Kildare A, B, C are the villages that utilize the rangelands in the medium rainfall zone (mesic mid region) and the rangelands in the low rainfall zone (dry east region) is utilized by the villages known as Justicia, Lillydale B and Huntington (Fig 2.1). For villages Ireagh B and Agincourt, 2 pairs of plots were sampled (n=4) per village. For villages Justicia, Lillydale B, Ireagh A and Xanthia, 3 pairs of plots were sampled (n=6) per village. For villages Huntington, Kildare A, B, C and Cunningmore B, 4 pairs of plots were sampled (n=8) per village. This resulted in 10 pairs of plots (n=20) being sampled for the dry east zone (Justicia, Lillydale B and Huntington) and 9 pairs of plots (n=18) being sampled for mesic mid (Ireagh A, Ireagh B and Kildare A, B, C) and wet west (Xanthia, Cunningmore B and Agincourt) zone (Fig 2.1).

2.3.2.2 Field sampling procedures

Circular plots were used for all woody vegetation sampling (Fig 2.2). Each plot consisted of a 6m radius plot nested within a 50m radius plot. The central point for both 6m plot and 50m plot was marked with a metal stake cemented into the ground and GPS co-ordinates were recorded. A fixed-point photograph was taken in a southerly direction, 2m north of the marker stake at 5mm focal length, so that the top of the stake is in the photograph allowing for future comparison.

All trees within the circular plot with radius of 6 m (area=113m^2) were recorded. The perimeter was marked by tying red tape or ribbon to tree branches along the perimeter. The perimeter of the 6m plot was determined using a Haglöf ultasonic distance meter (Haglöf DME 201 cruiser with 360° adaptor and T3 transponder, manufactured in Sweden). Trees larger than 6m in height were recorded in the 50m radius (area=7854m^2) plot. As large trees had lower densities compared to smaller trees, the sampling area was increased in order to track what happens to large trees over time. Whether a tree over 6m in height on the edge of the plot was included or excluded in the 50m radius plot was determined using a Nikon laser rangefinder. In cases where vegetation obscured line of sight from the mid-point of the plot, the distance of a tree from the centre marker was determined using a Garmin GPS (with the co-ordinates of the marker entered). The following was recorded, for every woody stem in both the 6m radius and 50m radius plots: 1) species, 2) height class ($\leq$0.5m, 0.6-1m, 1.1-2m, 2.1-4m, 4.1-6m, 6.1-8m, 8.1-10.0m, >10.0m), 3) whether or not there were signs of fruiting over the last year, 4) number of harvested and unharvested stems in the following diameter classes ($\leq$1cm (excluding new seedlings), 1.1-4.0cm, 4.1-10.0cm, 10.1-20.0cm, 20.1-40.0cm, >40.1cm) (diameter measured 30cm above ground), 5) evidence of coppicing and 6) evidence of branches harvested. If the plot showed signs of recent or previous burning, it was also noted. Harvested stems were defined as any stems with signs of recent (less than 12 months old) cutting or removel of stems from the selected tree. If cuttings were more than 12 months old, it was excluded due to possiblity of being recorded in the previous year. Cutting refers to stems that showed a cut that is smooth and has no ragged edges (clean cut) as in the case of broken branches.

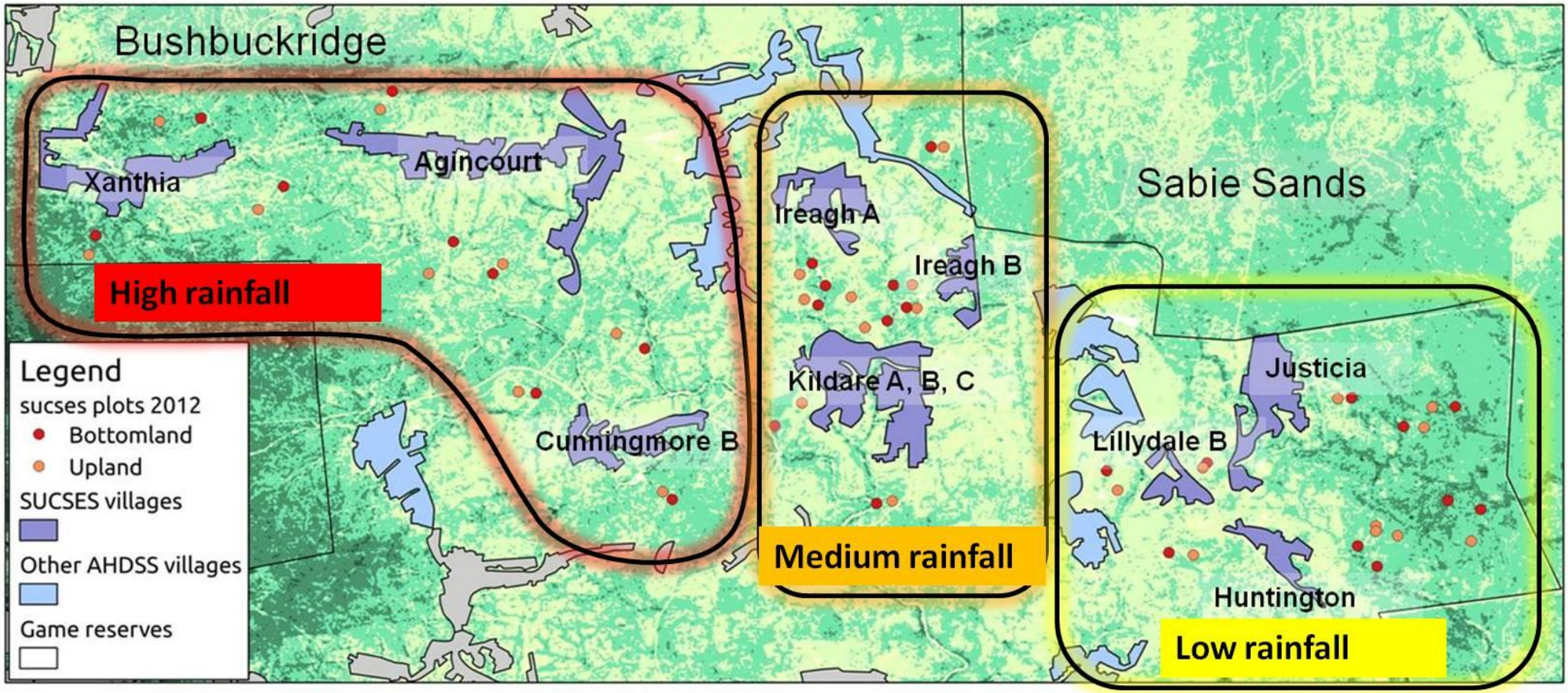


Figure 2.1 Graphical display of sampling plots (n=56). All plots randomly generated in GIS. All plots stratified by rainfall zone ('wet west', 'mid', 'semi-dry east') and catenal position (bottomland and uplands) over 2011 to 2013

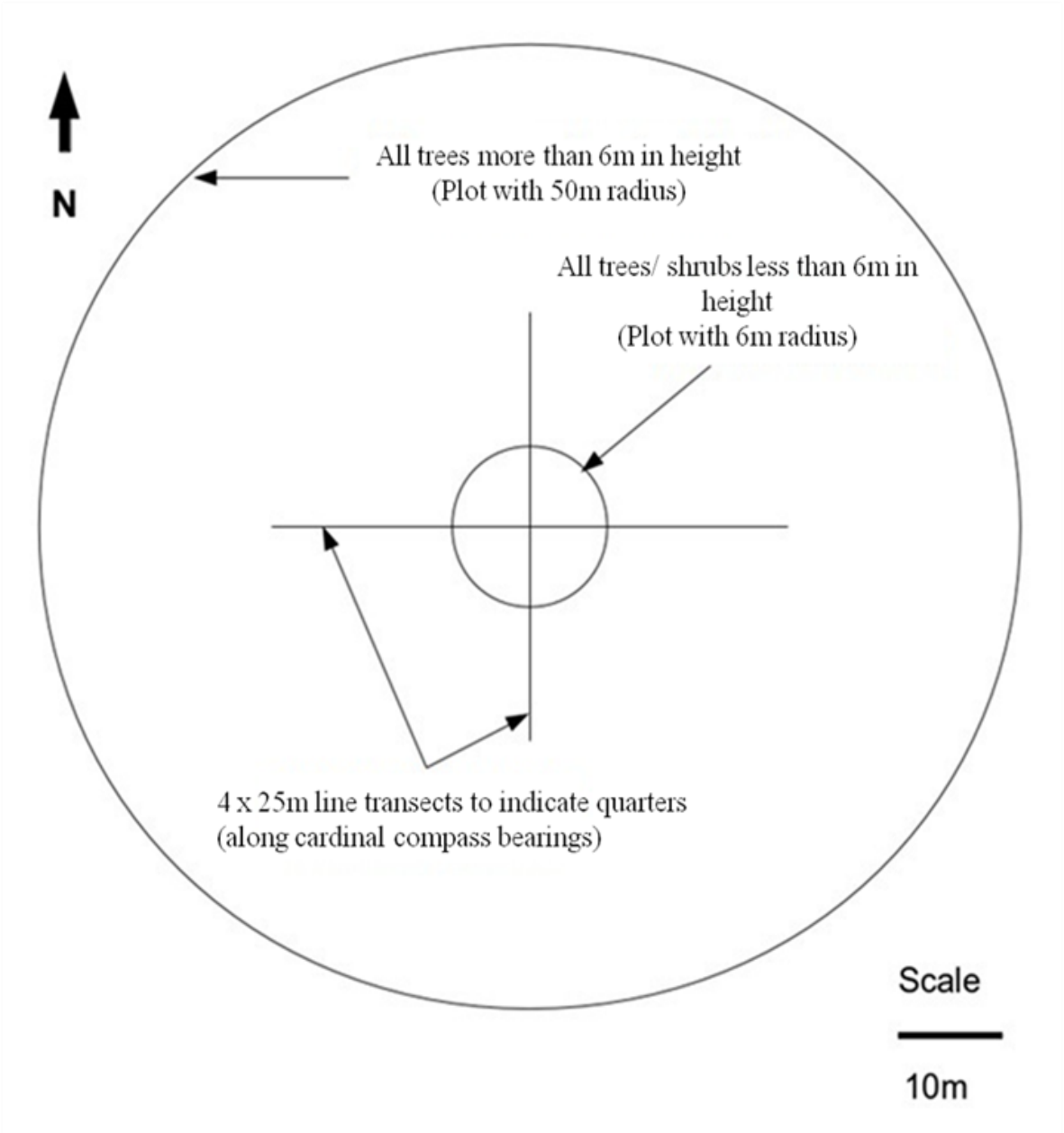


Figure 2.2 Diagrammatic layout of the sampling plots. A circular plot of 50m radius was used for all trees taller than 6m in height and a circular plot of 6m radius nested centrally within the 50m plot for all small trees <6m in height. Transect lines along cardinal compass bearings for indication of quarters.

2.3.3 Data analysis

All data analysis was done in the open source R2.1.0 statistical program and its contributing packages (R Development Core Team 2005). All variables were tested for normality with Shapiro-Wilk normality tests and data were log transformed if necessary. As 2011 only had 28 plots sampled and 2012 and 2013 had 56 plots, two sets of analyses were

done (a) for the same 28 plots for 2011, 2012 and 2013 as well as (b) for the 28 plots in 2011 and 56 plots in 2012 and 2013. Throughout the rest of the text, the number of plots (28 or 56) of each year will be seen in subscript next to the selected year, for example, for the 28 plot datasets: 2011_{28}; 2012_{28}, 2013_{28} and for 56 plots: 2012_{56} and $2013_{56.}$ Most analyses were done separately for large (>6m in height) and small trees (<6m in height).

2.3.3.1 Change in density

Tree and stem frequency values per plot were converting to density (trees per ha and stems per ha). Density for trees and stems was calculated as following:

$$Density = (Abundance/Plot\ area\ (m^2)) \text{ x } 10000.$$

For stem density at the plot level, one-way ANOVAs were used to (a) statistically compare stem density between the three rainfall zones and (b) between catenal positions. For stem density at the plot level, two-way ANOVAs were also done to statistically compare between rainfall zones, catenal positions as well as the interactions between the two. If the ANOVAs detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

2.3.3.2 Differences in size structure

Size structure was analysed as both height and stem diameter. The >6 m tall trees of the 50m radius plots were more sparsely distributed than the <6m tall trees of the 6m radius plot. For the combination of large and small trees, a scaling factor was calculated, as the large trees were assessed in the 50m radius plots while the small trees were only assessed in the much smaller 6m radius plots. The scaling factor is required due to the difference in area of the 6m plot (area=113m^2) and the 50m plot (area=7854m ²). The scaling factor is the area of the 50m plot in relation to the 6m plot ($Area_{50}/Area_6$), which is used to scale up the small plot to the area of the large plot. This was calculated by the following equation:

$$Scaling\ factor = \left(\frac{area\ of\ 50m\ radius\ plot}{area\ of\ 6m\ radius\ plot}\right)$$

$$\text{Hence: } Scaling\ factor = \left(\frac{7854\text{m}^2}{113\text{m}^2}\right) = 69.5$$

Height Structure: Two-way ANOVAs were used to compare mean tree abundance between combinations of rainfall and catenal categories for each of the eight different height classes (≤0.5m, 0.6-1m, 1.1-2m, 2.1-4m, 4.1-6m, 6.1-8m, 8.1-10.0m, >10m). One-way

ANOVAs were done to compare (a) between the size classes of the three rainfall zones (high, medium and low) and (b) between the landscape positions (bottomland and upland), for each year separately (2011 to 2013). If the ANOVA test detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

The Kolmogorov-Smirnov (KS) two-sample test was used to contrast tree height size class distributions (SCD_{ht}) across the three years ((i) 2011 vs. 2012, (ii) 2011 vs. 2013 & (iii) 2012 vs. 2013) in order to assess if the overall population structure had changed.

Stem diameter structure: Two-way ANOVAs were done to compare mean stem abundance between combinations of rainfall and catenal categories for each of the five stem diameter size class categories. Adjusting of size classes was done due to the size classes used in 2011 (≤1cm (excluding new seedlings), 2-5cm, 6-10cm, 11-15cm, 16-20cm, 21-25cm, 26-30cm, 31-35cm, 36-40cm, 41-45cm, >45cm) being different from 2012 and 2013 (≤1cm (excluding new seedlings), 1.1-4.0cm, 4.1-10.0cm, 10.1-20.0cm, 20.1-40.0cm, >40.1cm). In order to compare between years, the data was adjusted (≤1cm (excluding new seedlings), 1.1-10.0cm, 10.1-20.0cm, 20.1-40.0cm, >40.1cm) into fewer size classes. Once again, a Tukey post-hoc test was done if ANOVA was significant.

The Kolmogorov-Smirnov (KS) two-sample test was also used to contrast stem diameter size class distributions (SCD_{diam}) across the three years in order to assess if the overall population structure had changed.

2.4 RESULTS

2.4.1 Change in density and structure

Mean stem density of trees over 6m did not change significantly between 2011_{28}, 2012_{28} and 2013_{28} (Fig 2.3A) or between 2012_{56} and 2013_{56} (Fig 2.3B). Similarly, there was no change in density in 2011_{28}, 2012_{28} and 2013_{28} for small trees (Fig 2.3C). A significant decrease ($p<0.05$) in stem density of trees under 6m was observed from 2012_{56} to 2013_{56} (Fig 2.3D).

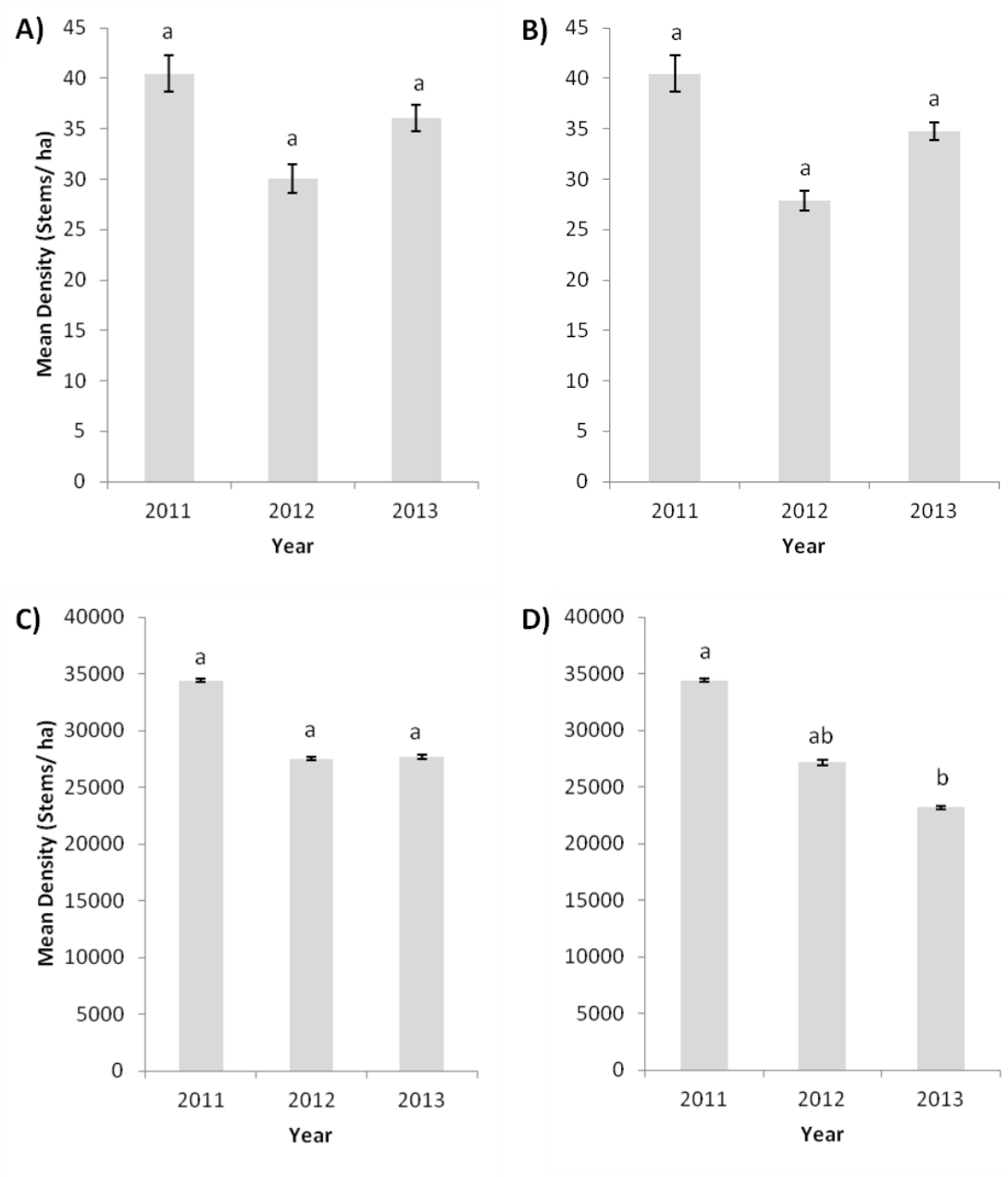


Figure 2.3 Overall mean (± SE) density (cut and uncut stems combined) for original 28 plots only datasets for (A) large and (C) small trees, as well as for all plot datasets (28 in 2011 and 56 in 2012 and 2013) for (B) large and (D) small trees, from 2011 to 2013. Different letters indicate significant differences between years ($P<0.05$, Tukey).

The height size class distributions (SCD_{ht}) (Fig 2.4) were not different between the years (Table 2.1). There was however a difference in abundance between height size classes within each year with the small trees (<6m in height) being by far the most abundant (more than 80%) while the large trees (>6m in height) were less than 20% for all three years (Fig 2.4).

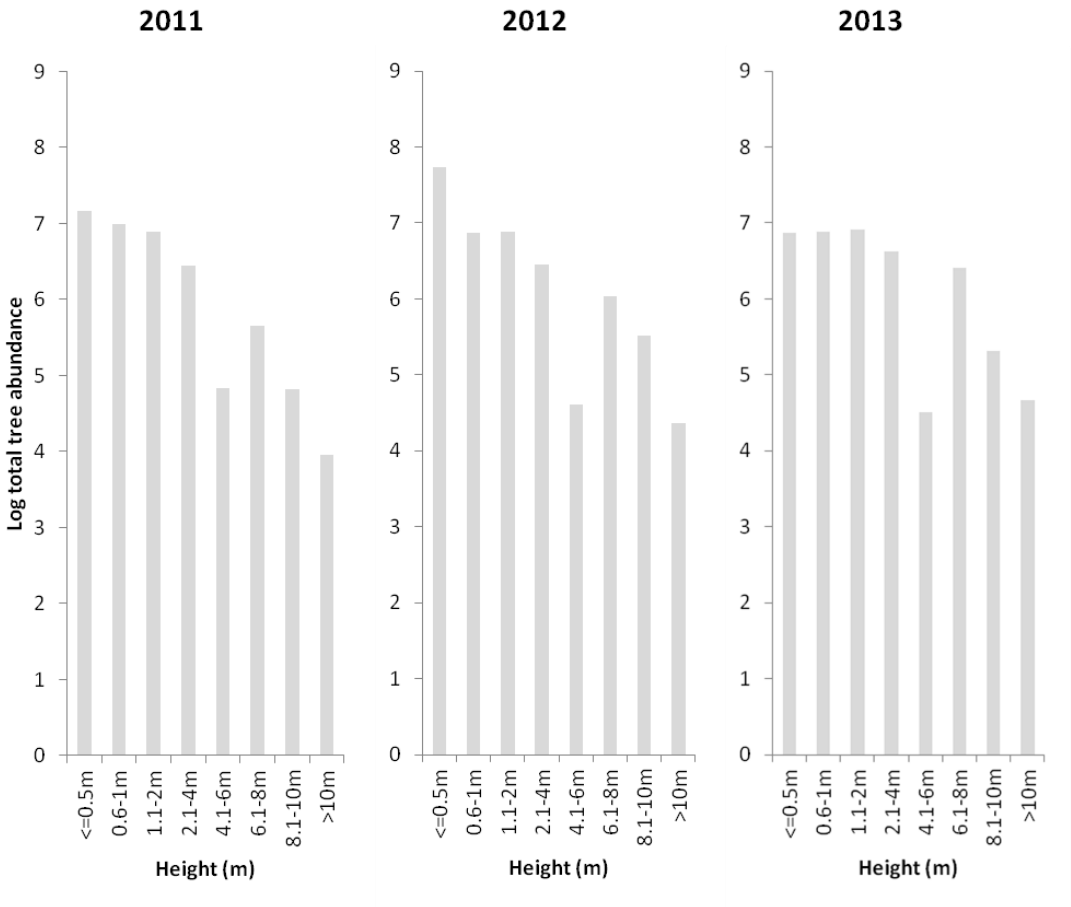


Figure 2.4 Comparison of height size class distributions (SCD_{ht}) in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 2.1 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) between years for all trees (large and small trees combined).

Comparison	Kolmogorov-Smirnov (KS) Test	
	D value	p-value
2011 vs. 2012	0.250	0.970
2011 vs. 2013	0.250	0.934
2012 vs. 2013	0.250	0.953

The stem diameter size class distribution (SCD_{diam}) (Fig 2.5) showed no difference in the distributions between each pair of years (Table 2.2). There is a very skewed distribution between stem diameter size classes for each year with the smallest two stem diameter classes (<10.1cm) being by far the most abundant (more than 90%) and the remaining three larger stem diameter classes (>10.1cm) the least abundant with less than 10% (Fig 2.5).

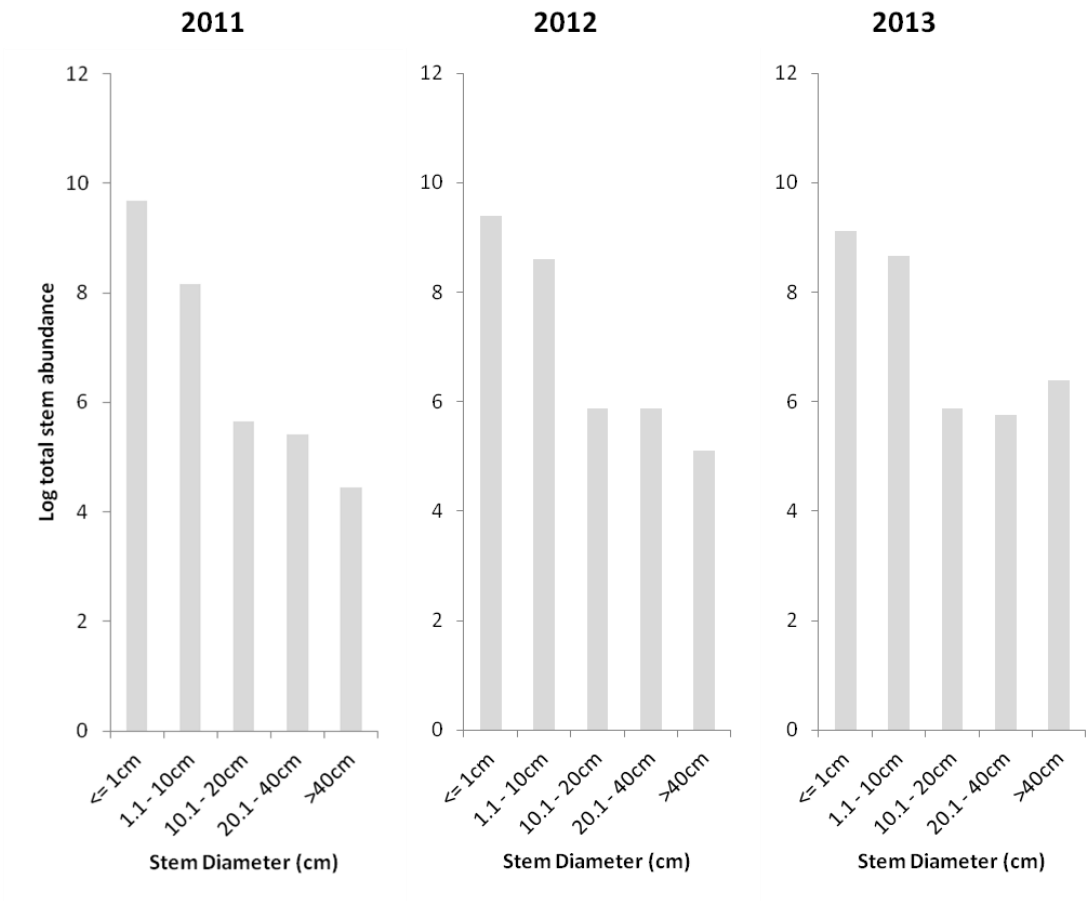


Figure 2.5 Comparison of stem diameter size class distributions (SCD_{diam}) in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 2.2 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) between years for all trees (large and small trees combined).

Comparison	Kolmogorov-Smirnov (KS) Test	
	D value	p-value
2011 vs. 2012	0.400	0.809
2011 vs. 2013	0.600	0.358
2012 vs. 2013	0.200	1.000

2.4.2 Difference in density and structure across rainfall zones

Mean stem density (± SE) was significantly different between rainfall zones for large trees whether comparing between the 28 plots (Fig 2.6A) or the 56 plots (Fig 2.6B) in each of the three survey years. Large tree stem density was highest in the high rainfall zone and lowest in the medium rainfall zone ($p<0.05$) (Fig 2.6A and B). Small tree stem density was

different ($p<0.05$) between rainfall zones for 2011_{28} and 2012_{28} (Fig 2.6C) with the high rainfall zone having higher stem densities compared to low and medium rainfall zones. In 2013_{28} only the high rainfall zone had higher stem densities compared to the low rainfall zone (Fig 2.6C). Similarly, small tree density for 2012_{56} and 2013_{56} was different between rainfall zones with the high rainfall zone also having higher ($p<0.05$) densities compared to the low and medium rainfall zones (Fig 2.6D). There were no differences in either large or small tree stem densities between years per rainfall zone.

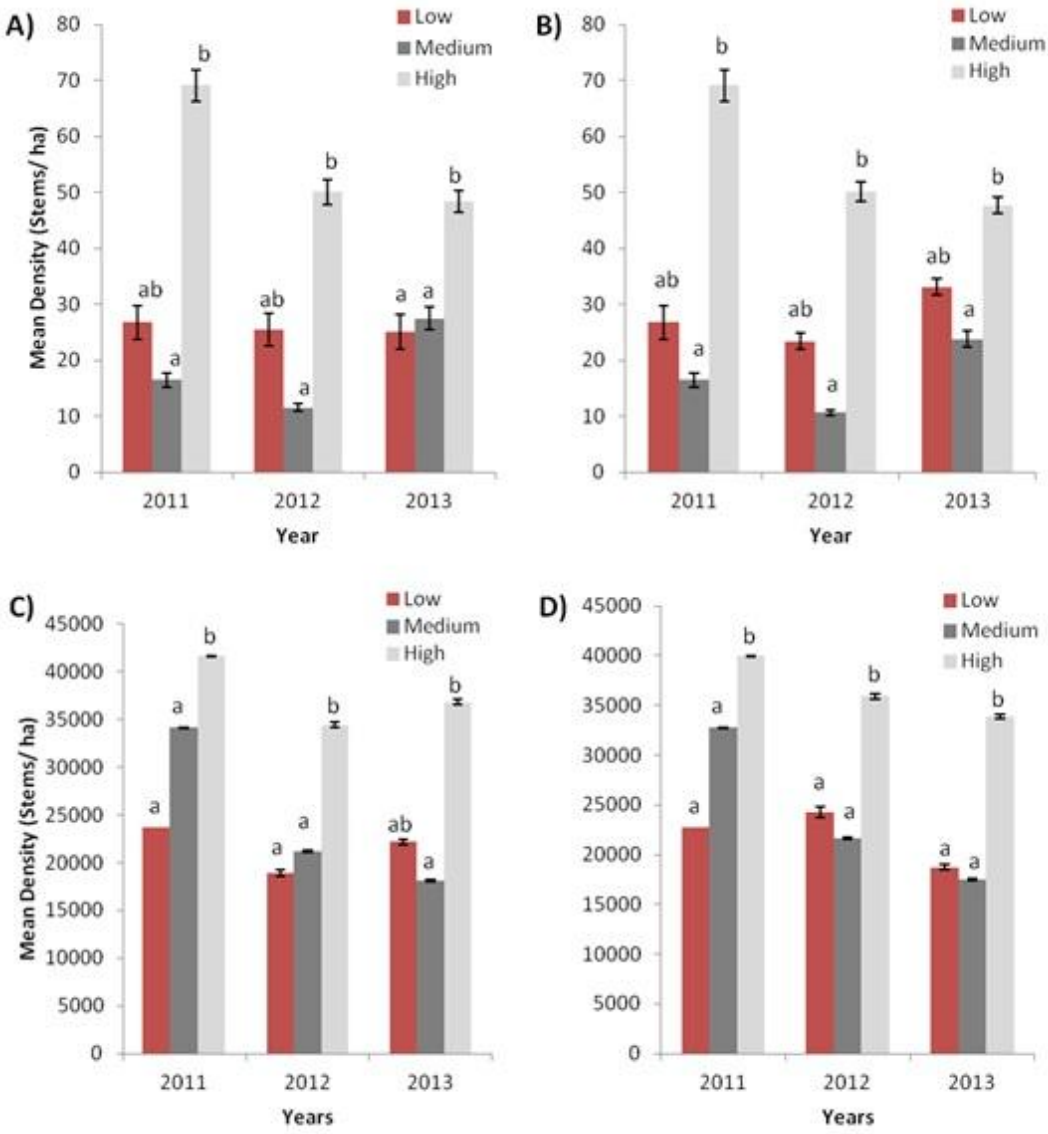


Figure 2.6 Overall mean (± SE) density (cut and uncut stems combined) between rainfall zones for original 28 plots only datasets for (A) large and (C) small trees, as well as for all plot datasets (28 in 2011 and 56 in 2012 and 2013) for (B) large and (D) small trees, from 2011 to 2013. Different letters indicate signific ant differences between years ($P<0.05$, Tukey).

SCD_{ht} did not differ significantly between rainfall zones within the three survey years (Fig 2.7). There are more trees in the high rainfall zone, especially in the 0.1-1m and 6.1->10m height classes, which might be related to the higher rainfall in that zone. Smaller trees were more abundant than larger trees throughout. The SCD_{ht} of the low, medium and high rainfall zones were not different between years (Table 2.3).

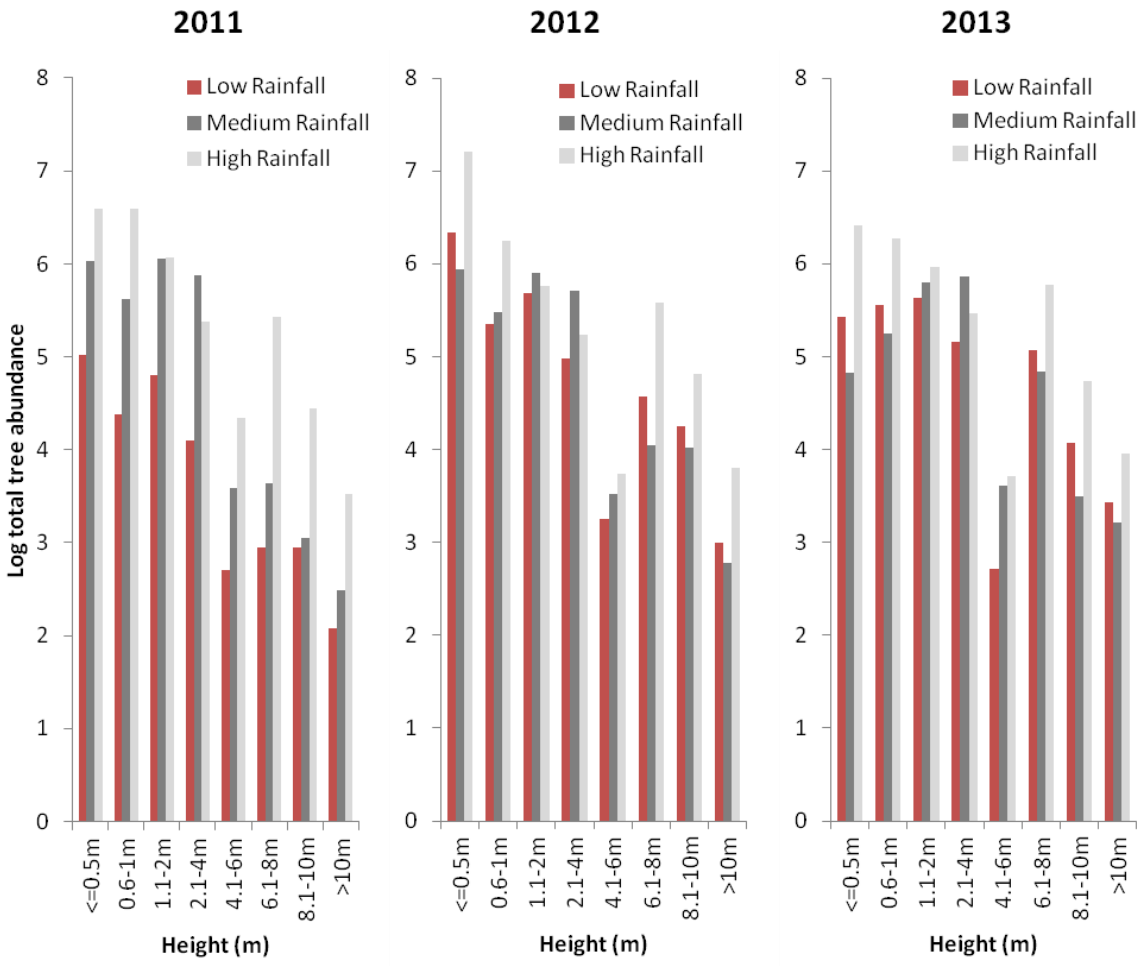


Figure 2.7 Comparison of height size class distributions (SCD_{ht}) between rainfall zones in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 2.3 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) within rainfall zones between years for all trees (large and small trees combined).

Comparison	Rainfall zone	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Low	0.250	0.967
2011 vs. 2013	Low	0.250	0.969
2012 vs. 2013	Low	0.250	0.978
2011 vs. 2012	Medium	0.250	0.937
2011 vs. 2013	Medium	0.375	0.624
2012 vs. 2013	Medium	0.250	0.898
2011 vs. 2012	High	0.125	1.000
2011 vs. 2013	High	0.250	0.953
2012 vs. 2013	High	0.250	0.971

SCD_{diam} did not differ significantly between rainfall zones in any of the three survey years (Fig 2.8). The distributions of the low, medium and high rainfall zones did not show any trending differences between years (Table 2.4).

Table 2.4 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) within rainfall zones between years for all trees (large and small trees combined).

Comparison	Rainfall zone	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Low	0.200	1.000
2011 vs. 2013	Low	0.400	0.810
2012 vs. 2013	Low	0.400	0.812
2011 vs. 2012	Medium	0.600	0.284
2011 vs. 2013	Medium	0.600	0.350
2012 vs. 2013	Medium	0.400	0.808
2011 vs. 2012	High	0.200	1.000
2011 vs. 2013	High	0.400	0.807
2012 vs. 2013	High	0.200	1.000

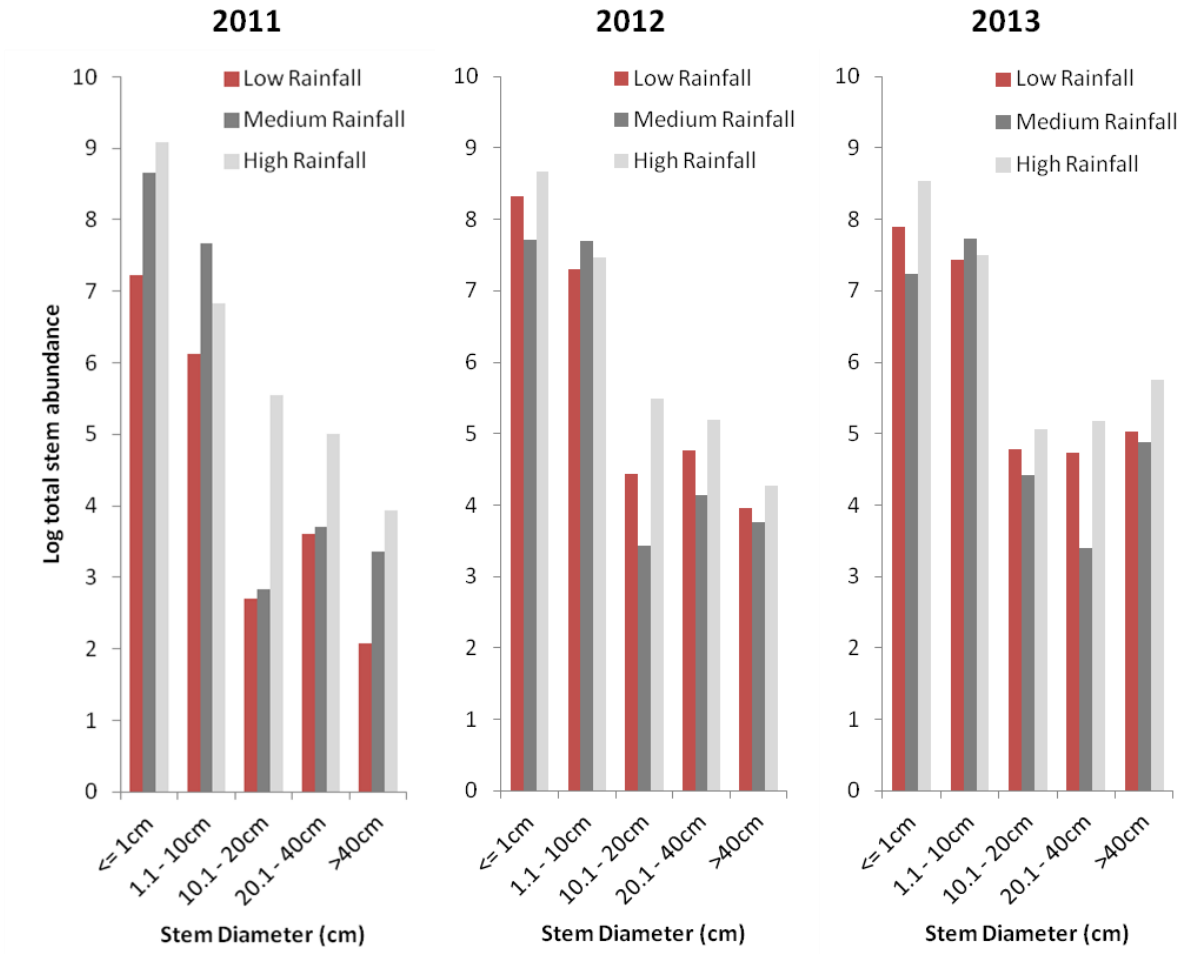


Figure 2.8 Comparison of stem diameter size class distributions (SCD_{diam}) between rainfall zones in 2011, 2012 and 2013 for all trees (large and small trees combined).

2.4.3 Difference in density and structure across catenal positions

Mean stem density was significantly higher in upland than bottomland plots for large trees in 2011_{28}, but not in 2012_{28} and 2013_{28} (Fig 2.9A). In both 2012_{56} and 2013_{56} (Fig 2.9B), mean stem density was significantly higher in upland than bottomland plots for large trees ($p<0.05$). There was however no difference in density for either of the catenal positions between the survey years. Small tree stem density in 2011_{28}, 2012_{28} and 2013_{28} was not significantly different between upland and bottomland plots (Fig 2.9C). Similarly, in 2012_{56} and 2013_{56} also showed no difference in densities between upland and bottomland plots, but there was a significant decrease ($p<0.05$) in density over time in both upland and bottomland plots (Fig 2.9D).

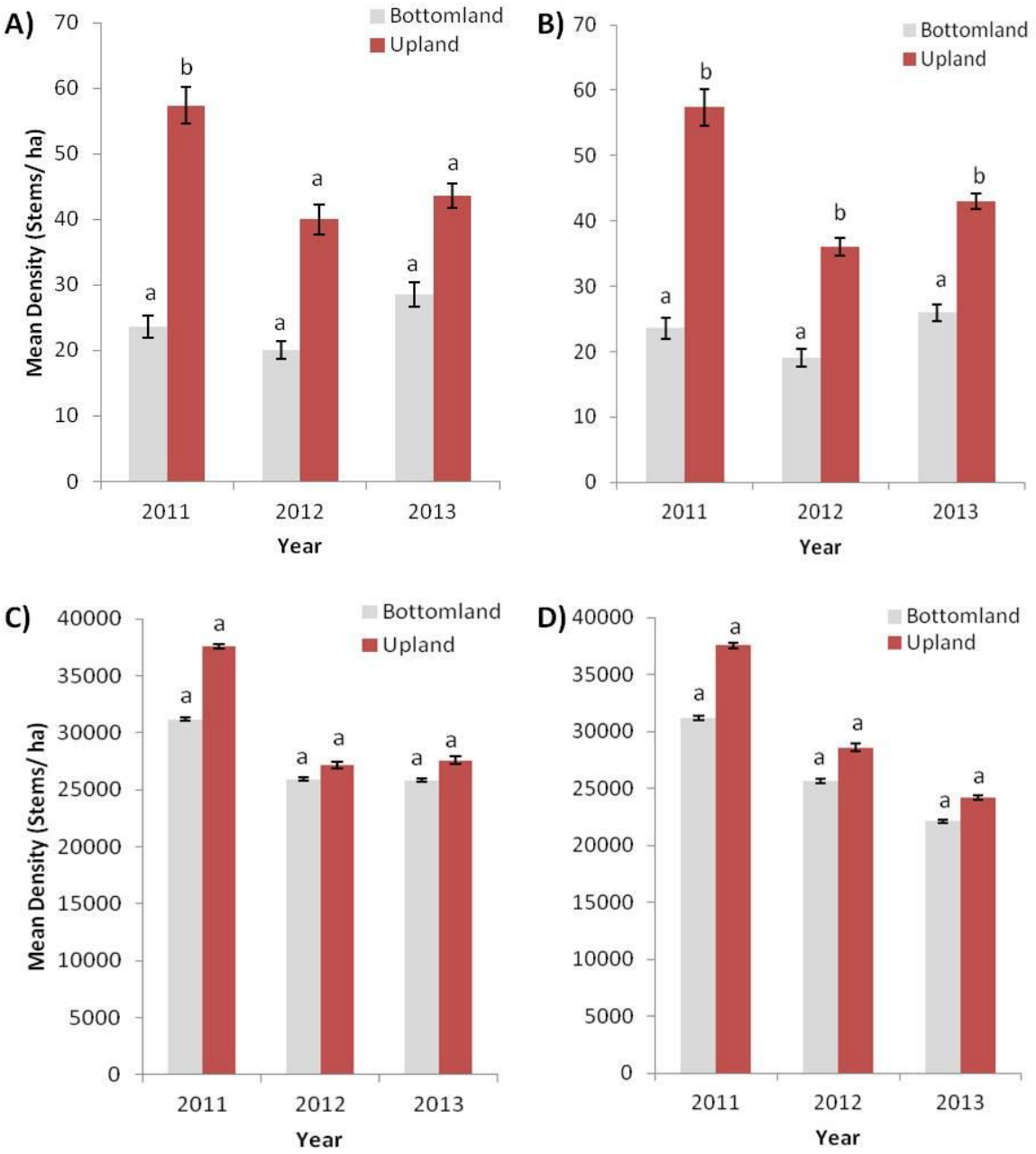


Figure 2.9 Overall mean (± SE) density (cut and uncut stems combined) between catenal positions for original 28 plots only datasets for (A) large and (C) small trees, as well as for all plot datasets (28 in 2011 and 56 in 2012 and 2013) for (B) large and (D) small trees, from 2011 to 2013. Different letters indicate significant differences between years.

SCD_{ht} showed similar abundance overall within bottomland and upland catenal positions within each of the three survey years (Fig 2.10). Large trees were more abundant in the upland relative to bottomland plots whereas small trees were similar in abundance between upland and bottomland plots. There was however no significant change over time for either upland or bottomland plots. The distributions of each year for the upland and

bottomland positions showed no differences between 2011 and 2012, 2011 and 2013 or 2012 and 2013 (Table 2.5).

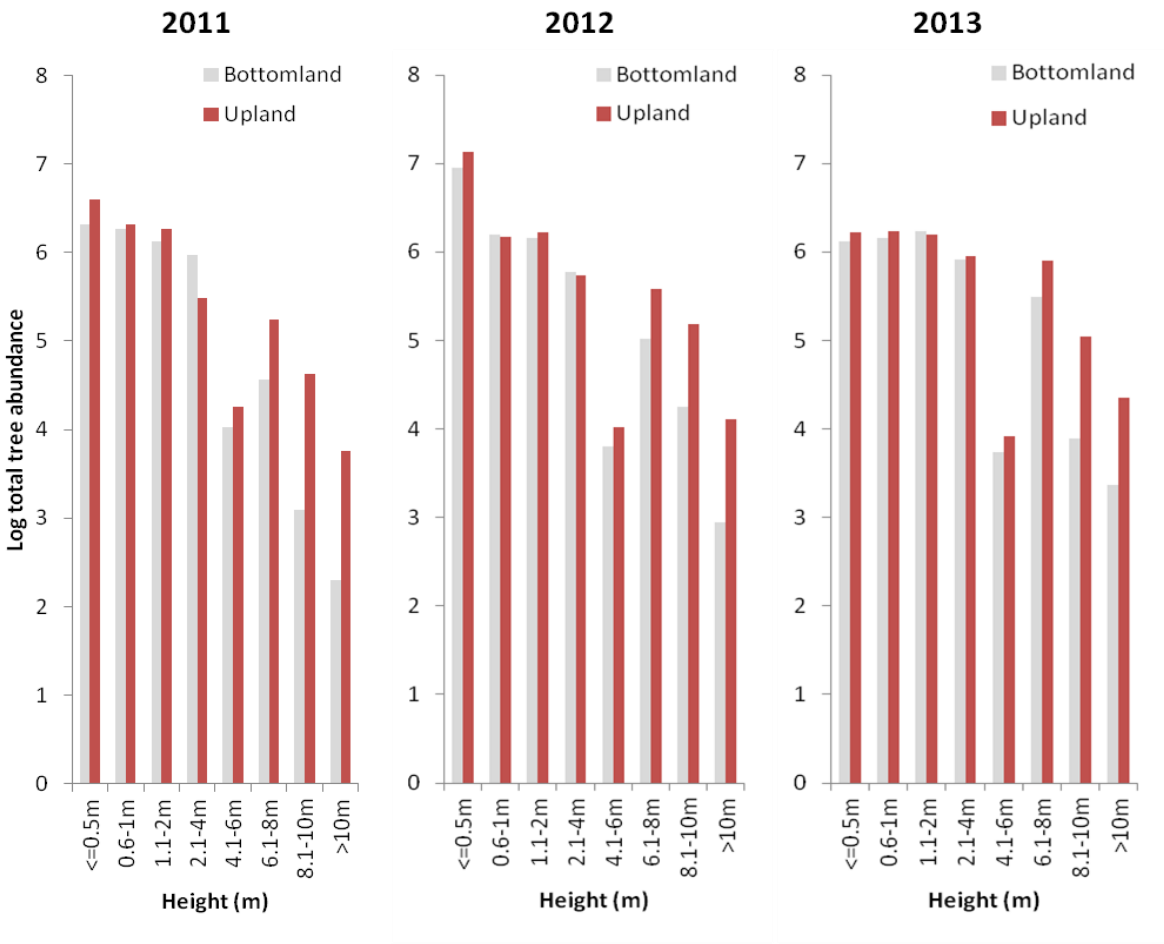


Figure 2.10 Comparison of height size class distributions (SCD_{ht}) between catenal positions in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 2.5 Kolmogorov-Smirnov (KS) comparisons of height size class distributions **(**SCD_{ht}**)** within catenal positions between years for all trees (large and small trees combined).

Comparison	Catenal position	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Bottomland	0.250	0.971
2011 vs. 2013	Bottomland	0.250	0.934
2012 vs. 2013	Bottomland	0.250	0.969
2011 vs. 2012	Upland	0.250	0.966
2011 vs. 2013	Upland	0.375	0.623
2012 vs. 2013	Upland	0.250	0.938

SCD_{diam} did not differ significantly between catenal positions within or across years (Fig 2.11). The distributions between upland and bottomland catenal positions showed no difference in abundance for any of three years (Table 2.6).

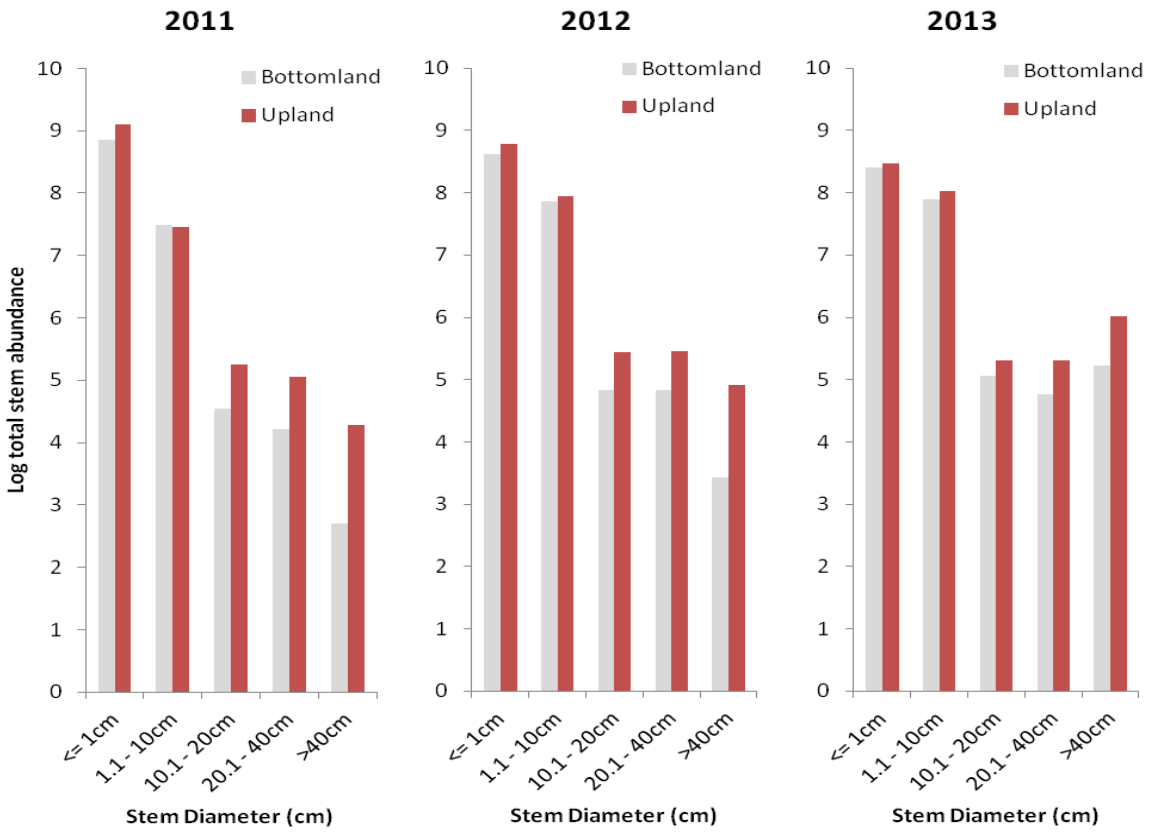


Figure 2.11 Comparison of stem diameter size class distributions **(**SCD_{diam}) between catenal positions in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 2.6 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) within catenal positions between years for all trees (large and small trees combined).

Comparison	Catenal position	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Bottomland	0.200	1.000
2011 vs. 2013	Bottomland	0.600	0.283
2012 vs. 2013	Bottomland	0.600	0.293
2011 vs. 2012	Upland	0.200	1.000
2011 vs. 2013	Upland	0.400	0.812
2012 vs. 2013	Upland	0.200	1.000

2.4.4 Difference in density and structure across a combination of rainfall zones and catenal positions over time

Rainfall zones had an effect on woody vegetation density and structure more often than catenal positions. There was no interaction between catenal positions and rainfall zones for either large or small trees. Rainfall zones had a stronger effect on the difference in woody vegetation density and structure of large trees in 2011_{28}, 2012_{28} and 2012_{56}. Rainfall had no significant effect on the density and structure of large trees in $2013_{28\&56}$ (Table 2.7). Similarly, rainfall zones had a stronger effect on the difference in density and structure of small trees in 2011_{28}. Different to large trees, rainfall zones did have a stronger effect on the difference in density over the three survey years and structure of small trees in $2013_{28\&56}$ but no effect on the difference in density and structure of $2012_{28\&56}$ (Table 2.7). Catenal position only had a stronger effect in the difference of structure and density of large trees in 2012_{56}. There was however no effect by catenal position on the difference in density and structure for large trees in 2011_{28}, 2012_{28} or $2013_{28\&56}$ or for all small trees of the three survey years (Table 2.7). Similarly, there was no interaction between catenal/rainfall combinations and thus no effect on the difference in density and structure for large trees or small trees in any of the three survey years (Table 2.7).

Table 2.7 Two-way ANOVAs comparing the effects of rainfall zone, catenal position and the interaction between them on stem density for large (>6m in height) and small trees separately (<6m in height). Significant p-values in bold type.

Tree size	Year	Plots sampled	Rainfall zones	Catenal position	Rainfall* Catenal Interaction
			p-value	p-value	p-value
Large Trees	2011	28	**0.035**	0.705	0.309
	2012	28	**0.029**	0.122	0.350
		56	**0.001**	**0.038**	0.464
	2013	28	0.319	0.282	0.272
		56	0.089	0.052	0.320
Small Trees	2011	28	**0.005**	0.610	0.550
	2012	28	0.077	0.836	0.952
		56	0.264	0.672	0.454
	2013	28	**0.022**	0.768	0.755
		56	**0.003**	0.556	0.851

Large tree stem density was significantly higher in upland plots in the high rainfall zone than bottomland plots in the medium rainfall zones in 2011_{28} and 2012_{28} (Fig 2.12A). In 2013_{28} the large tree stem densities in the upland plots in the high rainfall zone were significantly higher than the other catenal/rainfall combinations (Fig 2.12A). Large tree stem density was significantly higher in upland plots in the high rainfall zone than the bottomland plots in the medium rainfall zone in 2011_{28} (Fig 2.12B). In 2012_{56} the upland plots in the high rainfall zone had significantly higher densities than the bottomland plots in the low rainfall zone, the bottomland and upland plots in the medium rainfall zone (Fig 2.12B). In 2013_{56}, the stem densities in the upland plots in the high rainfall zone were significantly higher compared to the bottomland plots in the low rainfall zone, the bottomland and upland plots in the medium rainfall zone and the bottomland plots in the high rainfall zone (Fig 2.12B). The density of small trees in 2011_{28} was higher in the upland plots of the high rainfall zone than all other catenal/rainfall combinations. In 2012_{28} and 2013_{28} the stem densities in the upland and bottomland plots in the high rainfall zone were significantly higher than all other catenal/rainfall combinations (Fig 2.12C). Similarly, density of small trees was significantly higher in upland plots in the high rainfall zone than all other combinations in 2011_{28} (Fig 2.12D). In 2012_{56} the stem densities were significantly higher in the upland and bottomland plots in the high rainfall zone, as well as upland plots in the low rainfall zone than all other catenal/rainfall combinations (Fig 2.12D). Stem density in 2013_{56} was significantly higher in the upland and bottomland plots in the high rainfall zone than all other catenal/rainfall combinations (Fig 2.12D).

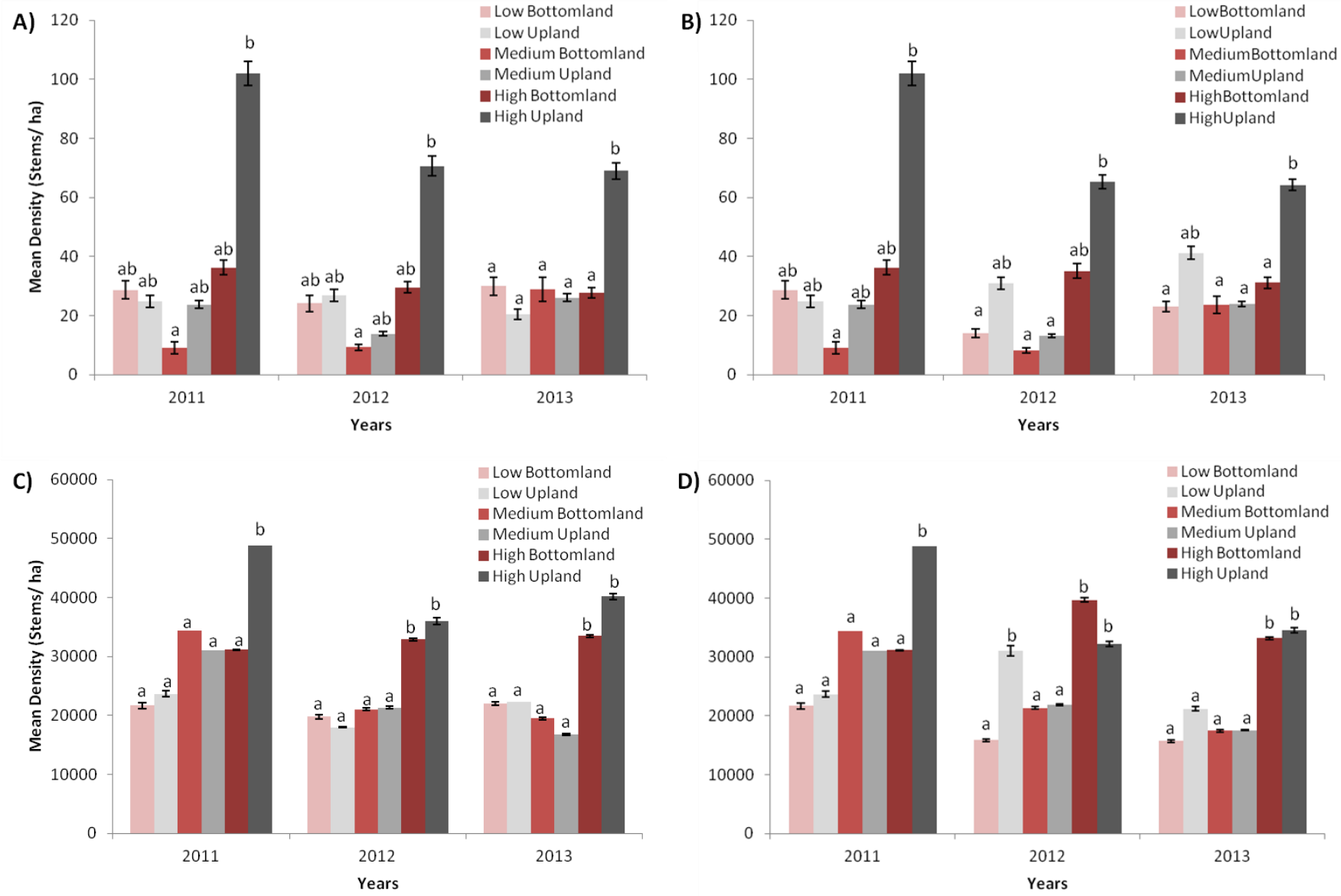


Figure 2.12 Overall mean (± SE) density (cut and uncut stems combined) between catenal position and rainfall zone combinations for original 28 plots only datasets for (A) large and (C) small trees, as well as for all plot datasets (28 in 2011 and 56 in 2012 and 2013) for (B) large and (D) small trees, from 2011 to 2013. Different letters indicate significant differences between catenal position and rainfall zone combinations within years ($P<0.05$, Tukey).

SCD_{ht} did not differ significantly between catenal/rainfall combinations across the three years (Table 2.8) but did show a difference between the different catenal/rainfall combination within each year (Fig 2.13). In 2011, the lowest abundance was in the bottomland plots of the low rainfall zone, except that the >10m trees in the bottomland plots of the medium rainfall zone had the lowest abundance. Similarly, the upland plots in the high rainfall zone of 2012 and 2013 had the highest abundance of the larger height size classes. The smaller height classes in 2012 and 2013 had similar abundance between all the catenal/rainfall combinations.

Table 2.8 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) for each catenal position/rainfall zone combination between years for all trees (large and small trees combined).

Comparison	Rainfall zone and catenal position interaction	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Low Bottomlands	0.250	0.952
2011 vs. 2013	Low Bottomlands	0.250	0.981
2012 vs. 2013	Low Bottomlands	0.125	1.000
2011 vs. 2012	Low Uplands	0.125	1.000
2011 vs. 2013	Low Uplands	0.250	0.897
2012 vs. 2013	Low Uplands	0.375	0.619
2011 vs. 2012	Medium Bottomlands	0.250	0.956
2011 vs. 2013	Medium Bottomlands	0.250	0.954
2012 vs. 2013	Medium Bottomlands	0.250	0.952
2011 vs. 2012	Medium Uplands	0.250	0.956
2011 vs. 2013	Medium Uplands	0.375	0.619
2012 vs. 2013	Medium Uplands	0.250	0.957
2011 vs. 2012	High Bottomlands	0.250	0.953
2011 vs. 2013	High Bottomlands	0.250	0.956
2012 vs. 2013	High Bottomlands	0.250	0.956
2011 vs. 2012	High Uplands	0.125	1.000
2011 vs. 2013	High Uplands	0.250	0.969
2012 vs. 2013	High Uplands	0.250	0.971

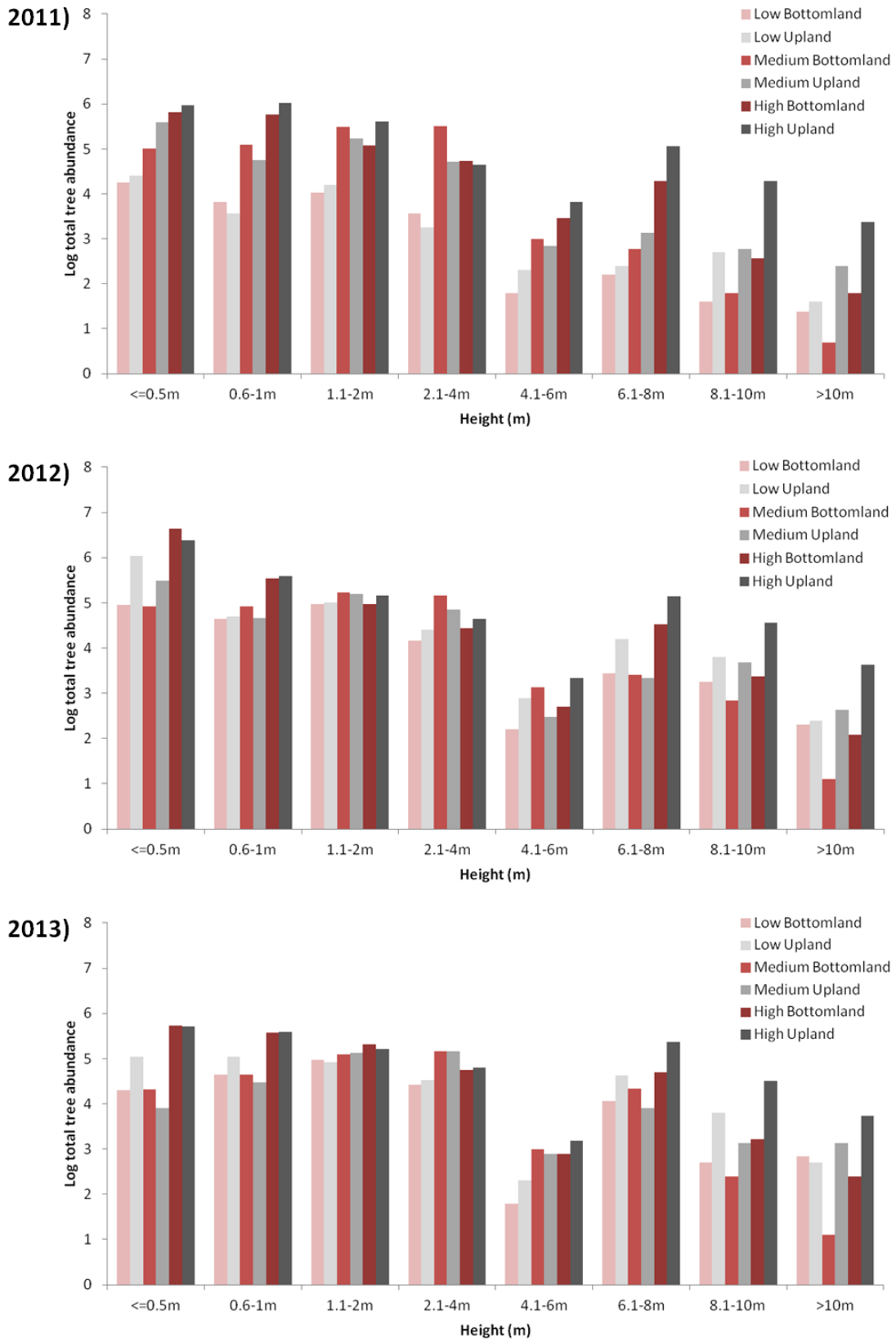


Figure 2.13 Comparison of height size class distributions (SCD_{ht}) between catenal position and rainfall zone combinations in 2011, 2012 and 2013 for all trees (large and small trees combined).

SCD_{diam} did not differ significantly between rainfall and catenal combinations (Fig 2.14). Stem abundance was higher in upland plots of the high rainfall zone in 2011, except that the 1.1-10cm size class in the bottomland plots in the medium rainfall zone had the highest abundance. Similar to the SCD_{ht} in 2011, the lowest abundance was in the bottomland plots of the low rainfall zone, except that the >40m stem diameter trees in the bottomland plots of the medium rainfall zone had the lowest abundance. Similarly, the upland plots in the high rainfall zone of 2012 and 2013 had the highest abundance in the larger size classes. The smaller stem diameter size classes in 2012 and 2013 had similar abundance between the catenal/rainfall combinations, especially in the 1.1-10cm size class. The distributions for each catenal/rainfall combination showed no difference between 2011 and 2012, 2011 and 2013 or 2012 and 2013 (Table 2.9).

Table 2.9 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) within catenal position/rainfall zone combinations between years for all trees (large and small trees combined).

Comparison	Rainfall zone and catenal position interaction	Kolmogorov-Smirnov (KS) Test	
		D value	p-value
2011 vs. 2012	Low Bottomlands	0.200	1.000
2011 vs. 2013	Low Bottomlands	0.400	0.808
2012 vs. 2013	Low Bottomlands	0.200	1.000
2011 vs. 2012	Low Uplands	0.200	1.000
2011 vs. 2013	Low Uplands	0.400	0.812
2012 vs. 2013	Low Uplands	0.400	0.806
2011 vs. 2012	Medium Bottomlands	0.400	0.720
2011 vs. 2013	Medium Bottomlands	0.600	0.361
2012 vs. 2013	Medium Bottomlands	0.400	0.715
2011 vs. 2012	Medium Uplands	0.200	1.000
2011 vs. 2013	Medium Uplands	0.400	0.876
2012 vs. 2013	Medium Uplands	0.200	1.000
2011 vs. 2012	High Bottomlands	0.200	1.000
2011 vs. 2013	High Bottomlands	0.200	1.000
2012 vs. 2013	High Bottomlands	0.200	1.000
2011 vs. 2012	High Uplands	0.200	1.000
2011 vs. 2013	High Uplands	0.400	0.808
2012 vs. 2013	High Uplands	0.200	1.000

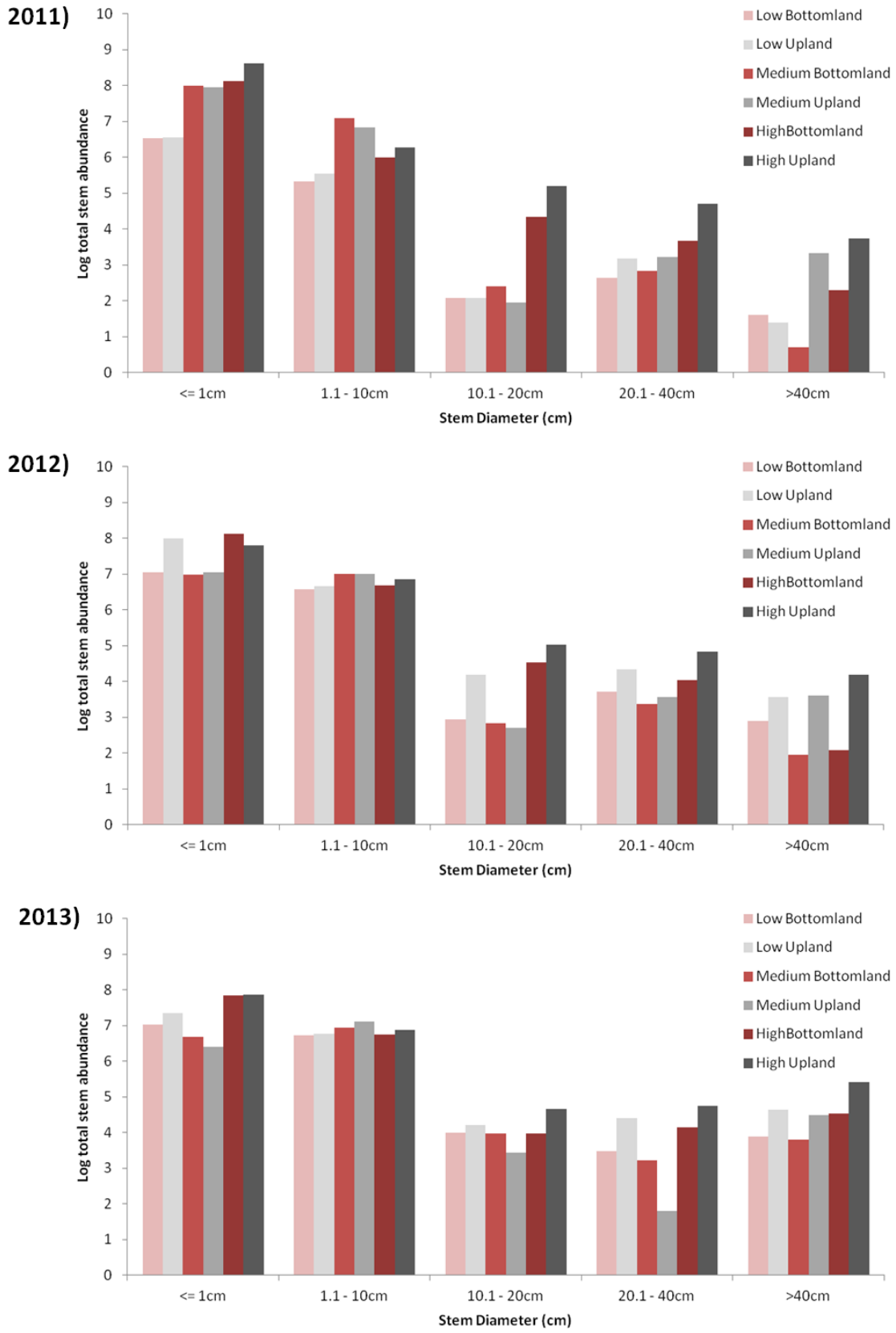


Figure 2.14 Comparison of stem diameter size class distributions (SCD_{diam}) between catenal position and rainfall zone combinations in 2011, 2012 and 2013 for all trees (large and small trees combined).

2.5 DISCUSSION

Focusing on how woody vegetation density and structure differ across the rainfall gradient and between catenal positions in this human-impacted landscape across time, a decrease in small tree density occurred over time while large trees had no change. The high rainfall zone had higher stem densities compared to the low and medium rainfall zones. Large tree stem density was higher in upland plots compared to bottomland plots whereas small tree stem density was similar between upland and bottomland plots. Stem density was higher in upland plots in the high rainfall zones compared to other catenal/rainfall combinations.

2.5.1 Change in density and structure across time

In this study, there was no change to stem density over time for large trees. There was however, a decrease in stem density for small trees within the 56 plots. As the practice of different land uses is another major determinant of savannas according to various studies (Breshears and Barnes 1999; Fairbanks 2004; Fisher *et al.* 2011; Gilson *et al.* 2003; Higgins *et al.* 1999; Kristensen and Lykke 2003; Scholes and Archer 1997), harvesting is a possible reason for the change in the structure of these savannas (Chapter 3).

The lack of change in large tree density might be due to large trees not being impacted as much by harvesting as the smaller trees, as local law forbids harvesting of large trees (Fisher *et al.* 2011; Wessels *et al.* 2011). Matsika *et al.* (2013b) found that the preferred size class for firewood were stems with a diameter of 4-10cm. This could also explain the lack of change in large tree density. As for structural changes over time, there was no change between the distributions for either tree height or stem diameter between years. Both SCD_{ht} and SCD_{diam} displayed a stable size class distribution (classic reverse–J shape size class distribution) with much higher abundance in the smaller size classes and lower abundance in the larger size classes. The abundance of small stems in the rangelands are higher due to the occurrence of harvesting which in turn results in the increase in abundance of smaller size classes due to coppice regrowth (Higgins *et al.* 1999; Jurisch *et al.* 2012; Kaschula *et al.* 2005; Twine 2005). Almost all savanna tree species have the ability to produce coppice regrowth if stems are damaged or killed (Luoga *et al.* 2004; Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). The impacts of the stem harvesting are thus alleviated in a sense that the coppice regrowth grows faster than old stems (Twine 2005). The increased cutting of live stems and widespread coppice regrowth has changed the tree morphology of many woody species (Higgins *et al.* 1999; Twine 2005). The most noticeable change is the increase of coppice regrowth production (Higgins *et al.* 1999; Twine 2005). The structure of the most

utilised species and their populations has become characterised by a lack of large mature stems and an increased abundance of smaller stems (Higgins *et al.* 1999; Jurisch *et al.* 2012; Kaschula *et al.* 2005; Twine 2005).

2.5.2 Difference in density and structure across rainfall zones

Water limits vegetation growth by 40% on a global scale and thus the availability of water is one of the key environmental determinants of changes in vegetation structure and composition (Nemani *et al.* 2010). As mentioned earlier, annual rainfall, infiltration capacity, soil composition and texture are responsible for the amount of water that is available to the surrounding vegetation (Kanniah *et al.* 2010). Stem density was higher in the high rainfall zone compared to the low and medium rainfall zones during this study. Sankaran *et al.* (2005) and Shackleton and Scholes (2011) found that woody vegetation density was higher in area with higher rainfall across savannas. Various studies have found stem density to be lower in the low rainfall areas and higher in the high rainfall areas (Buitenwerf *et al.* 2012; Shackleton and Scholes 2011; Smith and Goodman 1986). This study found similar results, with the stem density being higher with higher rainfall along the gradient. This study also found that the abundance of trees (SCD_{ht}) and stems (SCD_{diam}) was also higher in the high rainfall zone compared to the low and medium rainfall zones. Shackleton and Scholes (2011) and Smith and Goodman (1986) also found that the stem diameter, height of trees and number of species were all higher in the areas of higher rainfall and available soil moisture.

2.5.3 Differences in density and structure across catenal positions

Topography is also an important environmental determinant for vegetation structure, both in savannas and on a global scale across different biomes (Coughenour and Ellis 1993; Fisher *et al.* 2009; Fisher *et al.* 2011; Kanniah *et al.* 2010; Kaschula *et al.* 2005; Shackleton 1999; Wessels *et al.* 2011; Witkowski and O'Connor 1996). Overall, no trending difference was seen between the density in upland and bottomland plots. Other studies however found upland plots to have higher density and structural differences compared to the bottomland plots (Colgan *et al.* 2012; Daultrey 1970; Fisher *et al.* 2009; Fisher *et al.* 2011; Khomo *et al.* 2011; Wessels *et al.* 2011). Higher density in the upland plots compared to the bottomland plots was only found in the large tree stem densities in 2011_{28} and all the large tree stem densities in 2012_{56} and 2013_{56}. This could be attributed to the different availability of moisture and nutrients (Fisher *et al.* 2011; Shackleton 1999; Wessels *et al.* 2011). Shackleton (1999) and Colgan *et al.* (2012) found soil properties associated with catenal position, such as particle size or texture is often the primary determinant of infiltration rates and water

retention and tends to have an effect on the structure of vegetation. Shackleton (1999) and Colgan *et al.* (2012) found bottomlands to have greater soil moisture but reduced availability due to the higher clay content whereas the uplands had lower soil moisture but higher availability due to the lower clay content. The coarse-textured soils in uplands allow trees access to the through flow whereas the bottomlands with higher clay content is often dominated by overland flow instead of through flow (Colgan *et al.* 2012). Tree abundance (SCD_{ht}) and stem abundance (SCD_{diam}) was similar between upland and bottomland plots for smaller size classes. The larger size classes had higher abundance of trees (SCD_{ht}) and stems (SCD_{diam}) in the upland plots compared to the bottomland plots.

2.5.4 Difference in density and structure across a combination of rainfall zones and catenal positions over time

Rainfall zones had an effect on woody vegetation density and structure more often than the effect of catena positions. There were no significant interactions between rainfall zone and catenal position (Table 2.7). The differences between rainfall zones coincides with the findings of various studies which state rainfall is important for the differences within savanna landscapes (Belsky 1990; Colgan *et al.* 2012; Coughenour and Ellis 1993; Daultrey 1970; Fisher *et al.* 2011; Kanniah *et al.* 2010; Khomo *et al.* 2011; Pinto et al. 2006; Shackleton 1999; Walker 1987; Wessels *et al.* 2011; Witkowski and O'Connor 1996). This study found no difference between uplands and bottomlands, whereas the studies mentioned above did find differences in topography and thus state topography is also a key driver of change in vegetation.

With regard to the differences between rainfall zones and catenal positions combinations, upland plots in the high rainfall zone had higher stem densities compared to the other catenal/rainfall combination. A possible reason for this could be the difference in species composition. In Chapter 5, the ordination biplots of all three survey years showed that there was no relationship between rainfall and catenal position in their influence on species composition among large, small or all trees. It also found that the species composition in the uplands was different from those in the bottomlands and likewise, the high rainfall zone plots had different species composition to those of the low and medium rainfall zones (Chapter 5). This is one possible reason for no significant interactions between rainfall zone and catenal position, being based on the difference in species composition, which results in differences in stem densities due to the different growth patterns of different species. The relatively short

period of time of this research project is also a possible explanation as to why there were no interactions detected.

Tree abundance (SCD_{ht}) tended to be higher in the upland plots in the high rainfall zone compared to all other catenal/rainfall combinations. This was true for the majority of the height classes but with two exceptions. Firstly, in the 1.1-2m size class, bottomland plots in the medium rainfall zone tended to have the highest tree abundance in 2011 and 2012, while in 2013, the upland and bottomland plots in the medium rainfall zone tended to have higher abundance than the other two zones. Secondly, in the 2.1-4m size class, the bottomland plots in the medium rainfall zone tended to have higher tree abundance in 2012, while in 2013, the bottomland plots of the high rainfall zone tended to have higher tree abundance than the other two zones. The abundance can once again be attributed to the density difference between catenal/rainfall combinations (Buitenwerf *et al.* 2012; Colgan *et al.* 2012; Coughenour and Ellis 1993). The two exception height classes can possibly be attributed to harvesting as harvesting occurs mainly on trees of lower heights (Jurisch *et al.* 2012; Higgins *et al.* 1999; Kaschula *et al.* 2005; Shackleton 1993; Twine 2005). The lack of harvesting on large trees might be due to local traditions that forbid harvesting of large fruit bearing trees (Fisher *et al.* 2011; Wessels *et al.* 2011).

Similarly, stem abundance (SCD_{diam}), also had higher abundance in the upland plots in the high rainfall zone compared to all other catenal/rainfall combinations. There were also two exceptions, the first was in the ≤1cm size class where in 2012, the bottomland plots in the medium rainfall and the upland plots in the low rainfall zone had higher stem abundance and in 2013 where the upland and bottomland plots of the high rainfall zone had higher tree abundance. The second exception was in the 1.1-10cm size class, where in 2011 the bottomland plots in the medium rainfall zone had highest stem abundance, while in 2012 the upland and bottomland plots in the medium rainfall zone had the highest stem abundance, and in 2013 the upland plots in the medium rainfall zone had higher abundance. The abundance can once again be attributed to the density difference between catenal/rainfall combinations (Buitenwerf *et al.* 2012; Colgan *et al.* 2012; Coughenour and Ellis 1993; Khomo *et al.* 2011; Pinto et al. 2006; Shackleton 1999; Shackleton *et al.* 1994; Shackleton *et al.* 2007). The two exception height classes can also possibly be attributed to harvesting as harvesting, similar to height preferences, has a preference for smaller stem sizes (Higgins *et al.* 1999; Jurisch *et al.* 2012; Kaschula *et al.* 2005; Shackleton 1993; Twine 2005)

2.6 CONCLUSION

In conclusion, rainfall zones had a stronger effect on woody density and structure than catenal position, but rainfall zones and catenal position showed no significant interactions. The study found than higher rainfall did have an influence on the vegetation, density increased as the rainfall increased and the structure changed as the number of larger trees increased. We did not find the two catenal positions to have a strong influence on vegetation density and structure as other studies did, but the species composition did however differ (Chapter 5).

This study aimed to determine how woody vegetation density and structure differ along a rainfall gradient and between catenal positions in a human-impacted landscape across time. This study also assessed the relative importance of these two environmental factors, and the interactions between them. The first question, "how does density and structure change over time (2011-13), ignoring effects of rainfall zone and catenal position?" found when the 28 plots were used, that there was no change in density. If the 56 plots were used, the density of small trees did decrease. The second question, "how does density and structure differ across rainfall zones over time?" found the highest density was in the high rainfall zone and the low rainfall zone had the lowest density. The third question, "how does density and structure differ across catenal positions over time?" found no difference between upland and bottomland plots as both uplands and bottomlands had similar densities if one used the 28 plots. The large tree densities were however higher in the uplands if the 56 plots were used. The final question, "how does density and structure differ across a combination of rainfall zones and catenal positions over time?" found the uplands in high rainfall zone did have higher densities.

Future studies should rather have a longer monitoring period as the possibility of change occurring in such a short period of three years is relatively unlikely. By establishing a long term monitoring program, this research would be valuable not only to the science community but might be vital to help manage available resources in a sustainable way and thus ensuring the future to a vast number of individuals who are dependent on the resources provided by the surrounding environment. Future studies should also avoid changes in the sample size, which greatly complicates the analyses and interpretations. Nonetheless, the change in sample size did bring about more involved analyses during this study with the goal of making the best use of the available data.

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3 Chapter 3: Effect of harvesting on woody vegetation density and structure in communal rangelands across catenal and rainfall gradients (2011 – 2013)

3.1 ABSTRACT

Fuelwood is the primary energy source for the majority of rural households in African savannas. Harvesting affects the composition, structure and function of vegetation within the rangelands. Changes in vegetation structure have implications for both biodiversity and the resource users. Due to the many interactions between anthropogenic disturbances and environmental determinants, it is difficult to establish the most important drivers of change in woody species composition and structure over time. The aim of this study was to determine how the density and structure of woody vegetation differs along rainfall and catenal (environmental) gradients, together with the impacts of wood harvesting (anthropogenic disturbance), from 2011 to 2013 in the woodlands of Bushbuckridge, Mpumalanga Province. Three zones were selected that differed in annual rainfall: (a) wet west (>700mm), (b) mesic (600-700mm), and semi-dry east (<600m), with three villages per zone. For the rangeland of each village, plots were sampled in 2011, 2012 and 2013 to cover the variation between the upland and bottomland catenal positions. All harvested and unharvested trees >6m in height, and their individual harvested and unharvested stems, were counted and measured within a total of 56 circular plots (only 28 in 2011) each with a radius of 50m. Trees <6m, and their harvested and unharvested stems, were counted and measured in a circular plot with a radius of 6m, nested centrally within each 50m plot. Frequency of harvesting was based on number of harvested trees and stems. Frequency of harvesting increased over time among trees over 6m, whereas small trees did not show any change over time. The most utilized tree heights were from 0.6-4m and stem diameters from 1.1-10cm. Harvesting was higher in the medium rainfall zone, while both catenal positions had similar harvesting intensities. Differences in harvesting intensity across rainfall zones had a stronger influence on tree density and structure than catenal position.

Keywords: Density, fuelwood, harvesting, rangelands, structure

3.2 INTRODUCTION

People in different areas and with different incomes have different needs for wood. . Within these communities, the range of services and goods provided by wooded ecosystems are of great importance (Pote et al. 2006). These include wood fuels, timber, fruits, wild herbs, mushrooms, honey, shade, shelter and materials for making household utensils, to name but a few (Arnold 1987; Higgins *et al.* 1999; Moe and Rackman 1992; Pote et al. 2006; Twine 2005). The ecological importance of trees in the surrounding ecosystems include fodder provision for both wild and domestic animals, nesting sites and habitats for both birds and reptiles, micro-habitats for germination, sub-canopy environments and rich nutrient pools within a landscape (Pote et al. 2006).

Natural vegetation plays a vital role in the survival and livelihoods of rural households (Dovie *et al.* 2004; Giannecchini *et al.* 2007; Shackleton *et al.* 2005; Twine *et al.* 2003a; Twine 2005; Williams and Shackleton 2002). Harvesting of these natural resources is a land-based livelihood strategy which provides for both daily needs and enables income generation during times of unemployment and financial difficulties (Giannecchini *et al.* 2007; Shackleton *et al.* 2005; Twine 2005). The use of natural resources is not restricted to poor households, as is commonly believed (Madubansi and Shackleton 2007; Shackleton and Shackleton 2006; Twine *et al.* 2003a). The only difference found by Twine *et al.* (2003a) between poor and wealthy households in rural Limpopo Province is the level of reliance on the resources. Poor households rely more on fuelwood as their main fuel source whereas wealthier households will rely on both fuelwood and other different types of fuel resources (Arnold 1987; Madubansi and Shackleton 2007). Shackleton and Shackleton (2006) found no differences in the reliance on natural resources between household of different wealth status in the Kat River valley in the Eastern Cape. This shows that the relationship is not consistent across localities and different socio-economic or ecological contexts. However, wealthy households typically use more resources than poor households (Twine *et al.* 2003, Shackleton and Shackleton 2006). As all wood used in developing countries is mainly for fuelwood purposes within households, fuelwood is one of the many important resources to poor and rural communities (Arnold 1987; Dovie *et al.* 2004; Madubansi and Shackleton 2007).

Even with the availability of electricity as an energy substitute, both poor and wealthy households continue to use fuelwood as the primary source of energy (Dovie *et al.* 2004; Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013). This is because fuelwood harvested from surrounding woodlands provides households with a free or cheap

energy source that does not require the use of expensive appliances (Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013). It has been shown that even in the cases where communities were supplied with electricity, the use of fuelwood is still widespread as the cost of electrical appliances and electrical power is unaffordable (Madubansi and Shackleton 2007; Twine *et al.* 2003a; Wessels *et al.* 2013). The use of energy substitutes increased the financial burdens of rural and poor household and did not bring any relief to their fuel-dependent status (Wessels *et al.* 2013). This is mainly as the energy substitutes are more expensive than fuelwood and the monetary income of the household is not increasing to ensure the possibility of affording the substituted energy supplies (Dovie *et al.* 2004; Wessels *et al.* 2013).

The availability of fuelwood is one important requirement for livelihoods within the rural municipality of Bushbuckridge, Mpumalanga Province, South Africa. In this region, 95% of households use fuelwood, with 80% relying on fuelwood as their primary fuel source (Madubansi and Shackleton 2007). The remaining 15% use fuelwood occasionally (Madubansi and Shackleton 2007). The other uses for fuelwood include heating and lighting (O'Keefe and Raskin 1985; Madubansi and Shackleton 2007; Twine 2005). In the past, only dead wood was harvested, but live branches and stems are now harvested as deadwood is scarce or completely absent from surrounding areas (Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Williams and Shackleton 2002). As much as 93% of the demand for fuelwood is met by live wood that is harvested in an unsustainable way (Neke *et al.* 2006). Wood collected is often harvested coppice stems or pollarded shoots (Van Gelder *et al.* 1983; Williams and Shackleton 2002; Matsika *et al.* 2013a). The scarcity of wood often results in wood purchasing increasing (Matsika *et al.* 2013a). In 2002, 31% of households in Bushbuckridge in Mpumalanga Province, purchased fuelwood (Madubansi and Shackleton 2007; Matsika *et al.* 2013a).

The harvesting of fuelwood has an impact on the ecosystem (Jurisch *et al.* 2012; Pote et al. 2006; Shackleton *et al.* 2007). The most noticeable at the community level is the change in physiognomy by the removal of certain size classes and the increased production of coppice regrowth (Higgins *et al.* 1999; Twine 2005). The structure of the most utilised species populations has become characterised by a decline in large mature stems and an increased abundance of smaller stems (Jurisch *et al.* 2012; Higgins *et al.* 1999; Kaschula *et al.* 2005; Twine 2005). Harvesting and resprouting results in sexually mature individuals reverting to a functionally juvenile growth phase and reducing the production of seeds

(Kaschula *et al.* 2005; Twine 2005). Most savanna tree species have the ability to coppice if stems are damaged or killed (Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). Coppicing mitigates, to some degree, the impacts of fuelwood harvesting on stem density (Twine 2005). The increased harvesting of live stems and widespread coppice regrowth has changed the tree morphology of many woody species (Higgins *et al.* 1999; Twine 2005).

Changes in spatial patterns of vegetation structure of savannas are driven by environmental determinants such as rainfall and soil, but also by different land use practices, as seen in communal rangelands (Breshears and Barnes 1999; Colgan *et al.* 2012; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Shackleton *et al.* 1994; Shackleton 1999; Witkowski and O'Connor 1996). Topography plays a key role in determining savanna vegetation structure (Coughenour and Ellis 1993; Fisher *et al.* 2009; Kanniah *et al.* 2010; Shackleton 1999; Witkowski and O'Connor 1996). Savannas consist of catenal sequences which generally have distinct uplands and bottomlands, especially in granitic landscapes (Colgan *et al.* 2012; Parsons *et al.* 1997; Scholes and Walker 1993). The granite landscapes have steeper gradients than basalt landscapes in the Lowveld (Colgan *et al.* 2012). Different topographical locations have different vegetation composition and structure which is adapted to the particular topographic position (Colgan *et al.* 2012). On hill crests on granitic soils (deep sandy soil), the woody vegetation composition is dominated by broad-leaved trees whereas the bottomlands (sodic clay soil) are often dominated by fine-leaved trees (Colgan *et al.* 2012; Dzerefos *et al.* 2003; Parsons *et al.* 1997; Witkowski and O'Connor 1996). The structure of communities, within the heavily utilized areas of this study, which occur in the bottomlands, are often short and multi-stemmed such as *Dichrostachys cinerea,* whereas the communities on the hill crests are often tall with single stems such as *Sclerocarya birrea* (Fraser *et al*. 1987; Kaschula *et al.* 2005; Smith and Walker 2010).

The typical savanna experiences strongly contrasting seasonal conditions, with rainfall being largely unpredictable and variable between years (Colgan *et al.* 2012; Frost *et al.* 1986; Le Roux and Bariac 1998). Savannas are generally considered water-limited systems. Water limits vegetation growth by 40% on a global scale, and the availability of water is thus one of the key environmental determinants of change in vegetation structure and composition, not only in savannas, but globally as well (Archibald and Scholes 2007; Colgan *et al.* 2012; Kanniah *et al.* 2010; Nemani *et al.* 2003; Scholes and Archer 1997; Smith and Goodman 1986). The availability of water is dependent on the annual rainfall, infiltration and

retention capacity of the soil, to name a few (Kanniah *et al.* 2010). The vegetation structure differs between rainfall zones, with the high rainfall zones having more tall and dense woody vegetation than the dry rainfall zones which have less dense and shorter woody vegetation (Fraser *et al.* 1987).

With the possible interactions between anthropogenic disturbances and environmental determinants it is difficult to distinguish and single out which of the two has a greater role in the differences observed in the composition and structure of the woody vegetation (Dube and Pickup 2001; Jurisch *et al.* 2012; Shackleton 1999). Each component of woody vegetation is driven by various factors, some are more important drivers than others, but in particular combination result in the observed differences in structure and composition (Coughenour and Ellis 1993). If one is to establish the reason for change within a savanna ecosystem, a combination of various factors is of importance (Belsky 1990; Colgan *et al.* 2012; Coughenour and Ellis 1993; Kanniah *et al.* 2010; Shackleton 1999; Walker 1987; Witkowski and O'Connor 1996).

The aim of this study was to determine how the density and structure of woody vegetation differs along rainfall and catenal (environmental) gradients for harvested and unharvested trees, from 2011 to 2013 in the woodlands of Bushbuckridge, Mpumalanga Province. This was determined by answering four questions. Firstly, how does woody vegetation density and structure of harvested and unharvested trees differ over time? Secondly, how does woody vegetation density and structure of harvested species differ across rainfall zones over time? Thirdly, how does woody vegetation density and structure of harvested species differ across catenal positions over time? Finally, how does woody vegetation density and structure of harvested species differ across a combination of rainfall zones and catenal position over time?

3.3 MATERIALS AND METHODS

3.3.1 Study site

See Chapter 2 section 2.3.1

3.3.2 Study design

See Chapter 2 sections 3.2.2.1 and 3.2.2.2

3.3.3 Data analysis

All data analysis was done in the open source R2.1.0 statistical program and its contributing packages (R Development Core Team 2005). All variables were tested for normality with Shapiro-Wilk normality tests and data were log transformed if necessary. As 2011 only had 28 plots sampled and 2012 and 2013 had 56 plots, two sets of analyses were done (a) for the same 28 plots for 2011, 2012 and 2013 as well as (b) for the 28 plots in 2011 and 56 plots in 2012 and 2013. Throughout the rest of the text, the number of plots (28 or 56) of each year, will be seen in subscript next to the selected year, for example, for the 28 plot datasets: 2011_{28}, 2012_{28}, 2013_{28} and for 56 plots: 2012_{56} and 2013_{56}**.** In the case where a tree was harvested and height was unattainable, due to main tree stem being cut down at basal level, the tree was classified as a large tree if the stem was >20cm in diameter and as a small trees if the stem diameter was <20cm in diameter.

3.3.3.1 Change in density of harvested stems/plants

Harvested and unharvested tree and stem frequency values per plot were converted to density (trees per ha and stems per ha), (see Chapter 2 section 2.3.3.1). For harvested and unharvested stem density at the plot level, one-way ANOVAs were used to (a) statistically compare means between the three rainfall zones and (b) between catenal positions (harvested and unharvested trees separately). For harvested and unharvested stem density at the plot level, two-way ANOVAs were also done to statistically compare means between rainfall zones, catenal positions as well as the interactions between the two. If the ANOVAs detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

3.3.3.2 Difference in size structure

Size structure was analysed as (a) harvested and (b) unharvested stems for both height structure and stem diameter structure. The >6m tall trees of the 50m radius plots were more sparsely distributed than the <6m tall trees of the 6m radius plot. For the combination of large and small trees, a scaling factor was calculated (see Chapter 2 section 2.3.3.2).

Height Structure: Two-way ANOVAs were used to compare (a) harvested and (b) unharvested abundance between combinations of rainfall and catenal categories for each of the eight different height classes ($\leq$0.5m, 0.6-1m, 1.1-2m, 2.1-4m, 4.1-6m, 6.1-8m, 8.1-10.0m, >10m). One-way ANOVAs were done to compare abundance (a) between the size classes for (i) harvested and (ii) unharvested stems of the three rainfall zones (high, medium

and low) and (b) between catenal positions (bottomland and upland), for each year separately (2011 to 2013). If the ANOVA test detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

The Kolmogorov-Smirnov (KS) two-sample test was used to contrast tree height size class distributions (SCD_{ht}) for harvested and unharvested trees (combined) across the three years ((i) 2011 vs. 2012, (ii) 2011 vs. 2013 & (iii) 2012 vs. 2013) in order to assess if the overall population structure had changed.

Stem diameter structure: Two-way ANOVAs were used to compare mean stem abundance for (a) harvested and (b) unharvested trees between combinations of rainfall and catenal categories for each of the five stem diameter size class categories. Adjusting of size classes was done due to the 2011 size class distributions (≤1cm (excluding new seedlings), 2-5cm, 6-10cm, 11-15cm, 16-20cm, 21-25cm, 26-30cm, 31-35cm, 36-40cm, 41-45cm, >45cm) being different from 2012 and 2013 (≤1cm (excluding new seedlings), 1.1-4.0cm, 4.1-10.0cm, 10.1-20.0cm, 20.1-40.0cm, >40.1cm). In order to compare between years, the data was adjusted (≤1cm (excluding new seedlings), 1.1-10.0cm, 10.1-20.0cm, 20.1-40.0cm, >40.1cm) into new size class distributions with fewer classes. One-way ANOVAs were done to compare abundance (a) between the size classes for (i) harvested and (ii) unharvested stems of the three rainfall zones (high, medium and low) and (b) between catenal positions (bottomland and upland), for each year separately (2011 to 2013). If the ANOVA test detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

The Kolmogorov-Smirnov (KS) two-sample test was used to contrast tree height size class distributions (SCD_{ht}) for harvested and unharvested trees (combined) across the three years ((i) 2011 vs. 2012, (ii) 2011 vs. 2013 & (iii) 2012 vs. 2013) in order to assess if the overall population structure had changed.

3.4 RESULTS

3.4.1 Recent harvesting impact over time

The mean density of recently harvested stems of large trees over 6m increased significantly between 2012 and 2013 for both datasets (Fig 3.1A and B). Densities of unharvested stems were not different over time for both 28 and 56 plots. For small tress, density of harvested stems only increased significantly ($p<0.05$) over time in the 28 plots (Fig

3.1C). Densities of unharvested stems for small trees were not significantly different over time (Fig 3.1C). Density of harvested stems in the 56 plots did not differ significantly over time but the unharvested stem density did however decrease (Fig 3.1D).

The impact of harvesting within height size class distributions (SCD_{ht}) was mostly seen between the 0.6-4m tree heights in 2011 (Fig 3.2). Recent harvesting of small trees (<6m in height) in 2011 was 5% of total tree abundance, 17% in 2012 and 9% in 2013. Recent harvesting of large trees (>6m in height) was absent in 2011. Harvesting became more apparent in large trees in 2012 and 2013 (Fig 3.2). The SCD_{ht} for recently harvested trees were not different between each pair of years but unharvested tree abundance of 2012 was significantly higher in 2011 and 2013 (Table 3.1).

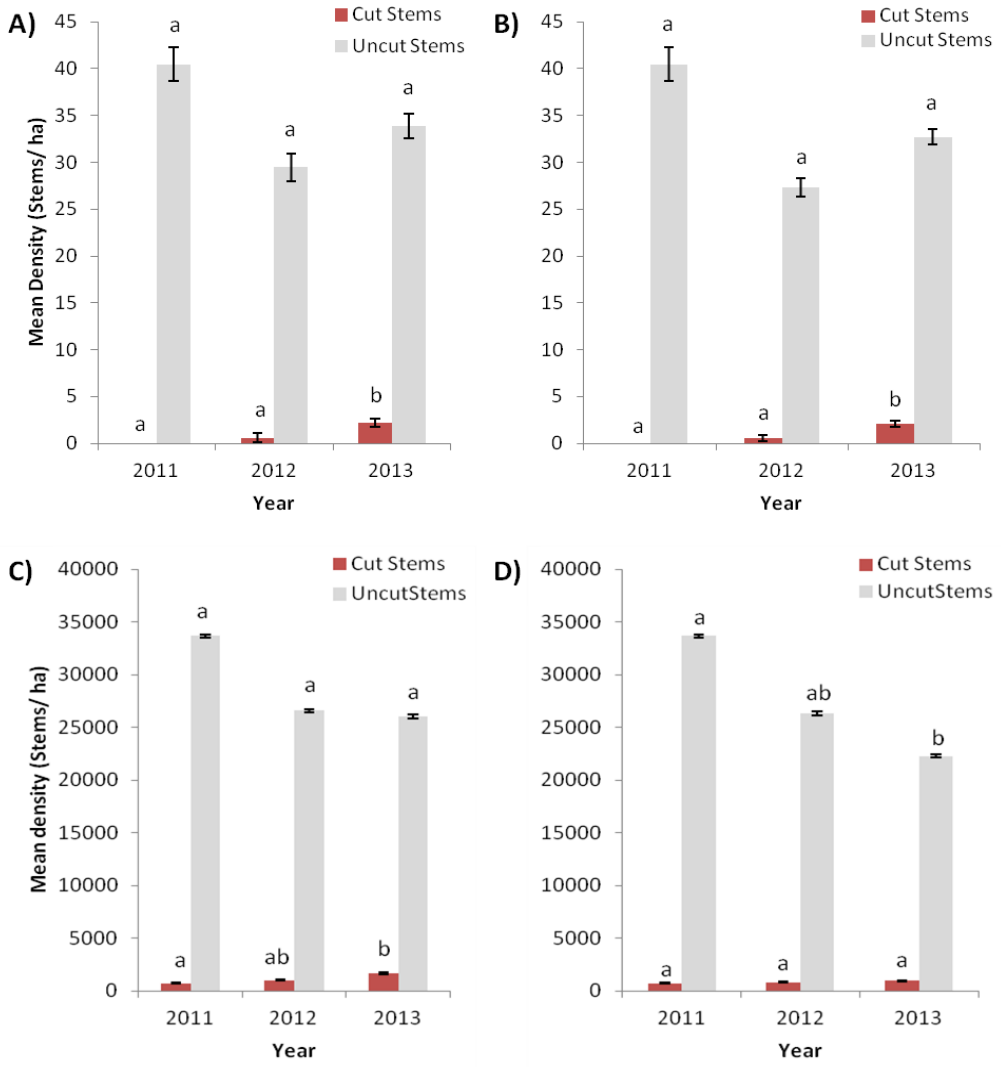


Figure 3.1 Overall mean (± SE) density of harvested (=cut) and unharvested (=uncut) stems for original 28 plots only datasets for (A) large and (C) small trees, as well as for all plot datasets (28 in 2011 and 56 in 2012 and 2013) for (B) large and (D) small trees, from 2011 to 2013. Different letters indicate significant differences between years (P<0.05, Tukey).

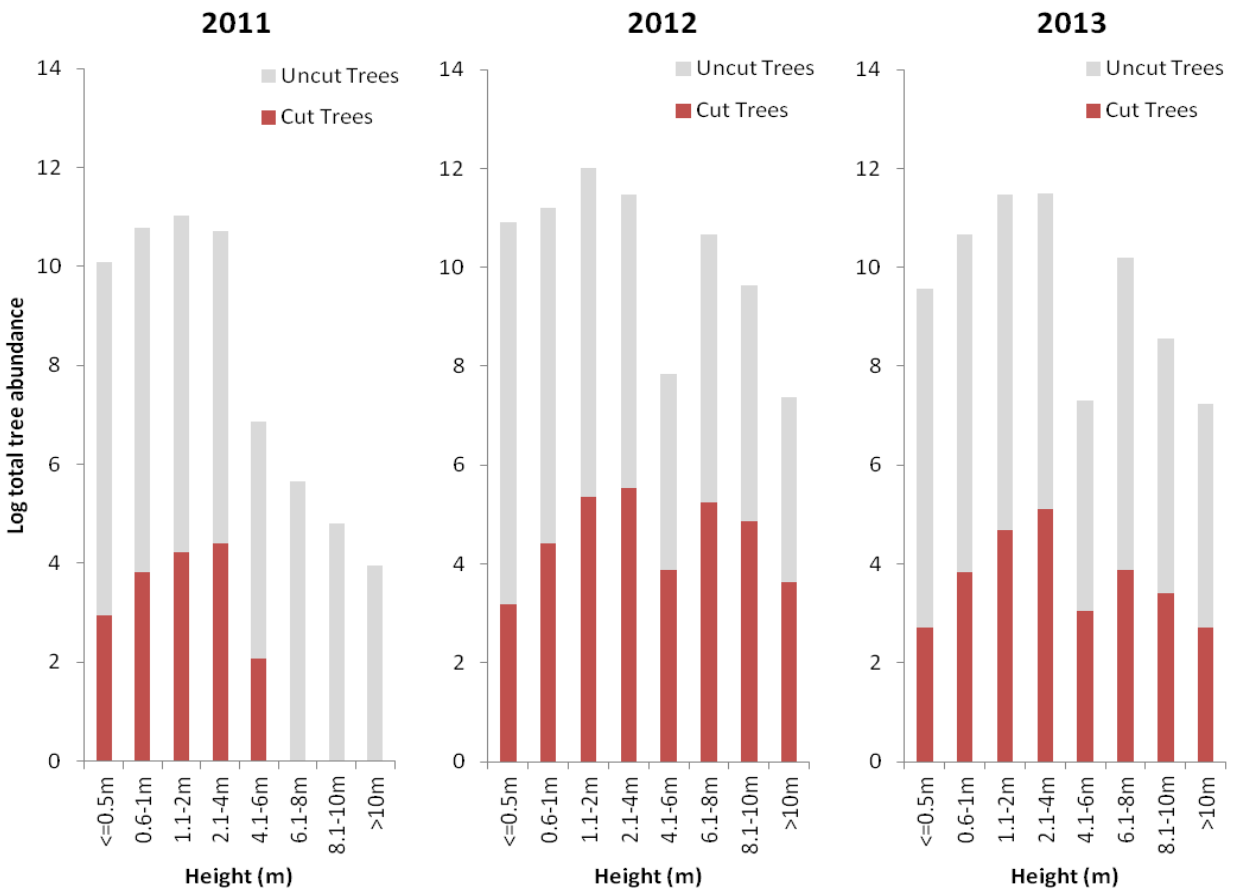


Figure 3.2 Comparison of height size class distributions (SCD_{ht}) for recently harvested and unharvested tree abundances (combined to give total abundance) in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 3.1 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) for recently harvested and unharvested trees between years for all trees (large and small trees combined). Significant p-values in bold type.

Comparison	Kolmogorov-Smirnov (KS) Test			
	Harvested trees		Unharvested trees	
	D value	p-value	D value	p-value
2011 vs. 2012	0.500	0.142	0.658	**0.003**
2011 vs. 2013	0.250	0.675	0.250	0.932
2012 vs. 2013	0.250	0.926	0.652	**0.002**

The impact of harvesting on the stem diameter size class distribution (SCD_{diam}) was mostly in the 1.1-10cm class for each year, expressed as a proportion of stems it increased over time from 2% in 2011, to 3% in 2012, and 4% in 2013 (Fig 3.3). The SCD_{diam} of both recently harvested and unharvested stems showed no difference in the distributions between each pair of years (Table 3.2).

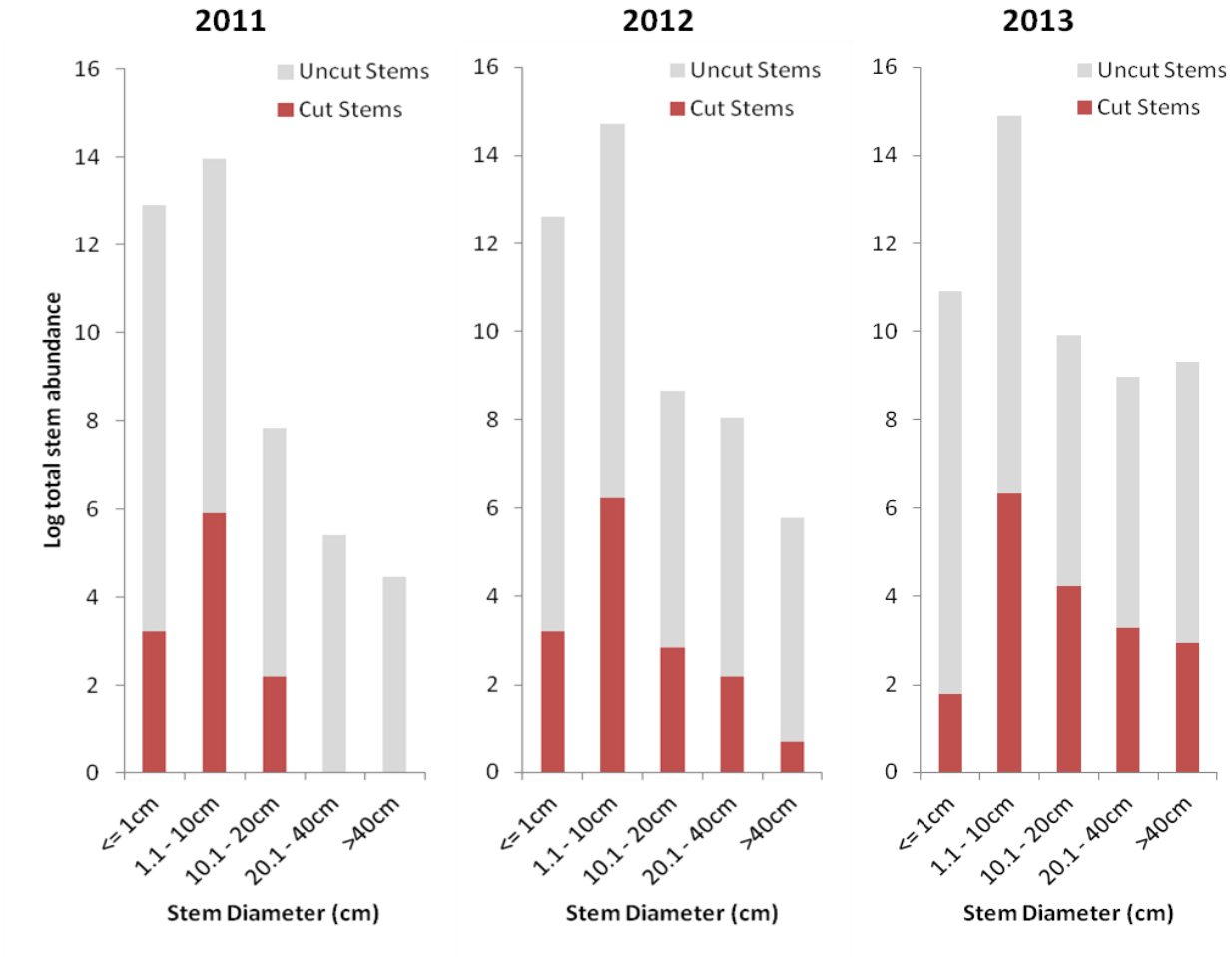


Figure 3.3 Comparison of stem diameter size class distributions (SCD_{diam}) for recently harvested and unharvested stem abundance (bars combine them to give total abundance) in 2011, 2012 and 2013 for all trees (large and small trees combined).

Table 3.2 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) for recently harvested and unharvested stems between years for all trees (large and small trees combined).

Comparison	Kolmogorov-Smirnov (KS) Test			
	Harvested stems		Unharvested stems	
	D value	p-value	D value	p-value
2011 vs. 2012	0.200	1.000	0.400	0.815
2011 vs. 2013	0.200	1.000	0.600	0.352
2012 vs. 2013	0	1.000	0.200	1.000

The difference between years in harvesting intensity seems higher in SCD_{ht} (Fig 3.2) than SCD_{diam} (Fig 3.3). This is because SCD_{ht} was based on abundance of whole trees (Fig 3.2), whereas SCD_{diam} were based on abundance of stems (Fig 3.3). Due to some trees being multi-stemmed, the difference in harvesting is higher in the SCD_{ht} than in the SCD_{diam}.

3.4.2 Recent harvesting across rainfall zones over time

Density of harvested stems over time did not change within any rainfall zone between 2011_{28}, 2012_{28} and 2013_{28} for large trees (Fig 3.4A), but did increase significantly ($p<0.05$) in all three rainfall zones from 2012_{56} to 2013_{56} (Fig 3.4C). There was no difference between the rainfall zones for harvested stems of large trees (Fig 3.4A and C). Density of unharvested stems for large trees did not change over time in either the 28 or 56 plots (Fig 3.4B and D). The density of unharvested stems among large trees in the high rainfall zone was significantly higher ($p<0.05$) than the low and medium rainfall zones for both the 28 and 56 plots (Fig 3.4B and D). Harvested stem density for small trees was only significantly higher in the medium rainfall zone in 2011_{28} compared to the low and high rainfall zones (Fig 3.4E). No significant difference in harvested stems was seen in 2013_{28} between rainfall zones (Fig 3.4E). Harvested stem density was significantly higher in the medium rainfall zone compared to the low and high rainfall zones for 2012_{56} (Fig 3.4G). Unharvested stem density was significantly higher in the high rainfall zone compared to the low and medium rainfall zones in $2011_{28,}$ 2012_{28} and 2013_{28} (Fig 3.4F). Similarly, unharvested stem density was higher in the high rainfall zone compared to the low and medium rainfall zones for 2012_{56} and 2013_{56} (Fig 3.4H).

The frequency of recent harvesting on SCD_{ht} between rainfall zones (Fig 3.5) was mainly in the smaller height classes (0.6-4m) but was more prevalent in the medium rainfall zone(Fig 3.5D-F) compared to the low (Fig 3.5A-C) and high (Figure 3.5G-I) rainfall zones for all three survey years. In 2011, the proportion of all harvested trees (large and small trees combined) was higher (10%) in the medium rainfall zone (Fig 3.5D) compared to the high rainfall zone (1%) (Fig 3.5G). The medium rainfall zone (Fig 3.5E) had the highest tree harvesting (24%) compared to the lowest harvesting in the high (11%) rainfall zone in 2012 (Fig 3.5H). The medium rainfall zone in 2013 had lower tree harvesting (13%) compared to 2012 but was still the highest impacted rainfall zone (Fig 3.5F). The most utilized tree height classes for harvesting varied between years and between rainfall zones. The most utilized height ranged between ≤0.5m-1.2m in the low rainfall zone (Fig 3.5A-C), 2.1-4m in the medium rainfall zone (Fig 3.5D-F) and 0.6-8m in the high rainfall zone (Fig 3.5G-I). SCD_{ht} only differed between 2011 and 2012 in the low rainfall zone for harvested trees (Table 3.3). All other SCD_{ht} did not differ between years (Table 3.3). Similarly, only the SCD_{ht} of the unharvested trees in the medium rainfall zone, between 2011 and 2013 was significantly different ($p<0.05$). All other SCD_{ht} did not differ between years (Table 3.3).

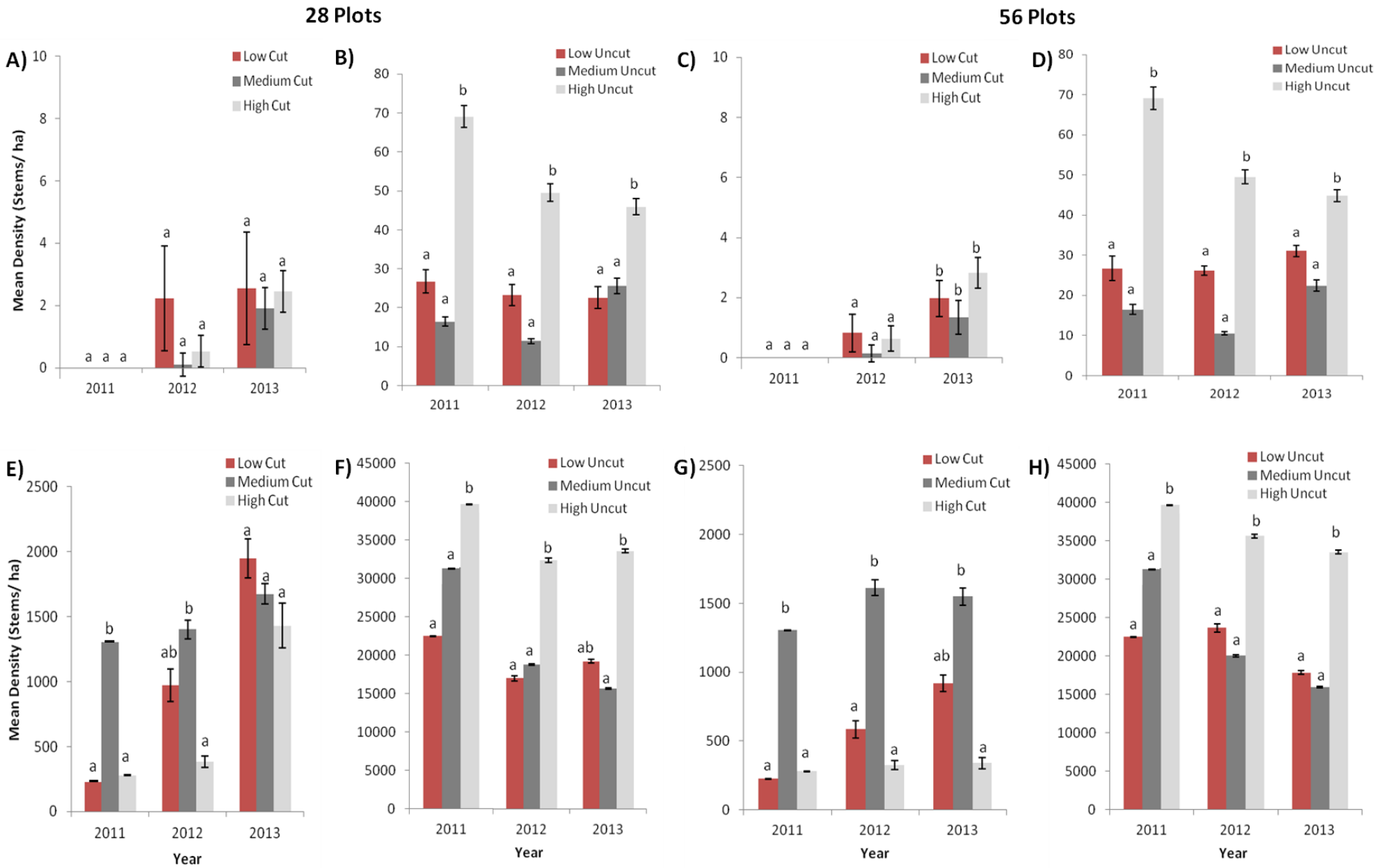


Figure 3.4 Overall mean (±SE) density of recently **harvested stems** (=cut) between rainfall zones (low, medium, high) for 28 plots (A) and 56 plots (C) of large harvested trees and 28 plots (E) and 56 plots (G) of small harvested trees from 2011 to 2013. Similarly, overall mean (±SE) density of **unharvested stems** (=uncut) between rainfall zones for 28 plots (B) and 56 plots (D) of large unharvested trees and 28 plots (F) and 56 plots (H) of small unharvested trees from 2011 to 2013. Different letters indicate significant differences between rainfall zones within each year ($P<0.05$, Tukey).

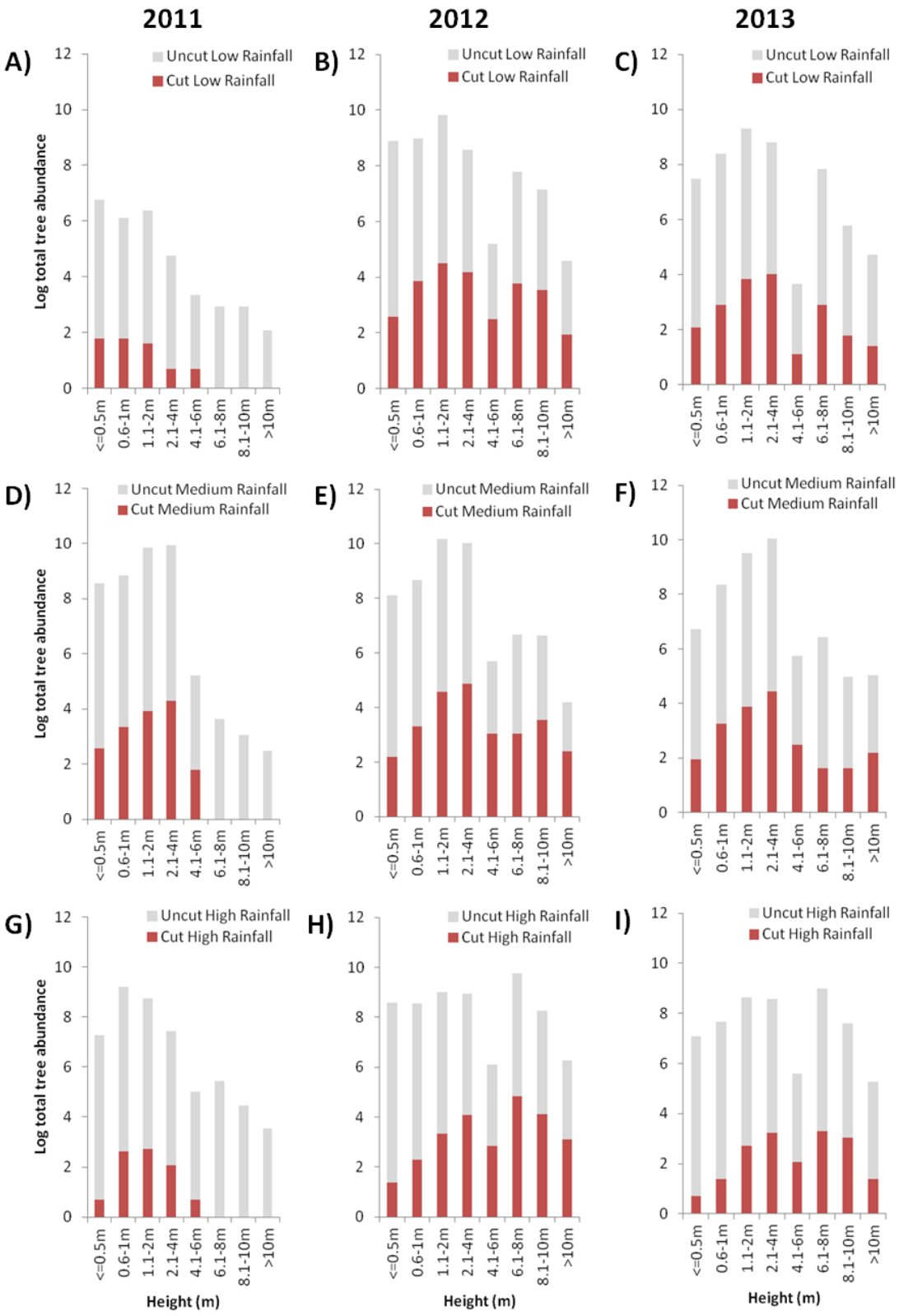


Figure 3.5 Comparison of height size class distributions (SCD_{ht}) for recently harvested (=cut) and unharvested (=uncut) trees (combined to total abundance) between rainfall zones (low, medium, high) in 2011, 2012 and 2013 for all trees (large and small trees combined). Rows illustrate rainfall zones and columns illustrate years.

Table 3.3 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) for recently harvested and unharvested trees within rainfall zones between years for all trees (large and small trees combined). Significant p-values in bold type.

Comparison	Rainfall zone	Kolmogorov-Smirnov (KS) Test			
		Harvested trees		Unharvested trees	
		D value	p-value	D value	p-value
2011 vs. 2012	Low	0.625	**0.030**	0.250	0.930
2011 vs. 2013	Low	0.250	0.787	0.250	0.956
2012 vs. 2013	Low	0.375	0.442	0.250	0.904
2011 vs. 2012	Medium	0.500	0.155	0.250	0.927
2011 vs. 2013	Medium	0.125	1.000	0.818	< **0.001**
2012 vs. 2013	Medium	0.375	0.517	0.693	0.251
2011 vs. 2012	High	0.500	0.135	0.250	0.971
2011 vs. 2013	High	0.250	0.615	0.250	0.956
2012 vs. 2013	High	0.375	0.288	0.250	0.934

The impact of harvesting on SCD_{diam} between rainfall zones (Fig 3.6A-I) was mainly in the smaller diameter classes (≤1cm-10cm) and was also more prevalent in the medium rainfall zone across time (Fig 3.6D-F). The medium rainfall zone (Fig 3.6D-F) had the highest stem harvesting compared to the low (Fig 3.6A-C) and high (Fig 3.6G-I) rainfall zone for 2011, 2012 and 2013. Recent harvesting of stems increased from 4% in 2011, to 7% in 2012 and 9% in 2013 in the medium rainfall zone (Fig 3.6D-F). The most utilized stem diameter for harvesting was dominated by the 1.1-10cm size class across all three rainfall zones and the three survey years (Fig 3.6). Harvesting of larger stems (>20cm diameter) was absent in 2011 but became more prevalent over time. SCD_{diam} did not differ significantly for harvested or unharvested stems between rainfall zones in any of the three survey years (Table 3.4).

Table 3.4 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) for recently harvested and unharvested stems within rainfall zones between years for all trees (large and small trees combined).

Comparison	Rainfall zone	Kolmogorov-Smirnov (KS) Test			
		Harvested stems		Unharvested stems	
		D value	p-value	D value	p-value
2011 vs. 2012	Low	0.200	1.000	0.200	1.000
2011 vs. 2013	Low	0.200	1.000	0.400	0.813
2012 vs. 2013	Low	0.200	1.000	0.400	0.804
2011 vs. 2012	Medium	0.200	1.000	0.400	0.807
2011 vs. 2013	Medium	0.200	1.000	0.600	0.362
2012 vs. 2013	Medium	0.200	1.000	0.400	0.813
2011 vs. 2012	High	0	1.000	0.200	1.000
2011 vs. 2013	High	0	1.000	0.400	0.806
2012 vs. 2013	High	0	1.000	0.200	1.000

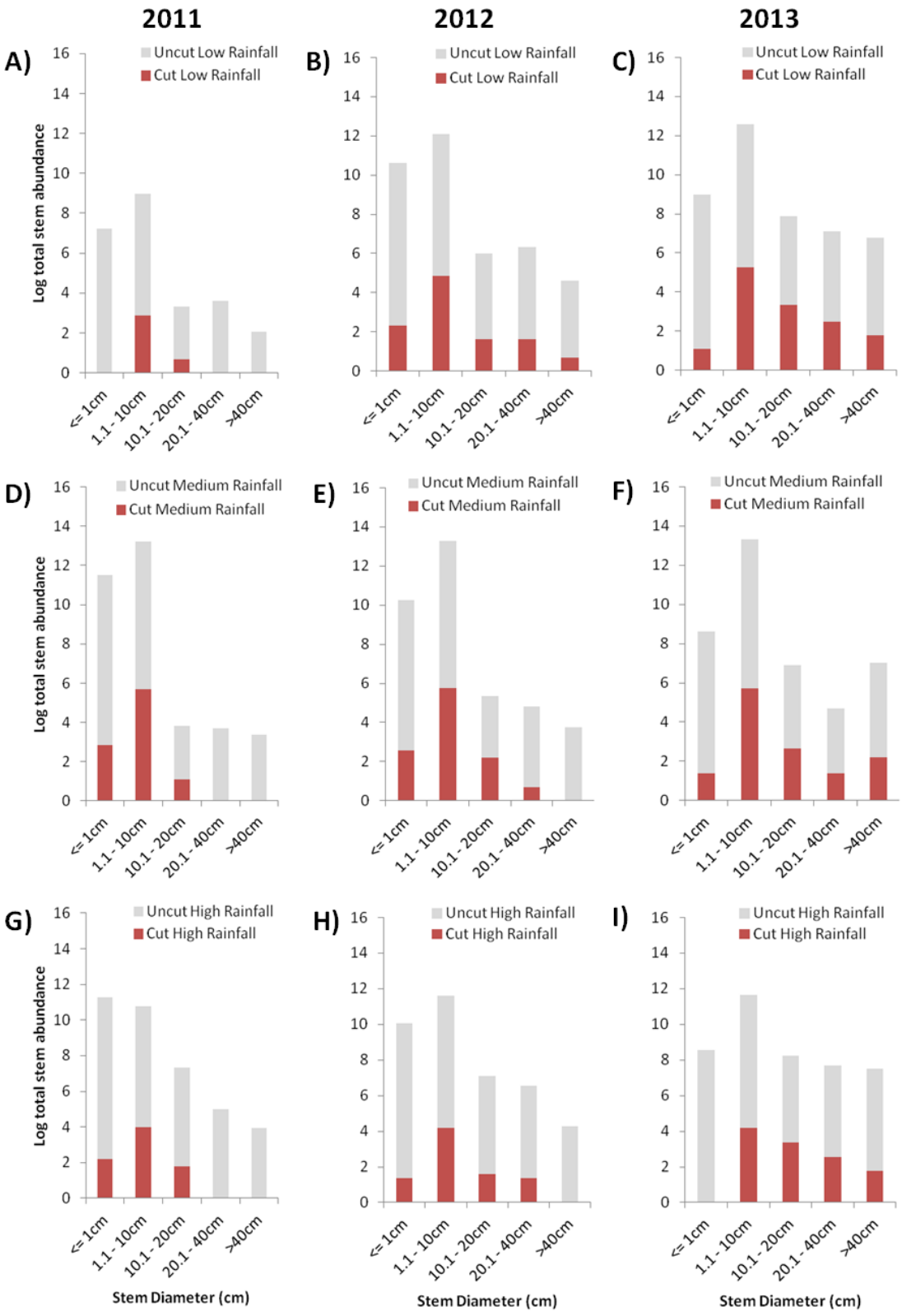


Figure 3.6 Comparison of stem diameter size class distributions (SCD_{diam}) for recently harvested (=cut) and unharvested (=uncut) trees (combined to total abundance) between rainfall zones (low, medium, high) within 2011, 2012 and 2013 for all trees (large and small trees combined). Rows illustrate rainfall zones and columns illustrate years.

3.4.3 Recent harvesting across catenal position over time

Density of harvested stems increased significant among large trees from $2012_{28\&56}$ to $2013_{28\&56}$ in both upland and bottomland plots (Fig 3.7A and C). Density of unharvested stems among large trees decreased from 2011_{28} to 2012_{28} in the upland plots and but there was no change in the bottomland plots (Fig 3.7B). Unharvested stem density was significantly higher in the uplands than in the bottomland plots for 2011_{28} whereas for 2012_{28} and 2013_{28}, stem densities did not differ between upland and bottomland plots (Fig 3.7B). Unharvested stem density was higher in the uplands than bottomland plots for large trees in 2012_{56} and 2013_{56} (Fig 3.7D). Small tree stem density had no difference between catenal position for both harvested and unharvested stems of both 28 and 56 plots (Fig 3.7 E- H). There was no change over time in harvested stems among small trees for both 28 (Fig 3.7E) and 56 plots (Fig 3.7G). Only unharvested stem density tended to decreased for the 56 plots among small trees (Fig 3.7H) from 2011 to 2013 but there was no change over time for the 28 plots (Fig 3.7F).

SCD_{ht} showed a preferred harvesting height that ranged between 0.6-4m for both upland and bottomland plots across the three survey years (Fig 3.8A-F). The proportion of harvested trees was very similar between upland and bottomland plots. Harvesting in the bottomland (7%) and upland (3%) plots was only different in 2011 whereas 2012 (17%) and 2013 (9%) had equal harvesting between upland and bottomland plots (Fig 3.8). The most preferred height for harvesting was found to range between 2.1-4m in the bottomlands (Fig 3.8A-C) and between 2.1-4m in the uplands (Fig 3.8D-F) across the three survey years. The distributions of each year for the upland and bottomland positions showed no differences between 2011 and 2012, 2011 and 2013 or 2012 and 2013 for either harvested or unharvested trees (Table 3.5).

SCD_{diam} had a preferred harvesting of 1.1-10cm diameter size class for both upland and bottomland plots across the three survey years (Fig 3.9A-F). Harvesting was absent from larger stems (>20cm diameter) in the upland and bottomland plots of 2011. The distributions between upland and bottomland catenal positions showed no difference in abundance for any of three years for either harvested or unharvested stems (Table 3.6).

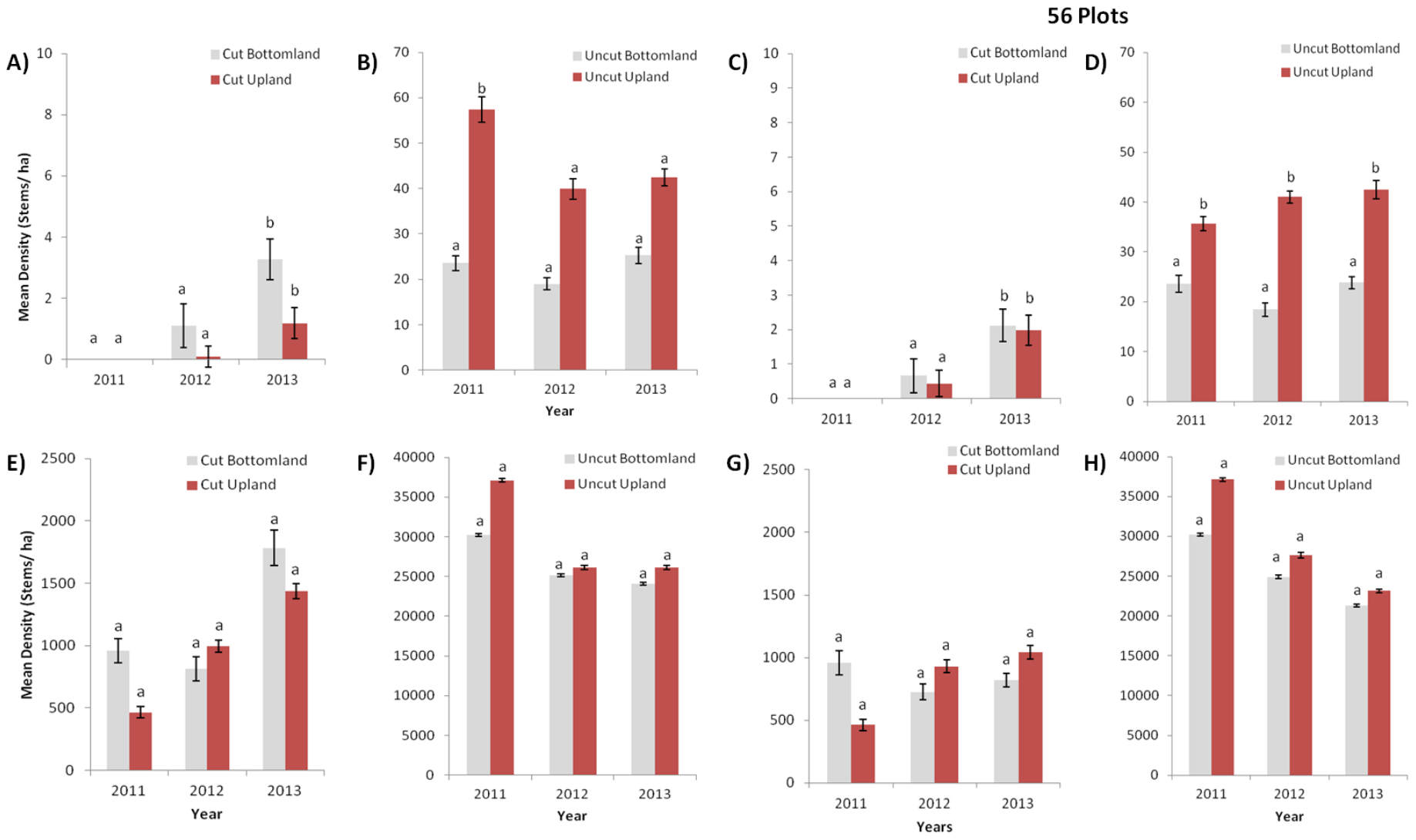


Figure 3.7 Overall mean (±SE) density of recently **harvested stems** (=cut) between catenal positions for 28 plots (A) and 56 plots (C) of large harvested trees and 28 plots (E) and 56 plots (G) of small harvested trees from 2011 to 2013. Similarly, overall mean (±SE) density of **unharvested stems** (=uncut) between catenal positions for 28 plots (B) and 56 plots (D) of large unharvested trees and 28 plots (F) and 56 plots (H) of small unharvested trees from 2011 to 2013. Different letters indicate significant differences between catenal positions within each year.

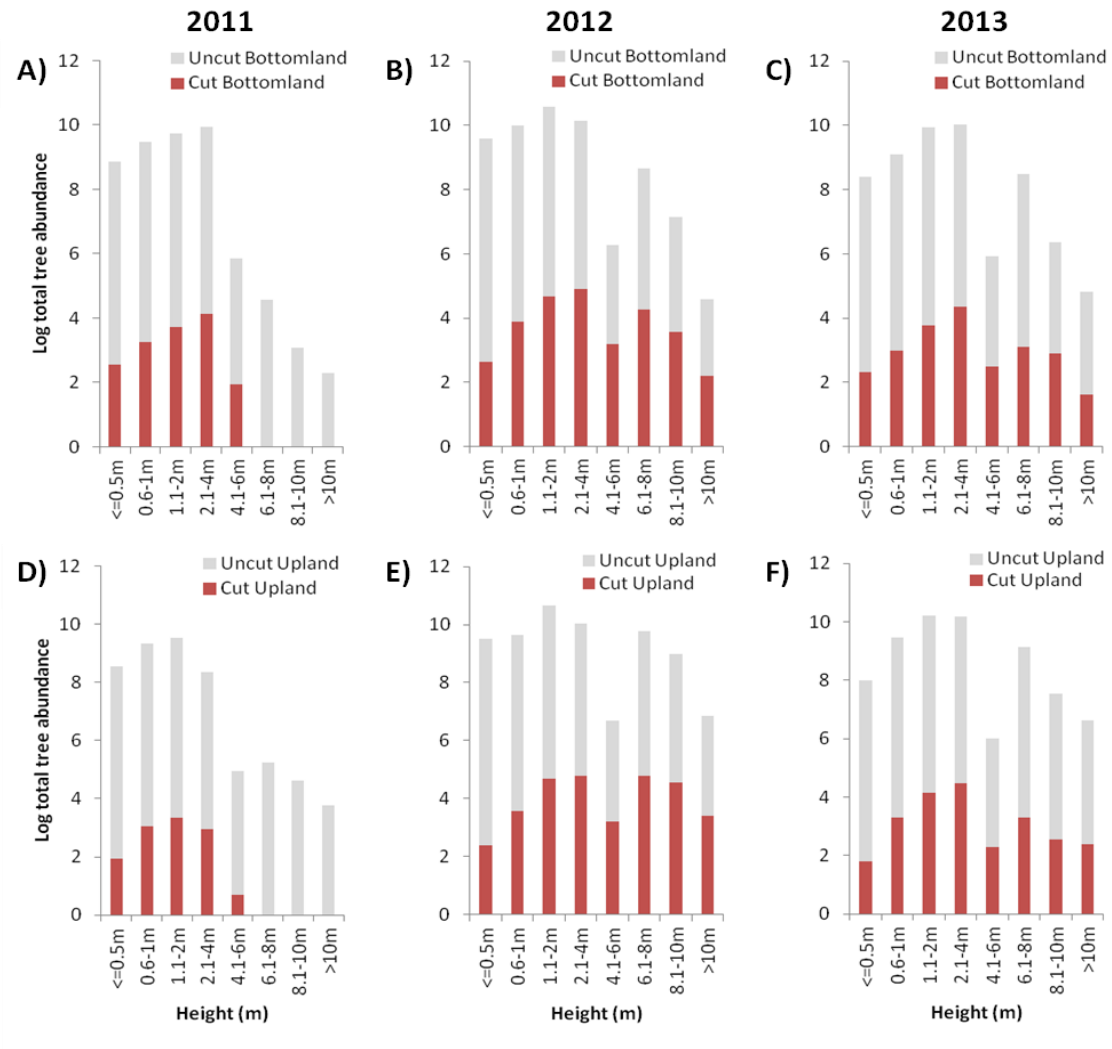


Figure 3.8 Comparison of height size class distributions (SCD_{ht}) for recently harvested (=cut) and unharvested (=uncut) trees (combined to total abundance) between catenal positions in 2011, 2012 and 2013 for all trees (large and small trees combined). Rows illustrate catenal position and columns illustrate years.

Table 3.5 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) for recently harvested and unharvested trees within catenal positions between years for all trees (large and small trees combined).

Comparison	Catenal position	Kolmogorov-Smirnov (KS) Test			
		Harvested trees		Unharvested trees	
		D value	p-value	D value	p-value
2011 vs. 2012	Bottomland	0.250	0.923	0.250	0.968
2011 vs. 2013	Bottomland	0.250	0.875	0.250	0.949
2012 vs. 2013	Bottomland	0.250	0.886	0.250	0.927
2011 vs. 2012	Upland	0.500	0.176	0.400	0.385
2011 vs. 2013	Upland	0.250	0.604	0.250	0.980
2012 vs. 2013	Upland	0.375	0.461	0.400	0.358

Table 3.6 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{diam}) for recently harvested and unharvested stems within catenal positions between years for all trees (large and small trees combined).

Comparison	Catenal position	Kolmogorov-Smirnov (KS) Test			
		Harvested stems		Unharvested stems	
		D value	p-value	D value	p-value
2011 vs. 2012	Bottomland	0	1.000	0.200	1.000
2011 vs. 2013	Bottomland	0	1.000	0.400	0.813
2012 vs. 2013	Bottomland	0	1.000	0.400	0.813
2011 vs. 2012	Upland	0.200	1.000	0.200	1.000
2011 vs. 2013	Upland	0.200	1.000	0.400	0.803
2012 vs. 2013	Upland	0.200	1.000	0.200	1.000

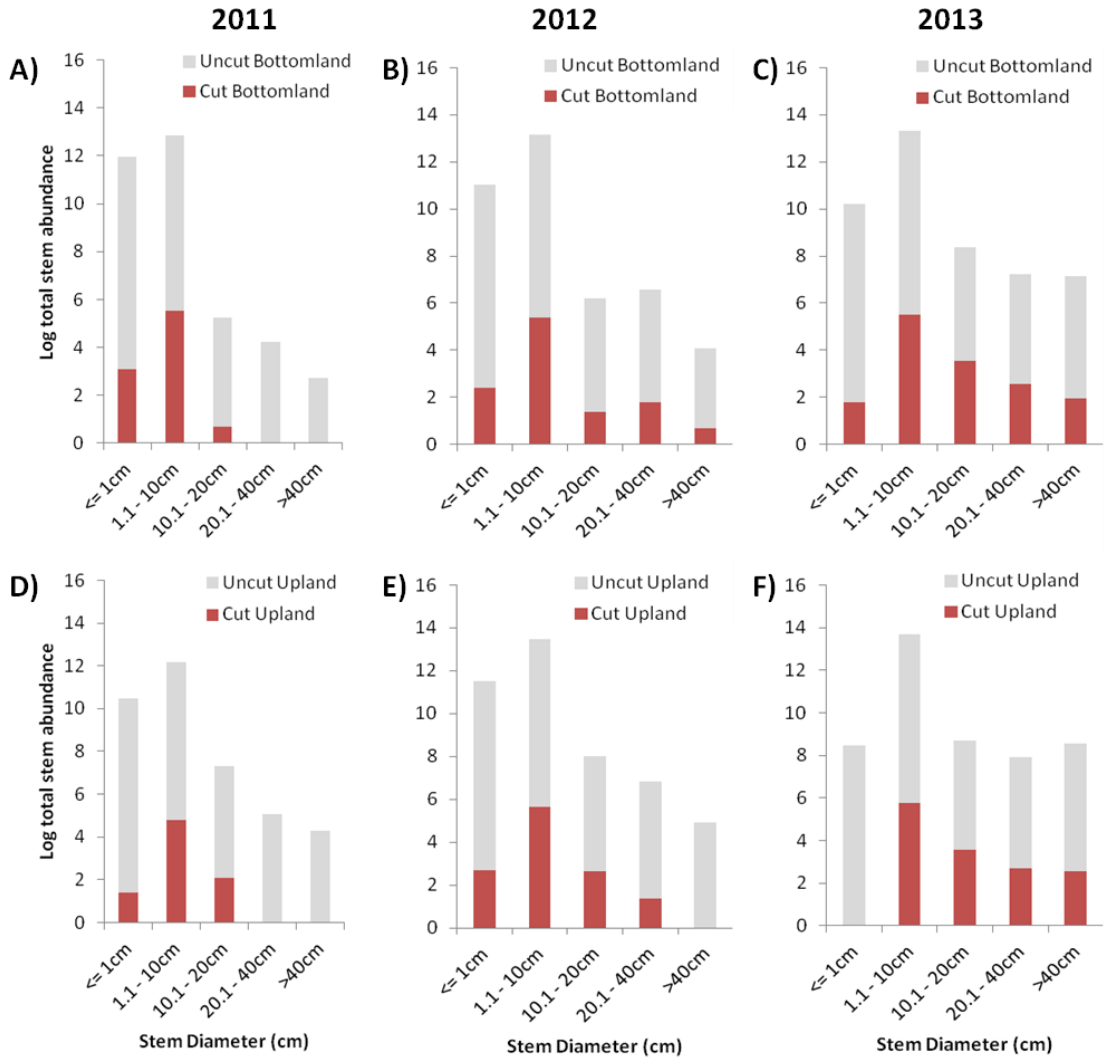


Figure 3.9 Comparison of stem diameter size class distributions (SCD_{diam}) for recently harvested (=cut) and unharvested (=uncut) stems (combined to total abundance) between catenal positions in 2011, 2012 and 2013 for all trees (large and small trees combined). Rows illustrate catenal position and columns illustrate years

3.4.4 Recent harvesting across a combination of rainfall zones and landscape position over time

Recent harvesting was only affected by rainfall zones and not by catenal positions over time (Table 3.7). Harvesting across rainfall zones tended to only influence the change of small tree density over time. Harvesting across catenal position had no influence on the change in density and structure over time (Table 3.7). There was no interaction between harvesting across catenal position and rainfall zones and thus had no influence on the change of density and structure for either large or small trees in any of the three survey years.

Harvested trees and stems: Harvesting across rainfall zones had no significant effect on the density and structure of large trees in either 28 or 56 plots of the three survey years (Table 3.7). Similarly, harvesting across rainfall zones also had no effect on the density and structure of small trees in 2011_{28} and 2013_{28}. Harvesting across rainfall zones did however have a significant effect on the change of density and structure of small trees in $2012_{28\&56}$ as well as in 2013_{56} (Table 3.7). Harvesting across catenal position had no effect on the change in density and structure of either large or small trees for any of the three survey years (Table 3.7).

Unharvested trees and stems: Rainfall zones had a stronger effect on woody vegetation density and structure than catenal positions. Rainfall zones had a stronger effect on the difference in woody vegetation density and structure of large trees in 2011_{28}, 2012_{28} and 2012_{56}. Rainfall had no significant effect on the density and structure of large trees in $2013_{28\&56}$ (Table 3.7). Different to large trees, rainfall zones did have a stronger effect on the difference in density over the three survey years and structure of small trees in $2013_{28\&56}$ but no effect on the difference in density and structure of either 2011_{28} or $2012_{28\&56}$ (Table 3.7). Catenal position only had a stronger effect in the difference of structure and density of large trees in $2012_{56}$and 2013_{56}. There was however no effect by catenal position on the difference in density and structure for large trees in 2011_{28}, 2012_{28} or 2013_{28} or for all small trees of the three survey years (Table 3.7).

Table 3.7 Two-way ANOVAs comparing the effects of rainfall zone, catenal position and the interaction between them for recently harvested and unharvested stem density for large (>6m in height) and small trees (<6m in height) separately. Significant p-values in bold type. No apparent harvesting of large trees in 2011.

Tree size	Year	Plots sampled	Harvested stems			Unharvested stems		
			Rainfall zones	Catenal position	Rainfall* Catenal Interaction	Rainfall zones	Catenal position	Rainfall* Catenal Interaction
			p-value	p-value	p-value	p-value	p-value	p-value
Large trees	2011	28	-	-	-	**0.035**	0.705	0.309
	2012	28	0.801	0.108	0.074	**0.028**	0.103	0.355
		56	0.382	0.577	0.841	**0.001**	**0.033**	0.446
	2013	28	0.939	0.107	0.575	0.298	0.201	0.244
		56	0.377	0.833	0.827	0.093	**0.040**	0.288
Small trees	2011	28	0.052	0.225	0.188	0.319	0.372	0.498
	2012	28	**0.011**	0.535	0.147	0.055	0.859	0.939
		56	**<0.001**	0.267	0.874	0.220	0.694	0.460
	2013	28	0.882	0.628	0.451	**0.017**	0.717	0.691
		56	**<0.001**	0.317	0.693	**0.002**	0.592	0.832

The density of harvested large tree stems had more significant differences between catenal/rainfall combinations than the unharvested large tree stems (Fig 3.10A-H). In 2011, no large trees were harvested (Fig 3.10A and B). Harvested stem density for large trees tended to increase significantly ($p<0.05$) in the bottomland plots in the low rainfall zone from 2012_{28} to 2013_{28} (Fig 3.10A). Harvested stem density in the bottomland plots in the low rainfall zone was significantly higher ($p<0.05$) than the other catenal/rainfall combinations for 2012_{28} and 2013_{28} (Fig 3.10A). Harvested stem density for large trees had no differences between catenal/rainfall combinations in 2011_{28} and 2013_{56} (Fig 3.10B). Stem density for harvested stems in 2012_{56} was higher in the bottomland plots of the low rainfall zone compared to the other catenal/rainfall combination (Fig 3.10B). Unharvested stem density for both 28 and 56 plots did not differ over time (Fig 3.10C and D). The unharvested stem density in $2013_{28\&56}$ was higher in the upland plots in the high rainfall zone compared to all other catenal/rainfall combinations (Fig 3.10C and D).

Harvested small tree stem density in the 28 plots also showed no trending differences over time for catenal/rainfall combinations (Fig 3.10E). Harvested small tree stem density did however increase from 2011_{28} to 2012_{56} in the upland and bottomland plots in the medium rainfall zone (Fig 3.10F). Harvested small tree stem density did not differ between catenal/rainfall combinations (Fig 3.10F) for 2011_{28} whereas the harvested stem density in 2012_{56} was higher in the upland and bottomland plots in the medium rainfall zone compared to the bottomland plots in the low rainfall zone and the upland and bottomland plots in the

high rainfall zone (Fig 3.10F). Similarly, the harvested stem density in 2013_{56} were higher in the upland and bottomland plots in the medium rainfall zones compared to the upland and bottomland plots in the high rainfall zone (Fig 3.10F). Unharvested small tree stem density in the 28 plots was not different over time for catenal/rainfall combinations (Fig 3.10G). Unharvested small tree stem density did however show a trend towards an increase in the bottomland plots in the high rainfall zone from 2011_{28} to 2012_{56} (Fig 3.10H). The unharvested stem density in 2011_{28} was higher in the upland plots in the high rainfall zone compared to all other catenal/rainfall combinations (Fig 3.10H). Whereas, the unharvested stem density in $2012_{28\&56}$ was higher in the upland plots in the low rainfall zone as well as the upland and bottomland plots in the high rainfall zone compared to uplands in the low rainfall zone as well as the uplands and bottomlands in the medium rainfall zone (Fig 3.10H). Similar to 2011_{28}, the unharvested stem density in $2013_{28\&56}$ was only higher in the upland and bottomland plots in the high rainfall zone compared to the other catenal/rainfall combinations (Fig 3.10H).

The impact of recent harvesting within SCD_{ht} between catenal position/rainfall zone combinations were greater in the smaller height classes (Fig 3.11A-R) and was more prevalent in the upland and bottomland plots in the medium rainfall zone (Fig 3.11G-I, J-L). Harvested trees had a higher (15%) relative abundance in the bottomland plots in the medium rainfall zone in 2011 (Fig 3.11G) and the lowest relative abundance (1%) in the bottomland plots in the high rainfall zone (Fig 3.11M). This increased in 2012 with the highest harvesting (27%) being in the bottomland plots of the medium rainfall zone (Fig 3.11H) and the lowest harvesting (9%) being in the bottomland plots in the high rainfall zone (Fig 3.11N). Whereas in 2013, harvesting decreased with the highest harvesting (18%) being in the upland plots in the medium rainfall zone (Fig 3.11L) and the lowest harvesting (4%) being in the upland plots in the high rainfall zone (Fig 3.11R). Harvesting of large trees (>6m) was absent in 2011 (Fig 3.11A, D, G, J, M, P) but was however prevalent in 2012 (Fig 3.11B, E, H, K, N, Q) and 2013 (Fig 3.11C, F, I, L, O, R).

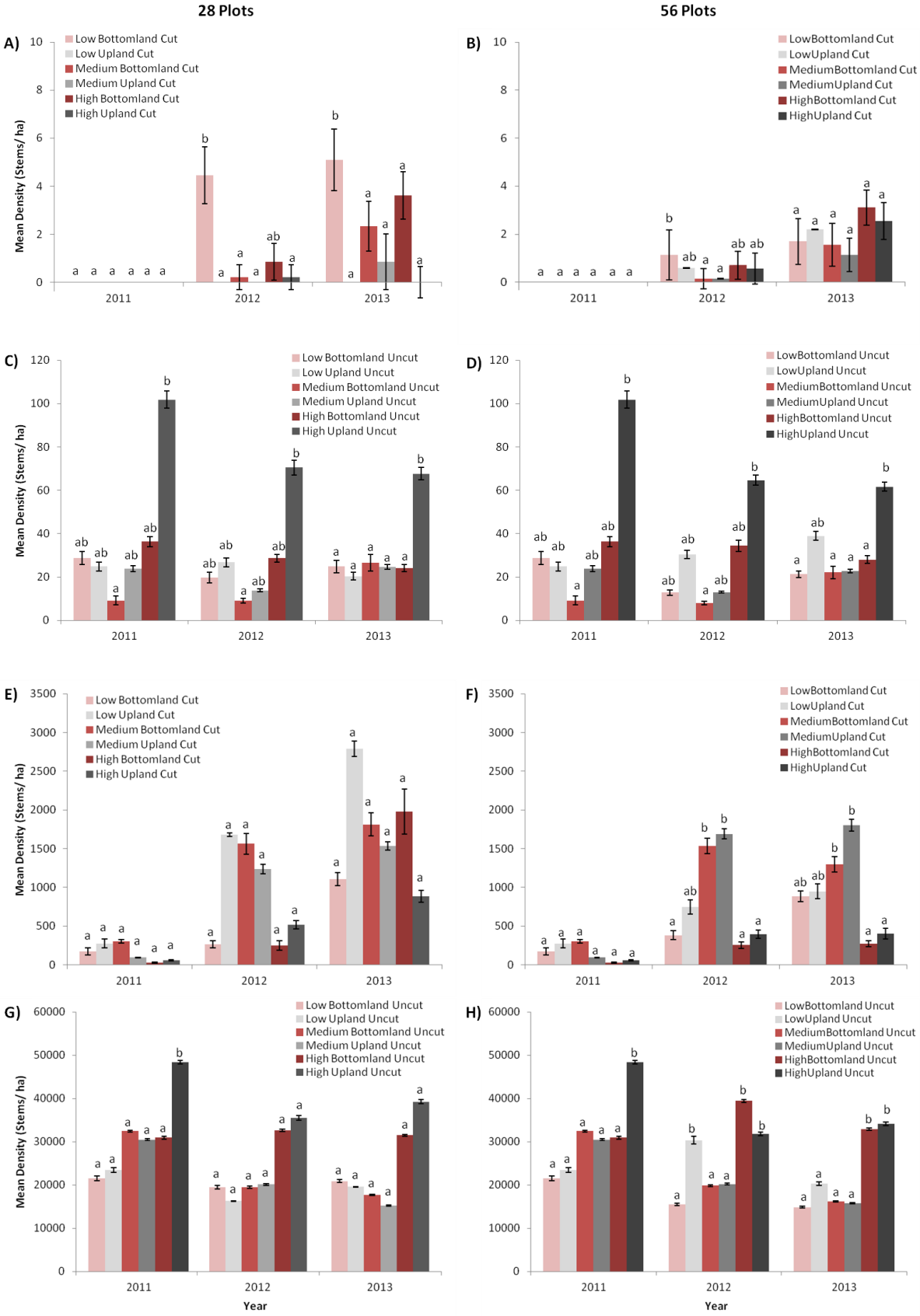


Figure 3.10 Overall mean (±SE) density of recently **harvested stems** (=cut) between catenal position and rainfall zone combinations for 28 plots (A) and 56 plots (B) of large harvested trees and 28 plots (E) and 56 plots (F) of small harvested trees from 2011 to 2013. Similarly, overall mean (±SE) density of **unharvested stems** (=uncut) between catenal position and rainfall zone combinations for 28 plots (C) and 56 plots (D) of large unharvested trees and 28 plots (G) and 56 plots (H) of small unharvested trees from 2011 to 2013. Different letters indicate significant differences between catenal positions within each year ($P<0.05$, Tukey).

The most utilized tree height for harvesting varied between years and between catenal/rainfall combinations. The most utilized tree height in the bottomland plots in the low rainfall zone ranged between ≤0.5-4m in height (Fig 3.11A-C). The most utilized tree height in the upland plots in the low rainfall zone was between 1.1-4m in height (Fig 3.11D-F).The bottomland plots in the medium rainfall zone stayed consistent in the most utilized tree height between 2.1-4m in height (Fig 3.11G-I). The most utilized tree height in the upland plots in the medium rainfall zone ranged between 1.1-4m in height (Fig 3.11J-L). The bottomland plots in the high rainfall zone, the most utilized tree height ranged between 1.1-10m in height (Fig 3.11M-O). The most utilized tree height in the upland plots in the high rainfall zone ranged between 0.6-8m in height (Fig 3.11P-R). The distribution of recently harvested trees for low rainfall bottomland plots was significantly different between 2011 and 2012 (Table 3.8). The SCD_{ht} for the rest of the catenal/rainfall combination showed no differences between 2011 and 2012, 2011 and 2013 or 2012 and 2013 for either harvested or unharvested trees (Table 3.8).

Table 3.8 Kolmogorov-Smirnov (KS) comparisons of height size class distributions (SCD_{ht}) for recently harvested and unharvested trees for each catenal position/rainfall zone combination between years for all trees (large and small trees combined). Significant p-values in bold type.

Comparison	Rainfall zone and catenal position interaction	Kolmogorov-Smirnov (KS) Test			
		Harvested trees		Unharvested trees	
		D value	p-value	D value	p-value
2011 vs. 2012	Low Bottomlands	0.750	**0.010**	0.250	0.932
2011 vs. 2013	Low Bottomlands	0.375	0.282	0.250	0.956
2012 vs. 2013	Low Bottomlands	0.375	0.536	0.250	0.954
2011 vs. 2012	Low Uplands	0.625	0.062	0.250	0.936
2011 vs. 2013	Low Uplands	0.375	0.405	0.250	0.953
2012 vs. 2013	Low Uplands	0.250	0.937	0.375	0.669
2011 vs. 2012	Medium Bottomlands	0.250	0.899	0.250	0.955
2011 vs. 2013	Medium Bottomlands	0.250	0.875	0.250	0.970
2012 vs. 2013	Medium Bottomlands	0.250	0.812	0.250	0.955
2011 vs. 2012	Medium Uplands	0.500	0.138	0.125	1.000
2011 vs. 2013	Medium Uplands	0.250	0.807	0.250	0.933
2012 vs. 2013	Medium Uplands	0.250	0.925	0.250	0.973
2011 vs. 2012	High Bottomlands	0.500	0.075	0.250	0.933
2011 vs. 2013	High Bottomlands	0.375	0.195	0.250	0.952
2012 vs. 2013	High Bottomlands	0.250	0.613	0.250	0.926
2011 vs. 2012	High Uplands	0.500	0.137	0.250	0.897
2011 vs. 2013	High Uplands	0.250	0.607	0.250	0.970
2012 vs. 2013	High Uplands	0.375	0.286	0.375	0.659

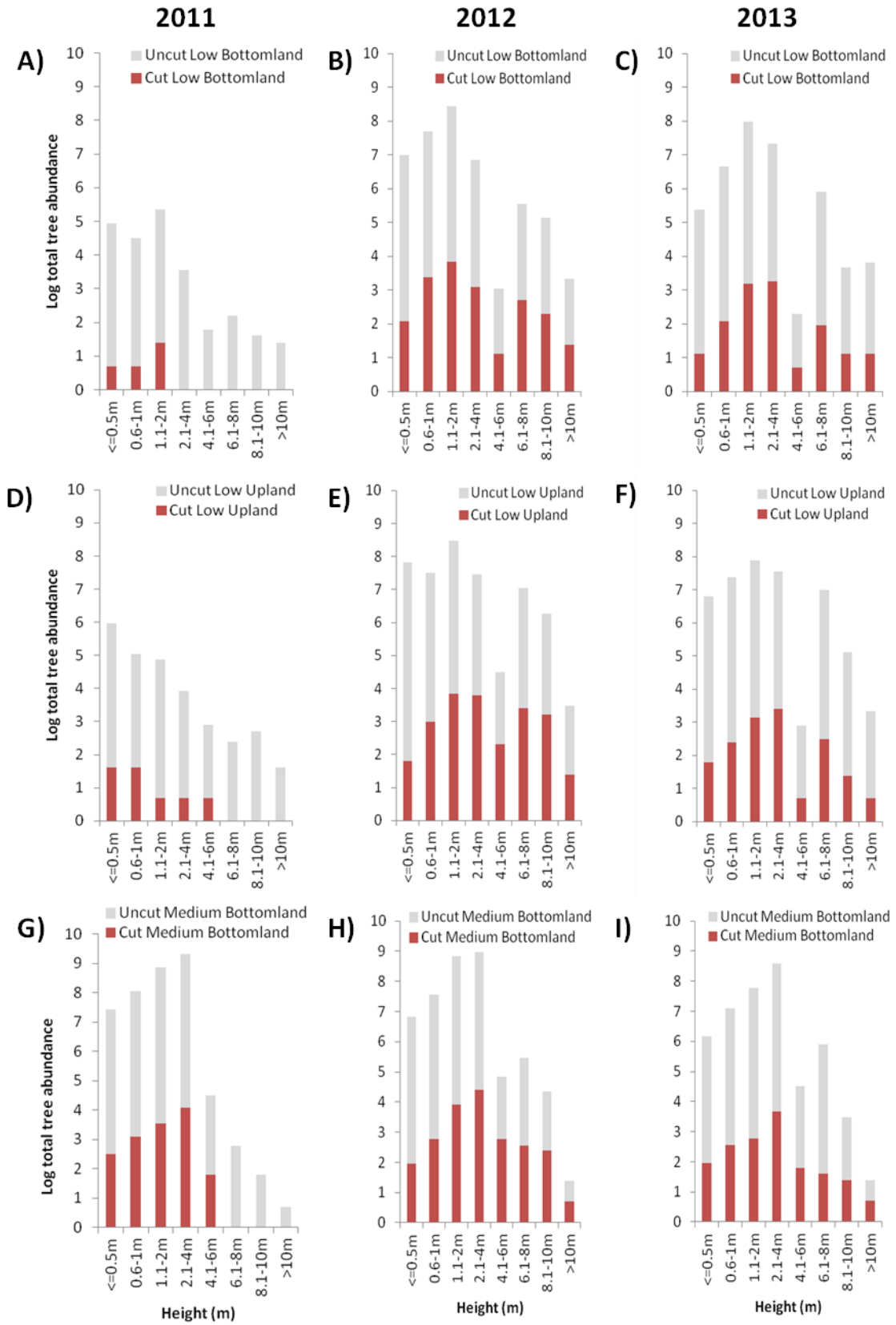


Figure 3.11 Comparison of height size class distributions (SCD_{ht}) for recently harvested (=cut) and unharvested (=uncut) trees (combined to total abundance) between rainfall and catenal position combinations in 2011, 2012 and 2013 for all trees (large and small trees combined). Rows catenal/rainfall combinations and columns illustrate years

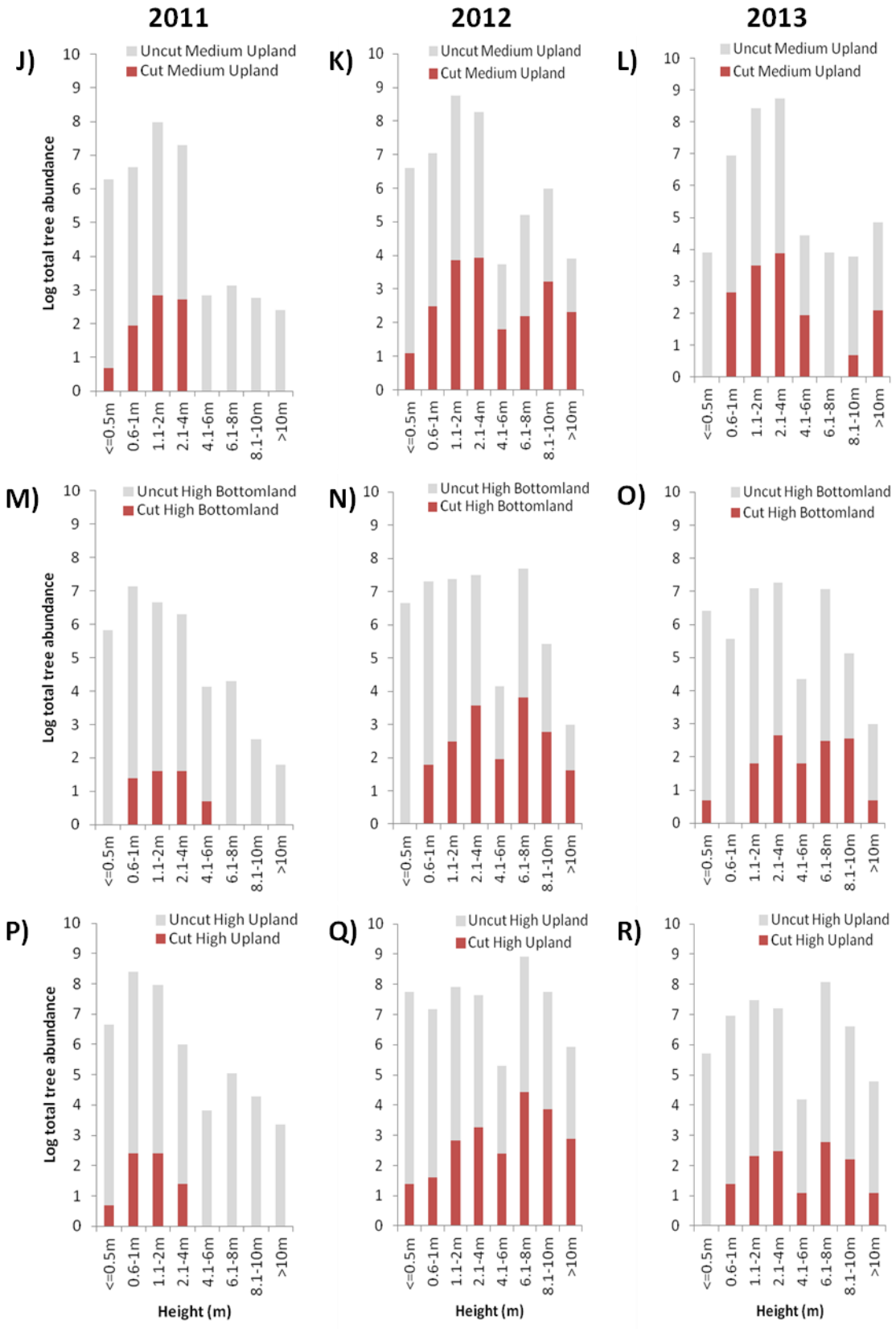


Figure 3.11 (Continued)

The SCD_{diam} where harvesting was most commonly seen between catenal/rainfall combinations (Fig 3.12) were in the smaller diameter classes but were more prevalent in the upland and bottomland plots in the medium rainfall zone across time (Fig 3.12G-L). Harvested stem density was highest (5%) in the bottomland plots in the medium rainfall zone (Fig 3.12G) for 2011 and with no harvesting in the bottomland plots in the high rainfall zone (Fig 3.12M). This increased in 2012 with the highest harvesting (7%) being in the upland and bottomland plots of the medium rainfall zone (Fig 3.13H and K) and the lowest harvesting (1%) in the upland and bottomland plots in the high rainfall zone (Fig 3.12N and Q). Similarly in 2013, harvesting increased with the highest harvesting (9%) being in the upland plots in the medium rainfall zone (Fig 3.12L) and the lowest harvesting (1%) in the upland and bottomland plots in the high rainfall zone (Fig 3.12O and R). The most utilized stem diameter for harvesting was consistent with stems between 1.1-10cm in diameter being the preferred size for harvesting across all catenal/rainfall combinations. The distributions for each catenal/rainfall combination showed no difference between 2011 and 2012, 2011 and 2013 or 2012 and 2013 for either harvested or unharvested stems (Table 3.9).

Table 3.9 Kolmogorov-Smirnov (KS) comparisons of stem diameter size class distributions (SCD_{ht}) for recently harvested and unharvested stems within catenal position/rainfall zone combinations between years for all trees (large and small trees combined).

Comparison	Rainfall zone and catenal position interaction	Kolmogorov-Smirnov (KS) Test			
		Harvested stems		Unharvested stems	
		D value	p-value	D value	p-value
2011 vs. 2012	Low Bottomlands	0.200	1.000	0.200	1.000
2011 vs. 2013	Low Bottomlands	0.200	1.000	0.400	0.814
2012 vs. 2013	Low Bottomlands	0.200	1.000	0.200	1.000
2011 vs. 2012	Low Uplands	0.200	1.000	0.200	1.000
2011 vs. 2013	Low Uplands	0.200	1.000	0.400	0.819
2012 vs. 2013	Low Uplands	0.200	1.000	0.400	0.813
2011 vs. 2012	Medium Bottomlands	0.200	1.000	0.400	0.809
2011 vs. 2013	Medium Bottomlands	0.200	1.000	0.600	0.282
2012 vs. 2013	Medium Bottomlands	0.000	1.000	0.400	0.808
2011 vs. 2012	Medium Uplands	0.200	1.000	0.200	1.000
2011 vs. 2013	Medium Uplands	0.200	1.000	0.200	1.000
2012 vs. 2013	Medium Uplands	0.200	1.000	0.200	1.000
2011 vs. 2012	High Bottomlands	0.200	1.000	0.200	1.000
2011 vs. 2013	High Bottomlands	0.200	1.000	0.200	1.000
2012 vs. 2013	High Bottomlands	0	1.000	0.200	1.000
2011 vs. 2012	High Uplands	0	1.000	0.200	1.000
2011 vs. 2013	High Uplands	0	1.000	0.200	1.000
2012 vs. 2013	High Uplands	0	1.000	0.200	1.000

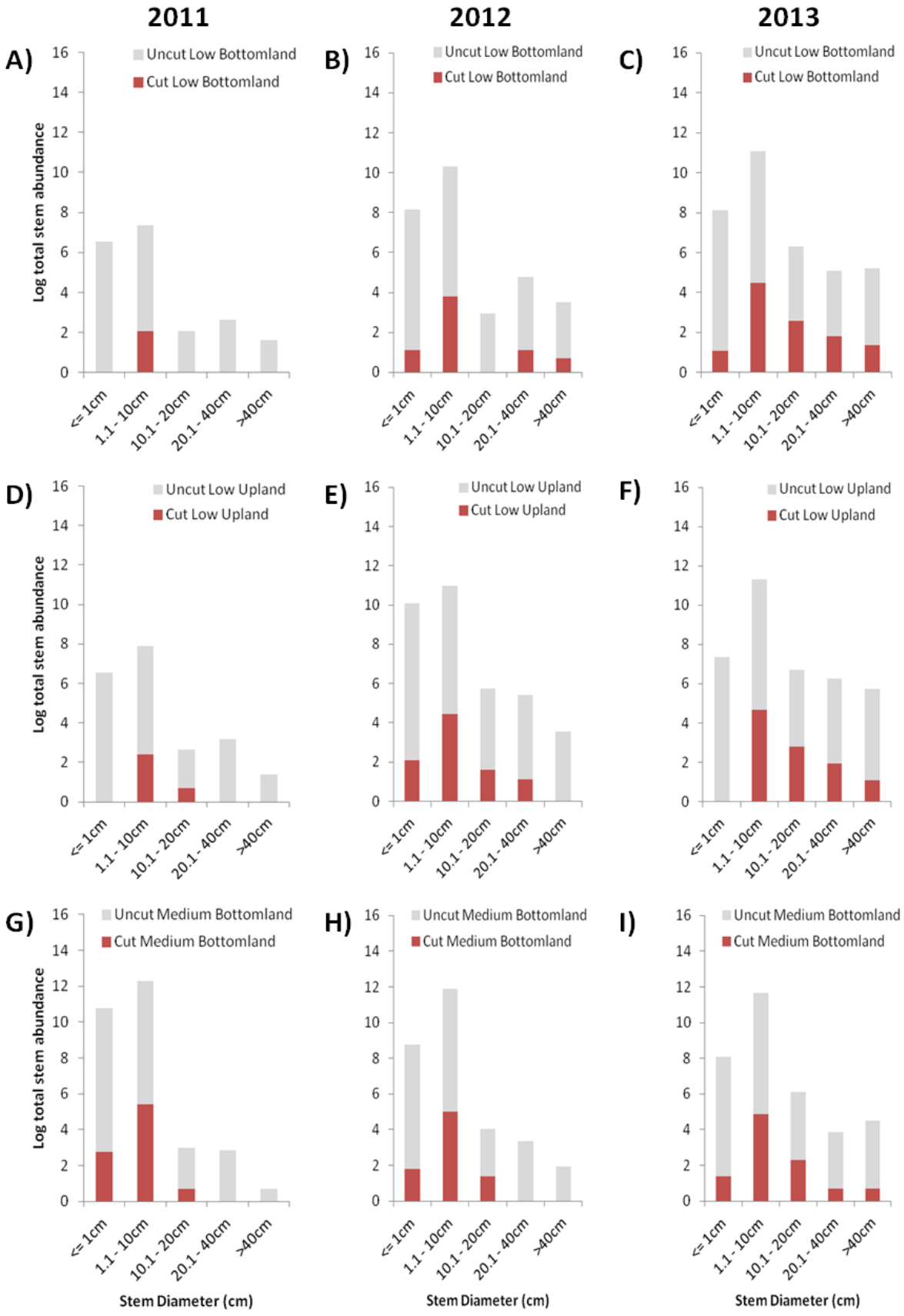


Figure 3.12 Comparison of stem diameter size class distributions (SCD_{diam}) for recently harvested (=cut) and unharvested (=uncut) stems (combined to total abundance) between catenal position and rainfall zone combinations in 2011, 2012 and 2013 for all trees (large and small trees combined). Rows illustrate catenal/rainfall combinations and columns illustrate years

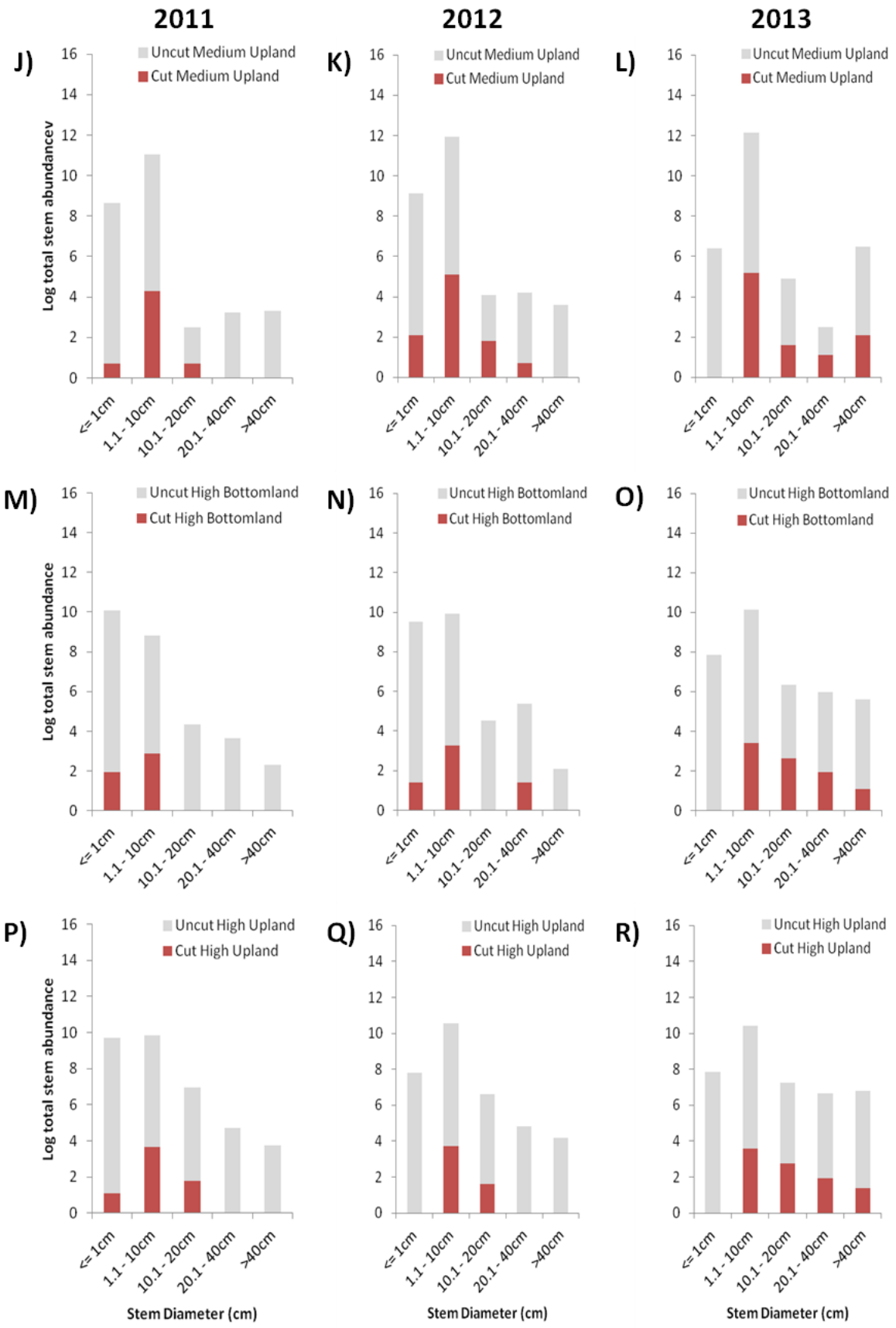


Figure 3.12 (Continued)

3.5 DISCUSSION

Focusing on determining the impacts of harvesting, density of recently harvested stems for large trees increased from 2012 to 2013 in all three rainfall zones. Harvested stem density was higher in the medium rainfall zone for all three survey years. Density of recently harvested stems increased in large trees from 2012 to 2013 in both upland and bottomland plots. Recent harvesting across rainfall zones only influenced the change of small tree density over time. Harvesting across catenal position had less influence on the change in density and structure over time than rainfall zones (Table 3.7). There was no interaction between harvesting across catenal position and rainfall zones in any of the three survey years. The preferred size of trees to harvest was between 0.6-4m in height and 1.1-10cm in diameter.

3.5.1 Recent harvesting impact over time

The change in vegetation density and structure has been attributed to the transformation of land due to the different land uses (Breshears and Barnes 1999; Colgan *et al.* 2012; Fairbanks 2004; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Scholes and Archer 1997; Shackleton *et al.* 1994; Shackleton 1999; Witkowski and O'Connor 1996). Density of harvested stems for large trees (>6m) in this study increased between $2012_{28\&56}$ and $2013_{28\&56}$, but the overall stem density did not show any change over time. This implies that the harvesting intensity on large trees is low at present. This is likely due to the availability of fuelwood decreasing as fuelwood markets increase (Kirkland *et al.* 2007; Matsika *et al.* 2013a). Density of harvested small tree stems increased over time for the 28 plots but did not change in the 56 plots. Unharvested stems for small trees did not change in the 28 plots but the unharvested stem density in the 56 plots decreased over time. This implies that coppice regrowth is replacing the harvested small trees at a similar rate that harvesting is occurring at. The lack of change within the overall small tree density might also be due to small trees responding to harvesting by producing coppice regrowth (Fisher *et al.* 2011; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kaschula *et al.* 2005; Luoga *et al.* 2004; Neke *et al.* 2006; Shackleton 2001; Twine 2005; Wessels *et al.* 2011). The increase in harvesting occurrence from 2011 to 2012 and 2013 was possibly due to the 28 additional plots included in 2012 and 2013 survey years. The harvesting of large trees increases with 4% from 2012 to 2013 which was significant compared to the small tree harvesting which increased with 1% for each year. A possible reason in the increase in harvesting of large trees is the development of rural and urban fuelwood markets (Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton *et al.* 2006). Rural households increasingly buy fuelwood due to the shortage of

dead wood within surrounding rangelands (Madubansi and Shackleton 2007; Matsika *et al.* 2013a). Harvesting for these markets are often on a large scale as harvesters have access to motor-vehicles and mechanised equipment (Matsika *et al.* 2013a; Shackleton *et al.* 2006). This type of harvesting allows for larger live trees to be harvested (Matsika *et al.* 2013a; Shackleton *et al.* 2006).

Structural changes due to harvesting in the SCD_{ht} and SCD_{diam}, was mostly seen in the smaller classes. The most utilized size structure of trees to be harvested is dependent on the use of the harvested wood according to the study by Shackleton (2001).The preferred size for harvesting was trees between 0.6-4m in height and 1.1-10cm in stem diameter. This indicates that this is the size which is easy to transport in bundles on foot (usually headloads) (Dovie *et al.* 2004; Neke *et al.* 2006; Van Gelder *et al.* 1983). The most utilized stem diameter of 1.1-10 cm, falls within the size found by Neke *et al.* (2006) and Van Gelder *et al.* (1983) that is easy to use for daily cooking and heating needs. Harvesting of large trees was absent in 2011 but does become more apparent in 2012 and 2013. This is possibly due to the commercialization of fuelwood which allows larger trees to be harvested by chainsaw and it is possible to transport the large harvested wood by means of trucks or bakkies (Dovie *et al.* 2004; Matsika *et al.* 2013a; Twine 2005; Van Gelder *et al.* 1983).

3.5.2 Recent harvesting across rainfall zones over time

Recent harvesting was highest in the medium rainfall zone and lowest in the high rainfall zone. The density of harvested stems for large trees in the 28 plots did not change over time whereas the density of harvested stems for small trees did increase from 2012 to 2013 in all three rainfall zones. The demand for fuelwood is often determined by the human population size that uses the resource as well as the sustainability of the intensity of harvesting for wood (Banks *et al.* 1996). The increase in harvesting can thus possibly be due to the depletion of wood on the village periphery (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). There was no difference between the rainfall zones for percentage of harvested stems of large trees. Various studies (Giannecchini *et al.* 2007; Shackleton 1993; Twine *et al.* 2003b) state that the lack of harvesting of large fruit-bearing species is due to the local customary law that forbids it. However, the increase in large tree harvesting, especially fruit-bearing species is a clear indication of the shortage of fuelwood and the lack or weakening of the power of local traditional institutions to enforce these local laws (Kirkland *et al.* 2007). The density of unharvested stems was higher in the high rainfall zone. Low rainfall areas had little to no

increase in unharvested stem density whereas higher rainfall areas did show a significant increase in unharvested stem density (Buitenwerf *et al.* 2012; Shackleton and Scholes 2011; Smith and Goodman 1986). This coincides with the density being higher in the high rainfall zone when compared to the low and medium rainfall zones (Buitenwerf *et al.* 2012; Shackleton and Scholes 2011; Smith and Goodman 1986). Harvested stem density for small trees was higher in the medium rainfall zone than the low and high rainfall zones in 2011_{28} and 2012_{28} whereas 2013_{28} had no difference between rainfall zones. Similarly, harvested stem density, was higher in the medium rainfall zone for 2011_{28}, 2012_{56} and 2013_{56}. Woody biomass decreased as harvesting increased. The increase in distance from villages resulted in a decrease in harvesting (Fisher *et al.* 2011; Luoga *et al.* 2002; Shackleton *et al.* 1994). The confounding influence of density of villages probably contributed to the higher harvest intensity in the medium rainfall zone, which had a higher density of villages than the other two zones (see Chapter 2 Section 2.3.2.1 Figure 2.1). Unharvested stem density was higher in the high rainfall zone for 2012 and 2013. The low density of harvested stems in the high rainfall zone is possibly due to the high density of unharvested stems. Studies done by Sankaran *et al.* (2005) and Shackleton and Scholes (2011) found that the woody vegetation biomass increased as the amount of water increased.

The abundance of harvested trees (SCD_{ht}) and harvested stems (SCD_{diam}) was higher in the smaller size classes and higher in the medium rainfall zone for all three survey years. This study also found harvesting to be more prevalent in the smaller size classes, across all of the rainfall zones. There was also some consistency in most utilized size of the stems and trees that were harvested which coincides to other studies that found preference in size does occur when harvesting fuelwood (Dovie *et al.* 2004; Neke *et al.* 2006; Van Gelder *et al.* 1983).

3.5.3 Recent harvesting across catenal position over time

Recent harvesting was similar between uplands and bottomlands. There was no change in harvesting over time, except for the increase in harvesting of large trees from 2012 to 2013. This study found that there was no preference for harvesting in either uplands or bottomlands, whereas the study by Kaschula *et al.* (2005) found there was a preference in catenal position, with more harvesting preference occurring in the uplands. They also found that by being selective in harvesting in catenal position, coppice regrowth of multi-stemmed species such as *D. cinerea* can produce more coppice shoots, which allow for more wood (Kaschula *et al.* 2005). . Other studies did however find upland plots to have higher density and structure differences compared to bottomland plots (Colgan *et al.* 2012; Daultrey 1970;

Fisher *et al.* 2009; Fisher *et al.* 2011; Khomo *et al.* 2011; Wessels *et al.* 2011). Similarly, unharvested stem density was higher in the upland plots than bottomland plots for large trees in the 56 plots across the three survey years. Small tree stem density had no difference between catenal position for both recent harvested and unharvested stems of both 28 and 56 plots. This indicates the possibility that the effect of harvesting could be at a fixed harvest rate or demand (Higgins *et al.* 1999; Jurisch *et al.* 2012). Some savanna tree species have the ability to produce coppice regrowth if stems are damaged or killed (Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). The removal of stems mitigates some of the impacts of fuelwood harvesting by producing coppice regrowth (Twine 2005).

Both uplands and bottomlands had similar size most utilized for harvesting. The study by Luoga *et al.* (2002) found that harvesting was more prevalent in the smaller size classes. This study also found harvesting to be more prevalent in the smaller size classes across both uplands and bottomlands, with increasing harvesting of larger trees. Again, the selection of preferred size classes was similar to other studies (Dovie *et al.* 2004; Neke *et al.* 2006; Van Gelder *et al.* 1983).

3.5.4 Recent harvesting across a combination of rainfall zones and catenal position over time

Recent harvesting was only effected by rainfall zones and not by catenal positions over time (Table 3.7). Harvesting across catenal position had less influence on the change in density and structure over time (Table 3.7). There was no interaction between harvesting across catenal position and rainfall zones and thus had no influence on the change of density and structure for either large or small trees in any of the three survey years. A possible reason for this could be the difference in species composition of harvested species (Chapter 5). In Chapter 5, the ordination biplots of all three survey years showed that there was no relationship between rainfall and catenal position in their influence on harvested species composition among large, small or all trees. It also found that the harvested species composition in the uplands was different from those in the bottomlands and likewise, the high rainfall zone plots had different harvested species composition to those of the low and medium rainfall zones (Chapter 5). This is one possible reason for one to expect significant interactions between harvesting across rainfall zone and catenal position, being based on the difference in harvested species composition, which results in differences in stem densities due to the different growth patterns of the harvested species.

In general, between the catenal position/rainfall zone combinations, the bottomland plots in the low rainfall zone tended to have the highest harvesting of large trees, especially in $2012_{28\&56}$ and $2013_{28\&56}$. If vegetation density is low due to low rainfall, the harvesting will be high as the harvesting is driven by the demand of population size, assuming similar human population density to other rainfall zones (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). Populations continue to increase, resulting in a shortage of fuelwood (Coetzer *et al.* 2010; Fisher *et al.* 2011). This is contradicted as the harvesting of small trees was only different between catenal/rainfall combinations in the 56 plots, where the upland and bottomland plots in the medium rainfall zone had the highest harvested density. As explained earlier, the high density of harvesting in the medium rainfall zone could be due to the medium rainfall zone having a higher density of villages. The unharvested stem density was in general higher in the upland plots of the high rainfall zone for both large and small trees. Sankaran *et al.* (2005) and Shackleton and Scholes (2011) found that the woody vegetation increased as the amount of water increased. This coincides thus with the high rainfall zone having higher density of unharvested vegetation.

Abundance of harvested trees and stems was higher in the upland and bottomland plots in the medium rainfall zone when compared to the other catenal/rainfall combinations, which is related to the higher density of harvested trees and stems within this rainfall zone. Luoga *et al.* (2004), Neke *et al.* (2006) and Shackleton (2001) found that the occurrence of harvesting is related to the abundance of species within an area. If a selected species is found to occur in a selected rainfall zone or catenal position, it is possible that the harvesting in that catenal/rainfall zone will be higher when compared to an area where the species does not occur. This might be the reason behind the high levels of harvesting in the upland and bottomland plots of the medium rainfall zone. Harvesting preference was similar to harvesting across rainfall and catenal position. Again, the consistency in the size most utilized of the stems and trees that were harvested which coincided to other studies (Dovie *et al.* 2004; Neke *et al.* 2006; Van Gelder *et al.* 1983).

3.6 CONCLUSION

In conclusion, focusing on how the density and structure of woody vegetation differs along rainfall and catenal (environmental) gradients, together with the impacts of wood harvesting (anthropogenic disturbance), from 2011 to 2013 in the woodlands of Bushbuckridge, Mpumalanga Province. Recent harvesting across rainfall zones did however

only influence the change of small tree density over time. There was however no interaction between harvesting across catenal position and rainfall zones across the three survey years for either large or small trees.

The first question "how does woody vegetation density and structure of harvested species differ over time?" found that wood harvesting will cause the change in vegetation density and structure over time. With the increase in harvesting intensity, an increase in density and relative abundance was seen in specific size classes (height and stem diameter size classes) for trees below 6m in height. This can be due to coppice regrowth occurring after harvesting of smaller stems. The second question "how does woody vegetation density and structure of harvested species differ across rainfall zones over time?" found that the medium rainfall zone had the highest level of harvesting and the high rainfall zone did have the highest vegetation density and lowest harvesting intensity. The third question "how does woody vegetation density and structure of harvested species differ across catenal positions over time?" found that both uplands and bottomlands had similar harvesting intensities and similar vegetation densities. The final question "how does woody vegetation density and structure of harvested species differ across a combination of rainfall zones and landscape position over time?" found the combination of anthropogenic and environmental factors had a larger impact on the density and structure of woody vegetation than the impacts of them individually. The harvesting intensity was found to be less impacted by the combination of the two environmental factors than by the individual environmental factors. Further studies are needed to answer this last hypothesis to the extent of have a definite answer.

The increase in harvesting of large trees, especially fruit-bearing species is a possible indication of the shortage of fuelwood and the lack or weakening of the power of local traditional institutions and their enforcement of local laws that forbid the harvesting of live trees, especially large fruiting species. Small trees had higher harvesting in the medium rainfall zone. This is a possible indication that the coppice production in this area is not producing quickly enough to meet the demand of fuelwood required by surrounding communities. As the preferred height for harvesting was below 2m in height and the preferred stem diameter was 1.1-10cm, the availability of the preferred size class will become less available if the coppice production is less than the harvesting rate. This in turn can lead to more large trees above 2m in height and above 10cm in stem diameter being harvested. With the less available preferred size trees, the existence of local fuelwood markets become more common. Many of the people who supply to these markets have equipment (chainsaws,

vehicles, etc.) available to harvest larger trees. If this is to occur, the sparsely dispersed large trees will become less and so will the production on seed become less. In future it is possible that the large trees will only exist in protected area.

Future studies would help resolve difficulties that arose during this study. The location of large trees was in some cases an obstacle. As the large trees were not GPS tagged, it is not possible to indicate what happened to the selected tree over long time scales. It was unclear if a large tree was harvested or died of natural causes in some case. Other times the large trees had been harvested, but only the top branches, resulting in trees that were smaller than the previous year. If the large trees were to be GPS tagged, it will ensure a way to locate the specific tree in future as well as to indicate if new trees are reaching the larger size classes or not. By establishing a long term monitoring program, the research would be valuable not only to the science community but might be vital to help manage available resources in a sustainable way and thus ensuring the future to a vast number of individuals who are dependent on these resources. Also, individual species need to be looked at as other studies have done with regards to elephant impacts. This also opens up the possibility of undertaking comparative studies between humans and elephants and the impact caused by them on their environment.

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4 Chapter 4: Difference in species richness, diversity and evenness of harvested and unharvested woody vegetation across catenal and rainfall gradients (2011 – 2013)

4.1 ABSTRACT

Species richness, diversity and evenness are used to investigate the variations in plant and animal communities across a variety of environmental conditions in many ecological models and conservation strategies. Species richness is the number of species in the selected area, and diversity is the relative abundance and the distribution thereof among species, whereas evenness is the measure of the equality of abundances within a community. The main aim of this study was to determine how species richness, diversity and evenness of woody vegetation differ over time along rainfall and catenal gradients. Secondly, to assess the species richness, diversity and evenness of harvested and unharvested tree species.. Three zones were selected that differed in annual rainfall: (a) wet west (>700mm), (b) mesic (600-700mm), and semi-dry east (<600m), with three villages per zone. For the rangeland of each village, plots were sampled in 2011, 2012 and 2013 to cover the upland and bottomland variations in catenal position. All trees >6m in height, and their individual stems, were identified, counted and measured (stem diameter and height) within a total of 56 circular plots (only 28 in 2011) each with a radius of 50m. Trees <6m, and their stems, were identified, counted and measured (stem diameter and height) in a circular plot with a radius of 6m, nested centrally within each 50m plot. The high rainfall zone had significantly higher species richness, diversity and evenness than the low and medium rainfall zones, whereas there was no difference between catenal positions for both large and small trees in all three survey years. There was no interaction between rainfall zones and catenal positions. All three survey years display similar patterns in the species accumulation and rarefaction curves for both the large and small trees, leading us to conclude that the species are distributed at random across the plots. The most abundant large tree species were *Sclerocarya birrea* > *Philenoptera violacea* > *Pterocarpus angolensis*, whereas the most abundant species among small trees were *Dichrostachys cinerea, Terminalia sericea, Acacia exuvialis, Strychnos madagascariensis* and *Combretum hereroense*. Harvesting intensity increased from 2011 to 2012 to 2013 for large trees with a greater species richness, diversity and evenness of harvested trees in 2013. Species that were most harvested for large trees comprised *Combretum collinum, Acacia gerrardii, T. sericea, Acacia robusta, Combretum zeyheri* and *S. birrea,* whereas harvested small trees comprised *D. cinerea, T. sericea, A. exuvialis* and *C. hereroense*.

Keywords: BiodiversityR, evenness, harvesting, Shannon-Wiener Index, Simpson's Index

4.2 INTRODUCTION

Biological diversity, or biodiversity, refers to variety within the living world or among and between living organisms (Kaennel 1998; Swingland 2001). DeLong (1996) is more comprehensive and defined biodiversity as an attribute of an area and specifically refers to the variety within and among living organisms, assemblages of living organisms, biotic communities, and biotic processes, whether naturally occurring or modified by humans. The most commonly cited definition of biodiversity (OTA 1987) is the "variety and variability among living organisms and the ecological complexes in which they occur" (Noss 1990). This definition however excludes the abiotic and biotic processes which are crucial to maintain biodiversity (Noss 1990).

Biodiversity consists of multiple levels of biological organization and has three primary attributes; composition, structure and function (Noss 1990). The three attributes can be considered in a nested hierarchy of genes, species populations, communities, and landscapes (Noss 1990). DeLong (1996) gave the following as a definition for biodiversity, "Biodiversity can be measured in terms of genetic diversity and the identity and number of different types of species, assemblages of species, biotic communities, and biotic processes, and the amount (abundance, biomass, cover or rate) and structure of each. It can be observed and measured at any spatial scale ranging from micro sites and habitat patches to the entire biosphere". This definition given by DeLong (1996), allows for modification, depending on the context in which it is used (Swingland 2001). Species diversity is one of the many basic concepts of ecology (DeJong 1975). It has been used in the past and present to characterize both communities and ecosystems (DeJong 1975).

4.2.1 What are species richness, diversity and evenness?

Species richness is the number of species in the selected area or sample (Ma and Eriksson 2005; Magurran 1988; Smith and Wilson 1996; Williams *et al.* 2007; Wilsey and Stirling 2006) and diversity is the relative abundance or biomass and the distribution thereof among species (Ma and Eriksson 2005; Magurran 1988; Pielou 1977; Wilsey and Stirling 2006). Evenness according to Alatalo (1981) is the measure of the equality of abundances within a community. The measurement of evenness should measure the equality of abundance within a selected community and maximum evenness is reached when all species are equally abundant (Alatalo 1981).

4.2.2 Importance of species richness, diversity and evenness

Biodiversity is often equated with species richness and/or evenness (Colwell *et al.* 2004; Colwell *et al*. 2012; DeJong 1975; Gotelli and Colwell 2011; Lande *et al.* 2003; Nagendra 2002; Pavoine and Bonsall 2010; Ugland *et al.* 2003; Williams *et al.* 2007). As species are the fundamental descriptive units of the living world, species diversity is often used as a synonym for species richness (Swingland 2001). A simple count of species in not sufficient if one is to understand the composition and interactions within communities (Colwell *et al.* 2004; Gotelli and Colwell 2001; Magurran 1988; Nagendra 2002; Noss 1990; Swingland 2001; Ugland *et al.* 2003). For this reason, a vast number of methods have been designed to determine species richness and diversity within communities (Colwell *et al.* 2004; Gotelli and Colwell 2001; Magurran 1988; Noss 1990).

Communities with higher species richness are often more complex as a greater variety of species means a greater array of interactions (Fromm 2000; Nagendra 2002; Reddy *et al.* 2009). Species richness is determined by the role played by environmental factors such as soil fertility, climate as well as human disturbances such as harvesting and livestock grazing (Reddy *et al.* 2009; Rutherford and Powrie 2013). Humans and their activities influence the rate of change that occurs in the world's ecosystems structure and functioning by altering the species composition and structure of the surrounding landscape (Elmqvist et al 2004; Nagendra 2002; Reddy *et al.* 2009; Rutherford and Powrie 2013; Terlizzi *et al.* 2014). Changes in landscape structure and organization are believed to have a significant effect on the integrity and distribution of ecosystems, and their functioning. This in turn has an effect on species richness and diversity (Elmqvist et al 2004; Nagendra 2002). Many ecological models and conservation strategies are underlined by species richness, which is why many ecologists often need to know how many species are within a predefined area (Colwell *et al.* 2004; Colwell *et al*. 2012; Gotelli and Colwell 2011; Gotelli and Colwell 2001; Lande *et al.* 2003; Magurran 1988; Nagendra 2002; Pavoine and Bonsall 2010; Terlizzi *et al.* 2014; Ugland *et al.* 2003; Williams *et al.* 2007).

4.2.3 How to determine species richness, diversity and evenness

Diversity indices, such as Shannon-Wiener index, H' (Shannon and Weaver 1949) and Simpson's index D (Simpson 1949) are the most commonly used (DeJong 1975; Colwell *et al.* 2004; Magurran 1988; Smith and Wilson 1996; Wilsey and Stirling 2006). Another basic feature of biological communities is the distribution of abundance among species (Smith and Wilson 1996). The easiest way to assess this distribution is by measuring evenness (DeJong 1975; Colwell *et al.* 2004; Magurran 1988; Smith and Wilson 1996;

Wilsey and Stirling 2006). Evenness indices standardize abundance, which ranges from 0 to 1. When most individuals in a community belong to a few dominant species, the value is close to 0 but when different species are nearly equally abundant, it is close to 1 (Smith and Wilson 1996; Wilsey and Stirling 2006). In other words, high evenness in a community occurs when each species present is equally abundant and low evenness when the species differ widely in abundance (Smith and Wilson 1996). If species diversity in communities is only used to describe the number of species, important aspects of the quantitative structure of these communities can be missed, such as whether some species are rarer than others (Ma and Eriksson 2005).

Another way to analyse species richness is by use of species accumulation curves. A species accumulation curve is a graph of the cumulative number of observed species as a function of some measure of sampling effort (Colwell *et al.* 2004; Thompson *et al*. 2007 Williams *et al.* 2007). It is thus a way to record the rate at which new species are added with continued sampling effort (Thompson & Withers 2003). Species accumulation can be useful in understanding the species richness within a selected area (Thompson & Withers 2003; Thompson *et al*. 2007).These curves are also a way to establish if adequate sampling has been done (Thompson *et al*. 2007). As species richness is influenced by sample size, a difference in species richness may be the result of a difference in sample size (DeJong 1975; Colwell *et al.* 2004; Gotelli and Colwell 2011; Lande *et al.* 2003; Magurran 1988; Thompson & Withers 2003; Thompson *et al*. 2007), and hence for comparisons between two sites to be meaningful, the same sample size or sampling effort needs to be undertaken at both sites. Species richness can thus be said to increase non-linearly with the number of individuals encountered or the number of samples collected or the area sampled (Colwell *et al.* 2012).

Rarefaction, allows species richness to be rarefied to the same number of individuals, reducing the problem of difference in sample size (Colwell *et al.* 2004; Gotelli and Colwell 2011). Rarefaction is thus a way to produce a smoothed curve that is statistically the expectation of the corresponding accumulation curve (Colwell *et al.* 2004; Gotelli and Colwell 2011, Williams *et al.* 2007). The purpose of rarefaction is to make direct comparisons amongst communities based on the number of individuals in the smallest sample (Magurran 1988). Hence species accumulation and rarefaction are often used to compare observed species richness in two communities at a common sample size (Colwell *et al.* 2004; Gotelli and Colwell 2011; Magurran 1988). Species accumulation curves record the total number of species collected and additional sampled units are added to the pool of all previously collected individuals or samples (Gotelli and Colwell 2001). This may be either

individual-based or sample based. Rarefaction curves on the other hand, are produced by re-sampling the pool of individuals or samples at random and the average number of species represented by individuals or samples, are then plotted (Gotelli and Colwell 2001). Sampling is thus done without replacement within each re-sampling (Gotelli and Colwell 2001). In a small collection of individuals or samples drawn at random from a large pool of individuals, the expected number of species is generated by rarefaction. (Gotelli and Colwell 2001).

Rank abundance curves are another way to analyse species diversity. Rank abundance curves list species in decreasing order of abundance (Kindt and Coe 2005). These are also sometimes referred to as dominance-diversity curves (Magurran 1988; Smith and Wilson 1996). One advantage of a rank abundance curve is that the contrasting patterns of species richness are clearly displayed (Magurran 1988). Even when the species are relatively few, all the information concerning their relative abundance is visible (Magurran 1988). Rank abundance curves are also a way to highlight the differences in evenness among assemblages (Magurran 1988; Smith and Wilson 1996). The rank abundance curve is also useful in illustrating the changes through succession or following an impact caused by the environment (Magurran 1988). The rank abundance curve provides a visual representation of species richness and species evenness (Kindt and Coe 2005; Oksanen *et al.* 2005). Species richness can be viewed as the number of different species on the graph and species evenness is derived from the slope of the line that fits the graph (Kindt and Coe 2005). The rank abundance curve can thus be seen as a way to infer which species abundance model best describes the data (Magurran 1988). In other words, if the gradient is steep, low evenness is indicated as the high ranking species have much higher abundances compared to the low ranking species, whereas a shallow gradient indicates high evenness as the abundances of different species are more similar (Kindt and Coe 2005; Magurran 1988; Oksanen *et al.* 2005; Smith and Wilson 1996).

4.2.4 Environmental and anthropogenic determinants of species richness, diversity and evenness

Ecologists are often concerned with the association between species and environmental gradients and many ecological studies investigate the variations in plant and animal communities across a variety of environmental conditions (Anderson and Willis 2003; Colwell *et al.* 2004; Colwell *et al*. 2012; DeJong 1975; Gotelli and Colwell 2011; Lande *et al.* 2003; Legendre 2008; Leps and Smilauer 2003; Maestre 2004; Nagendra 2002; Pausa and Austin 2001; Pavoine and Bonsall 2010; Ugland *et al.* 2003; Williams *et al.* 2007). Patterns of species richness were regarded by Huston (1979, 1994) as “the interaction of disturbance

with environmental gradients and competitive exclusion". Nuñez-Olivera *et al.* (1995); Richerson & Lum (1980); Knight *et al.* (1982) and O'Brien (1993) found mean annual rainfall to be an important environmental determinant of species richness and diversity. Whereas, Richardson *et al.* (1995) concluded that topographic and soil variability is also an important environmental determinant. It can thus be seen that more than one environmental factor is important for the species richness and diversity within a given area, or that vegetation in different ecological contexts is driven by different primary determinants (Pausa and Austin 2001). Botha *et al.* (2002) state that various studies (Dublin *et al.* 1990; Moloney & Levin 1996) found that species richness is affected by disturbance, whether by humans, mega-herbivores or other agents, all common within a variety of natural systems and populations. It is thus clear that in order to understand the biodiversity of selected areas both species richness and diversity need to be understood with the inclusion of both environmental and anthropogenic determinants.

4.2.5 Purpose of using species richness, diversity and evenness in this study

With species richness, diversity and evenness being important elements of biodiversity, this study investigated the species richness, diversity and evenness of the woody component of savanna vegetation and how environmental and anthropogenic factors influence them over time. The main aim of this study was to determine how species richness, diversity and evenness of woody vegetation differ over time along rainfall and catenal gradients. Secondly, to assess the species richness, diversity and evenness of tree species that was harvested. The first objective was to determine how species richness, diversity and evenness differ between rainfall zones and catenal positions. The second objective was to determine how species richness, diversity and evenness differ across rainfall zones and catenal positions when only focusing on the harvested species.

Key questions for Objective 1:

1) How do species richness, diversity and evenness change over time in general?
2) How do species richness, diversity and evenness differ between rainfall zones while controlling for time by assessing three different time periods?
3) How do species richness, diversity and evenness differ between catenal positions while controlling for time by assessing three different time periods?
4) How do species richness, diversity and evenness differ between a combination of rainfall zones and catenal positions while controlling for time by assessing three different time periods?

Key questions for Objective 2:

1) How do species richness, diversity and evenness of harvested species differ over time?
2) How do species richness, diversity and evenness of harvested species differ across rainfall zones over time?
3) How do species richness, diversity and evenness of harvested species differ across catenal positions over time?
4) How do species richness, diversity and evenness of harvested species differ across a combination of rainfall zones and catenal position over time?

4.3 MATERIALS AND METHODS

4.3.1 Study site

See Chapter 2 section 2.3.1

4.3.2 Study design

See Chapter 2 sections 2.3.2.1 and 2.3.2.2

4.3.3 Data analysis

In this chapter the species richness, diversity and evenness, for both total and recently harvested trees, for the large and small trees separately, were analysed for each study year separately, namely 2011, 2012 and 2013. This was done by means of indices (species richness, Simpson's, Shannon-Wiener, evenness), rank abundance curves, as well as species accumulation and rarefaction curves. These analyses were done to compare the effects of two environmental factors, namely (1) rainfall zone (low, medium and high) and (2) catenal position (bottomland and upland), as well as the combination of catenal position and rainfall zone. All variables were tested for normality with Shapiro-Wilk normality tests and data were log transformed if necessary. As 2011 only had 28 plots sampled and 2012 and 2013 had 56 plots, two sets of analyses were done (a) for the same 28 plots for 2011, 2012 and 2013 and (b) for the 56 plots in 2012 and 2013. Throughout the rest of the text, the number of plots (28 or 56) of each year will be subscripted next to the selected year, e.g. for 28 plots: 2011_{28}; 2012_{28}, 2013_{28} and for 56 plots: 2012_{56} and 2013_{56}**.**

The species abundance data (see Chapter 2) were analysed in this chapter for each of the three years, for the large (above 6m in height) and small trees (below 6m in height) separately. The large trees sampled in the 50m radius plots were more sparsely distributed

than the small trees sampled in the 6m radius plots. As there was no attempt made to search the 50m radius plots for the occurrence of new species that did not already occur in the 6m radius plots, the two could not be combined. For this reason, analysis of species richness, diversity and evenness had to be done separately for the large and the small trees. All analyses were undertaken on (a) all trees and (b) recently harvested (within the last 12 month) trees.

Species richness, Shannon-Wiener, Simpson's index, J-evenness, rank abundance, species accumulation and rarefaction, were compared between the three rainfall zones (low, medium and high), between the two catenal positions (uplands and bottomlands) and between the combination of rainfall zone and catenal position. For species richness, Shannon-Wiener, Simpson's index and evenness at the plot level, one-way ANOVAs were used to (a) statistically compare means between the three rainfall zones and (b) between catenal positions. For species richness, Shannon-Wiener, Simpson's index, evenness at the plot level, two-way ANOVAs were also done to statistically compare means between rainfall zones, catenal positions as well as the interactions between the two. If the ANOVAs detected an overall significant difference, a Tukey post-hoc test was then done to compare pairs of means.

All data analysis was done in the open source R2.1.0 statistical program and its contributing packages (R Development Core Team 2005). Species richness, Shannon-Wiener, Simpson's index and evenness were determined using the BiodiversityR software developed by Roeland Kindt (Kindt and Coe 2005), building on the open source R2.1.0 statistical program and its contributing packages such as the vegan community ecology package (Oksanen *et al.* 2005; R Development Core Team 2005). Similarly, the species accumulation and rarefaction curves and rank abundance curves were also determined using BiodiversityR. All commands (step by step) in the BiodiversityR programme (Appendix 1) were adapted from Kindt and Coe (2005).

4.3.3.1.1 Species richness, diversity and evenness

Species Richness

The summed number of species per plot was used for species richness.

Species Diversity (Shannon and Simpson's index)

The equation for Shannon-Wiener index and Simpson's index can be seen in various articles (Shannon and Weaver 1949; Simpson 1949; Smith and Wilson 1996). For the

Shannon-Wiener function, the higher the index value, the higher the species diversity. Unlike the Shannon-Wiener index values which indicate higher diversity with higher index values, Simpson's index values indicate lower values for higher species diversity.

Evenness

The values of evenness fall between 0-1. The equation for evenness can be seen in various articles (Hill 1979; Pielou 1969; Smith and Wilson 1996). For calculation methods of species richness, Shannon-Wiener, Simpson's index and evenness in BiodiversityR, see Appendix 1A and B.

Rank abundance, species accumulation and rarefaction curves

The natural log equation was selected for the rank abundance curves due to the abundance data not being normal. For calculation methods of the rank abundance curves, species accumulation and rarefaction curves in BiodiversityR, see Appendix 1C and D.

4.4 RESULTS

4.4.1 Difference in species richness, diversity and evenness

4.4.1.1 How do species richness, diversity (Shannon-Wiener index, Simpson's index) and evenness differ over time in general?

Diversity Indices

Large trees: Species richness at a plot scale did not change over time for either 28 or 56 plot datasets (Table 4.1). Species richness of large trees at a plot scale was significantly lower in the 56 plots compared to the 28 plots (Table 4.1). Similarly, species diversity (Shannon-Wiener index, Simpson's index) did not change over time for large trees over the three survey years (Table 4.1). The evenness of large trees did not change over the three survey years (Table 4.1).

Small trees: Species richness at a plot scale did change over time for 28 plot datasets, for small trees (Table 4.1). Species richness of small trees at a plot scale was significantly lower in the 56 plots compared to the 28 plots (Table 4.1). Similarly, species diversity did change over time for small trees over the three survey years (Table 4.1). The evenness of small trees did change over the three survey years but the small trees in the 56 plot dataset were more evenly distributed than those in the 28 plots (Table 4.1).

Species accumulation and rarefaction curves

Large and small trees: All three survey years display similar patterns between the species accumulation and rarefaction curves for both the large and small trees, thus it can be concluded that the species are distributed at random across the plots (Fig 4.1). Species accumulation and rarefaction curves both indicate that the increase in sampling sufficiency increases the species richness.

Rank abundance

Large trees: The three most abundant species were consistently *Sclerocarya birrea* > *Philenoptera violacea* > *Pterocarpus angolensis,* and did not differ between years (Fig 4.2). Abundance of trees increased with the increase in the number of plots sampled in 2012_{56} and 2013_{56} when compared with 2011_{28} (Fig 4.2). The species diversity and evenness were similar between the three survey years.

Small trees: The most abundant species differed between survey years and comprised *Dichrostachys cinerea, Terminalia sericea, Acacia exuvialis, Strychnos madagascariensis* and *Combretum hereroense* (Fig 4.2). The rank abundance curves and evenness were otherwise similar between the three survey years (Fig 4.2).

Table 4.1 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small trees across three survey years (2011-2013). Values in the same column for the 28 and 56 plot datasets separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Year		Large trees (>6m height)			
	Number of plots	Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	28	$5.0 \pm 0.16_a$	$1.1 \pm 0.03_a$	$0.6 \pm 0.01_a$	$0.8 \pm 0.01_a$
2012_{28}	28	$5.1 \pm 0.14_a$	$1.1 \pm 0.03_a$	$0.6 \pm 0.01_a$	$0.8 \pm 0.01_a$
2013_{28}	28	$5.9 \pm 0.15_a$	$1.3 \pm 0.03_a$	$0.6 \pm 0.01_a$	$0.8 \pm 0.01_a$
2012_{56}	56	$4.3 \pm 0.06_a$	$1.0 \pm 0.01_a$	$0.5 \pm 0.01_a$	$0.8 \pm <0.01_a$
2013_{56}	56	$5.3 \pm 0.07_a$	$1.2 \pm 0.01_a$	$0.6 \pm 0.01_a$	$0.8 \pm <0.01_a$
Year		**Small trees (< 6m height)**			
	Number of plots	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	28	$17.8 \pm 0.23_a$	$2.1 \pm 0.02_a$	$0.8 \pm 0.01_a$	$0.5 \pm <0.01_a$
2012_{28}	28	$14.2 \pm 0.20_b$	$1.9 \pm 0.02_a$	$0.8 \pm 0.01_a$	$0.5 \pm <0.01_a$
2013_{28}	28	$13.1 \pm 0.19_b$	$1.9 \pm 0.02_a$	$0.8 \pm 0.01_a$	$0.6 \pm <0.01_b$
2012_{56}	56	$12.0 \pm 0.10_a$	$1.8 \pm 0.01_a$	$0.7 \pm <0.01_a$	$0.6 \pm <0.01_a$
2013_{56}	56	$11.3 \pm 0.10_a$	$1.8 \pm 0.01_a$	$0.6 \pm <0.01_a$	$0.6 \pm <0.01_a$

4.4.1.2 How do species richness, diversity and evenness differ between rainfall zones over time?

Diversity Indices

Large and small trees: For large and small trees, the high rainfall zone had higher species richness and diversity when compared to the low and medium rainfall zones (Table 4.2). Evenness for large trees was significantly lower in the low rainfall zone for 2011_{28}, 2012_{28} and 2013_{28} (Table 4.2), but not different for 2012_{56} and 2013_{56}, while there were no differences for the small trees in any of the three survey years (Table 4.2).

Species rarefaction curves

Large trees: In 2011_{28}, the high rainfall zone had higher species richness compared to the low and medium rainfall zones (Fig 4.3). In 2012_{28} and 2013_{28}, the high rainfall zone had higher species richness compared to the low and medium rainfall zones (Fig 4.3). In 2012_{56} and 2013_{56}, the high rainfall zone had higher species richness compared to the low and medium rainfall zones (Fig 4.3).

Small trees: In all three survey years the high rainfall zone had higher species richness compared to the low and medium rainfall zones (Fig 4.3).

Rank abundance

Large trees: The most abundant species within the low rainfall zone differed between the three survey years and comprised *S. birrea, Combretum apiculatum, Combretum collinum, Combretum zeyheri, Lannea discolor* and *Acacia nigrescens*. The most abundant species within the medium rainfall zone differed between survey years and comprised *S. birrea, P. violacea,* S*pirostachys africana* and *Diospyros mespiliformis*. The three most abundant species within the high rainfall zone were the same for each year, namely *S. birrea > P. angolensis > P. violacea*.

Small trees: The most abundant species within the low rainfall zone differed between survey years and comprised *A. exuvialis, S. madagascariensis, D. cinerea, T. sericea* and *Dalbergia melanoxylon* The three most abundant species within the medium rainfall zone were consistently *D. cinerea > S. madagascariensis > T. sericea*. The most abundant species within the high rainfall zone differed between survey years and comprised *D. cinerea, T. sericea, Diospyros lycioides, C. hereroense* and *Senna petersiana*.

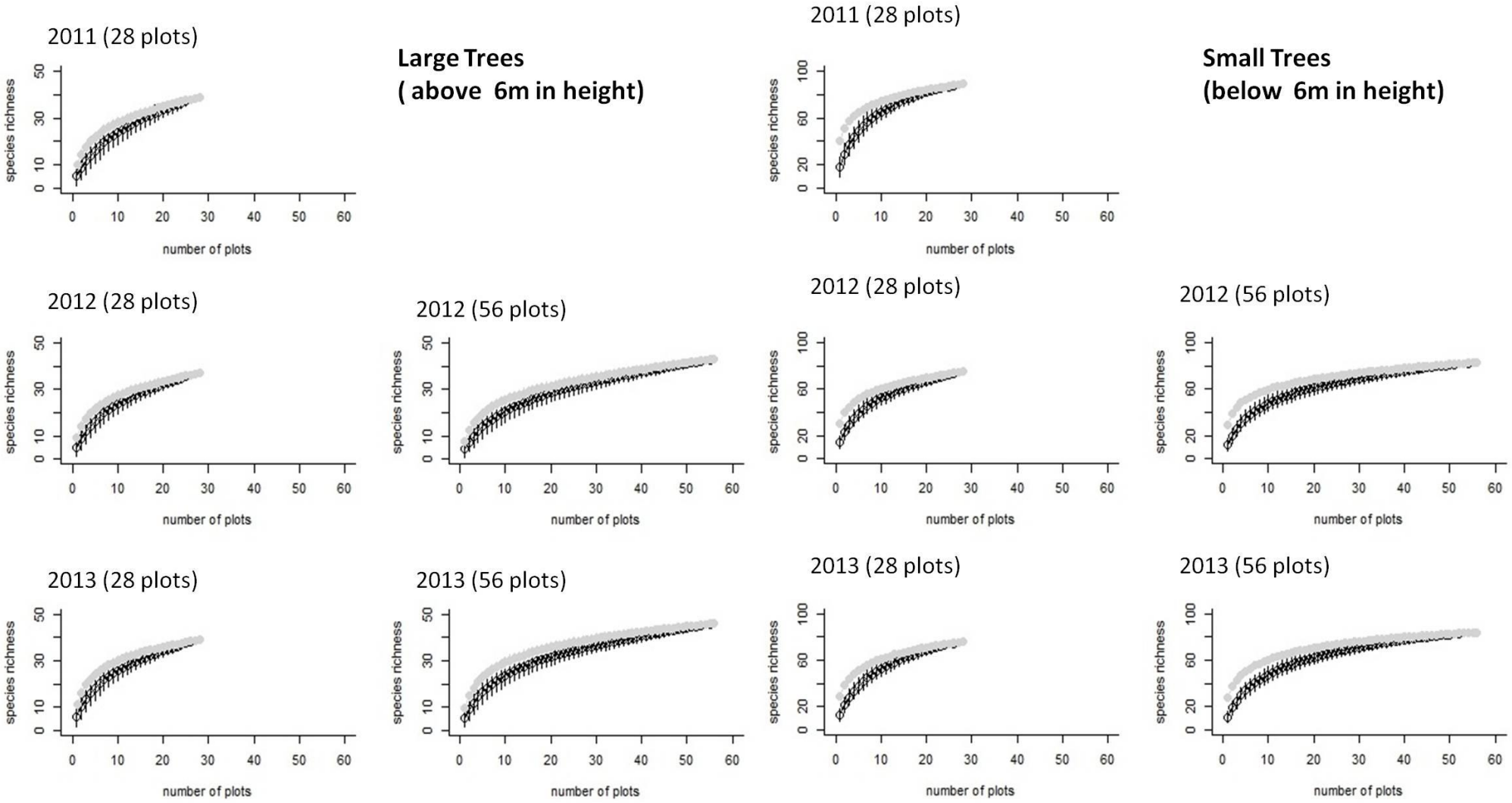


Figure 4.1 The species accumulation (open symbols (○)) and species rarefaction (solid symbols (●)) curves for large (left) and small (right) trees for each of the survey years. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size.

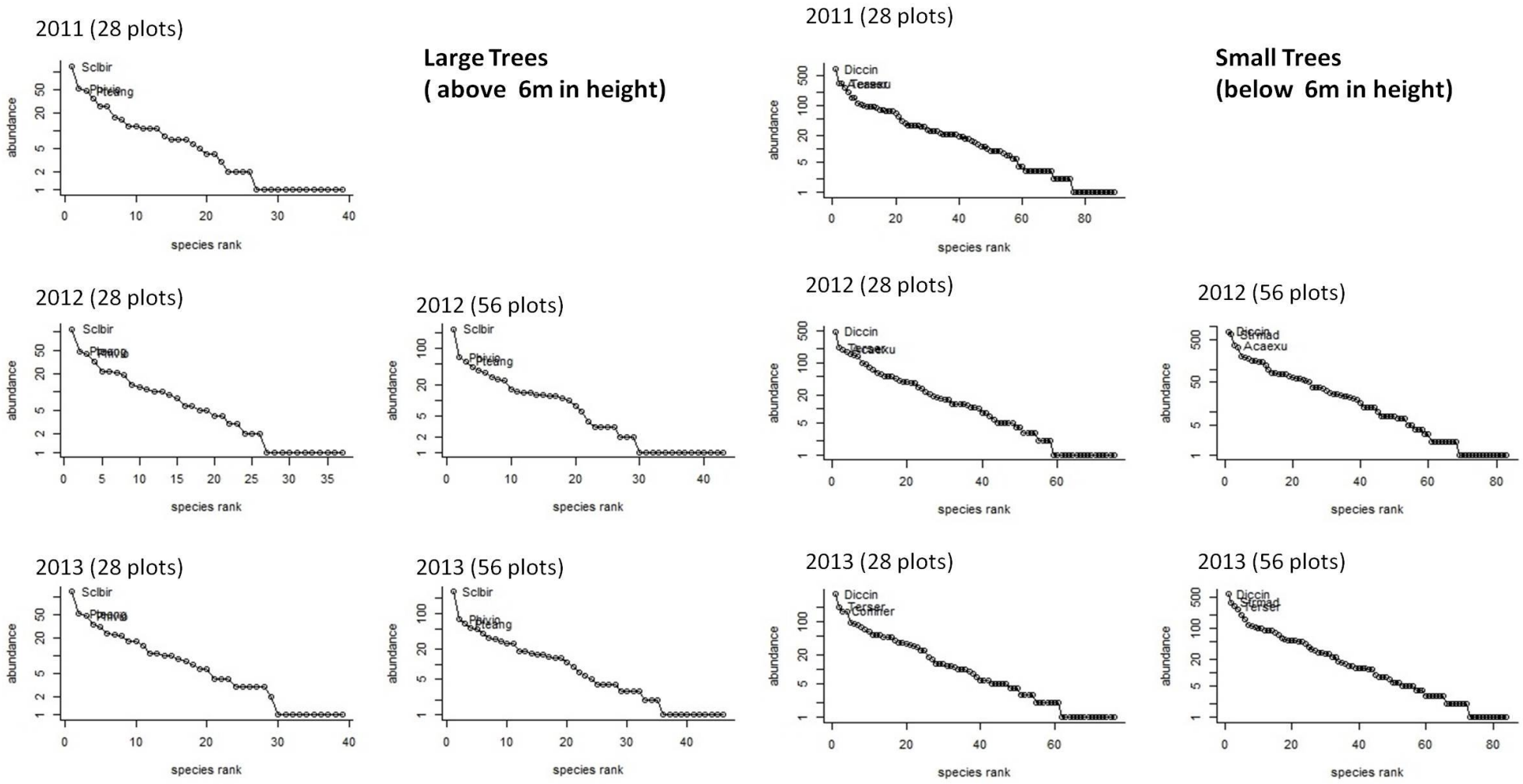


Figure 4.2 Rank abundance curves for both the large (left) and small (right) trees, showing the three highest ranked dominant species for each of the survey years. These rank abundance curves are based on the natural log of abundance. Rows indicate years and columns indicate tree size. Species abbreviations are the first three letters of the genus name and the first three letters of the species name (for full species list, see Chapter 5 Appendix 1).

4.4.1.3 How do species richness, diversity and evenness differ between catenal positions over time?

Diversity Indices

Large and small trees: Species richness, diversity and evenness were similar between bottomlands and uplands for both large and small trees across the three survey years (Table 4.3).

Species rarefaction curves

Large trees: The bottomlands and uplands had similar species richness in all of the three survey years (Fig 4.4).

Small trees: In 2011_{28} and 2013_{56}, the uplands and bottomlands had similar species richness (Fig 4.4). Whereas in $2012_{28\&56}$ and 2013_{28}, the uplands had higher species richness compared to the bottomlands (Fig 4.4).

Rank abundance

Large trees: The most abundant species within the bottomlands differed between survey years and comprised *S. birrea, S. madagascariensis, C. collinum, Albizia harveyi, Acacia gerrardii, P. violacea, P. angolensis* and *S. africana*. The three most abundant species within the uplands were consistently *S. birrea* > *P. angolensis* > *P. violacea*.

Small trees: The most abundant species within the bottomlands differed between survey years and comprised *D. cinerea, A. exuvialis, C. hereroense* and *Catunaregam spinosa*. The three most abundant species within the uplands were consistently *D. cinerea* > *S. madagascariensis* > *T. sericea*.

Table 4.2 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small trees between rainfall zones across three survey years (2011-2013). Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Years	Number of plots	Large trees (>6m height)				
		Rainfall Zone	Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	4	Low	$3.5 \pm 0.78_{ab}$	$0.7 \pm 0.16_{a}$	$0.6 \pm 0.09_{ab}$	$0.5 \pm 0.09_{a}$
	12	Medium	$2.3 \pm 0.14_{a}$	$0.6 \pm 0.05_{a}$	$0.4 \pm 0.03_{a}$	$0.8 \pm 0.02_{b}$
	12	High	$8.3 \pm 0.39_{b}$	$1.7 \pm 0.06_{b}$	$0.7 \pm 0.02_{b}$	$0.8 \pm 0.01_{b}$
2012_{28}	4	Low	$3.8 \pm 0.97_{ab}$	$0.7 \pm 0.20_{a}$	$0.6 \pm 0.11_{ab}$	$0.5 \pm 0.10_{a}$
	12	Medium	$3.3 \pm 0.20_{a}$	$0.8 \pm 0.06_{a}$	$0.4 \pm 0.02_{a}$	$0.9 \pm 0.01_{b}$
	12	High	$7.5 \pm 0.35_{b}$	$1.6 \pm 0.06_{b}$	$0.7 \pm 0.02_{b}$	$0.8 \pm 0.01_{b}$
2013_{28}	4	Low	$4.0 \pm 1.06_{ab}$	$0.7 \pm 0.21_{a}$	$0.6 \pm 0.11_{ab}$	$0.5 \pm 0.10_{a}$
	12	Medium	$4.2 \pm 0.29_{a}$	$1.0 \pm 0.05_{a}$	$0.5 \pm 0.02_{a}$	$0.8 \pm 0.01_{b}$
	12	High	$8.3 \pm 0.35_{b}$	$1.7 \pm 0.05_{b}$	$0.8 \pm 0.01_{b}$	$0.8 \pm 0.01_{b}$
2012_{56}	20	Low	$3.4 \pm 0.12_{a}$	$0.8 \pm 0.03_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.01_{a}$
	18	Medium	$2.8 \pm 0.12_{a}$	$0.7 \pm 0.04_{a}$	$0.4 \pm 0.02_{a}$	$0.9 \pm 0.01_{a}$
	18	High	$7.0 \pm 0.22_{b}$	$1.5 \pm 0.04_{b}$	$0.7 \pm 0.02_{b}$	$0.8 \pm 0.01_{a}$
2013_{56}	20	Low	$4.3 \pm 0.16_{a}$	$0.9 \pm 0.04_{a}$	$0.5 \pm 0.02_{a}$	$0.8 \pm 0.01_{a}$
	18	Medium	$3.7 \pm 0.16_{a}$	$0.9 \pm 0.03_{a}$	$0.5 \pm 0.01_{a}$	$0.8 \pm 0.01_{a}$
	18	High	$7.9 \pm 0.21_{b}$	$1.7 \pm 0.03_{b}$	$0.8 \pm 0.01_{b}$	$0.8 \pm 0.01_{a}$
Years	**Number of plots**	**Small trees (< 6m height)**				
		Rainfall Zone	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	4	Low	$9.0 \pm 0.35_{a}$	$1.4 \pm 0.11_{a}$	$0.6 \pm 0.05_{a}$	$0.5 \pm 0.04_{a}$
	12	Medium	$17.3 \pm 0.45_{b}$	$2.1 \pm 0.04_{ab}$	$0.8 \pm 0.01_{a}$	$0.5 \pm 0.01_{a}$
	12	High	$21.2 \pm 0.84_{c}$	$2.2 \pm 0.05_{b}$	$0.8 \pm 0.01_{a}$	$0.5 \pm 0.01_{a}$
2012_{28}	4	Low	$7.8 \pm 0.43_{a}$	$1.4 \pm 0.13_{a}$	$0.6 \pm 0.06_{a}$	$0.5 \pm 0.05_{a}$
	12	Medium	$13.7 \pm 0.34_{ab}$	$2.0 \pm 0.04_{ab}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	12	High	$16.8 \pm 0.50_{b}$	$2.1 \pm 0.04_{b}$	$0.8 \pm 0.01_{a}$	$0.5 \pm 0.01_{a}$
2013_{28}	4	Low	$7.8 \pm 0.69_{a}$	$1.4 \pm 0.15_{a}$	$0.6 \pm 0.06_{a}$	$0.6 \pm 0.04_{a}$
	12	Medium	$12.9 \pm 0.37_{ab}$	$2.0 \pm 0.04_{b}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	12	High	$15.1 \pm 0.50_{b}$	$2.0 \pm 0.04_{b}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
2012_{56}	20	Low	$8.4 \pm 0.13_{a}$	$1.5 \pm 0.03_{a}$	$0.7 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	18	Medium	$11.9 \pm 0.25_{b}$	$1.8 \pm 0.03_{ab}$	$0.7 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	18	High	$16.2 \pm 0.33_{c}$	$2.0 \pm 0.03_{b}$	$0.8 \pm 0.01_{a}$	$0.5 \pm 0.01_{a}$
2013_{56}	20	Low	$8.2 \pm 0.14_{a}$	$1.5 \pm 0.02_{a}$	$0.7 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	18	Medium	$11.6 \pm 0.25_{b}$	$1.8 \pm 0.03_{ab}$	$0.7 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	18	High	$14.7 \pm 0.29_{c}$	$2.0 \pm 0.03_{b}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$

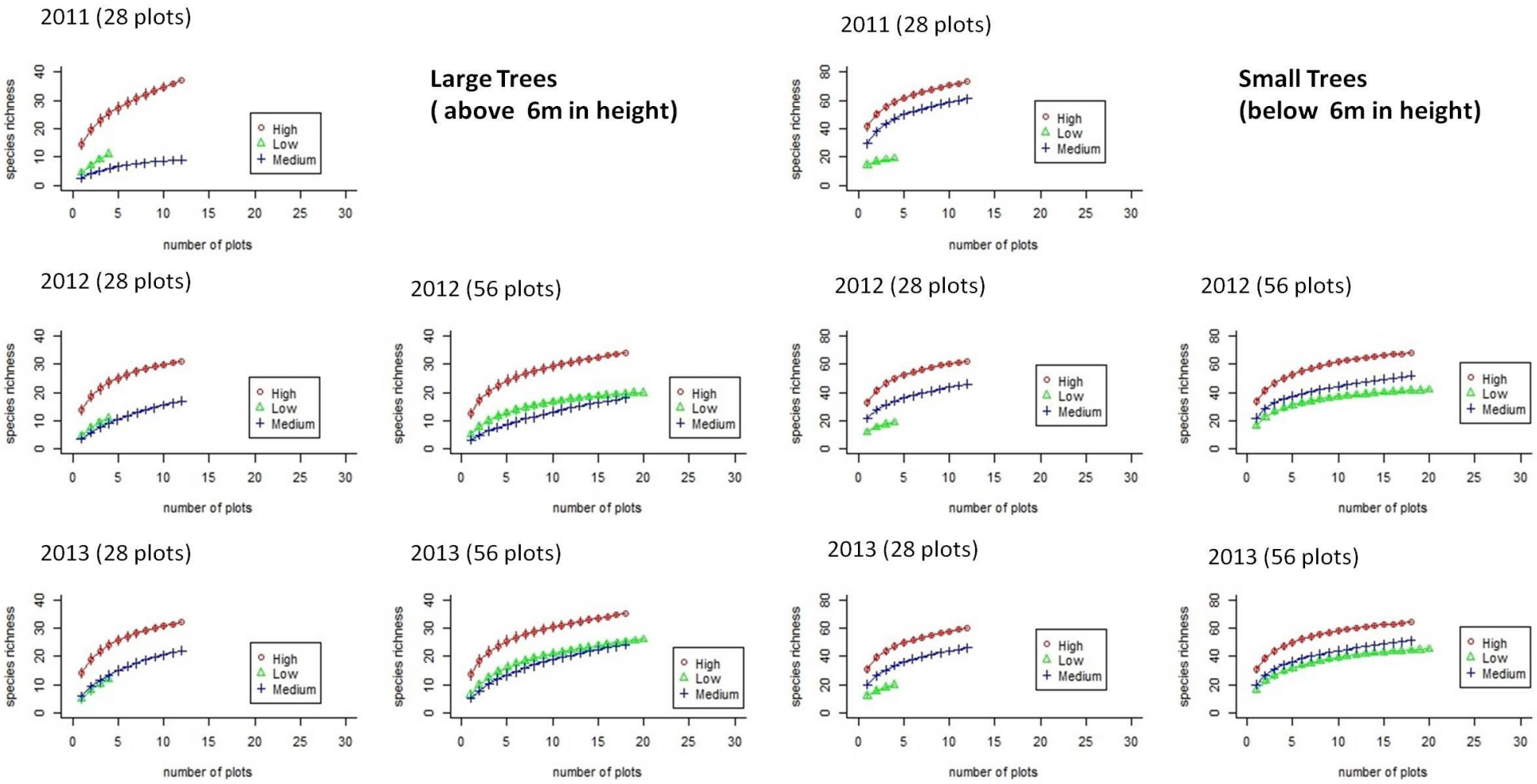


Figure 4.3 The species rarefaction curves for large (left) and small (right) trees compared between rainfall zones (low (Δ), medium (+) and high (○)) for each of the survey years. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size

Table 4.3 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small trees between catenal positions across three survey years (2011-2013). Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly.

Years	Number of plots	Large trees (>6m height)				
		Catenal position	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	14	Bottomlands	$3.8 \pm 0.23_a$	$0.9 \pm 0.06_a$	$0.6 \pm 0.03_a$	$0.8 \pm 0.02_a$
	14	Uplands	$6.3 \pm 0.37_a$	$1.2 \pm 0.05_a$	$0.5 \pm 0.02_a$	$0.7 \pm 0.01_a$
2012_{28}	14	Bottomlands	$4.5 \pm 0.24_a$	$1.1 \pm 0.05_a$	$0.6 \pm 0.02_a$	$0.8 \pm 0.02_a$
	14	Uplands	$5.8 \pm 0.32_a$	$1.2 \pm 0.05_a$	$0.5 \pm 0.02_a$	$0.8 \pm 0.01_a$
2013_{28}	14	Bottomlands	$5.4 \pm 0.29_a$	$1.2 \pm 0.05_a$	$0.7 \pm 0.02_a$	$0.8 \pm 0.02_a$
	14	Uplands	$6.5 \pm 0.34_a$	$1.3 \pm 0.05_a$	$0.6 \pm 0.02_a$	$0.8 \pm 0.01_a$
2012_{56}	28	Bottomlands	$4.1 \pm 0.12_a$	$1.0 \pm 0.03_a$	$0.5 \pm 0.01_a$	$0.9 \pm 0.01_a$
	28	Uplands	$4.6 \pm 0.13_a$	$1.0 \pm 0.03_a$	$0.5 \pm 0.01_a$	$0.8 \pm 0.01_a$
2013_{56}	28	Bottomlands	$5.1 \pm 0.14_a$	$1.2 \pm 0.03_a$	$0.6 \pm 0.01_a$	$0.8 \pm 0.01_a$
	28	Uplands	$5.4 \pm 0.13_a$	$1.1 \pm 0.02_a$	$0.5 \pm 0.01_a$	$0.8 \pm 0.01_a$
Years	**Number of plots**	**Small trees (< 6m height)**				
		Catenal position	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	14	Bottomlands	$17.2 \pm 0.58_a$	$2.0 \pm 0.04_a$	$0.8 \pm 0.01_a$	$0.5 \pm 0.01_a$
	14	Uplands	$18.4 \pm 0.63_a$	$2.2 \pm 0.04_a$	$0.8 \pm 0.01_a$	$0.5 \pm 0.01_a$
2012_{28}	14	Bottomlands	$13.4 \pm 0.39_a$	$1.8 \pm 0.04_a$	$0.7 \pm 0.01_a$	$0.5 \pm 0.01_a$
	14	Uplands	$15.0 \pm 0.41_a$	$2.1 \pm 0.03_a$	$0.8 \pm 0.01_a$	$0.6 \pm 0.01_a$
2013_{28}	14	Bottomlands	$12.8 \pm 0.39_a$	$1.8 \pm 0.04_a$	$0.7 \pm 0.01_a$	$0.5 \pm 0.01_a$
	14	Uplands	$13.4 \pm 0.39_a$	$2.0 \pm 0.03_a$	$0.8 \pm 0.01_a$	$0.6 \pm 0.01_a$
2012_{56}	28	Bottomlands	$12.0 \pm 0.21_a$	$1.8 \pm 0.02_a$	$0.7 \pm 0.01_a$	$0.6 \pm 0.01_a$
	28	Uplands	$12.1 \pm 0.19_a$	$1.7 \pm 0.02_a$	$0.7 \pm 0.01_a$	$0.5 \pm 0.01_a$
2013_{56}	28	Bottomlands	$11.6 \pm 0.19_a$	$1.9 \pm 0.02_a$	$0.8 \pm 0.01_a$	$0.6 \pm 0.01_a$
	28	Uplands	$11.1 \pm 0.17_a$	$1.7 \pm 0.02_a$	$0.7 \pm 0.01_a$	$0.6 \pm 0.01_a$

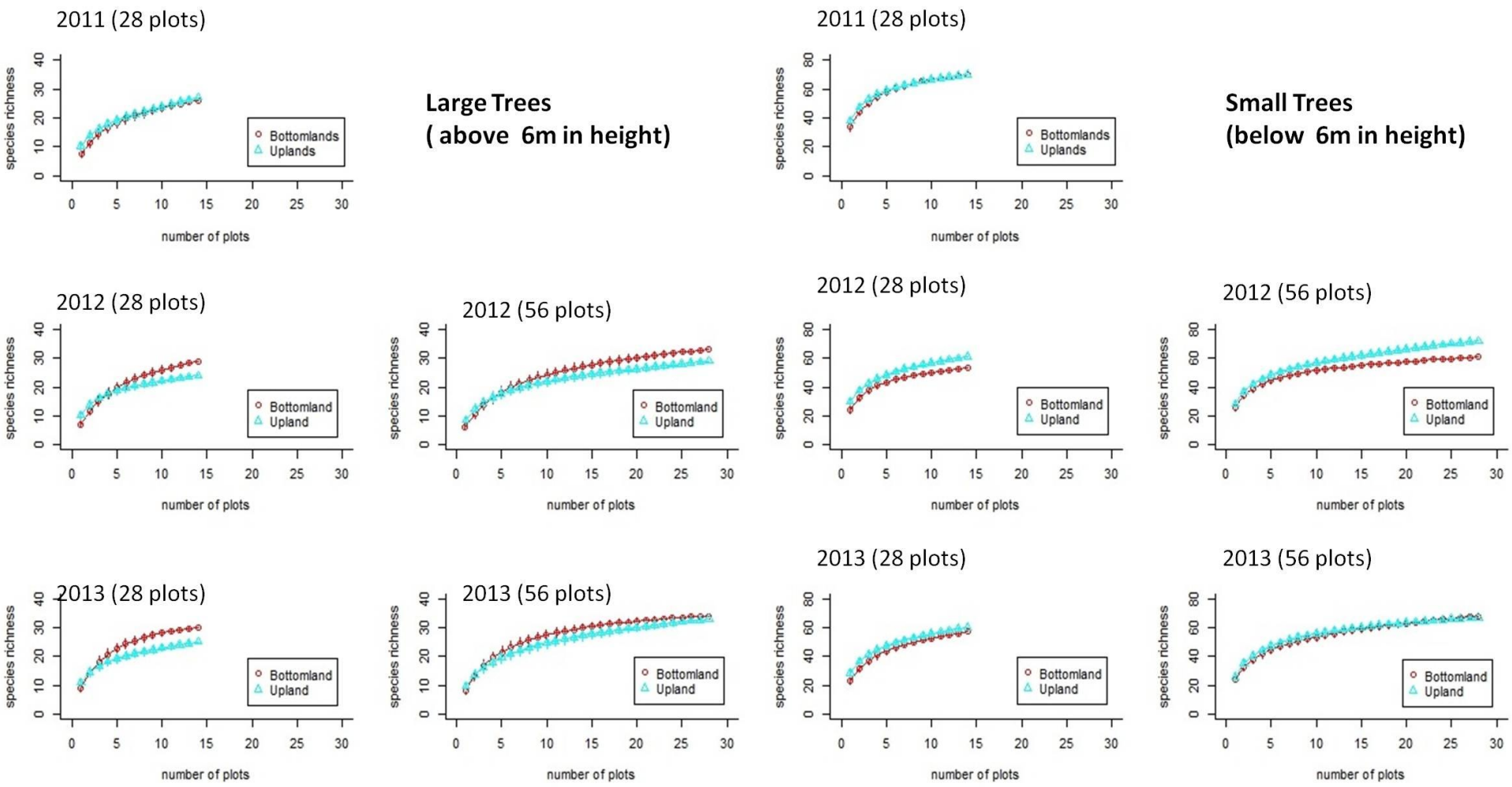


Figure 4.4 The species rarefaction curves for large (left) and small (right) trees compared between catenal positon (bottomlands (○) and uplands (Δ)) for each of the survey years. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size.

4.4.1.4 How do species richness, diversity and evenness differ between a combination of rainfall zones and catenal position over time?

Rainfall zones showed greater statistical differences between them than the difference between the catenal positions. Rainfall zones were significant on the change of both species richness and Shannon's diversity for all three the survey years for both large and small trees, except for the small trees in 2013_{28} (Table 4.4). For Simpson's diversity, rainfall only had a significant change in the large trees of 2011_{28}, 2012_{56} and $2013_{28\&56}$. There was however no effect by catenal position on the change in Simpson's diversity for large trees in 2012_{28} or for the small trees of the three survey years (Table 4.4). Rainfall zones were only significant on the evenness for the large trees of 2012_{28} and 2013_{28}, but there was no change in the large trees in 2011_{28}, 2012_{56} or 2013_{56} or small trees any of the three survey years (Table 4.4). Catenal position was only significant on the change of species richness of large trees in 2011_{28}. There was however no effect by catenal position on the change in species richness for large trees in $2012_{28\&56}$ or $2013_{28\&56}$ or for the small trees of the three survey years (Table 4.4). Catenal position had no effect on Shannon's and Simpson's diversity or evenness for either large or small trees in any of the three survey years (Table 4.4). Similarly, there was no interaction between catenal/rainfall combinations and thus no effect on the change of species richness and Shannon's diversity for large or small trees in any of the three survey years (Table 4.4). There was however an interaction between catenal positions and rainfall zones in the Simpson's diversity in 2013_{28} for large trees and in the evenness in $2012_{28\&56}$ and 2013_{28} of large trees (Table 4.4). There was no interaction between catenal/rainfall combinations for Simpson's diversity and evenness in the small trees in any of the three survey years (Table 4.4).

<u>Diversity Indices</u>

Large trees: Species richness was highest in the upland plots in the high rainfall zone, and in the uplands and bottomlands of the medium rainfall zone (Appendix 2). Both diversity indices indicated no difference in species diversity for the large trees in 2011_{28}, 2012_{28} or 2013_{28} (Appendix 2). Diversity was higher in the upland plots of the high rainfall zone compared to the other rainfall zone and catenal position combinations for 2012_{56} and 2013_{56} (Appendix 2). Species were not evenly distributed in 2011_{28}, 2012_{28} or 2013_{28} but was however evenly distributed in 2012_{56} and 2013_{56} (Appendix 2).

Small trees: Species richness was highest in the upland and bottomland plots of the high rainfall zone compared to the other catenal position/rainfall zone combinations

(Appendix 3). Species richness based on Shannon-Wiener did not differ between catenal position/rainfall zone in 2011_{28}, 2012_{28} or 2013_{28} but did differ in 2012_{56} and 2013_{56} (Appendix 3). The diversity index of Simpson indicated the opposite to that of Shannon-Wiener, as it indicated the differences between catenal position/rainfall zone combinations to be in 2011_{28}, 2012_{28} or 2013_{28} and not in 2012_{56} and 2013_{56} (Appendix 3). Species diversity was still highest in the upland and bottomland plots in the high rainfall zone in all tree survey years, except in 2013_{28} where the upland plots in the low and medium rainfall zone were equal to that of the uplands in the high rainfall zone (Appendix 3). The species were evenly distributed across the catenal position/rainfall zone combinations across the three survey years (Appendix 3).

Species rarefaction curves

Large trees: The uplands in the high rainfall zone had the highest species richness compared to the other catenal position/rainfall combinations for all three survey years (Fig 4.5). In the lower sampling effort, the bottomlands in the high rainfall zone had the highest species richness for all three survey years. For 2011_{28}, the other catenal position/rainfall zone combinations are similar in low sampling effort (Fig 4.5). In 2012_{28} and 2013_{28}, the species richness was similar between the bottomlands of the low and medium rainfall zones and the species richness was similar between the uplands of the low and medium rainfall zones (Fig 4.5). The uplands of the low and medium rainfall zone had the lowest species richness for both 2012_{56} and 2013_{56} (Fig 4.5).

Small trees: Again, the uplands in the high rainfall zone for small trees had the highest species richness in high sampling effort (Fig 4.5). In 2011_{28}, the uplands and bottomlands in the high rainfall zone and the bottomlands in the medium rainfall had similar species richness. The uplands and bottomlands in the low rainfall zone had the lowest species richness, partly due to the sample size (Fig 4.5). In 2012_{28} and 2013_{28}, the uplands in the high rainfall zone were slightly higher compared to the species richness of the bottomlands in the medium and high rainfall zones for small trees (Fig 4.5). The uplands and bottomlands in the low rainfall zone had the lowest species richness. In 2012_{56} and 2013_{56}, the species richness was very similar between catenal position/rainfall zone combinations (Fig 4.5).

Table 4.4 Two-way ANOVAs comparing species richness, evenness and diversity (Shannon's and Simpson's index) between rainfall zone, catenal position and the interaction between rainfall zone and catenal position for large (>6m in height) and small trees (<6m in height). Significant p-values in bold type.

			Species Richness			**Evenness**		
Tree size	**Year**	**Plots sampled**	**Rainfall zones**	**Catenal position**	**Rainfall* Catenal Interaction**	**Rainfall zones**	**Catenal position**	**Rainfall* Catenal Interaction**
			p-value	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Large Trees	2011_{28}	28	< **0.001**	**0.048**	0.251	0.055	0.709	0.314
	2012_{28}	28	**0.015**	0.327	0.209	**0.003**	0.476	**0.010**
	2013_{28}	28	**0.029**	0.436	0.182	**0.019**	0.685	**0.021**
	2012_{56}	56	< **0.001**	0.517	0.247	0.299	0.266	**0.041**
	2013_{56}	56	**0.001**	0.705	0.182	0.785	0.181	0.161
Small Trees	2011_{28}	28	**0.027**	0.681	0.101	0.916	0.145	0.670
	2012_{28}	28	**0.009**	0.362	0.153	0.468	0.234	0.672
	2013_{28}	28	0.051	0.730	0.132	0.648	0.086	0.754
	2012_{56}	56	< **0.001**	0.762	0.374	0.280	0.336	0.202
	2013_{56}	56	< **0.001**	0.820	0.255	0.407	0.266	0.120

			Shannon's Diversity			**Simpson's Index**		
Tree size	**Year**	**Plots sampled**	**Rainfall zones**	**Catenal position**	**Rainfall* Catenal Interaction**	**Rainfall zones**	**Catenal position**	**Rainfall* Catenal Interaction**
			p-value	**p-value**	**p-value**	**p-value**	**p-value**	**p-value**
Large Trees	2011_{28}	28	**0.001**	0.294	0.681	**0.042**	0.592	0.144
	2012_{28}	28	**0.024**	0.791	0.415	0.073	0.070	0.528
	2013_{28}	28	**0.008**	0.756	0.528	**0.024**	0.402	**0.022**
	2012_{56}	56	**0.001**	0.948	0.410	**0.006**	0.602	0.225
	2013_{56}	56	< **0.001**	0.835	0.615	**0.001**	0.334	0.447
Small Trees	2011_{28}	28	**0.029**	0.239	0.087	0.091	0.247	0.144
	2012_{28}	28	**0.032**	0.130	0.179	0.106	0.149	0.261
	2013_{28}	28	0.067	0.213	0.173	0.125	0.151	0.179
	2012_{56}	56	**0.005**	0.782	0.239	0.074	0.501	0.406
	2013_{56}	56	**0.009**	0.501	0.345	0.121	0.368	0.431

Rank abundance

Large trees: The most abundant species within each catenal position/rainfall zone differed between combinations and between survey years. The most abundant species within the bottomlands in the low rainfall zone comprised *S. birrea*, *C. apiculatum*, *A. nigrescens*, *C. collinum*, and *A. gerrardii*. The most abundant species within the uplands in the low rainfall zone comprised *S. birrea*, *L. discolor*, *C. zeyheri*, *P. violacea*, *P. angolensis*, *A. nigrescens* and *C. collinum*. The most abundant species within the bottomlands in the medium rainfall zone comprised *S. birrea*, *P. violacea*, *S. africana*, *Acacia burkei*, *D. mespiliformis* and *P. violacea*. The most abundant species within the uplands in the medium rainfall zone comprised *S. birrea*, *P. violacea*, *S. madagascariensis* and *D. mespiliformis*. The most abundant species within the bottomlands in the high rainfall zone comprised *S. birrea*, *S. madagascariensis*, *C. collinum*, *A. harveyi*, *A. gerrardii*, *A. burkei*, *C. zeyheri* and *D. mespiliformi*. The three most abundant species for trees within the uplands in the high rainfall zone were consistently *S. birrea* > *P. angolensis* > *P. violacea*.

Small trees: The most abundant species within each catenal position/rainfall zone differed between combinations and between survey years. The most abundant species within the bottomlands in the low rainfall zone comprised *A. exuvialis*, *Pterocarpus rotundifolius*, *T. sericea*, *D. cinerea*, *C. apiculatum* and *Ormocarpum trichocarpum*. The most abundant species within the uplands in the low rainfall zone comprised *A. exuvialis*, *S. madagascariensis*, *D. melanoxylon*, *D. cinerea*, *A. exuvialis* and *T. sericea*. The most abundant species the bottomlands in the medium rainfall zone comprised *D. cinerea*, *A. exuvialis*, *C. spinosa* and *C. hereroense*. The three most abundant species within the uplands in the medium rainfall zone were consistently *S. madagascariensis* > *T. sericea* > *D. cinerea*. The most abundant species within the bottomlands in the high rainfall zone comprised *D. cinerea*, *C. spinosa*, *C. hereroense*, *D. lycioides*, *C. collinum* and *T. sericea*. The most abundant species within the uplands in the high rainfall zone comprised *D. cinerea*, *S. petersiana*, *D. lycioides*, *Combretum molle*, *C. collinum* and *T. sericea*.

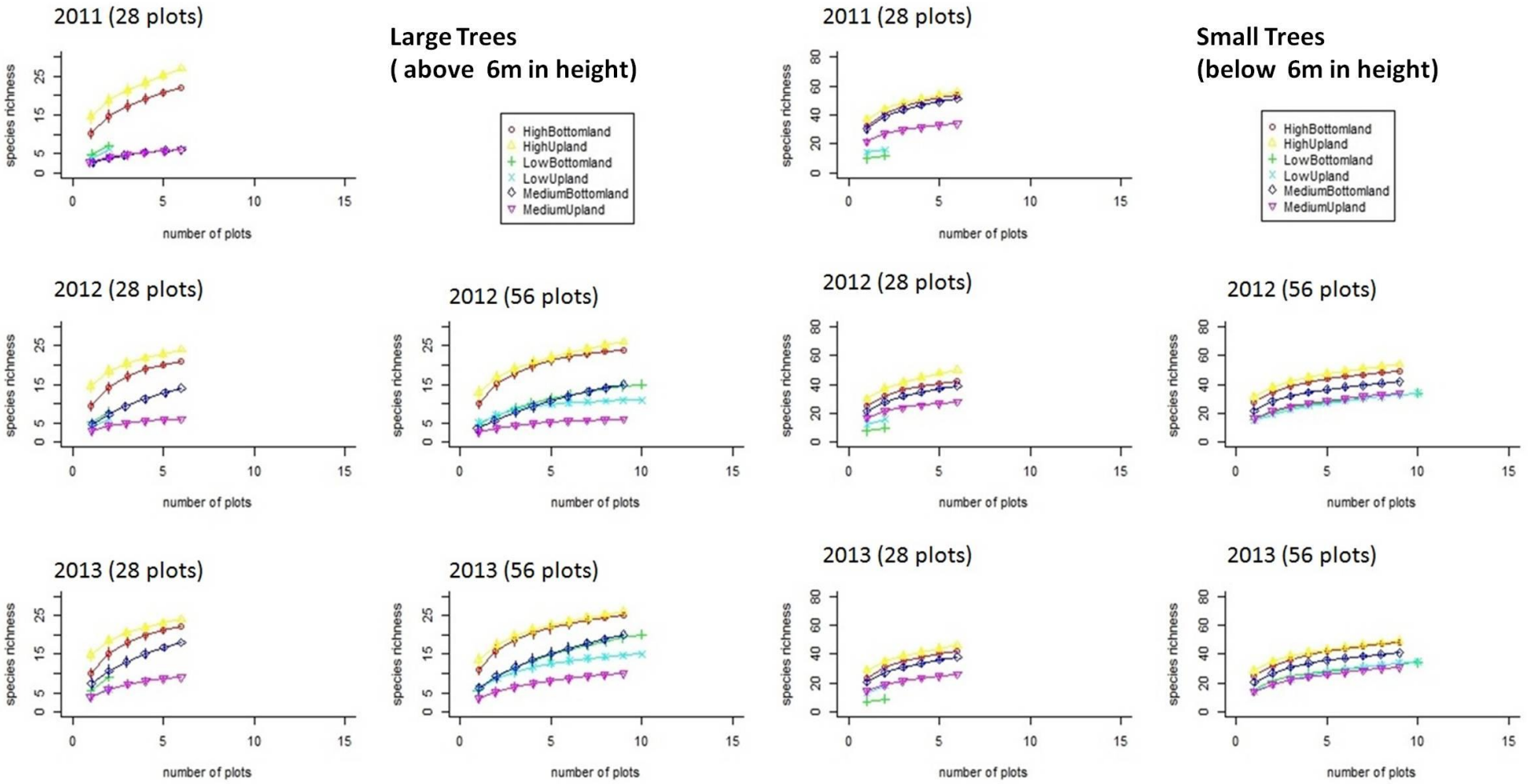


Figure 4.5 The species rarefaction curves for large (left) and small (right) trees compared between catenal position and rainfall zone combinations (bottomland (+) and upland (X) in low rainfall, bottomland (◊) and upland (∇) in medium rainfall and bottomland (○) and upland (Δ) in high rainfall) for each of the survey years. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size

4.4.2 Difference in species richness, diversity and evenness of harvested trees

4.4.2.1 How do species richness, diversity and evenness of harvested trees differ over time in general?

Diversity Indices

Large trees: Recent harvesting was absent in 2011_{28} but increased from $2012_{28\&56}$ to $2013_{28\&56}$ (Chapter 3 and 5). Species richness, diversity and evenness were lower in recently harvested trees in $2012_{28\&56}$ compared to $2013_{28\&56}$ (Table 4.5).

Small trees: In comparison, species richness, species diversity or species distribution of most harvested trees did not differ in any of the three survey years (Table 4.5).

Table 4.5 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small harvested trees across three survey years (2011-2013). Values in the same column for the 28 and 56 plot data separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$). In 2011 there was apparently no harvesting on the large trees.

Year		Large trees (>6m height)			
	Number of plots	Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	28	-	-	-	-
2012_{28}	28	$0.3 \pm 0.03_a$	$0.1 \pm 0.01_a$	$0.9 \pm 0.01_a$	$0.1 \pm 0.01_a$
2013_{28}	28	$1.3 \pm 0.05_b$	$0.3 \pm 0.02_b$	$0.6 \pm 0.02_b$	$0.6 \pm 0.02_b$
2012_{56}	56	$0.3 \pm 0.01_a$	$0.05 \pm <0.01_a$	$0.9 \pm 0.01_a$	$0.2 \pm 0.01_a$
2013_{56}	56	$1.1 \pm 0.02_b$	$0.3 \pm 0.01_b$	$0.6 \pm 0.01_b$	$0.6 \pm 0.01_b$
Year		**Small trees (< 6m height)**			
	Number of plots	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	28	$2.4 \pm 0.08_a$	$0.5 \pm 0.02_a$	$0.4 \pm 0.01_a$	$0.8 \pm 0.01_a$
2012_{28}	28	$2.6 \pm 0.06_a$	$0.7 \pm 0.02_a$	$0.5 \pm 0.01_a$	$0.8 \pm 0.01_a$
2013_{28}	28	$2.7 \pm 0.07_a$	$0.7 \pm 0.02_a$	$0.4 \pm 0.01_a$	$0.9 \pm 0.01_a$
2012_{56}	56	$2.2 \pm 0.03_a$	$0.6 \pm 0.01_a$	$0.4 \pm 0.01_a$	$0.8 \pm 0.01_a$
2013_{56}	56	$2.6 \pm 0.03_a$	$0.7 \pm 0.01_a$	$0.5 \pm 0.01_a$	$0.8 \pm 0.01_a$

Species accumulation and rarefaction curves

Large trees: Recent harvesting was absent in 2011_{28} and thus no species accumulation curve could be produced (Fig 4.6). The curves of $2012_{28\&56}$ and $2013_{28\&56}$ show the increase of species richness of harvested trees (Fig 4.6). Both $2012_{28\&56}$ and $2013_{28\&56}$ display similar patterns concluding that the species are distributed at random over the plots (Fig 4.6).

Small trees: All three survey years also display similar patterns to the large trees and thus species are also distributed at random over the plots (Fig 4.6).

Rank abundance

Large trees: The most harvested species differed between survey years and comprised *C. collinum, A. gerrardii, T. sericea, Acacia robusta C. zeyheri* and *S. birrea* (Fig 4.7). The species diversity of harvested trees was very different between $2012_{28\&56}$ and $2013_{28\&56}$. In $2012_{28\&56}$, very low species diversity is seen compared to $2013_{28\&56}$ (Fig 4.7). Evenness of harvested trees between $2012_{28\&56}$ and $2013_{28\&56}$ was also different with $2012_{28\&56}$ having less evenly distributed harvested species compared to $2013_{28\&56}$ (Fig 4.7).

Small trees: The most harvested species differed between survey years and comprised *D. cinerea, T. sericea A. exuvialis* and *C. hereroense* (Fig 4.7). The harvested trees were similar in richness and diversity in the three survey years (Fig 4.7). Evenness for the harvested trees was slightly different between the years, with 2011_{28} having the less evenly distributed species compared to $2012_{28\&56}$ and $2013_{28\&56}$ (Fig 4.7).

4.4.2.2 How do species richness, diversity and evenness of harvested trees differ between rainfall zones over time?

Diversity Indices

Large trees: The species richness of recently harvested trees was unaffected by the rainfall gradient (Table 4.6). Species richness and diversity of harvested trees were similar between the three rainfall zones for all three survey years (Table 4.6). Similarly, evenness was also similar between rainfall zones and survey years except for 2013_{56}, where the high rainfall zone had more evenly distributed harvested species (Table 4.6).

Small trees: In comparison, species richness in harvested trees was higher in the high rainfall zone of 2011_{28} but was similar for $2012_{28\&56}$ and $2013_{28\&56}$ between the three rainfall zones (Table 4.6). Species diversity and evenness had no difference between the rainfall zones in each of the survey years (Table 4.6).

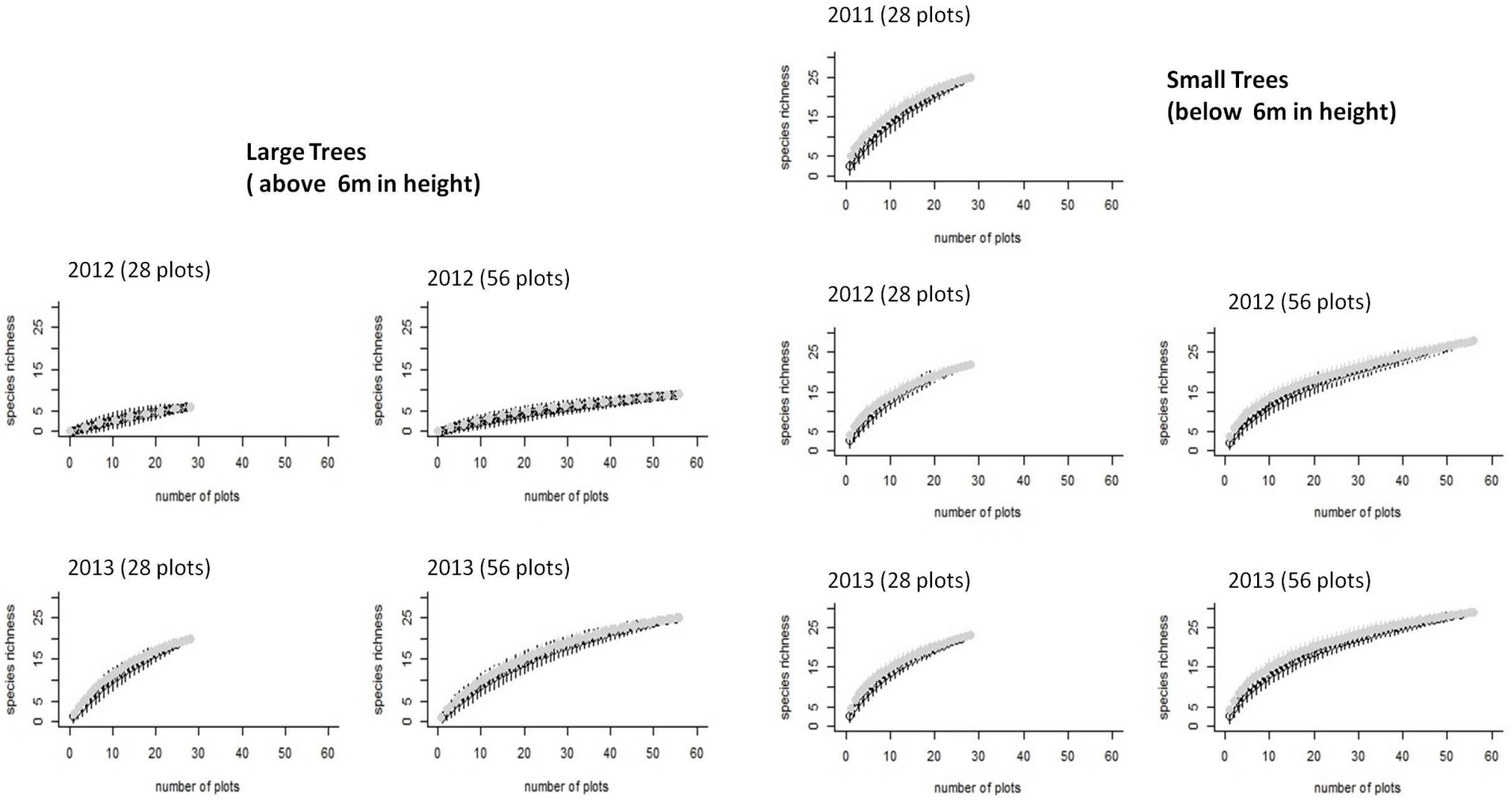


Figure 4.6 The species accumulation (open symbols (○)) and species rarefaction (solid symbols (●)) curves for recently harvested large (left) and small (right) trees for each of the survey years. Harvesting of large trees was absent in 2011. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size.

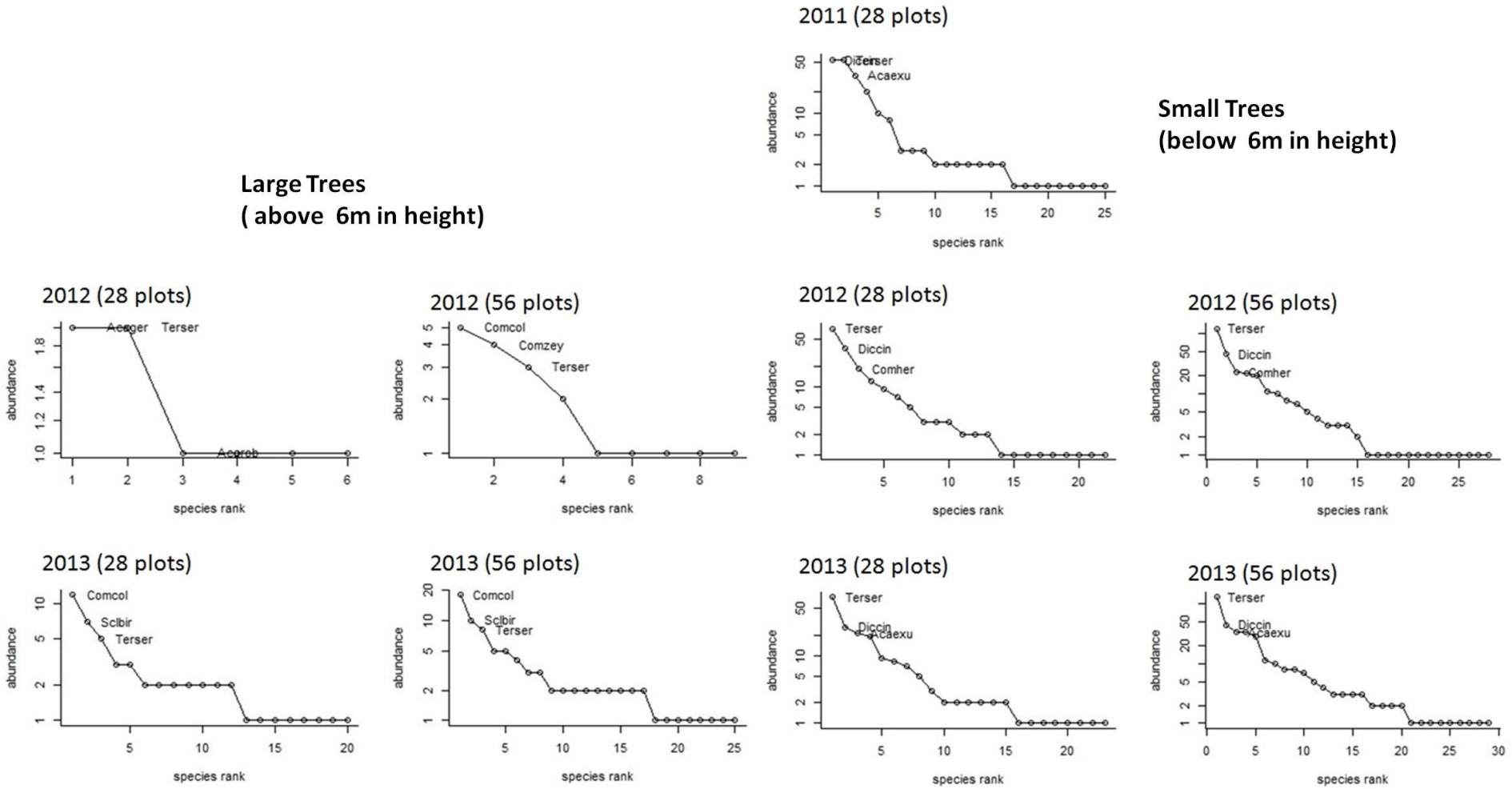


Figure 4.7 Rank abundance curves of recently harvested large (left) and small (right) trees, showing the three highest ranked dominant species for each of the survey years. These rank abundance curves are the natural log of abundance. Harvesting of large trees was absent in 2011. Rows indicate years and columns indicate tree size. Species abbreviations are the first three letters of the genus name and the first three letters of the species name (for full species list, see Chapter 5 Appendix 1).

Table 4.6 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small harvested trees between rainfall zones across three survey years (2011-2013). Values in the same column for the 28 and 56 plot data separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$). Harvesting was absent in the large trees of 2011.

Years	Number of plots	Large trees (>6m height)				
		Rainfall Zone	Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	4	Low	-	-	-	-
	12	Medium	-	-	-	-
	12	High	-	-	-	-
2012_{28}	4	Low	$1.0 \pm 0.50_{a}$	$0.3 \pm 0.17_{a}$	$0.9 \pm 0.03_{a}$	$0.3 \pm 0.13_{a}$
	12	Medium	$0.1 \pm 0.02_{a}$	-	$0.9 \pm 0.02_{a}$	$0.1 \pm 0.02_{a}$
	12	High	$0.3 \pm 0.05_{a}$	$0.1 \pm 0.02_{a}$	$0.9 \pm 0.03_{a}$	$0.2 \pm 0.03_{a}$
2013_{28}	4	Low	$1.3 \pm 0.63_{a}$	$0.4 \pm 0.20_{a}$	$1.0 \pm 0.03_{a}$	$0.3 \pm 0.13_{a}$
	12	Medium	$0.9 \pm 0.10_{a}$	$0.2 \pm 0.04_{a}$	$0.6 \pm 0.04_{a}$	$0.5 \pm 0.04_{a}$
	12	High	$1.7 \pm 0.11_{a}$	$0.4 \pm 0.04_{a}$	$0.4 \pm 0.03_{a}$	$0.8 \pm 0.03_{a}$
2012_{56}	20	Low	$0.4 \pm 0.05_{a}$	$0.1 \pm 0.02_{a}$	$0.8 \pm 0.02_{a}$	$0.2 \pm 0.02_{a}$
	18	Medium	$0.1 \pm 0.02_{a}$	-	$0.9 \pm 0.02_{a}$	$0.1 \pm 0.02_{a}$
	18	High	$0.3 \pm 0.04_{a}$	$0.1 \pm 0.01_{a}$	$0.8 \pm 0.02_{a}$	$0.2 \pm 0.02_{a}$
2013_{56}	20	Low	$1.0 \pm 0.07_{a}$	$0.2 \pm 0.02_{a}$	$0.6 \pm 0.02_{a}$	$0.5 \pm 0.03_{ab}$
	18	Medium	$0.7 \pm 0.06_{a}$	$0.1 \pm 0.02_{a}$	$0.7 \pm 0.02_{a}$	$0.4 \pm 0.03_{a}$
	18	High	$1.7 \pm 0.07_{a}$	$0.4 \pm 0.03_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.02_{b}$
Years	**Number of plots**	**Small trees (< 6m height)**				
		Rainfall Zone	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	4	Low	$2.3 \pm 0.24_{ab}$	$0.6 \pm 0.12_{a}$	$0.4 \pm 0.07_{a}$	$0.9 \pm 0.02_{a}$
	12	Medium	$3.5 \pm 0.21_{a}$	$0.8 \pm 0.05_{a}$	$0.4 \pm 0.03_{a}$	$0.8 \pm 0.02_{a}$
	12	High	$1.3 \pm 0.12_{b}$	$0.3 \pm 0.04_{a}$	$0.5 \pm 0.04_{a}$	$0.6 \pm 0.04_{a}$
2012_{28}	4	Low	$3.3 \pm 0.43_{a}$	$0.9 \pm 0.15_{a}$	$0.5 \pm 0.08_{a}$	$0.9 \pm 0.04_{a}$
	12	Medium	$2.8 \pm 0.17_{a}$	$0.6 \pm 0.05_{a}$	$0.4 \pm 0.02_{a}$	$0.9 \pm 0.01_{a}$
	12	High	$2.1 \pm 0.10_{a}$	$0.7 \pm 0.04_{a}$	$0.6 \pm 0.02_{a}$	$0.8 \pm 0.03_{a}$
2013_{28}	4	Low	$3.5 \pm 0.32_{a}$	$1.0 \pm 0.09_{a}$	$0.6 \pm 0.04_{a}$	$0.8 \pm 0.03_{a}$
	12	Medium	$1.8 \pm 0.09_{a}$	$0.7 \pm 0.05_{a}$	$0.4 \pm 0.03_{a}$	$0.9 \pm 0.01_{a}$
	12	High	$2.7 \pm 0.09_{a}$	$0.6 \pm 0.04_{a}$	$0.5 \pm 0.03_{a}$	$0.9 \pm 0.02_{a}$
2012_{56}	20	Low	$3.2 \pm 0.20_{a}$	$0.4 \pm 0.03_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.02_{a}$
	18	Medium	$3.0 \pm 0.10_{a}$	$0.7 \pm 0.03_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.01_{a}$
	18	High	$3.2 \pm 0.12_{a}$	$0.6 \pm 0.03_{a}$	$0.6 \pm 0.02_{a}$	$0.7 \pm 0.02_{a}$
2013_{56}	20	Low	$2.0 \pm 0.09_{a}$	$0.7 \pm 0.03_{a}$	$0.5 \pm 0.02_{a}$	$0.8 \pm 0.02_{a}$
	18	Medium	$1.8 \pm 0.07_{a}$	$0.8 \pm 0.03_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.01_{a}$
	18	High	$1.9 \pm 0.07_{a}$	$0.6 \pm 0.03_{a}$	$0.5 \pm 0.02_{a}$	$0.8 \pm 0.02_{a}$

Species rarefaction curves

Large trees: In 2012_{28} harvesting was absent in the high rainfall zone and species richness was similar between the low and medium rainfall zone (Fig 4.8). In 2012_{56}, harvesting in the low rainfall zone had the highest species richness whereas in 2013_{28}, the

species richness was highest in the high rainfall zone (Fig 4.8). There was however no difference in species richness between the three rainfall zones in 2012_{28} whereas in 2013_{56}, species richness was highest in the high rainfall zone (Fig 4.8).

Small trees: In all three survey years (2011_{28} $2012_{28\&56}$, $2013_{28\&56}$) harvesting in the medium rainfall zone had the highest species richness (Fig 4.8).

Rank abundance

Large trees: The most harvested species within the low rainfall zone differed between survey years and comprised *T. sericea*, *A. nigrescens*, *C. zeyheri*, *C. collinum*, *C. apiculatum* and *A. nigrescens*. The most harvested species within the medium rainfall zone differed between survey years and comprised *Acacia robusta*, *D. cinerea*, *S. birrea*, *A. burkei*, *C. collinum* and *A. gerrardii*. The most harvested species within the high rainfall zone differed between survey years and comprised *A. gerrardii*, *C. collinum*, *T. sericea* and *C. apiculatum*.

Small trees: The most harvested species within the low rainfall zone differed between survey years and comprised *A. exuvialis*, *T. sericea*, *D. cinerea*, *C. collinum* and *A. burkei*. The most harvested species within the medium rainfall zone differed between survey years and comprised *T. sericea*, *D. cinerea*, *C. hereroense* and *A. exuvialis*. The most harvested species within the high rainfall zone differed between survey years and comprised *D. cinerea*, *T. sericea*, *Peltophorum africanum*, *C. collinum* and *C. hereroense*.

4.4.2.3 How do species richness, diversity and evenness of harvested trees differ between catenal positions over time?

Diversity Indices

Large and small trees: Species richness of harvested species was similar between the two catenal positions for both large and small harvested trees (Table 4.7). Both Shannon-Wiener and Simpson's diversity index had similar diversities for the harvested trees in the bottomlands and uplands (Table 4.7). Likewise, both catenal positions had similar evenness of species distribution of harvested species for large and small trees (Table 4.7).

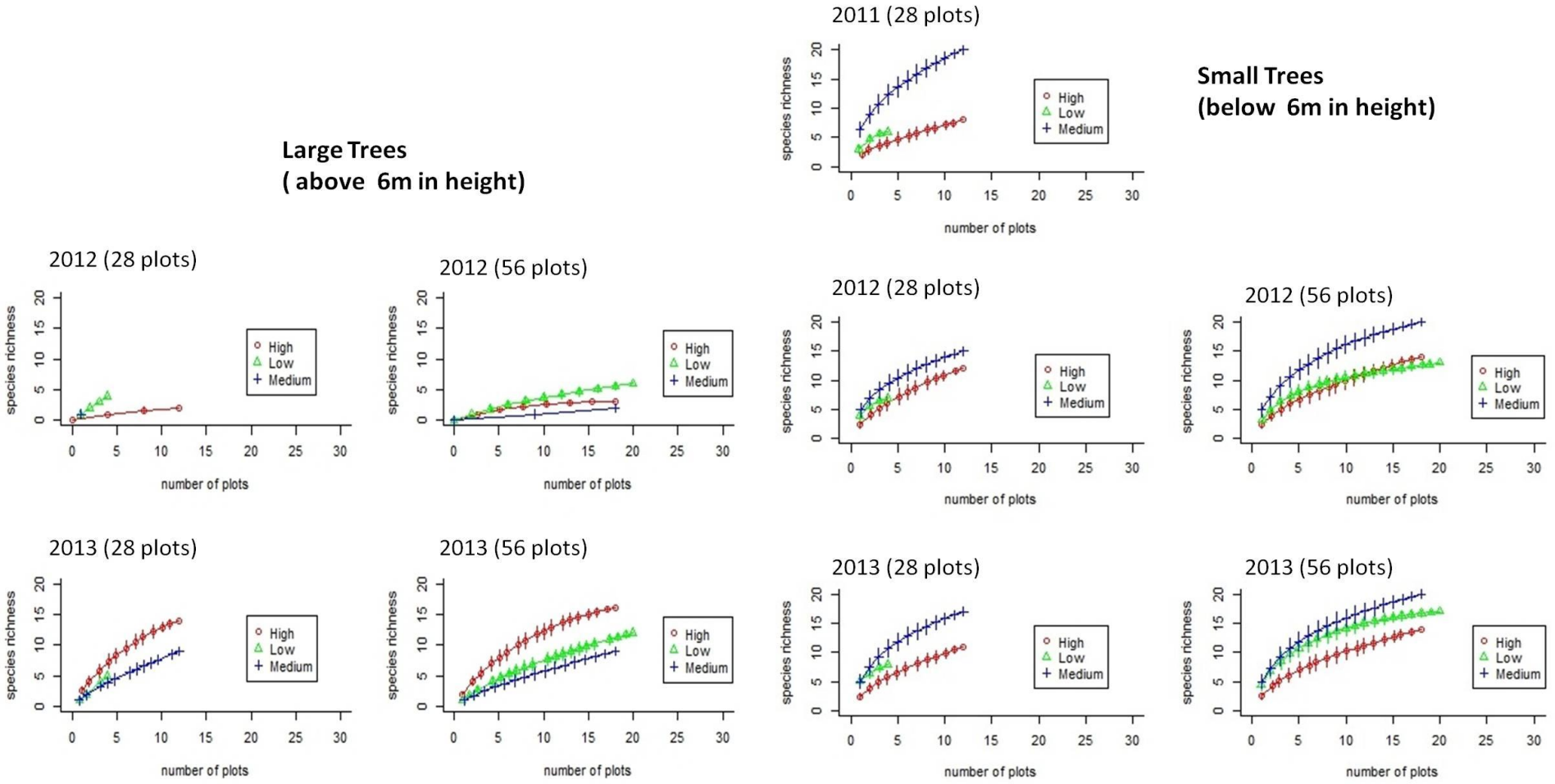


Figure 4.8 The species rarefaction curves for recently harvested large (left) and small (right) trees compared between rainfall zones (low (Δ), medium (+) and high (○)) for each of the survey years. Harvesting of large trees was absent in 2011. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size

Table 4.7 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for the large and small harvested trees between catenal positions across three survey years (2011-2013). Values in the same column for the 28 and 56 plot data separately accompanied by the same subscript do not differ significantly. Harvesting was absent in the large trees of 2011.

Years	Number of plots	Large trees (>6m height)				
		Catenal position	Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	14	Bottomlands	-	-	-	-
	14	Uplands	-	-	-	-
2012_{28}	14	Bottomlands	$0.6 \pm 0.08_a$	$0.1 \pm 0.03_a$	$0.8 \pm 0.03_a$	$0.3 \pm 0.03_a$
	14	Uplands	-	-	-	-
2013_{28}	14	Bottomlands	$1.7 \pm 0.13_a$	$0.5 \pm 0.04_a$	$0.6 \pm 0.03_a$	$0.7 \pm 0.03_a$
	14	Uplands	$0.9 \pm 0.07_a$	$0.2 \pm 0.03_a$	$0.6 \pm 0.03_a$	$0.5 \pm 0.04_a$
2012_{56}	28	Bottomlands	$0.4 \pm 0.03_a$	$0.1 \pm 0.01_a$	$0.8 \pm 0.01_a$	$0.2 \pm 0.02_a$
	28	Uplands	$0.2 \pm 0.02_a$	$0.02 \pm <0.01_a$	$0.9 \pm 0.01_a$	$0.1 \pm 0.04_a$
2013_{56}	28	Bottomlands	$1.1 \pm 0.06_a$	$0.3 \pm 0.02_a$	$0.6 \pm 0.02_a$	$0.5 \pm 0.02_a$
	28	Uplands	$1.1 \pm 0.04_a$	$0.3 \pm 0.02_a$	$0.6 \pm 0.01_a$	$0.6 \pm 0.02_a$
Years	**Number of plots**	**Small trees (< 6m height)**				
		Catenal position	**Richness**	**Shannon-Wiener**	**Simpson**	**Evenness**
2011_{28}	14	Bottomlands	$2.6 \pm 0.19_a$	$0.6 \pm 0.05_a$	$0.4 \pm 0.03_a$	$0.7 \pm 0.03_a$
	14	Uplands	$2.1 \pm 0.11_a$	$0.5 \pm 0.04_a$	$0.4 \pm 0.03_a$	$0.8 \pm 0.03_a$
2012_{28}	14	Bottomlands	$2.6 \pm 0.25_a$	$0.7 \pm 0.04_a$	$0.5 \pm 0.02_a$	$0.8 \pm 0.03_a$
	14	Uplands	$2.6 \pm 0.09_a$	$0.7 \pm 0.03_a$	$0.4 \pm 0.02_a$	$0.9 \pm 0.01_a$
2013_{28}	14	Bottomlands	$2.9 \pm 0.16_a$	$0.8 \pm 0.04_a$	$0.5 \pm 0.02_a$	$0.8 \pm 0.02_a$
	14	Uplands	$2.5 \pm 0.10_a$	$0.6 \pm 0.04_a$	$0.4 \pm 0.02_a$	$0.9 \pm 0.01_a$
2012_{56}	28	Bottomlands	$2.2 \pm 0.06_a$	$0.6 \pm 0.02_a$	$0.4 \pm 0.01_a$	$0.8 \pm 0.01_a$
	28	Uplands	$2.2 \pm 0.06_a$	$0.6 \pm 0.02_a$	$0.5 \pm 0.01_a$	$0.8 \pm 0.01_a$
2013_{56}	28	Bottomlands	$2.9 \pm 0.08_a$	$0.8 \pm 0.02_a$	$0.6 \pm 0.01_a$	$0.8 \pm 0.01_a$
	28	Uplands	$2.3 \pm 0.05_a$	$0.6 \pm 0.02_a$	$0.4 \pm 0.01_a$	$0.8 \pm 0.01_a$

Species accumulation curves

Large trees: For harvested species between catenal positions, the bottomlands and uplands had similar species richness in all of the three survey years except for 2012_{28}, where harvesting was absent in the uplands (Fig 4.9).

Small trees: For harvested species, the bottomlands and uplands had similar species richness in all three survey years except for 2011_{28}, 2012_{28} and 2013_{56} where the bottomlands had higher species richness than the bottomlands (Fig 4.9).

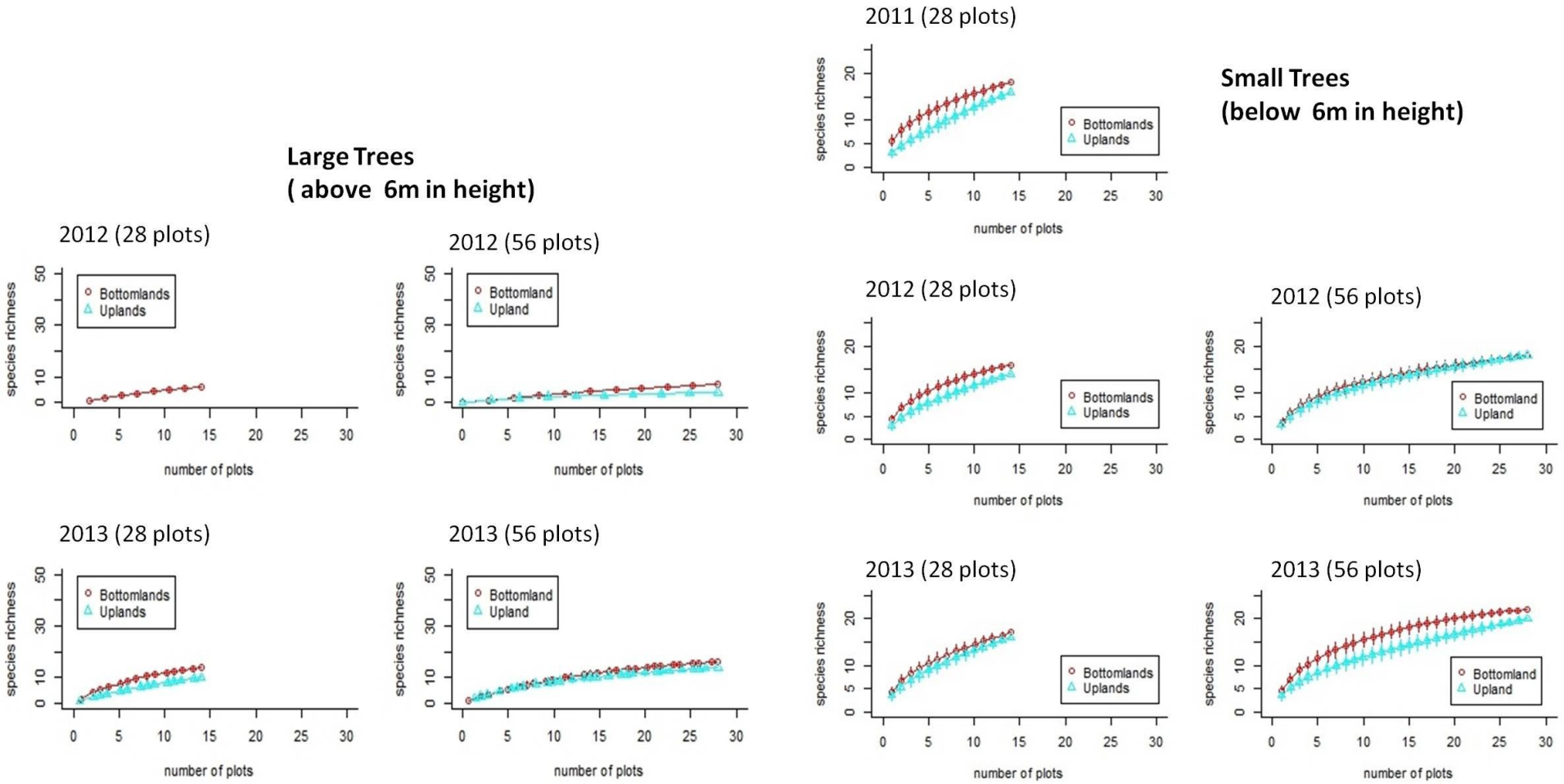


Figure 4.9 The species rarefaction curves for recently harvested large (left) and small (right) trees compared between catenal positon (bottomlands (○) and uplands (Δ)) for each of the survey years. Harvesting of large trees was absent in 2011. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size

Rank abundance

Large trees: The most harvested species within the bottomlands differed between survey years and comprised *A. gerrardii, C. collinum, T. sericea, A. robusta, Ziziphus mucronata* and *P. rotundifolius*. The most harvested species within the uplands also differed between survey years and comprised *T. sericea, S. birrea, C. zeyheri, C. apiculatum, C. collinum* and *C. zeyheri*.

Small trees: The most harvested species within the bottomlands differed between survey years and comprised *D. cinerea, C. hereroense, A. exuvialis* and *T. sericea*. The most harvested species within the uplands differed between survey years and comprised *T. sericea, D. cinerea, A. exuvialis, C. molle* and *C. collinum.*

4.4.2.4 How do species richness, diversity and evenness of harvested trees differ between rainfall zones and catenal positions over time?

There was no difference in species richness, diversity or evenness between rainfall zones and catenal positions for large trees in any of the survey years, neither was there an interaction between them for large trees in any of the survey years (Table 4.8). There was only an interaction between catenal positions and rainfall zones in species richness and Shannon's diversity of harvested trees in 2011_{28} and $2012_{28\&56,}$ as well as for Simpson's diversity in 2012_{56} for small trees (Table 4.8). Rainfall zones showed greater statistical differences between them than the difference between the catenal positions on the change of species richness in 2011_{28} and 2012_{56} as well as on the change of diversity in 2011_{28} (Table 4.8). Rainfall also had an effect on the evenness of large trees in $2013_{28\&56}$ as well as in 2012_{28} for small trees (Table 4.8). There was however no effect by catenal position on the change in species richness, Shannon's and Simpson's diversity and evenness for large and small trees of the three survey years except for the large trees in 2012_{28} (Table 4.8).

Diversity Indices

Large trees: Species richness and diversity for harvested trees did not show any change from $2012_{28\&56}$ to $2013_{28\&56}$ between catenal position/rainfall zone combinations (Appendix 4). The species richness and diversity for harvested trees were similar between catenal position/rainfall zone combinations for each of the survey years except for 2012_{28}, where the bottomlands in the medium and high rainfall zone had lower species richness and the bottomlands in the high rainfall zone had lower species diversity than other catenal position/rainfall zone combinations (Appendix 4). There was no difference in species

distributions in the catenal position/rainfall zone combinations in any of the three survey years (Appendix 4).

Table 4.8 Two-way ANOVAs comparing species richness, evenness and diversity (Shannon's and Simpson's index) between rainfall zone, catenal position and the interaction between rainfall zone and catenal position for large (>6m in height) and small harvested trees (<6m in height). Significant p-values in bold type.

			Species Richness			**Evenness**		
Tree size	**Year**	**Plots sampled**	**Rainfall zones p-value**	**Catenal position p-value**	**Rainfall* Catenal Interaction p-value**	**Rainfall zones p-value**	**Catenal position p-value**	**Rainfall* Catenal Interaction p-value**
Large Trees	2011_{28}	28	-	-	-	-	-	-
	2012_{28}	28	0.127	0.056	0.127	0.680	**0.041**	0.680
	2013_{28}	28	0.471	0.138	0.456	**0.082**	0.230	0.493
	2012_{56}	56	0.513	0.290	0.723	0.671	0.408	0.651
	2013_{56}	56	0.078	0.840	0.743	**0.022**	0.816	0.702
Small Trees	2011_{28}	28	**0.019**	0.407	**0.043**	0.261	0.848	0.913
	2012_{28}	28	0.257	1.000	**0.003**	**0.738**	0.208	0.249
	2013_{28}	28	0.175	0.514	0.099	0.969	0.435	0.910
	2012_{56}	56	**0.037**	0.905	**0.034**	0.621	0.414	0.894
	2013_{56}	56	0.095	0.234	0.385	0.918	0.726	0.821

			Shannon's Diversity			**Simpson's Index**		
Tree size	**Year**	**Plots sampled**	**Rainfall zones p-value**	**Catenal position p-value**	**Rainfall* Catenal Interaction p-value**	**Rainfall zones p-value**	**Catenal position p-value**	**Rainfall* Catenal Interaction p-value**
Large Trees	2011_{28}	28	-	-	-	-	-	-
	2012_{28}	28	0.073	0.128	0.073	0.902	0.078	0.902
	2013_{28}	28	0.589	0.220	0.483	0.107	0.558	0.836
	2012_{56}	56	0.526	0.348	0.487	0.854	0.564	0.490
	2013_{56}	56	0.165	0.835	0.676	0.163	0.717	0.925
Small Trees	2011_{28}	28	**0.055**	0.847	**0.032**	0.878	0.985	0.183
	2012_{28}	28	0.638	0.837	**0.005**	0.181	0.347	0.159
	2013_{28}	28	0.337	0.452	0.121	0.564	0.172	0.320
	2012_{56}	56	0.110	0.974	**0.010**	0.114	0.846	**0.030**
	2013_{56}	56	0.576	0.163	0.385	0.379	0.084	0.579

Small trees: Species richness for 2011_{28}, 2012_{28} and 2013_{28} of harvested trees was highest in the bottomlands of the medium rainfall zone (Appendix 5). Species diversity and species distributions of harvested trees in 2011_{28}, 2012_{28} and 2013_{28} were similar between

catenal position/rainfall zone combinations (Appendix 5). Species richness and species diversity of harvested trees were highest in the bottomlands of the high rainfall zone in 2012_{56}. Both species richness and diversity of harvested trees were similar between catenal position/rainfall zone combinations for 2013_{56} (Appendix 5). There was no difference in species distributions in the catenal position/rainfall zone combinations in any of the three survey years (Appendix 5).

Species rarefaction curves

Large trees: Recent harvesting occurred more in $2013_{28\&56}$ than in $2012_{28\&56}$ across the different catenal position/rainfall zone combinations. In $2012_{28\&56}$ the bottomlands in the low rainfall zone had the higher species richness for harvested trees whereas in $2013_{28\&56}$, the species richness was higher in the uplands in the high rainfall zone compared to the uplands of the low and medium rainfall zones (Fig 4.10).

Small trees: Recent harvesting occurred more in the bottomlands in the medium rainfall zone compared to the other catenal position/rainfall zone combinations for the three survey years (Fig 4.10). In all three the survey years, the species richness was highest in the bottomlands in the medium rainfall zone compared to the other catenal position/rainfall zone combinations (Fig 4.10).

Rank abundance

Large trees: Recently harvested trees differed between survey years for all catenal position/rainfall zone combinations. The most harvested species within the bottomlands in the low rainfall zone comprised *C. apiculatum, A. nigrescens, C. collinum, Balanites maughamii* and *D. melanoxylon*. The most harvested species within the uplands in the low rainfall zone comprised *T. sericea, A. nigrescens, C. zeyheri, C. collinum, C. apiculatum* and *P. angolensis*. The most harvested species within the bottomlands in the medium rainfall zone comprised *A. robusta, A. burkei, C. collinum, A. gerrardii* and *D. cinerea*. The most harvested species within the uplands in the medium rainfall zone comprised *Acacia robusta, D. cinerea, S. birrea, C. collinum, L. discolor* and *Euclea divinorum*. The most harvested species within the bottomlands in the high rainfall zone comprised *A. gerrardii, C. collinum, T. sericea, P. rotundifolius* and *C. hereroense*. The most harvested species within the uplands in the high rainfall zone comprised *A. gerrardii, C. apiculatum, C. collinum, T. sericea* and *Parinari curatellifolia*.

Small trees: Recently harvested trees differed between survey years for all catenal position/rainfall zone combinations. The most harvested species within the bottomlands in the

low rainfall zone comprised *A. exuvialis, C. hereroense, C. apiculatum, T. sericea, C. collinum* and *C. zeyheri*. The most harvested species in the uplands in the low rainfall zone comprised *A. exuvialis, T. sericea, D. cinerea, C. collinum, A. burkei* and *S. madagascariensis*. The most harvested species within the bottomlands in the medium rainfall zone comprised *D. cinerea, C. hereroense, A. exuvialis* and *T. sericea*. The most harvested species within the uplands in the medium rainfall zone comprised *T. sericea, D. cinerea, C. molle, Gymnosporia buxifolia* and *Gymnosporia glaucophylla*. The most harvested species within the bottomlands in the high rainfall zone comprised *D. cinerea, C. hereroense, Combretum imberbe, C. collinum, T. sericea* and *P. africanum*. The most harvested species within the uplands in the high rainfall zone comprised *D. cinerea, T. sericea, Antidesma venosum, C. molle* and *Annona senegalensis*.

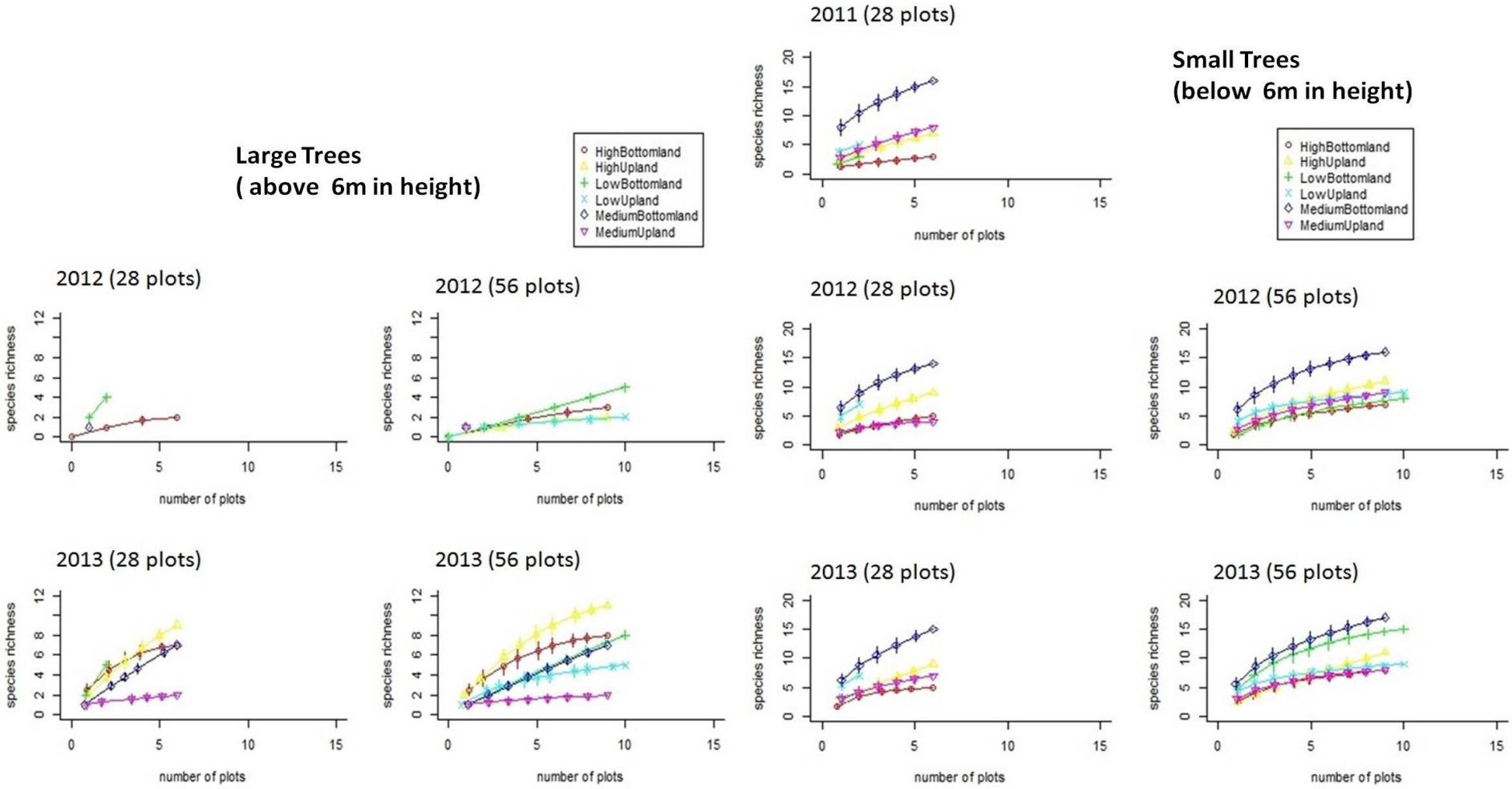


Figure 4.10 The species rarefaction curves for recently harvested large (left) and small (right) trees compared between catenal position and rainfall zone combinations (bottomland (+) and upland (X) in low rainfall, bottomland (◊) and upland (▽) in medium rainfall and bottomland (○) and upland (Δ) in high rainfall) for each of the survey years. Harvesting of large trees was absent in 2011. Bars indicate 95% confidence interval. Rows indicate years and columns indicate tree size.

4.5 DISCUSSION

The first objective of this study was to determine how species richness, diversity and evenness of woody vegetation differ over time along rainfall and catenal gradients. The second objective was to assess the richness, diversity and eveness of tree species that were harvested. The study found species richness, diversity and evenness was higher in the high rainfall zone than the low and medium rainfall zones for both large and small trees. There was no difference in species richness, diversity and evenness between catenal positions. The species richness and diversity of large harvested trees was higher in $2013_{28\&56}$ than in $2012_{28\&56}$, which indicates harvesters became less selective in the species harvested. There was no interaction between rainfall zones and catenal positions except for the evenness of large trees in $2012_{28\&56}$ and 2013_{28}, as well as in the Simpson's diversity in2013_{28} of large trees.

4.5.1 Difference in species richness, diversity and evenness over time

4.5.1.1 General difference in species richness, diversity and evenness over time

This study found that as the abundance of individual trees increased, the species richness and diversity also increased. This matches the results of other studies of both general plants, and of savanna trees, that higher richness was found where density was higher (Shackleton 2000; Tuomisto and Dahlberg 2000). For large trees, the species richness and diversity was higher in the 56 plots than the 28 plots. Shackleton (2000) found that species richness and diversity will increase with the increase in sample size. There was no change in richness, diversity and evenness over the three survey years for large trees but small trees showed a decrease in richness and diversity from 2011 to 2013. This coincides with the decrease in density and increase in harvested intensity (% of trees/ stems harvested) seen in Chapter 2 and 3. Species were distributed randomly across the landscape which was similar to other studies (Shackleton 2000; Wessels *et al.* 2013). The most abundant large tree species were consistently *S. birrea* > *P. violacea* > *P. angolensis.* As local law forbids harvesting of live trees, especially fruit bearing trees, *S. birrea* will be most abundant (Kirkland *et al.* 2007; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b). Species of small trees in higher abundance comprised *D. cinerea, T. sericea, A. exuvialis, S. madagascariensis* and *C. hereroense*.

4.5.1.2 Difference in species richness, diversity and evenness between rainfall zones over time

Rainfall zones had a larger influence on species richness, diversity and evenness than catenal position. Several other studies found rainfall to be an important driver in changes seen in vegetation density and structure over time within savannas (Dahlberg 2000; Dube and Pickup 2001; Hassler *et al.* 2010; Kanniah *et al.* 2010; Medinski *et al.* 2010; Sankaran *et al.* 2005; Shackleton and Scholes 2011). Both large and small trees had higher species richness, diversity and evenness in the high rainfall zone compared to the low and medium rainfall zone. The large trees are more sparsely dispersed than small trees, and with vegetation density being higher in the high rainfall zone (Chapter 2), the high rainfall zone had more large trees than the low and medium rainfall zones. This is possibly the reason for higher evenness in large trees within the high rainfall zone. The evenness of small tree distribution was not influenced by rainfall zones. The small trees were more evenly distributed across the rainfall zones, possibly due to the fact that small trees were more abundant than large trees.

4.5.1.3 Difference in species richness, diversity and evenness between catenal positions over time

This study found that catenal position had no influence on the richnessand evenness of species. This coincides with the findings in chapter 2 where the two catenal positions had similar densities. There was however a difference in species richness. Various studies also found topographical location did have an influence on the richness and diversity of species within the landscape (Chen *et al.* 1997; Dahlberg 2000; Lite *et al.* 2005; Medinski *et al.* 2010). Shackleton (2000) also found the bottomlands and uplands to have no difference in species richness and diversity. There is a possibility that the duration of the study was too short to indicate any influence of catenal position on the change in species richness over time.

4.5.1.4 Difference in species richness, diversity and evenness between combinations of rainfall zones and catenal positions over time

Rainfall zones showed greater statistical differences between them than the difference between the catenal positions on the change of species richness in 2011_{28} and 2012_{56}, and on the change of Shannon's diversity in 2011_{28}, as well as on the Simpson's diversity of 2011_{28}, 2012_{56}, and $2013_{28\&56}$. Rainfall zones also had an effect on the evenness of large trees in 2012_{28} and 2013_{28}. There was no interaction between rainfall zones and catenal positions except for the evenness of large trees in $2012_{28\&56}$ and 2013_{28}, as well as in the Simpson's diversity in2013_{28} of large trees (Table 4.4). Again, the influence of rainfall is larger than that

of catenal position (Chapter 2). Various studies described rainfall to be a more important driver of change within vegetation than catenal position, which was similar to the results of this study (Dahlberg 2000; Dube and Pickup 2001; Kanniah *et al.* 2010; Medinski *et al.* 2010; Sankaran *et al.* 2005; Shackleton 1999). This study also found similar results with other studies, with species richness and diversity being affected by the rainfall gradient resulting in the high rainfall zone to have higher species richness and diversity.

4.5.2 Difference in species richness, diversity and evenness of harvested trees over time

4.5.2.1 General difference in species richness, diversity and evenness of harvested trees over time

The influence of harvesting on vegetation density increased from $2012_{28\&56}$ to $2013_{28\&56}$ for large trees (Chapter 3). The species richness and diversity of recently harvested large trees was found to increase from $2012_{28\&56}$ to $2013_{28\&56}$, which is possibly an indication of less selection in regards to the species chosen for harvesting. The species richness, diversity and eveness of harvested small trees did not change over time.

In the past, all wood collected was generally dead wood with little preference to species, but at present, live trees are being harvested as dry wood is scarce or completely absent from surrounding areas (Kirkland *et al.* 2007; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Matsika *et al.* 2013b; Wessels *et al.* 2011; Wessels *et al.* 2013; Williams and Shackleton 2002). According to Neke *et al.* (2006), Madubansi and Shackleton (2007) and Wessels *et al.* 2013, as much as 93% of the demand for fuelwood in South Africa is not met by dead wood but by live wood that is harvested. The preference of the size and species tree to be harvested according to Shackleton (2001) is dependent on the use of the harvested wood.. The study by Kaschula *et al.* (2005), Neke *et al.* (2006) and Shackleton (2001) found that *T. sericea* was a preferred species in the rangelands as it is a good fuelwood, building material and fencing pole providing species. The preference for selected species was in proportion to the relative abundance of each species during this study. Preference to certain species occurs even if the abundance of the species is lower than less preferred species, which was also found by Neke *et al.* (2006) to be the case. The preference of species also depends on the need of the harvested wood. The preferred species according to Williams and Shackleton (2002) and Ferm and Kauppi (1990) are species that provide hardwood. This is due to hardwood producing longer lasting coals, yield more heat and emit less smoke (Williams and Shackleton 2002). This study found the most harvested species of

large and small trees varied between years and plot sample size (28 and 56 plots). For large trees, the most harvested species comprised *C. collinum, A. gerrardii, T. sericea, A. robusta, C. zeyheri* and *S. birrea* whereas for small trees, the most harvested species comprised *D. cinerea, T. sericea, C. hereroense* and *A. exuvialis*.

4.5.2.2 General difference in species richness, diversity and evenness of harvested trees between rainfall zones over time

Species richness and diversity differed less between rainfall zones for large trees than small trees. There was no change in species richness, diversity and eveness over time for large harvested trees. If the theory mentioned by Lite *et al.* (2005) is true, some disturbance is needed to result in the change of species richness and diversity. As levels of large tree harvesting is low (which was found to increase in Chapter 3), the required disturbance is possibly insufficient (Lite *et al.* 2005). The distribution of species was also similar between rainfall zone except for 2013_{56} large trees, where the distribution of harvested trees was more even in the high rainfall zone compared to the low and medium rainfall zones. Harvesting of small trees had a larger difference between rainfall zones. The harvesting of small trees was higher in the medium rainfall zone (Chapter 3) and in 2011_{28} harvested tree species richness was higher in the medium rainfall zone than the low and high rainfall zone. As harvesting was highest in the medium rainfall zone and lowest in the high rainfall zone (Chapter 3), the significant difference in species richness seen here, which coincides to the significant difference of harvesting intensity. The species richness between small harvested species was similar between rainfall zones in 2012 and 2013.

4.5.2.3 Difference in species richness, diversity and evenness of harvested trees between catenal positions over time

Just as rainfall is seen as a driver of change in savannas, topography also plays an important role in the determining of savanna vegetation structure and composition (Coughenour and Ellis 1993; Fisher *et al.* 2009; Fisher *et al.* 2011; Kanniah *et al.* 2010; Kaschula *et al.* 2005; Shackleton 1999; Wessels *et al.* 2011; Witkowski and O'Connor 1996). Catenal position had no influence on selection of species to harvest. Species richness, diversity and evenness of woody vegetation were not different between bottomlands and uplands for either large or small harvested trees in any of the three survey years. This study found that there was no preference for harvesting to either uplands or bottomlands whereas the study by Kaschula *et al.* (2005) found there was a preference in catenal position, with more harvesting preference occurring in the uplands. This study coincides with findings of

Chapter 3, where there was also no difference found between the harvesting intensity in the bottomlands and uplands.

4.5.2.4 Difference in species richness, diversity and evenness of harvested trees between a combination of rainfall zones and catenal positions over time

Species composition of savannas is driven by both environmental determinants and anthropogenic disturbances (Breshears and Barnes 1999; Buitenwerf *et al.* 2012; Colgan *et al.* 2012; Dahlberg 2000; Dube and Pickup 2001; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Shackleton *et al.* 1994; Shackleton 1999; Shackleton and Scholes 2011; Smith and Goodman 1986; Wessels *et al.* 2011; Witkowski and O'Connor 1996). There was an interaction between rainfall zones and catenal position in the species richness and Shannon's diversity of small harvested trees in 2011_{28} and $2012_{28\&56}$, as well as in the Simpson's diversity of small harvested trees in 2012_{56} (Table 4.8) Rainfall zones showed greater statistical differences between them than the difference between the catenal positions on the change of species richness in 2011_{28} and 2012_{56} as well as on the change of Shannon's diversity in 2011_{28}. Rainfall also showed an effect in the evenness of large trees in $2013_{28\&56}$ and small trees in 2012_{28}. The interaction between the two environmental determinants on harvested species produced similar results to other studies, stating that more than a single environmental variable causes the change in species richness and diversity (Dahlberg 2000; Lite *et al.* 2005; Medinski *et al.* 2010; Tuomisto and Dahlberg 2000; Wessels *et al.* 2013).

4.6 CONCLUSION

In conclusion, focusing on determining how species richness, diversity and evenness of woody vegetation differ over time along rainfall and catenal gradients, species richness, diversity and evenness was influenced by more by rainfall than catenal position. Secondly, focusing on assessing the species richness, diversity and evenness of tree species that were harvested, it was found that harvesting played an important role in the change seen in species richness, diversity and evenness.

My first objective was to determine how species richness, diversity and evenness differ between rainfall zones and catenal positions. The first question for this objective, "how do species richness, diversity and evenness change over time in general?" found that the species richness, diversity and evenness of large trees did not change but did decrease for

small trees over the three years survey. The second question, "how do species richness, diversity and evenness differ between rainfall zones while controlling for time by assessing three different time periods?" found the high rainfall zone had higher species richness, diversity and evenness across both large and small trees in all three survey years. The third question, "how do species richness, diversity and evenness differ between catenal positions while controlling for time by assessing three different time periods?" found the bottomlands and uplands to have similar species richness, diversity and evenness. The final question for the first objective, "how do species richness, diversity and evenness differ between a combination of rainfall zones and catenal positions while controlling for time by assessing three different time periods?" found the uplands in the high rainfall zone did have higher species richness, diversity and evenness across the three survey years.

My second objective was to determine how species richness, diversity and evenness differ across rainfall zones and catenal positions when only focusing on the harvested species. The first question for this objective, "how do species richness, diversity and evenness of harvested species differ over time?" found the species richness of harvested trees did increase for large trees and was similar between years for small trees. The second question, "how do species richness, diversity and evenness of harvested species differ across rainfall zones over time?" found that the medium rainfall zone had the highest species richness and diversity between large and small harvested trees. The third question, "how do species richness, diversity and evenness of harvested species differ across catenal positions over time?" found the uplands and bottomlands to have similar species richness, diversity and eveness due to similar levels of harvesting. The final question for the second objective, "how do species richness, diversity and evenness of harvested species differ across a combination of rainfall zones and catenal position over time?" found the specie richness, diversity and eveness being similar between catenal position/rainfall zone combinations in both large and small trees in all three survey years.

Future studies would help resolve difficulties that arose during this study. These include an improved design which will allow large (above 6m height) and small (below 6m in height) trees to be combined in order to asses species richness, diversity and evenness. As large and small trees differ in distribution, the plots used for large trees need to be surveyed to see new species that did not occur in the smaller plots, occur in the larger area (similar to the modified Whittaker plot design (Stohlgren *et al.* 2005)). This will simplify the difficulty found during this study of having large and small trees separate. Future studies should also

try having a longer monitoring period as the possible of change occurring in such a short period of three years is likely. By establishing a long term monitoring program, the research would be valuable not only to the science community but might be vital to help manage available resources in a sustainable way and thus ensuring the future to a vast number of individuals who are dependent on the resources provided by surrounding environment.

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APPENDIX 1

Appendix 1 All commands (step by step) in the BiodiversityR programme for A) species richness, B) species diversity and evenness, C) species accumulation and rarefaction curves and D) rank abundance curves. All steps were adapted from Kindt and Coe (2005). All steps were done for both total species and harvested species for large and small tree.

A)

To calculate the species richness (number of species)
Biodiversity > Analysis of diversity > Diversity indices...
- Diversity index: richness
- Calculation method: all
- Calculation method: separate per site (alternative to all)
- Subset option: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)

B)

To calculate diversity indices (Shannon-Wiener, Simpsons and Evenness)
Biodiversity > Analysis of diversity > Diversity indices...
- Diversity index: Shannon
- Diversity index: Simpson (alternative indices)
- Diversity index: Eevenness (alternative indices)
- Calculation method: All
- Calculation method: separate per plot (alternative to all)
- Subset options: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)
- Subset: .

C)

To calculate a sample-based species accumulation curve
Biodiversity > Analysis of diversity > Species accumulation curves...
- Accumulation method: exact
- Accumulation method: random (alternative to the exact method)
- Subset option: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)

To calculate an individual-based species accumulation curve (Rarefaction curve)
Biodiversity > Analysis of diversity > Species accumulation curves...
- Accumulation method: rarefaction
- Subset option: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)

To calculate a sample-based species accumulation curve and an individual-based species accumulation curve (Rarefaction curve) on same graph (both curves plotted at the same scale)
Biodiversity > Analysis of diversity > Species accumulation curves...
- Accumulation method: exact
- Subset option: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)
- Click OK and plot graph ("plot" tab)
- Change accumulation method and click "add plot" block on right hand side
- Accumulation method: rarefaction
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)
- Click OK and plot graph ("plot" tab)

D)

To calculate and plot a rank-abundance curve:
Biodiversity > Analysis of diversity > Rank abundance...
- Plot option: abundance
- Plot option: logabun (alternative to abundance)
- Subset options: All
- Subset options: Subset choice: e.g. Rainfall zone, catenal position subset (alternative to All)
- Subset: .

APPENDIX 2

Appendix 2 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for large trees between rainfall zones and catenal position combinations across three survey years (2011-2013). Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Years	Number of plots	Rainfall Zone & Catenal position	Large trees (>6m height)			
			Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	2	Low Bottomland	$3.5 \pm 2.46_{ab}$	$0.8 \pm 0.54_{a}$	$0.9 \pm 0.10_{a}$	$0.3 \pm 0.24_{a}$
	2	Low Upland	$3.5 \pm 1.06_{ab}$	$0.6 \pm 0.10_{a}$	$0.3 \pm 0.02_{a}$	$0.6 \pm 0.13_{ab}$
	6	Medium Bottomland	$1.8 \pm 0.29_{a}$	$0.5 \pm 0.10_{a}$	$0.4 \pm 0.07_{a}$	$0.8 \pm 0.07_{b}$
	6	Medium Upland	$2.8 \pm 0.25_{ab}$	$0.7 \pm 0.08_{a}$	$0.4 \pm 0.04_{a}$	$0.8 \pm 0.02_{b}$
	6	High Bottomland	$5.8 \pm 0.49_{ab}$	$1.4 \pm 0.12_{a}$	$0.7 \pm 0.06_{a}$	$0.9 \pm 0.02_{b}$
	6	High Upland	$10.7 \pm 0.82_{b}$	$1.9 \pm 0.10_{a}$	$0.8 \pm 0.02_{a}$	$0.7 \pm 0.02_{b}$
2012_{28}	2	Low Bottomland	$4.0 \pm 2.83_{ab}$	$0.8 \pm 0.57_{a}$	$0.9 \pm 0.10_{a}$	$0.3 \pm 0.22_{a}$
	2	Low Upland	$3.5 \pm 1.77_{ab}$	$0.5 \pm 0.38_{a}$	$0.2 \pm 0.18_{a}$	$0.7 \pm 0.18_{ab}$
	6	Medium Bottomland	$3.7 \pm 0.52_{ab}$	$0.9 \pm 0.14_{a}$	$0.5 \pm 0.05_{a}$	$0.9 \pm 0.01_{b}$
	6	Medium Upland	$2.8 \pm 0.25_{a}$	$0.7 \pm 0.11_{a}$	$0.4 \pm 0.04_{a}$	$0.8 \pm 0.02_{b}$
	6	High Bottomland	$5.5 \pm 0.54_{ab}$	$1.3 \pm 0.13_{a}$	$0.6 \pm 0.05_{a}$	$0.9 \pm 0.01_{b}$
	6	High Upland	$9.5 \pm 0.74_{b}$	$1.8 \pm 0.10_{a}$	$0.8 \pm 0.02_{a}$	$0.7 \pm 0.02_{ab}$
2013_{28}	2	Low Bottomland	$4.5 \pm 3.18_{ab}$	$0.9 \pm 0.61_{a}$	$0.9 \pm 0.09_{a}$	$0.3 \pm 0.22_{a}$
	2	Low Upland	$3.5 \pm 1.77_{a}$	$0.5 \pm 0.38_{a}$	$0.2 \pm 0.18_{a}$	$0.7 \pm 0.18_{ab}$
	6	Medium Bottomland	$4.8 \pm 0.80_{ab}$	$1.0 \pm 0.12_{a}$	$0.5 \pm 0.05_{a}$	$0.9 \pm 0.03_{b}$
	6	Medium Upland	$3.5 \pm 0.26_{a}$	$0.9 \pm 0.07_{a}$	$0.5 \pm 0.03_{a}$	$0.8 \pm 0.02_{b}$
	6	High Bottomland	$6.2 \pm 0.51_{ab}$	$1.5 \pm 0.09_{a}$	$0.7 \pm 0.02_{a}$	$0.9 \pm 0.01_{b}$
	6	High Upland	$10.5 \pm 0.72_{b}$	$1.9 \pm 0.09_{a}$	$0.8 \pm 0.02_{a}$	$0.7 \pm 0.02_{ab}$
2012_{56}	10	Low Bottomland	$3.6 \pm 0.31_{a}$	$0.9 \pm 0.08_{ab}$	$0.6 \pm 0.03_{ab}$	$0.7 \pm 0.04_{a}$
	10	Low Upland	$3.2 \pm 0.20_{a}$	$0.7 \pm 0.06_{a}$	$0.4 \pm 0.03_{a}$	$0.8 \pm 0.02_{a}$
	9	Medium Bottomland	$3.0 \pm 0.30_{a}$	$0.7 \pm 0.09_{a}$	$0.4 \pm 0.04_{a}$	$1.0 \pm 0.01_{a}$
	9	Medium Upland	$2.6 \pm 0.15_{a}$	$0.6 \pm 0.05_{a}$	$0.3 \pm 0.03_{a}$	$0.8 \pm 0.01_{a}$
	9	High Bottomland	$5.8 \pm 0.42_{ab}$	$1.3 \pm 0.09_{ab}$	$0.6 \pm 0.04_{ab}$	$0.9 \pm 0.01_{a}$
	9	High Upland	$8.2 \pm 0.45_{b}$	$1.7 \pm 0.06_{b}$	$0.8 \pm 0.01_{b}$	$0.8 \pm 0.01_{a}$
2013_{56}	10	Low Bottomland	$4.7 \pm 0.47_{a}$	$1.0 \pm 0.09_{ab}$	$0.6 \pm 0.04_{ab}$	$0.7 \pm 0.03_{a}$
	10	Low Upland	$3.9 \pm 0.22_{a}$	$0.9 \pm 0.06_{a}$	$0.4 \pm 0.03_{a}$	$0.8 \pm 0.02_{a}$
	9	Medium Bottomland	$4.1 \pm 0.45_{a}$	$0.9 \pm 0.07_{a}$	$0.5 \pm 0.03_{a}$	$0.9 \pm 0.02_{a}$
	9	Medium Upland	$3.2 \pm 0.16_{a}$	$0.8 \pm 0.05_{a}$	$0.4 \pm 0.02_{a}$	$0.8 \pm 0.01_{a}$
	9	High Bottomland	$6.6 \pm 0.37_{ab}$	$1.6 \pm 0.06_{ab}$	$0.7 \pm 0.02_{ab}$	$0.9 \pm 0.01_{a}$
	9	High Upland	$9.3 \pm 0.44_{b}$	$1.8 \pm 0.05_{b}$	$0.8 \pm 0.01_{b}$	$0.7 \pm 0.01_{a}$

APPENDIX 3

Appendix 3 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for small trees between rainfall zones and catenal position combinations across three survey years (2011-2013). Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Years	Number of plots	Rainfall Zone & Catenal position	Small trees (< 6m height)			
			Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	2	Low Bottomland	$8.0 \pm 0_{a}$	$1.2 \pm 0.18_{a}$	$0.5 \pm 0.11_{a}$	$0.4 \pm 0.08_{a}$
	2	Low Upland	$10.0 \pm 0.71_{a}$	$1.7 \pm 0.22_{a}$	$0.7 \pm 0.06_{ab}$	$0.6 \pm 0.08_{a}$
	6	Medium Bottomland	$20.2 \pm 0.96_{b}$	$2.2 \pm 0.08_{a}$	$0.8 \pm 0.02_{ab}$	$0.5 \pm 0.02_{a}$
	6	Medium Upland	$14.5 \pm 0.55_{ab}$	$2.0 \pm 0.06_{a}$	$0.8 \pm 0.02_{ab}$	$0.5 \pm 0.02_{a}$
	6	High Bottomland	$17.3 \pm 1.63_{ab}$	$1.9 \pm 0.09_{a}$	$0.7 \pm 0.03_{ab}$	$0.5 \pm 0.02_{a}$
	6	High Upland	$25.0 \pm 1.59_{b}$	$2.5 \pm 0.09_{a}$	$0.9 \pm 0.02_{b}$	$0.6 \pm 0.01_{a}$
2012_{28}	2	Low Bottomland	$6.5 \pm 0.35_{a}$	$1.1 \pm 0.29_{a}$	$0.5 \pm 0.16_{a}$	$0.5 \pm 0.16_{a}$
	2	Low Upland	$9.0 \pm 0.71_{ab}$	$1.6 \pm 0.20_{a}$	$0.7 \pm 0.06_{ab}$	$0.5 \pm 0.07_{a}$
	6	Medium Bottomland	$14.8 \pm 0.92_{ab}$	$2.0 \pm 0.10_{a}$	$0.8 \pm 0.03_{ab}$	$0.6 \pm 0.02_{a}$
	6	Medium Upland	$12.5 \pm 0.31_{ab}$	$1.9 \pm 0.05_{a}$	$0.8 \pm 0.02_{ab}$	$0.6 \pm 0.03_{a}$
	6	High Bottomland	$14.2 \pm 0.83_{ab}$	$1.8 \pm 0.07_{a}$	$0.7 \pm 0.02_{ab}$	$0.6 \pm 0.01_{a}$
	6	High Upland	$19.5 \pm 1.02_{b}$	$2.3 \pm 0.07_{a}$	$0.8 \pm 0.02_{b}$	$0.6 \pm 0.02_{a}$
2013_{28}	2	Low Bottomland	$5.5 \pm 0.35_{a}$	$1.0 \pm 0.32_{a}$	$0.5 \pm 0.17_{a}$	$0.6 \pm 0.14_{a}$
	2	Low Upland	$10.0 \pm 0.71_{ab}$	$1.8 \pm 0.17_{a}$	$0.8 \pm 0.05_{b}$	$0.5 \pm 0.06_{a}$
	6	Medium Bottomland	$14.8 \pm 0.92_{ab}$	$2.1 \pm 0.08_{a}$	$0.8 \pm 0.02_{b}$	$0.6 \pm 0.02_{a}$
	6	Medium Upland	$11.0 \pm 0.35_{ab}$	$1.9 \pm 0.06_{a}$	$0.8 \pm 0.02_{b}$	$0.6 \pm 0.03_{a}$
	6	High Bottomland	$13.2 \pm 0.81_{ab}$	$1.8 \pm 0.07_{a}$	$0.7 \pm 0.02_{ab}$	$0.6 \pm 0.01_{a}$
	6	High Upland	$17.0 \pm 1.13_{b}$	$2.3 \pm 0.09_{a}$	$0.8 \pm 0.02_{b}$	$0.6 \pm 0.01_{a}$
2012_{56}	10	Low Bottomland	$8.3 \pm 0.36_{a}$	$1.6 \pm 0.06_{a}$	$0.7 \pm 0.02_{ab}$	$0.7 \pm 0.02_{a}$
	10	Low Upland	$8.4 \pm 0.20_{a}$	$1.4 \pm 0.04_{a}$	$0.6 \pm 0.02_{a}$	$0.5 \pm 0.02_{a}$
	9	Medium Bottomland	$12.7 \pm 0.62_{ab}$	$1.9 \pm 0.06_{ab}$	$0.8 \pm 0.02_{a}$	$0.6 \pm 0.02_{a}$
	9	Medium Upland	$11.1 \pm 0.36_{ab}$	$1.7 \pm 0.06_{a}$	$0.7 \pm 0.02_{a}$	$0.6 \pm 0.02_{a}$
	9	High Bottomland	$14.9 \pm 0.66_{ab}$	$1.9 \pm 0.05_{ab}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	9	High Upland	$17.6 \pm 0.64_{b}$	$2.2 \pm 0.05_{b}$	$0.8 \pm 0.01_{a}$	$0.5 \pm 0.01_{a}$
2013_{56}	10	Low Bottomland	$8.0 \pm 0.40_{a}$	$1.6 \pm 0.06_{a}$	$0.7 \pm 0.02_{a}$	$0.7 \pm 0.02_{a}$
	10	Low Upland	$8.3 \pm 0.20_{a}$	$1.5 \pm 0.04_{a}$	$0.7 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	9	Medium Bottomland	$13.0 \pm 0.61_{ab}$	$2.0 \pm 0.05_{ab}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.02_{a}$
	9	Medium Upland	$10.1 \pm 0.32_{ab}$	$1.7 \pm 0.06_{a}$	$0.7 \pm 0.02_{a}$	$0.6 \pm 0.02_{a}$
	9	High Bottomland	$13.8 \pm 0.52_{ab}$	$2.0 \pm 0.05_{ab}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$
	9	High Upland	$15.6 \pm 0.65_{b}$	$2.1 \pm 0.06_{b}$	$0.8 \pm 0.01_{a}$	$0.6 \pm 0.01_{a}$

APPENDIX 4

Appendix 4 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for large harvested trees between rainfall zones and catenal position combinations across three survey years (2011-2013). Harvesting was absent in 2011. Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Years	Number of plots	Rainfall Zone & Catenal position	Large trees (>6m height)			
			Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	2	Low Bottomland	-	-	-	-
	2	Low Upland	-	-	-	-
	6	Medium Bottomland	-	-	-	-
	6	Medium Upland	-	-	-	-
	6	High Bottomland	-	-	-	-
	6	High upland	-	-	-	-
2012_{28}	2	Low Bottomland	$2.0 \pm 1.41_a$	$0.7 \pm 0.49_a$	$0.9 \pm 0.09_a$	$0.5 \pm 0.35_a$
	2	Low Upland	-	-	-	-
	6	Medium Bottomland	$0.2 \pm 0.07_b$	-	$0.8 \pm 0.07_a$	$0.2 \pm 0.07_a$
	6	Medium Upland	-	-	-	-
	6	High Bottomland	$0.5 \pm 0.14_b$	$0.1 \pm 0.05_b$	$0.8 \pm 0.07_a$	$0.3 \pm 0.09_a$
	6	High upland	-	-	-	-
2013_{28}	2	Low Bottomland	$2.5 \pm 1.77_a$	$0.8 \pm 0.57_a$	$0.9 \pm 0.07_a$	$0.5 \pm 035_a$
	2	Low Upland	-	-	-	-
	6	Medium Bottomland	$1.3 \pm 0.25_a$	$0.3 \pm 0.10_a$	$0.5 \pm 0.08_a$	$0.7 \pm 0.09_a$
	6	Medium Upland	$0.5 \pm 0.14_a$	$0.1 \pm 0.04_a$	$0.7 \pm 0.07_a$	$0.3 \pm 0.08_a$
	6	High Bottomland	$1.8 \pm 0.29_a$	$0.5 \pm 0.10_a$	$0.4 \pm 0.07_a$	$0.8 \pm 0.07_a$
	6	High upland	$1.5 \pm 0.18_a$	$0.4 \pm 0.08_a$	$0.4 \pm 0.06_a$	$0.8 \pm 0.07_a$
2012_{56}	10	Low Bottomland	$0.6 \pm 0.15_a$	$0.2 \pm 0.05_a$	$0.9 \pm 0.04_a$	$0.2 \pm 0.05_a$
	10	Low Upland	$0.2 \pm 0.04_a$	-	$0.8 \pm 0.04_a$	$0.2 \pm 0.04_a$
	9	Medium Bottomland	$0.1 \pm 0.04_a$	-	$0.9 \pm 0.04_a$	$0.1 \pm 0.04_a$
	9	Medium Upland	$0.1 \pm 0.04_a$	-	$0.9 \pm 0.04_a$	$0.1 \pm 0.04_a$
	9	High Bottomland	$0.4 \pm 0.08_a$	$0.1 \pm 0.03_a$	$0.7 \pm 0.05_a$	$0.3 \pm 0.06_a$
	9	High upland	$0.2 \pm 0.07_a$	$0.1 \pm 0.02_a$	$0.9 \pm 0.02_a$	$0.1 \pm 0.04_a$
2013_{56}	10	Low Bottomland	$1.0 \pm 0.18_a$	$0.3 \pm 0.06_a$	$0.7 \pm 0.05_a$	$0.4 \pm 0.06_a$
	10	Low Upland	$1.0 \pm 0.12_a$	$0.2 \pm 0.04_a$	$0.6 \pm 0.04_a$	$0.5 \pm 0.05_a$
	9	Medium Bottomland	$0.9 \pm 0.15_a$	$0.2 \pm 0.05_a$	$0.7 \pm 0.05_a$	$0.4 \pm 0.06_a$
	9	Medium Upland	$0.4 \pm 0.08_a$	$0.1 \pm 0.02_a$	$0.7 \pm 0.05_a$	$0.3 \pm 0.05_a$
	9	High Bottomland	$1.6 \pm 0.17_a$	$0.4 \pm 0.06_a$	$0.5 \pm 0.05_a$	$0.8 \pm 0.05_a$
	9	High upland	$1.8 \pm 0.13_a$	$0.5 \pm 0.06_a$	$0.4 \pm 0.04_a$	$0.9 \pm 0.04_a$

APPENDIX 5

Appendix 5 Species richness, diversity and evenness indices (mean ± SE) calculated at plot level for both 28 and 56 plot datasets for small harvested trees between rainfall zones and catenal position combinations across three survey years (2011-2013). Values in the same column for each year and plot dataset separately accompanied by the same subscript do not differ significantly (Tukey, $p < 0.05$).

Years	Number of plots	Rainfall Zone & Catenal position	Small trees (< 6m height)			
			Richness	Shannon-Wiener	Simpson	Evenness
2011_{28}	2	Low Bottomland	$1.5 \pm 0.35_{ab}$	$0.3 \pm 0.20_{ab}$	$0.2 \pm 0.13_{a}$	$0.9 \pm 0.04_{a}$
	2	Low Upland	$3.0 \pm 0_{ab}$	$0.1 \pm 0.03_{ab}$	$0.6 \pm 0.01_{a}$	$0.9 \pm 0.02_{a}$
	6	Medium Bottomland	$4.8 \pm 0.48_{b}$	$1.1 \pm 0.10_{a}$	$0.6 \pm 0.05_{a}$	$0.8 \pm 0.03_{a}$
	6	Medium Upland	$2.2 \pm 0.22_{ab}$	$0.5 \pm 0.09_{ab}$	$0.3 \pm 0.05_{a}$	$0.9 \pm 0.03_{a}$
	6	High Bottomland	$0.8 \pm 0.13_{a}$	$0.1 \pm 0.04_{b}$	$0.4 \pm 0.08_{a}$	$0.6 \pm 0.08_{a}$
	6	High upland	$1.7 \pm 0.31_{ab}$	$0.4 \pm 0.11_{ab}$	$0.6 \pm 0.07_{a}$	$0.6 \pm 0.08_{a}$
2012_{28}	2	Low Bottomland	$2.0 \pm 0.71_{ab}$	$0.5 \pm 0.39_{a}$	$0.3 \pm 0.24_{a}$	$1.0 \pm 0_{a}$
	2	Low Upland	$4.5 \pm 0.35_{ab}$	$1.2 \pm 0.01_{a}$	$0.6 \pm 0.02_{a}$	$0.8 \pm 0.05_{a}$
	6	Medium Bottomland	$4.0 \pm 0.38_{b}$	$1.0 \pm 0.10_{a}$	$0.5 \pm 0.05_{a}$	$0.8 \pm 0.02_{a}$
	6	Medium Upland	$1.7 \pm 0.14_{ab}$	$0.3 \pm 0.06_{a}$	$0.2 \pm 0.04_{a}$	$0.9 \pm 0.03_{a}$
	6	High Bottomland	$1.3 \pm 0.20_{a}$	$0.4 \pm 0.08_{a}$	$0.6 \pm 0.06_{a}$	$0.6 \pm 0.08_{a}$
	6	High upland	$2.8 \pm 0.13_{ab}$	$0.9 \pm 0.05_{a}$	$0.6 \pm 0.02_{a}$	$0.9 \pm 0.02_{a}$
2013_{28}	2	Low Bottomland	$2.5 \pm 0.35_{a}$	$0.7 \pm 0.06_{a}$	$0.4 \pm <0.01_{a}$	$0.8 \pm 0.07_{a}$
	2	Low Upland	$4.5 \pm 0.35_{a}$	$1.3 \pm 0.02_{a}$	$0.7 \pm 0.03_{a}$	$0.9 \pm 0.08_{a}$
	6	Medium Bottomland	$4.2 \pm 0.46_{a}$	$1.0 \pm 0.11_{a}$	$0.5 \pm 0.05_{a}$	$0.8 \pm 0.03_{a}$
	6	Medium Upland	$2.2 \pm 0.25_{a}$	$0.4 \pm 0.09_{a}$	$0.3 \pm 0.05_{a}$	$0.9 \pm 0.03_{a}$
	6	High Bottomland	$1.8 \pm 0.22_{a}$	$0.6 \pm 0.08_{a}$	$0.5 \pm 0.06_{a}$	$0.8 \pm 0.07_{a}$
	6	High upland	$2.2 \pm 0.16_{a}$	$0.6 \pm 0.08_{a}$	$0.4 \pm 0.05_{a}$	$0.9 \pm 0.02_{a}$
2012_{56}	10	Low Bottomland	$1.2 \pm 0.09_{a}$	$0.2 \pm 0.05_{a}$	$0.2 \pm 0.04_{a}$	$0.9 \pm 0.04_{a}$
	10	Low Upland	$2.3 \pm 0.20_{ab}$	$0.5 \pm 0.06_{ab}$	$0.5 \pm 0.04_{a}$	$0.8 \pm 0.04_{a}$
	9	Medium Bottomland	$3.8 \pm 0.21_{b}$	$1.0 \pm 0.05_{b}$	$0.6 \pm 0.03_{a}$	$0.9 \pm 0.02_{a}$
	9	Medium Upland	$2.2 \pm 0.15_{ab}$	$0.4 \pm 0.04_{ab}$	$0.2 \pm 0.03_{a}$	$0.8 \pm 0.02_{a}$
	9	High Bottomland	$1.6 \pm 0.13_{a}$	$0.5 \pm 0.05_{ab}$	$0.5 \pm 0.04_{a}$	$0.8 \pm 0.05_{a}$
	9	High upland	$2.1 \pm 0.15_{ab}$	$0.7 \pm 0.05_{ab}$	$0.6 \pm 0.03_{a}$	$0.7 \pm 0.05_{a}$
2013_{56}	10	Low Bottomland	$2.8 \pm 0.22_{a}$	$0.8 \pm 0.07_{a}$	$0.5 \pm 0.04_{a}$	$0.8 \pm 0.04_{a}$
	10	Low Upland	$2.5 \pm 0.17_{a}$	$0.7 \pm 0.06_{a}$	$0.5 \pm 0.03_{a}$	$0.9 \pm 0.03_{a}$
	9	Medium Bottomland	$4.0 \pm 0.29_{a}$	$1.0 \pm 0.07_{a}$	$0.5 \pm 0.03_{a}$	$0.9 \pm 0.01_{a}$
	9	Medium Upland	$2.4 \pm 0.17_{a}$	$0.5 \pm 0.05_{a}$	$0.3 \pm 0.03_{a}$	$0.8 \pm 0.02_{a}$
	9	High Bottomland	$1.9 \pm 0.15_{a}$	$0.6 \pm 0.06_{a}$	$0.6 \pm 0.03_{a}$	$0.8 \pm 0.05_{a}$
	9	High upland	$1.9 \pm 0.12_{a}$	$0.5 \pm 0.05_{a}$	$0.5 \pm 0.04_{a}$	$0.8 \pm 0.04_{a}$

5 Chapter 5: Multivariate analysis of species composition and harvesting intensity in communal rangelands across catenal and rainfall gradients (2011 – 2013)

5.1 ABSTRACT

The change in vegetation composition over time, in terms of climate change and human influences, has long been a major focus of vegetation ecology. Similarly, a vast number of ecological studies investigate the relationships between species distributions and associated environmental variables. The investigation of the variation of plant and animal communities across a variety of environmental variables is done with the aim of understanding the relationships that underpin the composition of multispecies communities. Canonical Correspondence Analysis (CCA) is an ordination technique that helps to examine these relationships. The aim of this study was to determine how woody plant species composition changes across a rainfall gradient and with catenal position for harvested and unharvested trees in a human-impacted landscape over time in the woodlands of Bushbuckridge, Mpumalanga Province. Three zones were selected that differed in annual rainfall: (a) wet west (>700mm), (b) mesic (600-700mm), and semi-dry east (<600m), with three villages per zone. For the rangeland of each village, plots were sampled in 2011, 2012 and 2013 to cover the upland and bottomland variations in catenal position. All trees >6m in height, and their individual stems, were counted and measured within a total of 56 circular plots (only 28 in 2011) each with a radius of 50m. Trees <6m, and their stems, were counted and measured in a circular plot with a radius of 6m, nested centrally within each 50m plot. Species composition differed between uplands and bottomlands, with fine-leaved species being more abundant in the bottomlands and broad-leaved species being more abundant in the uplands. The species composition in the high rainfall zone differed to those occurring in the low and medium rainfall zones, which were similar to each other. Harvesting intensity was higher in the bottomlands than the uplands and likewise, higher in the low and medium rainfall zones than in the high rainfall zone. This resulted in some species having higher abundance than others. Harvesting had less influence on species composition than catenal position or rainfall zone.

Keywords: Canonical Correspondence Analysis (CCA), catenal position, harvesting, ordination, rainfall, rangelands

5.2 INTRODUCTION

5.2.1 Importance of ordination

Many ecological studies investigate the variation of plant and animal communities across a variety of environmental conditions (Anderson and Willis 2003; Legendre 2008; Leps and Smilauer 2003; ter Braak 1986; ter Braak 1987). With these investigations, large differences in species composition are often found between the studied communities (Legendre 2008; Leps and Smilauer 2003; ter Braak 1987). The differences can be due to external factors such as environmental variation and internal processes such as the overlapping requirements of individual species for selected environmental factors such as available soil moisture or available nutrients, light and other factors (competition for resources) (Legendre 2008; Leps and Smilauer 2003; Wagner 2004). These factors are often referred to as gradients of species composition change within ecological studies (Leps and Smilauer 2003). Internal processes such as competition and dispersal are false gradients and external factors such as environmental variation are true gradients (Legendre 2008; Wagner 2004). Gradient analysis is used for the study of spatial patterns of vegetation and seeks to understand the variation in vegetation composition and structure of a landscape in terms of spatial gradients on three levels (Whittaker 1967). These three levels (Whittaker 1967) are (i) environmental factors, (ii) species populations and (iii) characteristics of a community. The environment level includes topographic position or the range of magnitudes of environmental factors in which a selected type of community occurs (Whittaker 1967). The species population level includes species which are usually present and the number of individuals in the community (Whittaker 1967). The overall characteristics of the community includes the structure of the vegetation, the total number of species present and the total mass of organic material and rate of production in the community (Whittaker 1967). Gradient analysis is thus a way to explain the difference in species composition within and between biotic communities (Wagner 2004; Whittaker 1967, ter Braak and Prentice 1988).

Statistical methods can summarize the variation in biotic communities, but with the continuity of change in community composition, a simple method is needed to analyse and visualize these relationships between species and environmental variables (Anderson and Willis 2003; Leps and Smilauer 2003; ter Braak 1986; ter Braak 1987). Ordination is seen as one of these methods to describe the variation in biotic communities and is a popular method for gradient analysis (Anderson and Willis 2003; Gauch and Wentwort 1979; Leps and Smilauer 2003; Okland 1996; Okland 1999; ter Braak 1986; ter Braak 1987; Wagner 2004;

Whittaker 1967). Since the early 1950's, ordination has been used by ecologists to investigate the change in species composition across various environmental gradients (Leps and Smilauer 2003; Okland 1996; Whittaker 1967). The main goal of ordination is to reveal the relationships between biotic communities and environmental variables in the data (Gauch and Wentwort 1979; Leps and Smilauer 2003; Okland 1996). Ordering of samples and/or species along axes that represent the main compositional gradients in the data set is the main aim of ordination (Leps and Smilauer 2003; Okland 1996).

5.2.2 Ordination techniques

5.2.2.1 Types of ordination

Ordination can be classified as either constrained or unconstrained (Anderson and Willis 2003; Legendre and Gallagher 2001; Leps and Smilauer 2003; Okland 1996; Okland 1999; ter Braak 1994; Wagner 2004). The unconstrained ordination is also called indirect gradient analysis and the constrained ordination is called direct gradient analysis (Anderson and Willis 2003; Legendre and Gallagher 2001; Leps and Smilauer 2003; Okland 1996; Okland 1999; ter Braak 1994; Wagner 2004; Whittaker 1967). Constrained or direct methods use species and environment data in a single integrated analysis to determine the relationships between biotic communities and environmental variables, whereas unconstrained or indirect methods use the species data only to determine the relationships between biotic communities only (ter Braak 1994; Whittaker 1967). Constrained ordination can be best defined as a search for the best explanatory variables whereas unconstrained ordination is best defined as any variable that best explains the species composition (Leps and Smilauer 2003; Whittaker 1967). Based on the underlying species response model and whether the ordination is constrained or unconstrained, there are four basic ordination techniques (Anderson and Willis 2003; Leps and Smilauer 2003; ter Braak 1994; ter Braak & Prentice, 1988). For linear methods, the basic unconstrained ordination technique is principal components analysis (PCA) and the basic constrained ordination technique is redundancy analysis (RDA) (Anderson and Willis 2003; Leps and Smilauer 2003; ter Braak 1994; ter Braak & Prentice, 1988; Wagner 2004). For weighted averaging methods, the basic unconstrained ordination technique is correspondence analysis (CA) and the basic constrained technique is canonical correspondence analysis (CCA) (Anderson and Willis 2003; Leps and Smilauer 2003; ter Braak 1994; ter Braak & Prentice, 1988; Wagner 2004).

5.2.2.2 Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) was developed by ter Braak in 1986 and examines the relationships between species distributions and the distributions of environmental factors and gradients (Ahmad 2011; ter Braak 1986). CCA is one of many correspondence analysis techniques but it differs from other correspondence analysis techniques, in that the ordination axes are constrained to be linear combinations of environmental variables (ter Braak 1987). CCA visualises not only the pattern of community variation as in the case of CA, but also the main features of the composition of species corresponding with a number of environmental variables within the selected study area (ter Braak 1987). Not only is CCA a method for detecting species-environment relations but also a method for investigating specific questions about the response of species to the environmental variables (ter Braak 1987). CA was found to be influenced by species-poor sites which often contain rare species. CCA is not influenced by this 'fault' of species poor sites (ter Braak 1986; ter Braak 1987). CCA extracts the best combination of environmental variables that maximizes the variance of the weighted average species positions (Doledec *et al.* 2000). CCA also implies that the number of individuals per site is proportional to the importance of the environmental measurements (Doledec *et al.* 2000).

According to ter Braak (1986; 1987), CCA constrains the linear combinations of environmental variables on which the species distributions are separated along as maximally as possible. The eigenvalues produced measure these separations (ter Braak 1986; ter Braak 1987). The diagram produced by CCA, displays sites, species and environmental variables (ter Braak 1986; ter Braak 1987). The sites and species points display variation in species composition across the sites, similar to CA diagrams (ter Braak 1986; ter Braak 1987). The environmental variables are represented by arrows (ter Braak 1986; ter Braak 1987). The arrows point in the direction of maximum change across the diagram for the selected environmental variable (ter Braak 1986; ter Braak 1987). The length of the arrows is proportional to the rate of change in the selected direction. According to ter Braak (1986; 1987), environmental variables which have long arrows are more strongly correlated with the ordination axis than those with short arrows. The better the correlation, the better the match between the field situation and the ordination will be (ter Braak 1986; ter Braak 1987).

In ordinary statistical tests, the value of the test statistic calculated from the data is compared with the expected distribution of the statistic under the null hypothesis (Leps and Smilauer 2003). Based on this comparison, we estimate the probability of obtaining results as

different from those that are expected (Leps and Smilauer 2003). The statistical test distribution is derived from the assumptions made about the distribution of the original data (Leps and Smilauer 2003). In CANOCO (CANOCO is an extension of DECORANA (Detrended Correspondence Analysis; Hill 1979) and formerly stood for canonical correspondence analysis (ter Braak 1986, ter Braak 1987)), the distribution of the test statistic under the null hypothesis is not known (Leps and Smilauer 2003). This distribution depends on the number of environmental variables, and the abundance of species and environmental variable correlation structure (Leps and Smilauer 2003). The distribution can be simulated in CANOCO by using a Monte Carlo permutation test (Leps and Smilauer 2003). In the Monte Carlo permutation test, an estimate of the distribution of the test statistic under the null hypothesis is obtained (Leps and Smilauer 2003). The null hypothesis states that the species composition (response) is independent of the environmental variables (Leps and Smilauer 2003). The values of the environmental variables are randomly assigned to the individual samples (species composition) (Leps and Smilauer 2003). The ordination is then performed with the permutation data set and the test statistic is calculated (Leps and Smilauer 2003). Both the distribution of the species composition and the correlation structure of the explanatory variables remains the same, not only in the real data but also in the null hypothesis simulated data (Leps and Smilauer 2003).

5.2.3 Purpose of using ordination in this study

This study aimed to determine how woody plant species composition changes across a rainfall gradient and with catenal position for harvested and unharvested trees in a human-impacted landscape over time. By focusing on the species-environment relationships among large and small trees across time, I sought to establish if species composition differs as a result of these environmental variables. By adding time as a component, it was be possible to see if (and to what degree) species composition changes over the time period of three years and in relation to the other components (rainfall zones and catenal position). This was determined by answering two questions. Firstly, how does species composition differ in response to environmental variables (a rainfall gradient and catenal position) and a disturbance gradient (harvesting intensity) in each of the study years (2011, 2012 and 2013)? Secondly, how does species composition change in response to these environmental variables and the disturbance gradient over time (2011-2013)?

5.3 MATERIALS AND METHODS

5.3.1 Study site

See Chapter 2 section 2.3.1

5.3.2 Study design

See Chapter 2 sections 2.3.2.1 and 2.3.2.2

5.3.3 Data analysis

In this chapter the species abundance data for the large and small trees (see Chapter 2), both separately and in combination, were analysed using multivariate analyses (ordinations) for each study year separately (2011, 2012 and 2013). Three environmental variables were used in all these ordinations, namely (1) rainfall zone (low, medium and high), (2) catenal position (bottomland and upland) and (3) harvesting intensity (proportion of trees harvested per study year). Note that harvesting intensity is seen as a disturbance variable which impacts the environment and was thus included as an environmental variable in ordinations. A final set of ordinations were then undertaken by combining the results from all three study years, and for these analyses time (or year) was an additional environmental variable. For the analyses where the large and small trees were combined, a scaling factor was calculated, as the large trees were assessed in the 50m radius plots while the small trees were only assessed in the much smaller 6m radius plots. The scaling factor is required due to the difference in area of the 6m plot (area=113m^2) and the 50m plot (area=7854m^2). The scaling factor is the area of the 50m plot in relation to the 6m plot ($Area_{50}/Area_6$), which is used to scale up the small plot to the area of the large plot (see Chapter 2 section 2.3.3.2). All the tree abundance data were tested for normality with Shapiro-Wilk normality tests and these data were natural log transformed to improve distribution if not normally distributed. Harvesting intensity was calculated at the plot level as the number of cut trees divided by the total number of trees. This provides a value between 0 and 1. If the value obtained is closer to 0, the harvesting intensity is very low. If the value is 1, all trees were harvested. This was done for both large and small trees separately as well as for the combination of the two for each of the three survey years.

Canonical correspondence analysis (CCA) was done for each of the three survey years (2011, 2012 and 2013) for both the 28 plots and 56 plots (only 2012 and 2013). This was done for large and small trees separated as well as the combination of the two. Each of the three survey years was tested separately in order to assess the influences of the environmental

variables for each of the survey years separately and see how they varied from year to year. Time (year) as a variable was established by combining the survey years, (three years with 28 plots and two years with 56 plots) and was done for large and small trees separately as well as the combination of the two. This was tested in order to assess the influences of the environmental variables for the combination of the survey years

All CCA analyses were done using the computer program CANOCO. CANOCO is an extension of DECORANA (Detrended Correspondence Analysis; Hill 1979) and formerly stood for canonical correspondence analysis (ter Braak 1986, ter Braak 1987, ter Braak 1988). However, it now includes both indirect and direct techniques (ter Braak 1986, ter Braak 1987, ter Braak 1988). CANOCO version 4.5 was used in this study (ter Braak and Smilauer 2002) with all default settings. The Monte Carlo permutation test was done for all CCA ordinations to test the significance of (a) the first canonical axis and (b) the first four canonical axes. The typical ordination diagrams of axis 1 against axis 2 were used for this study in interpreting the difference in species composition. All other data analysis was done in the open source R2.1.0 statistical program and its contributing packages (R Development Core Team 2005).

5.4 RESULTS

Throughout the rest of the text, the number of plots (28 or 56) of each year will be seen in subscript next to the selected year, for example, for the 28 plot datasets: 2011_{28}; 2012_{28}, 2013_{28} and for 56 plots: 2012_{56} and 2013_{56}.

5.4.1 Harvesting intensity

Table 5.1 shows the results for harvesting intensity (mean proportion of trees harvested ±SE) for both the large and small trees for each of the three survey years.

Large trees: Note that in 2011 there was no apparent harvesting of large trees. Harvesting intensity ranged between 0% in 2011, 2.3% in 2012 and 10.6% in 2013, with harvesting intensity being highest in 2013_{28}. Harvesting tended to increase over time, from 2011_{28} to $2012_{28\&56}$ to $2013_{28\&56}$ (Table 5.1). The harvesting intensity ranged between 2.6% and 6.5% in the low rainfall zone, between 1.4% and 10.7% in the medium rainfall zone and between 2.7% and 11.9% in the high rainfall zone (Table 5.1). Harvesting intensity ranged

between 2.9% and 14.7% in the bottomlands and between 1.8% and 7.4% in the uplands (Table 5.1).

Small trees: Harvesting intensity ranged between 6.5% and 12.2%, and was highest in 2013_{56}. Harvesting increased from 2011_{28} to $2013_{28\&56}$ (Table 5.1). The harvesting intensity ranged between 4% and 20.6% in the low rainfall zone, between 10.1% and 17.7% in the medium rainfall zone and between 3% and 6.1% in the high rainfall zone (Table 5.1). Harvesting intensity ranged between 6.2% and 10.6% in the bottomlands and between 5.7% and 14.5% in the uplands (Table 5.1). The harvesting intensity of smaller trees was higher than that of the large trees.

Table 5.1 Harvesting intensity index (mean proportion of trees harvested ±SE) for both large and small tree data sets for each of the three survey years. Harvesting intensity for (a) overall (plots combined), (b) rainfall zones and (c) catenal position are presented. *In 2011 there was no apparent harvesting of large trees.

Large trees

Year	No plots	Overall	Rainfall zone						Catenal position			
			No plots	Low	No plots	Medium	No plots	High	No plots	Bottomland	No plots	Upland
2011*	28	0.000±0.000	4	0.000±0.000	12	0.000±0.000	12	0.000±0.000	14	0.000±0.000	14	0.000±0.000
2012	28	0.025±0.013	4	0.053±0.053	12	0.014±0.014	12	0.028±0.021	14	0.051±0.024	14	0.000±0.000
2013	28	0.106±0.023	4	0.063±0.063	12	0.107±0.036	12	0.119±0.034	14	0.147±0.032	14	0.064±0.028
2012	56	0.023±0.008	20	0.026±0.013	18	0.017±0.012	18	0.027±0.016	28	0.029±0.013	28	0.018±0.009
2013	56	0.082±0.013	20	0.065±0.017	18	0.078±0.027	18	0.105±0.024	28	0.090±0.020	28	0.074±0.017

Small trees

Year	No plots	Overall	Rainfall zone						Catenal position			
			No plots	Low	No plots	Medium	No plots	High	No plots	Bottomland	No plots	Upland
2011	28	0.065±0.014	4	0.040±0.013	12	0.101±0.026	12	0.037±0.017	14	0.073±0.023	14	0.057±0.018
2012	28	0.088±0.015	4	0.121±0.035	12	0.127±0.025	12	0.037±0.015	14	0.074±0.021	14	0.101±0.023
2013	28	0.116±0.020	4	0.206±0.044	12	0.142±0.024	12	0.061±0.032	14	0.088±0.022	14	0.145±0.034
2012	56	0.080±0.012	20	0.068±0.016	18	0.142±0.027	18	0.030±0.010	28	0.062±0.012	28	0.098±0.021
2013	56	0.122±0.017	20	0.138±0.023	18	0.177±0.035	18	0.048±0.022	28	0.106±0.018	28	0.137±0.028

5.4.2 Multivariate analyses for large and small trees separately for each year (2011, 2012, & 2013 separately)

5.4.2.1 Summary of analysis and test of significance of canonical axes in relation to environmental variables

The eigenvalues for axis 1 ranged between 0.364-0.437 and 0.435-0.513 for the large and small tree analyses respectively (Table 5.2). The species-environment correlations for axis 1 were all high, and ranged between 0.833-0.895 and 0.886-0.970 for the large and small tree analyses respectively (Table 5.2). On the other hand, the cumulative percentage variance of species data for axis 1-4 ranged between 13.8-21.1% and 15.0-26.8% for the large and small tree analyses respectively (Table 5.2). Furthermore, the cumulative percentage variance of species-environment relation for axis 1-4 added up to 100% for the large and small tree analyses respectively (Table 5.2). The distribution of species for axis 1 was significant (Monte-Carlo permutation tests) in all of the survey years, indicating the species distribution is dependent on the environmental variables (rainfall zones, catenal positions and harvesting intensity), except for $2011_{28,}$ 2012_{28} and $2013_{28}$for large trees and for all three survey years among small trees (Table 5.2). On the other hand, the distribution of species for axes 1-4 were significant (Monte-Carlo permutation tests) in all of the survey years, indicating dependence of species distribution on environmental variables, except for 2012_{28} for large trees and for each of the three survey years for small trees (Table 5.2)

5.4.2.2 Results of multivariate analyses

The ordination biplots for the 28 plots results in 2011, 2012 and 2013 are shown in Figs 5.1A, B (large, small trees), 5.2A, B and 5.3A, B, respectively. Similarly the ordination biplots for the 56 plots results in 2012 and 2013 are shown in Figs 5.4A, B (large, small trees) and 5.5A, B, respectively.

Species composition

Large and small trees: Species that are near the edge of the ordination biplots are more specialized than those closer to the center of the ordination biplots (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5). The more abundant large tree species includes *Sclerocarya birrea, Philenoptera violacea* and *Pterocarpus angolensis* and, whereas the more abundant small tree species include *Dichrostachys cinerea, Terminalia sericea, Acacia exuvialis, Strychnos madagascariensis* and *Combretum hereroense* (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5), (also see Chapter 4).

Fine-leaved species such as *A. exuvialis, Acacia gerrardii* and *Albizia harveyi* were more commonly seen in the bottomlands, whereas broad-leaved species such as *Lannea discolour, Euclea natalensis* and *P. angolensis* were more commonly seen in the uplands. *T. sericea* was commonly seen near the centre between the uplands and bottomlands which coincides with the change in composition that is seen when moving along the catena (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5). The most abundant large tree species within the bottomlands included *S. birrea, S. madagascariensis; C. collinum; A. harveyi; A. gerrardii; P. violacea*; *P. angolensis* and *S. africana* whereas the three most abundant species within the uplands were *S. birrea, P. angolensis* and *P. violacea* (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5), (also see Chapter 4). The most abundant small tree species within the bottomlands included *D. cinerea, A. exuvialis, C. hereroense* and *Catunaregam spinosa* respectively whereas the three most abundant species within the uplands were *D. cinerea*, *S. madagascariensis* and *T. sericea* (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5), (also see Chapter 4).

Each of the rainfall zones also had species that were specific to the zone but also shared a number of species (dominant species). The most abundant large tree species within the low rainfall zone included *S. birrea, Combretum apiculatum, Combretum collinum, Combretum zeyheri, L. discolor* and *Acacia nigrescens* respectively. The most abundant large tree species within the medium rainfall zone included *S. birrea, P. violacea,* S*pirostachys africana* and *Diospyros mespiliformis* and the three most abundant large tree species within the high rainfall zone were *S. birrea*, *P. angolensis* and *P. violacea* (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5), (also see Chapter 4). The most abundant small tree species within the low rainfall zone included *A. exuvialis, S. madagascariensis, D. cinerea, T. sericea* and *Dalbergia melanoxylon* respectively. The three most abundant small tree species within the medium rainfall zone were *D. cinerea, S. madagascariensis* and *T. sericea* and the most abundant small tree species within the high rainfall zone included *D. cinerea, T. sericea, Diospyros lycioides, C. hereroense*, *Senna petersiana* and *T. sericea* (Fig. 5.1, 5.2, 5.3, 5.4, and 5.5), (also see Chapter 4).

Table 5.2 Summary of Canonical Correspondence Analysis results for the three survey years for both 28 and 56 plots among large and small trees. Significant results (P<0.05) for the Monte Carlo test with a maximum of 945 permutations are indicated in bold type. *In 2011 there was no apparent harvesting of large trees.

Large Trees (>6m height)							
						Monte Carlo Test	
2011 (28 plots)*	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.424	0.334	0.088	0.047	F- ratio	2.337	1.737
Species-Environment correlation	0.888	0.851	0.502	0.000	P-value	0.056	**0.012**
Cumulative percentage variance of:							
species data	9.6	17.2	19.2	21.1			
species-environment relation	50.1	89.6	100	0			
2012 (28 plots)							
Eigenvalue	0.380	0.326	0.185	0.074	F- ratio	1.884	1.378
Species-Environment correlation	0.891	0.859	0.812	0.526	P-value	0.200	0.086
Cumulative percentage variance of:							
species data	7.9	14.7	18.5	20.0			
species-environment relation	39.4	73.1	92.3	100			
2013 (28 plots)							
Eigenvalue	0.437	0.324	0.208	0.072	F- ratio	2.050	1.400
Species-Environment correlation	0.895	0.868	0.809	0.521	P-value	0.068	**0.042**
Cumulative percentage variance of:							
species data	8.5	14.8	18.9	20.3			
species-environment relation	42	73.1	93.1	100			
2012 (56 plots)							
Eigenvalue	0.364	0.254	0.139	0.060	F- ratio	3.273	1.997
Species-Environment correlation	0.833	0.763	0.627	0.498	P-value	**0.004**	**0.002**
Cumulative percentage variance of:							
species data	6.1	10.4	12.8	13.8			
species-environment relation	44.6	75.7	92.7	100			
2013 (56 plots)							
Eigenvalue	0.381	0.240	0.214	0.075	F- ratio	3.225	2.115
Species-Environment correlation	0.866	0.787	0.704	0.479	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.1	9.9	13.3	14.5			
species-environment relation	41.9	68.3	91.8	100			
Small Trees (< 6m height)							
						Monte Carlo Test	
2011 (28 plots)	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.482	0.362	0.234	0.087	F- ratio	3.127	1.106
Species-Environment correlation	0.970	0.903	0.840	0.731	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	10.7	18.8	24.0	26.0			
species-environment relation	41.3	72.4	92.5	100			
2012 (28 plots)							
Eigenvalue	0.513	0.293	0.260	0.083	F- ratio	3.127	2.106
Species-Environment correlation	0.958	0.878	0.829	0.722	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	12.0	18.8	24.9	26.8			
species-environment relation	44.7	70.1	92.7	100			
2013 (28 plots)							
Eigenvalue	0.509	0.299	0.277	0.115	F- ratio	2.936	2.093
Species-Environment correlation	0.961	0.887	0.871	0.763	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	11.3	18.0	24.1	26.7			
species-environment relation	42.4	67.4	90.4	100			
2012 (56 plots)							
Eigenvalue	0.441	0.370	0.107	0.074	F- ratio	3.651	2.255
Species-Environment correlation	0.886	0.827	0.710	0.550	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.7	12.3	13.9	15.0			
species-environment relation	44.4	81.7	92.5	100			
2013 (56 plots)							
Eigenvalue	0.435	0.341	0.169	0.093	F- ratio	3.615	2.393
Species-Environment correlation	0.907	0.821	0.812	0.599	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.6	11.8	14.4	15.8			
species-environment relation	41.9	74.7	91	100			

Environmental variables

Large and small trees seperately: For all three survey years (2011_{28}, $2012_{28\&56}$, $2013_{28\&56}$), the species composition of large (A) and small (B) trees in the uplands and bottomlands tended to be different (Fig 5.1, 5.2, 5.3, 5.4 and 5.5). The arrow length of both uplands and bottomlands are long, illustrating a relatively large influence of catenal position on species composition (Fig 5.1, 5.2, 5.3, 5.4 and 5.5). The species composition associated with the high rainfall zone was different compared to that of the medium and low rainfall zones (Fig 5.1, 5.2, 5.3, 5.4 and 5.5). However, the species compositions of the low and medium rainfall zones were similar to each other (Fig 5.1, 5.2, 5.3, 5.4 and 5.5). There was however no relationship between rainfall zones and catenal position because arrows was at about 90 degrees to each other (Fig 5.1, 5.2, 5.3, 5.4 and 5.5). All of the environmental variables except for harvesting intensity had a relative strong influence on the species composition (Fig 5.1B, 5.2, 5.3, 5.4 and 5.5).

Large trees: In the ordination biplots of the large trees of 2011_{28}, recent harvesting was absent (Fig 5.1A). In the ordination biplots of the large trees in $2012_{28\&56}$ and $2013_{28\&56}$, although recent harvesting was present, it had the smallest influence on species composition compared to the other environmental variables (Fig 5.2A, 5.3A, 5.4A and 5.5A). Influence of harvesting was greater in the bottomlands compared to the uplands in $2012_{28\&56}$ and in $2013_{28\&56}$ (Fig 5.2A, 5.3A, 5.4A and 5.5A). Influence of harvesting was also higher in the low and medium rainfall zones than in the high rainfall zone in 2012_{28} (Fig 5.2A) Influence of harvesting was higher in the low rainfall zone compared to that of the medium and high rainfall zone in 2012_{56} (Fig 5.3A) and 2013_{28} (Fig 5.4A) but in 2013_{56}, influence of harvesting was similar between the three rainfall zones due to the arrows being at about 90 degrees to each other (Fig 5.5A).

Small trees: The small trees in all three survey years (2011_{28}, $2012_{28\&56}$, $2013_{28\&56}$) showed that all of the environmental variables had some influence on the species composition and that the influence of recent harvesting was the smallest influence on species composition (Fig 5.1B, 5.2B, 5.3B, 5.4B and 5.5B). Influence of harvesting was higher in the bottomlands than in the uplands in 2011_{28} (Fig 5.1B) but was similar between the two catenal positions in $2012_{28\&56}$ (Fig 5.2B, 5.4B) and in $2013_{28\&56}$ (Fig 5.3B, 5.5B) due to the arrows being at about 90 degrees to each other. The influence of harvesting was higher in the low rainfall zone compared to the medium and high rainfall zone in 2011_{28} (Fig 5.1B). The influence of

harvesting was higher in the low and medium rainfall zones than that of the high rainfall zone in $2012_{28\&56}$ (Fig 5.2B, 5.4B) and in $2013_{28\&56}$ (Fig 5.3B, 5.5B).

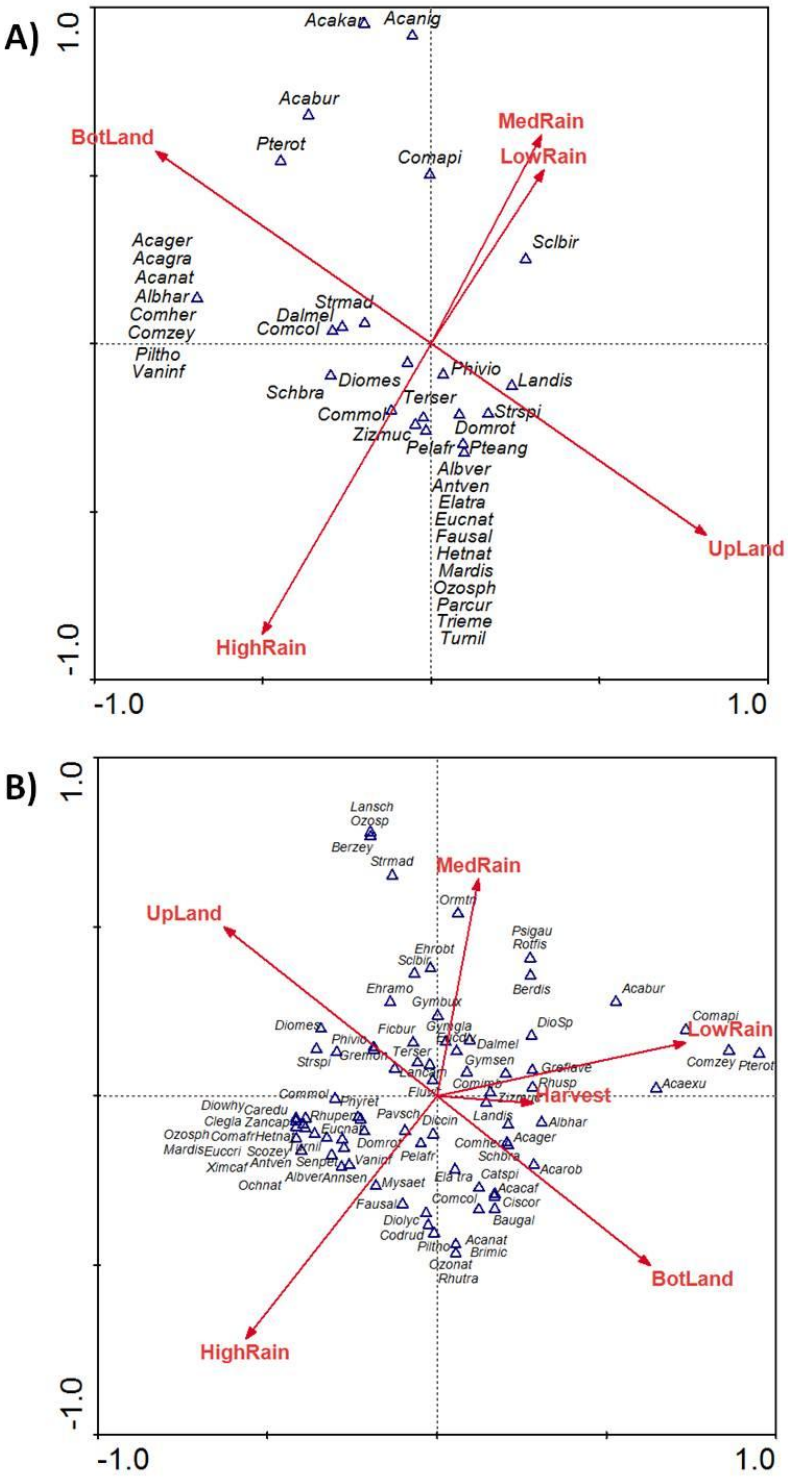


Figure 5.1 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in 2011 (28 plot dataset). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone and HighRain – High rainfall zone. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

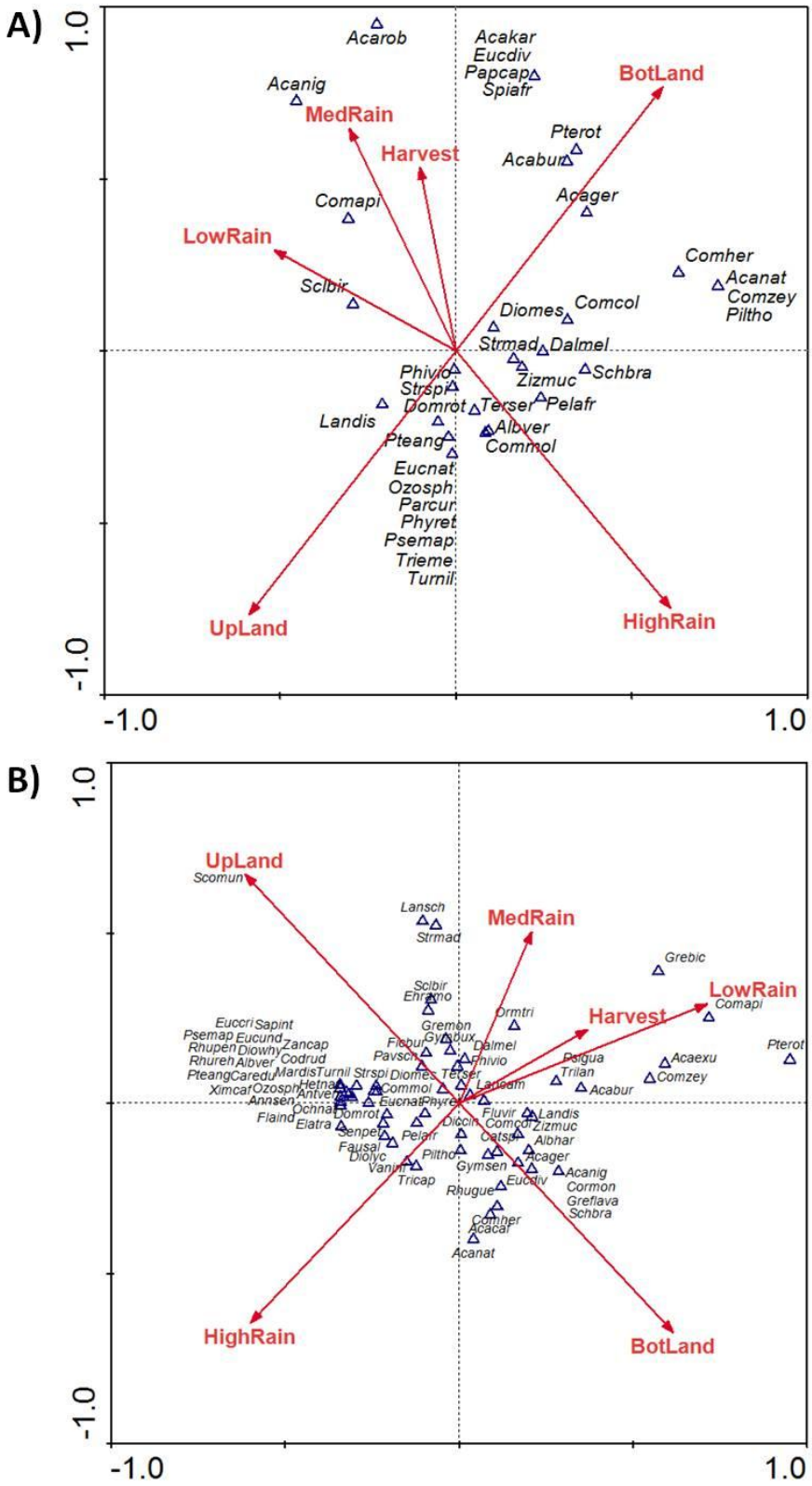


Figure 5.2 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in 2012 (28 plot dataset). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

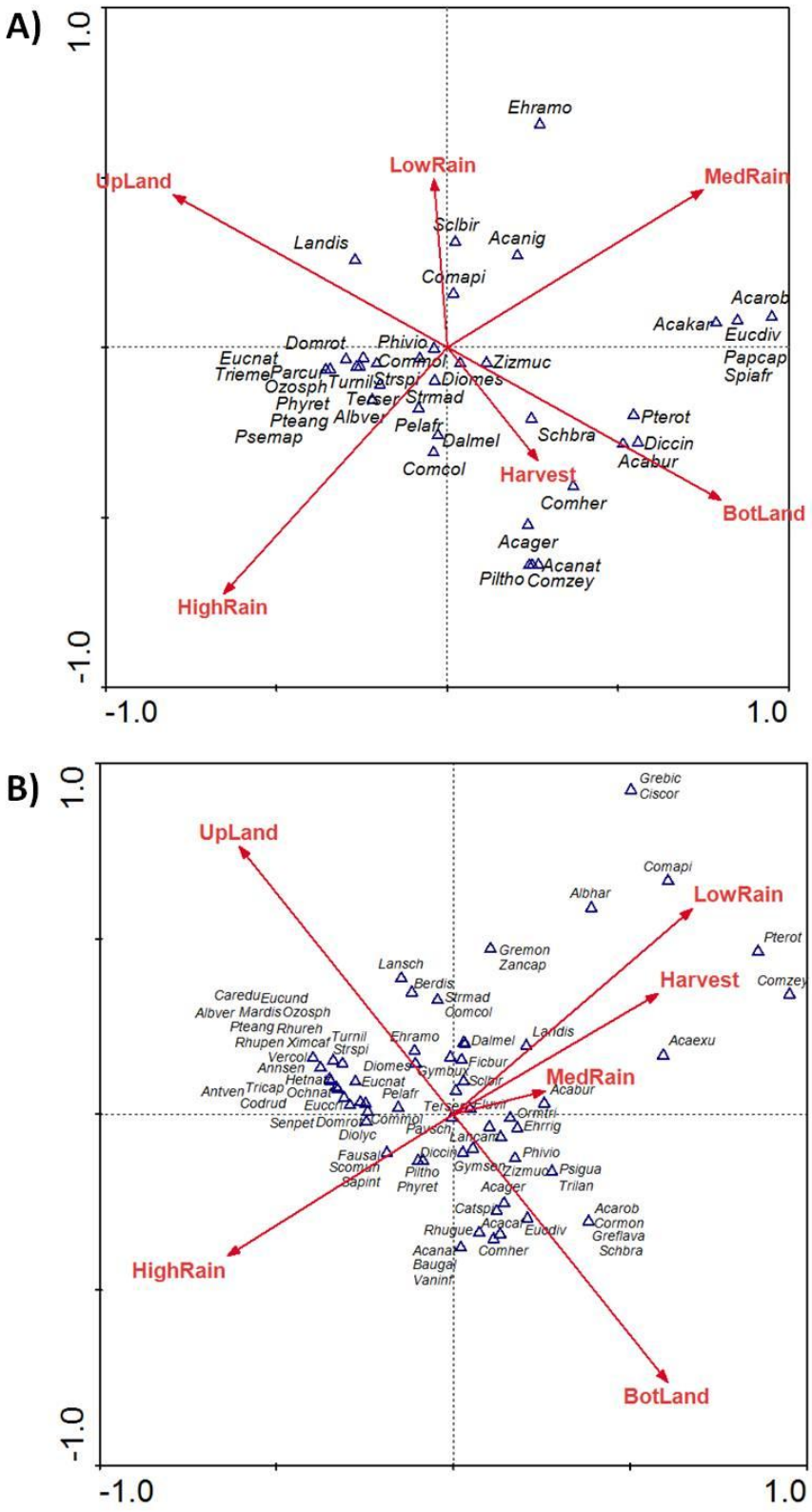


Figure 5.3 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in 2013 (28 plot dataset). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

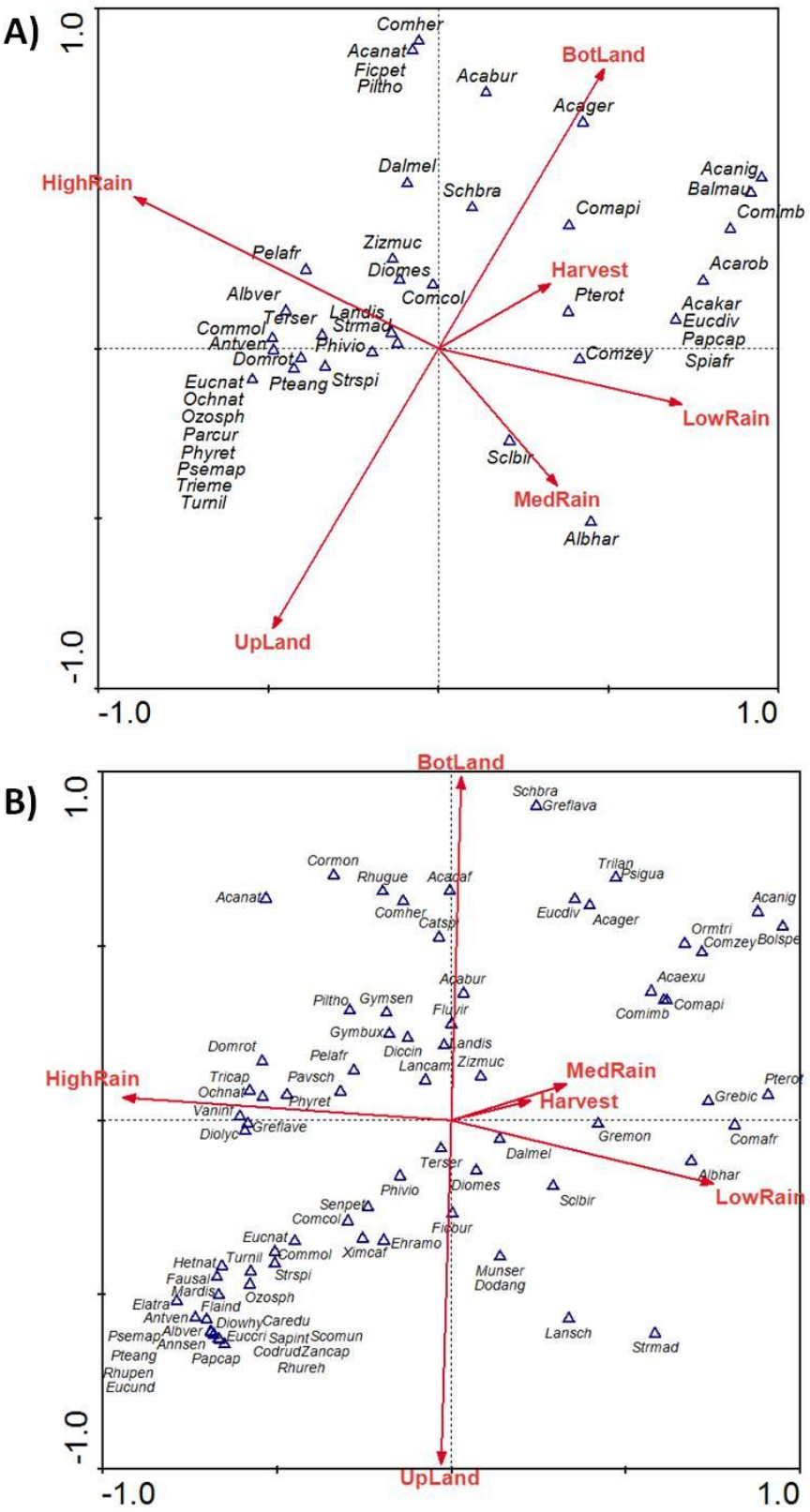


Figure 5.4 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in 2012 (56 plot dataset). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

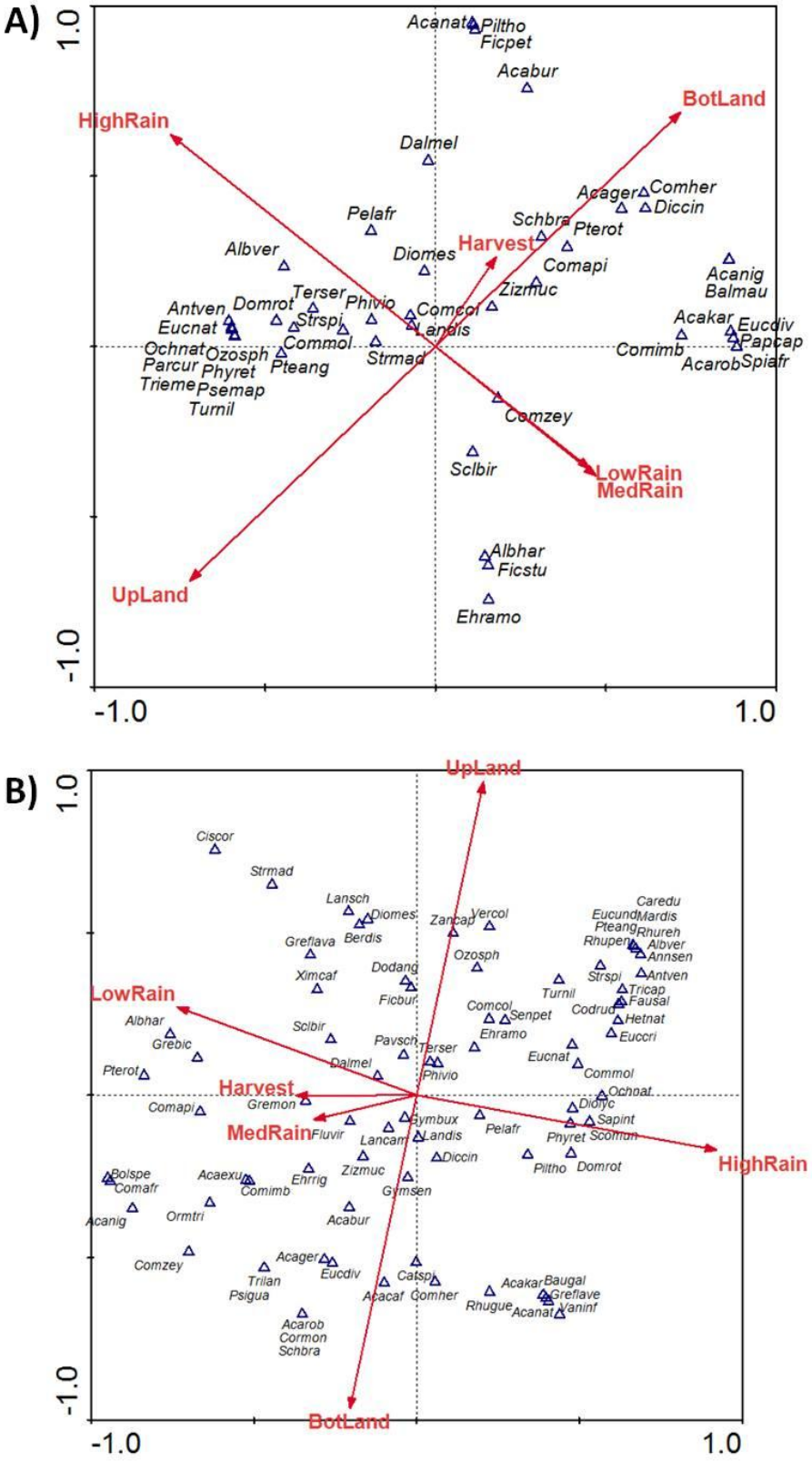


Figure 5.5 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in 2013 (56 plot dataset). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

5.4.3 Multivariate analyses for large and small trees combined for each year (2011, 2012, & 2013 separately)

5.4.3.1 Summary of analysis and test of significance of canonical axes in relation to environmental variables

The eigenvalues for axis 1 ranged between 0.436-0.521 for all tree (large and small trees combined) analysis (Table 5.3). The species-environment correlations for axis 1 were all high, and ranged between 0.889-0.969 for all tree analysis (Table 5.3). On the other hand, the cumulative percentage variance of species data for axis 1-4 ranged between 15.1-27.3% for all tree analysis (Table 5.3). Furthermore, the cumulative percentage variance of species-environment relation for axis 1-4 added up to 100% for all tree analysis (Table 5.3). The distribution of species for axis 1 and axis 1-4 were significant (Monte-Carlo permutation tests) in each of the survey years among all trees, indicating dependence of species distribution on environmental variables, (Table 5.3).

Table 5.3 Summary of Canonical Correspondence Analysis results for the three survey years for both 28 and 56 plots among the combination of large and small trees. Significant results (P<0.05) for the Monte Carlo test with a maximum of 945 permutations are indicated in bold type.

Combined Trees (small and large trees)							
						Monte Carlo Test	
2011 (28 plots)	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.476	0.362	0.230	0.088	F- ratio	2.855	2.106
Species-Environment correlation	0.969	0.902	0.838	0.734	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	11.0	19.4	24.8	26.8			
species-environment relation	41.2	72.5	92.4	100			
2012 (28 plots)							
Eigenvalue	0.521	0.288	0.269	0.099	F- ratio	3.158	2.158
Species-Environment correlation	0.964	0.878	0.828	0.699	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	12.1	18.8	25.0	27.3			
species-environment relation	44.2	68.7	91.6	100			
2013 (28 plots)							
Eigenvalue	0.506	0.294	0.268	0.097	F- ratio	2.935	2.029
Species-Environment correlation	0.960	0.888	0.854	0.689	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	11.3	17.9	23.9	26.1			
species-environment relation	43.4	68.7	91.6	100			
2012 (56 plots)							
Eigenvalue	0.441	0.367	0.109	0.077	F- ratio	3.665	2.269
Species-Environment correlation	0.889	0.824	0.712	0.554	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.7	12.3	13.9	15.1			
species-environment relation	44.4	81.3	92.3	100			
2013 (56 plots)							
Eigenvalue	0.436	0.342	0.172	0.110	F- ratio	3.649	2.469
Species-Environment correlation	0.909	0.824	0.814	0.627	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.7	11.9	14.5	16.2			
species-environment relation	41.2	73.4	89.6	100			

5.4.3.2 Results of multivariate analyses

The ordination biplots for all trees (large and small trees combined) for the 28 plots results in 2011, 2012 and 2013 are shown in Figs 5.6A, B and C, respectively. Similarly the ordination biplots for all trees for the 56 plots results in 2012 and 2013 are shown in Figs 5.6D and E, respectively.

Species composition

Similar patterns (see section 5.4.2.2) in species composition in regards to dominant species and species type across rainfall zones and catenal positions was seen when time was included as a variable (Fig 5.6).

Environmental variables

The species composition between catenal position and rainfall zones in all three survey years (2011_{28}, $2012_{28\&56}$, $2013_{28\&56}$), for all trees (large and small combined), (Fig 5.6A, B, C, D and E) were similar to the pattern seen in the separate ordination biplots of large and small trees (Fig 5.1-5.5). Harvesting only had a strong influence on the species composition in 2013_{28} (Fig 5.6C). Influence of harvesting was higher in the bottomlands than in the uplands in 2011_{28} (Fig 5.6A) but was similar between the two catenal positions in $2012_{28\&56}$ (Fig5.6B and D) and in $2013_{28\&56}$ (Fig 5.6C and E), similar to the pattern seen when large and small trees are separate. Influence of harvesting was higher in the low and medium rainfall zones compared to the high rainfall zone in 2011_{28} (Fig 5.6A) and in 2013_{28} (Fig 5.6C). Influence of harvesting was higher in the low rainfall zone than that of the medium and high rainfall zones in 2012_{28} (Fig 5.6B). Influence of harvesting was higher in the medium rainfall zone than that of the low and high rainfall zones in 2012_{56} (Fig 5.6D) and 2013_{56} (Fig 5.6E).

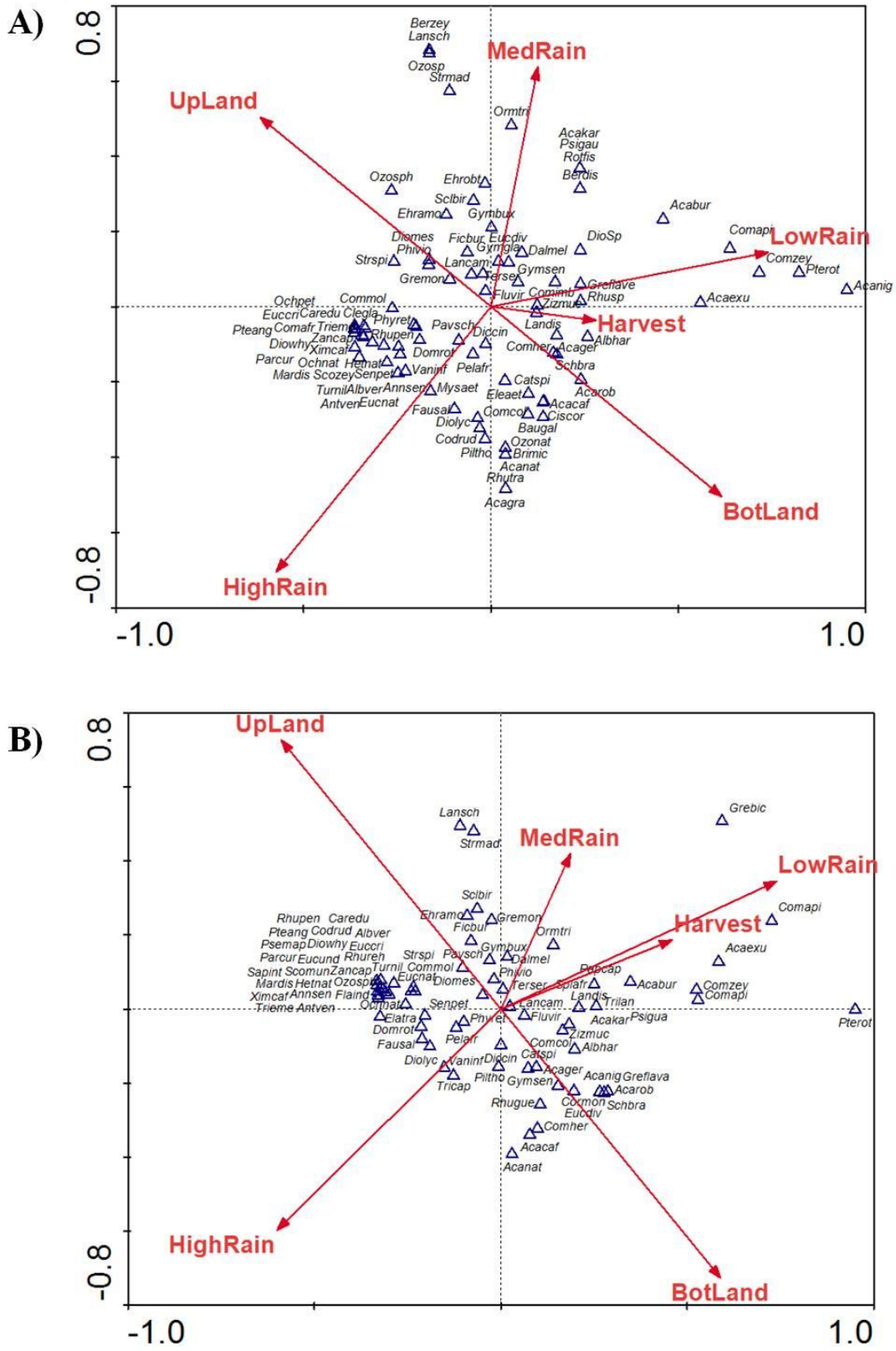


Figure 5.6 Canonical correspondence analysis (CCA) of species and environmental variables among all trees (combined large and small trees) in the 28 plot dataset in 2011 (A), 2012 (B) and 2013 (C) and 56 plot dataset in 2012 (D) and 2013 (E). Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name

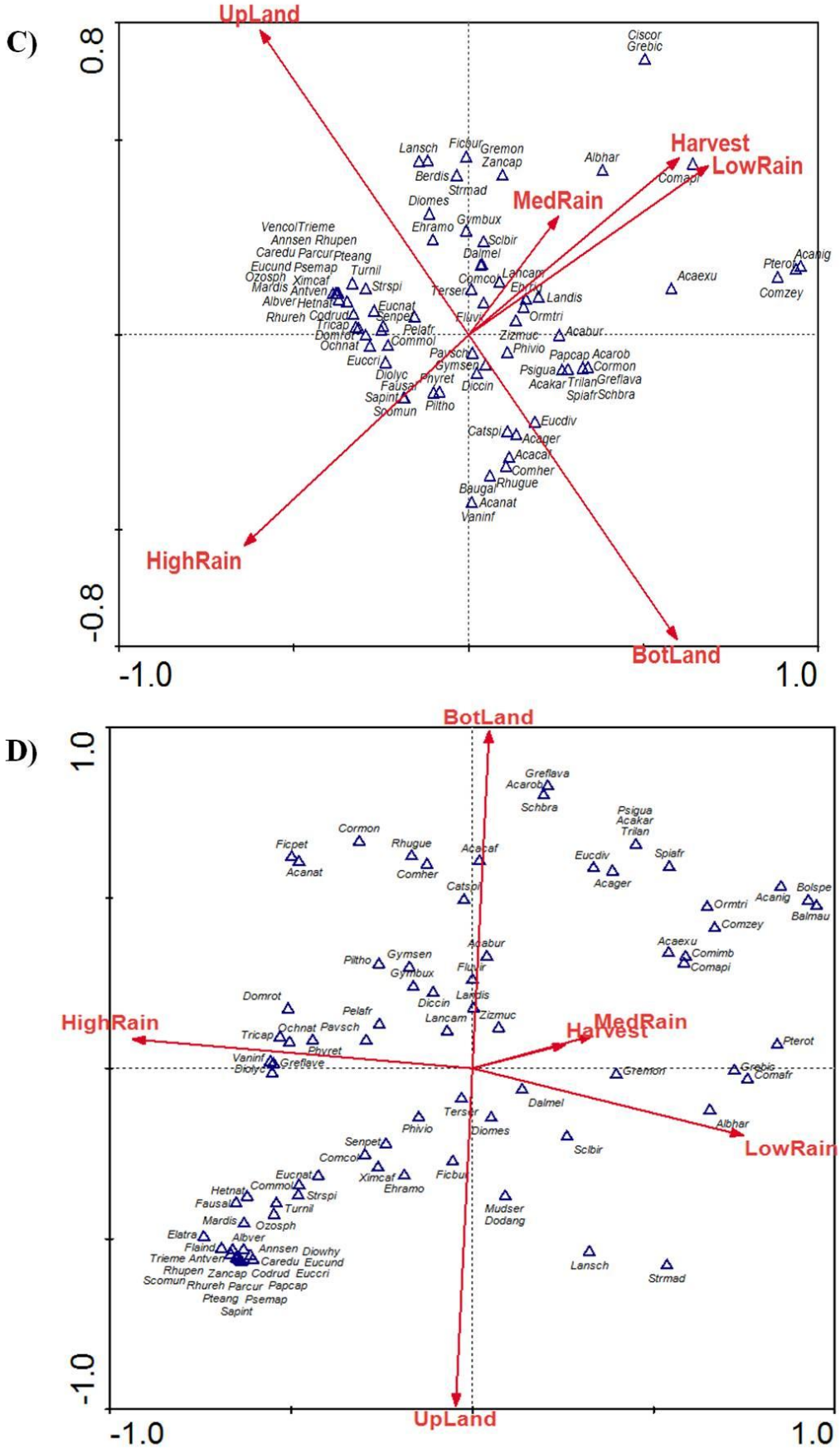


Figure 5.6 (Continued)

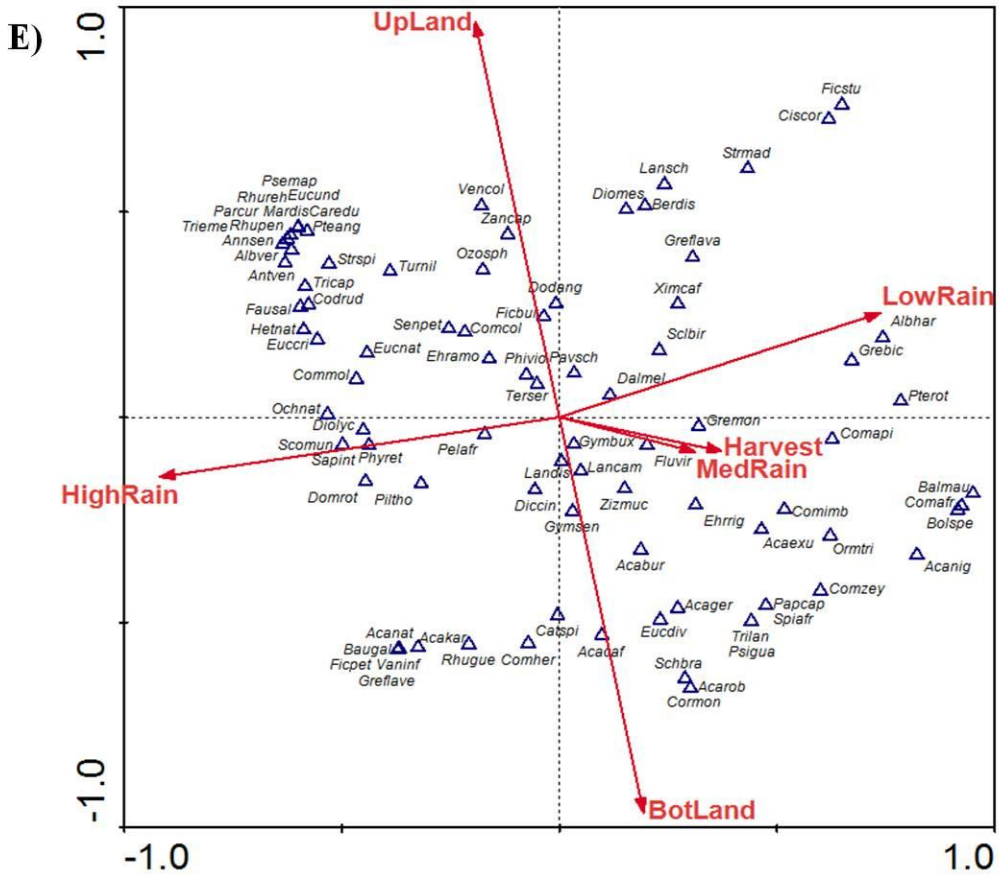


Figure 5.6 (Continued)

5.4.4 Multivariate analyses for large and small trees separately and combined for the three years (2011, 2012, & 2013) combined

5.4.4.1 Summary of analysis and test of significance of canonical axes in relation to environmental variables

28 plots: The eigenvalues for axis 1 was 0.381, 0.485 and 0.489 for the large, small and all tree analyses respectively (Table 5.4). The species-environment correlation for axis 1 were all high, and were 0.882, 0.959 and 0.958 for the large, small and all tree analyses respectively (Table 5.4). On the other hand, the cumulative percentage variance of species data for axis 1-4 was 16.2%, 20.6% and 20.7% for the large, small and all tree analyses respectively (Table 5.4). Furthermore, the cumulative percentage variance of species-environment relation for axis 1-4 added up to 95% for the large, small and all tree analyses respectively (Table 5.4). The distribution of species for axis 1 and axis 1-4 were significant (Monte-Carlo permutation tests) (p=0.002) in all of the survey years among large, small and all trees, indicating dependence of species distribution on environmental variables, (Table 5.4).

56 plots: The eigenvalues for axis 1 was 0.367, 0.434 and 0.894 for the large, small and all tree analyses respectively (Table 5.4). The species-environment correlation for axis 1 were high, and were 0.849, 0.894 and 0.894 for the large, small and all tree analyses respectively (Table 5.4). On the other hand, the cumulative percentage variance of species data for axis 1-4 was 12.9%, 14.4% and 14.4% for the large, small and all tree analyses respectively (Table 5.4). Furthermore, the cumulative percentage variance of species-environment relation for axis 1-4 added up to 99% for the large, small and all tree analyses respectively (Table 5.4). The distribution of species for axis 1 and axis 1-4 were significant (Monte-Carlo permutation tests) (p=0.002) in all of the survey years among large, small and all trees, indicating dependence of species distribution on environmental variables, (Table 5.4).

Table 5.4 Summary of Canonical Correspondence Analysis results for the combination of the three survey years for both 28 and 56 plots among large, small and the combination of large and small trees. Significant results (P<0.05) for the Monte Carlo test with a maximum of 945 permutations are indicated in bold type.

Large Trees (>6m height)							
						Monte Carlo Test	
28 plots	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.381	0.350	0.142	0.065	F- ratio	5.149	2.478
Species-Environment correlation	0.882	0.851	0.674	0.412	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.6	12.6	15.1	16.2			
species-environment relation	38.9	74.7	89.2	95.9			
56 plots							
Eigenvalue	0.367	0.245	0.181	0.048	F- ratio	6.227	3.141
Species-Environment correlation	0.849	0.772	0.650	0.385	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	5.6	9.4	12.2	12.9			
species-environment relation	43.1	71.8	93	98.7			
Small Trees (< 6m height)							
						Monte Carlo Test	
28 plots	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.485	0.300	0.235	0.060	F- ratio	7.952	3.672
Species-Environment correlation	0.959	0.862	0.822	0.584	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	9.4	15.2	19.7	20.6			
species-environment relation	42.1	68.1	88.5	93.7			
56 plots							
Eigenvalue	0.434	0.353	0.127	0.077	F- ratio	7.126	3.656
Species-Environment correlation	0.894	0.811	0.742	0.553	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.3	11.4	13.3	14.4			
species-environment relation	42.8	77.7	90.2	97.8			
Combined Trees (small and large trees)							
						Monte Carlo Test	
28 plots	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**		**1st axis**	**Axes 1--4**
Eigenvalue	0.489	0.287	0.240	0.053	F- ratio	8.049	3.643
Species-Environment correlation	0.958	0.856	0.820	0.631	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	9.5	15.0	19.7	20.7			
species-environment relation	42.8	67.9	88.9	93.6			
56 plots							
Eigenvalue	0.434	0.353	0.127	0.077	F- ratio	7.125	3.655
Species-Environment correlation	0.894	0.811	0.742	0.553	P-value	**0.002**	**0.002**
Cumulative percentage variance of:							
species data	6.3	11.4	13.3	14.4			
species-environment relation	42.8	77.7	90.2	97.8			

5.4.4.2 Results of multivariate analyses

The ordination biplots for the results in 2011_{28}, 2012_{28} and 2013_{28} are shown in Figs 5.7A, B (large, small trees) respectively. Similarly the ordination biplots for the results in 2012_{56} and 2013_{56} are shown in Figs 5.8A, B (large, small trees) respectively. The ordination biplots for all trees (large and small trees combined) for the results of 2011_{28}, 2012_{28} and 2013_{28} are shown in Figs 5.9A and the ordination biplots for all trees for the results in 2012_{56} and 2013_{56} are shown in Figs 5.9B respectively.

Species composition

The same patterns (see section 5.4.2.2) in species composition in regards to dominant species and species type across rainfall zones and catenal positions was seen when time was included as a variable (Fig 5.7, 5.8 and 5.9).

Environmental variable

Large and small trees separate

Large and small trees: In all three survey years (2011_{28}, $2012_{28\&56}$, $2013_{28\&56}$) for the species composition of large (A) and small (B) trees, the environmental variables (catenal position, rainfall zones and harvesting), was the same as those used earlier. Time had a small influence on species composition but a relationship (small) can be seen between the composition and the predictors (rainfall zones, catenal positions, harvesting intensity and time).

Large trees: The species composition for large trees in 2013_{28} was different from those in 2011_{28} and 2012_{28} (Fig 5.7A). The species composition for large trees in 2012_{56} was different from those in 2013_{56} (Fig 5.8A).

Small trees: The species composition for small trees in 2011_{28} was different from those in 2012_{28} and 2013_{28} (Fig 5.7B). The species composition for small trees in 2012_{56} was different from those in 2013_{56} (Fig 5.8B)

Large and small trees combined

The species composition for all tress in 2011_{28} was different from those in 2012_{28} and 2013_{28} (Fig 5.9A). The species composition for all trees in 2012_{56} was different from those in 2013_{56} (Fig 5.9B).

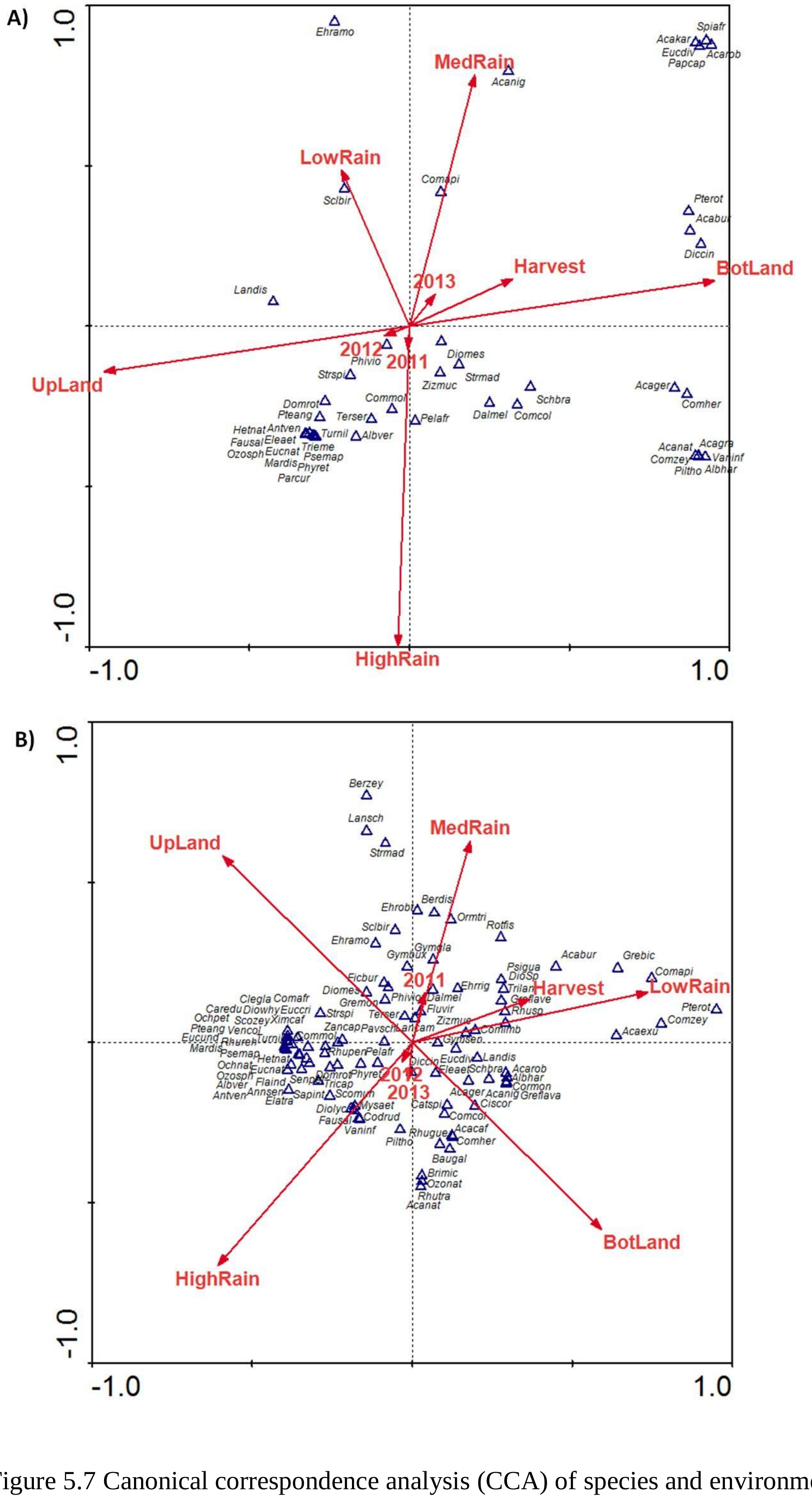


Figure 5.7 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in the 28 plot dataset. Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name

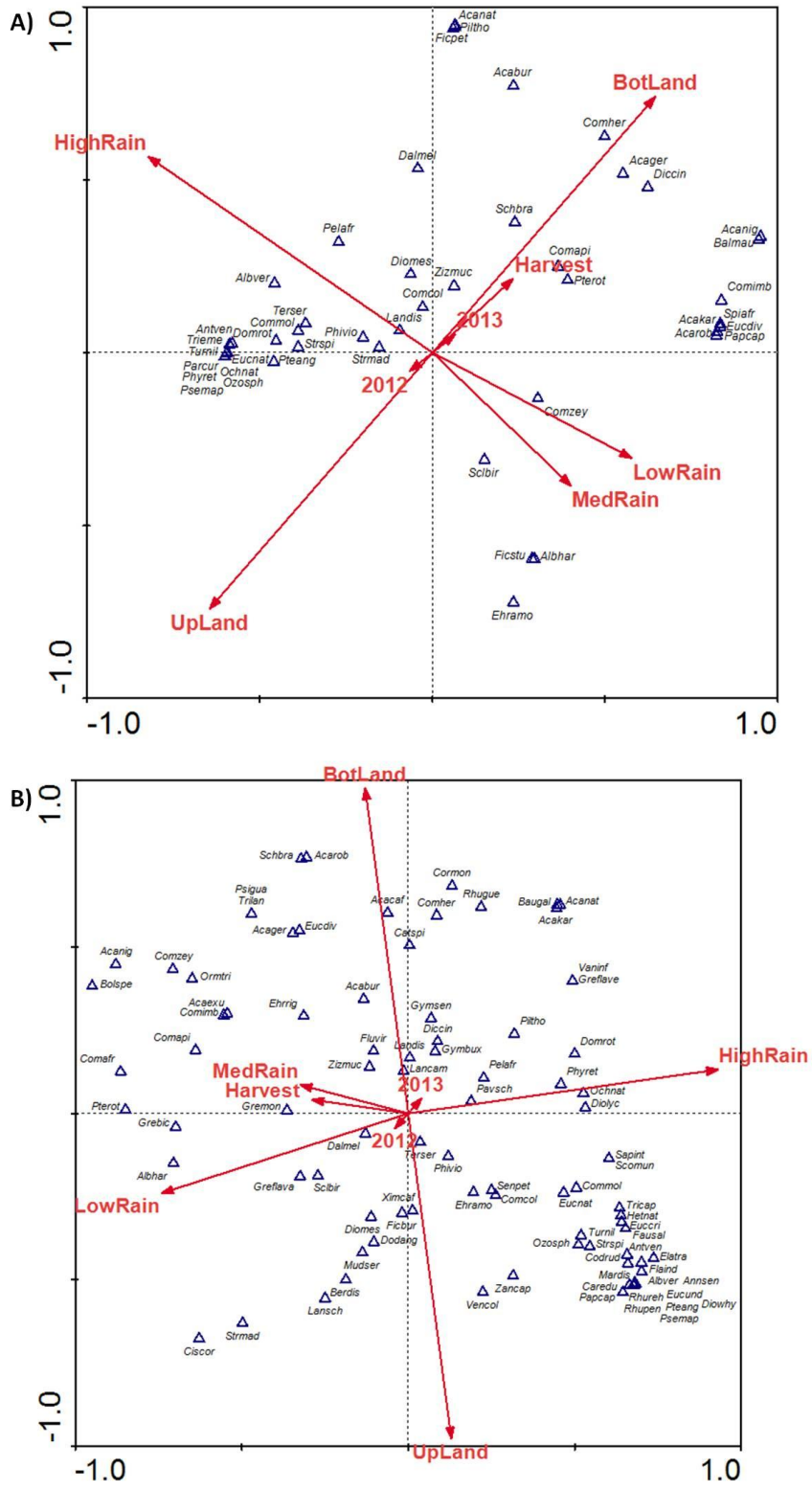


Figure 5.8 Canonical correspondence analysis (CCA) of species and environmental variables among (A) large trees and (B) small trees in the 56 plot dataset. Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name

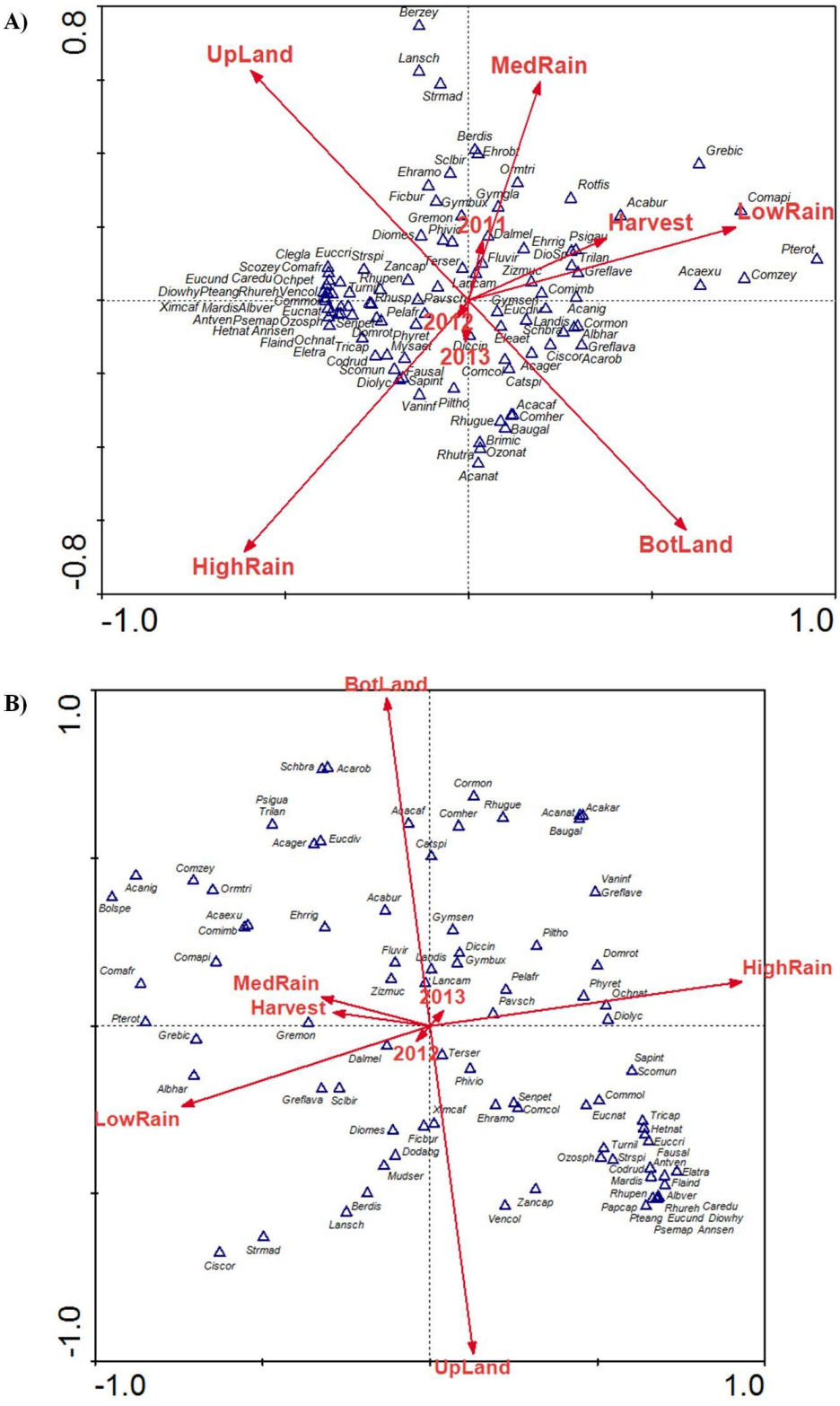


Figure 5.9 Canonical correspondence analysis (CCA) of species and environmental variables among all trees (combined large and small trees) in the (A) 28 plot dataset and (B)56 plot dataset. Key to environmental variables: BotLand – Bottomland catenal position; UpLand – Upland catenal position; LowRain – Low rainfall zone; MedRain – Medium rainfall zone; HighRain – High rainfall zone and Harvest – Harvesting intensity. Key to species: see Appendix 1. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name

5.5 DISCUSSION

The ordinations provided meaningful descriptions of the relationships between species composition and the included environmental variables. In general, harvesting intensity had the least influence on the species composition across the three survey years, among large and small trees separately and combined. The ordination biplots of all three survey years showed that there was no interaction between rainfall and catenal position in their influence on species composition among large, small and all trees. The arrows representing these two environmental variables were mostly at 90 degrees to each other, indicating no correlation between them. Across all three survey years and rainfall zones, species composition in the uplands was consistently different to that in the bottomlands among large, small and all trees. The ordination biplots of all three survey years, among large, small and all trees, also showed that the influence of higher rainfall resulted in the difference in species composition when compared to the species composition of the low and medium rainfall zone which had similar species composition. The influence of harvesting combined with rainfall zones and catenal positions resulted in the difference in species composition. Influence of harvesting was higher in the bottomlands than the uplands and similarly, the low and medium rainfall zones had higher influence of harvesting than the high rainfall zone in the three survey years among large, small and all trees. Time had little influence on species composition among large, small and all trees.

5.5.1 Difference in species composition between rainfall zones and catenal position

Both rainfall and topography are key drivers in compositional differences seen within savannas (Buitenwerf *et al.* 2012; Coughenour and Ellis 1993; Dahlberg 2000; Dube and Pickup 2001; Fisher *et al.* 2009; Fisher *et al.* 2011; Hassler *et al.* 2010; Kanniah *et al.* 2010; Kaschula *et al.* 2005; Nemani *et al.* 2003; Shackleton 1999; Shackleton and Scholes 2011; Smith and Goodman 1986; Wessels *et al.* 2011; Witkowski and O'Connor 1996). The study found similar findings to those mentioned above that both rainfall and topography were important for compositional differences in large, small and all trees.

Difference in species composition associated with each of these two environmental variables (rainfall zones and catenal position) was observed in this study. In all of the ordination biplots, large, small and all trees across the three survey years, species composition between the two different catenal positions were different from each other. The bottomlands contained more fine-leaved species whereas the uplands contained more broad-leaved species. This coincides with other studies that found that the species commonly found on the hill crest

included *Combretum* spp., *Diospyros mespiliformis*, *Peltophorum africanum*, *Terminalia sericea* and *Sclerocarya birrea* (Dzerefos *et al.* 2003; Parsons *et al.* 1997). The species composition of the bottom lands generally includes *Acacia* spp., *Dichrostachys cinerea*, *Albizia harveyi*, *Euclea* spp. and *Gymnosporia* spp. (Dzerefos *et al.* 2003; Parsons *et al.* 1997). A study by Colgan *et al.* (2012) found that the change in composition and structure can be seen when moving along the catena as the vegetation structure changes from a predominantly broadleaf species composition to a predominantly fine leaf species composition with a visible seep line in between after a fringe of *Terminalia sericea* on the upslope position of the seep line. This is what was expected as various studies state that species composition of bottomland catenal position is different to that of upland catenal position (Colgan *et al.* 2012; Daultrey 1970; Fisher *et al.* 2009; Fisher *et al.* 2011; Khomo *et al.* 2011; Wessels *et al.* 2011; see also the results of Chapter 2). This is mainly due to the differences in both soil properties (soil composition and texture) and water availability (annual rainfall and infiltration capacity) (Colgan *et al.* 2012).

The results of this study also showed that the species composition in the high rainfall zone was different to that of the low and medium rainfall zone for both large and small trees and all trees in all three survey years. This was also expected as most studies also found the species composition to differ between the high and low rainfall areas (Chapter 2). This coincides with the difference in species composition seen between the high rainfall zone with the species composition seen in the low and medium rainfall zone.

5.5.2 Difference in species composition between environmental variables and harvesting

The composition and structure of savannas have not only been formed by environmental determinants such as rainfall and soil, but has also been influenced and manipulated by anthropogenic disturbances, such as harvesting of fuelwood, which result in the transformation of the land (Breshears and Barnes 1999; Buitenwerf *et al.* 2012; Colgan *et al.* 2012; Dahlberg 2000; Dube and Pickup 2001; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Shackleton *et al.* 1994; Shackleton 1999; Shackleton and Scholes 2011; Smith and Goodman 1986; Wessels *et al.* 2011; Witkowski and O'Connor 1996). The study also found similar findings to those mentioned above, concluding that both environmental and anthropogenic disturbances are important for compositional differences in large, small and all trees.

The influence of harvesting on species composition was relatively small when compared to the influence of rainfall zones and catenal positions. Harvesting of large trees was absent in 2011_{28}, but was apparent in 2012_{28} and 2013_{28} (see Chapters 3 and 4). The lack of harvesting on large trees might be due to local traditions that forbid harvesting of large fruit bearing trees (Fisher *et al.* 2011; Wessels *et al.* 2011). The increase in harvesting of large trees is possibly due to the commercialization of fuelwood which allows larger trees to be harvested by chainsaw and transported by means of trucks or bakkies (Dovie *et al.* 2004; Matsika *et al.* 2013a; Twine 2005; Van Gelder *et al.* 1983). Literature mentioned above is based on long term studies, whereas this study was only longitudinal over a short period. The increase in harvesting seen from 2011 to 2012 to 2013 is possibly due to the general variation in harvesting between years and between locations (rainfall zones) because the harvesting was more evedent in the medium rainfall zone, which had a smaller rangelande and larger villages surrounding it that that of the low and high rainfall zones. The increase can also be due tot the rapidly increasing harvesting pressure which is linked to the shortage of wood. In general, influence of harvesting was similar between low and medium rainfall zones, being higher in these two rainfall zones than the high rainfall zone and also being higher in the bottomlands than the uplands. This is to be expected, as harvesting occurred more in the low and medium rainfall zones and bottomland catenal position (Chapter 3 and 4). Various studies found harvesting to be driven by the demand of human population density (Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). Harvesting intensity was low in the high rainfall zone and in the upland catenal position (Chapter 3 and 4). The low density of human population surrounding the high rainfall zone is possibly why the harvesting of this area is lower than that of the low and medium rainfall zone.

5.5.3 Difference in species composition between environmental variables (rainfall zone, catenal position and harvesting intensity) over time

During this study, it was found that the influence of time on species composition was small to none when compared to the influence of rainfall zones, catenal positions and harvesting intensity. The specie composition for large trees in 2013_{28} was different from those in 2011_{28} and 2012_{28} as was the species composition in 2012_{56} different from those in 2012_{56}. The species composition for small trees in 2011_{28} was different from those in 2012_{28} and 2013_{28} as was the species composition in 2012_{56} different from those in 2012_{56}. The

species composition for all tress in 2011_{28} was again different from those in 2012_{28} and 2013_{28} as was the species composition in 2012_{56} different from those in 2012_{56}.

Differences in vegetation structure and composition of savannas are not only driven by environmental variables but also by different land use practices (Colgan *et al.* 2012; Fisher *et al.* 2011; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Kanniah *et al.* 2010; Shackleton *et al.* 1994; Shackleton 1993; Witkowski and O'Connor 1996). In order to see change in species structure, short time periods are sufficient (Chapter 2 and 3) but for change in composition, a longer time period is needed. Shackleton (1993) found that change in vegetation structure occurs before the change in species composition. These results of Shackleton (1993) were similar to those of this study. Even though differences were seen in species composition between the different years and different sample sizes, a longer time frame is required to see significant change in species composition.

5.6 CONCLUSION

In conclusion, I was able to establish that both rainfall and catenal position had a larger influence on the species composition than harvesting intensity. Also, I established that while species compositions were different in response to these environmental drivers, they showed little or no change over the three year time span of the study. Species composition did not change substantially over the three survey years, as substantial change takes time to occur, a longer time period is required in order to see change in structure and species composition.

Future studies should try establishing longer time periods in order to establish change in species composition. By establishing a long term monitoring program, the research would be valuable not only to the science community but might be vital to help manage available resources in a sustainable way and thus ensuring the future to a vast number of individuals who are dependent on the resources provided by their surrounding environment. Future studies should also incorporate more environmental and human population variables in similar multivariate analyses in order to better determine the drivers of species composition change. Other possible drivers to include in future studies are grazing, fire, distance from village, distance from roads and soil composition. This will help in understanding the variation seen within the vegetation within these rangelands.

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APPENDIX 1

Appendix 1 Key to species abbreviations used in CCA diagrams for both large and small tree data sets across the three survey years. First three letters in an abbreviation refers to the genus name and second three letters refers to the species name.

Abreviation	**Species name**
Aca bur	*Acacia burkei*
Aca caf	*Acacia caffra*
Aca exu	*Acacia exuvialis*
Aca ger	*Acacia gerrardii*
Aca kar	*Acacia karroo*
Aca nat	*Acacia natalitia*
Aca nig	*Acacia nigrescens*
Aca rob	*Acacia robusta*
Aca gra	*Acacia grandicornuta*
Alb har	*Albizia harveyi*
Alb ver	*Albizia versicolor*
Ann sen	*Annona senegalensis*
Ant ven	*Antidesma venosum*
Bal mau	*Balanites maughamii*
Ber dis	*Berchemia discolour*
Ber zey	*Berchemia zeyheri*
Bol spe	*Bolusanthus speciosus*
Bau gal	*Bauhinia galpinii*
Car edu	*Carissa edulis*
Cat spi	*Catunaregam spinosa*
Cis cor	*Cissus cornifolia*
Cle gla	*Clerodendrum glabrum*
Cod rud	*Coddia rudis*
Com afr	*Commiphora Africana*
Com api	*Combretum apiculatum*
Com col	*Combretum collinum*
Com her	*Combretum hereroense*
Com imb	*Combretum imberbe*
Com mol	*Combretum molle*
Com zey	*Combretum zeyheri*
Cor mon	*Cordia monoica*
Dal mel	*Dalbergia melanoxylon*
Dic cin	*Dichrostachys cinerea*
Dio lyc	*Diospyros lycioides*
Dio mes	*Diospyros mespiliformis*
Dio spi	*Diospyros spinosa*
Dio why	*Diospyros whyteana*
Dod ang	*Dodonaea angustifolia*
Dom rot	*Dombeya rotundifolia*
Ehr amo	*Ehretia amoena*

Ehr obt	*Ehretia obtusifolia*
Ehr rig	*Ehretia rigida*
Ela tra	*Elaeodendron transvaalense*
Euc div	*Euclea divinorum*
Euc nat	*Euclea natalensis*
Euc und	*Euclea undulata*
Euc cri	*Euclea crispa*
Fau sal	*Faurea saligna*
Fic bur	*Ficus burkei*
Fic pet	*Ficus petersii*
Fic stu	*Ficus stuhlmannii*
Fla ind	*Flacourtia indica*
Flu vir	*Flueggea virosa*
Gre bic	*Grewia bicolor*
Gre mon	*Grewia monticola*
Gre flava	*Grewia flava*
Gre flavescens	*Grewia flavescens*
Gym bux	*Gymnosporia buxifolia*
Gym sen	*Gymnosporia senegalensis*
Gym gla	*Gymnosporia glaucophylla*
Het nat	*Heteropyxis natalensis*
Lan cam	*Lantana camara*
Lan dis	*Lannea discolor*
Lan sch	*Lannea schweinfurthii*
Mar dis	*Margaritaria discoidea*
Mun ser	*Mundulea sericea*
Mys aet	*Mystroxylon aethiopicum*
Och nat	*Ochna natalitia*
Orm tri	*Ormocarpum trichocarpum*
Ozo sph	*Ozoroa sphaerocarpa*
Pap cap	*Pappea capensis*
Par cur	*Parinari curatellifolia*
Pav sch	*Pavetta schumanniana*
Pel afr	*Peltophorum africanum*
Phi vio	*Philenoptera violacea*
Phy ret	*Phyllanthus reticulatus*
Phy vil	*Phylica villosa*
Pil tho	*Piliostigma thonningii*
Pse map	*Pseudolachnostylis maprouneifolia*
Psi gua	*Psidium guajava*
Pte ang	*Pterocarpus angolensis*
Pte rot	*Pterocarpus rotundifolius*
Rhu gue	*Rhus gueinzii*
Rhu pen	*Rhus pentheri*
Rhu reh	*Rhus rehmanniana*
Rhu spp	*Rhus spp*

Rhu tra	*Rhus transvaalensis*
Rot fis	*Rothmannia fischeri*
Sap int	*Sapium integerrimum*
Sch bra	*Schotia brachypetala*
Scl bir	*Sclerocarya birrea*
Sco mun	*Scolopia mundii*
Sco zey	*Scolopia zeyheri*
Sen pet	*Senna petersiana*
Spi afr	*Spirostachys africana*
Str mad	*Strychnos madagascariensis*
Str spi	*Strychnos spinosa*
Ter ser	*Terminalia sericea*
Tri cap	*Tricalysia capensis*
Tri eme	*Trichilia emetica*
Tri lan	*Tricalysia lanceolata*
Tur nil	*Turraea nilotica*
Van inf	*Vangueria infausta*
Ver col	*Vernonia colorata*
Xim caf	*Ximenia caffra*
Zan cap	*Zanthoxylum capense*
Ziz muc	*Ziziphus mucronata*

6 CHAPTER 6: SYNTHESIS AND CONCLUSION

6.1 INTRODUCTION

As over one-third of South Africa's surface area is covered by savanna woodlands, their existence is highly important to both humans and biodiversity (Grace *et al.* 2006; Hassler *et al.* 2010; Hejcmanova *et al.* 2009; Higgins *et al.* 2007; Kanniah *et al.* 2010; Low and Rebelo 1996; Mucina and Rutherford 2006; Scholes and Archer 1997; Scholes and Walker 1993). The vegetation composition and structure of savannas are determined by precipitation, fire regime, soil type and herbivory (Belsky 1990; Colgan *et al.* 2012; Fisher *et al.* 2009; Govender *et al.* 2006; Hassler *et al.* 2010; Hejcmanova *et al.* 2009; Le Roux and Bariac 1998; Sankaran *et al.* 2005; Scholes and Archer 1997; Scholes and Walker 1993; Wessels *et al.* 2011; Witkowski and O'Connor 1996). In addition to these environmental factors, the practice of different land uses is another major determinant of savanna structure and composition (Fairbanks 2004; Higgins *et al.* 1999; Kalema and Witkowski 2012; Scholes and Archer 1997). Land use, such as the uses of communal rangelands, is a major driver of change in the structure and composition of savannas (Breshears and Barnes 1999; Fisher *et al.* 2011; Gilson *et al.*, 2003; Higgins *et al.*, 1999; Kristensen and Lykke 2003; Neke *et al*. 2006). The vegetation in the communal rangelands plays a vital role in the livelihoods of the majority of rural communities throughout South Africa, through the range of resources and services that they provide (Dovie *et al.* 2002; 2003; 2004; 2006; Giannecchini *et al.* 2007; Pote et al. 2006; Shackleton and Shackleton 2004; Shackleton *et al.* 2005; Twine *et al.* 2003; Twine 2005; Williams and Shackleton 2002).

The aim of this study was to determine the individual and interactive influences of rainfall and catenal position on woody vegetation composition and structure across time (2011-2013), in human-impacted woodlands. The overall findings clearly show that both environmental and anthropogenic influences are important if one is to assess differences in woody vegetation structure and composition across gradients and over time (Fig 6.1). Various other studies have also found that both environmental and anthropogenic determinants can individually and in combination result in changes in the species composition and structure of savannas (Breshears and Barnes 1999; Colgan *et al.* 2012; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Shackleton *et al.* 1994; Shackleton 1999; Wessels *et al.* 2013; Witkowski and O'Connor 1996).

6.2 INFLUENCE OF ENVIRONMENTAL AND ANTHROPOGEIC VARIABLES

Numerous differences were found in the woody vegetation structure and composition between the three rainfall zones (low, medium, high), as well as smaller differences in the numbers and species selection of recently harvested trees (Fig 6.1). The results of this study show that when comparing across time between rainfall zones, the densities, species richness, Shannon's, Simpson's diversity and evenness, were higher in the high rainfall zone than in the low and medium rainfall zones (Chapter 2-4). The species composition in the high rainfall zone was also different compared to the low and medium rainfall zones (Chapter 4 and 5). Unlike the rainfall zones, catenal position was found to have little or no significant influence on vegetation structure, species richness and diversity or on the amount of recent tree harvesting (Fig 6.1). This study also showed that when comparing the densities, species richness, Shannon's, Simpson's diversity and evenness over time between catenal positions, there were no difference between uplands and bottomlands (Chapter 2-4). Even with there being no difference in density, structure, species richness, diversity or harvesting intensity, the species composition did however differ between uplands and bottomlands. The bottomlands had more abundant fine-leaved species and the uplands had more abundant broad-leaved species (Chapter 5). Harvesting in general had an influence on the change of both vegetation structure and composition and similarly, so did vegetation structure and composition have an influence on harvesting (Fig 6.1). This study showed that the intensity of harvesting increased for large trees over time, whereas small trees did not show any change over time. The most harvested trees were between 0.6-4m in height and 1.1-10cm in stem diameter (Chapter 3). A greater species richness and diversity of harvested trees were observed in 2013 when compared to 2011 and 2012. Large tree species that were most harvested comprised *Combretum collinum, Acacia gerrardii*, *T. sericea, Acacia robusta, Combretum zeyheri* and *S. birrea,* whereas small trees comprised *D. cinerea, T. sericea, A. exuvialis* and *C. hereroense* (Chapter 4). This study also found that harvesting intensity was similar between uplands and bottomlands, but higher in the low and medium rainfall zones than in the high rainfall zone. (Chapter 3-5).

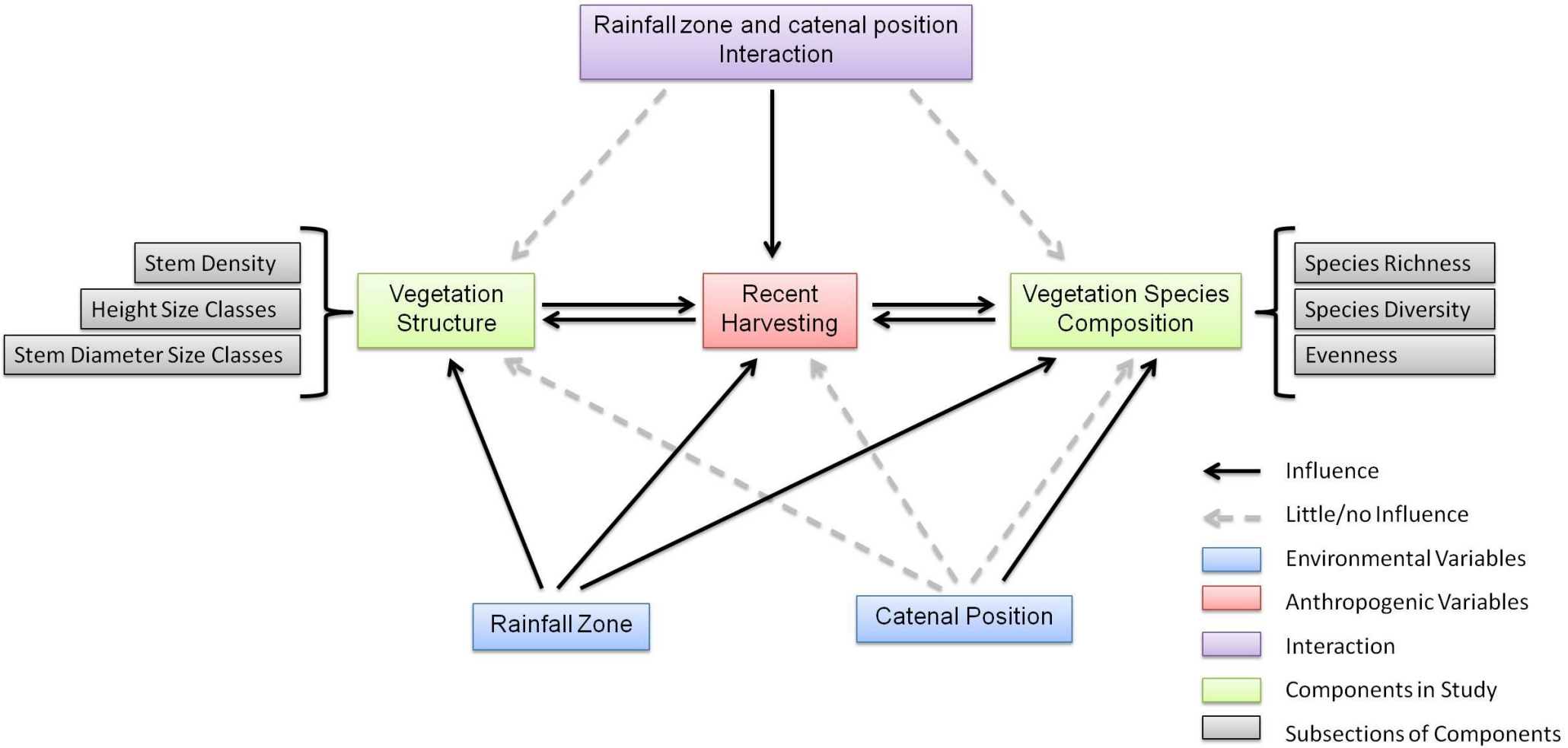


Figure 6.1. Flow diagram showing the breakdown of the components in the study, as well as the influences of rainfall zones (low, medium, high), catenal position (upland, bottomlands), harvesting and the interactions between them. Solid arrows indicate influences and dashed line indicates little or no influence during the study period.

6.2.1 Rainfall zones

Woody vegetation density and structure (Chapter 2 and 3) as well as species composition (Chapter 4 and 5) were clearly different between rainfall zones (Fig 6.1). The high rainfall zone had higher stem densities and higher tree abundance than the low and medium rainfall zones (Chapter 2 and 3). This links in to the findings of Sankaran *et al.* (2005), Shackleton and Scholes (2011) and Smith and Goodman (1986) stating that density and abundance of trees are influenced by water availability. Shackleton and Scholes (2011) also found that the stem diameter, height of trees, and number of species all increased with the increased in available water. The high rainfall zone was also found to have a different species composition when compared to that of the other two rainfall zones (Chapter 5). The mean species richness at the plot levels was also found to be higher in the high (8.3 species/plot for large and 21.2 species/plot for small trees) rainfall zone when compared to the low (4.3 and 9 species/plot, respectively) and medium (4.2 and 17.3 species/plot, respectively) rainfall zones (Chapter 4). This again agrees with the literature that rainfall does influence species richness (Buitenwerf *et al.* 2012; Kanniah *et al.* 2010; Sankaran *et al.* 2005; Shackleton and Scholes 2011; Smith and Goodman 1986).

6.2.2 Catenal position

Unlike the rainfall zones, catenal position was found to have little to no significant influence on either vegetation structure (Chapter 2 and 3) or species richness, diversity and evenness (Chapter 4) (Fig 6.1). Catenal position did however differ in the species composition between uplands and bottomlands (Chapter 5) (Fig 6.1). As the soil differs between uplands and bottomlands, the difference in species composition (Chapter 5) was expected (Colgan *et al.* 2012; Fisher *et al.* 2009; Fisher *et al.* 2011; Khomo *et al.* 2011; Shackleton 1999; Wessels *et al.* 2011; Witkowski and O'Connor 1996). The study found that even with there being no difference in density, structure, species richness, diversity or harvesting intensity (Chapter 2-4), the species composition did however differ between uplands and bottomlands (Chapter 5). Vegetation composition changes along the catena from a predominantly broad-leaf species composition to a predominantly fine-leaf species composition with a visible seep line in between, with a fringe of *T. sericea* on the upland edge (Colgan *et al.* 2012). This difference in species composition could be attributed to the different availability of moisture and nutrients (Fisher *et al.* 2011; Shackleton 1999; Wessels *et al.* 2011). Shackleton (1999) and Colgan *et al.* (2012) found soil properties associated with catenal position, such as texture or particle size is often the primary determinant of infiltration rates and water retention and tends to have an effect on the vegetation structure.

Bottomlands generally have greater soil moisture but reduced availability due to the higher clay content whereas the uplands have lower soil moisture but higher availability due to the lower clay content (Colgan *et al.* 2012; Shackleton 1999). The coarse-textured soils in uplands allow trees access to the through flow whereas the bottomlands with higher clay content is often dominated by overland flow instead of through flow (Colgan *et al.* 2012).

6.2.3 Recent harvesting

Harvesting in general had an influence on differences in both vegetation structure (Chapter 2 and 3) and composition Chapter 4 and 5) and similarly, so did vegetation structure and composition have an influence on harvesting (Fig 6.1). Various studies have attributed differences in woody vegetation structure and composition to the different land uses (Breshears and Barnes 1999; Colgan *et al.* 2012; Fairbanks 2004; Fisher *et al.* 2011; Gilson *et al.* 2003; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Scholes and Archer 1997; Shackleton *et al.* 1994; Shackleton 1999; Witkowski and O'Connor 1996).

The recent harvesting was found to be increasing in the larger trees. As the demand for fuelwood is often determined by the human population size that uses the resource, the increase in harvesting can be attributed to the increase in population density which results in a higher requirement for fuelwood (Banks *et al.* 1996; Coetzer *et al.* 2010; Fisher *et al.* 2011; Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton 2004). Various studies (Giannecchini *et al*. 2007; Shackleton 1993; Twine *et al.* 2003) state that the lack of harvesting of large fruit-bearing species is due to the local law that forbids it. However, Kirkland *et al.* (2007) found that most people, who harvest large fruit-bearing trees, do not respect or abide the local laws, or the traditional authorities are unable to implement it. Another possible reason in the increase in harvesting of large trees is due to the development of rural and urban fuelwood markets (Madubansi and Shackleton 2007; Matsika *et al.* 2013a; Shackleton *et al.* 2006). With the increase in human population size, and the scarcity of fuelwood from surrounding rangelands, the existence of fuelwood markets is fast becoming a part of daily live as it ensures fuelwood for daily usage such as cooking. Rural households are increasingly buying more fuelwood due to the shortage of dead wood within surrounding rangelands (Madubansi and Shackleton 2007; Matsika *et al.* 2013a). Harvesting for fuelwood markets are often on a large scale, as harvesters have access to motor-vehicles and mechanized equipment (Matsika *et al.* 2013a; Shackleton *et al.* 2006). This type of harvesting allows for larger, live trees to be harvested (Matsika *et al.* 2013a; Shackleton *et al.* 2006).

The rate of demand and the rate of reproduction through coppice regrowth seem to be stable. The harvesting on small trees did not increase. This is possibly due to the production of coppice. The harvesting of fuelwood has an impact on the ecosystem (Jurisch *et al.* 2012; Pote et al. 2006; Shackleton *et al.* 2007). The most noticeable change at community level is the change in physiognomy by the removal of certain size classes and the increased production of coppice regrowth (Higgins *et al.* 1999; Twine 2005). The structure of the most utilised species populations has become characterised by a decline in large mature stems and an increased abundance of smaller stems (Jurisch *et al*. 2012; Higgins *et al.* 1999; Kaschula *et al.* 2005; Twine 2005). Harvesting and resprouting results in sexually mature individuals reverting to a functionally juvenile growth phase (Kaschula *et al.* 2005; Twine 2005). The reverting back to a juvenile growth phase reduces the production of seed by mature trees (Kaschula *et al.* 2005; Twine 2005). Most savanna tree species have the ability to produce coppice regrowth if stems are damaged or killed (Kaschula *et al.* 2005; Neke *et al.* 2006, Twine 2005). The removal of stems alleviates some of the impacts of fuelwood harvesting by producing coppice regrowth (Twine 2005). The increased cutting of live stems and widespread coppice regrowth has changed the tree morphology of many woody species (Higgins *et al.* 1999; Twine 2005).

Recent harvesting was more common among trees below 2m in height and trees with stems of 1.1-10cm in diameter. The preference for particular stem sizes that are harvested is dependent on the use of the harvested wood (Shackleton 2001). The preferred harvested stem size is also dependent on ease of transport. For example, for fuelwood, carrying bundles on foot (usually headloads) that are used for daily cooking and heating needs, the smaller stems are preferred (Dovie *et al*. 2004; Neke *et al.* 2006; Van Gelder *et al*. 1983). The influence of harvesting on species richness and diversity was mainly in the areas where harvesting intensity was high. The increase in harvested species richness of the large trees was mainly due to the increase in harvesting over time from 2011 to 2013. The more consistent rate of harvesting on small trees between years resulted in no changes in species richness and diversity over time.

6.3 CONCLUSION AND RECOMMENDATIONS

In conclusion, monitoring of woody vegetation structure and composition will ensure that changes over time and differences between environmental and/or anthropogenic disturbances are detected. This study found that woody vegetation structure and composition were more different between rainfall zones than between catenal positions. It also found harvesting did have a small influence on changes in both woody vegetation structure and

composition. It can thus be concluded that as far an environmental/disturbance factors are concerned, rainfall zones >> harvesting ≥ catenal position on overall composition and structure of these communal woodlands. These findings coincide with the results of various other studies, as both environmental and anthropogenic determinants are important for monitoring change in vegetation composition and structure (Colgan *et al.* 2012; Fairbanks 2004; Fisher *et al.* 2011; Gilson *et al.* 2003; Godínez-Alvarezv *et al.* 2009; Hejcmanova *et al.* 2009; Higgins *et al.* 1999; Jurisch *et al.* 2012; Kanniah *et al.* 2010; Kristensen and Lykke 2003; Scholes and Archer 1997; Shackleton *et al.* 1994; Shackleton 1999; Witkowski and O'Connor 1996).

These data were collected for a larger long-term monitoring project (SUCSES), and the real value of these results is the usefulness for monitoring purposes. As vegetation structure and composition are seen as two of the most commonly used indicators in many ecosystems, the results of this study are of great interest for the future of the rangelands as well as for the future of natural resources (Godínez-Alvarezv *et al.* 2009). Monitoring will not only allow for possible future improved management of these natural resources, but it also allows for the communities to get involved in protecting the resources which are so vital for their daily living.

In terms of future studies, I put forward the following recommendations:

- Future monitoring is necessary in order to determine which of the environmental and anthropogenic determinants plays a larger part in the changes seen over time in the woody vegetation. Additional determinants such as geology, grazing, fire and temperature (climate), need to be included as well.
- The data collected during the survey of these sampling areas, should be incorporated with LiDAR data (if available) in order to supplement the LiDAR data in the <2m height structure.
- Future studies should also sample sites in the cultivated fields and yards of the surrounding villages. In this way, trees occurring in a "semi-protected" area can also be monitored. This will allow us to establish whether these trees are more "protected" as they are essentially "owned" by someone.
- A greater focus on individual species is also needed if one is to establish how harvesting influences the change in woody vegetation composition and structure in more depth.

- Large trees and also “rare” or “important” (for use or as indicator) species should ideally be GPS tagged in order to monitor more adequately what is happening to the large trees within these rangelands, as some members of the community do not appear to respect the local traditional law that forbids harvesting of large, living fruit-bearing trees.
- Having a sampling design that allows for the combining of large and small trees for analysis of species diversity, will make a large difference in obtaining a conclusive result. In the case of this study, large trees and small trees had to be analysed separately in most of the analyses.
- Finally, a sampling size must be selected that’s large enough to cover the variation within these rangelands. During this study, the sample size was increased from the original 28 plots to 56 plots. This did present some difficulties as the results suggested differences which could be questioned as being merely an effect of the increase in tree abundance due to the increase in sample size.
- The implications of this study will be useful for future management of natural resources and should thus be incorporated with local knowledge to establish what species are preferred and the usage of these species can then be determined and monitored.

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