SELECTED KEY ECOSYSTEM SERVICES, FUNCTIONS, AND THE RELATIONSHIP WITH BIODIVERSITY IN NATURAL FOREST ECOSYSTEMS

by
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DECLARATION

I declare that the research reported in this thesis, submitted for the degree of Doctor of Philosophy in Forestry at the University of Stellenbosch, is the result of my own original research, except where otherwise indicated. This thesis has not been submitted for any degree or examination at any other university.

December 2016, Sylvanus Mensah

ABSTRACT

Ecosystem services (ES) are the benefits people obtain from ecosystems. Biodiversity is a relevant component in this context, as it supports most ecosystem functions. The worldwide decline in natural ecosystem biodiversity and degradation of ecosystems will likely limit the opportunities to improve the services provided if an explicit focus is not put on their maintenance and improvement in future management decisions. This thesis aims at contributing to the knowledge base of ES provision and its relation with biodiversity in South African Mistbelt forests.

First, a socio-empirical study was conducted with households from different localities in Limpopo province to assess the relative importance and use of ES by local population. Questionnaires, descriptive rank analysis, logistic regressions and Poisson mixed effect models were used. Results revealed that provisioning and supporting ES (timber and firewood, edible plants and honey) were the most important, and that age, gender, income as well as prior recreational experiences played important roles in respondents' perceptions. "Timber and firewood" and "honey" were selected for further investigation in Mistbelt natural forests in Limpopo.

Second, the potential of Mistbelt forests as foraging habitat for managed honey bees, and as tree biomass and carbon sinks was investigated. Forest inventory was conducted to collect data on woody plant species (plant density, diameter, total height, pollen and nectar values of honey bee plant species; branch and wood core samples, leaf area, plant maximum height).

The diversity of honey bee plant species, temporal availability of honey bee forage and relationship of plant diversity with forage production, were explored, using descriptive analysis and general linear models. As results, 48% of the woody plant species recorded in the inventory were honey bee plant species. The highest potential of forage supply was observed during the last quarter of the year. Bee plant species richness, not overall plant richness, showed the greater effect on forage provision.

New multispecies biomass models were established and used to estimate aboveground biomass and carbon stocks, and examine the relationship of aboveground carbon with tree species diversity and structural variables. Allometric models with "DBH^2xH" were the best fitting. Biomass and carbon stand values of 358.1 Mg ha^{-1} and 179.0 Mg ha^{-1}, respectively, were obtained. Basal area of most important species, and of largest trees, as well as plant richness were positively correlated with carbon stock.

The relationship of biomass and carbon stock with biodiversity components was the final focus. An analysis scrutinised the effects of taxonomic diversity on carbon storage. Correlations were explored through functional traits-based diversity and dominance, using structural equation and linear mixed-effects models. Results showed that taxonomic diversity effects on carbon stock were positive, and mediated by functional diversity and functional dominance. The effects, however, were greater for functional diversity than for functional dominance.

In sum, a novel contribution was made to the ES provision of South African Mistbelt forests, which provides a base for the assessment of these forests and their contribution and underpins the need to protect these ecosystems as a natural heritage.

OPSOMMING

Ekostelsel dienste (ED) is voordele vir menselike gebruik wat verkry word uit ekostelsels. In hierdie konteks, is biodiversiteit ʼn relevante komponent, aangesien dit ondersteuning verleen aan verskeie ekostelseldienste. Die wêreldwye afname in natuurlike- ekostelsel biodiversiteit en die agteruitgang van ekostelsels sal moontlik die geleenthede beperk om die dienste te verbeter, indien instandhouding en verbetering nie ʼn prioriteit is in toekomstige bestuursbesluite nie. Die doel van hierdie tesis is om ʼn bydra te lewer tot die basiese kennis van ED voorsiening en die verwantskap tussen ED en biodiversiteit in Suid-Afrikaanse Afromontaan woude.

Eerstens is ʼn sosio-empiriese studie uitgevoer onder plaaslike huishoudings verspreid oor die Limpopo provinsie om die behoefte en gebruik van ED deur die bevolking te assesseer. Daar is van vraelyste, ʼn beskrywende rangontleding, logistiese regressie en Poisson-gemengde-effek modelle gebruik gemaak. Die resultate het getoon dat die voorsienende-en ondersteunende-ED (hout en vuurmaakhout, eetbare plante en heuning) die belangrikste was en dat ouderdom, geslag, inkomste en vorige ervarings ʼn belangrike rol gespeel het in die respondente se terugvoer. Die “hout en vuurmaakhout” en “heuning” veranderlikes is gekies vir verdere ondersoek.

Tweedens is daar ondersoek ingestel om die potensiaal van Misgordel woude om byeplase van voeding te voorsien te evalueer, asook die potensiaal vir die gebruik van Misgordel woude as ʼn bron van boom biomassa en die vermoë van die woud om as ʼn koolstofstoor op te berg.

Bosopmetings is uitgevoer op houtagtige plantspesies om die volgende inligting te bekom: plantdigtheid, boomdeursnee, totale hoogte, stuifmeel en nektar waardes vir heuningby plantspesies; tak en kernhout monsters, blaaroppervlakte en maksimum plant hoogte. Die diversiteit van plant spesies wat deur bye benut word, tydelike beskikbaarheid van heuningby voer en die verhouding tussen plantdiversiteit en voerproduksie is ondersoek. Lineêre modelle en beskrywende statistiek is gebruik. Resultate het getoon dat 48% van die opgetekende houtagtige plant spesies deur bye benut word. Die grootste voerpotensiaal was tydens die laaste kwartaal van die jaar waargeneem.

Nuut geformuleerde multispesie biomassa modelle is gebruik om die bogrondse biomassa en koolstofvoorraade te bereken, asook om die verhouding tussen bogrondse koolstof opberging met boomspesie diversiteit en strukturele veranderlikes te ondersoek. Allometriese modelle met “DBH^{2}xH” was die mees geskikte modelle. Waardes vir biomassa en koolstofinhoud van die opstand was 358.1 Mg ha^{-1} en 179.0 Mg ha^{-1} onderskeidelik. Die basale-oppervlakte van die belangrikste en die grootste bome, asook plant spesie diversiteit het positief gekorreleer met die koolstofvoorraade.

Laastens is die verhouding tussen biomassa en koolstofvoorraade met die biodiversiteit komponente ondersoek. Korrelasies is ondersoek deur die integrasie van funksionele diversiteit en dominansie in strukturele en lineêre gemengde-effek-modelle. Resultate het bewys dat die effek van taksonomiese diversiteit op die koolstofstoorvermoë positief is en dat dit deur funksionele diversiteit en funksionele dominansie bepaal word. Die effekte was meer beduidend vir funksionele diversiteit.

Ten slotte, is ŉ nuwe bydrae gemaak tot die voorsiening van ED in Afromontaan woude. Dit dien as ŉ basis vir die assessering van hierdie woude en hulle bydrae, en dit ondersteun die noodsaaklikheid om hierdie ekostelsels as ŉ natuurlike erfenis te beskerm.

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LIST OF ORIGINAL ARTICLES PUBLISHED AND IN REVIEW

This thesis is based on the following research articles (published and in review):

1. Mensah S, Veldtman R, Assogbadjo A, Cori H, Glèlè Kakaï R & Seifert T (2016). Ecosystem service importance and use vary with socio-environmental factors: a case study from household-surveys in local communities of South Africa. Ecosystem Services http://dx.doi.org/10.1016/j.ecoser.2016.10.018

2. Mensah S, Veldtman R, & Seifert T. Potential supply of foraging resources to managed honey bees – identification of key variables affecting forage provision in a natural forest. (In review)

3. Mensah S, Veldtman R, & Seifert T (2016). Allometric Models for Height and Above Ground Biomass of Dominant Tree Species in South African Mistbelt Forests. Southern Forests 79; http://dx.doi.org/10.2989/20702620.2016.1225187

4. Mensah S, Veldtman R, du Toit B, Glèlè Kakaï R & Seifert T (2016). Aboveground biomass and carbon in a South African Mistbelt forest, and the relationship with tree species diversity and forest structures. Forests 7(4) 79; http://dx.doi.org/10.3390/f7040079

5. Mensah S, Glèlè Kakaï R & Seifert T (2016). Patterns of biomass allocation between foliage and woody structure: the effects of tree size and specific functional traits. Annals of Forest Research 59 (1): 49-60, http://dx.doi.org/10.15287/afr.2016.458

6. Mensah S, Veldtman R, Assogbadjo A, Glèlè Kakaï R & Seifert T (2016). Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. Ecology & Evolution, http://dx.doi.org/10.1002/ece3.2525

AUTHOR´S CONTRIBUTION

Sylvanus Mensah, Ruan Veldtman and Thomas Seifert jointly designed the methodology for this project. Sylvanus Mensah collected and analysed the data, and wrote all the articles of this thesis with editorial support of Ruan Veldtman, Thomas Seifert, Assogbadjo Achille and Ben du Toit, and further statistical assistance from Romain Glèlè Kakaï. Chapter 1 (Introduction) and Chapter 7 (Conclusion) were written by Sylvanus Mensah, with the editorial support of Thomas Seifert and Ruan Veldtman.

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Chapter 1. General introduction

This chapter introduces the reader to the terms that are central to this thesis. It provides a brief description of the concepts of ecosystem services, ecosystem functions and biodiversity. It also presents the state of knowledge on important links between biodiversity, ecosystem functions and ecosystem services. A brief overview of the current status of South African forestry with regards to natural forests is given. It finally outlines the research objectives, research questions and provides some guidance on the contents of other chapters of this thesis.

1.1. Background

1.1.1. Ecosystem services as a concept

A large proportion of the world's ecosystems have been modified to meet the increasing basic demands for food fibre and energy (Foley et al. 2005). More than 50% of the world's ecosystems are being over-exploited or used unsustainably to maximise a limited number of benefits in the short term (Verburg et al. 2013). In the meantime, biodiversity loss has become inevitably the concern of the century, as every year, fractions of natural ecosystems are lost as result of agricultural intensification, deforestation and degradation (Ellis and Ramankutty 2008; Chirwa et al. 2015). This poses a true threat since it is assumed that biodiversity forms the base for several benefits from ecosystems, by supporting ecosystem functioning. Therefore, a loss of biodiversity would not only represent an irreversible loss of species, but also directly threaten human well-being by affecting key ecosystem services.

The current trend in sustainable management that provides an acceptable compromise for policy makers, scientists and stakeholders at different scales, is to approach agricultural intensification and land management in general, in a way to conserve biodiversity and ecosystem functions for a sustainable provision of multiple ecosystem services (MEA 2005; TEEB 2011). In this context three concepts are of specific importance: "biodiversity", "ecosystem functions" and "ecosystem services".

The Convention on Biological Diversity defines biodiversity as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (CBD 1992). Commonly, biodiversity is measured as richness and evenness (Magurran 1988); richness refers to the number of unique life forms while evenness refers to the equitability among life forms (Cardinale et al. 2012).

Ecosystem functions are the natural or ecological processes (biological, geochemical, physical) that control the exchanges and fluxes of energy, nutrients and organic matter in an ecosystem

(Cardinale et al. 2012). An example of an ecosystem function includes nutrient cycling, which is the process by which biologically essential nutrients are captured, released and then recaptured (Lavelle et al. 2005; Cardinale et al. 2012). There are several other ecosystem functions that play important roles such as primary production, plant growth, carbon storage, trophic regulation, parasite suppression and pollination (Díaz and Cabido 2001; Şekercioğlu 2010).

Ecosystem services (ESs; Figure 1.1) represent a human centred perspective on ecosystems and nature by defining benefits that humans derive from nature (MEA 2005). The Millennium Ecosystem Assessment (MEA) has identified four categories of ESs, which are: provisioning services, regulating services, supporting services and cultural services. The provisioning ESs are the physical goods for direct human use; for example, medicinal resources (plants), indigenous fruits and edible plants, which can be harvested from forest ecosystems for direct consumption. Timber falls in that category as it can also be harvested directly. The regulating ESs are benefits from ecosystem processes, and include local climate and air quality regulation, global climate regulation through carbon storage, erosion control, water purification and pollination (de Groot et al. 2002; MEA 2005). Regulating ES can also contribute to mitigate extreme events and are also sources of biological control by regulating pests and vector borne diseases that affect crops, livestock and people (TEEB 2011). Cultural ESs enhance the quality of human life and consist of non-material benefits from recreation, tourism, spiritual experience, aesthetic experiences, cognitive development. Supporting ESs are the services that form the foundation of the basic life-support processes. They also underpin almost all other ESs. These include the maintenance of biodiversity and genetic diversity and habitats for presence and survivorship of individual plants and animals (TEEB 2011).

Sustainable management of ecosystem services requires an understanding of their importance to the involved stakeholders and of the contribution of land use to the provision of these services, since the spatial and sociological contexts matter (Castro et al. 2013; Cuni-Sanchez et al. 2016). Understanding the importance of ecosystem services to people is a significant aspect of ESs assessment (Castro et al. 2013), likely because these services only “exist” if these people are benefiting from them. A point to consider in this context is that the delivery of an ecosystem service, although contributing to the well-being of the people, may not guarantee optimal use, because different people gain benefits from these services in different ways, according to their access to these resources and what value they place on its judicious management (Hein et al. 2006; Kozak et al. 2011). The concept of ES is being used as a way to inform and support landscape management. However, most studies have been oriented towards ecosystems’ potential to supply services and economic value (Burkhard et al. 2012; Costanza et al. 1997; Maes et al. 2012; Ninan and Inoue 2013; Seppelt et al. 2011; Xie et al. 2010). Very few studies have approached the demand side of ES, leading to a scarcity of information on the social aspect of ecosystem services assessment (Geijzendorffer and Roche 2014; Villamagna et al. 2013). The social perception towards ecosystem services is relevant in order to identify not only the most important or relevant services to people, but also the trade-off between ecosystem services (Martín-López et al. 2012; Meijaard et al. 2013).

Figure 1.1. Ecosystem services diagram, source: metrovancouver.org

1.1.2. Links between biodiversity, ecosystems functions and services

The role of biodiversity in ecosystem delivery has been increasingly debated in the past years, and one of the key points to strengthen the argument for biodiversity conservation is to support and implement the ecosystem services framework (MEA 2005; TEEB 2011). The framework provides a starting point for defining, monitoring and valuing ESs. It also helps to increase awareness of the importance of conserving biodiversity, natural habitats and ecosystems. To date, much research effort has gone into biodiversity and ecosystem services (Balvanera et al. 2014; Cardinale et al. 2012; Isbell et al. 2011), and although for some studies, biodiversity was treated as an ecosystem service itself (Egoh et al. 2010, 2009), the general idea that biodiversity in a particular ecosystem sustains most of the services delivered by that ecosystem, is accepted (Isbell et al. 2011; Gamfeldt et al. 2013).

Delivery of ecosystem services relies on ecosystem functioning, and on the extent to which species contribute to that functioning (Gamfeldt et al. 2013). This makes the ecosystem function concept a very complex issue. Currently, two well-debated mechanisms have been offered to explain the role of biodiversity in ecosystem functioning: selection effects or sampling effects (Huston 1997) and niche complementarity/facilitation effects (Hector et al. 1999); the selection effect hypothesis assumes that in ecosystem with higher diversity, there is a higher probability of the occurrence of dominant species or traits that influence ecosystem functioning. The niche complementarity hypothesis suggests that highly diverse ecosystems allow for a greater variety of functional traits and provide opportunities for a more efficient resource utilisation, thereby increasing ecosystem functions. Generally, both niche complementarity and facilitation are lumped together under the term “complementarity effect”, because in practice it is difficult to distinguish between them (Loreau and Hector 2001). An illustrative example of both hypotheses in forest ecosystems is that forest biomass and productivity can increase due to a few highly productive and dominant species (Finegan et al. 2015), or a better performance of all the species present through facilitation and increased resource use efficiency (Forrester and Bauhus 2016).

The ongoing decline of ecosystem service delivery (de Groot et al. 2002; McMichael et al. 2005; Zarandian et al. 2016), coupled with the alarming rate of ecosystem degradation (Achard et al. 2002; Foley et al. 2007; Turner 1996), have placed the issues on the links between biodiversity and ecosystem function and services high on research agendas (Kremen 2005; MEA 2005; Thompson et al. 2011). Understanding these relationships is not only important to support theoretical hypotheses (niche complementarity and selection effects), but also to develop strategies for safeguarding of both biodiversity and ecosystem services (Balvanera et al. 2014; Cardinale et al. 2012).

Over the last two decades, the role of biodiversity in ecosystem functioning and service delivery has been intensively investigated (Cardinale et al. 2012; Naeem and Wright 2003). A meta-analysis by Cardinale et al. (2011) suggested that plant litter diversity enhanced decomposition and recycling of elements after organism death. Another example, and by far the most common of ecosystem functions in plant communities, is stand productivity and/or biomass. Stand biomass has been used as primary productivity in some former studies (Hector et al. 1999; Tilman et al. 1997), however, increment of biomass, basal area or carbon could be appropriate metrics for aboveground biomass productivity (Finegan et al. 2015; Forrester and Bauhus 2016). An analysis of the relationship between mean biomass and gross primary production based on data from Stiling (1996), showed a positive correlation across different forest ecosystems (Figure 1.2), suggesting that biomass can be used as proxy for productivity. Among the biodiversity-productivity relationships described by Mittelbach (2001), only 14% actually measured productivity, and biomass was used as proxy in 34.4% of the studies (Jenkins 2015). In addition, Jenkins (2015) who generally warned against a careless use of biomass to predict productivity, pointed out that log-log productivity-biomass data showed models, suggesting high correlation between productivity and biomass. Yet, most biodiversity and ecosystem function studies based on productivity or biomass, have focussed on natural and experimental grasslands systems (Feßel et al. 2016; Hector et al. 1999; Tilman et al. 1996), mixed temperate forest stands and less diverse forest ecosystems (Paquette and Messier 2011; Ruiz-Jaen and Potvin 2010; Vilà et al. 2013) while comparatively, less effort has gone into tropical natural forests (Barrufol et al. 2013; Con et al. 2013). In grasslands, with some exceptions, however (Adler et al. 2011; Feßel et al. 2016; Šímová et al. 2013), evidence is mounting that increasing biodiversity influences ecosystem functions positively. In contrast, for natural forests, there is little agreement across studies that have examined the relationship between biodiversity and productivity (Seidel et al. 2013).

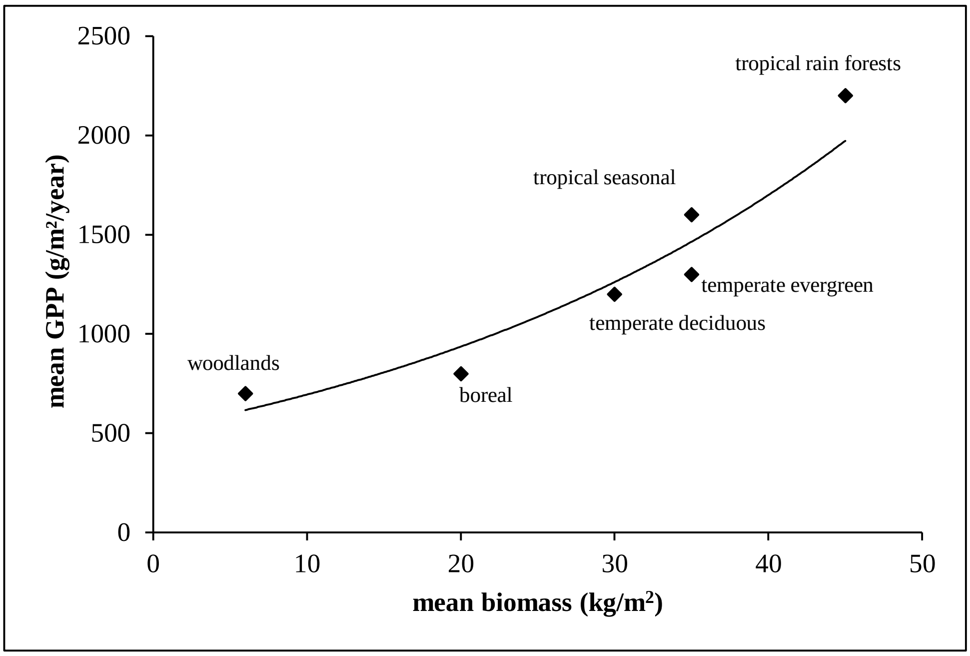

Figure 1.2. Relationship between mean biomass and gross primary production across different forest ecosystems (data from Whittaker cited in Stiling (1996)).

If it is assumed that an increase in plant diversity in forest ecosystems also increases ecosystem functions, and consequently that biodiversity loss has a negative influence on the ecosystem functioning and the services delivered (Balvanera et al. 2006; Cardinale et al. 2012; Gamfeldt et al. 2013), it must be stated that the current understanding of the mechanisms is limited (Paquette and Messier 2011; Ruiz-Jaen and Potvin 2010; Vilà et al. 2013) and many aspects are still subject of the scientific discussion (Balvanera et al. 2014; Lasky et al. 2014). On the one hand, studies on forest ecosystems suggest that productivity as an ecosystem function increases with diversity (Paquette and Messier 2011; Ruiz-Benito et al. 2014; Vilà et al. 2013); but most of these studies were carried out in temperate or boreal forests, which are characterised by rather low number of species (Paquette and Messier 2011; Vilà et al. 2013). On the other hand, studies by Ruiz-Jaen and Potvin (2011) in natural forests of Barro Colorado Island in Central Panama, Szwagrzyk and Gazda (2007) in natural forests of central Europe, and An-ning et al. (2008) in natural forest communities in Northwest China revealed a negative relationship between species diversity and biomass production. Other studies found such relationships non-significant (Gairola et al. 2011). While the controversy of findings, especially in forest ecosystems, may suggest that the mechanisms that drive the biodiversity-ecosystem function relationship may be variable according to the environment, an important conclusion emerging from the available literature is that natural tropical forests are largely under-represented. This is the case, despite the fact that these forests can harbour hundreds of species of different functional traits, and the results from temperate mixed species or less diverse forest ecosystems may not apply to them.

It is also important to mention that, for years, richness (species richness) as a simple measure of biodiversity, has been used to elaborate on the relationship between biodiversity and ecosystem functions. Interest in exploring other measures of biodiversity has only recently emerged (Chalcraft et al. 2009; Con et al. 2013; Lasky et al. 2014; Vance-Chalcraft et al. 2010), and the current trend is to examine how functional diversity, phylogenetic diversity and functional dominance play a major role in ecosystem functioning (Baraloto et al. 2012; Clark et al. 2012; Ouyang et al. 2016; Ruiz-Jaen and Potvin 2011). The functional diversity is known as ‘‘the value and range of functional traits of the organisms present in a given ecosystem’’(Díaz and Cabido 2001, pp 654), and might be more important to predict the functional role of individual species in ecosystem level processes. As pointed out by Mouchet et al. (2010), functional diversity can be used as a proxy to quantify the niche space and the niche differentiation among species, and thus can be used to test the niche complementarity hypothesis. Functional dominance is a measure of the degree to which a functional trait is more dominant than other traits (Figure 1.3); it is commonly used to test dominance patterns and selection effect hypothesis (Cavanaugh et al. 2014; Finegan et al. 2015). Phylogenetic diversity, known as the evolutionary history of a community, has also been proposed to be used to predict ecosystem functions (Cadotte et al. 2008; Cardinale et al. 2015; Srivastava et al. 2012). Understanding whether and how functional diversity, functional dominance and/or phylogenetic diversity transmit the full effects of diversity on ecosystem function will help to answer the question, which mechanism is the more relevant one.

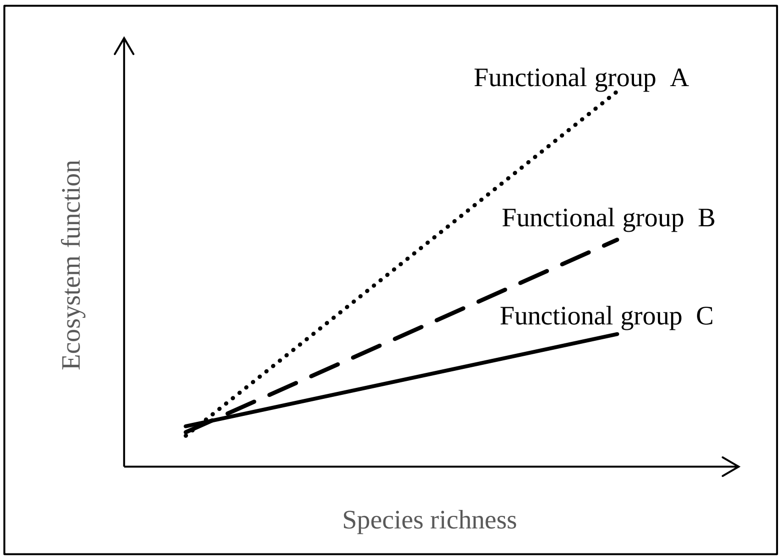

Figure 1.3. Relationship between ecosystem function and species richness for each functional group species. Modified from Figure 1(B) of Wu et al. (2015). It is assumed that species within each functional group are similar in terms of functional traits, while species of different functional groups are different.

In the next section, we gave a brief overview of the current status of South African forestry with regards to the natural forests.

1.2. South Africa's forestry sector

As a global pattern, the ongoing rapid growth of the world population has increased the demand for services that, in turn, have raised the rate of exploitation and degradation of natural forests to the point of diminishing returns (Foley 2005; de Groot and van der Meer 2010). As a subsequent response, forest plantations have been developed to produce wood, fibre and other resources and reduce the threats on natural habitats (Kanninen 2010; Seifert et al. 2016). Globally, thousands of people depend on both natural and planted forests as the source of various direct services (e.g. food, timber, fodder, fuel wood and medicinal plants) and indirect services (e.g. climate, soil and water regulation, habitats for pollinating species), for sustaining their well-being (de Groot and van der Meer 2010; Ninan 2011; Mander 2012).

In many countries around the world, the introduction of commercial forestry has become a necessity to fill the gap created by overexploitation of natural forests. Plantation forests add an important percentage of forest to the total forested area in many countries where natural forests are limited. For instance, forest plantations area covers more than 50 percent of total forested area of countries such as Lesotho, Rwanda, Ireland, the UK, Denmark, Israel, Syria and Burundi, and even nearly 100 percent of the total forest area in others countries such as Egypt, Libya, Cape Verde, Bahrain, Kuwait, Oman, United Arab Emirates and Malta (Kanninen 2010).

South Africa is a developing country on the threshold of industrialisation, with a growing population and highly increasing demand for resources. South Africa has successfully developed a well organised forest industry, especially with the establishment of commercial plantations based on exotic species, which cover about 1% of the land area (FSA 2013) and are about double the area of the indigenous forests. Plantations in South Africa have mainly been established on pristine grasslands and savannahs, so they have not replaced indigenous forests (Germishuizen 2012). However, this also means that plantations have been established in (pristine) fire prone environments in contrast to the indigenous forests that have developed mainly in fire protected areas.

Unlike plantation forests, indigenous forests in South Africa are not commercially relevant and spatially significant (approximately 0.56% of the total land area of the country), but they support a high proportion of the country's floral diversity (Mucina and Rutherford 2006) and contribute important ecosystem services to the local population (Rankoana 2016). Eight indigenous forest groups have been identified in South Africa (Geldenhuys 2002; Mucina and Geldenhuys 2006). There are: Southern Afrotemperate Forests, Northern Afrotemperate Forests, Northern Mistbelt Forests, Southern Mistbelt Forests, Scarp Forests, Northern Coastal Forests, Southern Coastal Forests, and Azonal Forests. Detailed information about each of these forests can be found in Geldenhuys (2002). Most of these indigenous forests have faced severe threats from logging exploitation by colonial woodcutters (King 1941), fire events, habitat fragmentation and also from conversion into subsistence agriculture. In many areas, these indigenous forests are represented as fragmented patches, and surrounded by exotic pine and *Eucalyptus* plantations. Geldenhuys (2002) pointed out that most of these disturbances were ended by 1939, and that the change in fire regimes to protect the surrounding plantations, has promoted the natural succession of vegetation communities and the recovery of natural forest in many degraded areas. Today most of South Africa's natural forests are formally protected and form an essential source of non-timber forest products and other ecosystem services for the surrounding population (Cunningham 1993; SA Government 1996; Ngubeni 2015). These services include timber for housing and fencing; edible fruits, sap for brewing of beer and wine, bark for medicinal products and ropes; bulbs, leaves and roots for medicinal resources, honey, edible insects, mushrooms and other edible plants as well as grass for grazing cattle (SA Government 1996).

1.3. Objectives, research questions and outline of the thesis

Failing to consider ecosystem services, functions and biodiversity conservation in management decisions will probably limit the opportunities to conserve biodiversity while maintaining the functions and the services provided. For example, a lack of knowledge on how plant diversity influences carbon storage in a specific forest type limits the opportunities to enhance this function for an optimal contribution to global climate regulation. Therefore, understanding how plant biodiversity influences ecosystem functions is important if we are to manage these functions and services provided. This thesis aims to study key ecosystem services and functions in indigenous South African Northern Mistbelt forests and their relationship with biodiversity. It is expected that the results will deepen the understanding of the role of biodiversity in ecosystem functioning and the delivery of ecosystem services. The overarching objective of this thesis is addressed with the following research objectives and questions:

Objective 1: Identify key important ecosystem services valued by local communities.
The following specific questions were addressed:

1.1. What are the local people's perceptions of the importance given to different categories of ecosystem services (provisioning, cultural, regulating and supporting services)? This question calls for another question which is: what socio-economic factors are associated with these perceptions?

1.2. What ecosystem services do local people use the most, and what are the underlying socio-environmental reasons for the use?

To answer the abovementioned research questions, a socio-empirical study (Chapter 2) was conducted with households from different localities in Limpopo province, to establish the most relevant/important ecosystem services.

Key ecosystem services identified from Chapter 2, were "timber and firewood" and "honey".

Objective 2: Quantify the functions responsible of the selected key services in natural forest ecosystems.
Primary production of biomass and forage resources (nectar and pollen) to honey bee species in forest ecosystems are relevant for timber availability and beekeeping activities, respectively. The following specific objectives were therefore addressed:

2.1. Examine the potential of Mistbelt forests to harbour honey bee plant species,
2.2. Explore the temporal availability of honey bee forage (nectar and pollen resources) in the Mistbelt forests
2.3. Determine how plant diversity (bee plant richness and the overall plant richness) influences the forage production.

2.4. Develop multispecies aboveground biomass models in natural forest ecosystems
2.5. Quantify the amount of biomass and carbon stored in the aboveground compartment

2.6. Examine the relationship of aboveground carbon with tree species diversity and structural variables

Firstly, the potential and temporal availability of the honey bee forage was assessed in Mistbelt forests in the Limpopo (Chapter 3; objectives 2.1, 2.2 and 2.3). This is important not only for consideration of these forests in the apiculture calendar of the regions, but also for opportunities of using these forests to maintain honey bee colonies during forage shortage periods, and for further pollination of crops in surrounding environments.

Secondly, new allometric biomass models were established to determine the amount of tree biomass and carbon in Mistbelt forests (Chapter 4; objectives 2.4, 2.5 and 2.6). While these information are useful for determination of the volume of timber wood in natural forest ecosystem, they are also key to understand the role of these forests in regulating global climate.

Objective 3. Examine the relationship between biodiversity components and ecosystem functions

To address this objective, only tree biomass and carbon storage were considered and the following research questions were investigated:

3.1. Do functional traits (leaf area and specific wood density), tree size (diameter), species identity influence the allocation of biomass between foliage and wood (stem plus branch)? If yes how?

3.2. Are diversity effects on carbon stock mediated through functional traits-based diversity and dominance? If yes, which of functional diversity and functional dominance exhibit the greater effects on carbon storage?

These questions were addressed in Chapters 5 and 6. In Chapter 5 (research question 3.1.), the focus was on tree biomass at species level, and the potential specific functional traits that influence the allocation of biomass. These functional traits are important to address two most debated components of biodiversity (functional diversity and functional dominance), which were the focus in Chapter 6.

In Chapter 6 (research question 3.2), the relationship between plant diversity and carbon storage was investigated through functional diversity and functional dominance, to determine whether niche complementarity, and or selection effects were the major mechanisms. The results showed that niche complementarity effects were greater than selection effects, and that the latter were mainly transmitted through the plant maximum height, reflecting the importance of forest vertical stratification for diversity-carbon relationship.

The findings from Chapter 2 to Chapter 6 were synthesised in Chapter 7 (Conclusion). The specific implications of the results for managing these functions and services in the natural forests were also discussed in the Conclusion chapter (Fig. 1.4).

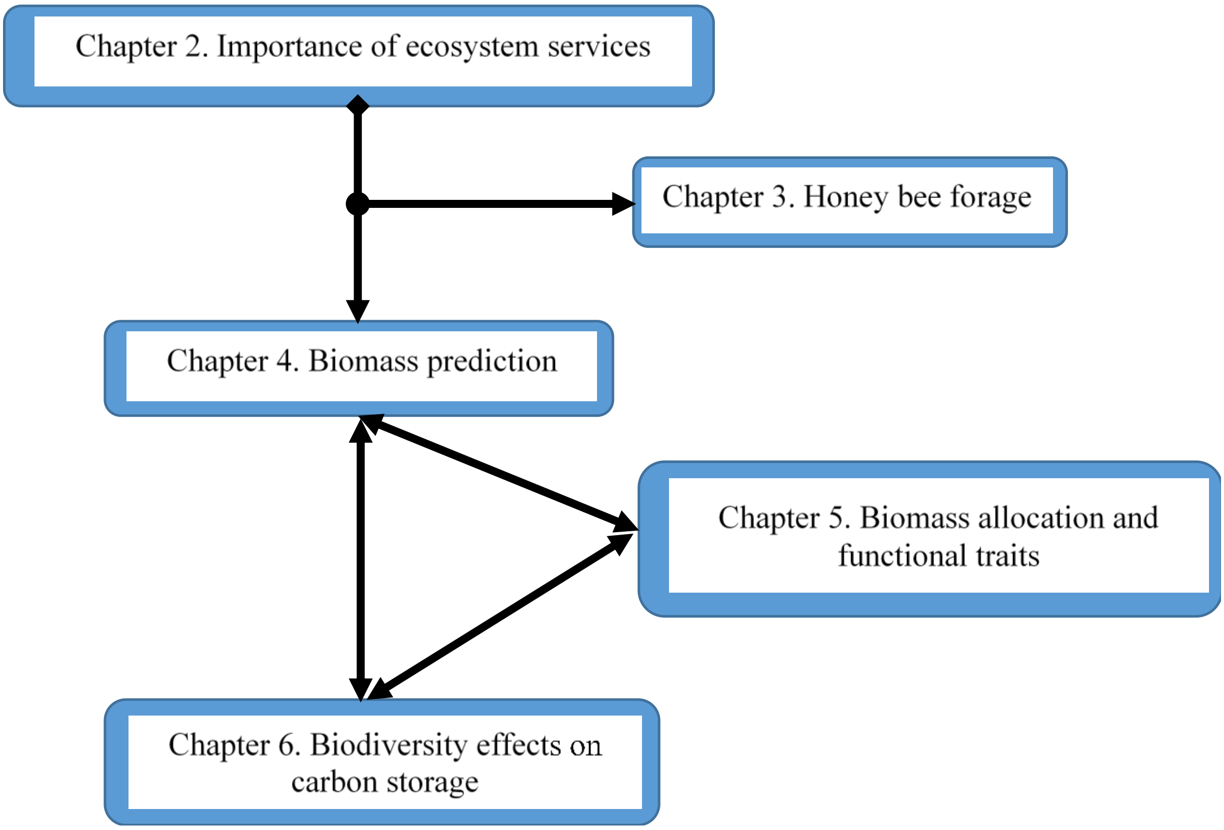

Figure 1.4. Diagram showing the linkages between the different chapters of this thesis

Chapter 2. Importance and use of ecosystem services within local communities of South Africa

Abstract

Ecosystem services (ESs) underpin human livelihoods around the world. Our understanding of how people benefit from these services, and of the social and environmental aspects that influence the interest and use is generally limited. Conducting surveys in eighty six households in four villages in the Limpopo province of South Africa, we assessed the relative importance and the use of ESs by rural inhabitants. The importance attributed to each ES was evaluated using a descriptive rank analysis. Separate logistic regressions were used to test whether and how socioeconomic factors influenced the importance attributed to ESs. The most used services were determined, based on the frequency of citation and actual use, which was further modelled as count data using a Poisson mixed effects model – as response of social and environmental factors. Supporting and provisioning ES were ranked the most important, followed by regulating and cultural ES. Among the provisioning ES, timber, firewood and edible plants were the most cited and used. Age, gender, income and prior recreational experiences played important roles in people's perceptions towards ES. As suspected, the frequency of collection of provisioning ES declined significantly with increasing distance to the forest and presence of foothills in landscape, which formed a natural barrier. The study also revealed that employed householders benefited from these services more than unemployed householders. Contrary to our expectations, income did not significantly influence the use of these provisioning ESs, suggesting that the collection of goods is more likely oriented towards a domestic usage. The implications of the results for ESs management in local development planning are discussed.

Keywords: livelihoods, households, local valuation, social factors, provisioning services

2.1. Introduction

Humans depend on ecosystems as sources of goods and services for a sustainable well-being. More than one billion people are directly supplied with provisioning services, e.g. non-timber forest products, fire wood, fresh water, and fish (Ninan 2011). In the meantime, there is a high dependency on other ecosystem services (ESs), such as regulating ESs (e.g. climate regulation, water purification, and pollination), supporting ESs (e.g habitat for species) and cultural ESs (e.g. tourism, recreation). The dynamic and complex interactions between people and ecosystems have triggered the need for further research, and the last decades have witnessed a considerable research effort in ES field (Bennett et al. 2009; Castro et al. 2011; Costanza et al. 1997; Egoh et al. 2007;

García-Nieto et al. 2013; Nelson et al. 2009). Yet, the concept of ES is still increasingly being debated between scientists, landscape managers and policy-makers. The establishment of many international initiatives such as the Millennium Ecosystem Assessment (MEA), The Economics of Ecosystems and Biodiversity (TEEB), and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) serves as testimony.

While the concept of ES is being used to inform and support management decisions at landscape level, most of the analytical efforts in ES assessment have been directed towards the capacity of ecosystems to supply these ES (Burkhard et al. 2012; Geijzendorffer and Roche 2014; Maes et al. 2012; Seppelt et al. 2011), and their economic valuation (Costanza et al. 1997; Ninan and Inoue 2013; Xie et al. 2010). Very few studies have approached the demand side of ES, which lead to a lack of information on the social aspects of ES assessment (Geijzendorffer and Roche 2014; Villamagna et al. 2013). It is inappropriate to neglect the social perspective of ES valuation, because ESs as a anthropocentric concept are per definition closely related to people (Castro et al. 2013). Hence, attempts to analyse ESs should not only focus on the supply side, but also on the demand side, i.e. the social demand for using a specific ES.

The social demand for ESs involves a wide range of stakeholders, from those directly or indirectly benefiting from these ESs to those involved in management and underlying policy development (Harrington et al. 2010). As different groups of stakeholders could have different interests in the services, with respect to their importance, and the value they place on those, the identification of the ES beneficiaries is a step forward in the ES valuation (Hein et al. 2006). For instance, the importance of ESs for rural populations would be a relevant information in ES valuation, because these ESs only exist if people benefit from them (Bennett et al. 2009; Paruelo 2012). In addition, the social perception towards the importance of ESs is particularly relevant to (1) identify the most valued ES, (2) infer on the most important/relevant ESs to people and (3) identify potential trade-offs between ESs (Martín-López et al. 2012; Meijaard et al. 2013).

In sociocultural valuation of ESs, the mere provision of a specific ES in a landscape, may not guarantee optimal use and people well-being, because the capacity of an ecosystem to produce a particular ES (Burkhard et al. 2012) may not indicate the actual production and use of that ES (Villamagna et al. 2013). Within a group of beneficiaries, the benefits are differently delivered, according to the access of these beneficiaries to the resource, and also according to the value they place on its wise management (Hein et al. 2006; Villamagna et al. 2013). There is mounting evidence that the access to a particular ES and the use of that service would be more strongly influenced by a wide range of social factors (ethical, ecological knowledge, demographic), spatial and environmental factors. For example, as pointed out by Kozak et al. (2011), the rate at which people benefit from recreational services, by visiting a free recreation site, diminishes as a function of distance to that particular site. Therefore, taking into account these factors could also improve our investigation on the importance and use of ES. The application of the socio-cultural and socio-environmental aspects is an advance in the multi-disciplinary assessment of ESs (Castro et al. 2013) since it improves the understanding of the complex interactions between people and the environment.

The present study assessed the importance and use of ESs by local inhabitants in Limpopo, the northernmost province of South Africa. In this province some of the most productive areas, in terms of commercial forestry and commercial farming are found. The area provides a wide range of ESs to both rural and urban people. In this study, we explored a range of ESs to account for different categories of services. The following questions were addressed:

(1) What are the local people's perceptions of the importance attributed to different categories of ESs (provisioning, cultural, regulating and supporting services)? This question called for another question which was: what socio-economic factors are associated with these perceptions?

(2) What ESs do local people in the proximity to a forest use the most, and what are the socio-environmental variables that form the foundation of the use?

2.2. Method

2.2.1. Study area

This study was conducted in the Greater Letaba Municipality, located in the Mopani District in the north-eastern part of the Limpopo Province (South Africa) (Figure 2.1). Greater Letaba Municipality shares borders with the Greater Tzaneen Municipality with an urban center in the south, the Greater Giyani Municipality in the east, the Molemole Municipality in the west and the Makhado Municipality in the north. The area is characterised by a highly variable topography, from zones of flat lowland plains to some zones of high mountains and a mosaic of foothills and low mountains. Zones of low mountains and foothills are dominated by commercial and small scale subsistence farming, commercial plantation forestry with pines and eucalypts managed by private forest companies, small fragments of natural forest habitats and degraded woodlots non-suitable for forest plantations.

A preliminary exploration was conducted in the Greater Letaba Municipality to identify the rural communities living around forested areas and making use of forest products to support their livelihoods. Four village communities, notably Magkoba, Maraka, Satlaleni and Mollong villages (Figure 2.1), were selected for this study. Magkoba village is surrounded by commercial forests and patches of natural forests. Communities living in Magkoba village depend on these forests as principal sources of wood and non-timber forest products. The last three villages (Maraka, Satlaleni and Mollong) are located in a mosaic of degraded bushvelds and forests. These lands are owned by the village communities, but generally unmanaged, and most of these inhabitants have access to forest products.

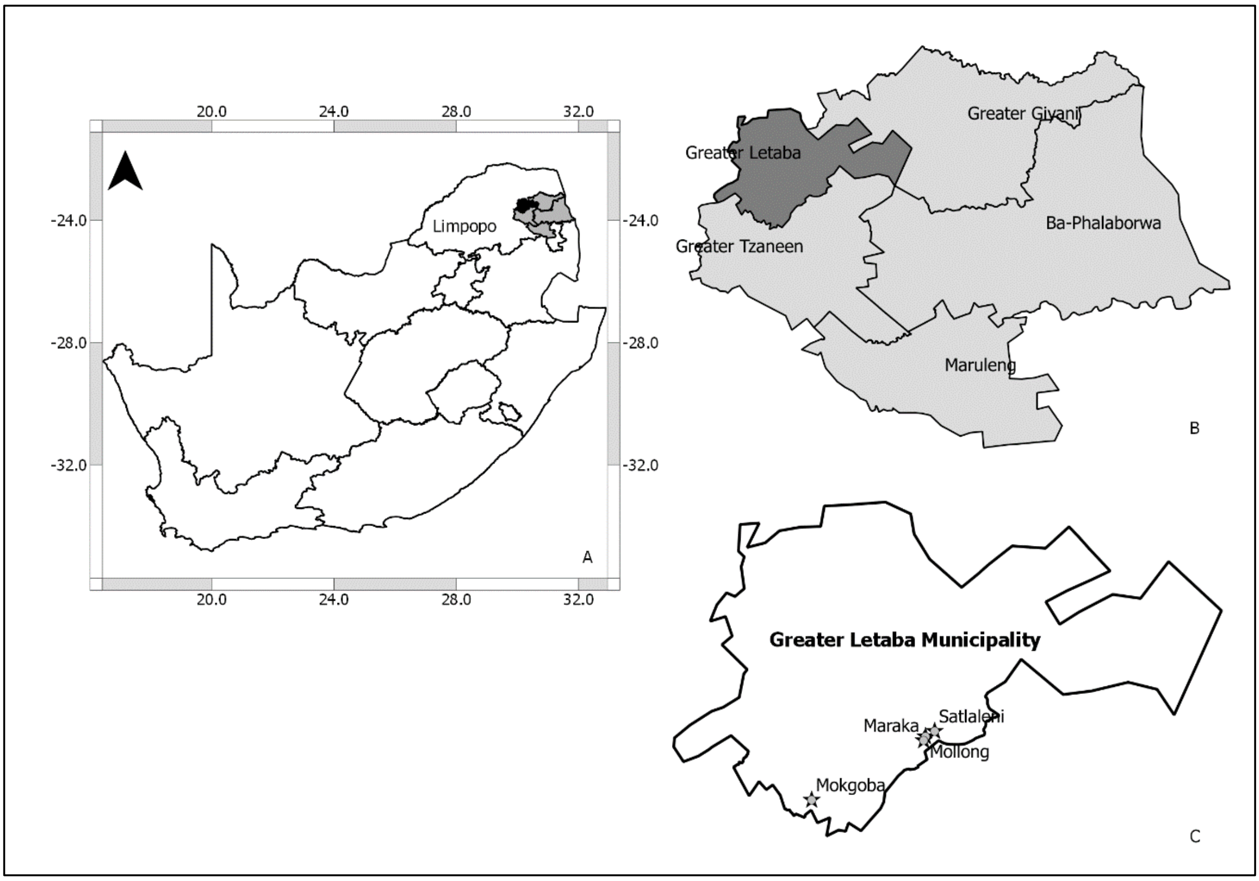

Figure 2.1. Location of the studied villages in the Greater Letaba Municipality.

2.2.2. Sampling and data collection

For the purpose of this study, a Human Research Ethics Committee permission was established and approved by the Research Ethic Committee of Stellenbosch University (http://www0.sun.ac.za/research/research-integrity-and-ethics/human-research-humanities-ethics-1) to adhere to the policy of safeguarding the rights, the safety and the dignity of the participants in this research. Before the survey was started, the legal representatives of the participants were informed and consent forms were signed.

In each village, a pilot survey was conducted with 50 randomly selected householders to calculate the proportion p of householders who benefit from any ES. The sample size was determined afterwards for each village, using the proportion p and the following formula (Köhl et al. 2006):

$$n = \frac{1}{e^2} p(1-p) {U^2}_{1-\frac{\alpha}{2}} \tag{1}$$

In this formula, n is the estimated sample size, U is the value of the normal random variable (1.96 for $\alpha = 0.05$) and e, the authorized margin error from this survey, held to be 10 %. Altogether, 86 householders (46 in Magkoba village, 10 in Maraka, 20 in Satlaleni and 10 in Mollong) were randomly selected and included in the survey. All participants were local residents. Some demographical characteristics of the studied samples are presented in Table 2.1.

Table 2.1. Characteristics of studied householders

Land uses	Villages	Sampled household	Employed householder (Yes/No)	Income (Yes/No)	Gender (Women/men)	Age (Young/Adult/Old)
Natural forests and Eucalypt plantations	Mokgoba	46	15/31	28/18	29/17	13/18/15
Degraded forest lands	Maraka	10	1/9	8/2	7/3	0/4/6
	Satlaleni	20	6/14	15/5	16/4	3/9/8
	Mollong	10	5/5	9/1	6/4	1/3/6

A questionnaire (Appendix A) was designed and administered to each householder, separately. The interview was conducted at informants' houses to record the geographic coordinates of each location. The concept of ES was explained, with some illustration, to each informant prior to the survey. Four categories of ESs (MEA 2005) were considered during the interviews. These included provisioning services (timber and firewood, edible plants, honey, edible fruits, edible insects, medicinal plants and mushrooms), regulating services (pest control, pollination), supporting services (healthy soil) and cultural services (tourism and recreation). First, householders were asked to provide some basic information on their age, the type of employment and the monthly income. Second, a list of ecosystem services was presented to each informant, who was asked to evaluate them in terms of importance, from "not important" to "extremely important". Each respondent was also given the possibility to select a "don't know" option. Then the respondents were requested to disclose information on the use of ecosystem services. Specifically, they were asked to select the provisioning forest ecosystem services they use and to tell about the approximated time (in hours) spent to obtain that service, the frequency of collection (number of times they get a particular service in a month). Because of the probable seasonal variation in the availability of provisioning services, informants were requested to disclose these information on an average basis. Finally, informants were told to mention any presence of barriers (e.g. rivers or foothills) that could affect their access to the forest ecosystems.

2.2.3. Data analysis

We applied a descriptive rank analysis to evaluate the relative importance given to each ES and category of ESs. A 4-point scale was used to rank the levels of importance attributed to each service (where 1: not important, 2: somewhat important, 3: important and 4: extremely important). To determine whether and how socio-economic factors influence the relative importance given to each category of ES, the informants were first grouped on the basis of their age (young householder: < 30 years; adult householder: 30-60 years; and old householder: > 60 years), employment (employed householder, unemployed householder), gender (women, men) and income (yes *vs* no). Because of the nature of response variable (ordered factor), separate ordered logistic regression models were performed for each category of ES. Predictors for these models were householder age used as categorical variable with three levels (young, adult and old householder), employment situation with two levels (yes if the respondent is employed and no if not), gender (men *vs* women) and income considered as dummy variable with two levels ('yes' if the respondent receives a monthly income and 'no' if not). An additional variable, indicating whether the respondent had once visited a recreational site or not, was considered for cultural ESs.

During this survey, it appeared that forest provisioning services were the ones mostly used in the studied local communities. Within provisioning services, the most used services were determined, based on the relative frequency of citation, which is the total number of citations for a particular provisioning service divided by the total number of respondents for that service. For a better representation of these results, a radar chart was used to highlight the most used provisioning services. Next, the use of provisioning ES was characterised, based on the frequency of collection (number of times people get a particular service in one month). The frequency of collection was modelled as count data, assumed to follow a Poisson distribution. Therefore, using a mixed effects GLM with Poisson error structure (GLMM), the frequency of collection was afterwards modelled as a function of socio-economic variables (employment and income) and environmental variables (presence of barrier, time spent to collect a good and the distance from forests). The approximate time was indicated by the informants, but the distance to travel was determined in a GIS software (Quantum GIS 2009), using the recorded geographic coordinates of each location. ES was considered as random factor, and GLMM with a Poisson link function was thus performed (Zuur et al. 2009). A Shapiro-Wilk test was used to determine whether the variation around the intercept, for each service, was normally distributed (Zuur et al. 2009). Statistical analyses were carried out using R software (R Development Core Team 2015) and at 5% significance level.

2.3. Results

2.3.1. Importance value of ESs

Healthy soil was the only supporting ES considered in this study, and was ranked the most important, followed by provisioning ES, and regulating ES (Table 2.2). The least important category was the one of cultural services. Within the provisioning services, timber and firewood, edible plants and honey were considered the most important whereas edible insects and mushrooms were less important for local respondents. As for regulating services, pest control was perceived more important than pollination.

Table 2.2. Importance value of provisioning, regulating, cultural and supporting ESs: average rank out of 4 ± SE (standard error).

		Importance value of ESs	
Type of ES	ES	Mean ± SE	Mean ± SE
Supporting ES	Healthy soil	3.81±0.04	3.81±0.04
Provisioning ES	Timber & firewood	3.80±0.04	3.26±0.03
	Edible plants	3.56±0.07	
	Honey	3.46±0.08	
	Medicinal plants	3.32±0.10	
	Edible fruits	2.96±0.06	
	Edible insects	2.82±0.07	
	Mushrooms	2.42±0.10	
Regulating ES	Pest control	2.92±0.10	2.79±0.07
	Pollination	2.64±0.11	
Cultural ES	Tourism	2.28±0.09	2.15±0.07
	Recreation	2.02±0.10	

2.3.2. Factors influencing the relative importance given to categories of ESs

Results from the ordered logistic regression models were summarized in Table 2.3. For all categories of ESs, there was no significant effect of the employment status. The main factors that influenced the perceived importance of ESs were age, gender, income and first visit (i.e. if the respondent has once visited a recreational/touristic site).

Old householders were significantly and positively associated with the importance of provisioning ESs. The regression coefficient for this group was positive and 0.57 higher than the ones for adult and young householders (Table 2.3). This suggests that older householders, compared with the younger, perceived provisioning ESs as more important. Gender also strongly influenced the ability of informants to value provisioning ESs; accordingly, men were negatively associated with the importance value of provisioning ESs. Unlike age and gender, income and employment status did not significantly influence the perceived importance of these provisioning ESs.

Table 2.3. Ordered logistic regression results showing the determinant socio-economic variables influencing the perceived importance of ecosystem services. Standard errors are shown in brackets.

	Provisioning ES	Regulating ES	Supporting ES	Cultural ES
Variables	Coefficient estimate (standard error)			
Old	0.57* (±0.27)	1.28** (±0.53)	3.61** (±1.29)	-0.39 (±0.47)
Adult	0.36 (±0.24)	0.56 (±0.47)	1.20 (±0.75)	0.12 (±0.42)
Employment Yes	0.34 (±0.37)	0.87 (±0.71)	2.02 (±1.17)	0.68 (±0.62)
Gender Men	-0.44* (±0.25)	-0.20 (±0.52)	-1.86* (±0.84)	0.16 (±0.44)
Income Yes	-0.24 (±0.23)	-0.27 (±0.46)	-1.92* (±0.97)	0.57 (±0.39)
First visit	-	-	-	0.98* (±0.53)
Cond. H	3.18E+01	5.90E+02	6.70E+01	8.40E+01

ES: Ecosystem services; Cond. H: Condition number of Hessian; *: $p < 0.05$; **: $p < 0.01$

As for regulating ES (biological control and pollination), there were no significant effects of respondent’s gender, employment and economic situations, except for the age category which showed significant positive perception of old householders towards their importance value ($p < 0.01$; Table 2.3).

Age was a significant predictor of householder ability to value supporting ES (healthy soil), which was perceived as more important for older householders, than for adult and younger householders. Gender and income were also significant predictors ($p < 0.05$; Table 2.3). Specifically, men exhibited less positive attitude towards that ES, while comparatively, women showed more positive attitude.

Neither the age and gender, nor the employment and economic situation had significant influence on the importance attributed to the cultural ESs. The results further showed that only respondents’ first visit to a recreational/touristic site determined their positive perception towards ESs ($p < 0.05$; Table 2.3).

2.3.3. Most used ecosystem services across study sites

Forest provisioning ESs were the most used among the respondents. The highest frequency of citation was recorded for timber and firewood (97.7%), followed by edible plants (83.7%), edible wild fruits (79.1%) and edible insects (69.8%). Mushrooms, medicinal plants and honey were less used. The results also indicated that the patterns of citation and use varied with the surrounding land uses; accordingly, edible plants, wild fruits and insects were more considerably used in Maraka, Satlaleni and Mollong villages, surrounded by degraded forest lands, than in Magkoba village, which is surrounded by established plantations and natural forest patches.

2.3.4. Factors influencing the use of provisioning ecosystem services

The results from the Generalised linear mixed effect models (Table 2.4) revealed that 67 % of the variance in the frequency of collection was explained by the fixed effects of environmental variables and employment status, and the random effects of provisioning ESs. The presence of foothills, the distance and the time spent had negative significant influence on the frequency of collection of these services ($p < 0.001$). There was also a significant ($p = 0.04$), but positive effect of employment status, suggesting that employed householders seemed to benefit from these ES more than unemployed householders. Income did not show any significant effect on the frequency of collection. The results further revealed a considerable variance (0.34) in the random effect of the provisioning ES (Table 2.4; Fig. 2.2). Examination of the random intercept (Fig. 2.2) suggests that the frequency of collection of provisioning ES increased due to the higher interest in timber and firewood, edible plants and edible fruits, while there was very little interest in the collection of other provisioning services such as edible insects, medicinal plants and mushrooms.

Table 2.4. Results of Poisson mixed effect model describing the effects of employment and environmental variables on the frequency of collection; SE: standard error

Variables	Estimate	SE	Z	Pr(>|z|)
(Intercept)	2.03	±0.25	8.23	< 0.001
Environmental variables				
Foothill Yes	-0.33	±0.07	-4.57	< 0.001
Time spent (hours)	-0.11	±0.03	-4.01	< 0.001
Distance to forest (km)	-1.12	±0.33	-3.39	< 0.001
Social variables				
Employed householder Yes	0.16	±0.08	2.07	0.04
Income Yes	-0.04	±0.08	-0.54	0.59
Variance random intercept (ESs)	0.34			
Conditional R Square (%)	67.02			
Marginal R Square (%)	11.34			
Shapiro-Wilk normality			0.931	0.56

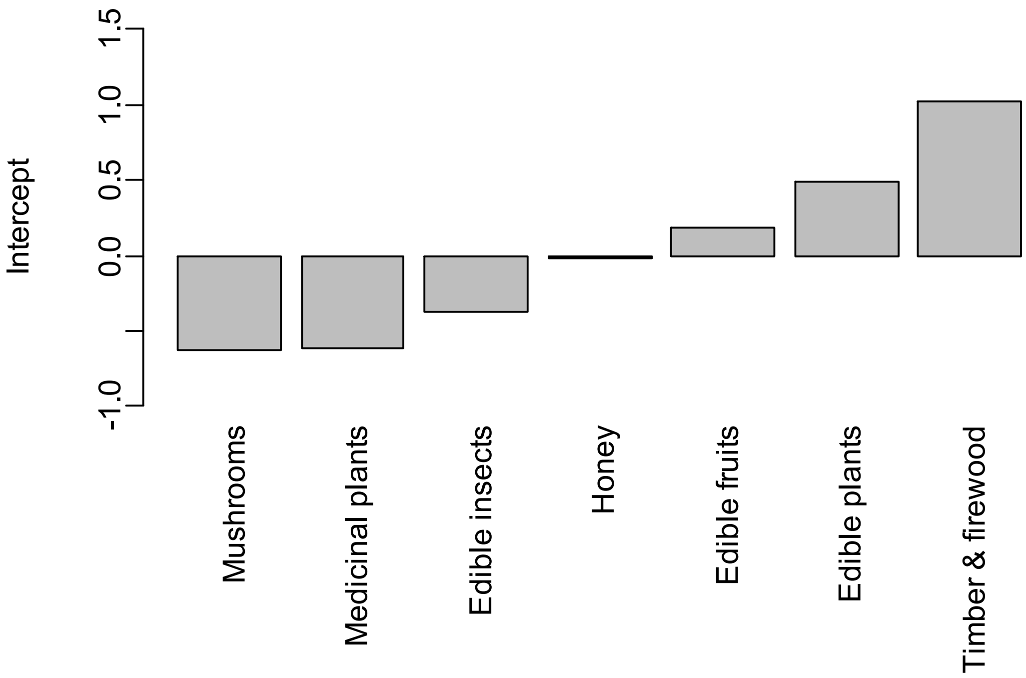

Figure 2.2. Random intercept for each ecosystem service

2.4. Discussion

2.4.1. User's perception on the importance of ESs

We found that supporting and provisioning ESs were perceived as the most important, compared with regulating and cultural ESs. This result is consistent with previous studies that have approached social aspects of ES assessment (Hartel et al. 2014; Hartter 2010; Martín-López et al. 2012). Among the provisioning ESs, timber, firewood and edible plants stood out as the most important. The interest of local people in these forest provisioning ESs concur with the ideas that rural communities show a high appreciation of material benefits from forest ecosystems, in contrary to urban communities (Martín-López et al. 2012) who rather seemed to highly appreciate cultural services such as aesthetic value, recreational activities, tourism, environmental education (Kroll et al. 2012). The fact that provisioning ESs are often highly valued within rural inhabitants may be because they have a close connection to the ecosystems (Martín-López et al. 2012). However, the high rank in the importance of supporting services (especially healthy soil) reflects more the level of awareness of local people of the soil quality. They depend on the soil as a production base for food. Indeed, in agricultural and forestry systems, soil quality has a major impact on the delivery of almost all other services (TEEB 2011), because soil influences the primary production through factors such as nutrient availability, water content and soil structure.

Age, gender, income and past touristic/recreational experiences played important roles in the perception of the importance of ESs. These findings accord with some recent studies that found age and gender as significant predictors of people's attitude towards ESs (Allendorf and Yang 2013;

Castro et al. 2011; Martín-López et al. 2012; Meijaard et al. 2013; Sodhi et al. 2010). Interestingly, our results further showed that these factors worked differently according to the category of ESs (Table 2.3). The positive attitude of women towards the importance of provisioning and supporting ESs is likely the result of the sense of duties that women have in the household, and how they are aware of the direct benefits from the environment (Allendorf and Yang 2013). Therefore, the gender effect on the perceived importance of ESs can be explained by the gender-related roles in the house (Martín-López et al. 2012). Local women have a close relationship with the collection of forest resources, and most of the provisioning ESs studied in this context (e.g. timber, firewood, edible plants, edible fruits, and medicinal plants) were harvested by women, as part of domestic roles.

Older community members had a more positive perception on provisioning ESs than younger members. This is likely because old people/householders generally support the basic necessities (e.g. water, foods) of the entire household. This result also seems to be supported by an indirect effect of knowledge, which is considered to be accumulated over time (Camou-Guerrero et al. 2008). Moreover, the positive attitude of old people towards regulating services and supporting services stresses the importance of knowledge transfer (Allendorf and Yang 2013), in that youngsters usually learn from elders. There was no significant effect of informants' employment status and income on the perceptions about provisioning, regulating and cultural ESs. This is surprising since unemployed or less wealthy people were expected to use more forest resources and to have a positive perception of their importance. This result, however, suggests that employment status has less influence on local people perceptions towards the importance of services.

Neither age and gender, nor the employment and economic situation had significant influence on the importance given to the cultural ESs. Interestingly, only informants who visited a recreational site in the past, were more aware of the importance of cultural ESs. This indicates that rural people, in general, do not strongly appreciate the cultural services from environment, unless they had acquired own experience in the past. This also means that the lack of information and prior experience has much influence on the perception about cultural services, and in turn the value they attribute to these services.

2.4.2. Use of ESs across study sites

The importance given to the ESs reflects the actual use of these services. Indeed, wood for construction and fuelwood were the major products rural people derive from the forests. This is in line with previous findings by Shackleton et al. (2007) about the importance of woodlands in rural livelihoods in South Africa. Fuelwood is still the main source of energy because most of the remote communities are exposed to an unreliable electricity supply (Gugushe et al. 2008). Except for timber and firewood which were both highly cited in the studied communities, there was a considerable difference in the frequency of citation for edible plants, edible fruits and edible insects.

Such differences reflect the influence of the surrounding land use. In fact, communities living in Maraka, Satlaleni and Mollong villages were surrounded by degraded forest vegetation and seemed to benefit from other forest provisioning services (e.g. edible plants, edible fruits and edible insects) more than people living in Makgoba village, surrounded by commercial eucalypt forests and small patches of natural forest habitats. The establishment of these eucalypt commercial plantations provided economic benefits to private owners and companies, and considerable quantities of wood for local people, but reduced the availability of other forest products, because the existing edibles fruit trees and edible plants are frequently treated as weeds. This means that wood and other timber products are greatly supplied to these local populations, at the expense of other provisioning ESs such as edible plants, indigenous fruits and edible insects, suggesting some trade-offs between provisioning services from managed landscapes (Bennett et al. 2009). But the fact that local people still use forest products even in areas where closed-canopy forests are absent, reinforce the importance of degraded indigenous forests for rural people's livelihoods (Meijaard et al. 2013), compared with commercial plantations.

Unlike timber and firewood, relatively low frequencies of citation were recorded for forest provisioning ESs such as mushrooms, medicinal plants and honey. This is likely the result of increase in community income and local people disinterest towards the collection of these forest products. The rural communities in South Africa are relatively similar to communities in other parts of the developing world (Gugushe et al. 2008), but the level of industrialisation makes the context different. For example, in Zambia, forest ecosystems, especially Miombo woodlands were revealed to provide a wide range of services (food, timber, firewood, health, and spiritual benefits) to local people (Kalaba et al. 2013). This is also the case in West Africa, for instance in Burkina Faso, where local people benefit from provisioning services such as firewood, construction material, medicinal plants (Ouédraogo et al. 2014). One could hypothesize that in South Africa, the development of forest industry combined with the conversion of natural lands, has a substantial contribution to the production of major services such as timber and fuelwood, and at the same time limits the provision of other services supplied by natural forests. The conversion of natural habitats into plantations has been found to negatively affect biodiversity (Stephens and Wagner 2007; Vellend 2004), and probably on the availability of medicinal and non-timber forest products.

Factors that significantly influenced the use of provisioning ESs were: presence of foothills in the landscape, the time spent and the distance to the forest. Specifically, the frequency of collection of forest provisioning ESs decreased with increasing distance to the forest and presence of foothills in the landscape. This is simply because communities close to forest stands benefit from forest services more than people living far away from these forests (Colfer et al. 2006). This underpins the influence of the spatial landscape context on ES provisioning. The effects of environmental variables on the frequency of collection of forest goods indicated that also small scale geographical and topographical patterns are important for use of ESs. Large scale environmental indicators (e.g. rural-urbans gradient) however would have strong influence, because of the spatially differential interest of beneficiaries in ESs (Hein et al. 2006; Kozak et al. 2011; Kroll et al. 2012). It was also found that ESs were more frequently used if the householder was employed. This is because most types of employment are related with timber harvesting in plantation stands and wood processing in sawmill. These jobs allowed rural employed householders to have more access to the forest provisioning services. Contrary to our expectations, there was no effect of income on the use of these provisioning services. This result, therefore, seemed not to support the influence of employment. However, the findings may be due to the nature of the income, which included state pensions, especially for aged people. The nonsignificant effect of income on the use of the provisioning ESs suggests that these services are not subject to trade in the studied areas, but instead, are used for domestic purposes, contrary to other rural communities where the trade of forest products is major source of household income (Kalaba et al. 2013).

Linking statement to Chapters 3 and 4

The scope of this thesis required a selection of important ES since the multitude of possible ES could not be modelled. The ES were selected based on a compromise of ES, which are of global importance and of such which were identified as locally importance in this survey. The results from this first chapter showed that provisioning services especially “timber and firewood” were the most important and valued. In addition, ecosystem services such as “edible plants” and “honey” were highly frequently cited. Two key ecosystem services were selected for further studies. There were “timber and firewood” and “honey”. Honey was selected over “edible plants” because (1) it was found valuable for communities; (2) honey bee forage is important for bee colonies survivorship and also for pollination of crops in agricultural farms. This is relevant, because most of the crops and fruits farms in the region of Limpopo rely on beekeepers and honey bee colonies for pollination. **Chapter 3**, therefore focussed on the honey bees’ forage. Particularly, the potential and temporal availability of the forage to honey bees was assessed in a natural Mistbelt forest. **Chapter 4** focussed on timber potential in a natural forest. Specifically, tree biomass and carbon were quantified in native tree species selected from Mistbelt forests, by developing allometric biomass models. The information on biomass and carbon are useful for determining the potential of timber in natural forest ecosystem, and are also key to understand the role of these forests in regulating global climate.

Chapter 3. Potential supply of foraging resources to managed honey bees – identification of key variables affecting forage provision in a natural forest

Abstract

Honey bees play a vital role in the pollination of flowers in many agricultural systems, while providing honey through well managed beekeeping activities. With the worldwide decline in insect pollinators, pollination services have become increasingly reliant on managed honey bees. The provision of pollen and nectar to managed honey bees is important for the survival and productivity of their colonies. The aims in this chapter were to (1) examine the potential of natural forests to harbour honey bee plant species, (2) explore the temporal availability of honey bee forage (nectar and pollen resources), and (3) elucidate how plant diversity (bee plant richness and the overall plant richness) determined the forage production.

A forage value index was defined on the basis of species-specific nectar and pollen values, and the expected flowering period. Forage provision was modelled using General Linear Models. Up to 50 % of the overall woody plant richness were found to be honey bee plant species, with varying flowering period. As expected, bee plant richness increased with overall plant richness. Interestingly, bee plants' flowering period was greatly distributed over the year season, but the highest potential of forage supply was observed during the last quarter. Few honey bee plant species contributed 90 percent of the forage provision. Surprisingly, overall plant richness did not influence the bee forage value. Rather, richness of bee plant species showed the greater effect. This suggests that conservation needs to be specifically oriented towards bee forage species in the Mistbelt forests to preserve and enhance their potential to maintain honey bee colonies.

Keywords: plant diversity; honey bee plant richness; floral resources; forage value; Mistbelt forests; South Africa.

3.1. Introduction

Insect pollinators provide a vital service of pollination to flowering plants by foraging and transferring the pollen from one flower to another. Of all insect pollinators, bees are seen as the most important, as they are fully dependent on floral resources (nectar and pollen) for forage provision (Buchmann and Nabhan 1996; Shepherd et al. 2003). Bees feed on the floral resources of a wide variety of flowering plants, from natural and semi-natural habitats to surrounding agricultural landscapes (Ricketts et al. 2008), and contribute to the pollination of more than 66 % of the world's crop species (Kremen et al. 2004).

With the increasing worldwide decline in insect pollinators (and thus reduction of pollination services) as results of landscape fragmentation and modern agricultural practice (Potts et al. 2010; Whitehorn et al. 2012), honey bees, as important pollinators that require floral resources, have increasingly been managed for apiculture and future provision of pollination services (Crane 1999; de Lange et al. 2013). For instance, honey bee colonies can be managed and maintained by beekeepers in natural and semi-natural biomes that provide floral resources, and moved afterwards, to other places (e.g. agricultural farms) when they are needed for pollination (Allsopp and Cherry 2004; de Lange et al. 2013; Johannsmeier 2005; Melin et al. 2014). Allsopp and Cherry (2004), and Johannsmeier (2005) documented the potential of forage supply by many eucalypt species to honey bees in Western Cape province of South Africa, with some being excellent sources of high quality pollen. These authors argued that beekeepers rely on the flowering season of eucalypt plantations to maintain honey bee colonies, which will provide pollination service for deciduous fruits (e.g. apples, avocados, mangoes and litchis) in the following season. In addition, the majority of honey bee colonies in the Western Cape are used for pollination purposes within the deciduous fruit industry, and are maintained after the fruit pollination season within eucalypt plantations (Allsopp and Cherry 2004). However, because these plantations are fast growing monocultures with short rotation periods, and do not usually harbour high species richness, they provide forage resources only for a certain period (Allsopp and Cherry 2004; de Lange et al. 2013). In addition to this but of lesser importance, pesticide use for biological control in plantation management is not always beneficial for pollinators. Contrary to these plantations, protected natural forests usually support high floral diversity, and are seen as primary sources of diversified floral resources for honey bees and other wild pollinators (de Lange et al. 2013). This is the case for the natural Fynbos in the Western Cape province of South Africa, which are reported as main forage sources for the beekeeping industry during the period from April to July (de Lange et al. 2013).

Limpopo (South Africa's northernmost province) is one of the most productive provinces, in terms of commercial timber (pine and eucalypt plantations) and agricultural farming (especially fruits and tea). The natural vegetation in Limpopo province is dominated by large and fragmented patches of Mistbelt forests (Mensah et al. 2016a), which surround these plantations and agricultural areas. Despite the high floral diversity in these Mistbelt forests, very little is known of their potential to provide floral and nesting resources for honey bees, which might suggest availability of good forage resources nearby. As a corollary, very little is also known about the possibilities for utilization of the available forage resources for beekeeping activities, and to use these natural forests as main or alternative sources of honey bee forage, in a typical forage-calendar year, as for the Fynbos in the Western Cape (de Lange et al. 2013; Melin et al. 2014). In this chapter, the aim was to quantify the availability of forage to honey bees in the Mistbelt forests, and more specifically, how the bee forage provision varied with honey bee plant diversity and the overall plant species diversity.

The diversity and abundance of floral resources reflect the continuous supply with forage from different species and therefore, are almost certainly one of the most important factors that will encourage honey bees to remain on site (Torné-Noguera et al. 2014). Yet, the availability of floral resources to honey bees in natural forests varies in several factors, namely the distance from the colony (Jha and Kremen 2013; Williams and Winfree 2013), the species-specific flowering phenology, tree size (Pardee and Philpott 2014; Scaven and Rafferty 2013), and the spatial distribution of honey bee plants, which in turn determines the spatial distribution of flower and nesting resources (Torné-Noguera et al. 2014).

The availability of floral resource at plant individual level, is governed by whether and how intensively a honey bee plant flowers, i.e. the flowering area (Hülsmann et al. 2015; Scaven and Rafferty 2013), although the flowering area can be a poor predictor of visitation (Hülsmann et al. 2015). On trees, flowers and leaves both originate from buds, which are carried by twigs. Thus, the flowering area for each honey bee flowering plant will likely correlate with the amount of foliage, which in turn correlates with tree size and age (Otárola et al. 2013). At the plant community and forest stand scales, the stand structural characteristics of bee plant species (density and stem basal area) will likely determine the potential amount of floral resources that attract honey bees from a distance (Fründ et al. 2010; Hülsmann et al. 2015; Jha and Kremen 2013; Pardee and Philpott 2014). These variables would also underlie the diversity of the floral resources because a new bee plant species in flowers, added to the community, would likely contribute new species-specific phenological characteristics such flower production, pollen and nectar production.

In this study, field plot inventories were carried out in natural evergreen Mistbelt forests in South Africa to (1) examine their potential to harbour honey bee plant species, (2) explore the temporal availability of honey bee forage (nectar and pollen resources), and (3) elucidate how plant diversity (bee plant richness and the overall plant richness) determines the forage production. For the first objective, the diversity of honey bee plants was assessed, and the most important honey bee forage plant species, identified. It was also asked whether the variation in plant diversity (all species) was positively associated with variation in bee forage plant species. Our rationale was based on the fact that such association may not be straightforward, as rich plots (in terms of species) can contain very few bee plant species. Also, at the plot level, bee plant species would represent a proportion of all plant species, but the strength of the association would depend on how such proportion is distributed across the study plots. In other words, no association would be expected if the distribution of honey bee plant richness, showed an early asymptotic trend with increasing number of plots. As for the second objective, a forage value index (FVI, based on the species-specific nectar and pollen value, and the expected flowering period) was defined, and the temporal availability of the nectar and pollen forage value was explored. Finally, the defined FVI was used as proxy for forage production to model its relationships with plant diversity (plant richness and bee plant richness). It was assumed that both, plant richness and bee plant richness would positively influence the forage value.

3.2. Material and methods

3.2.1. Study site

The study was carried out in the Limpopo province located in the northern part of South Africa. Spatially, the province is characterised by a succession of landscapes with highly varied topography, from zones of flat lowland plains to zones of high mountains, through mosaic of foothills and low mountains. The areas of low mountains and foothills are exploited for commercial and small scale subsistence farming, commercial timber managed by forest companies. Many fragmented patches of natural forests and degraded woodlots non-suitable for forest plantations, are also encountered (Geldenhuys 2002, 1997). Some crops fields (especially fruits) are established in the surrounding environment of natural and planted forests (eucalypt), and benefit from pollination services provided by wild pollinators and managed honey bees (Carvalheiro et al. 2010; Melin et al. 2014). The specific area selected for this study is the Woodbush natural forest (23°50'S, 30°03'E), considered as part of the Limpopo Mistbelt forests (Mucina and Rutherford 2006). The Woodbush-De Hoek forest covers a total area of about 6, 626 ha, and is the largest forest block along the North-eastern Escarpment (Cooper 1985; Geldenhuys 2002). The woody flora is predominated by species such as *Podocarpus latifolius*, *Combretum kraussii*, *Syzygium gerrardii* and some understorey species such as *Peddiea africana*, *Oricia bachmannii*, *Kraussia floribunda* (Geldenhuys 1997; Mucina and Rutherford 2006). More detailed information on Mistbelt forests are provided in section 4.2.1.

3.2.2. Sampling for floristic data

The data used in this study was collected from a sample plot survey, based on a stratified random sampling design set in a 708 ha (hectare) forest block in the Woodbush De Hoek forest. The stratification of the research area was based on three classes of slope (flat: 1.5%-15.3%, gentle: 15.3%-29.19% and steep: 29.19%-43.1%); four classes of aspect (North, South, West and East); and three classes of elevation (low: 1174-1332 m a.s.l., medium: 1332-1490 m and high: 1490-1648 m). The reason for stratifying the study area was to account for any environmental heterogeneity and floristic variation according to the topographic aspects (Yirdaw et al. 2015). Thirty 0.05 ha circular plots were randomly established within stratified compartments and used as sample plots for tree species above 10 cm diameter. The coordinates of these plots were randomly obtained in the

Quantum GIS software. Inside each 0.05 ha circular plot, a smaller circular plot of 0.025 ha was also set for recording species with 5 to 10 cm diameter. Tree species names, tree number and diameter at breast height (DBH) were recorded. Detailed information on abundance, density per plot and basal area of plant species (including bee plant species) recorded on the inventory plots are presented in Appendix B.

This floristic data was completed with information on honey bee forage resources for each plant species. The book on 'Beeplants of South Africa' (Johannsmeier 2005) was used to gather the information on nectar value, pollen value and flowering time of each plant species. The information is only applicable to the honey bee, as other pollinators have other specific preferences. Plant species names and synonyms were referenced using http://www.tropicos.org/ and http://www.ipni.org/. The nectar and pollen values of honey bee plants were ranked from 0 (no nectar/pollen is available to, or collected by honey bees) to 4 (very good and major source), with 1, 2 and 3 denoting poor, minor to medium, and medium to good source of nectar/pollen, respectively (Johannsmeier 2005). The nectar values assigned to a bee plant refer to the amount of nectar that is available to honey bees in a flower of that plant (Johannsmeier 2005). The author used the forager method (which consists of assessing the relative abundance of pollen foragers), pollen analysis of honey and evaluation of trapped pollen to rate the bee plants. The flowering time (number of months) refers to the period within which the forage plants are expected to flower.

3.2.3. Data analysis

3.2.3.1. Potential of Mistbelt forests to harbour honey bee plants

To evaluate the potential of honey bee plant species in the Mistbelt forests, the diversity of honey bee plants was first assessed, and the most important honey bee forage plant species, identified.

We used species richness (total number of bee plant species recorded) and Shannon-Wiener (H) diversity index (Magurran 1988) to assess honey bee plant diversity. Species-accumulation curves were additionally set based on sample plots. The species richness, Shannon-Wiener diversity index and the species-accumulation curves were performed with the FD package (Laliberté and Legendre 2010; Laliberté et al. 2015) in R software (R Development Core Team 2015). It was tested whether the variation in plant diversity (all species) was associated with variation in bee forage plant species. The individual effect of all plant richness on bee plant richness was tested using Generalised linear model (GLM). Bee plant richness was modelled as count data, using GLM with Poisson error structure. Count data is often over-dispersed. Over-dispersion in bee plant richness was checked using the "qcc.overdispersion.test" function of library "qcc" of the R statistical software.

To identify the most important honey bee plant species, a Forage Value Index (FVI) was defined for each plant species in each sample plot, based on the flowering time, nectar and pollen values, as follows:

$$FVI_{ij} = RD_{ij} \times (N_i + P_i) \times \frac{FT_i}{12} \qquad (2)$$

where FVI_{ij} is the Forage Value Index of the ith honey bee plant species in the jth sample plot. N_i, P_i and FT_i are respectively the nectar value, pollen value and the flowering time (number of months) of the ith honey bee plant species. The value 12 in the above formula refers to the number of months in a year. RD_{ij} denotes the relative density of the ith honey bee plant species in the jth sample plot, and is calculated as follows (Curtis 1982):

$$RD_{ij} = \frac{G_{ij}}{\sqrt{Dg_{ij}}} \qquad (3)$$

where G_{ij} and Dg_{ij} are the basal area of the stem and quadratic mean diameter of the ith honey bee plant species in the jth sample plot, respectively. The basal area (expressed in m^2) was computed as the sum of the cross-sectional area at 1.3 m above the ground level of all bee plants recorded inside a plot. The reason of using the relative density (as defined by Curtis (1982)) in the FVI index, is that it provides a simple and convenient scale of density that accounts for tree size, which scales with crown size and therefore with flowering area and amount of flowers (Otárola et al. 2013). The relative FVI (RFVI, %) of each honey bee plant species was thus assessed by dividing the plot-based average FVI of each bee plant species by the total (all bee plant species) plot-based average FVI. RFVI is indicative of the relative contribution of each honey bee plant species to the total forage value. RFVI was thus calculated using the following formula:

$$RFVI = \frac{\frac{1}{z}\times\sum_{j=1}^{z} FVI_{ij}}{\sum_{i=1}^{s}(\frac{1}{z}\times\sum_{j=1}^{z} FVI_{ij)}} \times 100 \qquad (4)$$

where z is the total number sample plots, s is the total number of honey bee plant species and FVI_{ij} is the Forage value index of the ith honey bee plant species in the jth sample plot.

3.2.3.2. Availability of forage resources (nectar and pollen)

To assess the availability of forage resources for honey bees, the distributions of nectar/pollen values and of the flowering time (number of months) based on the number of bee plant species, were first examined. The temporal repartition of honey bee flowering plant from January to December was explored afterwards.

A monthly forage value was also defined for the nectar and the pollen separately, by summing up the respective nectar and pollen values of all bee plant species flowering in that month. The total forage value (i.e. nectar plus pollen) was additionally considered. These monthly values were plotted to determine the period of greater potential availability of forage resources within a year period.

3.2.3.3. Modelling forage value and plant diversity (overall plant richness and bee plant richness)

Here, species richness at plot level was used to account for the variation of plant diversity (all plant species, including honey bee plants). For honey bee plant diversity, the plot level bee plant richness was considered. As for forage value, the plot level FVI (FVI_j) was calculated for all honey bee plant species by summing up the FVI_{ij} values as follows:

$$FVI_j = \sum_{i=1}^{s} FVI_{ij} \quad (5)$$

where s is the total number of honey bee plant species and FVI_{ij} is the Forage value index of the ith honey bee plant species in the jth sample plot. FVI was thus related to plant richness and honey bee plant richness by fitting separate GLMs with Gaussian error structure, FVI being normally distributed (Shapiro-wilk statistic = 0.936; p > 0.05). Specifically, the GLMs were fitted to assess (1) individual effect of plant diversity (all species richness), and (2) individual effect of bee plant richness. The GLMs were performed using the "glm" function in the R statistical software. The overall significance of the models were tested by comparing the obtained deviance with the asymptotic chi-square.

3.3. Results

3.3.1. Diversity of woody bee plants and important bee forage plant species

Out of 50 woody plant species identified during the inventory, 24 species (48 %) were honey bee plant species and belonged to 23 genera and 19 families. The Rutaceae and Stilbaceae families were ranked first and had the highest number of bee plants species (n=3, 12.5% each), followed by the Rubiaceae family (n=2, 8.33%). The remaining families were weakly represented, with only one species each. Of the 24 bee plant species, 15 species were enumerated between 5 and 10 cm DBH while 22 species were recorded for stem of >10 cm DBH. The Shannon diversity index was estimated at 2.17 for the > 5 cm DBH data, and did not vary much between 5-10 cm (H=2.07) and >10 cm DBH classes (H=2.08). The species-accumulation curves based on the number of plots showed an asymptotic trend towards a unique value (25 species; Fig. 3.1A), suggesting that the sampling was adequate and the actual value of bee plant richness was not far from being completely recorded within the study region. The results from the Poisson GLM showed that the diversity of bee plants increased with increasing all plant species richness (β = 0.08; p = 0.002). Plant diversity therefore was a significant predictor of bee plant richness, explaining 46.42 % of its variation (Figure 3.1B).

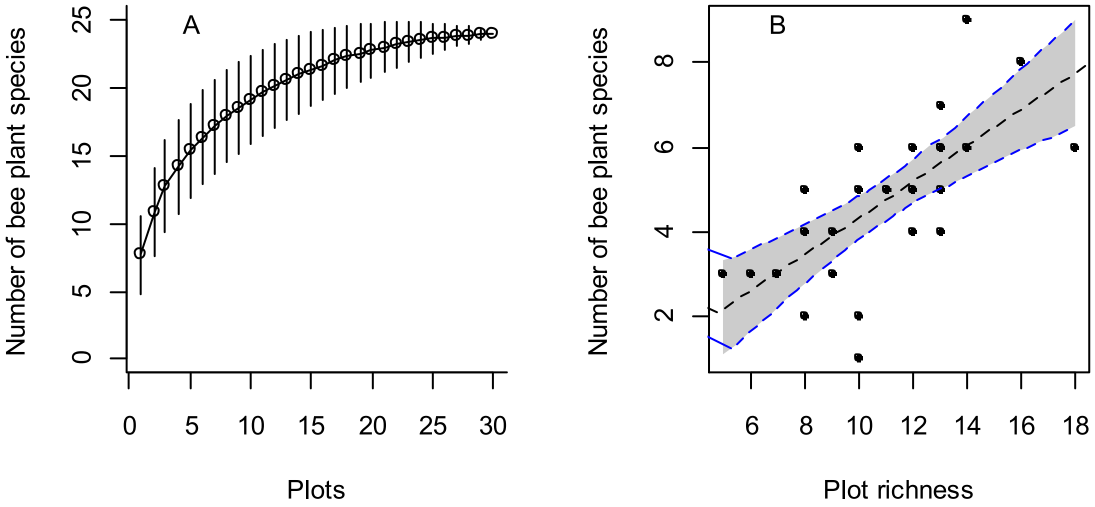

Figure 3.1. Species accumulation curves for bee plant species, based on the number of sampled plots (A), and scatterplot of the relationship between bee plant richness and all plant diversity (B).

3.3.2. Temporal availability of forage resources (nectar and pollen)

The patterns of availability of bee forage resources (nectar and pollen; Fig. 3.2) showed a tendency to a bell shape with more than 20 honey bee plant species being medium sources of nectar and pollen. Meanwhile, very few species (less than 5) were revealed to be excellent sources of nectar and pollen (Fig. 3.2).

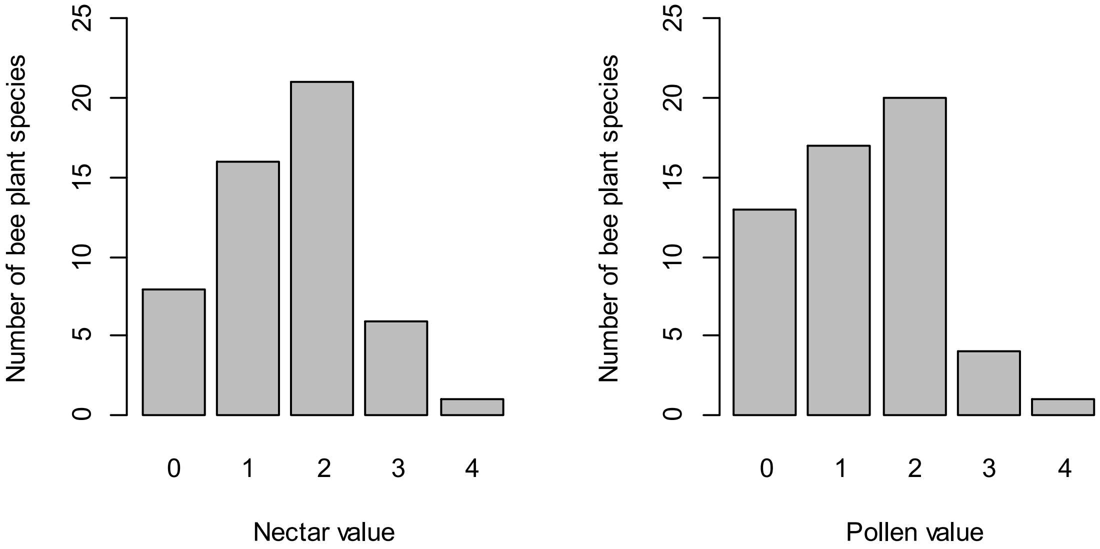

Figure 3.2. Distribution of bee plant species according to the nectar and pollen values

Examination of the distribution of the flowering period of bee forage plants revealed great variation in its length (Fig. 3.3). The flowering periods of five and six months were the most represented (13 species). The flowering periods overlapped for most species. However, the period from September to February was found to be the one at which several honey bee plants (from 10 to 18 species) produce flowers (Fig. 3.3).

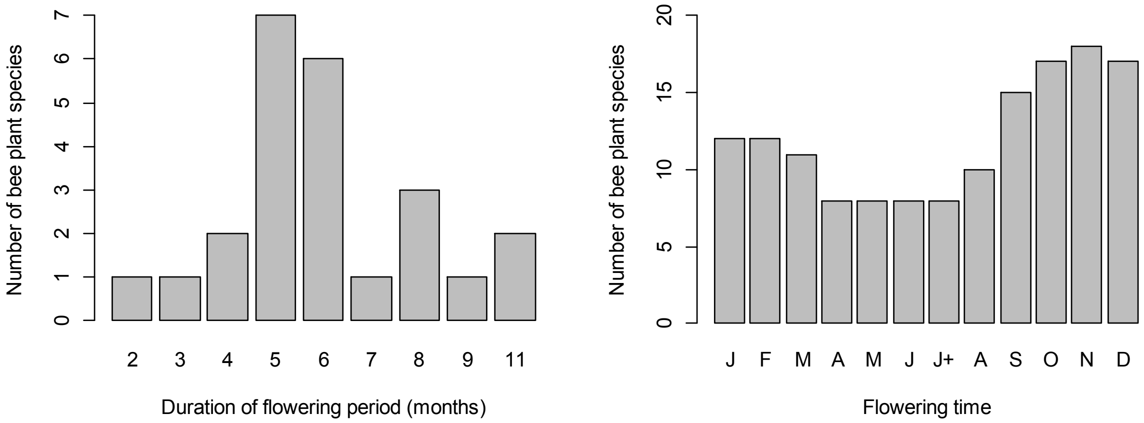

Figure 3.3. Distribution of bee plant species according to the flowering duration (months) and flowering time (month of the year)

October to November was the period of greatest production of pollen whereas November to December was the period of the greatest production of nectar (Fig. 3.4). Altogether, October to December was the period of year the forage value (and thus the forage provision) was at its maximum whereas April to July is the period of minimal forage provision (Fig. 3.4).

The important bee plant species based on the relative forage value index are shown in Table 3.1. Examination of FVI to reveal the important bee plant species showed that *Syzygium gerrardii* was the most important honey bee plant in terms of forage provision. It was followed by *Combretum kraussii*, *Ochna arborea*, *Nuxia floribunda* and *Nuxia congesta*. Out of the 24 identified honey bee plant species, the ten most important contributed 90.59 % of the total forage supply, mostly covered the period from September to December.

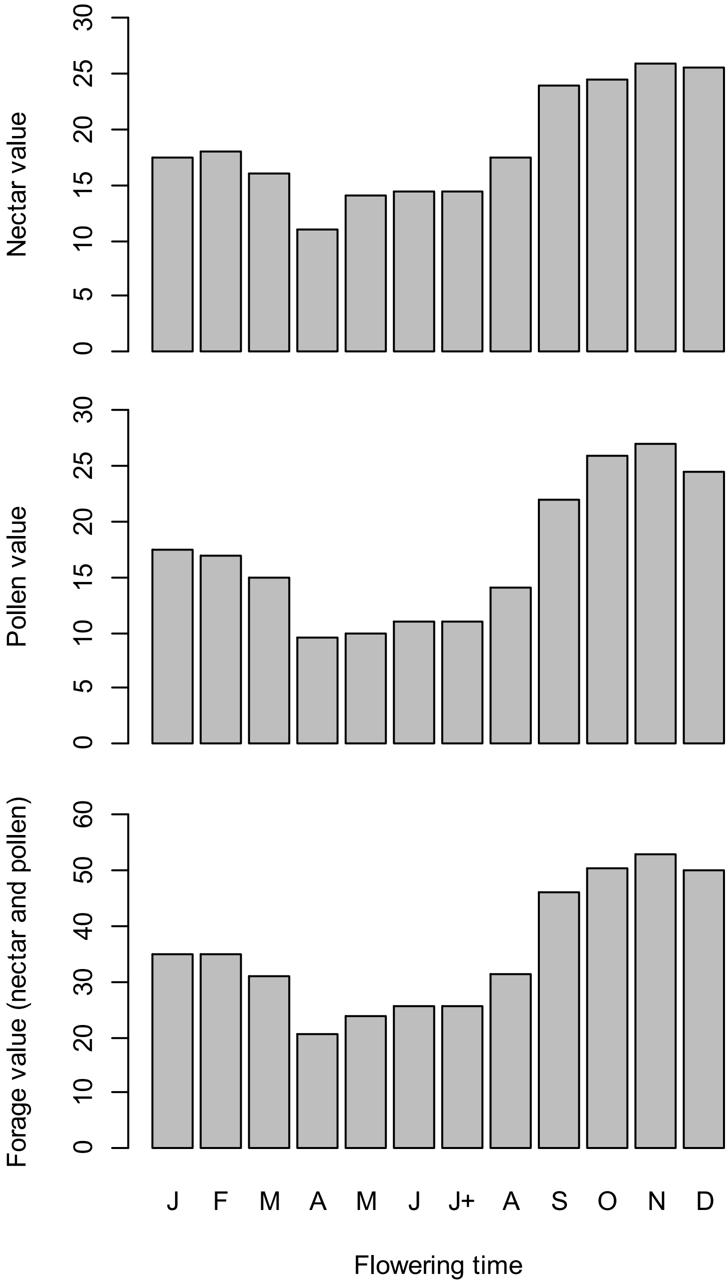

Figure 3.4. Distribution of the forage value (nectar and pollen values) according to the flowering time (month of the year).

3.3.3. Individual effect of plant diversity (richness) and honey bee plant richness on forage value

Results of GLMs describing the individual effects of plant richness and bee plant richness on forage value index are shown in Table 3.2. The forage value index was influenced by bee plant richness ($\beta = 0.004$; $p < 0.001$), but not by total plant richness ($p = 0.275$). The bee plant richness alone explained up to 40.31 % of the variation of the forage value index.

Table 3.1. Important honey bee plant species with their RFVI (relative forage value index) in the sample; the 10 most important species are highlighted in bold.

Family	Species	RFVI (%)
Myrtaceae	*Syzygium gerrardii*	34.81
Combretaceae	*Combretum kraussii*	10.76
Ochnaceae	*Ochna arborea*	7.90
Stilbaceae	*Nuxia floribunda*	7.42
Stilbaceae	*Nuxia congesta*	6.53
Rosaceae	*Prunus africana*	6.05
Curtisiaceae	*Curtisia dentata*	5.22
Asteraceae	*Brachylaena transvaalensis*	4.25
Euphorbiaceae	*Croton sylvaticus*	3.87
Rubiaceae	*Kraussia floribunda*	3.79
Achariaceae	*Kiggelaria africana*	3.57
Rutaceae	*Calodendrum capense*	0.89
Salicaceae	*Trimeria grandifolia*	0.85
Malvaceae	*Dombeya burgessiae*	0.83
Rutaceae	*Zanthoxylum davyi*	0.53
Rubiaceae	*Rothmania capensis*	0.53
Aquifoliaceae	*Ilex mitis*	0.47
Stilbaceae	*Halleria lucida*	0.43
Myrsinaceae	*Rapanea melanophloeos*	0.39
Fabaceae	*Calpurnia aurea*	0.27
Oleaceae	*Olea capensis ssp macrocarpa*	0.24
Rutaceae	*Clausena anisata*	0.18
Ebenaceae	*Diospyros whyteana*	0.18
Cannabaceae	*Celtis africana*	0.03

Table 3.2. Results of GLMs showing the individual effects of plant diversity (all plant richness and bee plant richness) on forage value index

Dependent variable	Independent variables						
		Est.	SE	t	*P*	Deviance	Pseudo R^2
Forage value index	(Intercept)	0.011	±0.008	1.37	0.181		
	All plant richness	0.0008	±0.0007	1.11	0.275	1.29	04.24
	(Intercept)	0.001	±0.005	0.11	0.911		
	Bee plant richness	0.004	±0.001	4.35	<0.001	15.49	40.31

3.4. Discussion

Many previous studies have elucidated the positive relationship of area of natural forests covered (within a certain foraging distance) with abundance of flower visiting insects (especially wild and managed bees), pollination success, seed set and fruit production in agricultural systems (Bennett and Isaacs 2014; Blanche et al. 2006; Munyuli 2011; Ricketts et al. 2004; Taki et al. 2011). This chapter provides evidence on the potential of forests to supply forage resources (nectar and pollen) to managed honey bees.

Twenty four plant species (accounting for 48 % of woody plant richness) with highly diversified genera and families, were identified as sources of nectar and pollen for honey bees. Such high diversity of bee plants suggests diversity of flowers and differences in plant nectar and pollen quality (Blüthgen and Klein 2011; Hülsmann et al. 2015), which would be prerequisites to attract and maintain honey bee colonies. As pointed out by Blüthgen and Klein (2011), pollen and nectar from different bee plant species could be more nutritious than pollen or nectar from a single plant species. Therefore, such diversity of bee plants in the Mistbelt forests would promote nutrition balance for honey bees, through mixed diet (pollen and nectar from different species) and enhanced complementary nutrition (Blüthgen and Klein 2011).

Although this study was only limited to woody and shrub plants, which could constitute a major gap as small shrubs and forbs also provide pollen and nectar resources (Johannsmeier 2005), the results point out the importance of Mistbelt forests to conserve bee plant species. This is reinforced by the Poisson GLM results, as it was found that bee plant richness increased with increasing plant diversity at plot level. These natural forests harbour several tree and shrubs species, and conserving of these forests will promote the availability of honey bee plant species utilisable for beekeeping activities.

Some bee forage plant species flower simultaneously, providing advantage for differential visitation and resource specialisation with other wild bees and insect pollinators (Taki et al. 2011). This is in line with Blüthgen and Klein (2011) who indicated that different pollinator species could utilise and pollinate different plant species, as results of complementary specialisation of plant-pollinator interactions. Across all bee plant species, there was highly varying flowering period, which is not a surprise, especially in hyper-diverse environments (Adgaba et al. 2013; Garbuzov and Ratnieks 2014). The variation in bee plants' flowering period is the reflection of high bee plant species richness, which could be beneficial for the management of honey bee colonies. Specifically, the variation in phenology of bee plant species increases the temporal availability of bee forage, and could help to sustain these colonies, either spatially or temporally (Blüthgen and Klein 2011). Given that managed honey bees can contribute to honey production and crop pollination (Allsopp et al. 2008; Crane 1999), the actual pattern of temporal availability of forage for honey bees indicates that opportunities exist to develop beekeeping activities for honey production, and to maintain honey bee colonies for future pollination services in surrounding environments (Melin et al. 2014). The finding that flowering occurred throughout the year suggests that beekeepers can exploit the honey for a long period, especially because some bee plants can even be more attractive than others due their longer flowering period (Garbuzov and Ratnieks 2014). This result suggests including these forests in the forage calendar of the apiculture industry in the Limpopo province to help beekeepers to successfully make use of the available floral resources on time.

Based on the finding that the number of bee plants flowering, as well as the nectar and pollen values peaked during the period from September to December, it is suggested that honey bee hives be placed close to these Mistbelt forests during that period. However, as flowering period is sensitive to rainfall and soil moisture conditions, and climate/micro-climate conditions are continually changing, long term research should be undertaken to determine whether the duration of the flowering time of these honey bee plants shifts over time.

The determination of the forage value index was based on the assumption that availability of floral resources would greatly increase with increasing bee plant structural characteristics (density and stem basal area). The use of honey bee plant structures (density and basal area) as weighing variables at plot level, can simply be explained by the importance of dominance patterns for the availability of flower resources (Otárola et al. 2013). In a recent study, Otárola et al. (2013) showed that the total flower coverage and the flowering time increased with increasing tree size. Similarly, Hülsmann et al. (2015) related the blooming product, which is a measure of the flowering area, with the abundance of flowering plants and the amount of floral resources. However, because this study was not based on observation of honey bees, it is important to cautiously make interpretations, as very abundant flowering plant taxa (family or species) can attract foraging bee species even much less than does a rare particular taxa. For instance, as suggested in other studies and for other bee species, particularly bumble bees, richness in pollen protein of particular plant families can have a marked influence on the observed visitation pattern (Goulson et al. 2005; Hanley et al. 2008) even if these families are not abundant (Hülsmann et al. 2015).

When analysing the contribution of bee plant species to the forage supply, it was found that, although plant species capable of attracting honey bees were diverse, only a few (10 species) contributed to the maximum forage provision. This finding agrees with Hülsmann et al. (2015) who reported similar patterns on other bee species (bumble bees). Thus not all honey bee plant species in a community, but rather only few are sources of major nectar and pollen used by honey bees. This result is also to some extent in agreement with Crane (1990) who reported that only a small percent of the world’s bee plants are source of most of the world’s honey. The greater contribution to the total forage value, made by few species in the study site can be explained by the fact that these species are abundant and colonise more easily the area. This suggests that conservation should prioritise these species in the Mistbelt forest, and that enrichment or reforestation programs can be developed using these species, especially in forest margins that are close to crops fields.

In attempting to model forage provision in response of plant diversity (overall plant species richness and bee plant species richness), it was first found that overall plant richness did not significantly influence the forage value. It has generally been shown that more diverse forest habitats offer more nesting opportunities (floral and nesting resources) than other natural habitats such as grasslands (Bennett and Isaacs 2014; Brosi et al. 2007), probably because these forests usually contain hundreds of species (trees and forbs) with diverse flowering time and nectar and pollen production. In this line, the nonsignificant effect of all plant richness on the forage value index, was somewhat surprising. This finding, however, could be due to the fact that the analysis of the diversity was only done at the plot level, rather than across different forest sites with different diversity level.

Unlike overall plant species richness, bee plant species richness showed significant positive effects with the forage value index, which supports the idea that higher bee plant diversity will provide continuous forage supply that is essential for long-lived bee colonies. Specifically, in highly diverse forest habitats, the more the bee plant species flower, the higher the foraging opportunities. Furthermore, as bees can exhibit a high degree of specialisation (Blüthgen and Klein 2011), the increased forage value (as result of increased bee plant richness) could offer the possibilities to support many honey bee hives. Altogether, the findings that overall plant richness promotes bee plant richness, and that increasing bee plant richness increases forage value index, suggest that plant diversity loss would have knock-on negative effects on forage resources (Carvell et al. 2006; Goulson et al. 2005). Basically, if the amount of forage provided decreases, fewer honey bees can remain on sites or less temporary hives can be supported. These results also suggest that conservation needs to be specifically oriented towards bee forage species in the Mistbelt forests to preserve and enhance their potential to maintain honey bee colonies.

Chapter 4. Aboveground biomass and carbon in a South African Mistbelt forest and the relationships with tree species diversity and forest structures

Abstract

Biomass and carbon stocks are key information criteria to understand the role of forests in regulating global climate. However, for a bio-rich continent like Africa, ground-based measurements for accurate estimation of carbon are scarce, and the variables affecting the forest carbon are not well understood. Here, we present the first biomass study conducted in South Africa Mistbelt forests. Using data from a non-destructive sampling of 59 trees of four species, we (1) evaluated the accuracy of multispecies aboveground biomass (AGB) models, using predictors such as diameter at breast height (DBH), total height (H) and wood density; (2) estimated the amount of biomass and carbon stored in the aboveground compartment of Mistbelt forests and (3) explored the variation of aboveground carbon (AGC) in relation to tree species diversity and structural variables. There were significant effects of species on wood density and AGB. Among the candidate models, the model that incorporated DBH and H as a compound variable (DBH^2xH) was the best fitting. AGB and AGC values were highly variable across all plots, with average values of 358.1 Mg ha^{-1} and 179.0 Mg ha^{-1}, respectively. Few species contributed 80% of AGC stock, probably as results of selection effect. Stand basal area, basal area of the ten most important species and basal area of the largest trees were the most influencing variables. Tree species richness was also positively correlated with AGC, but the basal area of smaller trees was not. These results enable insights into the role of biodiversity in maintaining carbon storage and the possibilities for sustainable strategies for timber harvesting without risk of significant biomass decline.

Keywords: climate regulation; non-destructive sampling; allometric equations; wood density; carbon density

4.1. Introduction

Tropical forests harbour a considerable number of plant species that underpin ecosystem functioning (Balvanera et al. 2005; Díaz and Cabido 2001; Ruiz-Jaen and Potvin 2010), provide forage resources to insect pollinators (Goulson 1999; Jha and Kremen 2013; Pywell et al. 2005), contribute to control biological invasion, and help alleviate the effects of climate change by storing atmospheric carbon (Pan et al. 2011; Saatchi et al. 2011). As pointed out by Pan et al. (2011), more than 40% of the global terrestrial carbon is contained in the living biomass of these forests. Assuming that most of these functions and services are vital for human beings, climate regulation services are particularly critical with regard to increasing anthropogenic greenhouse gas emissions in the atmosphere and its subsequent adverse effect on climate (Beer et al. 2010; Pan et al. 2011).

Carbon accounting and climate change mitigation activities are central topics in the landscape management debate (MEA 2005), and as a result, accurate and reliable information on contribution of land use to alleviate the effects of changing climate are needed. However, for much of Africa, there is still a lot of uncertainty about the amount of aboveground biomass (AGB) and belowground biomass and carbon stocks in indigenous forest ecosystems and in particular, in the tropical and sub-tropical regions (Chave et al. 2014, 2005).

Indigenous forests in South Africa are not spatially significant (approximately 0.56% of the total land area of the country), but they support a high proportion of the country's floral diversity (Mucina and Rutherford 2006) and contribute important ecosystem services to the local population. These indigenous forests have been intensely fragmented and exposed to illegal timber harvesting in the past (Geldenhuys 2002). The modification of fire regimes to protect the agricultural farms and plantations surrounding these forests, has favoured a natural successional development that has contributed to the conversion of some degraded forest areas into forest vegetation (Geldenhuys 2002). Mistbelt forests are some of the indigenous forests that have recovered from the modification of fire regimes. In the Limpopo province of South Africa, these forests occur as fragmented patches in zones of low and highland, and form with surrounding pine and eucalypt plantations and commercial farming areas, a succession of widely distributed landscapes with a great potential of supply of fibres and food.

With the large greenhouse gas emissions due to industrialisation, deforestation and forest degradation, care should be given to management policies aiming to balance the production of food, fibres and fuels with the protection of biodiversity and regulation of global climate change (Jose and Bardhan 2012). Accounting for the potential of biophysical units in a landscape to store atmospheric carbon is vital for policy and management decisions. More specifically, the clear understanding of the relative role of these forests in carbon sequestration and climate regulation would support the motives behind land relocation and landscape management schemes. To date, many studies have addressed the biomass and carbon stocks in common plantation genera such as *Pinus*, *Eucalyptus* and *Acacia* in South Africa (Dovey 2009; du Toit 2008; Phiri et al. 2015), while comparatively very little attention has been given to native species and natural woody vegetation (see for example, the study by Colgan et al. (2013) which is one of the rare biomass studies in natural woody vegetation in South Africa). This results in a lack of precise information about these forests, and appears as a drawback for accurate local and national carbon inventories. It is also a drawback for economic incentives and in particular, the implementation of carbon credit market mechanisms for the conserved forest areas (Lung and Espira 2015).

From previous studies, the quantification of forest biomass relies on different methods, from remote sensing techniques to tree-based allometric approaches (Chave et al. 2005; Kunneke et al.

2014; Magalhães and Seifert 2015; Picard et al. 2015; Seifert and Seifert 2014). Multispecies allometric equations have been extensively studied and offer possibilities to accurately estimate forest biomass at smaller scales, and to elucidate the relationships of forest biomass with stand variables. Recent studies have shed light on the influence of forest stand variables and tree species diversity on the forest biomass and carbon stocks (Day et al. 2014; Poorter et al. 2015; Sharma et al. 2010), and how these relationships can serve not only to suggest appropriate management strategies to increase carbon storage (Lung and Espira 2015), but also to test niche complementarity and selection effect hypotheses (Cavanaugh et al. 2014; Ruiz-Jaen and Potvin 2011). The niche complementary hypothesis suggests that higher diversity in forest ecosystems would allow a greater variety of functional traits and provide opportunities for efficient resource utilisation, thereby increasing ecosystem functions (for example, carbon storage). The selection effect hypothesis assumes that highly diversified ecosystem would allow higher probability of occurrence of dominant species or traits that would positively influence the ecosystem function. Both hypotheses have been subject to intense debate about the processes behind ecosystem functioning.

In this study, the aim was to quantify the stand biomass and carbon stocks in a Mistbelt forest, a typical multi-storey, multispecies forest in South Africa, and to understand their variation in relation to the stand characteristics and biodiversity. To our knowledge, this is the first biomass study in these Mistbelt forests in South Africa. The method was built upon forest inventory, tree sampling, laboratory processing and biomass modelling. Therefore, the objectives of this study were to:

(1) Develop three multispecies AGB equations and compare their ability to accurately estimate AGB at tree level; to do so, we first determined if wood density and AGB varied among study species. We next tested whether the inclusion of tree height and wood density in biomass equations reduced the estimation error.

(2) Estimate the total amount of biomass and carbon stored in the aboveground compartment in Mistbelt forests; we used the best multispecies AGB equation and the forest inventory data to upscale AGB from tree level to stand level; we next applied the carbon fraction commonly used in natural forests.

(3) Understand the aboveground carbon (AGC) variation in relation to the forest tree species diversity (richness) and stand characteristics. We assumed that selection effects and dominance patterns are the main drivers of carbon variation.

4.2. Materials and Methods

4.2.1. Study area

This study was conducted in the northern Mistbelt forests of Limpopo Province in South Africa (Mucina and Rutherford 2006), classified as part of the Afromontane Archipelago in Africa (White

1983). These Mistbelt forests are found in the Southern end of the Mpumalanga escarpment as small and fragmented patches, and along the Northern escarpment as a large forest complex (Cooper 1985; Geldenhuys 2002). Most of these forests occur at an altitudinal belt spanning from 1050 to 1800 m above mean sea level. The area covered in this study (707 ha) is located in Woodbush- De Hoek State Forest (23°50'S, 29°59'E), near Tzaneen in the Limpopo Province. Annual mean precipitation varies from 1800 mm at higher altitude to 600 mm at lower altitudes (Geldenhuys 2002). The vegetation in the Woodbush- De Hoek State Forest is dominated by species such as *Xymalos monospora* (Harv.) Baill., *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb., *Combretum kraussii* Hochst., *Syzygium gerrardii* (Harv. ex Hook.f.) Burtt Davy, *Cryptocarya transvaalensis* Burtt Davy in the canopy and sub-canopy layers, and *Oxyanthus speciosus* DC., *Peddiea Africana* Harv., *Oricia bachmannii* (Engl.) I. Verd., *Kraussia floribunda* Harv. in the understorey vegetation, while herb layer is made up of species genus like *Isoglossa, Plectranthus, Stachys, Galopina*, etc (Mucina and Rutherford 2006).

4.2.2. Forest inventory and biomass data

The study area was stratified into compartments based on different classes of aspect, slope and elevation based on a digital elevation model. A first phase forest inventory was carried out using thirty replicates of a nested plot design, which consisted of 0.025 ha (hectare) circular subplot inside a 0.05 ha larger circular plot. These plots were established based on a stratified random sampling design. Diameter at breast height (DBH) was measured with a diameter tape, inside each 0.025 ha plot for trees between 5-10 cm DBH class, and inside the 0.05 ha plots for trees having more than 10 cm DBH. Total height (H) was additionally measured where possible, using a Vertex hypsometer. In total, 50 species were enumerated, of which four species were selected, on the basis of their greater relative contribution to stand basal area, for further sampling and quantification of biomass. The four selected species namely *Combretum kraussii* (Combretaceae), *Croton sylvaticus* Hochst. (Euphorbiaceae), *Syzygium gerrardii* (Myrtaceae) and *Trichilia dregeana* Sond. (Meliaceae) contributed 42% of the stand basal area. Among the species that were not considered, *Xymalos monospora* (Monimiaceae) and *Cussonia sphaerocephala* Strey (Araliaceae) were also dominant and covered 29% of the stand basal area. The remaining species (n=44) contributed 29% of the total stand basal area.

For each species selected, fourteen to sixteen individual trees (a total of 59 trees; Table 4.1) were chosen across a wide range of DBH, and measured for biomass quantification. DBH, H and wood core samples were collected on all selected trees. Wood core samples were taken at breast height level and crown base level (i.e. the level of insertion of the first branch of the living crown). Diameter was measured on standing stems at 2 meter intervals up to the crown base with help of a tree climber. On larger branches (basal diameter > 15 cm), both thick and thin-end diameters, respectively at the base and the end of branch, and the distance between these two points were determined. On smaller branches (basal diameter <15 cm), only the branch basal diameter was measured. In addition, two to four branches per tree were sampled at different height levels (distance from the ground) from eight individual trees for each species, for further determination of dry mass. As results, 19, 18, 20 and 16 branches were sampled for *C. kraussii*, *C. sylvaticus*, *S. gerrardii* and *T. dregeana*, respectively. To obtain the dry mass, branch wood and leaf samples were oven-dried at 105°C until weight equilibrium was reached (Seifert and Seifert 2014). Data on branch dry mass were used to establish the branch biomass equations based on branch basal diameter, which explained 94.5%, 93.6%, 94.2% and 95.3% of the variation of the branch dry mass for *C. kraussii*, *C. sylvaticus*, *S. gerrardii* and *T. dregeana*, respectively. Wood density was determined by dividing the oven-dried mass of each wood core sample by its green volume (obtained from the water displacement method (Seifert and Seifert 2014)). The volume of standing stem plus larger branch sections was calculated by applying Smalian's formula (van Laar and Akça 2007), and the average values of wood density (based on the two wood core samples per tree) were used to calculate the wood biomass of the stem plus larger branches. The total AGB of each individual tree was then obtained by adding biomass of stem and larger branches to the branch biomass predicted from branch biomass regression equations. Table 4.1 shows descriptive summary of sampled trees.

Table 4.1. Descriptive summary (minimum and maximum values) of characteristics of measured tree species

Species	Number of trees	DBH (cm)	Height (m)	Wood density (g/cm^3)	AGB (Kg)
C. kraussii	16	1.5 - 91.0	3.1 - 24.2	0.51 - 0.66	0.26 - 4590.19
C. sylvaticus	14	4.8 - 64.0	5.4 - 28.0	0.38 - 0.50	4.17 - 5127.94
S. gerrardii	15	0.7 - 92.5	2.3 - 22.1	0.51 - 0.65	0.17 - 3423.33
T. dregeana	14	2.8 - 62.0	4.4 - 27.0	0.35 - 0.55	0.82 - 2357.97

4.2.3. Assessing the effect of species on wood density and AGB

We tested for the difference of wood density among species through a one-way analysis of variance (species as factor). Shapiro Wilk's statistic was used to test for the normality of the data. Because of the significant effect of species, Student-Newman-Keuls test was performed to classify the species according to their values of wood density. It was also tested whether (and how) the biomass allocated to the aboveground compartment varied with species. Because biomass allocation is size dependent, the effects of species (categorical variable) and tree size (DBH, continuous variable) were assessed by performing a Generalised Linear Model (Zuur et al. 2009). Additionally, interaction effects between tree size and species were tested to determine if the effects of tree size would vary by species.

4.2.4. Multispecies DBH-height and biomass allometric models

As result of the forest inventory, total tree height was measured for 461 individual trees, accounting for 37 species. Tree diameter and height relationship was explored using scatter plots. Because, the power function fitted well with the observed data, the allometric relationship between tree DBH and height (H) was developed for all species using function in Equation 6

$$H = \beta_0 \cdot DBH^{\beta_1} \cdot \varepsilon \tag{6}$$

where H is the response variable, DBH the predictor, and ε the random error. Equation 6 can be linearized by applying the natural logarithm to H and DBH to obtain its logarithmic form (7) (Sileshi 2014; van Laar and Akça 2007)

$$\ln H = \ln \beta_0 + \beta_1 \ln DBH + \varepsilon' \tag{7}$$

Three allometric equations 8, 9 and 10 taking into account DBH (cm), H (m) and wood density ρ (g /cm^3), were used to fit the multispecies biomass models:

$$\ln AGB = \ln \beta_0 + \beta_1 \ln \rho + \beta_2 \ln DBH + \varepsilon' \tag{8}$$

$$\ln AGB = \ln \beta_0 + \beta_1 \ln \rho + \beta_2 \ln DBH + \beta_3 \ln H + \varepsilon' \tag{9}$$

$$\ln AGB = \ln \beta_0 + \beta_1 \ln \rho + \beta_2 \ln(DBH^2 \times H) + \varepsilon' \tag{10}$$

where β_0, β_1, β_2 and β_3 are the regression coefficients, and ε' the additive error. The selection of the best multispecies equation was based on the values of adjusted R^2, root mean squared error (RMSE), Akaike information criterion (AIC), percent relative standard errors (PRSE, %) and mean absolute deviation (MAD, %), as suggested by Chave et al. (2005), Sileshi (2014) and Fayolle et al. (2013). PRSE is defined as follows:

$$PRSE = 100 \times \left(\frac{SE}{|\theta|}\right) \tag{11}$$

where SE is the standard error of model parameter (θ) (Dumont et al. 2013). Value of PRSE greater than 20 % indicate unreliable parameter (McCune and Grace 2002). MAD is calculated using the deviation of the predicted versus observed response variable (Chave et al. 2005), as defined below:

$$\delta D = 100 \times \frac{|\bar{y} - y|}{y} \tag{12}$$

In Equation 12, y and $\bar{y}$ are respectively the observed and predicted values of the response variable. All deviations were averaged based on the total number of observations. The use of logarithmic transformation in the equations 7, 8, 9 and 10 induces a systematic bias in the final estimation of the response variable (Chave et al. 2005). To account for that bias, the predicted values were back-transformed into the original values and corrected by applying the correction factor, as defined in Baskerville (1972):

$$CF = e^{\left(\frac{RSE^2}{2}\right)} \tag{13}$$

where RSE is the Residual Standard Error of the regression.

4.2.5. Quantifying AGB and AGC at stand level

The best multispecies biomass equation was used to predict AGB for the total pool of species, based on DBH, total height (predicted from DBH-height models), and wood density. Since wood density was determined only for the studied species, the values of wood density for the species not sampled, were obtained from the global publicly available wood density database (Chave et al. 2009; Zanne et al. 2009). Average wood density was used when multiple values were available for a single species. When the wood density value was missing for a given species, the average genus wood density was used. Similarly, when genus data on wood density was missing, mean wood density at family level was used. In the case a family was missing, the average wood density of the plot was used as proposed by Stegen et al. (2009).

To upscale from the tree level to the stand level, the predicted AGB was first calculated at plot scale and averaged, based on the total number of plots. The AGB density (kg.ha^{-1}) was upscaled to stand level by applying the surface expansion factor (area of hectare/area of plot). Because nested plots design was employed during forest inventory (0.025 ha circular subplot within 0.05 ha circular larger plot), the AGB was computed for each DBH size class, i.e. 5-10 cm DBH in small subplot and >10 cm DBH in the large subplot. The calculated values were summed up to obtain the total AGB at stand level. The AGC stock was afterwards determined by applying the carbon fraction of 0.50 (Lung and Espira 2015).

4.2.6. Assessing the structural variables influencing AGC

Stand variables such as stem density, mean diameter and basal area have positive effects on carbon stocks, because these variables are the stand level attributes that reflect the structures of the plant communities. However, combined use of basal area, diameter and tree density can lead to double accounting of tree size, as the stand basal area already integrates population density and tree size. To determine the most important stand variables, the plot level basal area was partitioned based on the contribution of small trees (5-30 cm DBH), medium sized trees (30-60 cm) and large trees (>60 cm) (Mensah et al. 2014; Reque and Bravo 2008). The selection effect hypothesis assumes that dominance patterns drive ecosystem functioning. Thus the basal area of the 10 most important species at each plot was additionally quantified. The ten most important species were identified on the basis of their importance value index IVI (Curtis and McIntosh 1951). This index was determined for each species by summing up the species relative frequency, relative density and relative dominance (basal area), as follows:

$$\mathrm{IVI} = \frac{n_i}{\sum_{i=1}^{s} n_i} + \frac{f_i}{\sum_{i=1}^{s} f_i} + \frac{c_i}{\sum_{i=1}^{s} c_i} \tag{14}$$

where n_i, f_i and c_i are respectively the density, frequency and basal area of the i^{th} species. As results, stand basal area, basal area of smaller trees, basal area of medium sized trees, basal area of largest trees, basal area of 10 most important species, and species richness were considered as candidate variables influencing AGC at plot level. The bivariate relationships between AGC and these variables were explored, using scatter plots and fitting regressions. The variables that significantly explained AGC storage in the bivariate analyses, were additionally combined in a multiple linear regression model and a stepwise model selection procedure, to select the best predictors. All statistical analyses were performed with the R statistical software.

4.3. Results

4.3.1. Effect of species on wood density and AGB

Analysis of variance showed that wood density varied significantly among species (F= 40.34, $p < 0.001$), with 68.21 % of the variation being explained. The highest values of wood density were recorded by *C. kraussii* (0.593 g/cm^3 ± 0.011) and *S. gerrardii* (0.571 g/cm^3 ± 0.011) while the lowest mean wood density values (0.459 g/cm^3 and 0.445 g/cm^3) were found with *C. sylvaticus* and *T. dregeana* (Figure 4.1). The results of the Generalised Linear Model (Table 4.2) showed significant interaction effects between DBH and species. For a given tree size, *C. sylvaticus* had a scaling coefficient which was 0.31 ± 0.13, being significantly higher than the baseline (*C. kraussii*, Table 4.2). These results mean that, for the same values of DBH, *C. sylvaticus* would have significantly higher mean AGB at tree level, as compared to *C. kraussii*, *S. gerrardii* and *T. dregeana* which would have similar average AGB values at tree level ($p > 0.05$).

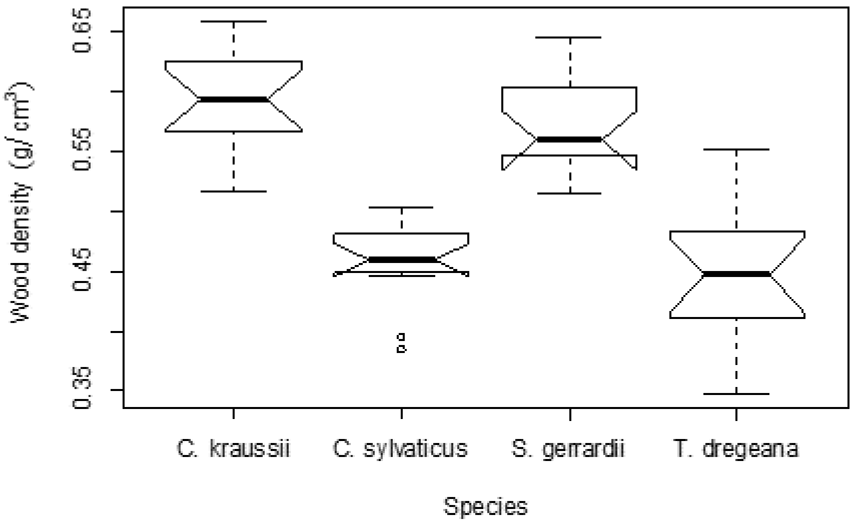

Figure 4.1. Variation of wood density (g/cm^3) among study species.

Table 4.2. Results of the Generalised Linear Models showing the effects of species and size on the aboveground biomass (AGB).

		Estimate	SE	t value	Pr(>|t|)
	(Intercept)	-1.963	±0.252	-7.791	0.000
Tree size	ln (DBH)	2.365	±0.079	30.036	< 0.001
Species	*C. sylvaticus*	-0.958	±0.439	-2.183	0.034
	S. gerrardii	0.403	±0.322	1.254	0.215
	T. dregeana	-0.465	±0.402	-1.155	0.253
Tree size: Species	ln (DBH): *C. sylvaticus*	0.309	±0.135	2.288	0.026
	ln (DBH): *S. gerrardii*	-0.132	±0.101	-1.305	0.198
	ln (DBH): *T. dregeana*	0.081	±0.125	0.644	0.523

4.3.2. Multispecies DBH-height and AGB allometric models

DBH and height data fitted well with the power law model used (Figures 4.2 and 4.3). Model coefficients, indicators for goodness of fit and correction factors of Equation 7 are summarised in Table 4.3. DBH explained 83.81% of the variation of total height, as shown by the value of adjusted R square. Model coefficients were highly significant ($p < 0.001$), indicating that tree diameter was a significant predictor of tree height for all species.

The comparison of the three fitted equations (Equations 8-10) for estimating AGB is also shown in Table 4.3. Equation 8 produced the poorest fits (non-existent effect of wood density, lowest R square, highest AIC, and highest residual standard and root mean square errors) while Equations 9 and 10 provided the best fit (highest variance explained and lowest residual errors and AIC), with additional significant effect of wood density ($p < 0.05$). Compared to Equation 10, Equation 9 proved to be less satisfactory because it showed high variance inflation factors (VIF) especially for the correlated variables such as DBH (8.105) and height (8.086). High VIF reflects collinearity between predictors and unreliable coefficients. Based on that, Equation 10 (incorporating DBH^2xH as single predictor) provided the best multispecies model for estimation of AGB. Taking that model into account, 98.45% of the variation in AGB is explained by positive and significant effects of wood density ($p < 0.05$) and DBH^2 x H ($p < 0.001$), with an associated correction factor of 1.03. The scatter plot of regression residuals versus predicted values did not show any heteroscedastic behaviour for the selected model (Figure 4.4). In addition, the trend in the observed and estimated values of AGB showed a very good coincidence with the linear equation ($y = x$) (Figure 4.4).

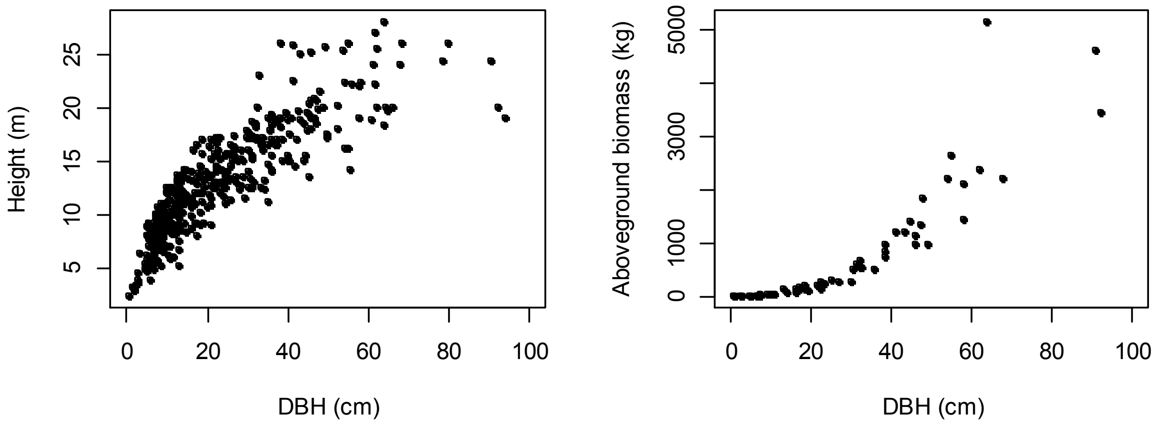

Figure 4.2. Variation of height and aboveground biomass (AGB) according to tree diameter.

Table 4.3. Multispecies DBH-height and aboveground biomass (AGB) equations with coefficient estimates and statistic fits. SE: Standard Error; R^2: Adjusted R Square; VIF: Variance Inflation Factor; RSE: Residual Standard Error and CF: Correction Factors.

Models	Equations	Predictors	Param.	Est	±SE	*P*	R^2	VIF	RSE	CF
Height	7	Intercept	ln (β_0)	1.01	0.03	<0.001	83.81	-	0.181	1.016
		DBH	β_1	0.51	0.01	<0.001				
AGB	8	Intercept	ln (β_0)	-1.89	0.25	<0.001	97.60	-	0.304	1.047
		Wood density	β_1	0.37	0.26	0.159		1.005		
		DBH	β_2	2.41	0.05	<0.001		1.005		
	9	Intercept	ln (β_0)	-2.84	0.27	<0.001	98.44		0.245	1.030
		Wood density	β_1	0.75	0.22	0.001		1.115		
		DBH	β_2	1.81	0.12	<0.001		8.105		
		Height	β_3	1.14	0.21	<0.001		8.086		
	10	Intercept	ln (β_0)	-2.69	0.21	<0.001	98.45		0.244	1.030
		Wood density	β_1	0.69	0.21	0.002		1.002		
		DBH^2xHeight	β_2	0.95	0.02	<0.001		1.002		

Height (m); DBH (cm); Wood density (g /cm^3) and AGB (kg)

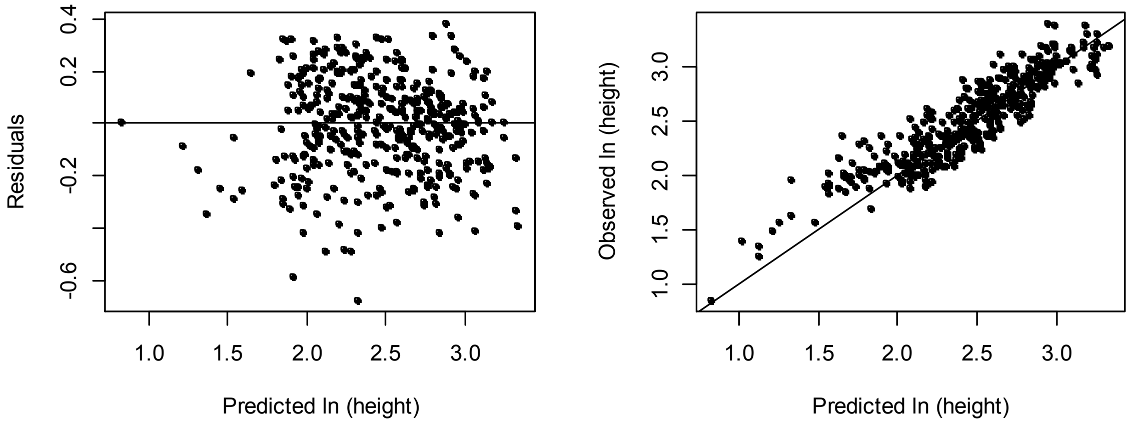

Figure 4.3. Residuals *vs.* predicted values and observed *vs.* predicted values of total height (Equation 7). Original units are in meter.

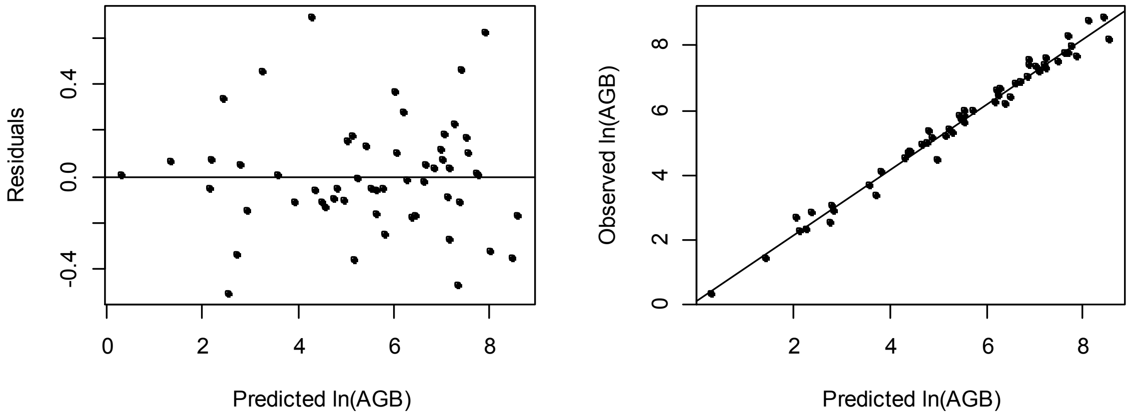

Figure 4.4. Residuals *vs.* predicted values and observed *vs.* predicted values of aboveground biomass (AGB). Values are predicted from Equation 10. Original units are in kilograms of dry mass.

4.3.3. AGB and AGC stocks at the stand level

The total AGB, when pooling all enumerated species together, was estimated at 358.1 ± 31.9 Mg ha^{-1} with a range of 98.2 – 952.2 Mg ha^{-1}. Approximate carbon stock of 179.0 ± 15.9 Mg ha^{-1} was estimated for aboveground component.

When assessing the contribution of species to the total pool of AGB and AGC, it was found that few species (8 out of 50 species) contributed 80%. The most substantial contribution came from *S. gerrardii* (25.3%), *Xymalos monospora* (15.4%), *T. dregeana* (12.8%) and *C. kraussii* (5.5%). *C. sylvaticus*, which is one of the focus species in this study, brought 4 % of the total AGB and AGC stocks. The pattern, however, differed from the forest understory layer (5 ≤ DBH < 10 cm), where some new species such as *Cassipourea malosana* (Baker) Alston, *Kraussia floribunda* and *Ochna arborea* var. *oconnorii* (E.Phillips) Du Toit contributed 30.2% of AGB and AGC stocks. Within that same layer, *S. gerrardii* and *Xymalos monospora* contributed 20.8%.

4.3.4. Factors influencing AGC stocks

AGC ranged from 49.1 Mg ha^{-1} to 476.1 Mg ha^{-1} across plots. Analyses of the bivariate relationships showed that stand basal area, basal area of the ten most important species and basal area of the largest trees (> 60 cm DBH) were the most influencing stand variables, with 95%, 77% and 59 % variation explained, respectively (Figure 4.5). Basal area of medium trees (30 - 60 cm DBH) and tree species richness were positively correlated with the AGC ($R^2 = 0.24$, $p = 0.006$ and $R^2 = 0.13$, $p = 0.04$, respectively Figure 4.5), but the basal area of smaller trees (5 - 30 cm DBH) was not (Figure 4.5). When all the stand variables that significantly correlated with AGC storage were combined in the multiple linear regression model, only stand basal area and basal area of the largest trees (>60 cm DBH) were retained in the final model, and best predicted positively AGC, overruling the species richness effect.

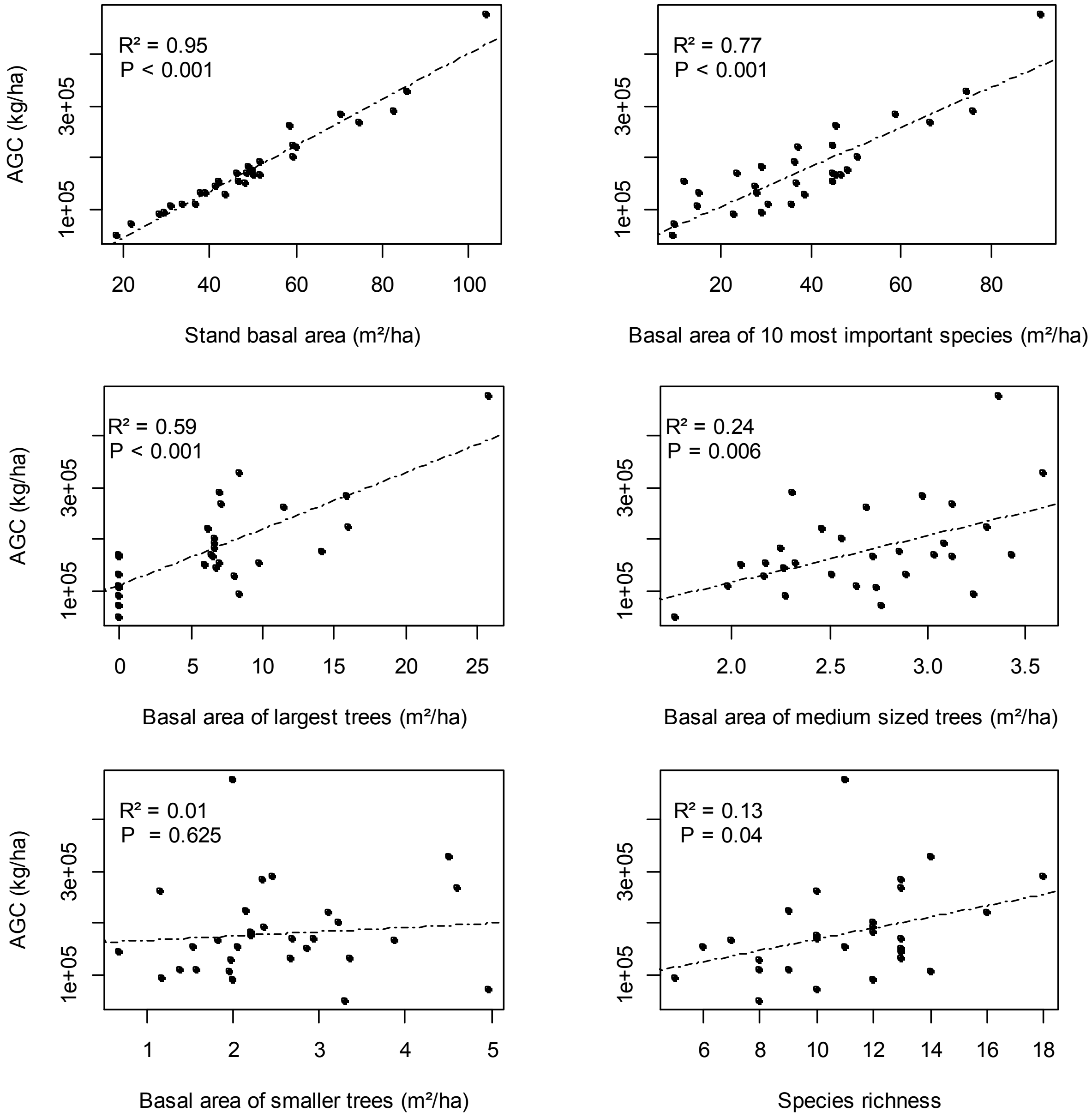

Figure 4.5. Bivariate relationships between aboveground carbon (AGC) and stand variables.

4.4. Discussion

4.4.1. Effect of species on wood density and AGB

The values of wood density found in this study are in the range of published values (Chave et al. 2009, 2006). The between species variation of wood density indicates that this variable is determinant for multiple species biomass assessments (Chave et al. 2006). By examining the effects of species on AGB, our results showed that species with relatively lower wood density had higher mean average wood biomass. This is in part because species with lower wood density typically grow faster than species with higher wood density (Wright et al. 2010). The significant effects of species on both wood density and AGB demonstrate that species perform differently in terms of resource acquisition and biomass production (Poorter et al. 2012). The fact that *C. sylvaticus* had higher biomass than *C. kraussii*, *S. gerrardii* and *T. dregeana* results from a greater foliage biomass production in *C. sylvaticus*, which seems to be consistent with the species leaf traits (Mensah et al. 2016b).

4.4.2. Uncertainties in the multispecies AGB equations

The AGB equations used in this study were based on a non-destructive sampling of 59 trees from four species. Commonly applied methods for accurate estimation of tree biomass rely on destructive tree sampling and measurement of samples' weight in the field. Accordingly, the non-destructive method used here might be a source of uncertainty in the allometric biomass prediction. However, in conserved natural forests (where tree felling is not authorized), this particular non-destructive method is the only available option.

Besides this, the representativeness of the selected species may be another source of uncertainty for the multispecies biomass equations. Indeed, four out of fifty species might not be sufficient enough to account for the variation in all species traits. Our methodological approach, which was based on branch biomass modelling in order to reconstruct the crown biomass, required an acceptable number and diameter range of branch samples; and due to the policy, time and resource constraints, it was relatively difficult to explore many species. Nevertheless, to quantify the biomass stocks at the stand level, it was assumed that the inclusion of multiple predictors (e.g. diameter, height and wood density) in the biomass equations would help to catch some variability of the characteristics of the species that could not be sampled in the field.

The actual sample size (59 trees) may not be entirely sufficient to account for the total variation of the species characteristics, and thus can also constitute a caveat for the reliability of our results. Larger sample data sets are often preferred, but are difficult to obtain especially for biomass studies in natural forests, because of their status and the amount of work that is required for measuring tree components (Ebuy et al. 2011). For instance, Ebuy et al. (2011), Deans et al. (1996), Henry et al. (2010) and Segura and Kanninen (2005) used respectively 12, 14, 42 and 19 trees to establish biomass allometric models. Although our sample size is low, it is higher than most of the sample sizes that are used in tree biomass studies in natural forests, with some exceptions however (Fayolle et al. 2013; Henry et al. 2011; Ngomanda et al. 2014). In addition, most of larger data sets used in tree biomass studies in natural forests, were obtained from a compilation of existing smaller data sets (Chave et al. 2014). To our knowledge the functions presented here are the first functions published for Mistbelt forests in South Africa.

4.4.3. Predictors for multispecies AGB equations

DBH, total height and wood density acted as potential predictors in the multispecies biomass equations, consistently to what is expected, and as also revealed in many recent studies (Chave et al. 2005; Fayolle et al. 2013; Ngomanda et al. 2014; Picard et al. 2015). DBH is commonly used because it is the most familiar and easily measured variable during national forest inventories. However, as pointed out by Fayolle et al. (2013), tree diameter should not be considered solely as a predictor for AGB, especially when dealing with several species or a species that does not show strong relationship between diameter and other tree characteristics (e.g. tree height). Contrary to DBH, the main reason why total height is often left out in evergreen tropical forests is because tree height is difficult to measure accurately within the complex or closed canopy forests (Fayolle et al. 2013). For that reason, and given the lower marginal variance that is often explained by additional use of height, some authors advocated using DBH alone as predictor of tree biomass (Fayolle et al. 2013; Segura and Kanninen 2005).

In reality, if height is included in biomass models as additional variable, then the implication is that any error in measuring height will propagate to tree level and further to stand level estimates (Garber et al. 2009). Even so, regarding the species-specific differences in DBH-height allometry, tree height is an important factor for biomass estimation (Picard et al. 2015; Temesgen et al. 2015). The inclusion of height as an additional variable helps accounting for variation in AGB among trees with same value of DBH (Picard et al. 2015), thus reducing the estimate errors (Chave et al. 2005). For instance, in this study, it was found that the additional use of height reduced the residual standard error by 19.73%. All being considered, for quantification of AGB stocks in multispecies forests, it is recommended that DBH and total height be measured for a reasonable number of trees from different species, in order to establish a multispecies DBH-height equation for estimation of total height for each individual tree, and account for it in AGB models.

While the use of both DBH and height is expected to improve the statistical fits of biomass equations, it is interesting to discuss how to allow for the simultaneous effects of DBH and height (Picard et al. 2015). Depending on how diameter and height are correlated, models can give rise to collinearity (Picard et al. 2015; Sileshi 2014), which deserves particular attention. In line with this, model that incorporated DBH^2xH as a compound variable, was the most parsimonious in that it helped accounting for within-species variation of height for same value of DBH while solving the problem of collinearity. DBH^2xH is expected to be good predictor because it is directly proportional to the volume of cylinder with diameter (DBH) and height (H). Chave et al. (2005) also found DBH^2xH as suitable predictor for tropical moist forest stand biomass. The results are also consistent with other recent studies that used DBH^2xH as variable in biomass models (Ngomanda et al. 2014; Picard et al. 2015).

Wood density was a good indicator of AGB, and thus for multispecies biomass equations (Chave et al. 2014). The significant effect of wood density indicates that within- and between species wood density patterns are important to explain biomass estimates. Between species variation would, however, strongly influence AGB because wood density affects tree specific growth and survival rate (Falster 2006). Accordingly, it has been documented that lower wood density allows for faster growth in size (Preece et al. 2015; Wright et al. 2010), probably because trees grow faster when the conductive tissue is less expensive (in terms of carbon) to construct (Chave et al. 2006; Suzuki 1999). The use of wood density is not common, although it is known to bring substantial improvement. The availability of global and regional wood density data bases should help to promote the use of that variable. However, the biomass estimates obtained by applying the values of wood density of such data bases (as used in this study) are not exempt from uncertainty. Fayolle et al. (2013) showed that using wood density from the global data base slightly increased the estimation errors. Therefore, the direct determination of wood density in field remains better for reliable biomass estimation, but not practical due to the great amount field and laboratory work, especially when dealing with several species.

4.4.4. AGB and AGC stocks at the stand level

When pooling all enumerated species together, the total AGB and AGC values for a diameter range above 5 cm across all plots are estimated at 358.1 ± 31.9 Mg ha^{-1} and 179.0 ± 15.9 Mg ha^{-1}, respectively. The average estimated AGB in the northern Mistbelt forests is above biomass estimates provided by Lung and Espira (2015) for an African tropical forest (279 ± 32.78 Mg ha^{-1}), but relatively lower than AGB values in Amazonian forests (312 - 464 Mg ha^{-1}) (Houghton et al. 2001), and in closed-canopy tropical forests (395.7 Mg ha^{-1}) (Lewis et al. 2013). Using the same diameter range, Fischer et al. (2015) estimated the total AGB at 385 Mg ha^{-1} for a tropical forest at Mt. Kilimanjaro. These comparisons showed that northern Mistbelt forests store substantially higher quantities of biomass and carbon stocks than some montane and sub-montane tropical forests (Baccini et al. 2008; Saatchi et al. 2011). A simple explanation for this is that these northern Mistbelt forests support, across a wide range of their geological and altitudinal gradients (Mucina and Rutherford 2006), not only a high floral diversity, but also a structurally diverse horizontal and vertical forest matrix (Geldenhuys 2002, 1997). As expected, the (taxonomic) diversity of trees and the stand structural variables such as (e.g. basal area, percentage of large trees) were found to explain a high variability of the estimated biomass and carbon density, as also reported in recent studies. More specifically, it was found that species richness was significantly and positively correlated with AGC. Indeed, it is a well-known pattern, especially at global scale, that carbon stocks increase with increasing diversity (Cavanaugh et al. 2014; Poorter et al. 2015; Wu et al. 2015). The positive relationships between tree species diversity and carbon stock in this study supports the idea that diversity-carbon patterns are also identifiable even at smaller spatial scales. In fact, tree species diversity correlates positively with carbon storage because higher species richness probably leads to higher stem density and higher forest productivity (Ruiz-Benito et al. 2014), i.e. basically, the more tree species are present in a plot, the more biomass is produced. While this seems to agree with the niche complementarity hypothesis (Tilman et al. 1997), the weak effect of trees species diversity on AGC suggests that dominance patterns are likely to be stronger.

Despite the higher biomass production of *C. sylvaticus* at tree level, our results showed that *S. gerrardii* was ranked first in terms of the relative contribution to AGB and AGC stocks. In addition, few species (8 out of 50 species) proved to greatly contribute to the biomass and carbon stocks (80%). These results reinforce the importance of other factors (e.g. stand related factors) influencing the biomass partitioning among species. More specifically, an important contribution of stand basal area, basal area of the ten most important species and basal area of the largest trees, was found in this order. The greatest influence of dominant stems has been evidenced in some previous studies (Chave et al. 2003; Slik et al. 2010). These information corroborate the fact that dominance patterns greatly influence the AGC stocks, thus supporting the selection effects hypothesis. In a recent study, Lung and Espira (2015) showed that tree stems larger than 50 cm have the greatest impact on forest biomass, and less than 16% of the species pool accounted for over 62% of the AGB. Ruiz-Jaen and Potvin (2011) and Cavanaugh et al. (2014) also showed that selection effects hypothesis contributes greatly to the carbon stocks.

Linking statement to Chapter 5

Understanding the relationship between biodiversity on the one side and biomass and carbon storage (as ecosystem function) on the other is one of the objectives of this thesis. A key result from the previous chapter was a significant increase in biomass and carbon stocks with increasing diversity, and an even stronger influence of most dominant species on the carbon variation, which suggests selection effects as the main mechanism. Recent research attempts to elucidate how diversity components (functional diversity and functional dominance, based on functional traits) drive biomass and carbon stocks, and the extent to which the findings support niche complementarity and selection effects hypotheses. In the next chapter (Chapter 5), we focussed on tree biomass at species level, and searched for the potential specific functional traits that influenced the allocation of biomass between the foliage and the wood components. We extended the analyses to six native species in the Mistbelt forests in South Africa.

Chapter 5. Patterns of biomass allocation between foliage and woody structure: the effects of tree size and specific functional traits

Abstract

Biomass allocation is closely related to species traits, resource availability and competitive abilities, and therefore it is often used to capture resource utilisation within plants. The aims in this study were to assess the patterns in biomass allocation between foliage and wood (stem plus branch), and how they changed with tree size (diameter), species identity and functional traits (leaf area and specific wood density). Using data on the aboveground biomass of 89 trees from six species in a Mistbelt forest (South Africa), the leaf to wood mass ratio (LWR) was evaluated. The effects of tree size, species identity and specific traits on LWR were tested using Generalised Linear Models. Tree size (diameter) was the main driver of biomass allocation, with 44.43 % of variance explained. As expected, LWR declined significantly with increasing tree diameter. Leaf area (30.17% explained variance) and wood density (12.61% explained variance) also showed significant effects, after size effect was accounting for. Results also showed clear differences among species and between groups of species. Per unit of wood mass, more biomass is allocated to the foliage in the species with the larger leaf area. Inversely, less biomass is allocated to the foliage in species with higher wood density. Moreover, with increasing diameter, lower wood density species tended to allocate more biomass to foliage and less biomass to stems and branches. Overall, our results emphasise the influence of plant size and functional traits on biomass allocation, but showed that neither tree diameter and species identity nor leaf area and wood density are the only important variables.

Keywords: Aboveground biomass, leaf area, leaf to wood mass ratio, Mistbelt forest, South Africa, partitioning, species identity, trunk diameter, wood density.

5.1. Introduction

Biomass production is a primary function of forest ecosystems that is influenced by an interplay of processes: roots capture nutrients from soil, stems and branches provide mechanical support and conduct water with nutrients, and leaves fix carbon (Poorter et al. 2012). Because plants have to balance the allocation of resources to roots, stem, branches and leaves in a way to enable necessary physiological activities for the functioning of these organs, only plants that are successful in acquisition of resources will maintain or achieve a regular growth (Bloom et al. 1985; Shipley and Meziane 2002). The extent to which acquisition and utilisation of resources vary among taxa would define the limit of plant biomass production (Reich 2002). Therefore, understanding the patterns of biomass partitioning within plants is of high importance in the field of tree physiology and plant ecology, and also has many applications for agriculture/forestry.

Biomass allocation has generally been used to capture resource utilisation by plants in empirical and simulation studies (e.g. Seifert and Müller-Starck 2009; Pretzsch et al. 2012; Rötzer et al. 2012; Tomlinson et al. 2014; Freschet et al. 2015). According to the optimal partitioning theory (OPT), plants should allocate more biomass to organs that have limited access to resources (Bloom et al. 1985). For instance, in water- and nutrient-limited environments, plants decrease the biomass allocation to foliage with increasing light availability (Shipley and Meziane 2002; Poorter et al. 2012). Similarly, in nutrient-limited soils, more biomass would be allocated to roots to increase use of water and nutrient resources (Deng et al. 2006; Poorter et al. 2012). Therefore, biomass allocation among plant organs is driven by above and belowground environmental conditions (Müller et al. 2000; Freschet et al. 2015), but plant size (Pino et al. 2002), ontogenic trends (Poorter et al. 2012; Xie et al. 2012), species competitive abilities (Ninkovic 2003; Dybzinski et al. 2011), species identity and functional traits (McCarthy et al. 2007; Poorter et al. 2015) can also act as potential covariates to define the investment in support tissues.

Many previous studies have emphasised the influence of plant size on biomass allocation (Bonser and Aarssen 2009; Poorter and Sack 2012; Xie et al. 2012), regardless of whether root to shoot ratio, or its inverse shoot to root ratio is used (Wilson 1988; Reich 2002; Mokany et al. 2006). The use of root to shoot ratio has the advantage of taking into account the whole plant, however, it condenses the total aboveground biomass into one compartment and therefore limits the investigation on the different organs (e.g. stem, branch, leaves) (Poorter et al. 2012). Whether the generalisation about plant size influence on biomass allocation also applies for aboveground organs alone, has received much less attention so far (Körner 1994; Poorter et al. 2015). In particular, as stem, branches and leaves have different physiological activities (Pearcy et al. 2005), analysing the patterns of biomass allocation between aboveground organs can produce additional information. Accurate quantification of wood (i.e. stem plus branch) and foliage biomass would allow for understanding such patterns, the extent to which they vary among species, groups of species, and according to specific traits.

Species groups, distinguished phylogenetically, morphologically or physiologically, are important because species from different groups may have different specialized strategies to optimize uptake of resources. Depending on plant traits, species are often grouped into woody or herbaceous species, angiosperms or gymnosperms, coniferous or broadleaved, deciduous or evergreen. Specific traits such as wood density, leaf area and maximum height could show strong influence on the allocation patterns (Mokany et al. 2006; Reich 2002). For instance, wood density is a good predictor of individual tree diameter increments (Wright et al. 2010), and correlates consistently with the biomass increment (Finegan et al. 2015). Besides wood density, specific leaf area is known to be related to the intensity of plant respiration and photosynthesis (Ivetić et al. 2014; Weraduwage et al. 2015), and thus plant growth. In the infancy of its growth, a plant would tend to allocate more resources to leaves so that to allow maximum interception of light and favour fixation of large amounts of C from atmosphere. As a result, leaf area would co-determine, through the rate of photosynthesis and respiration, the relative growth rate of the plant (Tomlinson et al. 2014).

In this study, the biomass allocation to wood (stem plus branch) and foliage was evaluated using our available data on the aboveground biomass of 89 trees from six species in a Mistbelt forest (South Africa). It was expected that tree size, species identity and functional traits would influence the biomass allocation, but their relative importance was unknown. The between-species variation in the biomass allocation was first examined, using the leaf to wood mass ratio (LWR). Because biomass allocation is size dependent, the effects of tree size (diameter at breast height, DBH) and species identity on LWR were assessed simultaneously. By further accounting for the effect of tree size, it was tested whether the biomass allocation in the aboveground compartment was influenced by species traits such as, individual leaf area and wood density. Finally, the trends of LWR and DBH scaling relationship were compared between groups of species. It was assumed that (i) LWR decreases with increasing tree diameter, but (ii) the effect of tree size works differently according to the species group. Specifically, we suspected that (iii) the slope of the trend line of LWR- DBH in the group of species with higher leaf area, would be larger than in the one of species with smaller leaf area.

5.2. Materials and Methods

5.2.1. Study species

On the basis of leaf area, specific wood density and the relative dominance in the forest, six species were considered for this study in Woodbush-De Hoek State Forest (See Chapter 4 for more information about the study area). They were *Celtis africana* Burm. f. (Cannabaceae), *Combretum kraussii* (Combretaceae), *Croton sylvaticus* Hochst. (Euphorbiaceae), *Syzygium gerrardii* (Myrtaceae), *Trichilia dregeana* Sond. (Meliaceae) and *Xymalos monospora* (Monimiaceae). *C. africana*, *C. kraussii* and *C. sylvaticus* are deciduous trees while *S. gerrardii*, *T. dregeana* and *X. monospora* are all evergreen species.

5.2.2. Aboveground biomass data and specific traits

Dry mass of branch foliage (obtained from Chapter 4) was used to estimate for each species, the foliage biomass equations at branch level as a function of branch basal diameter (Mensah et al. 2016c). Based on these specific foliage biomass equations and the branch basal diameter measured on standing trees, the foliage biomass was up-scaled from the branch level to the tree level. The same method was applied for the branch wood to determine the total dry mass of wood in smaller branches at tree level. In addition, the volume of larger branches and standing stems was calculated by applying Smalian's formula (van Laar and Akça 2007), and the average wood density was thus used to calculate the wood biomass for the stem and larger branches. The total aboveground wood mass of each individual tree was then obtained by adding the biomass of stem and larger branches to the total dry mass of wood in smaller branches (Table 5.1).

The plant traits used in this study were wood density (g/cm^3) and individual leaf area (cm^2). Wood density was obtained from laboratory analyses. Because wood cores were taken from two levels on each standing tree, the averaged wood density was used. The information on leaf area of these species was obtained from TRY database on biological traits (Kattge et al. 2011) and using the Trees of Southern Africa (Coates-Palgrave 2002). In case multiple values were available for a species, the average value was used. *C. africana*, *C. kraussii*, *S. gerrardii* and *X. monospora* have leaves with smaller area, whereas *C. sylvaticus* and *T. dregeana* have leaves with relatively greater area (Table 5.1).

Table 5. 1. Traits of study species and sampled trees.

Species	No. trees	DBH	Wood density	Aboveground biomass (Kg)
C. africana[a,d]	15	2.80 – 94.50	0.30 – 0.65	4.93 – 8871.97
C. kraussii[a,d]	16	1.50 – 91.00	0.51 – 0.66	0.26 – 4590.19
C. sylvaticus[b,c]	14	4.80 – 64.00	0.38 – 0.50	4.17 – 5127.94
S. gerrardii[a,d]	15	0.70 – 92.50	0.51 – 0.65	0.17 – 3423.33
T. dregeana[b,c]	14	2.80 – 62.00	0.35 – 0.55	0.82 – 2357.97
X. monospora[a,c]	15	2.00 – 54.50	0.39 – 0.54	2.61 – 3816.50

[a]: species with smaller leaf area; [b]:species with larger leaf area; [c]: species with lower wood density; [d]:species with higher wood density

5.2.3. Data analysis

We evaluated the biomass allocation to wood and foliage by calculating for each individual tree, the foliage mass to wood mass ratio (LWR), i.e. the biomass allocated to foliage per unit of wood mass. To assess the effect of species identity, the difference of LWR among study species was tested through a one-way analysis of variance applied to the log-transformed data. The normal distribution was checked using Shapiro Wilk statistic. Species were post-hoc compared by performing the Student-Newman-Keuls test. Next, it was tested whether the size dependency hypothesis of biomass allocation applies for wood and foliage components, and whether there were differences among species. A Generalised Linear Model (GLM) was used to estimate simultaneously, the effects of tree size (i.e., DBH) and species identity. As the distribution of LWR was positively skewed, a GLM with Gamma family and "log" link was fitted. GLMs were also used to examine the relative effects of specific traits (wood density and leaf area) on LWR. To do so, the variation of LWR due to tree size was controlled for, by using the residuals of LWR-DBH model as response variable, and each specific trait as explanatory variable. Finally, species were grouped and the trend lines of LWR-DBH scaling relationship were compared between groups of species. Specific functional traits were used as a grouping factor, thus distinguishing (1) between species with larger and smaller leaf area, and (2) between species with higher and lower wood density. After grouping, we found that the range for tree diameter was greater in the group of high wood density species (0.7 - 94.5 cm). Therefore, we excluded the largest trees from the set of study species to have approximatively the same range of tree diameter within each group, and to fairly compare the trends in LWR-DBH scaling relationship.

5.3. Results

5.3.1. Effects of tree diameter and species identity on biomass partitioning patterns

Within study species, the biomass allocated to foliage per unit of wood mass (LWR) ranged from 0.0038 to 0.0225 for *C. africana*, 0.0071 to 0.0704 for *C. kraussii*, 0.0200 to 0.0916 for *C. sylvaticus*, 0.0073 to 0.1443 for *S. gerrardii*, 0.0113 to 0.0485 for *T. dregeana* and 0.0053 to 0.0503 for *X. monospora* (Figure 1). There were significant differences between species ($F = 13.4$; $p < 0.001$). On average, *C. sylvaticus* and *T. dregeana* showed the highest values of LWR, followed by *C. kraussii* and *S. gerrardii*, while *C. africana* and *X. monospora* had the same and lowest values (Figure 5.1).

Tree diameter and species identity showed significant effects ($p < 0.001$) on the biomass allocation patterns, with 77.96 % of the total variance being explained (Table 5.2). Tree diameter alone explained 44.44 % of the variance of LWR for all species ($p < 0.001$). The effect of tree size was shown by a significant decrease in LWR with increasing tree diameter (Figure 5.2a), regardless of the species. Results from GLM also showed species' significant effects on the leaf to wood mass ratio ($p < 0.001$, Table 5.2), and a large variability of species-specific slopes. For a given tree diameter, *C. sylvaticus*, *T. dregeana*, *C. kraussii* and *S. gerrardii* showed slopes of 1.27±0.14, 1.13±0.14, 0.81±0.14 and 0.53±0.14 respectively, higher than the one in *C. africana*, which was considered as the baseline (Table 5.2). *X. monospora* was ranked last, and had a slope that did not differ significantly from the one in the baseline ($p = 0.320$).

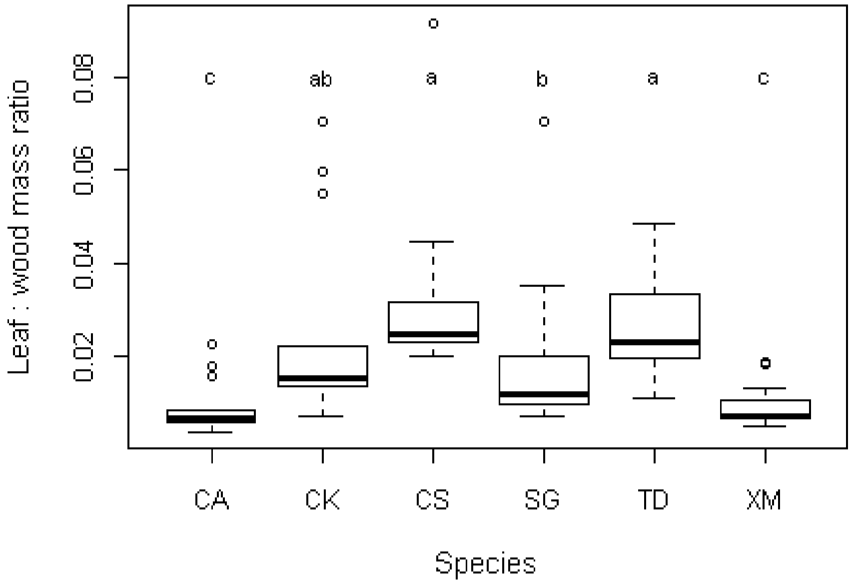

Figure 5.1 Distribution of leaf to wood mass ratio among studied species; CA = *C. africana*, CK = *C. kraussii*, CS = *C. sylvaticus*, SG = *S. gerrardii*, TD = *T. dregeana*, XM = *X. monospora*. Species with the same letter are not significantly different at p = 0.05 (Student-Newman-Keuls test).

Table 5.2. Output of GLMs describing the effects of tree diameter, species identity, wood density and leaf area on leaf to wood mass ratio.

	Estimate	SE	t	*P* (>|t|)	Deviance	*P* (>Chi)	Pseudo R square (%)
Intercept	-3.09	±0.16	-18.89	<0.001			77.96
Log (DBH)	-0.52	±0.04	-12.76	<0.001	24.79	<0.001	
Species					18.70	<0.001	
C. kraussii	0.81	±0.13	5.86	<0.001			
C. sylvaticus	1.27	±0.14	8.89	<0.001			
S. gerrardii	0.53	±0.14	3.77	<0.001			
T. dregeana	1.12	±0.14	7.86	<0.001			
X. monospora	0.14	±0.14	1.00	0.320			
Intercept	1.38	±0.40	3.44	<0.001			12.61
Wood density	-2.67	±0.76	-3.48	<0.001	4.11	<0.001	
Intercept	-0.46	±0.09	-4.97	<0.001			30.17
Leaf area	0.01	±0.00	6.13	<0.001	9.96	<0.001	

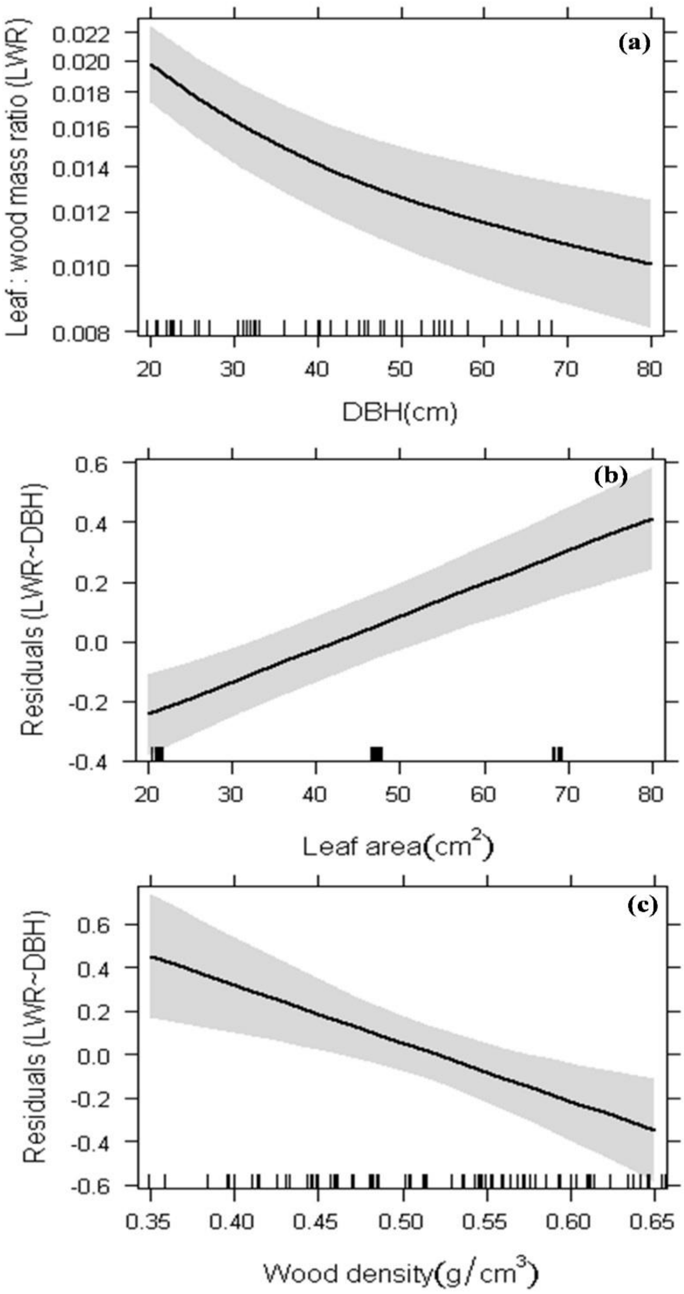

Figure 5.2. Individual effects of (a) tree size (DBH), (b) leaf area and (c) wood density on leaf to wood mass ratio. Grey areas stand for the prediction intervals. The regression coefficients (estimates) and values of pseudo R-square are given in Table 5.2.

5.3.2. Effects of leaf area and wood density on biomass partitioning patterns

Leaf area and specific wood density explained 30.17 % and 12.61 % respectively, of the variance of the leaf to wood mass ratio, after the effect of tree diameter was accounted for. The leaf to wood mass ratio increased significantly ($p < 0.001$) with increasing leaf area (Table 5.2; Figure 5.2b). Contrary to the leaf area, wood density showed a negative effect on the leaf to wood mass ratio (Table 5.2; Figure 5.2c). Figure 5.3 shows a significant decline in LWR with increasing tree diameter for all species groups (scaling coefficient < 0, Figure 5.3a-b). However, the biomass allocated to foliage per unit of wood mass decreased more steeply in higher wood density species (slope = -5.10^{-4}) than in lower wood density (slope = - 4.10^{-4}, Figure 5.3b). Accordingly, species with higher wood density had slightly lower LWR than species with lower wood density. In contrast, a more remarkable differentiation was noted between species with larger leaf area and species with smaller leaf area (Figures 5.3b): those with larger leaf area had greater slope and intercept, and therefore greater biomass allocated to foliage per unit of wood biomass.

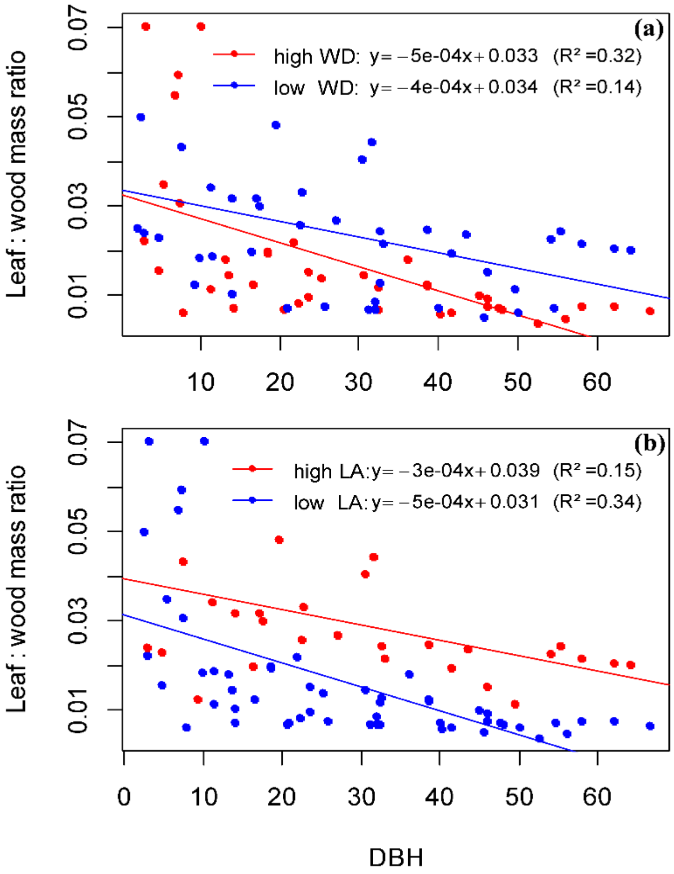

Figure 5.3. Regression lines fitting the distribution of leaf to wood mass ratio as a function of tree diameter (DBH; cm) in (a) higher and lower wood density (WD) species, and in (b) smaller and larger leaf area (LA) species.

5.4. Discussion

Our results showed that tree size (diameter) has a strong effect on the aboveground biomass partitioning patterns, as also revealed in other studies (Xie et al. 2012; Poorter et al. 2015). More specifically, LWR declined substantially with increasing tree diameter, regardless of the species. This means that as trees get larger, the biomass of the foliage per unit of wood mass tends to decrease. This outcome accords with other studies that reported for larger trees, an increasing relative contribution of stem and branches with a proportional decrease in the fraction of foliage (e.g. Pajtik et al. 2011; Luo et al. 2014). This is also consistent with the fact that an increase in wood biomass occurs often at the expense of foliage biomass (Helmisaari et al. 2002). Such a reduced production of foliage biomass is in part a result of the declining production of branch foliage when branches get older (King 1997). This is intrinsically linked with increasing amount of heartwood in stems and branches with increasing age and in line with the findings that sapwood area is highly correlated with total foliage biomass according to the pipe model theory (Shinozaki et al. 1964a,b; Marchand 1984; Morataya et al. 1999). The higher LWR in younger trees indicates that more carbohydrate resources might have been allocated to foliage to undertake photosynthetic activities and allow rapid vertical growth. In natural environments (e.g. natural forests), it is remarkable that resource partitioning among plant organs at early development stages is part of plant's strategy built as a response of competition for light. But as plant size increases, more resources are allocated for stem growth (height and diameter) to enable plants to compete with conspecific and heterospecific neighbours. In the meantime, additional resources are invested for root growth and for below ground mechanical safety (Poorter et al. 2015). Therefore, increasing tree size would result in different mechanical architectures that enable plants to differentially access the resources in the below and aboveground compartments (Fourcaud et al. 2008). While our results support the hypothesis of size-related allocation patterns, the variance explained by tree diameter leaves much part of variation to be attributed to species-specific differences (Weiner 2004; McCarthy et al. 2007; Poorter et al. 2015), and / or environmental effects (McCarthy and Enquist 2007; Reich et al. 2014).

The significant effect of species identity on the biomass partitioning patterns stresses the plasticity of different species in acquiring resources and adjusting biomass allocation. Indeed, different species are expected to obtain resources in various ways because of the interspecific variation in architectural branching and phenotypic plasticity (Poorter et al. 2006; Fourcaud et al. 2008; Lambers et al. 2006; Jarčuška and Barna 2011), and in functional traits (Xie et al. 2012; Freschet et al. 2015). For instance, when analysing the individual effect of each species, the highest slopes were observed for *C. sylvaticus* and *T. dregeana*. From a biological perspective, this result means that, for a given value of trunk diameter, *C. sylvaticus* and *T. dregeana* would exhibit higher foliage biomass per unit of wood mass, compared to *C. africana*, *C. kraussii S. gerrardii* and *X. monospora*. From a functional perspective, the relatively greater foliage biomass allocated in *C. sylvaticus* and *T. dregeana* is likely the result of the effects of functional traits that might be strongly involved in the construction of conductive tissues and the growth of plant.

Our results support the influence of plant functional traits, such as specific wood density and individual leaf area, on biomass allocation. Leaf area showed positive effects on the biomass allocated to foliage per unit of wood mass. Accordingly, species with larger average leaf area exhibited higher LWR than those with smaller leaf area. The leaf area seems to be a good explanatory variable of biomass allocation patterns because it defines not only the extent of interception of radiant energy, but also the absorption of CO_2, and facilitates the transfer of water between foliage and atmosphere (Margolis et al. 1995; Leuchner et al. 2012; Priesack et al. 2012; Weraduwage et al. 2015). Our results reinforce the importance of leaf traits for plant performance (Poorter and Bongers 2006). Specifically, larger leaves have greater potential for light interception and photosynthetic production. If the effect of leaf area can also explain the between-species variation of allocation patterns, then species leaf area should play an important role in determining the capacity of plant to capture aboveground resources (Freschet et al. 2015), and also a crucial role in plant competition.

Leaf to wood mass ratio decreased with increasing wood density. The latter has proved to be a good indicator of the aboveground biomass in many studies (Chave et al. 2014; Wright et al. 2010, Finegan et al. 2015; Mensah et al. 2016a), even though the relation between tree biomass and wood density is not always consistent (Stegen et al. 2009). Pajtik et al. (2011) found significant differences in whole tree biomass between beech, oak and pine species in Slovakia, and related this outcome to a probable effect of wood density. The here-reported influence of wood density could be explained by the fact that low wood density would allow for a faster tree growth (King et al. 2006; Wright et al. 2010), and when tree grows faster, more resources are allocated to the organ responsible for photosynthetic activities, thus stimulating the production of foliage. The faster growth in lower wood density tree is typical for pioneer tree species that enables them to fill forest canopy gaps quickly. On the contrary, in higher wood density species, the conductive tissues are more expensive to construct (Suzuki 1999), thus slowing tree growth. Furthermore, it was found that LWR declined with increasing tree size for both higher and lower wood density species, consistent with what is expected from the size-dependency hypothesis. However, the fact that LWR declines more steeply in higher wood density species than in lower wood density species indicates that the latter allocates more biomass to foliage and less biomass to stem and branches. This outcome suggests that additional resources have probably been allocated to foliage to maximize photosynthetic activities in low wood density species.

All being considered, it is worth mentioning that co-existing species show quite different patterns of aboveground allocation and different correlations with structural traits. This may serve as proof that competition in the Mistbelt forests is interacting with tree structure and morphology. However, it must be taken into account that the competition in these multi-species forests is complex and that trees might change their competitive abilities during their lifetime as shown in similarly structured Afrotemperate forests (Seifert et al. 2014).

Linking statement to Chapter 6

The results of the previous chapter provided further insights into the effects of plant size and functional traits (leaf area and wood density) of a species on biomass allocation. However these were not the only important variables. We used these functional traits to assess, two most debated components of biodiversity (functional diversity and functional dominance) in the following Chapter 6. We specifically analysed the relationship between plant diversity and carbon storage to determine whether niche complementarity and selection effects are the governing effects behind the biomass and carbon variation.

Chapter 6. Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance

Abstract

The relationship between biodiversity and ecosystem function has increasingly been debated as the cornerstone of the processes behind ecosystem services delivery. Experimental and natural field-based studies have come up with non-consistent patterns of biodiversity-ecosystem function, supporting either niche complementarity or selection effects hypotheses. Here, aboveground carbon (AGC) storage was used as proxy for ecosystem function in a South African Mistbelt forest, to analyse its relationship with species diversity, through functional diversity and functional dominance. It was hypothesised that: (1) diversity influences AGC through functional diversity and functional dominance effects; (2) effects of diversity on AGC would be greater for functional dominance than for functional diversity. Community Weight Mean (CWM) of functional traits (wood density, specific leaf area and maximum plant height) were calculated to assess functional dominance (selection effects). As for functional diversity (complementarity effects), multi-trait functional diversity indices were computed. The first hypothesis was tested using structural equation modelling. For the second hypothesis, effects of environmental variables such as slope and altitude were tested first, and separate linear mixed-effects models were fitted afterwards for functional diversity, functional dominance, and both. Results showed that AGC varied significantly along the slope gradient, with lower values at steeper sites. Species diversity (richness) had positive relationship with AGC, even when slope effects were considered. As predicted, diversity effects on AGC were mediated through functional diversity and functional dominance, suggesting that both, the niche complementarity and the selection effects are not exclusively affecting carbon storage. However, the effects were greater for functional diversity than for functional dominance. Furthermore, functional dominance effects were strongly transmitted by CWM of maximum plant height, reflecting the importance of forest vertical stratification for diversity-carbon relationship. We therefore argue for stronger complementary effects that would be induced also by complementary light-use efficiency of tree and species growing in the understorey layer.

Keywords: functional richness; carbon stock; niche complementarity; maximum plant height.

6.1. Introduction

The relationship between biodiversity and carbon storage is being debated as one of the current ecological topics (Cavanaugh et al. 2014; Day et al. 2014; Ruiz-Benito et al. 2014; Ruiz-Jaen and Potvin 2011), and some aspects of climate-related effects have been well investigated (Durán et al.

2015; Wu et al. 2015). Because biomass is an important component of forest stand productivity, the relationship between biomass carbon and biodiversity can also be assimilated to the one of biodiversity and ecosystem function (Lasky et al. 2014). Basically, two well-debated mechanisms are commonly used to explain the role of plant diversity in ecosystem resource dynamics, ecosystem processes and functions: niche complementarity effects and selection effects (Díaz and Cabido 2001; Tilman et al. 1997); the niche complementary effects hypothesis assumes increasing diversity would promote greater variety of functional traits and provide opportunities to species to efficiently use the available resources, thereby increasing ecosystem function; the selection effect hypothesis suggests that in ecosystems with higher diversity, there would be a higher probability of occurrence of dominant species or traits that influence ecosystem functioning. Currently, great research efforts are being made to elucidate how diversity components (taxonomic diversity, functional diversity and functional dominance) drive biomass and carbon stocks, and the extent to which the findings support niche complementarity and selection effects hypotheses.

Taxonomic diversity, expressed by species richness and alpha-diversity indices, has been commonly used as a simple measure of biodiversity (Mayfield et al. 2010; Tilman et al. 1997), and has been shown to correlate positively with carbon stocks. However, because a new species – with different functional traits – added to an ecosystem would likely contribute to the physiological processes, the effects of taxonomic diversity on carbon storage could be treated as different effects of functional diversity (accounting for niche complementarity) or/and functional dominance (comprising selection effects). The functional diversity is known as ‘‘the value and range of functional traits of the organisms present in a given ecosystem’’(Díaz and Cabido 2001, pp 654) therefore, might be the starting point of elucidating the mechanisms underlying the relation between biodiversity and carbon (Cadotte et al. 2011; Naeem 2002). Yet, some recent reviews showed controversy in the relationship between taxonomic and functional diversity (Mayfield et al. 2010; Naeem 2002; Song et al. 2014). On the one hand, following Tilman et al. (1997) and Mouchet et al. (2010), functional diversity was positively correlated with species richness, and in this case, taxonomic diversity can simply be used to replace functional diversity. On the other hand, it was pointed out that land use, the local species pool, etc. could also influence the relationship between functional and taxonomic diversity (Cadotte et al. 2011; Mayfield et al. 2010). Consequently, whether diversity (species richness) effects on ecosystem function are fully mediated by functional diversity, or co-determined by selection effects (dominance patterns) is still well debated. In tropical natural forests, where several species cohabit and fulfil the major ecosystem functions, it is common to observe the abundance and dominance of highly productive tree species, thus increasing the chances that diversity-carbon relationships are mediated by selection effects. This was partly confirmed by our previous observations in South African Mistbelt forests, especially the greater influence of the most dominant species on biomass stocks. More and more, research tends to show how functional diversity and/or functional dominance play a major role in ecosystem functioning (Baraloto et al. 2012; Clark et al. 2012; Ruiz-Jaen and Potvin 2011; Song et al. 2014). Understanding whether diversity effects on ecosystem function are more likely mediated through functional diversity than functional dominance, or *vice-versa*, will bring substantial insights into which mechanism is more relevant.

Very few studies have addressed the relationships between diversity and ecosystem function in natural multispecies tropical forests. Using aboveground tree carbon data in a Northern Mistbelt forest in South Africa, the relationship between diversity and carbon stocks was examined through the effects of functional diversity and functional dominance. It was hypothesised that (1) diversity influences tree carbon storage through both functional diversity and functional dominance effects. However, there are insights that diversity and carbon relationships can be caused by co-varying environmental factors (Cavanaugh et al. 2014; Ouyang et al. 2016). Therefore, altitude and slope were considered as the most physical gradients in these forests, and their effects on tree carbon storage were tested. In addition, while accounting for significant environmental gradient effects, it was also hypothesised that (2) effects of diversity on carbon storage would be greater for functional dominance than for functional diversity.

6.2. Materials and method

6.2.1. Study area, forest sampling and aboveground carbon data

The study was carried out on the same site (Northern Mistbelt forests in the Limpopo Province, South Africa). Stand data (species, canopy layer, tree density, basal area) were obtained by means of a stratified random sampling design set in a forest block in the Woodbush De Hoek forest, as described in Chapter 4. The plots were laid out in stratified compartments obtained by subdividing the research area on the basis of three classes of slope: flat (1.5%-15.3%), gentle (15.3%-29.19%) and steep (29.19%-43.1%); four classes of aspect (North, South, West and East); and three classes of elevation: low (1174-1332 m a.s.l.), medium (1332-1490 m) and high (1490-1648 m). The multispecies allometric biomass equation developed for the Northern Mistbelt forests (Mensah et al. 2016a) was used to calculate the aboveground biomass (AGB) for all individual trees present in the plots, as in Chapter 4. The allometric equation provided more accurate estimated biomass values, compared with the existing pantropical biomass equation (Chave et al. 2005; Mensah et al. 2016c). The formula for the allometric biomass equation is as follows:

$$AGB = 1.03 \times \exp(-2.69 + 0.69 \cdot \ln(SWD) + 0.95 \cdot \ln(DBH^2 \cdot H)) \qquad (15)$$

where *AGB* stands for the aboveground tree biomass in kilograms, SWD the specific wood density (g·cm^{-3}), DBH the diameter at breast height (cm) and *H* the total height (m). AGB was computed for each individual tree, upscaled to plot and stand level for each diameter class (i.e. for 5-10 cm DBH in the 30 smaller plots and for ≥ 10 cm DBH in the 30 larger plots), and summed up to obtain the values for DBH > 5 cm. Carbon values were determined afterwards as in Chapter 4, by multiplying the aboveground biomass by a factor of 0.5 (Lung and Espira 2015).

6.2.2. Diversity and dominance metrics

Diversity was measured using taxonomic diversity, at each plot. Species richness was used to characterise the taxonomic diversity (Magurran 1988). Species richness at plot level is simply defined as the number of distinct species enumerated inside each plot. To assess functional diversity, the functional traits that are relevant to the ecosystem function of interest (i.e. biomass and carbon storage) were considered. Because carbon storage is strongly dependent on wood and foliage structures, traits such as specific wood density (WD), specific leaf area (SLA), and maximum plant height (PHm) were used. Data on specific wood density was obtained from the Global Wood Density Database (Zanne et al. 2009). In case multiples values were available for a single species, the average wood density was used. When a particular species was missing, the average genus wood density was used. SLA and PHm were extracted from the TRY database (Kattge et al. 2011). As functional diversity metrics, Functional richness (Fric), Functional evenness (Feve), Functional divergence (Fdiv), Functional dispersion (Fdis) and Rao quadratic entropy (RaoQ) were estimated at plot level (Baraloto et al. 2012; Cavanaugh et al. 2014; Finegan et al. 2015; Villéger et al. 2008), using the values of the functional traits with the FD package in R (Laliberté et al. 2015). These diversity indices are multi-trait functional diversity metrics that combine both the relative weight of each species and the pairwise functional difference between species. Fric measures the amount of trait or niche space filled by the species within a community; low Fric indicates that some of the resources potentially available to the community are unused, thus reducing productivity (Mason et al. 2005). Feve measures the evenness of abundance distribution in the filled niche space, i.e. the degree to which the abundance distribution is spread over multivariate-trait space; Feve is higher when abundance distribution is homogeneous across the multivariate-trait space. Fdiv indicates the degree to which abundance distribution in niche space maximises divergence in functional characters within the community (Mason et al. 2005); High functional divergence indicates a high degree of niche differentiation, and thus low resource competition (Mason et al. 2005). A review of these measures can be found in Mouchet et al. (2010).

Functional dominance was assessed by estimating the plot-level community weight mean (CWM) for each functional trait. CWM is the mean of each species trait value weighted by the relative abundance (stem number) of that species (Cavanaugh et al. 2014). The per-plot CWM was estimated for WD, SLA and PHm, again using the FD package in R.

6.2.3. Data analyses

Here, two hypotheses were tested: (1) diversity effects on carbon storage are mediated through both functional diversity and functional dominance effects; and (2) effects of diversity on carbon storage are greater for functional dominance than for functional diversity. The first hypothesis was tested using structural equation models (SEM) while the second hypothesis was tested using linear mixed-effects models. For both SEM and linear mixed-effects models, AGC data was log-transformed to meet the normality assumption (Shapiro-Wilk statistic = 0.97, *P*-value = 0.628).

6.2.3.1. Structural equation modelling

SEM offers the possibility to test hypothesized patterns of direct and indirect relationships among the measured variables. This is particularly important, as it was assumed that the diversity effects would be transmitted through both functional diversity and functional dominance. Therefore, the indirect and direct effects of diversity (species richness) on aboveground carbon were examined. Two separate structural equation models were constructed: (1) full mediation (diversity effects are fully transmitted by functional diversity and dominance metrics); (2) partial mediation (there are both direct diversity effects and indirect diversity effects through functional diversity and functional dominance metrics). Due to presence of multiple measures for functional diversity, stepwise selection techniques were used to select the most relevant functional diversity metrics for the aboveground carbon data. As a result, only Functional Richness (Fric) and Functional evenness (Feve) were selected (*P-value* < 0.05). Environmental variables could have potential effects on the species diversity and aboveground tree carbon. Nevertheless, such effects could be better assessed in mixed modelling approach (addressed in the next paragraph), thus simplifying the outputs of the SEMs. The overall fit of the SEMs was assessed using $\chi 2$ test (a *P*-value > 0.05 would indicate an absence of significant deviations between data and model), the comparative fit index (CFI) and the Akaike information criterion (AIC) (Grace and Bollen 2005). The standardized coefficients were used to allow direct comparisons across paths (Grace and Bollen 2005). SEMs were fitted in the R statistical software package (R Development Core Team 2015), using the “sem” functions in the “lavaan” package version 0.5-19 (Rosseel 2012).

6.2.3.2. Linear mixed-effects models

Prior to the mixed-effect modelling, potential environmental variables and species richness effects on aboveground carbon storage were tested for. Environmental variables are expected to have effects on plant structures, growth and survival (Mensah 2014; Mensah et al. in press; Wang et al. 2006), and hence on standing above-ground biomass and carbon stocks. Here, the variables that are determinant and quantifiable in the area, i.e. topography (slope and altitude) (Geldenhuys 2002, 1997) were considered. Other environmental variables such as temperature and precipitation have also been proved to have much influence on productivity, biomass and carbon stocks (Cavanaugh et al. 2014; Durán et al. 2015), but were not explored here mainly because of their unavailability at the small scale in this study. Topography was characterised by classifying the slope and elevation in three categorical levels. Slope was categorized as flat (low slope), gentle (intermediate slope) and steep (high slope). As for elevation, low, medium and high categories were considered. Simple linear models were performed to test for slope and elevation effects on aboveground carbon storage. As a result, only the slope showed slightly significant impact on the carbon stock, and therefore, was considered for further analyses. Multiple linear regressions were also fitted on slope and species richness to test their effects on aboveground carbon storage. For both simple and multiple linear models, Shapiro-Wilk tests were used to check for the normality of the log-transformed AGC data and of the residuals. Additionally, Breusch-Pagan tests and Durbin-Watson statistics were used to test for homoscedasticity and autocorrelation between residuals, respectively.

We next examined the relationship of each diversity component (i.e. functional diversity and functional dominance) with carbon storage, by fitting separate linear mixed-effects models (Zuur et al. 2009). Species richness and slope were considered as random factors, and each measure of functional diversity (i.e. Fric, Feve, Fdiv, Fdis and RaoQ) and of functional dominance (i.e. CWM of WD, SLA and PHm) as fixed effects. The mixed-effects models were fitted to assess (1) individual effect of each functional diversity and functional dominance metric, (2) combined effects of functional diversity metrics, (3) combined effects of functional dominance metrics, and (4) combined effects of functional diversity and functional dominance metrics. The best models were selected by preforming a backward elimination of non-significant effects (*P-value* > 0.05). The linear mixed-effect models were performed using the “lmer” function of the “lmerTest” package of the R statistical software. The *P*-values reported were calculated from the *F* test based on Satterthwaite approximations to the degrees of freedom, in the package “lmerTest”. The significance of the random effects was assessed using likelihood ratio (LR) test, again in the package lmerTest. The performance of fitted models was assessed based on the fit statistics such as Akaike information criterion (AIC) and the marginal R square, which indicates the proportion of variance explained by fixed effects (Nakagawa and Schielzeth 2013).

6.3. Results

6.3.1. Diversity effects mediated through functional diversity and functional dominance

The outputs of the structural equation models fitted to assess the mediated effects of diversity (species richness) on AGC, through functional diversity and functional dominance, are summarized in Table 6.1 and Figure 6.1. The first model "full mediation" had chi-square value of 11.59 (df = 7; p = 0.115), indicating good fit and absence of significant deviations between data and model.

In the "full mediation" model, species richness showed a significant positive direct effect on functional richness ($R^2 = 0.47$; $\beta = 0.69$; $p < 0.001$; Table 6.1), which also showed positive and significant effect of AGC ($\beta = 0.47$; $p = 0.002$; Table 6.1). Therefore, species richness, through functional richness, had a positive significant effect on AGC ($\beta = 0.69*0.47 = 0.32$). There was a nonsignificant effect of species richness on functional evenness ($\beta = 0.02$; $p = 0.926$; Table 6.1), the latter however exhibited a significant negative effect on AGC. In addition, there was no significant correlation between functional richness and functional evenness ($\beta = 0.29$; $p = 0.090$; Table 6.1), which would suggest that the mediated effects of species richness were transmitted by functional richness only. Among the functional dominance metrics, the CWM of maximum plant height did not retain any significant path. Only the CWM of wood density showed significant responses to species richness ($R^2 = 0.15$; $\beta = 0.38$; $p = 0.028$), but did not significantly influence the AGC ($p = 0.275$). In contrast, the CWM of SLA had a negative significant effect ($\beta = -0.37$; $p = 0.039$; Table 6.1) on AGC, although not significantly influenced by species richness ($p = 0.324$). The significant residual correlation between CWM of wood density and CWM of SLA ($\beta = 0.45$; $p = 0.003$; Table 6.1) suggests that the mediated effects of species richness are also transmitted by these two factors.

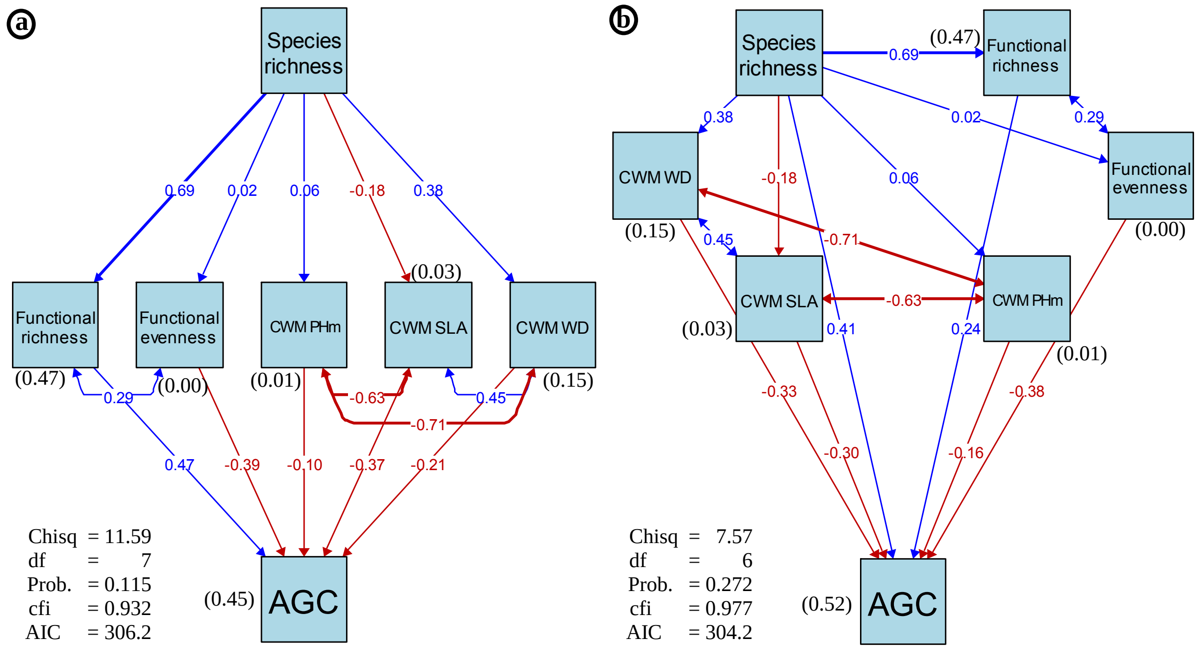

Figure 6.1. Summary of the path model relating species diversity (species richness), and measures of functional diversity and of functional dominance to the aboveground carbon (AGC); a: full mediation; b: partial mediation. CWM: community weight mean; PHm: maximum plant height; SLA: specific leaf area; WD: wood density. The figures with parentheses are the coefficients of determination (R^2), shown for dependent variables. The figures without parentheses are the standardized path coefficients. The single-pointed arrows represent causal paths, while the double-pointed arrows represent the residual correlations. The blue lines indicate the positive

effects while the red lines show negative effects; Chisq: Chi square statistic; df: degree of freedom indicating the number of paths omitted from the model; Prob.: probability of the data given the model; Prob > 0.05 indicates absence of significant discrepancy between the data and the model. cfi: comparative fit index; AIC: Akaike information criterion. The significance of each path is given in Table 6.1.

Note that the “partial mediation” model was fitted by only adding a direct path from species richness to AGC to the “full mediation” model. The chi-square value for the “partial mediation” model was 7.57 with 6 degrees of freedom and a p value of 0.272, also indicating good fit. There are similarities between the two models in terms of significant and non-significant paths (Table 6.1), but the “partial mediation” model exhibited slightly better fits (cfi = 0.932; R^2 = 0.52; AIC=304.2) than the “full mediation” model (cfi = 0.977; R^2 = 0.45; AIC = 306.2). The added causal path from species richness to AGC, was slightly significant at 0.05, suggesting an existing true direct effect of diversity on AGC. Both models suggest that species richness effects on aboveground carbon are mediated through functional diversity and functional dominance.

Table 6.1. Results of the structural equation modelling done to test the effects of species richness on carbon stocks (AGC) via functional diversity and functional dominance. Est.std: path standardized coefficients; SE: standard error; Fric: Functional richness; Feve: Functional evenness; CWM: community weight mean; PHm: maximum plant height; SLA: specific leaf area; WD: wood density.

	Est.std	SE	Z	P-value	Est.std	SE	Z	P-value
Regressions	Full mediation				Partial mediation			
Path from Species richness to Fric	0.69	±0.14	5.02	<0.001	0.69	±0.14	5.02	<0.001
Path from Species richness to Feve	0.02	±0.19	0.09	0.926	0.02	±0.19	0.09	0.926
Path from Species richness to CWM(PHm)	0.06	±0.19	0.32	0.750	0.06	±0.19	0.32	0.750
Path from Species richness to CWM(SLA)	-0.18	±0.19	-0.99	0.324	-0.18	±0.19	-0.99	0.324
Path from Species richness to CWM(WD)	0.38	±0.18	2.20	0.028	0.38	±0.18	2.20	0.028
Path from Fric to AGC	0.47	±0.16	3.04	0.002	0.24	±0.19	1.27	0.203
Path from Feve to AGC	-0.39	±0.14	-2.70	0.007	-0.38	±0.14	-2.75	0.006
Path from CWM(PHm) to AGC	-0.10	±0.22	-0.46	0.642	-0.16	±0.21	-0.77	0.440
Path from CWM(SLA) to AGC	-0.37	±0.18	-2.06	0.039	-0.30	±0.17	-1.74	0.081
Path from CWM(WD) to AGC	-0.21	±0.19	-1.09	0.275	-0.33	±0.20	-1.66	0.096
Path from Species richness to AGC					0.41	±0.20	2.00	0.046
Residual correlations								
Path from CWM(WD) to CWM(SLA)	0.45	±0.15	3.02	0.003	0.45	±0.15	3.02	0.003
Path from CWM(WD) to CWM(PHm)	-0.71	±0.09	-7.50	<0.001	-0.71	±0.09	-7.50	<0.001
Path from CWM(SLA) to CWM(PHm)	-0.63	±0.11	-5.54	<0.001	-0.63	±0.11	-5.54	<0.001
Path from Feve to Fric	0.29	±0.17	1.69	0.090	0.29	±0.17	1.69	0.090
Model fit statistics								
AIC	306.2				304.2			
P-value (Chi square)	0.115				0.275			
R^2	0.45				0.52			

6.3.2. Effects of environmental variables, functional diversity and functional dominance on carbon storage

Not surprisingly, there were significant effects of the environmental variables, especially the slope which explained 14.05 % of the variation of the aboveground carbon (Table 6.2). Low slope showed regression coefficient which was 0.53 significantly higher than the baseline (higher slope) whereas intermediate slope was not. This indicates that carbon stock was significantly higher at low slope sites than high slope sites. Unlike slope, altitude did not have any significant influence on the aboveground tree carbon (F-statistic = 1.381; p = 0.268; Table 6.2). Furthermore, even after accounting for the effects of the slope, species richness was significant and showed a positive relationship with AGC (β = 0.06; p = 0.016; Table 6.2).

Table 6.2. Results of simple and multiple linear models testing the effects of elevation, slope and richness on aboveground carbon stock; Est.: estimates of regression coefficients; SE: standard errors; SW: p-values for Shapiro-wilk normality tests; BP: p-values for Breusch-Pagan tests; DW: Durbin-Watson autocorrelation statistic.

		Est.	SE	t value	Pr(>|t|)	SW	BP	DW
Elevation								
	(Intercept)	12.15	±0.19	63.48	<0.001	0.849	0.240	1.68
	Low	-0.36	±0.24	-1.48	0.152			
	Medium	-0.09	±0.23	-0.40	0.691			
	Adjusted R Square (%)	2.56						
Slope								
	(Intercept)	11.67	±0.20	59.24	<0.001	0.927	0.211	1.69
	Low	0.53	±0.23	2.32	0.028			
	Medium	0.19	±0.24	0.84	0.409			
	Adjusted R Square (%)	14.05						
Slope + Species richness								
	(Intercept)	10.98	±0.32	34.19	<0.001	0.821	0.263	1.93
	Low	0.51	±0.21	2.45	0.021			
	Medium	0.16	±0.22	0.72	0.479			
	Species richness	0.06	±0.03	2.56	0.017			
	Adjusted R Square (%)	28.71						

The results of the separate linear mixed-effect models testing the individual effects of functional diversity metrics revealed that only Feve was significant effect, and had a negative effect on AGC (β = -1.6; p = 0.037; Table 6.3). Fdis, Fdiv, RaoQ showed high values of probability (from 0.359 to 0.528), while Fric had a slightly significant and positive effect on AGC (p = 0.079; Table 6.3). While assessing the combined effects of functional diversity metrics, it was found that Fdis, Fdiv and RaoQ were left out after backward selection for the final model (Table 6.3). The effects of functional diversity on AGC were thus shown by a significant positive effect of functional richness (β = 135.6; p = 0.013; Table 6.3) and a significant negative effect of functional evenness (β = -2.03; p = 0.006; Table 6.3). Both functional richness and evenness explained 27% of the variance of AGC.

Table 6.3. Results of linear mixed-effect models testing the effects of functional diversity on aboveground carbon stock; Est.: coefficient estimates; SE: standard errors; Sp.rich.: species richness; Rsd.: Residual variance; Marg. R^2: Marginal R square; Fric: functional richness; Feve: Functional evenness; Fdis: Functional dispersion; Fdiv : Functional divergence; RaoQ: Rao quadratic entropy

	Fixed effects					Random effects (variance)				
	Est.	SE	df	t	Pr(>|t|)	Sp.rich.	Slope	Rsd.	Marg. R^2	AIC
(Intercept)	11.76	±0.16	2.98	71.90	<0.001	0.00	0.05	0.15	0.09	30.74
Fric	103.06	±56.38	24.19	1.83	0.079					
(Intercept)	12.92	±0.48	25.97	27.11	<0.001	0.00	0.03	0.15	0.13	37.96
Feve	-1.66	±0.75	24.58	-2.21	0.037					
(Intercept)	11.75	±0.27	8.16	43.48	<0.001					
Fdis	1.00	±1.57	25.82	0.64	0.528	0.00	0.05	0.17	0.01	40.77
(Intercept)	12.30	±0.446	22.51	27.577	<0.001	0.01	0.02	0.16	0.03	41.95
Fdiv	-0.64	±0.686	25.47	-0.935	0.359					
(Intercept)	11.77	±0.22	4.18	53.14	<0.001					
RaoQ	3.82	±4.66	25.80	0.82	0.42	0.00	0.06	0.17	0.02	38.38
(Intercept)	12.97	±0.43	24.83	30.08	<0.001	0.00	0.04	0.12	0.27	23.83
Fric	135.59	±50.64	23.15	2.68	0.013					
Feve	-2.03	±0.68	23.32	-2.97	0.006					

Table 6.4. Results of linear mixed-effect models testing the effects of functional dominance on aboveground carbon stock; Est.: coefficient estimates; SE: standard errors; Sp.rich.: species richness; Rsd.: Residual variance; Marg. R^2: Marginal R square; CWM (SLA): community weight mean of specific leaf area; CWM (WD): community weight mean of wood density; CWM (PHm): community weight mean of maximum plant height.

	Fixed effects					Random effects				
	Est.	SE	df	t	Pr(>|t|)	Sp.rich.	Slope	Rsd.	Marg. R^2	AIC
(Intercept)	13.92	±0.66	18.99	21.15	<0.001	0.03	0.03	0.10	0.20	44.18
CWM (SLA)	-0.02	±0.01	17.55	-3.14	0.006					
(Intercept)	10.21	±0.51	20.18	20.14	<0.001	0.08	0.11^{**}	0.07	0.17	41.29
CWM (PHm)	0.07	±0.02	18.45	3.66	0.002					
(Intercept)	14.85	±1.19	16.42	12.46	<0.001	0.15	0.05	0.09	0.10	38.39
CWM (WD)	-4.86	±1.94	15.37	-2.50	0.024					
(Intercept)	6.06	±2.06	24.64	2.95	0.007	0.00	0.16^{**}	0.11	0.21	38.03
CWM(PHm)	0.11	±0.03	24.35	3.63	0.001					
CWM(WD)	5.35	±2.44	23.96	2.19	0.038					

**: significant at 0.01

All the three functional dominance metrics used in this study showed significant effects on the aboveground carbon (Table 6.4). Both CWM of SLA and CWM of WD showed negative effects, while CWM of maximum plant height exhibited a positive effect (Table 6.4). However, when assessing their combined effects on AGC, CWM of SLA was not retained by the final model, and the effects of functional dominance were only shown by positive and significant effects of CWM of maximum plant height and CWM of wood density, with 21% explained variance (Table 6.4).

Examination of separate mixed-effect models for functional diversity and functional dominance revealed that the marginal R square (variance explained by fixed factors) in the diversity-AGC relationship, was greater for functional diversity (27%) than for functional dominance (21%). When considering functional diversity and functional dominance measures in a same model, it was found that 34 % of the variations of AGC were explained by significant effects of functional richness, functional evenness and CWM of maximum plant height (Table 6.5). For all the selected models, species richness as random factor had much less variability than slope. The nonsignificant variability due to species richness in the mixed-effect models, suggests that much of its influence on AGC, has been considered by functional diversity and functional dominance, as confirmed by the SEM.

Table 6.5. Results of linear mixed-effect models testing the combined effects of functional diversity and functional dominance on aboveground carbon (AGC) stock; Est.: coefficient estimates; SE: standard errors; Fric: functional richness; Feve: Functional evenness; CWM (PHm): community weight mean of maximum plant height.

Model description			Est.	SE	df	t	Pr(>|t|)
Functional diversity + Functional dominance	Fixed effects	(Intercept)	11.39	±0.63	23.82	18.03	<0.001
		Fric	143.50	±42.65	21.99	3.37	0.003
		Feve	-1.72	±0.58	22.15	-2.95	0.008
		CWM(PHm)	0.06	±0.02	22.80	3.10	0.005
	Random effects (variance)	Species richness	0.00				
		Slope**	0.09				
		Residual	0.08				
		Marginal R^2	0.34				
		AIC	24.28				

**: significant at 0.01

6.4. Discussion

6.4.1. Effects of environmental variables on tree carbon storage

We did not detect any significant effect of altitude on tree carbon stock, according with Cavanaugh et al. (2014) who also reported in a global scale study, a lack of significant relationship between forest carbon and altitude. Yet, this finding runs contrary to many previous studies that examined the relationships between altitude and biomass or carbon storage (de Castilho et al. 2006; Ensslin et al. 2015; Sharma et al. 2010). On the one hand, some authors reported that biomass and carbon stocks can decline with increasing altitude in a central Amazonian and tropical montane forests (de Castilho et al. 2006; Moser et al. 2007). On the other hand, studies in moist temperate valley slopes of the Garhwal Himalaya (India) and temperate forests on Mt Changbai, Northeast China, found positive correlation between increasing tree carbon and increasing altitude (Gairola et al. 2011; Zhu et al. 2010). Furthermore, biomass and carbon stocks were found to increase up to a certain altitudinal limit (3000 m a.s.l.), and afterwards, decline sharply with higher altitudinal values (Ensslin et al. 2015; Singh et al. 1994). This lack of clarity on the relationship between altitude and forest biomass may partly due to the variation in the altitudinal range among studies. For instance, most of the abovementioned studies that reported significant effects of altitude, have covered greater altitudinal ranges well above 2500 m a.s.l; the relationship between altitude and carbon stocks in our study, might have been hidden due to the smaller altitude range covered (1000-1800 mm), which might have not been considerable enough to detect substantial variation in growth conditions and hence biomass and carbon stock.

Unlike altitude, slope showed significant influence, and accounted for 14% of carbon variance, evidencing that differences in carbon stocks can result from topological constraints, particularly difference in slope. Consistently to our results, slope has been identified as a potential environmental variable that affects tree carbon (Chave et al. 2003; de Castilho et al. 2006). Because aboveground carbon is intrinsically related to wood and biomass production, the influence of slope can be seen as prior impacts of environment on resources availability (de Castilho et al. 2006; Luizao et al. 2004), which in turn affect forest dynamics. For example, steeper slope will speed up nutrients and water run-off and constrain trees and will also favour highly water and nutrient efficient species against others. Taking this into account, it follows that tree growth and biomass production can be potentially reduced at higher slope sites, as results of moisture and nutrient stress (Clark et al. 2010; Durán et al. 2015), whereas flat and gentle slope sites would allow for more water availability, to which plant would likely respond positively. The significant effect of slope supports the fact that ecosystem functions in general and biomass and carbon storage in particular, are environment-structured (Wu et al. 2015).

6.4.2. Increasing species diversity promotes tree carbon storage

We found significant and positive effects of species richness on aboveground carbon, even when the effects of environmental factors (i.e. slope) were accounted for. While this finding accords with some recent studies that controlled for the effects of environmental variables (Wu et al. 2015; Ouyang et al. 2016), it also supports the commonly described pattern in highly diverse natural forests, i.e. biomass and carbon stocks increase with increasing diversity. Indeed, several local and global studies on forest ecosystems have shown positive relationship between species richness and forest biomass or carbon (Cavanaugh et al. 2014; Con et al. 2013; Day et al. 2014; Ruiz-Benito et al. 2014; Sharma et al. 2010; Wu et al. 2015). In addition, studies in boreal (Paquette and Messier 2011), temperate (Paquette and Messier 2011; Vilà et al. 2007) and tropical forests (Barrufol et al. 2013) have also reported increases in productivity with diversity.

One can expect that increasing species diversity would increase carbon storage because higher taxonomic diversity would lead to higher stem density and forest productivity (Ruiz-Benito et al. 2014). The positive effect of species diversity can also be explained through the benefits of plant-plant interactions such as facilitation, where by some species could enhance soil fertility (by fixing nitrogen) for the productivity of other species. This fact is even often used to support the reason why mixed species communities of plantations are far more productive than monospecific stands. But it is also possible that increasing species richness increases the chances of inclusion of highly productive and naturally favoured dominant species (Ruiz-Benito et al. 2014), as shown by our previous results on the influence of most dominant species on carbon stocks in Mistbelt forests (Mensah et al. 2016a).

While our dataset in the Mistbelt forests supports positive species richness-carbon relationship, it must be noted that evidence of the inverse effect, also exists. For instance, studies by Ruiz-Jaen and Potvin (2011) in natural forest of Barro Colorado Island in Central Panama, and Szwagrzyk and Gazda (2007) in natural forests of central Europe revealed negative relationship of species diversity with biomass and carbon stocks. Furthermore, others studies found such relationships nonsignificant (see Gairola et al. 2011). These controversial outcomes suggest that the effects of diversity on forest carbon may vary with other factors such as the types and the successional stages of the forests (Wu et al. 2015; Lasky et al. 2014), and also the specific dimension of the diversity measure used (Con et al. 2013; Lasky et al. 2014; Ouyang et al. 2016).

6.4.3. Diversity effects mediated through functional diversity and functional dominance

The use of multiple diversity measures to provide additional insights into the mechanisms behind diversity-productivity, has gained increasing interest in recent years (Cadotte et al. 2011; Conti and Díaz 2013; Finegan et al. 2015; Lasky et al. 2014; Ruiz-Benito et al. 2014; Vance-Chalcraft et al. 2010; Ziter et al. 2013). Accordingly, functional diversity and dominance metrics were also examined in this study. While most of these studies tended to compare the relative effects of species richness and other diversity measures, this study provided an additional example of exploring diversity effects on carbon stocks, through the assumption that these effects were mediated through functional diversity and functional dominance. The results on the structural equation modelling confirm this assumption, and therefore support the need to explore beyond species richness to better elucidate the mechanisms that govern diversity-productivity relationship. The results further support the idea that both complementarity and selection effects are not exclusively affecting carbon storage (Ruiz-Benito et al. 2014; Wu et al. 2015). Diversity (species richness) promotes carbon stock through effects of both functional diversity and functional dominance, partly because these diversity components are based on specific functional traits, which would reflect functional differences among the species (Diaz and Cabido 2001; Song et al. 2014). This finding can also be due to the fact that increased species richness indirectly accounted for differences among species, in terms of ecological niche and resource use.

6.4.4. Functional diversity effects on tree carbon storage

Out of the five functional diversity indices used in this study, only functional richness and functional evenness were found to explain variation in carbon stock. There is a variety of evidence for functional diversity effects on biomass and carbon. A study by Finegan et al. (2015) in tropical rain forests of Bolivia, Brazil and Costa Rica, found only functional richness – among other functional diversity indices – as significant predictor for biomass variation. Yet, a study in unmanaged forest fragments in Quebec revealed significant and positive relationships between functional dispersion and AGC (Ziter et al. 2013). Similarly, Ouyang et al. (2016) found significant but negative effects of the Rao quadratic entropy and stand biomass in subtropical forests in China. The positive effect of functional richness on the AGC, could be due to functional richness being positively correlated with species richness (SEM results; Villeger et al. 2008). Functional richness measures the amount of trait space occupied by the community (Clark et al. 2012); it would thus increase carbon storage because species with various traits would more efficiently use the resources for growth, thus reflecting the niche complementarity effects (Finegan et al. 2015). Unlike functional richness, functional evenness did not show any relationship with species diversity, however, it did exhibit negative influence on AGC. Vance-Chalcraft et al. (2010) and Con et al. (2013) found negative relationship of aboveground biomass with Simpson's and Shannon's evenness, respectively. Both effects of functional richness and functional evenness on AGC describe different aspects of functional diversity effects.

The unexpected lack of a strong individual effect of functional richness on aboveground carbon in this study, might be due to the number of functional traits used. In fact, only three functional traits were considered; although these traits were found to be crucial to explain biomass allocation patterns (Chave et al. 2009; Mensah et al. 2016b), they might not be as important as thought for complementary resource allocation. Similarly, these functional traits might not be sufficient enough to catch the entire variability needed to explain carbon variation. Adding other functional traits such as plant hydraulic conductivity, leaf mass per area and nitrogen fixing potential could have well captured the functional variability.

6.4.5. Functional dominance effects on tree carbon storage

Functional dominance effects varied with the functional trait. This is because functional dominance is a single trait community weight metric, contrary to the functional diversity indices, which are multi-trait functional indices. Specifically, CWM of wood density revealed negative and significant effect on carbon stocks. It is not surprising, given that wood density is a potential predictor of tree biomass, which highly correlates with the carbon stock. There are some insights that CWM of wood density is negatively related with the biomass increment, as being good predictor of individual tree diameter increments (Finegan et al. 2015). However, after examining biomass stocks in tropical forests, Stegen et al. (2009) pointed out that increasing wood density can decrease or increase the carbon stock, regardless of whether trees have high or low mean wood density. The authors therefore came to the conclusion that no general relationship exists between forest biomass and wood density. The present finding about CWM of wood density means that low wood density species grow faster and tend to store more biomass; thus it suggests that conserving and planting low wood density species would likely help to increase the carbon stock.

Similarly, CWM of specific leaf area exhibited significant and negative effects on carbon stocks. This is consistent with other studies that found negative relationship between specific leaf area and plant biomass (Finegan et al. 2015). Leaf area is important for the amount of radiant energy intercepted by the plant. It is also generally known to facilitate the transfer of CO_2 and water between foliage and atmosphere. Therefore, the significant influence of CWM of specific leaf area in this study, supports the idea that leaf area captures a strategy of the plant for resource consumption, especially light (Mensah et al. 2016b).

Community weight mean of maximum plant height showed positive relationship with carbon storage, as also reported in recent studies (Conti and Díaz 2013; Finegan et al. 2015; Ruiz-Jaen and Potvin 2011). This is probably because tree height is a key variable for species-specific or multispecies biomass regressions. In addition, maximal tree height is a potential species trait, as it defines the limits of competition for light and thus for light consumption (Poorter et al. 2006, 2005). Examination of combined effects of functional dominance metrics revealed that only CWM of wood density and of maximum plant height were retained in the final model, with maximum plant height being the most significant predictor. Furthermore, only maximum plant height was also retained among functional dominance metrics when the combined effects of functional dominance and functional diversity were assessed. Tree height being closely related to tree diameter, the significant and positive relationship between CWM of maximum plant height and carbon stocks reflects the potential importance of characteristics of dominant and adult trees for ecosystem functioning and productivity, thus supporting the selection effect hypothesis. The important contribution of dominant stems to forest biomass has well been evidenced in some recent studies

(Chave et al. 2003; Lung and Espira 2015). The study by Lung and Espira (2015) revealed that tree stems larger than 50 cm have the greatest impact on forest biomass, and less than 16% of the species pool accounted for over 62% of the aboveground biomass.

6.4.6. Functional diversity effects greater than those of functional dominance

When examining the percentage of variance explained, it was found that functional diversity explained more variance than functional dominance (Tables 6.2 and 6.4). This rejects our second hypothesis, and suggests that complementarity effects seem to be more important than selection effects. This finding contradicts Finegan et al.’s (2015) and Ruiz-Jaen and Potvin's (2011) results that selection effects were more important for the aboveground biomass and carbon stock in tropical forests. For this study, functional dominance metrics (community weight mean of functional traits) were calculated using species relative abundance, while Ruiz-Jaen and Potvin (2011) and Finegan et al. (2015) used species relative basal area and species relative biomass, respectively, as weighting variable. The strength of relationship between community weight mean of traits and the ecosystem function of interest could depend on the weighting variable. Biomass- or basal area-weighted communities mean values would likely show greater relation with biomass and carbon than abundance-based communities mean values. Further studies should elaborate on this and show the extent to which weighting variable can influence our understanding of weighted mean values’ effects on ecosystem functions.

All being considered, it is important to mention that our result actually supports the idea that these two hypotheses are not exclusive, and can contribute to ecosystem functioning. Previous evidence of both complementarity and selection effects on ecosystem function suggests they can also contribute at different proportions at different times of ecosystem development (Fargione et al. 2007). The selection effects reported here are strongly transmitted through specific maximum plant height, reflecting the importance of forest vertical stratification for diversity-carbon relationship. Therefore complementary effects would be induced also by complementary light use efficiency of species and trees growing in the understorey layer.

Chapter 7. Conclusions, implications for management and perspectives for future research

This thesis aimed to study key ecosystem services and functions provided by indigenous Northern Mistbelt forests and their relationship with biodiversity. The following overarching three objectives were addressed:

1. Identify key important ecosystem services valued by local communities.
2. Quantify the functions responsible of the selected key services in natural forest ecosystems.
3. Examine the relationship between biodiversity components and ecosystem functions.

7.1. Attributed importance of ecosystem services by local communities

7.1.1. Key results

Evaluating the importance of ecosystem services for people's livelihoods is an essential part of ecosystem service assessment framework. This enables the identification of the most relevant services to people. In this thesis, the importance and use of ecosystem services were assessed within local communities of a region in South Africa. It was found that these local communities valued forest provisioning services ("timber and firewood", "edible plants" and "honey") more than regulating and cultural services. Further, the results revealed how socio-economic factors such as age, gender, income and prior recreational/touristic experiences are associated with the importance value for certain ecosystem services. For instance, older householders had more positive perception on provisioning services than younger householders, while women exhibited a more positive attitude of towards importance of provisioning and supporting services than men. The results further highlighted that respondents' perceptions about ecosystem service importance reflect their actual use of these services. These results are important, and should be taken into account for management of ecosystem services in local development planning.

7.1.2. Implications for ecosystem services management and future research

The needs for the provisioning services will increase in the future if these forests (natural, planted, degraded) are not sustainably managed. Specifically, the finding that provisioning services are more valued (in terms of attributed importance) and used (based on the frequency of citation and collection) over regulating and cultural services, suggests new local development planning that should favour not only the delivery of provisioning, but also the supply and the explicit recognition of regulating and cultural services. As shown in this study, prior recreational/touristic experiences increased the probability that local people assign a higher value to cultural services. Therefore, as often included in management plans of urban localities, recreational areas should also be promoted in the rural localities to increase local people's interest in cultural services, and thus contribute to enhance local people livelihoods. The finding that local people still use and value forest provisioning services even from degraded bushvelds and woodlots, supports the need for sustainable management planning for conservation and enhancement of the provision of these services. Management interventions for sustainability should aim at restoring the native vegetation in most parts of these areas, and simultaneously reducing local people's dependency on major provisioning services such as timber and fuel wood. This could be achieved by facilitating access to electricity and markets, and also by creating more local employment opportunities. Indeed, planted forests in close proximity of natural forest areas are positive for conservation as they (1) help managing the fire in the area, (2) offer an alternative fuelwood source, and (3) create employment. In addition, some open areas should be identified and tested for suitability for community forests, in agreement with the local municipalities, to create more jobs. This, however, requires a training program for local people on sustainable management and protection of these forests against fire and degradation. The detailed information about the influence of social factors on ecosystem service importance value, can also be used to improve the institutional responses to local development planning. This could be done in a participative way, gathering local people, land managers and decision-makers to develop sustainable win-win scenarios (Chirwa et al. 2015). Specifically, the finding that older householders valued provisioning, regulating and supporting services more than younger householders, suggests increasing young people awareness for the importance of these services. A way to achieve this is the sensitisation and education of social groups. Management actions to enable these landscapes to sustainably produce services should focus on women who seemed to assign higher importance values to provisioning services, but should not neglect men in general. Similarly, the result that householders used forest provisioning services according to their location, is also worthy of consideration in local development planning. Management actions that involve households close to these landscapes could help to sustain the use of the services for the benefits of future generations. All being considered, the social valuation of ecosystem services has enabled the selection of two key ecosystem services namely "honey" and "timber and firewood", the latter investigated in natural forests as tree biomass.

7.2. Honey bee forage in Mistbelt forests

7.2.1. Key results

Harvesting honey is possible due to successful foraging activities of honey bees in forests and agricultural ecosystems. While the availability of foraging resources (nectar and pollen) is insured in agricultural fields during fruits and crops' flowering seasons, the potential of floral diverse Mistbelt forests to provide additional forage to managed honey bees was so far unknown.

When assessing the availability of honey bee plant species and forage in natural Mistbelt forests, it was found that (1) 48 % of woody plants were bee plant species; (2) bee plant richness significantly increased with overall plant richness; (3) bee plants' flowering period was greatly distributed over the year season; (4) the highest potential of forage supply was observed during the last quarter of the year; (5) few bee plant species greatly contributed the bee forage provision; and (6) bee plant richness, but not the overall plant richness significantly promoted the bee forage value.

7.2.2. Implications for management, beekeeping activities and future research

These results suggest that Mistbelt forests can support the management of honey bee colonies. From a functional perspective, bee plant richness is highly important for bee forage (nectar and pollen) availability. Given the bee plant richness in these forests, different flowering bee plant species would produce different flowers, and thus diverse nutritious resources to bee colonies (suggesting resource complementarity), and would also provide these resources at different times of the bees foraging activities (suggesting phenological complementarity). From a practical perspective, it is an interesting result, given the spatial context of these Mistbelt forests. Indeed, Limpopo province is one of the most productive provinces, in terms of agricultural farming. There is a variety of the actual crops/fruits produced that rely on honey bees pollination services. The prominent ones are sunflower, mango and avocado, which provide foraging resources during March-April, July-September and August, respectively; this emphasised the opportunities for beekeeping activities and honey production in Mistbelt forests, and thus the possibilities to consider these forests in the apiculture calendar of the area; honey bee hives can be, for example, placed close to these Mistbelt forests during the period from September to December, when the peak agricultural crops flowering time has passed and the maximum forage is available from Mistbelt forests. The benefits from the beekeeping industry in these Mistbelt forests can serve not only to contribute to the costs of promoting their conservation, but also to sustain the income of local beekeepers. In addition, most of the deciduous and sub-tropical fruit fields in the surrounding environments of these forests could also benefit from the pollination services. For crop fields which are isolated from natural habitats, field edges could be afforested or wind breaks established with important indigenous bee plant species of the Mistbelt forests. This will not only help to attract honey bees, but also contribute to sustain pollinator diversity at the proximity of these agricultural fields, thus increasing the benefits of local conservation and pollination services. Although this study has highlighted key aspects of management of honey bees, it is important to mention that the study did not consider any forb species, which are also known to provide nectar and pollen resources to managed honey bees. Therefore, further research studies will be necessary to investigate other functional groups of species and existing biomes in the area, to understand their potential contribution to the forage provision.

7.3. Biomass growth and carbon sequestration

7.3.1. Key results

Timber and firewood was identified as the most used and valued service (Chapter 2). Both plantation and natural forests, respectively supply timber resources. While the information on timber volume is mainly available from plantation forests owners and companies, the potential of timber in the natural systems is not well studied. A proxy that can account for timber (as provisioning ecosystem service, if harvested in natural forests), and also for the natural forests potential in global climate regulation (as regulating ecosystem service) is tree biomass and carbon. Up to date there are neither biomass information, nor allometric equations available to estimate either the volume of timber or the standing biomass in the Mistbelt forests. By developing allometric biomass equations and upscaling biomass and carbon values to stand level, it was found that (1): biomass and carbon values varied across the studied plots, average values being 358.1 Mg ha^{-1} and 179.0 Mg ha^{-1}, respectively; (2) few species contributed 80% of the carbon stock; (3) basal area of the ten most important species and of the largest trees were the most influencing variables; (4) tree species richness was also positively correlated with AGC, but the basal area of smaller trees was not.

7.3.2. Implications for management and future research

The estimated values of AGB in the northern Mistbelt forests are comparable to values in other important tropical African forests, thus providing evidence of their great potential for sequestration of CO_2. Due to the necessity for prioritisation of CO_2 mitigation actions, it is important to consider the carbon storage potential of these Mistbelt forests in landscape management planning.

The variation in biomass and carbon values on the survey plots is corroborated by the influence of structural variables. This information can also be used to design management and conservation plans. For example, the finding that basal area of most important species and of the largest trees greatly influenced biomass and carbon stock suggests that conservation of dominant tree species or trees with larger size (in terms of height or diameter) could be a strategy to increase carbon storage. Further, the unexpected lack of significant influence of smaller trees on the AGC can be used to support the idea that optimal solutions exist for sustainable harvesting of stems in the Mistbelt forests without risking a significant decline of the carbon storage. Because the largest trees may also die over time, an appropriate management strategy would consist of maintaining a balanced forest structure over time, by imposing a harvest regime that would target both smaller and larger trees. This, however, calls for more targeted research on long-term sustainability of timber and non-timber forest products' harvesting.

The correlation between biodiversity and carbon sequestration suggests a possible a win-win strategy where by local residents would benefit while conserving the forests for biodiversity and their ecosystem services. The promotion of the conservation of Mistbelt forests will reduce the risk of loss of biodiversity, while enhancing carbon stocks and mitigating the impact of global climate change. This also sheds light on the implications for REDD (reducing emissions from deforestation and degradation) schemes.

The finding that few species contributed 80% of the carbon stock, is likely due to increased chance of occurrence of a highly productive species, and suggests dominance patterns and selection effects on the carbon storage. This is corroborated by the significant positive but weaker effect of species richness on carbon stock. However, taxonomic diversity (species richness) only is insufficient to elucidate the mechanism behind biodiversity-carbon patterns. Thus, aspects of functional diversity (implying niche complementarity) and functional dominance (suggesting selection effects) were investigated. While carbon sequestration is well described with the results obtained from this thesis some further investigations would be needed to fully account for a sustainable supply of fuelwood and timber. These would have to address a quantification of the long term increment of Mistbelt forests for different stages of fuelwood and timber harvesting in order to break down the standing biomass in a stream of sustainably available timber and fuelwood. Long term monitoring and experimental sites are a way to achieve this. The fact that the Mistbelt forests are protected by law makes a management for timber quite unlikely. Thus this part was not put in the focus of this thesis but would definitely warrant some future investigations, in particular if the potential of converting degraded land into healthy natural forests for local supply of ecosystem services is considered.

7.4. Functional diversity and functional dominance effects on carbon storage

7.4.1. Key results

Understanding how plant biodiversity influences ecosystem functions (e.g. carbon storage) is important if we are to improve these functions. The results showed that (1) diversity effects on tree carbon stock were mediated through functional diversity and functional dominance; (2) functional diversity effects on tree carbon stock were greater than those of functional dominance; and (3) the specific effects of functional diversity and functional dominance on carbon stock varied with metrics and functional traits.

7.4.2. Implications for future research

These results actually support the fact that these two hypotheses (niche complementarity and selection effects) are not exclusive, and both contribute to ecosystem functioning. However, the effects of functional diversity were greater that functional dominance effects, suggesting that niche complementarity was the main mechanism. Moreover, the selection effects strongly influenced biomass and carbon amounts through the specific maximum plant height, which reflects the potential influence of dominant species. In multi-species, multi-storey natural forests, chances are high to observe dominant and taller species that increase stand productivity (Chapter 5), probably by achieving higher uptake of photosynthetically active radiation, and thus reducing the level of photosynthetic photon flux density available for understorey species. However, it must be noted that, even for these dominant species, interactions within ontogenic stages (for example, competition for light between seedlings, juveniles and adults) could define an efficient complementary use of light for greater productivity. Furthermore, efficient use of available photosynthetic photon flux density, and of decomposed litter (from canopy and dominant trees leaves), by the understorey species (limited to the sub-canopy layer) may likely reflect some complementary effects on stand productivity. Therefore, selection effects (dominant traits and species) on carbon storage were apparent, as predicted, but complementary effects were greater, probably as results of efficient use of limited resources. Like most tropical forests, Mistbelt forests exhibit a well-structured, multi-storey woody vegetation, made up by understorey species, canopy species and above canopy species (emergent). Coexisting and understorey species would promote greater carbon storage though efficient resource (light and decomposed litter) use. It is suggested that future research on the relation between diversity and forest carbon, be oriented towards a perspective of forest canopy (or dominant species *vs*. other species), to contribute further insights to our understanding of biodiversity-ecosystem function relationship.

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Appendix A. Questionnaire for assessing the importance and use of ecosystem services (ESs).

Stakeholder No:	**Village:**	**Name:**		
Date:		Age:	Employment status: YES or NO	Income status: YES or NO
Longitude:	Latitude:	Gender:	Employment type :	Description*

	Importance and Use of ESs							
List of ecosystem services	Not Important	Somewhat Important	Important	Very Important	Don't know	Do you collect these services? If yes, how often (monthly basis)?	How long (time) does it take to assess the collection sites?	Presence of natural barrier (river/foothills)
Medicinal plants								
Edible plants								
Edible insects								
Edible fruits								
Mushrooms								
Honey								
Timber & firewood								
						Do you visit a recreational/touristic site? If yes, how often?		
Tourism								
Recreation								
						Are you involved in agricultural activities? Do you benefit from pollination and pest control services? If yes how?		
Pollination								
Pest control								
						Do you restore the fertility of the agricultural lands? If yes how?		
Healthy soil								

*: monthly income from employment or state pension

Appendix B. Abundance, density per plot and basal area of plant species (including bee plant species) recorded on the inventory plots. SE: standard error; *: indicates honey bee plant species

Species	Number of individuals	Mean number of individuals per plot ± SE	Stem basal area m^2/ha
Aphloia theiformis (Vahl) Benn.	18	0.60±0.27	0.38
Bersama tysoniana Oliv.	4	0.13±0.06	0.03
Brachylaena transvaalensis Phill. & Schweick. p.p. *	9	0.30±0.15	0.92
Calodendrum capense Thunb. *	2	0.07±0.05	0.25
Calpurnia aurea Baker *	3	0.10±0.10	0.02
Cassipourea malosana (Baker) Alston	88	2.93±0.66	0.89
Celtis africana Burm. f. *	1	0.03±0.03	0.06
Chionanthus peglerae (C.H. Wright) Stearn	1	0.03±0.03	0.01
Clausena anisata (Willd.) Hook. f. ex Benth. *	2	0.07±0.07	0.01
Combretum kraussii Hochst. *	82	2.73±0.98	2.79
Croton sylvaticus Hochst. *	14	0.47±0.22	2.01
Cryptocarya transvaalensis Burtt Davy	24	0.80±0.27	1.46
Curtisia dentata (Burm.f.) C.A.Sm *	12	0.40±0.16	0.68
Cussonia sphaerocephala Strey	47	1.57±0.38	6.05
Diospyros whyteana (Hiern) F. White *	2	0.07±0.07	0.02
Dombeya burgessiae Gerrard ex Harv. & Sond. *	4	0.13±0.13	0.03
Drypetes gerrardii Hutch.	23	0.77±0.43	0.26
Eugenia natalitia Sond.	8	0.27±0.20	0.09
Ficus craterostoma Warb. ex Mildbr. & Burret	9	0.30±0.12	0.43
Halleria lucida L. *	2	0.07±0.07	0.04
Ilex mitis (L.) Radlk. *	2	0.07±0.05	0.06
Kiggelaria africana L. *	13	0.43±0.30	0.86
Kraussia floribunda Harv. *	51	1.70±0.41	0.28
Maytenus sp	19	0.63±0.53	0.27
Mimusops obovata Pierre ex Engl.	2	0.07±0.07	0.07
Nuxia congesta R. Br. ex Fresen. *	33	1.10±0.42	2.00
Nuxia floribunda Benth. *	28	0.93±0.47	1.65
Ochna arborea Burch. ex DC. *	48	1.60±0.59	0.50
Ochna holstii Engl.	16	0.53±0.20	0.19
Ocotea kenyensis Robyns & R. Wilczek	4	0.13±0.06	0.11
Olea capensis L. *	2	0.07±0.07	0.01
Oricia bachmannii (Engl.) I. Verd.	15	0.50±0.18	0.19
Oxyanthus speciosus DC	32	1.07±0.34	0.28
Pavetta galpinii Bremek.	1	0.03±0.03	0.01
Peddiea africana Hook.	22	0.73±0.41	0.12
Pleurostylia capensis Oliv.	1	0.03±0.03	0.01

Podocarpus falcatus (Thunb.) R. Br. ex Mirb.	6	0.20±0.11	0.12
Podocarpus latifolius (Thunb.) R. Br. ex Mirb.	10	0.33±0.10	0.49
Prunus africana (Hook. f.) Kalkman *	7	0.23±0.09	0.90
Pterocelastrus rostratus Walp.	18	0.60±0.22	0.12
Rapanea melanophloeos (L.) Mez *	12	0.40±0.27	0.02
Rawsonia lucida Harv. & Sond.	2	0.07±0.05	0.09
Rinorea angustifolia (Thouars) Baill.	49	1.63±0.95	0.36
Rothmania capensis Thunb. *	16	0.53±0.25	0.16
Syzygium gerrardii Burtt Davy *	212	7.07±1.24	12.63
Trichilia dregeana Sond.	31	1.03±0.48	3.71
Trimeria grandifolia (Hochst.) Warb. *	4	0.13±0.06	0.03
Xymalos monospora (Harv.) Baill. ex Warb.	247	8.23±0.76	8.32
Zanthoxylum capense (Thunb.) Harv.	1	0.03±0.03	0.00
Zanthoxylum davyi (I. Verd.) P.G. Waterman *	3	0.10±0.07	0.10