Spatio-temporal dynamics of woody vegetation structure in a human-modified South African savanna

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Declaration

I declare that this dissertation is my own, unaided work, unless otherwise noted within the text. It is being submitted for the degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any other degree or examination in any other university.

Penelope Jane Mograbi

25th day of October 2016 in Johannesburg, South Africa

For my grandmother, Dr. Sheila Mavis Osborn (1926- 2015),
A fiercely pragmatic and gentle woman of indomitable spirit who encouraged curiosity;
Equally versed in flower fairies, ehrlichiosis, mince pie pastry, and the taxonomic reshuffle of her rose garden beetles.

Abstract

Ecosystem services, nature's benefit to people, contribute to human well-being. Extensive reliance on, and unsustainable use of, natural resources is typical of the rural poor in developing countries and can lead to ecosystem degradation, decreased ecosystem service provision, and increased vulnerabilities of rural populations. Most ecosystem services are intangible or difficult to quantify, but fuelwood provisioning can be measured directly and can serve as a proxy for the status of other ecosystem services (e.g. aesthetic and spiritual services, nutrient cycling, carbon sequestration). South African rural communities have a high reliance on fuelwood despite extensive access to electricity. Within this context, live wood harvesting occurring around rural settlements in increasing amounts has been deemed unsustainable. However, the 'fuelwood crisis' of the 1970s, and subsequent predictions of woodland collapse through fuelwood supply-demand models, has still not occurred despite substantial population growth in developing countries. Hypothesised reasons for modelled supply-demand mismatches are based on underestimation of fuelwood supply and woodland regeneration, as well as overestimation of fuelwood demand by discounting behavioural adaptability of users. It is likely that the spatial configuration of fuelwood use allows for the co-adaptability of both humans and ecosystems. A lack of understanding of the spatial configuration of these social-ecological dynamics limits our insights into current and future adaptive responses and thus, the degree of sustainability. This thesis aimed to assess woody biomass stocks and vertical structure changes, as a proxy for provisioning ecosystem services, in a spatially and temporally explicit manner, to describe the status and impact of wood extraction in semi-arid, savanna communal lands. Using repeat, airborne light detection and ranging (LiDAR) data from 2008 and 2012, we surveyed three-dimensional woodland structure in Bushbuckridge Municipality communal lands – the grazing and harvesting areas for densely populated rural settlements in former Apartheid 'homelands' in South Africa. Woody biomass in 2008 ranged from 9 Mg ha^{-1} on gabbro geology to 27 Mg ha^{-1} on granitic geology. Land-use pressure was associated with compensatory regrowth of savanna tree species through post-harvest coppice in the 1-3m height class. Woody biomass increased at all sites, contrary to previous fuelwood models of the area. Change detection in the vertical canopy structure revealed that biomass increases were almost solely attributable to the 1-3m and 3-5m height classes. These changes were exacerbated by wood extraction intensity in the communal lands – the communal land with the highest wood extraction pressure experienced

the greatest biomass increases, likely a strong regrowth response to high harvesting levels. Within communal lands, areas closest to roads and settlements experienced substantial biomass increases as a result of shrub level gains. This relationship was mediated by the usage gradient – the greater the wood extraction pressure on the communal land, the larger and more spatially coalesced the 'hotspots' of shrub-level increases were in relation to ease of access to the communal land. However, biomass increases are not necessarily indicative of woodland recovery, as shrub-level increases were coupled with losses of trees >3m in height. To explore these tall tree dynamics further, we tracked >450 000 individual tree canopies over two years over contrasting landscapes – a private reserve containing elephants, two communal lands under different wood extraction pressures, and a nature reserve fenced off from both elephants and humans. Humans are considerable drivers of treefall (defined here as a ≥75% reduction in the maximum height of each tree canopy) in communal lands. Human-mediated biennial treefall rates were 2-3.5 fold higher than the background treefall rate of 1.5% treefall ha^{-1} (in the control site – the reserve containing neither elephants nor humans). Elephant-mediated treefall was five fold higher than the background rate. Rate and spatial patterns of treefall were mediated by geology and surface water provision in the elephant-utilised site where relative treefall was higher on nutrient-rich geology, and intense treefall hotspots occurred around permanent water points. Human-mediated rates and spatial patterns of treefall were influenced by settlement and crop-land expansion, as well as ease of access to communal lands. Frequent fires facilitated the persistence of trees >3m in height, but was associated with height loss in trees <3m. The combined loss of large trees and gain in shrubs could result in a structurally simple landscape with reduced functional capacity. Shrub-level increases in the communal lands are likely an interactive combination of newly established woody encroachers and strong coppice regrowth in harvested species. The more intensely used the communal land, the greater the bush thickening and the stronger the relationship between biomass gains and structural changes in the lowest height classes. The exacerbation of bush thickening in natural resource-dependent communities has critical implications for ecosystem service provision. There is potential for coppice regrowth to provide fuelwood to communities using 'tree thinning' programmes, but there is a lack of data on the quantity and quality of the regrowth, as well as the sustainability of coppice, the impacts of different harvesting methods, and the potential feedbacks with changing climate and CO_2 fertilisation. Woody resource spatial distribution in communal lands is centred around settlement-level wood extraction pressure, as well as natural resource accessibility in the woodlands. In highly utilised areas, woodland regenerative capacity has been underestimated. Additionally, natural

resource extraction is still highly localised, even at the communal land scale, with major structural changes occurring around the periphery or close to existing infrastructure. However, it is these underrated coupled adaptive responses in social-ecological systems that explain the failure of fuelwood supply-demand models' predictive abilities. Nevertheless, loss of large trees in the landscape and the persistence of 'functionally juvenile' coppice stands will have implications for seedling production and establishment in the landscape with repercussions for the future population structure and ecosystem service provision. I discuss the implications of increased natural resource reliance in an African development context and the positive feedback between rural poverty and environmental impoverishment. Potential constraints to the data are unpacked, together with opportunities for further research in this area.

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"It's no use going back to yesterday, because I was a different person then." – Lewis Carroll, Alice in Wonderland

Disclaimer

This thesis consists of content chapters which have been prepared for submission to scientific journals. As a result, styles may vary between chapters, and there may be some overlap to ensure publishable material. Author contributions and specific scientific journals have been specified in Chapter 1.

Table of Contents

List of Abbreviations

2-D	two-dimensional
3-D	three-dimensional
ACCESS	Applied Centre for Climate and Earth Systems Science
a.s.l.	above sea level
AToMS	Airborne Taxonomic Mapping System
CAO	Carnegie Airborne Observatory
CAR	Central African Republic
CC	canopy cover
CCA	canonical correspondence analysis
CHM	canopy height model
CTHB	Centre of Excellence in Tree Health Biotechnology
CSIR	Council for Scientific and Industrial Research
DIMACS/MBI	Center for Discrete Mathematics and Theoretical Computer Science/Mathematical Biosciences Institutite
DSM	digital surface model
DST	Department of Science and Technology
DTM	digital terrain model
ENSO	El Niño–Southern Oscillation
ES	ecosystem
ESS	ecosystem services
FAO	Food and Agriculture Organisation, United Nations
GPS	global positioning system
GLP	gains, losses and persistence
GDP	gross domestic product
H	height
H xCC	height x canopy cover
IMU	inertial management unit
IPBES	Intergovernmental Platform on Biodiversity and Ecosystem Services
ISRDP	Integrated Sustainable Rural Development Programme
K2C	Kruger to Canyons
KNP	Kruger National Park
KS	Kolmogorov-Smirnov
LAI	leaf area index
LANDSAT	Earth Resources Technology Satellite
LiDAR	Light Detection and Ranging
MA	Millenium Ecosystem Assessment
MAP	mean annual precipitation
MRC/WITS	Medical Research Council/University of the Witwatersrand
MODIS	Moderate-Resolution Imaging Spectroradiometer
NR	natural resource
NRF	National Research Foundation
OBIA	object based image analysis
REM	relative elevation model
RMSE	root mean square error
RSE	relative squared error
SAEON	South African Environmental Observation Network

SAWS	South African Weather Service
SD	standard deviation
SES	social-ecological system
SPOT	*Satellite Pour l'Observation de la Terre/*Satellite for Observation of the Earth
SSW	Sabi Sand Wildtuin
TPC	Thresholds of Potential Concern
voxel	volumetric pixel
VNIR	Visible-to-near infrared
VSWIR	visible-shortwave infrared
WITS	University of the Witwatersrand

Chapter 1: Introduction

"Natural systems are not so very fragile; they are ... complex adaptive systems … What is fragile … is the maintenance of the services on which humans depend." - Levin 1999

1.1 Rationale

Ecosystem services are the benefits that people derive from ecosystems and these can be categorised as provisioning (e.g. food, wood), regulating (e.g. flood attenuation, water purification), supporting (e.g. nutrient cycling, primary production) and cultural (e.g. aesthetic, spiritual) services (MA 2005). These ecosystem services provide the basis for human well-being (MA 2005). 'Well-being deprivation' defines poverty (World Bank 2001) and loss of biodiversity increases vulnerability to shocks (MA 2003). Unfortunately, as a direct result of the pervasive human presence on the globe, the substantial growth in human population and subsequent appetite for resources (Vitousek 1997; Ellis 2011), there has been extensive unsustainable use, and an accompanying decline, in ecosystem services (MA 2005; Egoh *et al.* 2008; Carpenter *et al.* 2009). The rural poor often disproportionately rely on natural resources and when human population growth outstrips resource growth, standards of living decrease (World Commission on Environment and Development 1987; Cervigni & Morris 2016). This can result in a "poverty-environment trap" where natural resources dynamics are non-linear and the coupled collapse of both human well-being and the natural environment become increasingly likely (World Commission on Environment and Development 1987; Cervigni & Morris 2016). Thus, areas that maintain ecosystem functioning should be carefully managed to ensure sustained coupled systems' well-being into the future (van Jaarsveld *et al.* 2005; Egoh *et al.* 2007), especially considering that 'spatial spillovers' may impact adjacent areas (Barrett *et al.* 2011). In order to better manage ecosystem services, one has to have some understanding of their current status, the factors that influence their dynamics and how they relate within social-ecological systems. Quantifying ecosystem services is not solely based on mapping of the ecosystem function that supports the services, but also identifying the beneficiaries and where these services are used (Egoh *et al.* 2007).

Historical consensus has been that ecosystem services rely on biodiversity (Ostfeld & LoGiudice 2003; MA 2005; Isbell *et al.* 2015), but there has been extensive debate on which biodiversity measures are accurate and/or useful surrogates and, subsequently, whether conserving biodiversity is an effective means of conserving ecosystem services (Egoh *et al.* 2007). Although most ecosystem services are intangible, some services (especially provisioning and supporting services) can be measured directly. Fuelwood harvesting can be measured, both directly as a provisioning ecosystem service, and indirectly, as a proxy for other services (e.g. regulating air quality, nutrient cycling, primary production, carbon sequestration).

Although the use of woody biomass stocks as fuelwood have slowly declined globally (charcoal consumption is increasing rapidly) (Arnold *et al.* 2003; Carpenter *et al.* 2009), localised shortages occur where fuelwood is still the predominant source of energy. Millions of people in southern and east Africa rely on woody vegetation for energy, extracted from both communal (Luoga *et al.* 2002; Stringer & Reed 2007; Kalema & Witkowski 2012) and protected areas (Abbot & Homewood 1999; Furukawa *et al.* 2011). Within southern Africa, South Africa has high per capita use of fuelwood as a primary energy supply; despite having considerable access to electricity (85% of national population) (Statistics South Africa 2014). Although the relative contribution of fuelwood is expected to decline, absolute growth in population is expected to increase; the FAO (United Nations' Food and Agriculture Organisation) predicted a 25% increase in woody consumption from 2001 onwards (van Jaarsveld *et al.* 2005; FAO 2008) and by 2030, fuelwood is still expected to represent 80% of household energy consumption in sub-Saharan Africa (Gazull & Gautier 2014).

Within this context, 93% of current fuelwood demands are no longer met by collection of dead wood (Dovie *et al.* 2004). Thus, live wood harvesting occurs around settlements (Shackleton & Scholes 2011). Fuelwood, and charcoal, harvesting are significant contributors to woodland degradation in semi-arid ecosystems in southern Africa (Stringer & Reed 2007; Shackleton & Scholes 2011), particularly in the South African Lowveld (low altitude) savannas, where woody vegetation is being harvested for live fuelwood and field-clearing (Banks *et al.* 1996; Shackleton & Scholes 2011; Wessels *et al.* 2011).This is of extreme concern as localised fuelwood scarcity is already being experienced and the situation is unlikely to improve in the future (Madubansi & Shackleton 2007). Indeed, localised fuelwood shortages have facilitated the development of fuelwood markets (Shackleton *et al.* 2006; Matsika *et al.* 2013), effectively increasing the harvestable area and thus the impacts of

fuelwood extraction may become less of a localised phenomenon. Despite fuelwood markets contributing to rural livelihoods (Shackleton *et al.* 2006), they have the unfortunate knock-on effect of artificially maintaining perceptions of fuelwood abundance (Twine *et al.* 2003a; Matsika *et al.* 2013). Although complete woodland collapse in Bushbuckridge, South Africa, was predicted to occur by 2011 (Banks *et al.* 1996) and more recently, by 2024 at current extraction rates (Wessels *et al.* 2013), the interactions between socioeconomic and environmental factors driving natural resource use are complex, non-linear systems that are challenging to quantify (Giannecchini *et al.* 2007). However, the above predictions do emphasise that woody vegetation harvesting, driven by increased demand and greater extraction amounts (often owing to the use of vehicles), is unsustainable (Twine 2005). Not only is the sustainability of fuelwood supply a concern, but resilience theory holds that if a system is pushed beyond its ability to absorb disturbance, the system can move into another stable state (Holling 1973), one which may be undesirable for people who depend on the system for their livelihood (Hobbs *et al.* 2014).

Woody biomass extraction changes the structure of woody vegetation in the landscape (Freitag-Ronaldson & Foxcroft 2003; Wessels *et al.* 2011; Fisher *et al.* 2012). Structural diversity of vegetation is linked to ecosystem functioning (Tews *et al.* 2004; Fischer *et al.* 2006; Hall *et al.* 2011; Davies & Asner 2014; Ilstedt *et al.* 2016) and can affect: productivity (Aguiar & Sala 1999; Ishii *et al.* 2004); edge effects (Harper *et al.* 2005); ecosystem health and integrity (Manning *et al.* 2006); habitability and the species richness of arthropods (Halaj *et al.* 2000), birds (Seymour & Dean 2009), mammals (Williams *et al.* 2002), amphibians (Atauri & de Lucio 2001) and reptiles (Smart *et al.* 2005). Thus, unsustainable harvesting of woody vegetation impacts ecosystem functions and the social-ecological systems that rely on the ecosystem services provided. Not only is general vegetation structure important, but individuals within the landscape also fulfil functional roles. Large trees play a uniquely important role in landscapes, supplying shade, reducing soil and plant temperatures (Belsky & Canham 1994), increasing below-canopy nutrient cycling (Manning *et al.* 2006; Treydte *et al.* 2008; Mills *et al.* 2012), decreasing under-canopy evapotranspiration (Belsky *et al.* 1993; Holdo & Mack 2014), improving grazing quality (Treydte *et al.* 2007) and providing nesting sites for arboreal species (Herremans 1995; Tews *et al.* 2004). Small trees and shrubs also play a role in landscape pattern and process. Shrubs and dead logs provide microhabitats for seedling germination and provide cover for small birds and mammals (White 2005). However, an increased presence of shrubs can be construed as bush encroachment. Human

influences are shifting savanna systems to increasingly woody states as a result of overgrazing, fire suppression and reduction in browser numbers (Archer *et al.* 2001). Bush encroachment reorganises savanna systems (Archer *et al.* 2001; Meik *et al.* 2002). Indeed, bush encroachment has been shown to result in lower livestock carrying capacity and decreased survival rate for calves (Oba *et al.* 2000). Bush encroachment may be exacerbated by continued harvesting of woody vegetation and the ensuing increased density of coppicing shoots in communal lands, together resulting is what we term here "bush thickening". Additionally, the loss of small trees and shrubs can lead to desertification. Bare patches have increased water run-off, decreased infiltration and a resultant loss of nutrients during erosion (Rietkerk & van de Koppel 1997). Intensive use of natural resources that changes the structural diversity threatens to transform the communal lands into a structurally homogeneous, functionally inferior landscape. This has serious implications for the communities that rely on ecosystem goods and services from communal lands in semi-arid savannas.

Past studies on wood extraction focused on relationships between wood supply and demand and provided detailed field studies on biomass loss in communal areas (e.g. de Montalembert & Clement 1983; Banks *et al.* 1996; Twine 2005; Kirkland *et al.* 2007; Madubansi & Shackleton 2007). However, these studies lacked detailed data over large extents, especially in the context of the heterogeneity inherent in savannas (Pickett *et al.* 2003). Small footprint, discrete return light detection and ranging (LiDAR) sensors estimate three-dimensional vegetation structure in detail (ca. 1 m laser spot spacing) over relatively large areas, providing landscape-scale estimates large enough to distinguish between local and regional variance (Colwell 1967). Airborne LiDAR has recently been applied in savanna ecosystems (Asner *et al.* 2009b; Levick *et al.* 2009; Smit *et al.* 2010; Colgan *et al.* 2012; Baldeck *et al.* 2014; Davies *et al.* 2014) with excellent results. LiDAR has also been applied successfully to assess fine scale vegetation trends over the communal lands (Wessels *et al.* 2011; Fisher *et al.* 2012) and to provide baseline biomass data for fuelwood supply-demand models (Wessels *et al.* 2013). Although woody vegetation structure has been studied in communal lands, little is known about temporal changes in vegetation structure and biomass as a result of land-use. LiDAR has been repeatedly demonstrated as a tool essential for the monitoring and management of a spatially and temporally heterogeneous ecosystem. Here we use LiDAR to estimate vegetation structure change over Bushbuckridge communal lands, a former 'Apartheid homeland', in the Mpumalanga province of South Africa.

1.2 Research aim, objectives and thesis structure

The overarching aim of this research is to examine woodland biomass and structural changes in response to harvesting in a communally utilised semi-arid savanna over varying levels of resource extraction pressure to infer woodland sustainability and the implications for continued ecosystem functioning.

1.2.1 Objective 1: Investigate height-specific changes in vegetation structure across a wood extraction gradient in a semi-arid, communally utilised savanna between 2008 and 2012.

a) Rationale:

Most research on structure change in savannas is either specific to one focal tree species (e.g. Helm & Witkowski 2012; Venter & Witkowski 2013) or overall size class distributions (e.g. Matsika *et al.* 2012). Measures of stem diameter are more frequently used to asses change in woodland structure (e.g. Walker 1976; Shackleton & Scholes 2011), but this is an inappropriate measure in an ecosystem dominated by coppice response as stump diameter (if harvested above the ground) is not a consistent predictor of shoot productivity (Kaschula *et al.* 2005). A specific investigation into savanna woodland recovery is worthwhile. Lowveld savanna studies suggest that environmental variables act as a stabilizing mechanism, driving heterogeneous species-specific biomass distribution (Colgan & Asner 2014). Even within species, different height classes can be driven by different processes (Helm and Witkowski 2012, Scholtz *et al.* 2014). Anthropogenic influences, especially in a natural-resource harvesting scenario, are fundamentally important to pattern and process and it is likely that they will play a role in height-class changes in savanna woodlands. The height-class specific growth characteristics of the woodland and the buffering ability of the ecosystem in response to continued fuelwood harvesting is particularly important for sustainably managing communal natural resources. This knowledge may contribute to knowledge on adaptive height-class dependent primary productivity response to varying land-use intensity.

b) Research Questions:

- How do the rates and patterns in height-specific gains, losses and persistence of woody cover differ between communal lands?

- What factors (e.g. geology, relative elevation, fire, perceived distance from settlements and roads) are associated with structural vegetation dynamics?

1.2.2 Objective 2: Investigate changes in woody biomass stocks and vertical vegetation structure at varying levels of wood extraction pressure between 2008 and 2012 in Bushbuckridge.

a) Rationale:

Remotely-sensed biomass, as a complex biophysical reflection of ecosystem functioning, is increasingly being used for management purposes. Yet, biomass estimations remain challenging in ecosystems with highly variable species composition and structural complexity. Biomass estimations, however, do not provide any information on the vertical location of that biomass change within the vertical vegetation profile. Vertical vegetation structure can be quantified using LiDAR volumetric pixel (voxel) data. Analysis of voxels is a useful aid in describing change in biomass, providing detail of where in the 3-D canopy the biomass changes are occurring. Changes in woody biomass may not necessarily be mirrored by changes in vertical woody vegetation structure and discrepancies in patterns of both biomass and vertical structure change may reveal previously unknown dynamics. This will also assist in identifying which portions of the woody vegetation canopy are contributing to the gain/loss of biomass in a spatially explicit manner.

b) Research Questions:

- What is the magnitude of woody biomass change at varying levels of wood extraction in the Bushbuckridge communal lands?
- What are the changes in 3-D vegetation structure at varying levels of wood extraction in the Bushbuckridge communal lands?
- What is the relationship between woody biomass and 3-D vegetation structure change at varying levels of wood extraction?

1.2.3 Objective 3: To examine the influence of anthropogenic drivers on woody biomass and vegetation structure change between 2008 and 2012 in communal lands with varying levels of wood extraction, in relation to abiotic and anthropogenic variables.

a) Rationale:

Wood extraction disturbance gradients are evident around settlements, but the gradient change threshold has increased from 100m in the 1980's to approximately 1 km from settlements in the 1990's (Giannecchini *et al.* 2007). Not only has the distance from settlement increased for fuelwood collection, the time taken to collect fuelwood has increased from 239 minutes per trip in 1992 to 268 minutes per trip in 2002 (Madubansi & Shackleton 2007). These figures explain the large difference in biomass seen beyond 1km from settlements in 2008 (Wessels *et al.* 2013). This relationship should also be present in woody vegetation biomass change detection maps. The extent of extraction can provide clues into the status of the villagers' well-being and their vulnerability. Patterns of extraction can give insight into the uses of extracted resources and identify heavily utilised areas. In the context of wood provisioning landscapes, the interplay between woody biomass, vegetation structure and anthropogenic variables is poorly understood. Change analysis of woody biomass stocks is vital information for future management of ecosystem services in communally-utilised woodlands.

b) Research questions

- How does the relationship between above ground woody biomass and vertical vegetation structure change between and within communal lands under different resource extraction levels?
- How does the relationship between woody biomass and vertical vegetation structure change, with respect to:
    - distance from the nearest settlements?
    - distance from the nearest roads?
    - the abiotic template?

1.2.4 Objective 4: To explore the relative impact of humans and elephants on height-specific treefall rates between 2010 and 2012 in sites containing either humans, elephants, or neither.

a) Rationale

Measures of whole tree loss/mortality in savannas have been the focus of many studies with respect to elephants (e.g. Laws 1970; Asner & Levick 2012) or fire (e.g. Govender *et al.* 2006) or the interaction between both (Moncrieff *et al.* 2008; Shannon *et al.* 2011; Helm & Witkowski 2013). Yet, humans are overlooked as agents of ecological change. Human effects alter savanna structure and function, and this is set to increase with projected population increases. Savanna woody cover determinants are often considered in terms of herbivore and abiotic drivers, but humans alter woody cover through land-use change (Belsky 1987; Higgins et al. 1999) and the use of fire (Bird and Cali 1998; Pyne 2001).

The importance of large trees for ecosystem function is often stressed in literature and in a semi-arid savanna context they form 'keystone' structures. Trees are also crucial to rural communities' wellbeing, through supply of fruit, as well as in their religious and cultural significance (Shackleton *et al.* 2003; McHale *et al.* 2013). In areas of severe, localised wood scarcity, large tree loss has been reported anecdotally in the lands despite tribal taboos (Kirkland *et al.* 2007). This research aims to quantify large tree loss in a communal land-specific context and identify people as drivers of savanna structure outside of fenced-off reserves.

b) Research questions

- How do the rates and spatial patterns of treefall differ between the sites?
- What affects the differences in rates and spatial patterns of treefall between the sites?
- What is the relative importance of other factors (e.g. fire, geology, hillslope, human-settlement specific traits) in treefall rates and patterns between sites?

1.2.5 Thesis structure

The thesis chapters, excluding the introductory (Chapter 1) and synthesis (Chapter 6) chapters, have been written in a free-standing format for submission to scientific journals. Whilst I endeavoured to avoid overlap between chapter components, it was at times unavoidable to ensure publishable material was maintained in a standalone context. This is

especially true of motivations for the study, study site descriptions and research methodology. Chapters 2 and 4 will soon be submitted for publication to appropriate journals. Chapter 3 has been published in *PLoS ONE* (Mograbi *et al.* 2015) and Chapter 5 is currently accepted in *Ecography* (Mograbi *et al.* in press).

Chapter 1 provides a rationale and introduction to the thesis, establishing the research context, and the aims and objectives. Chapter 2 investigates the vegetation structural dynamics across a wood extraction gradient, including the abiotic and anthropogenic factors associated with height-specific growth and loss. In Chapter 3 I derive above-ground woody biomass estimates, explore the challenges involved in biomass estimation, as well as the context of biomass change within the vertical structure of the vegetation canopy. Chapter 4 establishes the differences in patterns of biomass and vertical vegetation change both between and within communal lands, specifically examining the anthropogenic drivers of vegetation stocks and structure dynamics. I also compare rates and spatial patterns of treefall between human- and elephant-dominated sites in Chapter 4 to examine humans as drivers of savanna vegetation dynamics. The findings of each chapter are discussed in a more holistic context in Chapter 6, as well as addressing the constraints within which this research was conducted. The implications of the findings and possible opportunities within the social-ecological context of natural resource use are also considered.

I have also been involved as a co-author on the following publication:

Fisher, J.T., Witkowski, E.T.F., Erasmus, B.F.N., Mograbi, P.J., Asner, G.P., van Aardt, J.A.N., Wessels, K.J., & Mathieu, R. 2015. What lies beneath: Detecting sub-canopy changes in savanna woodlands using a 3D classification method. *Applied Vegetation Science,* 18(3): pp. 528-540 .

a) Author contributions

Due to the highly collaborative nature of the study, the papers on which Chapters 2-5 are based have vested involvement from a number of authors. The following list details the specific contributions of each co-author:

Mograbi, P. J.: Primary author conducted data extraction and analysis, wrote up chapters/papers

Witkowski, E. T. F.: PhD supervisor, provided guidance on theoretical ideas and data analysis for the papers, commented on various drafts of chapters/papers

Erasmus, B. F. N.: PhD supervisor, provided guidance on theoretical ideas and data analysis for the papers, commented on various drafts of chapters/papers

Asner, G. P.: PhD co-supervisor, CAO collaborator, developed and implemented CAO, provided LiDAR data, guidance on theoretical ideas and data analysis for the papers, commented on various drafts of chapters/papers

Wessels, K. J.: CSIR collaborator, commented on various drafts of papers

Mathieu, R.: CSIR collaborator, commented on various drafts of papers

Knapp, D.: CAO LiDAR data processing

Martin, R.: Planning, deployment and execution of CAO LiDAR campaigns

Main, R.: CSIR field-biomass estimates and initial field-LiDAR regression analyses, commented on an early draft of Chapter 3

Vaughn, N.: CAO LiDAR data processing, commented on an early draft of Chapter 5

1.3 Literature Review

1.3.1 Ecosystem Services

Ecosystem services are categorised by being: provisioning (often tangible 'goods': e.g. food, wood, medicinal); supporting (essentials for the production of other ecosystem services: e.g. nutrient cycling, primary production); regulating (benefits from ecosystem process regulating: e.g. flood attenuation, water purification); and cultural (services that enhance human living: e.g. aesthetic, spiritual) (MA 2003). From the above, it is clear that ecosystem services underpin human well-being (MA 2003). The establishment of the link between ecosystem services and human well-being clarifies ecosystem service valuation in anthropogenic terms, providing relevance and urgency that would not galvanise as much conservation effort from policy and management in isolation from human requirements (van Jaarsveld *et al.* 2005; van Wilgen & Wannenburgh 2016). This definition also provides a means of linking interventions to ecological concerns (e.g. desertification, biodiversity loss). The relationship between landscape processes and human well-being can be seen as a cascade of ecosystem services (Figure.1.1) (Haines-Young & Potschin 2010). However, ecosystem

services are not only the link between natural systems and human well-being, but ecosystem service provision processes also operate across spatial and temporal scales; changes to ecosystem functioning can also overflow into adjacent areas (Barrett *et al.* 2011), like conservation areas.

The link between nature (biodiversity and ecosystems), nature's benefit to people (ecosystem services), and quality of life (human well-being) has been formalised in the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) conceptual framework (Figure 1.2) (Díaz *et al.* 2015a). IPBES builds on the Millennium Ecosystem Assessment (MA) framework, but explicitly includes different knowledge systems (Figure 1.2) (Díaz *et al.* 2015a). A potential stumbling block to implementation of the IPBES assessments are the lengthy debates and compromises that come from being comprised of a purely governmental oversight body; in contrast, the MA came to consensus early on and easily, as the governing board comprised natural and social scientists, business communities and indigenous community leaders (Reid & Mooney 2016). That said, an MA shortcoming, that IPBES seeks to rectify, was the lack of institutional and governance representatives to support the science-policy interface (Díaz *et al.* 2015b).

Growing demand for ecosystem goods, especially food, fuel and water, are driving many ecosystem changes globally (MA 2005). Natural-resource dependence in communal areas is often a livelihood strategy and can be an effective buffer against poverty (Twine *et al.* 2003a). Although ecosystem goods and services have increased human well-being, these gains have been at the cost of ecosystem degradation and, thus, at the cost of decreasing the well-being of future generations who will rely on these compromised ecosystem services (MA 2005). This is a trade-off of the utilisation of ecosystem services that has to be made explicit (Carpenter *et al.* 2009). However, trade-offs become particularly difficult as ecosystem services manifest and are supplied to stakeholders at different scales; the composition of stakeholder groups also varies with institutional scale at different scales (Hein *et al.* 2006). In a fuelwood context, fuelwood provision is most important at the municipal scale, but woodland conservation is at the national level. Thus the processes that generate ecosystem services and socio-economic drivers of demand will change with scale. For example, fuelwood harvesting is sustainable at a national scale (Von Maltitz & Scholes 1995), but not on a local scale (Dovie *et al.* 2004). As ecosystem service production is spatially variable, it is important to identify essential areas to ensure continued ecosystem service provision and human well-being (van Jaarsveld *et al.* 2005).

Ecosystem services are generally difficult to quantify and biodiversity surrogates are often used in line with the asymptotic relationship between biodiversity and ecosystem function (MA 2003). Small changes in biodiversity can lead to small changes in ecosystem functioning, provided those biodiversity losses do not include unique roles (MA 2003). Nonetheless, some ecosystem services, especially goods, can be measured directly without the use of surrogates. For example, fuelwood stocks can be measured directly via woody biomass and change in woody vegetation structure and this is particularly relevant in communal harvesting areas. In this regard, woody vegetation can provide both a direct measure of an ecosystem good as well as an indirect measure of other ecosystem services via a proxy for regulating, supporting and cultural services. Specifically measuring large trees in rural commons can serve as a proxy for cultural ecosystem services as they are often valued for their spiritual significance as well as providing fruit and shade (Shackleton *et al.* 2003; Luoga *et al.* 2005; Kirkland *et al.* 2007). For example, in the South African Lowveld *Diospyros mespiliformis, Sclerocarya birrea* and *Strychnos* species are traditionally taboo

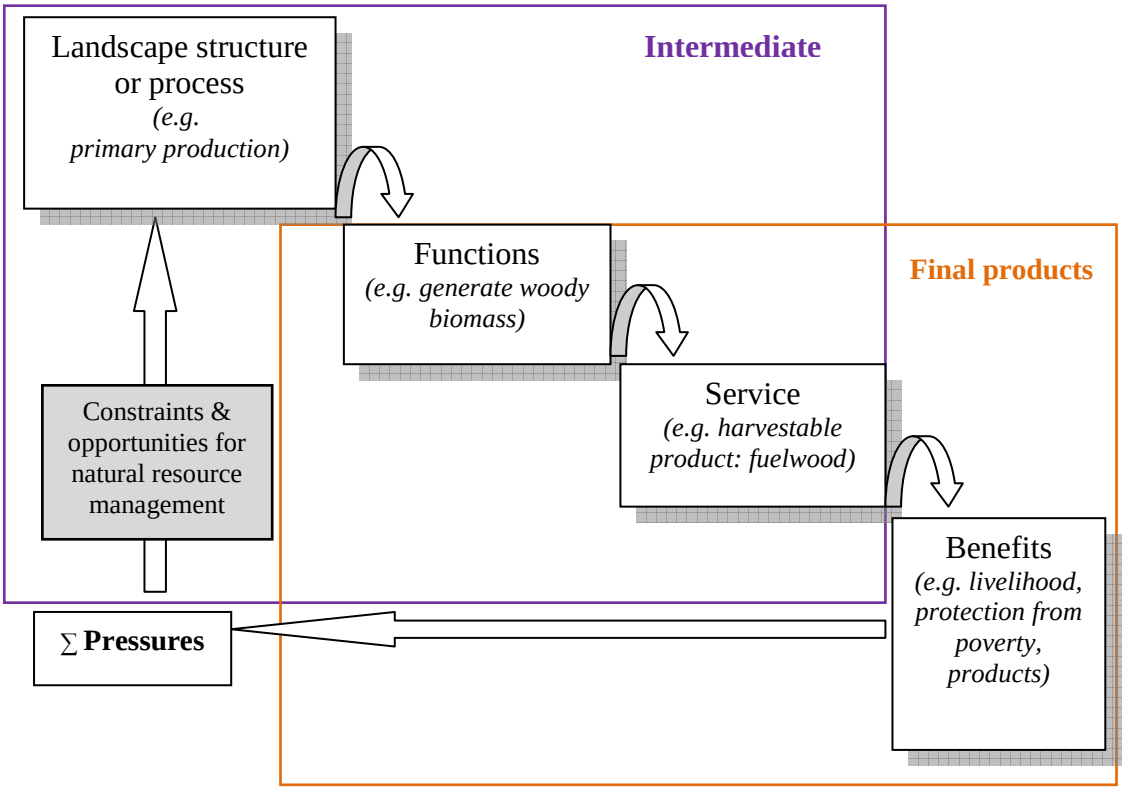

Figure.1.1. Conceptual diagram linking ecosystem functioning to human well-being through a series of service cascades [adapted from: Haines-Young & Potschin 2010]. "∑" refers to the "sum of".

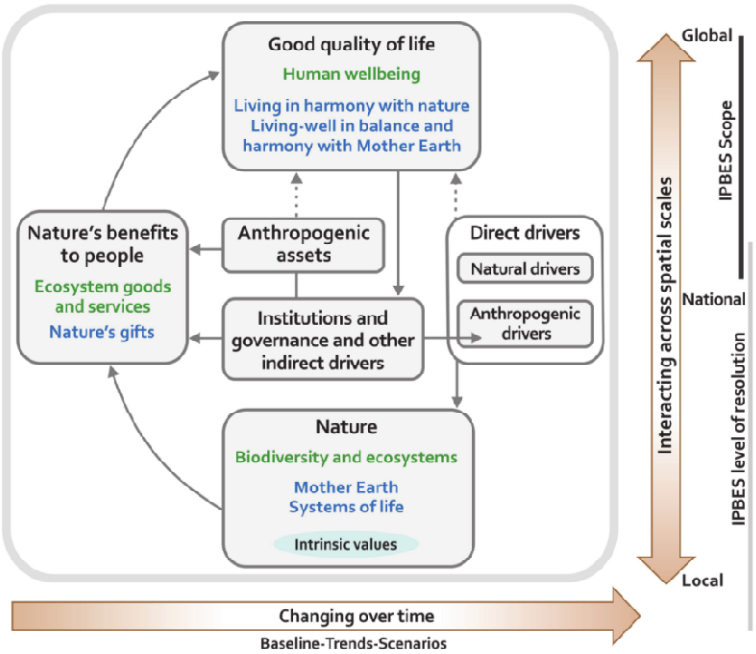

Figure 1.2. The IPBES Conceptual Framework. The main focus of the framework is the three elements of coupled social-ecological systems: nature, humans, and the benefits humans derive from nature. The blue and green texts denote scientific and equivalent knowledge systems for concepts. Dashed arrows are links that are acknowledged to be important, but are not the focus of the IPBES framework. The broad arrows denote spatial and temporal scales. Although IPBES assessments will be undertaken at the regional to global scale, they build on sub-national scale knowledge [from Díaz *et al.* (2015a)].

species for cutting (Madubansi & Shackleton 2007) and these trees can be seen in their conserved status within communal fields in the area (Wessels *et al.* 2011). Changes to the number and/or height of these large fruiting trees could be an indication of severe fuelwood shortages where locals are prepared to violate local taboos and harvest live wood from forbidden trees.

1.3.2 The 'Fuelwood Crisis'

Fuelwood use by developed countries has drastically decreased with convenient and efficient energy alternatives being provided, but wood-based energy use continues to be the dominant form of energy in developing countries (Arnold *et al.* 2003; Cervigni & Morris 2016). The use of woody biomass for heating and cooking does not require expensive or complicated equipment and only costs the labour and effort required to collect it. The 'fuelwood crisis' of the 1970s revolved around the socio-economic implications of people not being able to meet

their basic energy needs and concern over wide-spread destruction of forest resources (Arnold *et al.* 2003). However, predicted woodland collapses did not occur because the real reason for woodland degradation was driven by clearing for agricultural expansion (Arnold *et al.* 2003). People would not switch to alternatives and woodlot schemes were unsuccessful, yet woodfuel-dependent communities continued to find sources of energy. Fuelwood supply-demand models had overestimated fuelwood demand, and underestimated supply and woodland regenerative potential - people do not chop down whole trees for fuelwood, they lop branches and collect deadwood (Arnold *et al.* 2003). This led to a reduction in funding and research in the 1990s, but fuelwood has recently been revitalised as a concern for ecosystem service provision and sustainability in socio-economically compromised countries, representing a shift from an energy-crisis framework to a community-resources framework (Shackleton *et al.* 2004). This is particularly true of communal areas in African savannas commensurate with heavy population increases, and urban areas in African forest zones (de Montalembert & Clement 1983). Fuelwood sustainability research in Bushbuckridge Municipality has followed the trend of the new focus on community-resources, with recent work exploring social-ecological system resilience (e.g. Matsika *et al.* 2013), the association between natural resource use reliance with community health and well-being *(e.g. Hunter et al.* 2011), social dynamic effects on natural resource harvesting patterns (e.g. Twine *et al.* 2003), and woodland regenerative response to harvesting (e.g. Neke *et al.* 2006).

Fuelwood use is typical of 'wicked problems' with no simple solutions (Rittel & Webber 1973; Levin *et al.* 2009) – woodland degradation is both a cause and an effect of fuelwood shortages (Mercer & Soussan 1992). Woody resource use is a reflection of the local land-use pattern, generated by the 'integrated production system' (the relationship between the environmental capacity to supply the resources and peoples' interaction with the environment) (Figure 1.3) (Soussan 1988). But fuelwood shortages do not manifest as a lack of fuel, rather through deteriorating indicators of fuel availability and quality, increased effort required to collect resources, and tensions arising from competing uses and land-access constraints (Soussan 1988). Thus, supply-demand models often do not show the problem accurately and previous predictions of lack of fuel supply have not come to pass (e.g. de Montalembert and Clement 1983, Banks *et al.* 1996). Rather, fuelwood shortages manifest indirectly in adaptive behaviour from communities (e.g. changing cooking patterns, fuelwood commodification) and weakening social structure (e.g. men become involved in fuelwood provision, balance of power to people who control access to resources) (Soussan 1988).

Although fuelwood shortages are a global phenomenon, shortages need to be understood at a local level as it is produced and used at this level and are exceptionally context-specific (Soussan 1988; Giannecchini *et al.* 2007). However, increasing globalisation and modernisation has unintended consequences for local fuelwood demand. Urban migration in a developing world context creates "remittance landscapes" – land-use change driven by wages earned in urban centres and remitted to rural communal lands, altering the distribution of crop-land and common land use (Lambin *et al.* 2001), with repercussions for natural resource supply. Government policy changes designed to solve "tragedy of the commons" problems (Hardin 1968) – such as restriction of seasonal transhumance, removing tribal authority – inadvertently worsen the natural resource reliance situation by increasing unemployment levels and welfare dependencies, and altering power balances to those who control access to resources and land (Rohde *et al.* 2006).

1.3.3 Woody vegetation biomass and structure

Fuelwood harvesting changes the structure and composition of woodlands. Vegetation structure refers to the aboveground vertical and horizontal components that determine the position, extent, quantity and type of vegetation in space and time (Lefsky *et al.* 2002a). The composition and diversity of vegetation structure provides information about the functioning of the vegetation (Lefsky *et al.* 2002a). Indeed, it is structural information derived from vegetation structure studies that is required for understanding of biomass change estimations, clarifying the uncertainty of surface carbon exchange and changes in habitability and biodiversity (Hall *et al.* 2011).

Biodiversity, according to Noss's (1990) definition, includes structural, functional and compositional facets at multiple, hierarchical levels. However, compositional diversity is often elevated in disturbed areas relative to undisturbed areas and the effects of disturbance are seen in comparative structural diversity. Shackleton (2000) found significantly less herbaceous cover and lower vegetation height in communal lands than protected areas, yet the communal lands also had significantly higher species richness. The functional diversity aspect of biodiversity can often be inferred from structural diversity. Structural complexity has been linked with, amongst others, productivity (Aguiar & Sala 1999; Ishii *et al.* 2004), habitability and species richness (Halaj *et al.* 2000), regulation of edge effects (Harper *et al.* 2005), groundwater regulation (Ilstedt *et al.* 2016), and ecosystem health and integrity

(Manning *et al.* 2006). At landscape levels, the spatial heterogeneity of flora and fauna habitats and their complex interactions in three dimensional space affects the distribution of biodiversity (Tews *et al.* 2004; Hall *et al.* 2011). An often neglected aspect of structural diversity is vertical complexity. It has relevance to ecosystem function as canopy height is related to biomass and productivity (Lefsky *et al.* 2002b), biodiversity (Herremans 1995; Halaj *et al.* 2000; Lumsden & Bennett 2005) and contributes to structural heterogeneity (Hall *et al.* 2011). Edge effects can be beneficial to ecosystem functioning, as they constitute components of ecosystems across which processes operate (Cilliers 2001), but are also detrimental by contributing to fragmentation (Harper *et al.* 2005). Thus, structural heterogeneity is essential for biodiversity conservation (Fischer *et al.* 2006). Studies of landscape structural characteristics (e. g. structural richness, structural extent and structural diversity) and how they affect landscape biodiversity are essential (Waldhardt 2003) for natural resource management. In the context of agro-ecological landscapes, evidence suggests that heterogeneous landscapes which resemble natural patterns are more functional and productive than structurally simple landscapes (Fischer *et al.* 2006). Thus, if species composition is not a consistent indicator of disturbance impacts, and function can be inferred from structure, structural indicators are essential for measuring biodiversity in landscapes.

Although many studies emphasise the relationship between structural diversity, biodiversity and ecosystem function, 'keystone structures' may be just as important (Tews *et al.* 2004). In this context, 'keystone structure' refers to a spatial structure providing goods and services essential for other species' survival (Tews *et al.* 2004). An example of an ecosystem where 'keystone structures' are important is semi-arid savannas where large, solitary trees within a grass matrix become central functional components through a supply of shade (Tews *et al.* 2004), local nutrient hotspots (Treydte *et al.* 2007; Treydte *et al.* 2008; Mills *et al.* 2012), decreased local evapotranspiration (Belsky *et al.* 1993; Manning *et al.* 2006), and nesting sites for arboreal species (Herremans 1995). These effects have been recorded in numerous tree species in a South African savanna, including *Acacia haematoxylon, Boscia albitrunca, Acacia erioloba, Terminalia sericea* and *Peltophorum africanum* (Tews *et al.* 2004).

However, small trees and shrubs also play a role in landscape pattern and process. Increased presence of shrubs can be construed as bush encroachment, manifesting in unpalatable woody species increase and palatable grass species decrease. Both local and global drivers have been implicated as the cause behind woody encroachment (Archer *et al.* 1995; Stevens *et al.* 2015). Human influences are shifting savanna systems to increasingly woody states as a

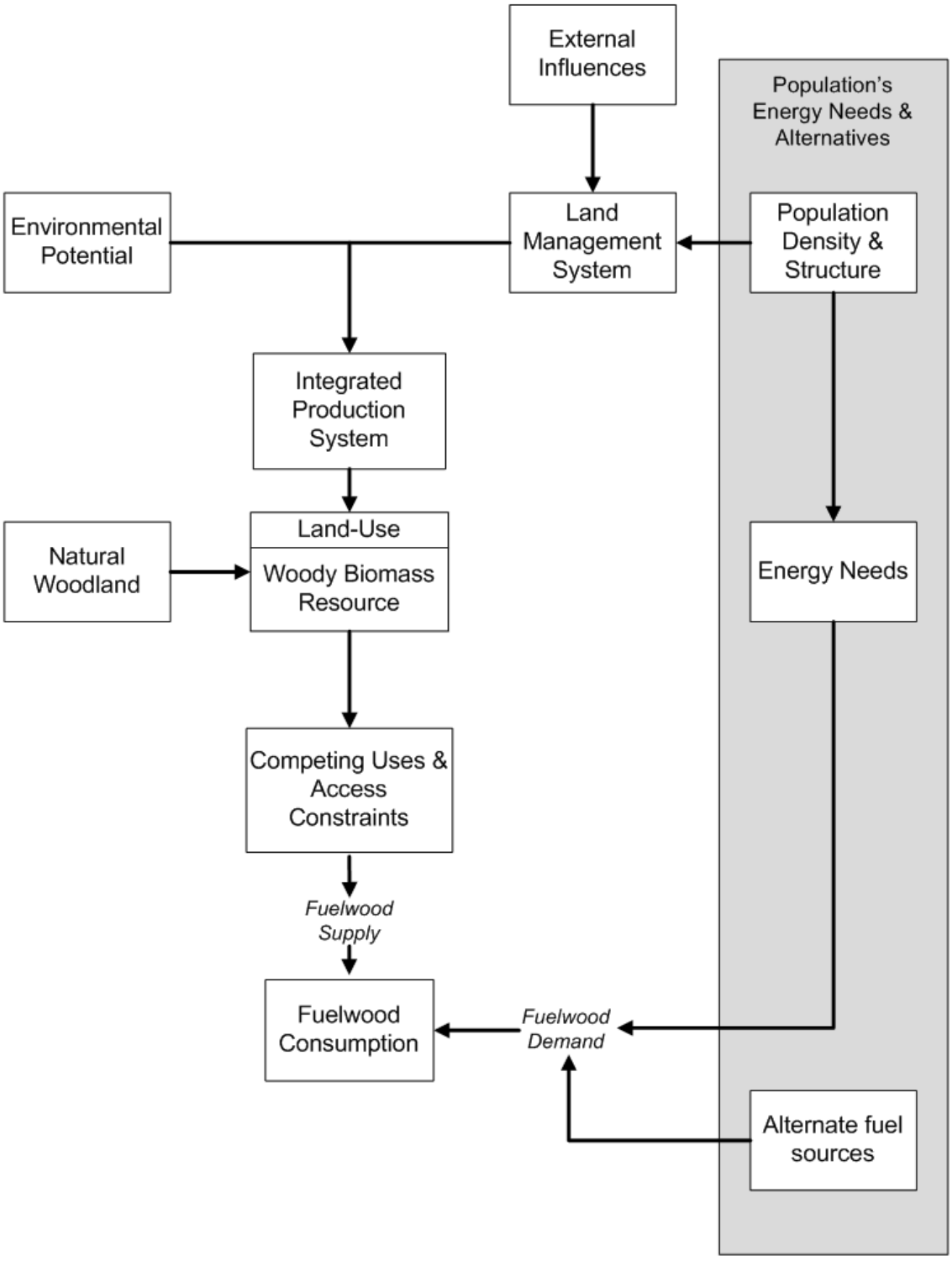

Figure 1.3. Soussan's (1988) fuel use and supply framework.

result of overgrazing, fire suppression and reduction in browser numbers (for historical list of studies documenting woody encroachment see review by Archer *et al.* 2001), particularly in Africa where encroachment is 2.5 fold greater than in Australian savannas (Stevens *et al.* 2016). Cattle farming is frequently implicated as a culprit of vegetation structure changes; the shifting grazing localities also mean that the effects of cattle on the landscape (e.g. increasing soil nutrients through defecation, increasing moisture availability & lowering fire frequency through grass removal, high grazer selectivity) are widespread (Moleele *et al.* 2002). Climate change and atmospheric CO_2 enrichment are also driving bush encroachment (Bond & Midgley 2012; Buitenwerf *et al.* 2012). Bush encroachment reorganises savanna systems (Archer *et al.* 2001; Meik *et al.* 2002). Indeed, bush encroachment has been shown to result in lower livestock carrying capacity and decreased survival rate for calves (Oba *et al.* 2000). Moreover, bush encroachment can change the behaviour of ungulates which avoid densely vegetated areas, creating a cascade of effects on the herbaceous vegetation (Riginos & Grace 2008). Bush thickening can be exacerbated by continued woody harvesting and coppicing shoots in communal lands. However, a complete lack of woody cover, desertification, is also detrimental for ecosystem functioning.

Desertified, bare patches have increased sheet flow, decreased infiltration and a resultant loss of nutrients (Rietkerk & van de Koppel 1997). This impaired recruitment of vegetation in bare patches, creates positive feedbacks of low water availability, soil crusting and extreme temperatures, resulting in persistent bare patches (Rietkerk & van de Koppel 1997). Implications of the alternate stable states model is that the bare patches' run-off facilitates vegetation growth in vegetated patches, but herbivore grazing behaviour changes to focus on the vegetated patches, reducing the biomass in the vegetated patches, perpetuating a large-scale ecosystem collapse (van de Koppel *et al.* 2002). Regime shifts, or changes to the structural diversity or even just a reduction in 'keystone structures', which affect ecosystem functioning, are expensive and restoration is a slow process (Milton *et al.* 1994), with social-ecological costs *en route*. As anthropogenic influences in savannas can sever complex regulatory mechanisms (Sankaran & Anderson 2009), restoration might not even be possible if a shift occurs to a different 'basin of attraction'. Conversely, anthropogenic influences may be crucial in maintaining optimal savanna ecosystem function through, for example, the use of fire.

Change is inherent in savannas and shifts in tree-grass ratios with regard to climatic, topoedaphic, fire, herbivory and anthropogenic drivers are expected (Scholes & Archer

1997). Dynamism across a spatial-temporal context is an integral component of ecosystems from the heterogeneity paradigm perspective (Rogers 2003). As fuelwood harvesting has functional implications for social-ecological systems, monitoring and management of heterogeneous landscapes cannot just occur in protected areas (Farina 2000; Fischer *et al.* 2006). The variety of land-uses and land-use intensities makes communal lands a heterogeneous landscape, but the intensity of use threatens to transform lands into a structurally homogeneous, functionally inferior landscape. Admittedly, the susceptibility of a landscape to homogenisation effects is dependent on: local socio-cultural and economic status; local population densities; the ecological context of the landscape being harvested; and the spatio-temporal accessibility of woody resources in the landscape. Communal landscapes are dynamic systems, which is reflected in the land-cover change, with drivers likely to be spatio-temporally distributed across the landscape (Coetzer *et al.* 2013). As a complex system, ecosystems are capable of reorganising after disturbances. Hence structural landscape changes could provide different ecological functions, albeit with ecological repercussions (van de Koppel *et al.* 2002; Hobbs *et al.* 2014). Loss of tall trees may result in increased forage availability for small ungulates through coppicing shoots; however it reduces the abundance of woodland birds, in particular the canopy specialists (Herremans 1995). Spatial heterogeneity has been linked to stabilising populations and functional heterogeneity (Owen-Smith 2004). Indeed, homogeneous landscapes are less resilient to global environmental changes and local disturbances (van de Koppel & Rietkerk 2004). This affects ecosystems' ability to provide ecosystem services.

At a broad scale, a trend in decreasing woodland cover had already been observed in the greater Kruger to Canyons (K2C) Biosphere Reserve (Coetzer *et al.* 2013; Coetzer-Hanack *et al.* 2016) and one would expect that this will affect both vegetation structural diversity of the area as well as loss of 'keystone structures' such as large trees. Accordingly, Wessels *et al.* (2011) found vegetation in the <5 m height class had half the woody cover than the same class in protected areas but, conversely, found a greater number of trees in communal areas than conserved areas as a result of culturally-protected trees. These findings were echoed in Fisher *et al.*'s (2012) communal lands study where high levels of wood harvesting reduced structural diversity, by changing the amplitude of height class distributions. Although coppice does occur in some harvested species, overharvesting skews the population structure. Under extreme circumstances, disturbance gradients decline in highly utilised areas and this is a warning of severe woodland degradation – for example, in highly utilised communal

lands, the phenomena of height class distribution changes with increasing distance from villages disappears, replaced by expanses of homogeneous vegetation structural profiles regardless of distance from disturbance centres (Fisher *et al.* 2012).There has also been an observable decrease in the coppice stem diameters being harvested, indicating localised shortages of desirable fuelwood size classes (Matsika 2012). This has implications for plant recruitment as the coppice may not reach reproductive maturity before it is harvested. This renders adult trees 'functionally juvenile' (Twine 2005). Fewer seedlings in the population reduces the future populations' survival rate (Lykke 1998). Indeed, both fewer reproductively mature plants and fewer seedlings were found in harvested areas relative to protected areas in Bushbuckridge (Neke 2005). If population size structures become drastically skewed as a result of preferential wood harvesting, it could lead to impaired woodland regeneration.

The preservation of large trees in communal lands is particularly important in the light of localised fuelwood shortages leading to live wood harvesting (Kirkland *et al.* 2007). Evidence suggests that even trees that are normally protected by traditional taboos, such as marulas (*Sclerocarya birrea*) which are valued for their fruit (Shackleton *et al.* 2003), are being targeted (Kirkland *et al.* 2007). In the context of Miller and Rudolph's (2011) stage-structured consequences for populations, large trees can be considered 'stage-structured refugia' which, if targeted, could change the entire ecosystem. Similarly, stage-structured harvesting effectively redistributes biomass within the stage-structures, affecting life history characteristics of the population (De Roos *et al.* 2007), and altering ecosystem functioning even if overall biomass remains constant (Miller & Rudolf 2011). Savannas, as complex tree-grass biomes (Scholes & Archer 1997), typify structural complexity.

1.3.4 Spatio-temporal dynamics of savannas

Savannas are multiple-use landscapes that are shaped by interactions between environmental and anthropogenic drivers. Ecosystem functioning derived from savannas is generated at a range of spatial scales and is utilised at different levels (Hein *et al.* 2006). For example: household utilisation of ecosystem services will differ from municipality utilisation (Hein *et al.* 2006). In a fuelwood scenario, harvested fuelwood can benefit households as energy but loss of landscape level air purification could jeopardise the health of the region. Thus, the drivers that shape these processes will differ across the landscape and at a range of spatial scales.

Generally, water availability sets the upper limit for woody cover with increasing biomass from arid to mesic areas (Sankaran *et al.* 2005) but realised woody cover is regulated by disturbances, such as fire and herbivory (Bond & Keeley 2005; Sankaran *et al.* 2008). Savanna distribution limits are less clearly defined in arid areas (~200mm rainfall p.a.), under high rainfall seasonality, or on high nutrient soils, implying herbivory extends savanna limits (Lehmann *et al.* 2011). Fire's effects on savanna woody cover occur mostly at tree sapling level. Tree saplings exposed to fire are vulnerable to top-kill, keeping saplings in the 'fire trap' (Higgins *et al.* 2000; Bond & Keeley 2005). Thus, frequent fires impose a demographic bottleneck on tree communities in savannas. In addition, large tree mortality is affected by intense fire events (Smit *et al.* 2016). Changes to fire regimes are inextricably linked to increased human ignitions as well as increase fragmentation of the landscape by humans (Archibald *et al.* 2013).

Anthropogenic land use has been acknowledged as a driver in savanna vegetation structure (Bird & Cali 1998; Pyne 2001; Bucini & Hanan 2007), but usually in association with fire, and secondary to topoedaphic features, fire and herbivory. However, current, and growing human land-use in savannas will increasingly alter woody vegetation cover. To date, savannas contain up to 33% of the global human population (Safriel *et al.* 2005), are characteristically rural, and heavily reliant on natural resources (Cervigni & Morris 2016).

1.3.5 Conservation and research priorities in savannas

Ecological research is predominantly focused on areas of high biodiversity, often areas with low human impacts. Yet formal protected areas only make up 17% of terrestrial land surface (IUCN 2014) and considerable biodiversity occurs outside reserves (Andelman & Willig 2003). In an era where land is an increasingly sought after economic resource and human population numbers are steadily rising, establishment of new 'fortress' style reserves is unrealistic and often impossible - real 'wilderness' areas are increasingly rare (currently, 75% of ice-free terrestrial land is already human-modified (Ellis & Ramankutty 2008). Conservation efforts need to extend beyond reserve fences into multi-use landscapes, establishing a compromise between conservation and sustainable development (UNESCO 1996). Indeed, biodiversity research outside of protected areas should be at the forefront of research as people's livelihoods and welfare depend on ecosystem functioning. Monitoring changes in woody vegetation structure can be equated with monitoring the sustainability of

rural wood-use. Using Banks *et al.*'s (1996) study as a baseline, Shackleton and Scholes (2011) estimated that up to 90% of woody biomass had been extracted as fuelwood and timber by the surrounding communities. Moreover, biomass structure distributions are more altered in communal than protected lands as a result of human impacts (Wessels *et al.* 2013). Disturbance gradients are predicted to merge around settlements as vegetation structure becomes more homogeneous (Fisher *et al.* 2012). The impacted vegetation footprint has already begun to coalesce, blurring boundaries between lands (Coetzer *et al.* 2013). The intensive use of woodland resources indicated by these studies suggests impending sustainability issues. However, resource usage is not equal over the landscape and usage patterns are settlement specific (Soussan 1988; Giannecchini *et al.* 2007), reflecting village-level characteristics within the broader national and global socio-economic context (Lambin & Geist 2006). Despite uneven resource extraction in communal lands, patches of disturbed areas can act as kernels to larger scale losses of vegetation (Luoga *et al.* 2005; Coetzer *et al.* 2010).

1.3.6 Sustainability, resilience and poverty-traps

'Sustainability' of ecosystem services encompasses society's reliance on the ecosystem in the present without compromising future delivery of ecosystem services by utilising ecosystem services within environmental limits; i.e. consumption rates for ecosystem services are less than production rates (Biggs *et al.* 2004). Sustainability is often measured according to biophysical parameters and associated thresholds beyond which ecosystem services start to collapse (Tacconi 2000). Sustainability science's goal is to manage ecosystems in areas where multiple human requirements interact in a complex manner with multiple ecosystem service requirements (Clark 2007). These areas are crucial to manage sustainably and can be referred to as ecosystem service 'hotspots'. Hence, sustainability science should revolve around managing both conservation and human welfare (Naidoo *et al.* 2008) through the concept of ecosystem services. Communal lands are an example of where trade-offs occur between human requirements and ecosystem services. When woody biomass extraction, like fuelwood harvesting, occurs beyond sustainable limits, it threatens the provision of other ecosystem services. Hence, sustainability science is instrumental in driving conservation beyond the boundaries of parks and into areas where people are considered part of the ecosystem in complex interactions, with the goal of sustaining ecosystem service provision (Daily & Matson 2008).

The implications of this type of conservation are that one cannot avoid looking at the socio-economic context that ecosystem services are being utilised in, as people and the environment shape each other interactively (Clark & Dickson 2003; Folke *et al.* 2010). For example, an assessment on the productivity of an ecosystem in the absence of understanding the cultural background behind why certain plants are protected over others or which sites are consider sacred might lead to incorrect conclusions about the system state and the motives of the people ingrained in the system (Whitfield & Reed 2012). The recognition of environmental issues embedded within cultural, political, economic and social landscapes means environmental assessments involve value judgements (Whitfield & Reed 2012).

Dealing with issues of sustainability in ecosystem services means certain trade-offs have to be made explicitly. Decisions have to be made in ecosystem service management between: different ecosystem services and the socio-economic benefits derived from them; current and future requirements of the community; and benefits at different institutional scales (Biggs *et al.* 2004) and within different spheres (e.g. cultural, political, economic, environmental) (Whitfield & Reed 2012). Troublesome trade-offs can occur when promoting an ecosystem benefit at the expense of other benefits (Biggs *et al.* 2004). For example, bush encroachment is considered land degradation to cattle owners who need grazing land, but could be considered a new service for goat owners who can utilise the additional browsing resource (Whitfield & Reed 2012). In addition, ecosystem services themselves are scale-dependent. Often provisioning services are studied on a fine scale, yet regulating services occur at landscape scales (van Jaarsveld *et al.* 2005). Thus, the trade-off decision also needs to be scale-explicit. Trade-offs are frequently quantified by assigning monetary values to ecosystem services (Biggs *et al.* 2004). However, estimates in financial terms are useful to translate the magnitude of the ecosystem services provided, but have no meaningful contribution in decision-making contexts (Costanza *et al.* 2014). The true value of an ecosystem service is often not financially quantifiable (Carpenter *et al.* 2009) and can portray the impression that the service is more easily substitutable than it actually is (Cowling *et al.* 2008).

A crucial aspect in sustainability science is the concept of an ecosystem's renewal and response to disturbances, known as resilience. Resilience is defined as "the capacity to absorb disturbance and reorganise while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks" (Walker *et al.* 2004). For example, woody biomass extraction within a resilient system would occur within a changeable system which

is capable of absorbing disturbances through adapting or reorganising while maintaining ecosystem functions. Ecosystem resilience provides adaptive capacity which is critical in the context of utilisation limits of ecosystem services (Elmqvist *et al.* 2003). From an ecosystem services perspective, biodiversity is seen as the foundation supporting ecosystem services and not just as a list of threatened charismatic species (Mace *et al.* 2012).

If resilience is thought of as a system with an 'identity', derived from the maintenance of its constituent components and interactions, then resilience can be defined by quantifying 'identity' and ascertaining the system's potential to change that identity (Cumming & Collier 2005; Cumming 2011). Unfortunately, quantifying the actual change in a system's state is difficult as a threshold can be crossed without any change in the measurable variable (Cumming 2011) (Figure 1.4).

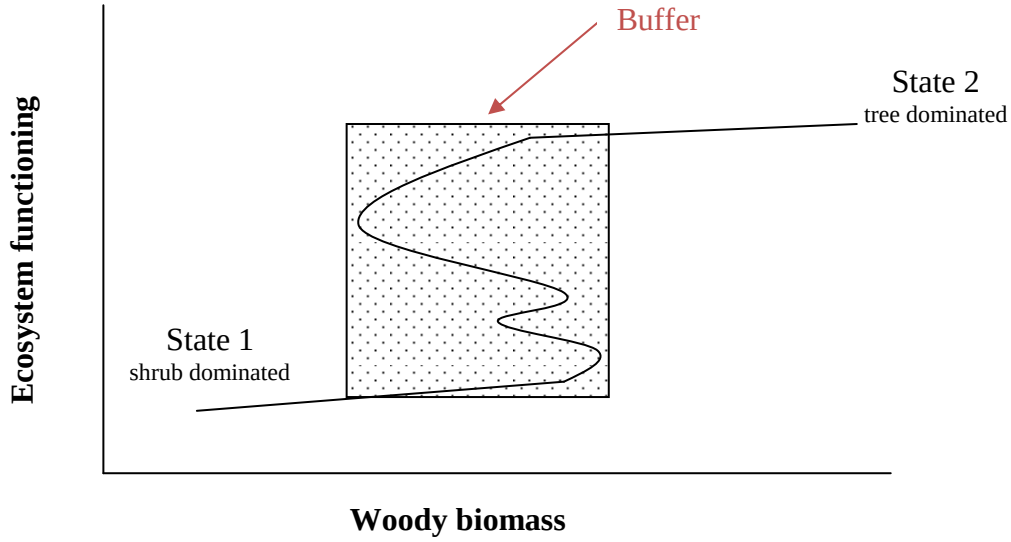

Figure 1.4. Conceptual diagram demonstrating the buffering capacity of a system. In order for the system to change state, it must exceed the loss of woody biomass and the buffering capacity. Quantifying biomass does not necessarily give an indication of what level of ecosystem functioning is occurring in relation to state changes as a result of the buffering capacity [adapted from: Cumming 2011].

Regular perturbations in ecosystems, both natural (e.g. droughts, floods) and anthropogenic (e.g. overharvesting), and in communities relying on the ecosystem (e.g. poverty, population growth) can become mutually reinforcing vulnerabilities (Barrett *et al.* 2011). This 'poverty trap' situation can be a result of positive feedbacks in coupled system interactions where

poverty, resource exploitation and human well-being become reinforcing cycles (Biggs *et al.* 2004). Unfortunately, in these situations fine-scale decisions compound into large-scale patterns that are spatially correlated with ecosystem fragility (Barrett *et al.* 2011). Resilience theory would advocate that spatio-temporal trade-offs and system resilience would be the ideal strategy to mitigate decline in ecosystem service provision (Béné *et al.* 2011). Yet, poverty-traps require trade-offs that cater for basic needs and fundamental rights provision first before general system resilience, especially in the short-term (Béné *et al.* 2011). Poverty-traps (also known as "green traps" *sensu* Cumming *et al.* (2014)) are characterised by "fixes that fail" (Senge 1990; Cumming 2011) where short-term fixes produce causal loops of unintended consequences, in this case, system collapse from unsustainable use of natural resources (Figure 1.5). Unfortunately, arid and semi-arid ecosystems are one of the least ecologically resilient systems to start with (Whitfield & Reed 2012) and, as such, are particularly vulnerable. Agropastoralist communities in developing countries are typically in "green traps" – a reinforcing loop of poverty and environmental degradation - resulting from inadequate food production and population growth without adequate socioeconomic reorganization (Cumming *et al.* 2014). However, "green traps" are notoriously 'sticky' and moving social-ecological systems into a sustainable "red loop" (that is, improving household wealth whilst maintaining environmental degradation within feasible levels) is the challenge facing both rural and the rapidly urbanising sectors of the developing world (Cumming *et al.* 2014).

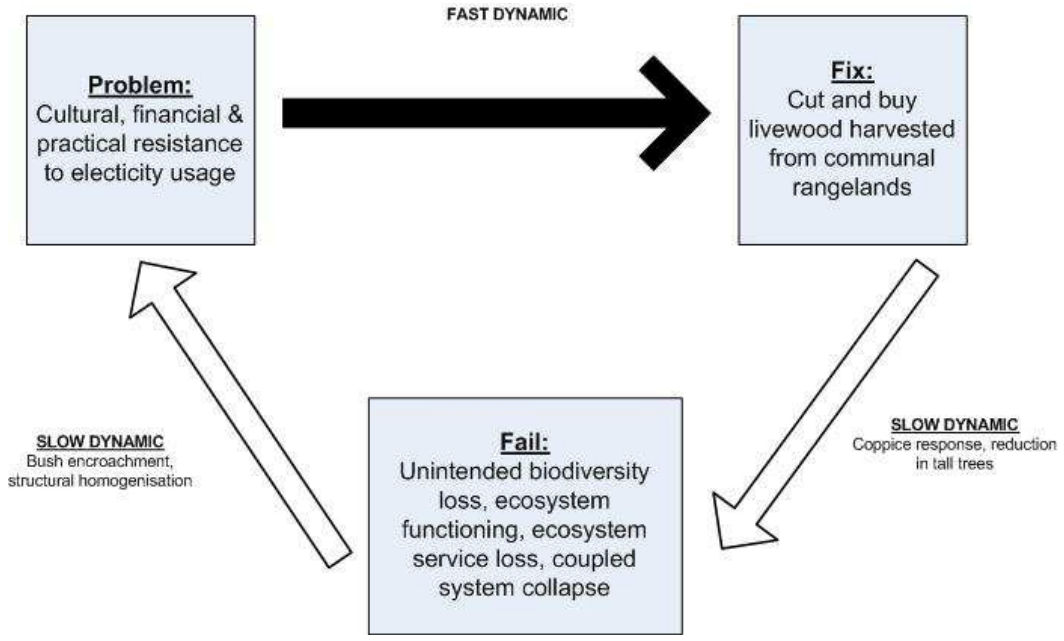

Figure 1.5. The causal loop that lead to "fixes that fail" consequences in unsustainable natural resource use. Slow variables are particularly important in ecosystem functioning and resilience [adapted from: Cumming 2011].

1.3.7 Light Detection and Ranging

Light Detection and Ranging (LiDAR) is an active remote-sensing method which has provided the opportunity to quantify vegetation structure and biomass over extensive areas by remotely sensing three-dimensional vegetation structure and the underlying terrain (Hall *et al.* 2011).The laser ranging method detects the precise time interval that it takes an emitted laser pulse to reach an object, reflect and return to the sensor (Lefsky *et al.* 2002a). The time taken for discrete time intervals can be taken (e.g. first and last return intervals) or a complete waveform of the returned signal can be measured (Figure 1.6). LiDAR metrics commonly employed to quantify woody vegetation include canopy cover, tree and canopy height, vegetation layers and volume measures (Lefsky *et al.* 2002a; Asner *et al.* 2007; Hall *et al.* 2011). LiDAR has mostly been used in temperate forest applications to measure fuel loads and structural attributes (see: Means *et al.* 1999; Lefsky *et al.* 2002a; Roberts *et al.* 2005; Patenaude *et al.* 2004) and tropical forest monitoring (see: Drake *et al.* 2002; Chave *et al.* 2005; Asner *et al.* 2008), but has recently been successfully applied in savanna ecosystems. Small-footprint, high point density, discrete return LiDAR provides fine-scale detail over areas much larger than possible with conventional field methods to assess savanna drivers.

a) The Carnegie Airborne Observatory (CAO)

The Carnegie Airborne Observatory (CAO) (https://cao.carnegiescience.edu/) was launched in order to study global ecosystem structure, function and composition. The products generated were aimed at assisting conservation, management and resource policy development with the aid of detailed, large-scale observational data (Asner *et al.* 2007). To date, they have performed macroscale ecosystem measurements in Argentina, Brazil, Borneo, California, Columbia, Costa Rica, Hawaii, Madagascar, Malaysia, Panama, Peru, and South Africa. The CAO Alpha system operated in South Africa in 2008 and 2010, and was decommissioned in 2011. The system had an integrated visible-to-near infrared (VNIR) imaging spectrometer and waveform LiDAR system (Asner *et al.* 2007). The in-flight fusion of both products, together with an integrated navigational and data processing capabilities, delivered high resolution vegetation structure (vegetation height, crown shape, vertical vegetation layering), biochemistry and physiology products, as well as information on surface waters, soil and the underlying terrain (Asner *et al.* 2007) (Table 1.1). The CAO-2 AToMS (Airborne Taxonomic Mapping System) operational platform replaced CAO Alpha and was launched in 2011. AToMS integrated very high fidelity visible-shortwave infrared (VSWIR) imaging spectrometer measuring the 380-2510 nm wavelength range (5nm spectral

resolution), a dual-laser, waveform LiDAR system, and a high-resolution visible-to-near infrared (VNIR) imaging spectrometer (365-1052 nm). The data fusion from all three sensors presents the highest dimensional data for terrestrial and aquatic habitats, data which are able to answer increasingly complex questions about biosphere change without the error associated with multiple sensors on multiple aircraft (Asner *et al.* 2012).

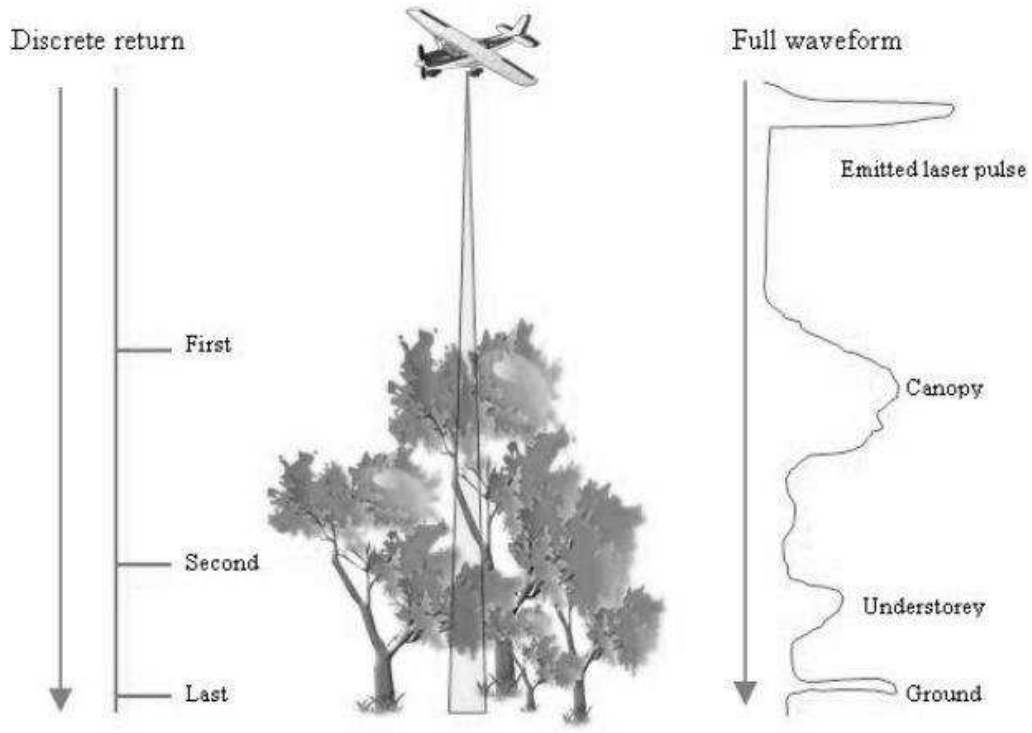

Figure 1.6. Discrete and full waveform LiDAR systems returning laser pulses off different vegetation heights within the canopy [from: Miura 2010].

CAO-2 AToMS was used to collect the 2012 LiDAR data in South Africa (Table 1.1). The data generated by the CAO have been used for a variety of applications, including: invasive species mapping (Asner *et al.* 2008), identifying the extent of illegal gold mining in the Peruvian Amazon (Asner *et al.* 2013), assessing animal behaviour through mapping landscape use hunting lions (Loarie *et al.* 2013) as well as arboreal primate canopy use (McLean *et al.* 2016), the effects of the 2012-2015 drought on California's forests (Asner *et al.* 2015b), the effects of roads on woody cover (Smit & Asner 2012),and mapping tropical carbon stocks (Asner & Mascaro 2014) (for a full list of CAO publications see https://cao.carnegiescience.edu/publications). Use of LiDAR in savannas is particularly

relevant as savannas are characterised by structural heterogeneity (Scholes & Archer 1997) which traditional 2-D remote sensing methods cannot adequately represent. Due to the enormous 3-D detail of LiDAR, the data are often simplified into summary statistics, including canopy cover and above-ground biomass estimations (Lefsky *et al.* 2002a; Anderson *et al.* 2006; Meyer *et al.* 2013) which do not express savanna heterogeneity in an ecologically meaningful context (Fisher *et al.* 2014). Thus, LiDAR application in savannas often makes use of voxels (volumetric pixels) which are a 2-D summary of the 3-D point cloud by binning LiDAR laser returns into aggregated 1m height classes (Weishampel *et al.* 2000). LiDAR data are also being used in object-based image analysis (OBIA) approaches, at an ecologically relevant scale which identifies individual tree 'objects' to gather vegetation parameters, circumventing per-pixel-based analysis and maintaining heterogeneity principles in the analysis (Johansen *et al.* 2010). The LiDAR product application to South African savanna ecosystems has produced many novel findings, including a description of the hierarchical impacts of mega-faunal disturbance on savanna structure (Asner *et al.* 2009b; Levick *et al.* 2009), and the relative influence of topo-edaphic factors (Colgan *et al.* 2012), biotic drivers (Levick *et al.* 2010; Davies *et al.* 2015), and fire (Smit *et al.* 2010) to landscape heterogeneity. LiDAR data have also been used effectively in savannas to describe the rate and spatial pattern of treefall across the landscape (Levick & Asner 2013), how these rates are mediated by herbivore disturbance (Asner & Levick 2012), and the effects on ecosystems (Asner *et al.* 2015a). Species-specific variation of plant communities across a savanna landscape (Cho *et al.* 2012; Baldeck *et al.* 2014) as well as the interactional relationships between plant species (Colgan & Asner 2014) have also been demonstrated with this technology. LiDAR studies have also contributed new classification methods for savannas using a 3-D approach (Fisher *et al.* 2014) and improved the accuracy of biomass estimation methods (Colgan *et al.* 2013). LiDAR has also been applied successfully to assess fine scale vegetation trends over the communal lands (Wessels *et al.* 2011; Fisher *et al.* 2012; Fisher *et al.* 2015) and to provide baseline biomass data for fuelwood supply-demand models (Wessels *et al.* 2013).

Table 1.1. Specifications of the Carnegie Airborne Observatory LiDAR systems for measurement and monitoring of ecosystem structure (after Asner *et al.* 2007, Asner *et al.* 2012).

Specification	2008 LiDAR data	2012 LiDAR data
LiDAR System	CAO-Alpha	CAO-AToMS
Flight height	2 000 m	2 000 m
Number of lasers	One	Dual
Wavelength	1064 nm	1064 nm
Laser pulse rate frequency	50 kHz	100 kHz
Discrete laser returns/pulse	Up to 4 returns	Up to 4 returns
Laser spot spacing	1.1 m	1 m
Laser point distribution	Evenly spaced across swath	Evenly spaced across swath

1.3.8 Contribution

This study can provide understanding on the sustainability of fuelwood collections and contribute to the management of social-ecological landscapes, specifically within the K2C Biosphere Reserve's mandate of conservation and maintenance of sustainable, multi-use landscapes. Configurations of woody vegetation resource stocks and the rates of utilisation of these stocks influences villagers' well-being and livelihoods directly (provisioning service) and indirectly (ecosystem regulation and cultural services). Quantifying the spatial variability in patterns of change of woody vegetation structure, as well as the potential regenerative capacity of communal woodlands, could be a powerful management tool in the sustainable management arsenal. This research may provide nuance to our current understandings of natural resource use management, particularly the adaptive responses of social-ecological systems. The methods used in this study can also provide a means for monitoring woody vegetation stocks within a management context. This study may also advance our understanding of LiDAR use in natural resource landscapes and savannas. Although a standard monitoring tool in forestry, LiDAR has not been used for natural resource monitoring and this thesis provides opportunities to demonstrate the usefulness of active remote sensing in human-impacted ecosystems.

1.4 Study Site

1.4.1 Biophysical characteristics

The Bushbuckridge Municipality is located in the Lowveld within the savanna biome in South Africa. The Lowveld sub-biome is classified as the low altitude (mostly below 600 m a.s.l.) area between the western foot slopes of the Drakensberg Escarpment and the eastern Mozambican coastal plains (Venter *et al.* 2003). The study area is in the north-eastern most portion of the Mpumulanga Province, South Africa (centred on 24.731◦S, 31.181◦E) between the Klaserie-Orpen road in the north and the Sabie River in the south. This is also the Transition zone of the K2C Biosphere Reserve which means that Bushbuckridge is surrounded by conservation land (both state-owned and private) (Coetzer *et al.* 2010) with pressures for grazing and harvesting occurring outside fenced-off areas. The terrain is shallowly undulating and the geology is dominated by granite with local Timbavati gabbro intrusions. Classic catenal sequences are common in the area with shallow, sandy, dystrophic soils on the uplands and deeper, clayey, eutrophic soils on the bottom slopes (Shackleton & Scholes 2011).

Summer rainfall (October to May) usually falls in convective thunderstorms and averages 750 mm per annum in the north-west and 550 mm per annum in the east. Summers are hot and humid with a mean daily maxima of 31 °C (minima 20 °C) and winters mild and dry with mean daily maxima of 26 °C (minima 8°C). Droughts can be prolonged and may be experienced every ten years.

The predominant vegetation is Granite Lowveld, but the region also contains Gabbro Grassy Bushveld on localised Timbavati Gabbro outcrops (Rutherford *et al.* 2006). Dominant plant species on the Granite Lowveld uplands (sandy, dystrophic soils) include: *Terminalia sericea, Combretum zeyheri* and *C. apiculatum;* the lowlands (deep, clay, sodium rich soils) are characterised by *Acacia nigrescens, Dichrostachys cinerea* and *Grewia bicolor* (Rutherford *et al.* 2006). Other frequently occurring species are *Sclerocarya birrea, Lannea schweinfurthii, Ziziphus mucronata, Dalbergia melanoxylon, Peltophorum africanum* and *Pterocarpus rotundifolius.* The majority of the woody biomass in the region is formed from *S. birrea, Pterocarpus angolensis* and *A. nigrescens* (Shackleton & Scholes 2011).

1.4.2 Historical land-use context

Ecologists tend to regard the effects of people on savannas as an 'unnatural' disturbance; but people have been an integral, and ancient, part of savanna structure and function (Scholes & Walker 1993). The impact of past land use is often unknown, but is likely to have some effect on current savanna form and function. Historically, the region was sparsely populated due to the prevalence of tsetse fly and malaria, and precolonial settlement relics (e.g. grinding stones, pots) are present in the Lowveld region but without any clearly-associated large-scale environmental impacts (Shackleton & Scholes 2011). Yet, the presence of Stone Age communities would have altered the frequency and location of bush fires and were likely to have a substantial impact on game populations (Kay 1995), but little is known. The Iron Age period was dominated by fairly residential pastoralists and hunters (Carruthers 1995) resulting in patches of agricultural-related homogenisation (Freitag-Ronaldson & Foxcroft 2003). European settlers arrived in the Lowveld in the late 1800's and early 1900's and this period was marked by game population decimation (Freitag-Ronaldson & Foxcroft 2003). The substantial reduction in the elephant population during this time would have altered the vegetation structure in the area, although to an unknown degree (Carruthers 1995). The conservation areas in the Lowveld were conceived during this period from the realisation that the hunting levels of the time were unsustainable (Freitag-Ronaldson & Foxcroft 2003). In the 1850's, Tsonga-speaking immigrants fleeing the war in Portuguese East Africa joined the local Sotho inhabitants (Neke 2005). The remaining land outside of the conservation areas was considered inhospitable since the region was rife with tsetse fly, malaria and the rinderpest, but also variable rainfall and high temperature (Pollard *et al.* 2003). Once the rinderpest epidemic (1896) and prolonged drought (1897 – 1913) reduced both tsetse fly and malaria risk in the Lowveld, the region became densely settled with white cattle farmers (Pollard *et al.* 2003). Apartheid followed in 1948, with the "Betterment and Villagisation" policies, including the the Promotion of Bantu Self-Government Act of 1959, which forced black South Africans to live in 'homelands' (Pollard *et al.* 2003) – centralised settlements on farms of 1000-2000 ha. Bushbuckridge Municipality was formed from the joining of two such farms, Mhala in Gazankulu and Mpulaneng in Lebowa, former Apartheid homelands formed under the Natives Land Act (No. 27) of 1913 (Thornton 2002). The settlement boundaries are defined by the old cadastral boundaries of the historical cattle ranches (Thornton 2002).

1.4.3 Political and socio-economic context

Although Bushbuckridge falls under state control, there is customary communal land tenure controlled by headmen who zone the land into residential, arable and communal areas for grazing of livestock and collection of timber and non-timber products (e.g. thatch, fruit, medicine) (Shackleton 2000). The settlements range from small, isolated villages to larger, dense settlements along major roads (Madubansi & Shackleton 2007). The human population density increased dramatically between 1972 and 1994 to approximately 300 people/km^2 (Pollard *et al.* 2011), but these growth rates have declined over the past ten years (Matsika 2012). Mean household size is six to seven members (Madubansi & Shackleton 2007). The land-use patterns reflect this population growth as before 1974 there were no patterns to land-use organisation; after 1974, disturbance gradients are evident (Matsika 2012). Commensurate with human population growth in the area, the spatial footprint of the residential regions has expanded (Giannecchini *et al.* 2007; Coetzer *et al.* 2010). The residential areas are surrounded by a heterogeneous mix of tree-less crop and 'park' land, then a shrubland buffer zone before transition into mixed woodland; as utilisation becomes more intensive and the settlement footprint expands, the land becomes more homogeneous (Matsika 2012).

Characteristic of Bushbuckridge's former homeland status, there is rampant unemployment (14% of adults are employed) (Phambili Energy 2009), poor infrastructure, high dependence on government-derived social grants and pensions, and reliance on migrant worker incomes (Shackleton *et al.* 2005; Madubansi & Shackleton 2007). Over 85% of BRR households live below the household subsistence level (Phambili Energy 2009). The South African Presidency proclaimed Bushbuckridge as needing development intervention (Mbeki 2001) and the area was declared a flagship node to lead the way in the Integrated Sustainable Rural Development Programme (ISRDP) (RSA 2000). In theory, the ISRDP would prioritise electrification and potable, running water (RSA 2000). Although most households have access to electricity, potable water is still a concern (Mhlongo & Dibakwane 2012). Despite the high level of electrification (Madubansi & Shackleton 2007), 90% of households still use fuelwood as their primary source of energy (Twine *et al.* 2003a). This has serious implications for the roll-out of electrification in other rural, high-poverty areas (Matsika 2012).

As a result of the dire socio-economic conditions in Bushbuckridge, many households diversify their risk by using a variety of informal activities to supplement their livelihoods,

including subsistence-level crop and livestock farming, collection of natural resources (e.g. fuelwood, thatch grass, medicinal plants), casual labour, migrant labour and small-scale ventures (Pollard *et al.* 1998; Dovie *et al.* 2006). An increasing activity is commercial harvesting of fuelwood, often with the use of a vehicle to be sold in fuelwood markets (Twine 2005). This has implications for the sustainability of natural resources as it implies that utilisation of the resource is not limited to the region immediately surrounding its source. Much of the natural resource shortages experienced by the local population is being blamed on 'outsiders', especially Mozambican immigrants (Twine *et al.* 2003b). Compounding the problem is that natural resource harvesting used to be restricted by cultural values and tribal authorities, but both these influences have decreased in context of high demand for woodland products (Higgins *et al.* 1999).

Within the context of grazing and harvesting pressures, poverty and unemployment in Bushbuckridge, there are a number of contributing socio-political complexities, including uncertainties over future land redistribution in the Lowveld. As Bushbuckridge is ethnically heterogeneous, conflicting understandings of land demarcation exist within the local population as there are cadastral boundaries registered in deeds offices as well as more organic tribal boundaries. There are also different layers of governance at odds with each other jostling for recognition within the new social relationships that have formed since the democratic elections in South Africa and tribal control has weakened in influence (Thornton 2002; Twine 2005). Unfortunately, the political and social issues are not always in the best interests of environmental and sustainability issues and these trade-offs need to be acknowledged explicitly.

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Chapter 2. Savanna woodland response to a land-use gradient in an African communal landscape

2.1 Abstract

The effects of fuelwood harvesting on woodland ecosystems continues to be a concern in developing countries where woody biomass is the primary source of energy. Underestimation of human-environmental systems' adaptive capacity has meant the "fuelwood crisis" predicted by fuelwood supply-demand models have not materialised. By identifying the response of woody canopy structure to different land-use intensities, we aimed to quantify height-specific woodland response to varying harvesting intensities in semi-arid savanna communal lands in Bushbuckridge, South Africa. Using repeat airborne light detection and ranging (LiDAR) surveys in 2008 and 2012, we measured changes in three-dimensional fine-scale vegetation structural dynamics. Wood extraction pressure drove spatially extensive compensatory regrowth in the 1-3m height class. Coupled with losses in trees taller than 3m, mostly due to agricultural and settlement expansion, structural homogenisation occurs in heavily utilised communal lands. Frequent fires facilitated persistence of tall trees (>3m), but was associated with height loss in vegetation <3m. Vegetation structural dynamics were also associated with ease of access in the communal lands, with compensatory growth peaking <800 m from the nearest settlement, reinforcing previous findings that wood harvesting occurs within 1km of settlements. Fuelwood harvesting as the primary driver of deforestation has been overstated – woodland regenerative capacity has been underrated, and taller tree loss was associated with settlement development. This has implications for the sustainability of natural resource use in a steadily shrinking communal land with compromised ecosystem functioning through reduction of vegetation structural complexity.

2.2 Introduction

Woody biomass remains the primary energy source in the developing world, accounting for 60% of energy demand in sub-Saharan Africa (International Energy Agency 2014). Although the sub-Saharan reliance on woodfuel is predicted to drop below 50% by 2040, 650 million people will still be using solid biomass fuels. The subsequent, often unsustainable, extraction of wood from the ecosystem places humans in the role of agents of structural and compositional change (Shackleton *et al.* 1994; House & Hall 2001; Galvin & Reid 2011). Wood extraction in developing countries has been implicated as a driver of forest and woodland degradation (Soussan 1988; Arnold *et al.* 2003). Fuelwood supply-demand models have predicted imminent "fuelwood crises" as (e.g. de Montalembert & Clement 1983; Banks *et al.* 1996; Wessels *et al.* 2013), which have not yet occurred, in large part because these models overestimated the adaptive capacity of natural-resource dependent communities (Dewees 1989; Mortimore & Adams 2001) and underestimated the regenerative capacity of woodlands (Dewees 1989; Foley 1987).

Although woodland collapse may not have been realised, high levels of wood extraction alters ecosystem structure and composition (Shackleton *et al.* 1994; Luoga *et al.* 2002), thereby affecting ecosystem functioning by reducing structural heterogeneity (Tews *et al.* 2004; Manning *et al.* 2006; McGranahan *et al.* 2016), as well as the quantity and quality of fuelwood available (Luoga *et al.* 2002; Matsika *et al.* 2012), and driving localised shortages. Thus, rural energy problems often do not manifest in a direct lack of woodfuel resources, but rather through adapted responses to localised fuelwood shortages (Soussan 1988). Adaptive responses include an increase in the average wood collection time, change of fuelwood species preference (e.g. Madubansi & Shackleton 2007), the development of fuelwood markets (Matsika *et al.* 2013), and more efficient collection and transportation systems (Twine *et al.* 2003a). Woodlands also have adaptive responses to harvesting, including the rapid regenerative regrowth typical of many savanna tree species (Bond & Midgley 2001). Coppice shoots form after woody plant disturbance (e.g. fire, herbivory, harvesting) with accelerated growth relative to saplings of the same size as they access reserves stored in mature tree rootstock (Holdo 2006). This regrowth response to harvesting mitigates fuelwood shortages substantially (Neke *et al.* 2006; Tredennick & Hanan 2015). These coupled responses, from both humans and ecosystems, forms part of a complex non-linear

relationship that is highly contextual (Mercer & Soussan 1992; Giannecchini *et al.* 2007) and difficult to disentangle.

As woody vegetation resource patterns form part of an 'integrated rural production system' - a reflection of the interaction between ecological response and the community land management (Soussan 1988) - monitoring change in canopy cover and structure will assist in describing changes in coupled human-environment systems. Woody vegetation canopies also reflect spatio-temporal processes operating at multiple scales (Watt 1947; Levick & Rogers 2011; Scholtz *et al.* 2014), at different life stages within species (Scholtz *et al.* 2014), interspecific interactions (Dean *et al.* 1999; Sankaran *et al.* 2005), and between ecosystem processes (Belsky 1994; Treydte *et al.* 2007). Predicting local ecosystem change, potential degradation, and coupled human-environment vulnerability requires an understanding of human-environmental changes associated with the ecosystem utilisation (Turner II *et al.* 2003; Lambin *et al.* 2006).

Here we use airborne light detection and ranging (LiDAR) technology to quantify three-dimensional woody vegetation dynamics over a wood extraction gradient. The surveyed communal lands form part of Bushbuckridge Municipality, South Africa, where extensive wood harvesting has changed ecosystem structure and composition (Shackleton *et al.* 1994; Shackleton & Scholes 2011), despite extensive electrification (Madubansi & Shackleton 2007). Specifically, we ask what are the rates and patterns in height-specific gains, loss and persistence of woody cover, and how do they differ between communal lands with varied use intensities? What factors (e.g. geology, relative elevation, fire, ease of access to communal lands) are associated with structural vegetation dynamics? Describing such ecosystem dynamics in a site-specific human-environmental context can provide insights into management of natural resource extraction for increased sustainability.

2.3 Methods

2.3.1 Study Site

Bushbuckridge municipality is in the north-eastern portion of South Africa, part of Mpumalanga province (Figure 2.1). The study site forms part of a UNESCO Biosphere Reserve – a multi-use conservancy integrating different land uses across core conservation

areas, buffer and transition zones (Coetzer *et al.* 2014). The area is characterised by hot, wet summers (900-500 mm p.a.; 20-31°C) and warm, dry winters (8-26°C). The geology is predominantly granitic and dominated by Granite Lowveld vegetation (Rutherford *et al.* 2006). Catenal sequences are recognised by *Terminalia sericea*, *Combretum zeyheri* and *C. apiculatum* on sandy, shallow, dystrophic uplands and *Acacia nigrescens*, *Dichrostachys cinerea* and *Grewia bicolor* on clayey, deep, eutrophic lowlands; seep zones are demarcated by stands of *T. sericea* (Rutherford *et al.* 2006). Localised Timbavati gabbro intrusions occur in the granite matrix (Figure 2.1), characterised by Gabbro Grassy Bushveld vegetation, dark clay soil which expand and shrink, forming an open savanna containing fewer scattered trees (Rutherford *et al.* 2006).

Bushbuckridge Municipality was formed from joining portions of two former Apartheid 'homelands' – Mhala from Gazankulu and Mpulaneng from Lebowa (Thornton 2002). The communal lands are state-owned, tribally controlled areas containing zones of settlement, cropland, and communal land; the latter is used for natural resource harvesting and livestock grazing. Settlements range from small, rural, isolated settlements to large, sprawling, urban areas along main transport routes. The Bushbuckridge area has the inherent socio-economic challenges of former 'homelands': high unemployment and low education levels, high population densities largely dependent on migrant worker remittances and social grants (Thornton 2002), and a reliance on natural resources in the area (Twine *et al.* 2003a). The spatial footprint of residential regions in the area have increased correspondingly with increasing human population (Coetzer *et al.* 2013).

Within Bushbuckridge, we surveyed three communal lands under varying wood extraction pressure: high wood extraction communal land (adjacent to the settlements of Croquetlawn, Ireagh and Kildare); an intermediate use communal land (adjacent to Justicia); and a low use communal land (adjacent to Xanthia and Agincourt) (Figure 2.1). Although communal lands are zoned for use by their adjacent settlements, both local and cross-border foreigners are known to harvest in them (Twine *et al.* 2003b). Communal land extraction pressure classification was derived from 2008 population and household density relative to communal land area: high (9.2 people ha^{-1}, 1.56 households ha^{-1}); intermediate (1.8 people ha^{-1}, 0.35 households ha^{-1}); and low (0.21 people ha^{-1}, 0.04 households ha^{-1}) (data from the ongoing MRC/WITS Rural Public Health and Health Transitions Research Unit demographic surveillance surveys – see Kahn *et al.* (2007)).

2.3.2 Light Detection and Ranging (LiDAR) data collection and individual tree detection

Repeat airborne Light Detection and Ranging (LiDAR) surveys were conducted in April 2008 and 2012 using the Carnegie Airborne Observatory (CAO) systems. Small-footprint, discrete-return LiDAR provides accurate three-dimensional (3-D) information on vegetation structure over large areas. CAO-Alpha and CAO-2 AToMS - flown in 2008 and 2012, respectively -operated on a laser pulse repetition frequency of 50 kHz and 100 kHZ, with actual point spacing of 4 hits m^{-2} (see Asner *et al.* (2007, 2012) for technical details).

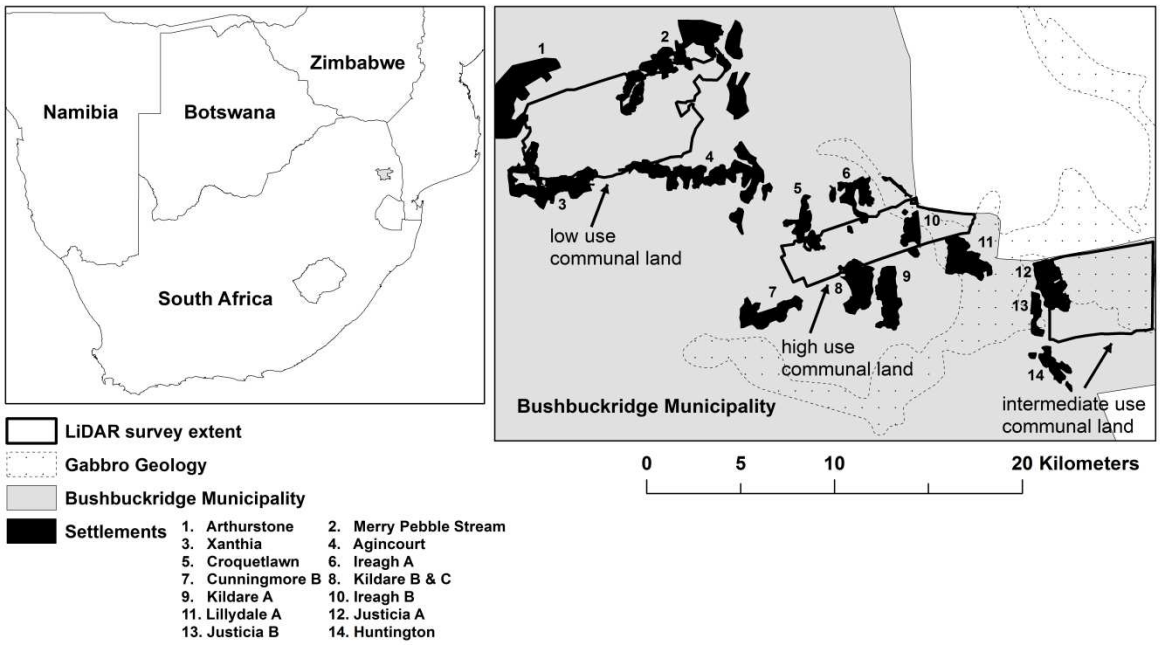

Figure 2.1. Bushbuckridge Municipality is situated in the north-east of South Africa. The predominant geology is granite with Timbavati gabbro outcrops. Communal lands are utilised by adjacent settlements. Numbered settlements are described in the legend.

Each system had an integrated Global Positioning System-Inertial Measurement Unit (GPS-IMU) providing each laser point with accurate locational data, producing a 3-D point 'cloud' of LiDAR data (Asner *et al.* 2007). The LiDAR point cloud was processed to identify first (top-of-canopy) and ground LiDAR returns using lasground tool in LAStools software (Rapidlasso). A digital terrain model (DTM) was produced by passing a 5m x 5m kernel over

each mapping area, with the lowest elevation point in each kernel considered the 'ground' point. Horizontal planes were fitted to these 'ground' point estimates to assess neighbouring points. If the neighbouring unclassified point was <5.5° and <1.5m difference in elevation, it was also classified as a 'ground' point (Smit *et al.* 2016). Once all points in the mapping area were evaluated, an interpolation was run on all 'ground' points to produce the DTM. The digital surface model (DSM) was interpolated from all LiDAR first (top-of-canopy) returns, including ground returns where only bare ground was present. The difference between the DSM and the DTM produced a canopy height model (CHM) at 1m spatial resolution.

We identified individual tree objects using an object-based image analysis approach using a local maximum search algorithm (Kaartinen *et al.* 2012). The CHM was smoothed (circular Gaussian kernel smoothing) - to optimise whole-canopy detection - and transformed to increase accuracy of individual object identification in clumped canopies, using the following equation:

$$f(x) = 10\sqrt{x}$$

where x is the smoothed vegetation height. The transformation exaggerates small height variations in shorter vegetation which reduces the chance of clumped CHM segments being joined (Asner *et al.* 2015; Vaughn *et al.* 2015). The centre point of each tree object was geotagged with locational coordinates and the maximum canopy height recorded. The change in maximum canopy height between 2008 and 2012 for each tree object was recorded. Growth or loss of each tree was classified as a change >1m to account for sensor noise. Residential and crop-field present in 2008 were removed from the CHM maps before further analysis.

2.3.3 Height-specific gains, loss and persistence of vegetation

The number of trees that had gained height (increase ≥ 1m), lost height (decrease ≥1m) or stayed unchanged (height change <1m) were aggregated per hectare. Each 1-ha grid cell was then marked as: gains (number of individuals that gained height exceeded the number that lost height or the number that stayed unchanged); loss (number of individuals that lost height exceeded the number that gained height or the number that stayed unchanged); and persistence (number of individuals that stayed unchanged exceeded or was equal to the number that gained or lost height). Patterns of vegetation structural dynamics were then examined through the creation of gains, loss and persistence maps created using 2008 and 2012 data. These data, together with various environmental and anthropogenic variables

(geology, relative elevation, burn frequency (Appendix Figure 2.1-2), distance from the nearest river, distance from the nearest settlement, and distance from the nearest road) were extracted using a spatial join for each hectare grid cell. The vertical vegetation profile was divided into ecologically-relevant height classes: 1-3m shrubs and small trees in the 'fire trap' (e.g. Bond & Keeley 2005), but also form part of the coppice regrowth height class (Mograbi *et al.* 2015); 3-5m trees in the 'elephant trap' (e.g. Asner & Levick 2012) but also a height class that is important to rural households (Paumgarten *et al.* 2009) ; 5-10m tall trees which contribute to ecosystem functioning (e.g. Dean *et al.* 1999) and are valuable to people as non-timber product generators (Shackleton *et al.* 2003); and very tall trees >10m acting as 'keystone structures' in savannas where their relatively small area occupied contributes disproportionally to ecosystem functions, often filling unique functional roles (e.g. Tews *et al.* 2004; Manning *et al.* 2006).

2.3.4 Data Analysis

We used a constrained ordination technique, canonical correspondence analysis (CCA), to explore height-specific vegetation dynamics in relation to a suite of known environmental and anthropogenic variables. Each ordination axis is a linear combination of different variables to explain 'species' abundance (here, each 'species' is a height-specific vegetation classes of gains, losses and persistence) using a multivariate direct gradient analysis (Ter Braak 1986). The analysis was conducted on a randomly selected subsample (n= 182, 213, 378 for the high, intermediate and low use communal lands, respectively) of hectare grid cell data including height-specific gains, losses and persistence. Spatial autocorrelation occurred within 40 m calculated from a semivariogram in SAGA GIS, but 160 m was enforced to avoid selecting adjacent grid cells in the random subsample. Known environmental and anthropogenic variables were chosen that have either been shown to affect savanna vegetation structure and composition (e.g. geomorphology, fire: (Huntley & Walker 1982)) or were related to perceived ease of access to communal lands (distance to the nearest settlement/road). Bushbuckridge settlement features were manually digitised using aerial images from 2009 and 2012 (50 cm resolution; www.ngi.gov.za). The relative elevation model (REM) was the "normalized height" product generated using the "Terrain Analysis" toolset in SAGA GIS (SAGA User Group Association 2010) using the LiDAR-derived DTM as an input. Distances from the nearest river, road and settlement were generated using the "Near" tool in ArcGIS v10.2 (ESRI 2012). Fire data were derived from monthly MODIS

burned area products (MCD45SA1-V051; 500m resolution) using R v3.2.1 (R Core Team 2013; packages: sp, rgdal, raster). Fire data were interpreted as binary burned/unburned and summed between June 2007 and March 2012. The CCA was performed using CANOCO v4.5 using manual forward selection and 999 Monte-Carlo permutations. Variables were added to the ordination model until at least 95% of the described variation was accounted for by variables' conditional effects. Variables were also tested for their marginal effect to the data set independently, using a Bonferroni correction to maintain the model's global type I error at $p < 0.05$ (Rice 1989; Cabin & Mitchell 2000). Variables that were non-significant in marginal effects but contributed substantially to conditional effects were kept in the model but displayed as non-significant variables in graphical outputs (see greyed out arrows in Figure 2.4). Co-linearity was present between sites and geology as each site was dominated by one type of geology, but both variables were kept in the model. The exception is the low use communal land where geology as a variable was removed as the site is located solely on granite. Total variation explained in each CCA was calculated using an R^2 analog of explained variance (all canonical eigenvalues) as a percentage of total variance (all eigenvalues).

2.4 Results

2.4.1 Landscape-scale vegetation structural dynamics

Using landscape-scale object-based tree identification methods, we detected over 650 000 individual trees >1m in height in 2008 across three communal rangelands. Of these, 32.6% changed in height by ≥1m; comprising 8.7% that decreased by ≤1m and 23.8% that increased by ≥1m (Table 2.1). The high use communal land had the greatest height change frequency at 42%, with most of this attributable to vegetation height gains (Table 2.1). The intermediate communal land had the highest recorded height frequency decreases and treefall (height reduction ≥75%) (Table 2.1). Treefall in the low use communal land was 1.6% of trees in the site. This site also had the smallest frequencies in vegetation height change (Table 2.1). Although the high use communal land seemed to have a relatively high tree density (Table 2.1), the bulk of these were trees <5m in height, evident in the right-skewed height class distribution (Figure 2.2). The intermediate use communal land 2008 height profile resembled that of the low use communal land (Figure 2.2).

Table 2.1. Vegetation structural dynamics in three communal lands in Bushbuckridge combined and within each site. 'H' refers to canopy height and 'n' to number of samples of individually detected trees. The percentage frequency of H changes ≥1m refers to both increases and decreases in canopy height. Height reduction ≥ 75% is termed 'treefall'.

Site	Site area (ha)	n (trees)	Tree density (trees ha^{-1})	Frequency of H changes ≥1m	Frequency of H increases ≥1m / Frequency of H decreases ≥1m	Frequency of 75% H reduction i.e. treefall
Combined sites	10 534	634 284	60.21	32.6%	23.8% / 8.7%	2.2%
High use communal land	2 155	97 104	45.06	41.9%	34.1% / 7.9%	2.6%
Intermediate use communal land	3 359	109 070	32.47	35.5%	25.3% / 10.25%	4.5%
Low use communal land	5 020	428 110	85.28	29.7%	21.1% / 8.6%	1.6%

2.4.2 Height-specific spatial patterns of vegetation gains, loss and persistence

The lower height classes (1-3m) mostly experienced gains in vegetation height (Figure 2.3). These gains were spatially associated with the river location in the intermediate use communal land, and a granite ridge running east-west across the centre of the low use communal land (Figure 2.3). Fewer patches of vegetation gains were noticeable with progressively taller vegetation, but patches of loss were evident in the 3-5m and 5-10m height classes (Figure 2.3). In the high and low use communal lands, these patches were adjacent to the settlement, whilst in the intermediate use communal land the patches of loss also occurred along the river and near the eastern fence line border with private conservation land (Figure 2.3). Most of the area covered by vegetation >3 m in height was classified as persistent with no change >1m (Figure 2.3). However, there were portions of the intermediate use communal land that had height loss in vegetation >10m (Figure 2.3).

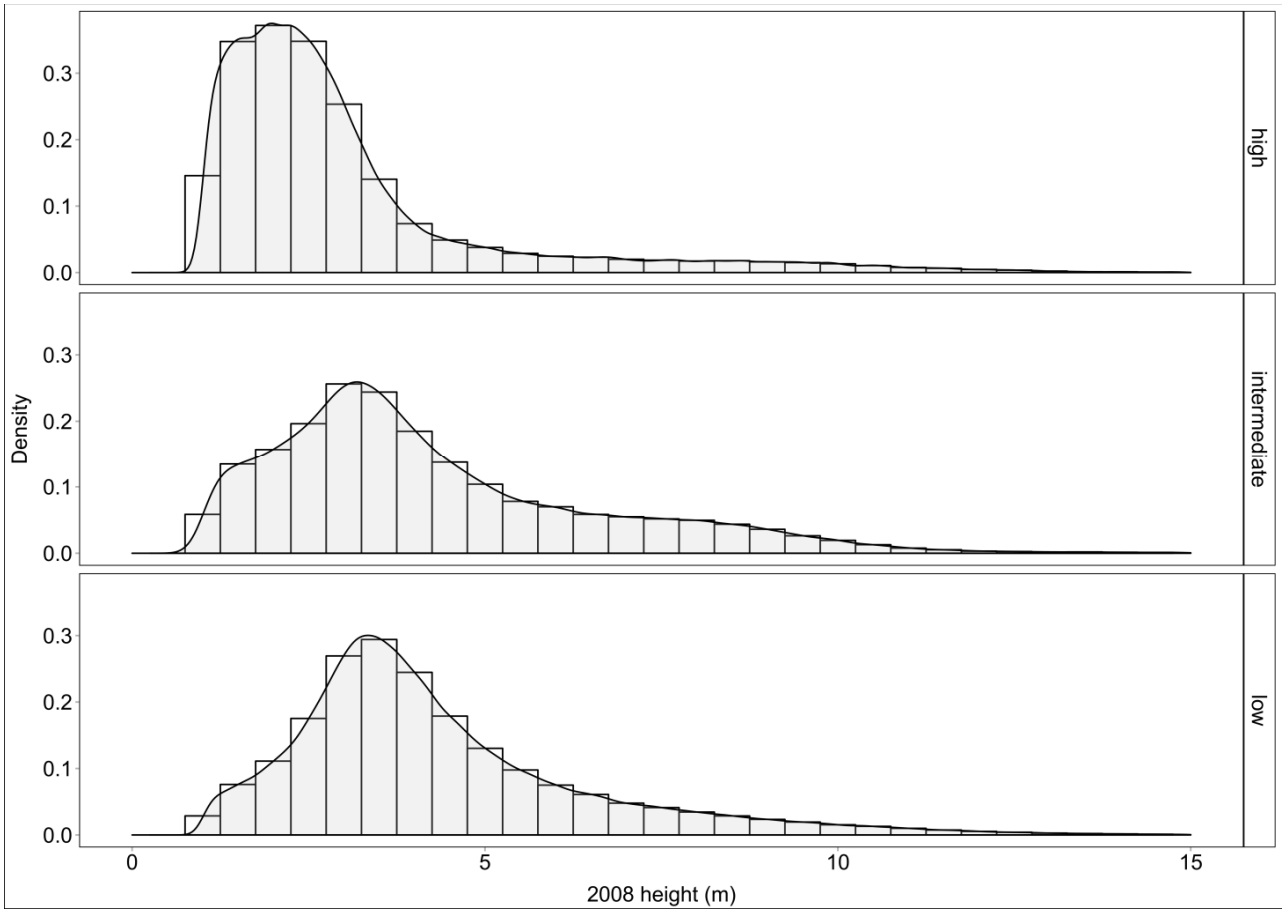

Figure 2.2. Density distribution of maximum canopy height in 2008, represented per land-use level per site (high, intermediate, low).

This height loss in tall trees was also reflected in the lowest persistence level of trees >10m in the intermediate use communal land relative to the other communal lands (Table 2.2), although persistence levels were >82% in this size class for all communal lands. The highest persistence of all vegetation >5m was in the low use communal land. Conversely, the high use site had the greatest persistence of 1-3m vegetation, and augmenting shrub dominance in this site was the transition from 3-5m to the 1-3m class over 4 years (Table 2.2). The strongest gain was a transition from the 1-3m height class to the 3-5m height class in all sites, especially in the intermediate use site (Table 2.2).

Table 2.2. Proportional transitions between vegetation height classes over 4 years in 3 communal lands under: a) high; b) medium; and c) low wood extraction pressure. Total proportions do not add up to 1 because of loss to <1m height class and the exclusion of growth and loss transitions <1m change threshold.

a) **high**

		2012				
		1-3 m	3-5 m	5-10 m	>10 m	total
2008	1-3 m	0.58	0.26	0.01	0.00	0.86
	3-5 m	0.11	0.58	0.11	0.00	0.80
	5-10 m	0.04	0.05	0.82	0.02	0.92
	>10 m	0.03	0.02	0.05	0.87	0.96

b) **intermediate**

		2012				
		1-3 m	3-5 m	5-10 m	>10 m	total
2008	1-3 m	0.42	0.36	0.01	0.00	0.79
	3-5 m	0.06	0.66	0.10	0.00	0.82
	5-10 m	0.04	0.04	0.83	0.01	0.91
	>10 m	0.04	0.04	0.04	0.82	0.94

c) **low**

		2012				
		1-3 m	3-5 m	5-10 m	>10 m	total
2008	1-3 m	0.41	0.32	0.01	0.00	0.74
	3-5 m	0.07	0.68	0.10	0.00	0.85
	5-10 m	0.02	0.06	0.87	0.01	0.95
	>10 m	0.01	0.02	0.05	0.90	0.97

2.4.3 Drivers of vegetation structural dynamics

Canonical correspondence analysis explained 18.7% of the total variation in height-specific gains, loss, and persistence for all sites combined (Figure 2.4a). Variation explained for the high, intermediate, and low use communal lands was 13.8%, 19.2%, and 7.2%, respectively (Figure 2.4b-d). Height-class specific patterns of gains, loss and persistence were most strongly associated with the high use site and this land-use gradient formed the major component of canonical axis 1 (Figure 2.4a, Appendix Table 2.2a). Specifically, this site was positively associated with gains in the 1-3m class whilst the low use site was negatively associated with gains in the 1-3m class (Figure 2.4a). The second most important factor influencing vegetation structural dynamics across all the communal lands and the major component of canonical axis 2 was distance from the nearest settlement (Figure 2.4a, Appendix Table 2.2a); losses in the height classes >5m were strongly associated with

distance from the nearest settlement (Figure 2.4a). Settlement-specific ordination patterns varied between settlements but height-specific gains, losses and persistence were associated with geology and distance from settlement (Figure 2.4b-d). The high use communal land reiterates that vegetation losses >3m in height were associated with distance from the nearest settlement (Figure 2.4b). The intermediate communal land had the highest percentage of variation explained by the included variables (Figure 2.4c) and, again, vegetation losses in height classes >3m were associated with distance from the nearest settlement. However, frequent burns were also associated with loss in vegetation >3m in height, despite this variable not being independently significant beyond its contribution to the model (Figure 2.4c). Very little variation (7.2%) in vegetation structural dynamics was explained by the included variables in the low use communal land. This site also had the lowest environment-species correlations (Appendix Table 2.1d). Here the distance to the nearest road was the most important variable (Figure 2.4d) which was indicative of this site being an inaccessible communal land relative to the other sites. The vegetation structural dynamics in the low use communal land were also associated with fire; specifically, 2 burns in 4 years associated closely with distance from the nearest settlement variable, and the 1-3m height classes were positively associated with no burns and negatively associated with frequent burns over 4 years (Figure 2.4d).

Site-specific changes in height-specific growth with increasing distance from the nearest settlement ran counter to land-use patterns. The high and intermediate use sites had varying mean proportional growth relative to settlement proximity (Figure 2.5). This was particularly true of the intermediate use site where proportional growth in the 3-5m and 5-10m height classes increased up to 800m from the nearest settlement and then decreased to 1400m (Figure 2.5). Spatially-specific proportional growth change in vegetation >10m were inconsequential at 5% overall (Figure 2.5). The intermediate site, again, had noticeably different patterns of spatially-explicit proportional loss, although the communal lands were similar in loss patterns in the 1-3m and 3-5m height classes (Figure 2.6). Proportional loss decreased up to 600m from the nearest settlement and then increased between 600-1000m from the settlement in the intermediate use communal land (Figure 2.6). The low use communal land had the lowest proportional loss relative to settlement proximity than the remaining communal lands (Figure 2.6).

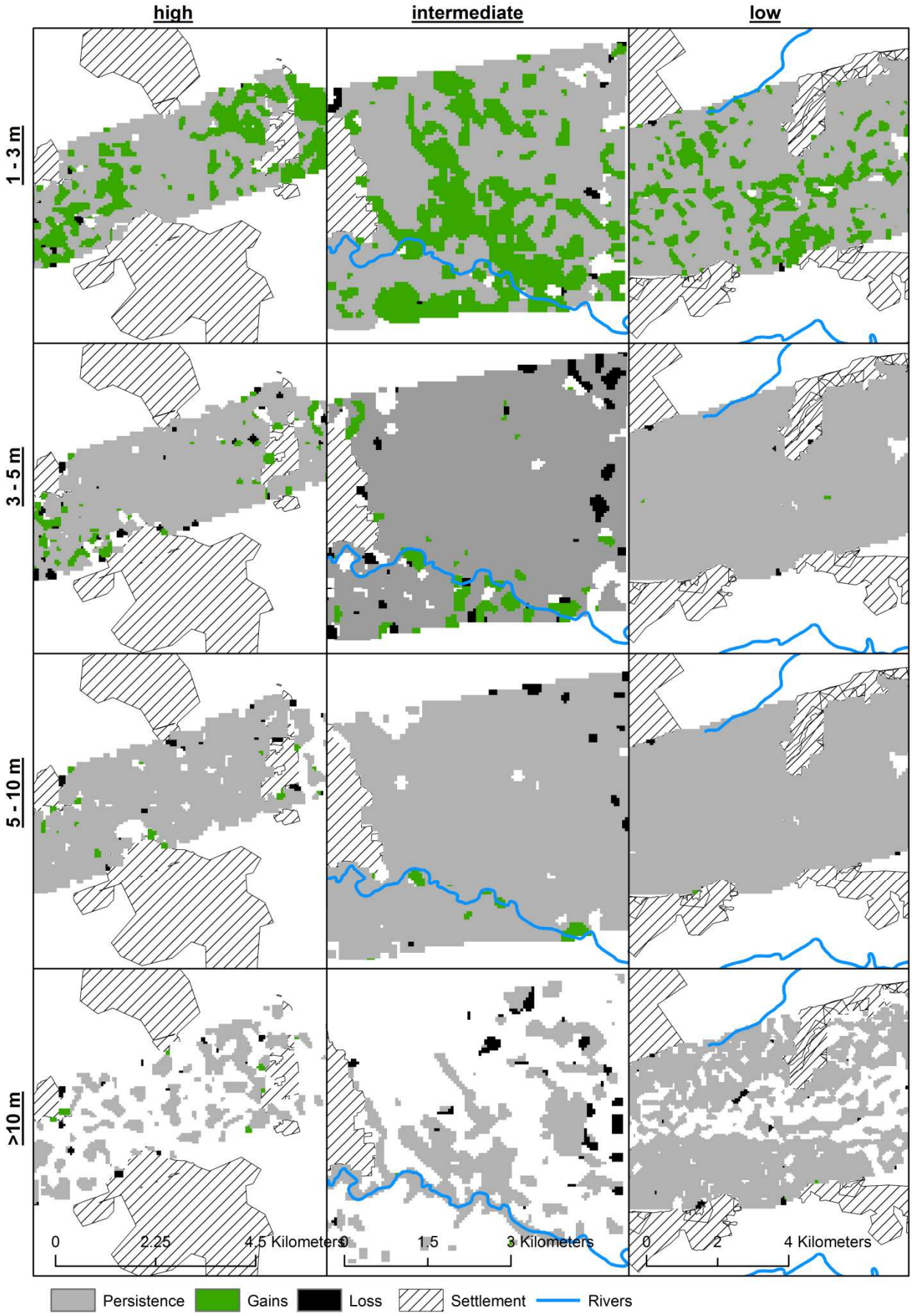

Figure 2.3. Maps of height-specific gains, losses and persistence aggregated per hectare in three communal lands with varying wood extraction pressure (high, intermediate, low).

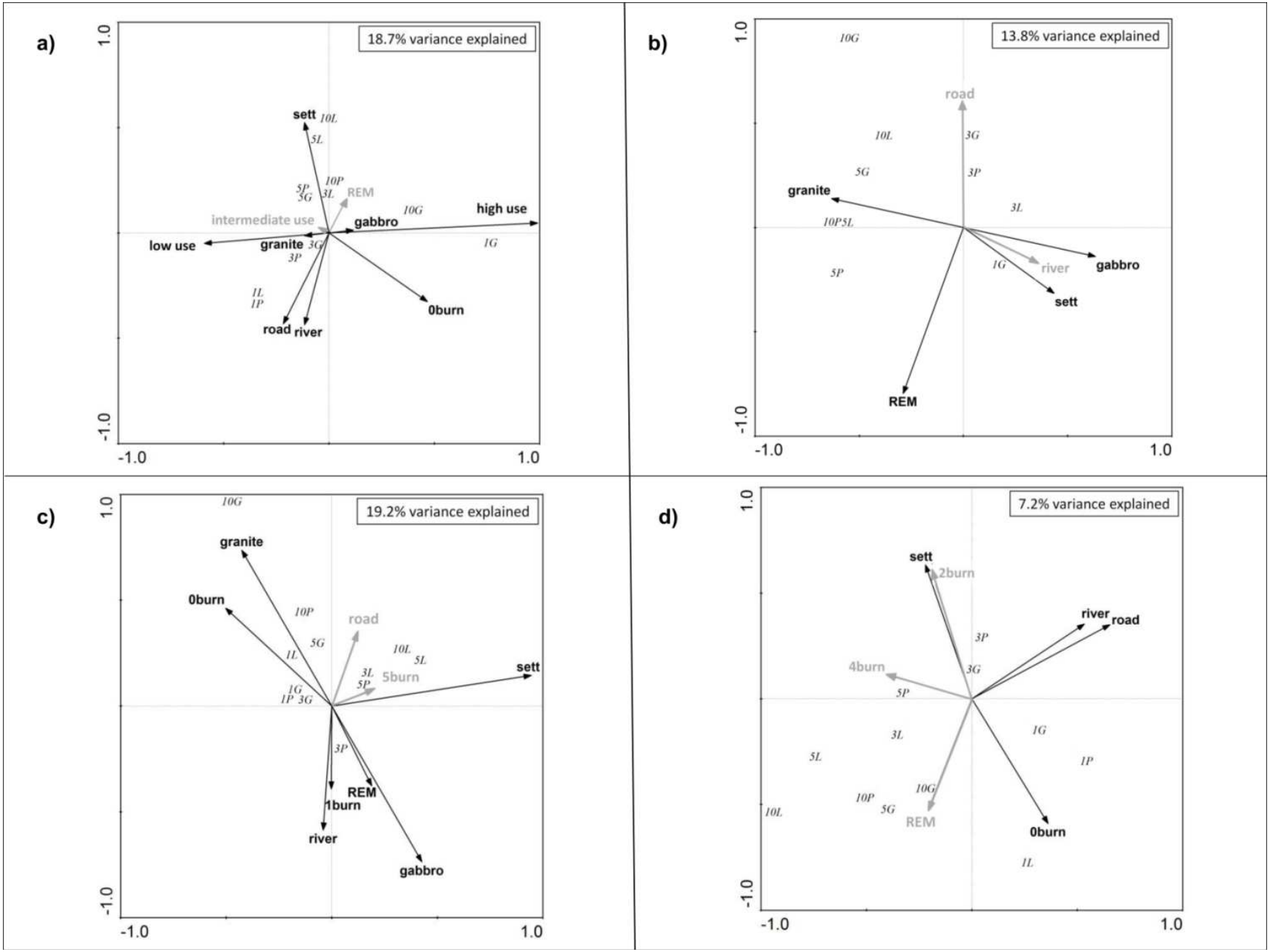
a)
18.7% variance explained
sett
10L
5L
5P
5G
10P
3L
REM
10G
high use
intermediate use
gabbro
low use
granite
3G
3P
1G
1L
1P
0burn
road
river
b)
13.8% variance explained
10G
road
10L
3G
5G
3P
granite
3L
10P5L
1G
river
gabbro
5P
sett
REM
c)
19.2% variance explained
10G
granite
0burn
10P
road
5G
10L
5L
1L
3L
5burn
sett
5P
1G
1P 3G
3P
REM
1burn
river
gabbro
d)
7.2% variance explained
sett
2burn
river
road
3P
4burn
3G
5P
3L
1G
5L
1P
10G
10P
5G
REM
10L
0burn
1L
1.0
-1.0

Figure 2.4. Canonical correspondence analysis (CCA) of a random subsample of height-class specific gains, loss and persistence abundance per hectare related to both anthropogenic and environmental explanatory variables in a) all sites combined, b) high wood extraction site, c) intermediate wood extraction site, and d) low wood extraction site. Arrow length indicates the strength of influence of the explanatory variable. Each arrow points in the direction of the expected steepest increase in that variable. Angles between arrows indicate correlations between explanatory variables (<90^0 = positive correlation, >90^0 = negative correlation, 90^0 = no correlation).The closer a size class is to an arrow head, the stronger the correlation between that size class and the explanatory variables. Similarly, arrows can be projected backwards to size classes to explore negative correlations. Size classes clustered around the origin indicate little to no correlation with the explanatory variables, while those in close proximity to each other correspond to sites occurring together (Lepš & Šmilauer 2003). Sett, road and river refer to distances from the nearest settlement, roads, and rivers, respectively. Height class codes are: 1 (1-3 m), 3 (3-5 m), 5 (5-10 m) and 10 (>10m). Letters following height class codes refer to: G (gains), L (loss), and P (persistence). (See Appendix Table 2.1 for model details.)

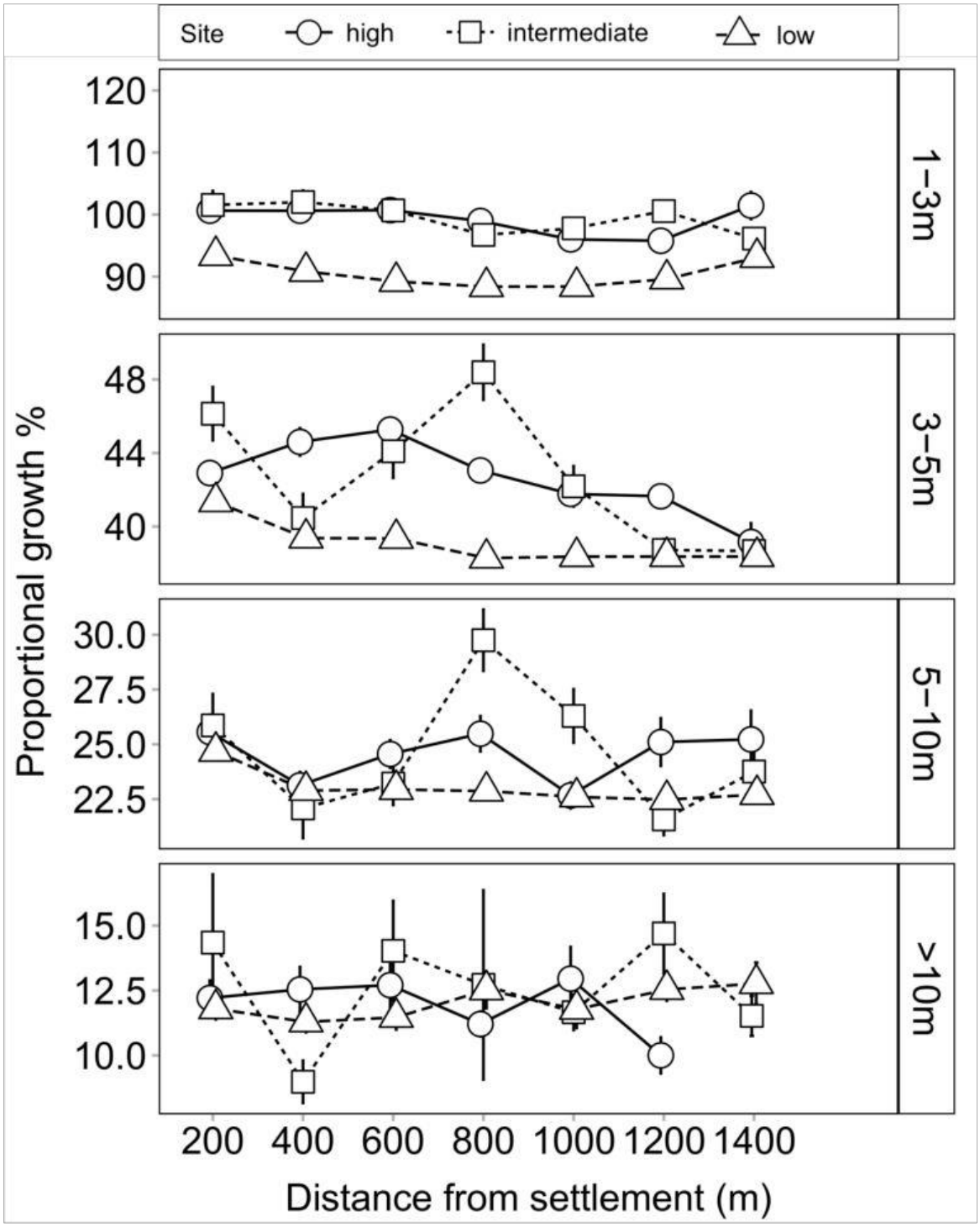

Figure 2.5. Proportional growth (%) of vegetation height per height class as a function of distance from the nearest settlement at varying wood extraction levels (high, intermediate, and low). Error bars denote standard error.

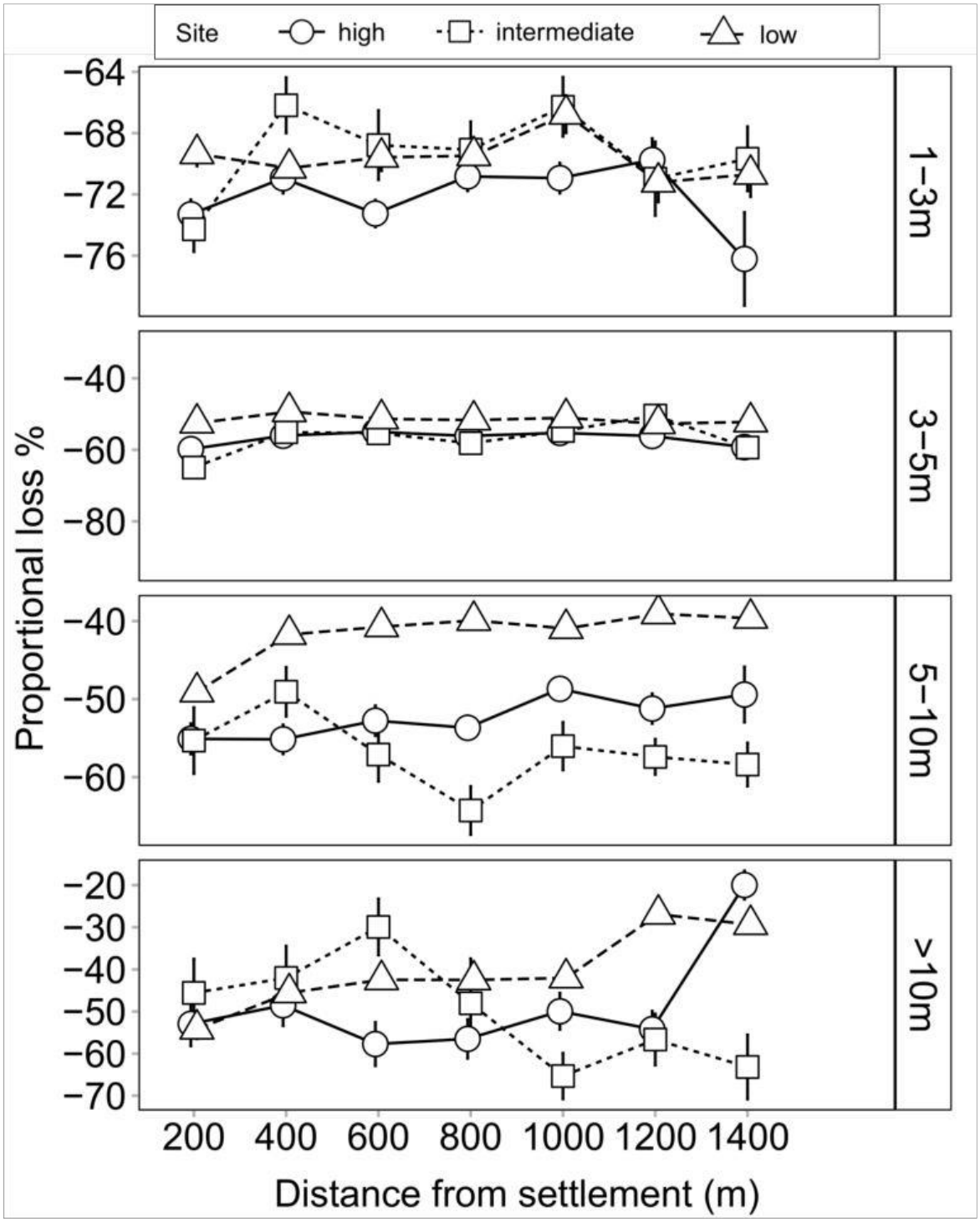

Figure 2.6. Mean proportional loss (%) of vegetation height per height class as a function of distance from the nearest settlement at varying wood extraction levels (high, intermediate, and low). Error bars denote standard error.

2.5 Discussion

2.5.1 Wood extraction intensity drives structural dynamics in communal lands

Vegetation structural dynamics reflect the communal land-use gradient in the three communal lands surveyed. Vegetation height gain trends followed the land-use gradient – i.e. high frequency of gains in high use communal lands and low frequency of gains in the low use communal land (Table 2.1). But this pattern is less obvious with other metrics; the intermediate use communal land had the most spatially extensive changes to all height classes (Figure 2.3) and the highest frequencies of losses >1m and treefall (Table 2.1). However, extensive losses of vegetation height and higher treefall in the intermediate communal land (Table 2.1) are indicative that there are still tall classes of vegetation available for harvest. Put another way, the high number of trees ha^{-1} in the high use communal land (Table 2.1) are inflated by low-height class shrub gains (Figure 2.2), skewing the frequency of loss trend and probably driven by compensatory growth as a result of high wood harvesting levels. This phenomenon is supported by earlier research on disturbance-related structural and composition change studies where species richness increased in proportion to the disturbance level on old lands (Armesto & Pickett 1985), and studies detailing increased woody cover and density in heavily-grazed areas (Skarpe 1990). Furthermore, Bushbuckridge communal lands have had documented woody vegetation structural diversity reductions with increasing land-use intensity in a space-for-time substitution study (Fisher *et al.* 2012) and vegetation gains across multiple height classes exceeding that of neighbouring conservation areas (Fisher *et al.* 2015).

2.5.2 Communal land accessibility and fire frequency affect woody vegetation dynamics

Not only is does the land-use gradient affect changes in overall gains, loss and persistence of canopies, it also affects height-specific dynamics. The high use communal land is associated with gains in the 1-3m height class (Figure 2.4a) - a combination of bush thickening (Twine & Holdo 2016), as well as persistent harvesting converting the 3-5m class to the 1-3m height class (Table 2.2). Fire frequency was an important variable in the intermediate use communal land (Figure 2.4c). Fire dynamics are seldom explored explicitly in communal land vegetation dynamics, largely due to a lack of fire history data (Trollope 1998). Although humans have been associated with more frequent fire ignitions, burns in anthropogenic areas

are from small, cool fires – a result of reduced grass biomass in rangeland areas and increased landscape fragmentation, preventing fire spread (Archibald *et al.* 2009). In contrast to the low and intermediate use communal lands, fire frequency was not an important feature of vegetation dynamics in the high use communal area, likely a consequence of very low biomass in a heavily encroached area, reinforced by a positive feedback loop where fire suppression and overgrazing have, in turn, been implicated in bush encroachment (Archer *et al.* 1995; Roques *et al.* 2001). Where fires do occur in communal lands, low height class vegetation dynamics were associated with low to no fires, whilst more frequent fires were associated with gains in the 3-5m height class and persistence in vegetation taller than 3m (Figure 2.4c,d). Presumably, as trees in the 'fire trap' (Bond & Keeley 2005) experience top-kill from burns, the thinned areas are released from competition, facilitating taller vegetation classes.

Vegetation structural dynamics in the low use communal land were related to ease of access (distance from the nearest road), reflecting the relative inaccessibility of this site (Figure 2.4d). In the other two communal lands, vegetation structural dynamics were associated with distance from the nearest settlement (Figure 2.4). Disturbance gradients radiating out from settlements are a well-established communal land phenomenon (e.g. Shackleton *et al.* 1994; Matsika *et al.* 2012). Changes in vegetation structural dynamics are related to an 800 m threshold in the intermediate communal land (Figure 2.5-6). The results hint at compensatory growth (i.e. coppicing) occurring <800m from settlement (Figure 2.5). This ties in with previous studies demonstrating that most fuelwood harvesting in this area occurs between 1-1.5km from the settlement, as most wood is carried in bundles or in wheelbarrows (Shackleton *et al.* 1994; Giannecchini *et al.* 2007; Wessels *et al.* 2013). In addition, previous studies on biomass disturbance gradients in this region have found biomass increases with increasing distance from settlement (Shackleton *et al.* 1994; Wessels *et al.* 2011). The growing use of vehicles to collect and transport fuelwood is likely to expand the harvesting footprint in these areas (Twine 2005).

2.5.3 Have fuelwood harvesting effects been overstated historically?

Height loss in trees >5m adjacent to settlements is indicative (Figure 2.3) of settlement and crop-land expansion (Coetzer *et al.* 2013), reducing the available land for natural resource provision – a twofold blow to ecosystem service provision from natural land with an

increasing population and decreasing savanna woodland (ecosystem service provision supplied by agricultural lands will increase). There were also large patches of height loss >3m on the eastern boundary of the communal land; this area is perceived to be more fertile for croplands and also contains abundant stands of *Acacia nigrescens*, a preferred construction timber (Tuinder 2009). Historically the blame for deforestation has been placed on fuelwood harvesting effects, but recent consensus is that agricultural and settlement expansion are the dominant drivers of degradation (Cline-Cole *et al.* 1990; Arnold *et al.* 2003; Defries *et al.* 2004). This is certainly true of Bushbuckridge settlements which have expanded multi-directionally, coalescing across boundaries with other settlements (Coetzer *et al.* 2013). In addition to over allocating deforestation to wood harvesting, previous studies have underestimated the regenerative capacity of woodlands (Arnold *et al.* 2003; Twine & Holdo 2016). Here we have seen substantive regrowth response with increasing harvesting intensity, supporting suggestions that annual woodland productivity estimates have been too conservative. Tredennick and Hanan (2015) demonstrated sustainable harvesting levels at all levels, bar the most extreme, as a result of savanna tree species regenerative responses to disturbance. However, changes to the functional profile of a savanna woodland under high harvesting intensity to a highly productive, but structurally homogeneous shrub layer in the 'fuelwood trap', will have implications for ecosystem functioning and ecosystem services to the community. For example, grass biomass will decline, affecting livestock carrying capacity, and loss of recruitment of vegetation in the tall tree class will impact on non-timber products (e.g. fruit). Natural resource use is part of the wider rural development crisis (Mercer & Soussan 1992) and unlikely to abate in Africa where southern Africa's population is expected to increase to >70 million people by 2050 (United Nations 2015), with limited economic growth prospects, where only 35.3% of sub-Saharan Africa has access to electricity (World Bank Development Indicators 2012). The functional consequences of previously underestimated woodland regenerative response, and possible interactions with CO_2 fertilisation (Midgley & Bond 2015), should be monitored to mitigate coupled human-environment vulnerabilities.

2.5.4 Concluding remarks

Our results show high levels of wood extraction in communal lands are associated with compensatory growth in the low height classes. Fuelwood harvesting effects do interact with fire frequency and distance to settlements and roads. Bush thickening with a concomitant loss

of tall trees in the vicinity of settlements is likely to lead to a reduction in vegetation structural complexity. Although the results of this study describe detailed changes in woody canopy dynamics, the information about shrub-level increases is not species specific. Shrub-level increases could be dominated by species that are not appropriate for fuelwood use (e.g. *Lantana camara*) (Shackleton 1993). A reduction in structural heterogeneity and a community composition dominated by species with harvesting-tolerant regrowth responses will reduce woodland diversity, and subsequently ecosystem functioning (Hooper *et al.* 2005). To effectively manage woodland systems sustainably, we need to be able to predict future woodland structure by adding fine-scale data over broad extents on germination and seedling survival; low height classes are crucial for monitoring as they determine future woodland structure and composition.

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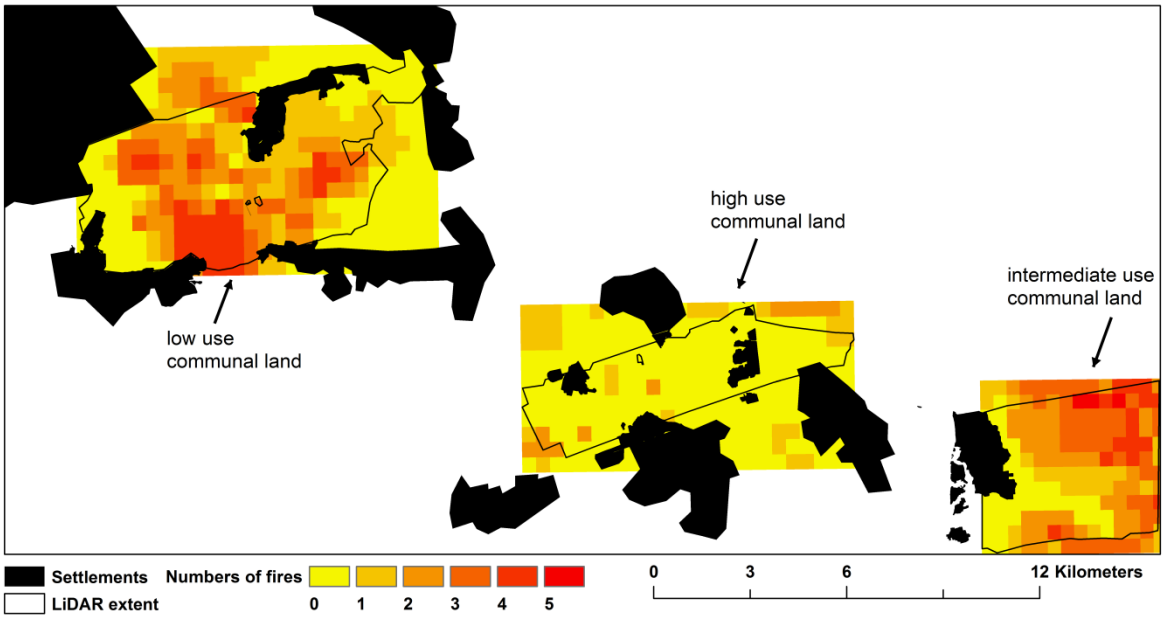
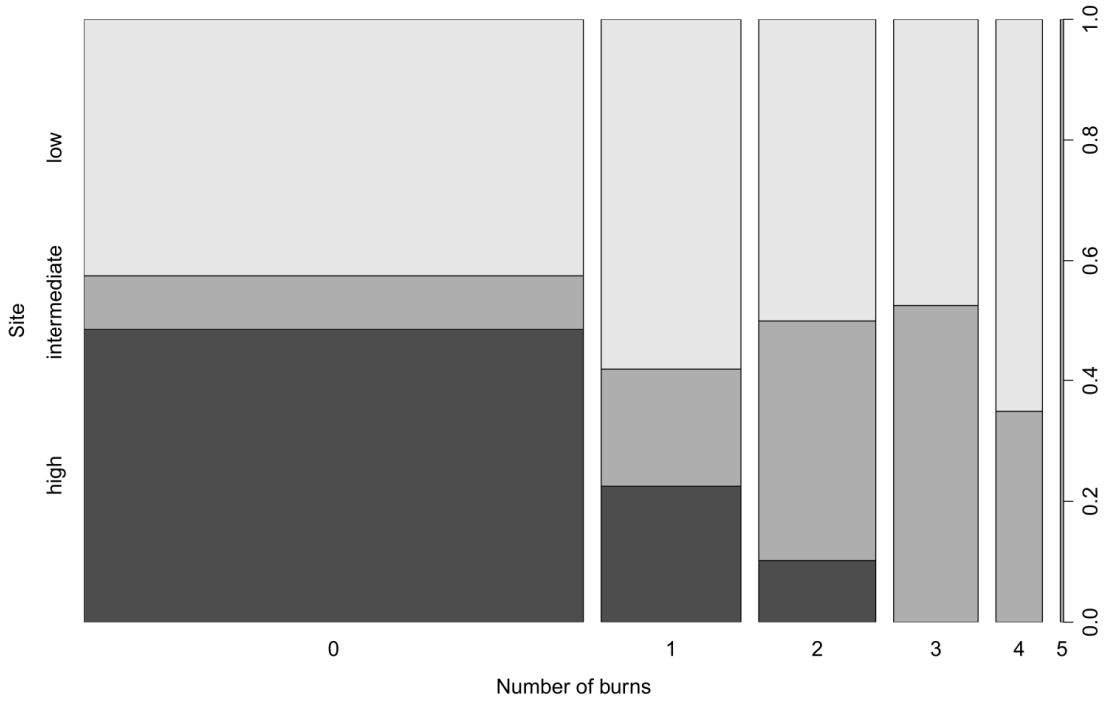
2.7 Appendix



Appendix Figure 2.1. Spatial distribution of burns in the Bushbuckridge communal lands between June 2007 and March 2012.



Appendix Figure 2.2. Proportional burn frequencies for high, intermediate and low wood extraction sites. Burn frequencies between sites showed marked differences (χ = 195.98 df = 4, p <0.001). The intermediate wood extraction site experienced more burns than the other sites between 2008 and 2012. Width of the bars on the x-plane represents the proportion of values in that burn category relative to all values. The intermediate wood extraction site is the only site containing areas that burned 5 times between 2008 and 2012.

Appendix Table 2.1. Canonical Correspondence Analysis (CCA) Eigenvalue details for a) all sites combined, b) high, c) intermediate, and d) low wood extraction sites. See Figure 2 in main document for graphical outputs.

a) All sites combined ** Summary ****

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.096	0.024	0.012	0.004	0.747
Species-environment correlations	:	0.767	0.408	0.386	0.271	
Cumulative percentage variance						
of species data	:	12.9	16.1	17.7	18.3	
of species-environment relation:		68.5	85.7	94.4	97.4	
Sum of all eigenvalues						0.747
Sum of all canonical eigenvalues						0.140

b) **high wood extraction site** **** Summary ****

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.072	0.035	0.006	0.002	0.848
Species-environment correlations	:	0.551	0.496	0.297	0.169	
Cumulative percentage variance						
of species data	:	8.5	12.6	13.3	13.5	
of species-environment relation:		62.2	92.2	97.2	99.0	
Sum of all eigenvalues						0.848
Sum of all canonical eigenvalues						0.116

c) intermediate wood extraction site**** Summary ****

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.076	0.064	0.022	0.011	0.937
Species-environment correlations	:	0.658	0.648	0.439	0.337	
Cumulative percentage variance						
of species data	:	8.1	14.9	17.2	18.4	
of species-environment relation:		42.3	77.5	89.5	95.9	

Sum of all eigenvalues	0.937
Sum of all canonical eigenvalues	0.180

d) low wood extraction site **** Summary ****

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.020	0.011	0.004	0.001	0.512
Species-environment correlations :	0.372	0.412	0.254	0.169	
Cumulative percentage variance					
of species data :	4.0	6.2	6.9	7.1	
of species-environment relation:	54.7	84.4	94.6	97.1	
Sum of all eigenvalues					0.512
Sum of all canonical eigenvalues					0.037

Appendix Table 2.2. Canonical Correspondence Analysis (CCA) species-environment correlation matrix details for a) all sites combined, b) high, c) intermediate, and d) low wood extraction sites. See Figure 2 in main document for graphical outputs. Canonical axes are in terms of species (Sp.) or environmental (Env.) variables. In this case, 'species' refers to the gains, losses or persistence of vegetation height classes (1-3m, 3-5m, 5-10, or >10m). Settlement, road and river refer to distances from the nearest settlement, roads, and rivers, respectively. REM refers to relative elevation model and 0burn, 1burn, 2burn, 3burn, 4burn, 5burn refer to burn frequency in the communal lands.

a)	**All sites combined**							
	Sp. Axis1	**Sp. Axis2**	**Sp. Axis3**	**Sp. Axis4**	**Env. Axis1**	**Env. Axis2**	**Env. Axis3**	**Env. Axis4**
Sp. Axis1	1							
Sp. Axis2	-	1						
Sp. Axis3	0.0057	0.1848	1					
Sp. Axis4	0.0679	-0.1796	0.0074	1				
Env. Axis1	0.7666	0	0	0	1			
Env. Axis2	0	0.4078	0	0	0	1		
Env. Axis3	0	0	0.3862	0	0	0	1	
Env. Axis4	0	0	0	0.2706	0	0	0	1

Granite	-	-0.0053	0.0612	-0.2275	-0.116	-0.013	0.1584	-0.8406
Gabbro	0.0889	0.0053	-0.0612	0.2275	0.116	0.013	-0.1584	0.8406
Intermediate use communal land	-0.0355	0.0093	0.0837	0.1969	-0.0463	0.0228	0.2168	0.7276
High use communal land	0.7591	0.0191	-0.0168	-0.0319	0.9902	0.0469	-0.0435	-0.118
Low use communal land	-0.4539	-0.0203	-0.0624	-0.1517	-0.5921	-0.0498	-0.1617	-0.5604
Road	-0.166	-0.1757	-0.1208	-0.028	-0.2166	-0.4309	-0.3128	-0.1033
Settlement	-	0.2133	-0.0958	0.1655	-0.1163	0.5232	-0.2482	0.6114
River	-	-0.1778	-0.1907	0.0683	-0.1156	-0.4361	-0.4939	0.2524
REM	0.0653	0.0682	0.1276	0.0713	0.0852	0.1671	0.3303	0.2636
0burn	0.3576	-0.1328	0.1898	0.051	0.4665	-0.3258	0.4914	0.1883

b)	**High wood extraction site**							
	Sp. Axis1	**Sp. Axis2**	**Sp. Axis3**	**Sp. Axis4**	**Env. Axis1**	**Env. Axis2**	**Env. Axis3**	**Env. Axis4**
Sp. Axis1	1							
Sp. Axis2	-	1						
Sp. Axis3	-	0.0236	1					
Sp. Axis4	-	-0.1662	-0.0183	1				
Env. Axis1	0.5514	0	0	0	1			
Env. Axis2	0	0.496	0	0	0	1		
Env. Axis3	0	0	0.297	0	0	0	1	
Env. Axis4	0	0	0	0.1687	0	0	0	1
Granite	-	0.0686	0.0203	-0.0572	-0.6332	0.1384	0.0684	-0.3392
Gabbro	0.3492	-0.0686	-0.0203	0.0572	0.6332	-0.1384	-0.0684	0.3392
Road	-	0.297	0.2139	-0.0424	-0.0058	0.5988	0.72	-0.2515
Settlement	0.2394	-0.1562	0.007	-0.1417	0.4342	-0.315	0.0235	-0.8397
River	0.2182	-0.0931	0.1635	0.1199	0.3957	-0.1878	0.5505	0.7105
REM	-	-0.3947	0.1205	-0.0016	-0.289	-0.7957	0.4056	-0.0097

c)	Intermediate wood extraction site							
	Sp. Axis1	**Sp. Axis2**	**Sp. Axis3**	**Sp. Axis4**	**Env. Axis1**	**Env. Axis2**	**Env. Axis3**	**Env. Axis4**
Sp. Axis1	1							
Sp. Axis2	0.1325	1						
Sp. Axis3	0.0484	-0.0068	1					
Sp. Axis4	-	-0.1152	0.1159	1				
Env. Axis1	0.6577	0	0	0	1			
Env. Axis2	0	0.6478	0	0	0	1		
Env. Axis3	0	0	0.4387	0	0	0	1	
Env. Axis4	0	0	0	0.3365	0	0	0	1
Granite	-	0.4765	0.1396	0.0431	-0.426	0.7355	0.3182	0.128
Gabbro	0.2802	-0.4765	-0.1396	-0.0431	0.426	-0.7355	-0.3182	-0.128
Road	0.0801	0.2214	-0.1738	-0.0297	0.1218	0.3418	-0.3962	-0.0882
Settlement	0.621	0.0939	0.0555	0.0002	0.9441	0.1449	0.1266	0.0006
River	-	-0.3794	-0.0624	0.0944	-0.0403	-0.5857	-0.1423	0.2804
REM	0.124	-0.244	-0.1259	0.125	0.1885	-0.3767	-0.287	0.3715
0burn	-	0.2993	0.0054	0.1535	-0.5029	0.462	0.0124	0.4562
1burn	-	-0.2536	0.2306	-0.0322	-0.0022	-0.3914	0.5256	-0.0957
5burn	0.1271	0.0517	-0.1398	0.1349	0.1933	0.0797	-0.3187	0.4009

d)	Low wood extraction site							
	Sp. Axis1	**Sp. Axis2**	**Sp. Axis3**	**Sp. Axis4**	**Env. Axis1**	**Env. Axis2**	**Env. Axis3**	**Env. Axis4**
Sp. Axis1	1							
Sp. Axis2	0.0004	1						
Sp. Axis3	0.1438	0.0146	1					
Sp. Axis4	-0.21	0.052	-0.2194	1				
Env. Axis1	0.3723	0	0	0	1			
Env. Axis2	0	0.4118	0	0	0	1		
Env. Axis3	0	0	0.2536	0	0	0	1	
Env. Axis4	0	0	0	0.1691	0	0	0	1
Road	0.2436	0.1443	-0.1008	-0.0115	0.6542	0.3503	-0.3972	-0.0681
Settlement	-	0.2608	-0.1332	0.0772	-0.2206	0.6332	-0.525	0.4565
River	0.1986	0.1456	-0.0816	0.0583	0.5334	0.3535	-0.3218	0.3449

REM	-	-0.215	-0.1688	-0.0436	-0.2057	-0.5221	-0.6655	-0.258
0burn	0.1344	-0.2427	-0.0004	0.0948	0.361	-0.5893	-0.0017	0.561
2burn	-	0.2462	-0.0138	-0.0305	-0.1898	0.5979	-0.0545	-0.1805
4burn	-	0.0456	0.0767	-0.002	-0.3959	0.1107	0.3023	-0.0116

Chapter 3. Biomass increases go under cover: Woody vegetation dynamics in South African rangelands**

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3.1 Abstract

Woody biomass dynamics are an expression of ecosystem function, yet biomass estimates do not provide information on the spatial distribution of woody vegetation within the vertical vegetation subcanopy. We demonstrate the ability of airborne light detection and ranging (LiDAR) to measure aboveground biomass and subcanopy structure, as an explanatory tool to unravel vegetation dynamics in structurally heterogeneous landscapes. We sampled three communal rangelands in Bushbuckridge, South Africa, utilised by rural communities for fuelwood harvesting. Woody biomass estimates ranged between 9 Mg ha^{-1} on gabbro geology sites to 27 Mg ha^{-1} on granitic geology sites. Despite predictions of woodland depletion due to unsustainable fuelwood extraction in previous studies, biomass in all the communal rangelands increased between 2008 and 2012. Annual biomass productivity estimates (10-14% p.a.) were higher than previous estimates of 4% and likely a significant contributor to the previous underestimations of modelled biomass supply. We show that biomass increases are attributable to growth of vegetation <5 m in height, and that, in the high wood extraction rangeland, 79% of the changes in the vertical vegetation subcanopy are gains in the 1-3m height class. The higher the wood extraction pressure on the rangelands, the greater the biomass increases in the low height classes within the subcanopy, likely a strong resprouting response to intensive harvesting. Yet, fuelwood shortages are still occurring, as evidenced by the losses in the tall tree height class in the high extraction rangeland. Loss of large trees and gain in subcanopy shrubs could result in a structurally simple landscape with reduced functional capacity. This research demonstrates that intensive harvesting can, paradoxically, increase biomass and this has implications for the sustainability of ecosystem service provision. The structural implications of biomass increases in communal rangelands could be misinterpreted as woodland recovery in the absence of three-dimensional, subcanopy information.

3.2 Introduction

Woody biomass is a fundamental expression of terrestrial ecosystem functioning, (e.g. primary productivity, land-atmosphere gas exchange and nutrient regulation), and can be used for the quantification of ecosystem services, such as fuelwood and carbon sequestration.

Biomass distribution reflects the spatial pattern of topo-edaphic and climatic gradients [1-3] and responses to disturbance [4-7]. However, biomass estimation remains challenging, particularly in environments with highly variable species composition and structural complexity [8-10].

Savannas, as complex tree-grass ecosystems, are structurally heterogeneous and are best described by three-dimensional metrics [11]. As such, savannas are ideal for examining the biomass dynamics in structurally complex vegetation. While total precipitation sets the upper boundaries on woody cover in savannas [12], their 'woody cover potential' is often unrealised [13-14] as a result of disturbances, such as fire [15-19] and herbivory [20-22]. A major driver in savanna ecosystem structure and function is the influence of people on the landscape [15,23], particularly through natural resource use, such as fuelwood harvesting [24]. Yet, the contributions of anthropogenic changes to savanna biomass dynamics are poorly understood.

Millions of people in Africa rely on woody vegetation for energy, extracted from both communal [25-27] and protected areas [28-29]. Within southern Africa, South Africa has a high per-capita use of fuelwood as a primary energy supply; despite having substantial access to electricity (66% of national population) [30]. Within this context, 93% of current fuelwood demands are no longer met by collection of dead wood [31]. Thus, live wood harvesting occurs around settlements and is a major driving force in woodland degradation in semi-arid ecosystems in southern Africa, particularly in the South African Lowveld (low altitude) savannas [7,24,32]. This is concerning because localised fuelwood scarcity is already being experienced, and the situation is unlikely to improve in the future [33]. Indeed, localised fuelwood shortages have facilitated the development of fuelwood markets [34-35], effectively increasing the harvestable area and thus the impacts of fuelwood extraction may become less of a localised phenomenon. Despite fuelwood markets contributing to rural livelihoods [34-35], they have the unfortunate knock-on effect of artificially maintaining perceptions of fuelwood abundance [36]. Although a depletion of woodland biomass was predicted to occur in Bushbuckridge, South Africa, by 2011 [24] and more recently, by 2024, at current extraction rates [32], the interactions between socioeconomic and environmental factors driving natural resource use are complex, non-linear systems that are difficult to quantify [37]. However, the above predictions do raise the concern that woody vegetation harvesting, driven by increased demand and greater extraction amounts is unsustainable [38]

and reduces the ability of ecosystems to provide ecosystem goods and services, fuelling the link between rural poverty and environmental impoverishment [39].

Wood harvesting changes not only biomass, but also vertical stratification of vegetation. Vertical vegetation complexity has relevance to ecosystem function as canopy height is related to biomass and productivity [40], biodiversity [41-43] and contributes to structural heterogeneity [44]. We submit that a method of understanding and, potentially, improving biomass change estimations, is to examine the vertical vegetation structure. We believe that by observing the interplay between woody biomass change and subcanopy structural change, drivers of biomass dynamics may be revealed.

Vertical subcanopy structure of vegetation canopies, however, cannot be derived from traditional two-dimensional remote sensing methods and top of canopy cover is a poor predictor of subcanopy cover [45]; three-dimensional (3-D) field-based efforts are impractical at landscape scales. Light detection and ranging (LiDAR) is a valuable tool for repeat estimation and monitoring of biomass, whilst providing subcanopy information, over large geographic areas and with fine-scale detail [46]. Repeat LiDAR campaigns have enabled tracking of woody biomass change as well as variation in the 3-D structure of the vegetation, providing the means to test previous fuelwood supply-demand model predictions [24,32], and to make inferences about the sustainability of wood provision under continued wood extraction pressure. The aim of this research is to utilize the power of airborne LiDAR to assess changes in aboveground biomass and subcanopy structure, as a unique window into unravelling vegetation dynamics in structurally heterogeneous landscapes.

3.3 Methods

3.3.1 Study Site

Permission to conduct fieldwork in the Bushbuckridge communal rangelands was granted by the local headmen. This study is part of a broad, long-standing relationship with the local community and the University of the Witwatersrand to conduct ecological research in their communal land. The field studies did not involve endangered or protected species. The study sites were located within the Bushbuckridge Municipality in the Lowveld region, a semi-arid savanna in South Africa. Summer rainfall (October to May) usually falls in convective

thunderstorms and ranges between >900 mm per annum in the west and 500 mm per annum in the east with an mean annual precipitation (MAP) coefficient of variation of 25%. Summers are hot and humid with mean daily maxima of 30 °C and winters are mild and dry with mean daily maxima of 23 °C. Droughts can be prolonged and may be experienced every ten years. Within the timeframe of this study (2008-2012), the 2006-2007 and 2007-2008 summer rainfall was below average and the 2011-2012 was a particularly wet summer. Within seasons, notable rainfall peaks occurred in April 2010 (4.1-fold more rain than the monthly 8-year average) and January 2012 (2.4-fold higher than the monthly 8-year average).

The terrain is shallowly undulating and the geology is dominated by granite with local Timbavati gabbro intrusions. Classic catenal sequences are common in areas with shallow, sandy, dystrophic soils on the uplands and deeper, clayey, eutrophic soils on the bottom slopes [7]. The predominant vegetation type is granite lowveld, but the region also contains gabbro grassy bushveld and legogote sour bushveld [47]. Common plant species on the granite Lowveld uplands include*: Terminalia sericea, Combretum zeyheri* and *C. apiculatum*; the bottom slopes are characterised by *Acacia nigrescens, Dichrostachys cinerea* and *Grewia bicolor* [47]. Other frequently occurring species are *Sclerocarya birrea, Lannea schweinfurthii, Ziziphus mucronata, Dalbergia melanoxylon, Peltophorum africanum and Pterocarpus rotundifolius*. The majority of the woody biomass in the region is formed from *S. birrea, Pterocarpus angolensis* and *A. nigrescens* [7].

Bushbuckridge is surrounded by conservation land (both state-owned and private) [48] which increases the pressure for grazing and harvesting outside of protected areas. An overgrazing land-use legacy exists from intensively stocked, white-owned cattle farms from 1913 onwards [49]. Apartheid followed in 1948, with the Promotion of Bantu Self-Government Act of 1959, which forced black South Africans to live in 'homelands' [49] – centralised settlements on farms of 1000-2000 ha. Bushbuckridge Municipality was formed from the joining of Mhala in Gazankulu and Mpulaneng in Lebowa (Matsika 2012), with settlement boundaries defined by the old cadastral borders of the historical cattle ranches [50]. Although Bushbuckridge falls under state control, there is customary communal land tenure controlled by headmen who zone the land into residential, arable and communal areas for grazing of livestock and collection of timber and non-timber products (e.g. thatch, fruit, medicine) [51]. The settlements range from small, isolated villages to larger, dense settlements along major roads [33]. Human population density sharply increased between 1972 and 1994 to approximately 300 people/km^2 [49] but these growth rates have declined over the past ten

years [35]. Commensurate with human population growth in the area, the spatial footprint of the residential regions has expanded [37,52]. A foreboding of this decline was an observed reduction in the size-class distribution of the woodland vegetation with increasing distance from certain settlements [53].

Within Bushbuckridge, three communal rangelands were chosen to represent different levels of natural resource utilisation. These rangelands are zoned for use by the following villages: Justicia; Croquetlawn, Ireagh and Kildare; Xanthia and Agincourt (Figure 3.1). The rangelands were classified according to the relative wood extraction pressure assessed using 2008 data on the number of people and households accessing a given rangeland and relative to this corresponding rangeland area: high (9.2 people ha^{-1}, 1.56 households ha^{-1}; using 2155 ha of rangeland); intermediate (1.8 people ha^{-1}, 0.35 households ha^{-1}; using 1815 ha of rangeland); and low (0.21 people ha^{-1}, 0.04 households ha^{-1}; using 4425 ha of rangeland) (see [53] for detailed demographic data). Although each rangeland is used by its corresponding settlements, use is not exclusive to these villages and foreigners (both local and cross-border immigrants) are known to harvest from these areas [38]. The intermediate-use intensity rangeland (Justicia) is the only example of exclusive access, as it is fenced on two sides by private conservation land and its location makes it more difficult to access from other villages [32].

3.3.2 Field-derived biomass estimates

All field data were collected concurrently with the airborne LiDAR campaigns in April 2012. Field-plots (total n = 56; high extraction site n = 16; intermediate extraction site n = 20; low extraction site n = 20) of 25 m x 25 m were established within the extent of the communal rangelands LiDAR coverage, and their locations recorded with a differential Global Positioning System (Trimble GeoXH Handheld GPS). All heights and basal stem diameters on stems thicker than 5 cm on trees taller than 1.5 m in height were recorded. A ‘tree’ may refer to a single-stemmed or multi-stemmed individual derived from the same rootstock, whilst ‘stem’ refers to the all branches derived from a single point on the ground. These height and basal stem diameter field data were used to estimate field biomass using allometric relationships from Colgan *et al.* [9], an extensive harvesting study with the same woody species composition as Bushbuckridge, in the form:

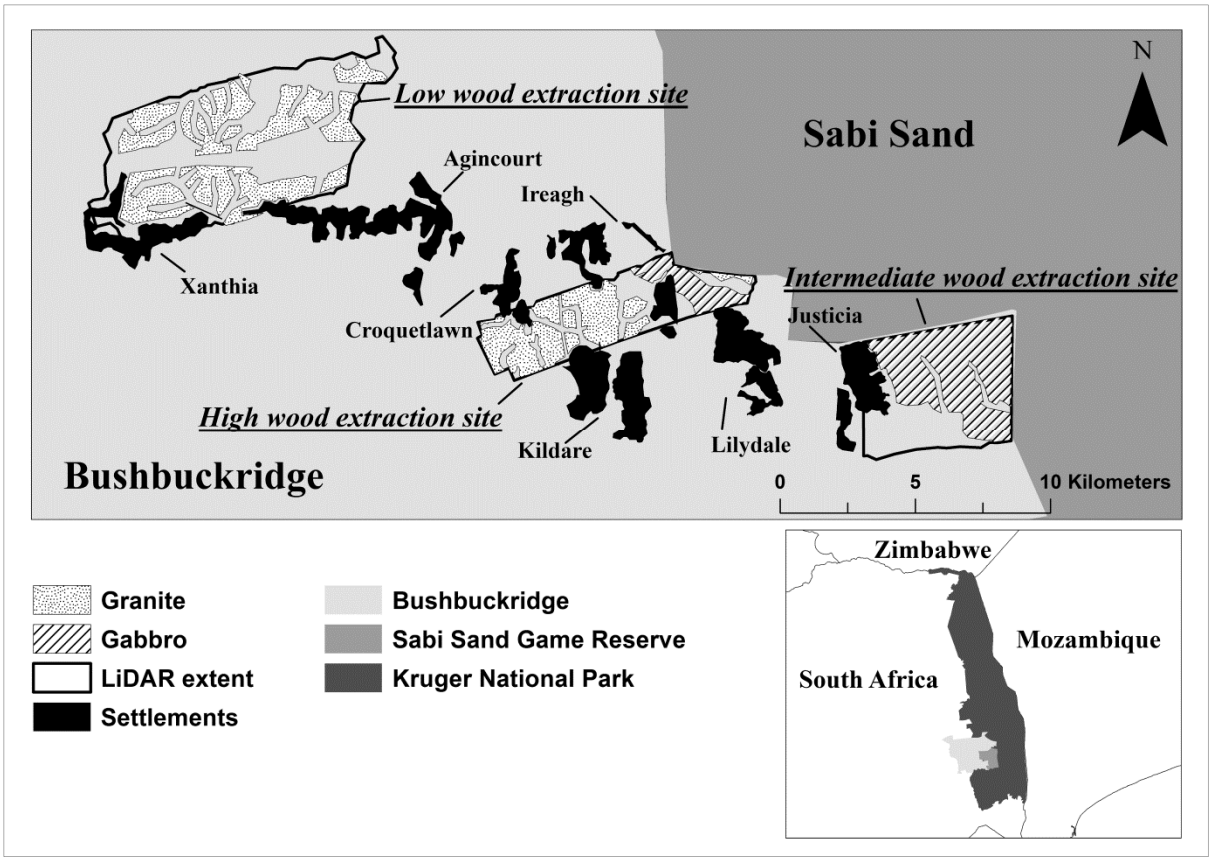

Figure 3.1. Study sites in Bushbuckridge municipality, located in the South African Lowveld. Sites are classified (from west to east) as low, high and intermediate wood extraction pressure based on the number of households and people utilising each rangeland. Settlements that utilise each rangeland are shown, including the names of the major settlements, as well as the location of the gabbro intrusions in the predominantly granitic landscape.

$$m = 0.109 D^{(1.39+0.14\ln(D))} H^{0.73} \rho^{0.80}$$

where m is dry aboveground stem mass (kg), D is stem diameter (cm), H is height (m) and ρ is a unitless wood-specific gravity constant. The individual stem masses where then summed within each 25 m x 25 m plot to obtain plot-level field biomass, reported in Mg ha^{-1}.

3.3.3 Light detection and ranging (LiDAR) data

The communal rangelands were surveyed with airborne laser mapping as part of a Carnegie Airborne Observatory (http://cao.ciw.edu/) campaign in April 2008 and April 2012, concurrently with the collected fieldwork data in 2012. Small footprint, discrete-return LiDAR is a remote sensing method which estimates 3-D vegetation structure over large areas.

The 2008 LiDAR data were collected from 2 000 m a.s.l. with the CAO-Alpha system with a laser pulse repetition frequency of 50 kHz and laser spot spacing of 1.1 m (see [54]); the 2012 data were collected with CAO-2 AToMS with a laser pulse repetition of 100 kHz and laser spot spacing of 1m (see [55]). The LiDAR system also provides accurate geo-locational information generated by a high performance inertial management unit (IMU) and global positioning system (GPS) [54]. The LiDAR product is a 3-D point cloud from which a canopy height model (CHM) was constructed from the difference between the digital terrain model (DTM, interpolated from the last LiDAR returns) and the digital surface model (DSM, interpolated from the first LiDAR returns). Spatial errors on the more coarse of the two products (2008 data) were <0.20 m vertically and <0.36m horizontally [54]. Although different sensors and processing methods were used for the 2008 and 2012 data, errors between corresponding DTM'S were <15cm.

Volumetric pixels (voxels) are formed by aggregating LiDAR laser returns into 1 m height classes [56]. The position of each voxel is taken from the voxel centroid relative to the ground. LiDAR return frequency, within each voxel, are reported as a percentage relative to the total number of LiDAR points in the complete vertical column, including the ground returns. These data are used to quantify subcanopy (i.e. vegetation beneath the canopy cover) structure.

3.3.4 LiDAR-derived biomass estimates

LiDAR-derived metrics of woody vegetation can be used to estimate allometric relationships and infer biomass [2,8,9,32,57-58]. We derived a biomass regression model according to previously established methods by correlating the plot-level field-allometry and a corresponding LiDAR-derived H x CC (height x canopy cover) predictor metric calculated for each 25 m x 25 m grid cell created to correspond to the 25 m x 25 m field plots; H is plot-averaged (mean pixel height values >1.5 m) and CC is the proportion of canopy cover per plot (proportion of pixels >1.5 m in height). Both values were extracted from the CHM (see [9] for details). The H x CC metric is not only ecologically meaningful as it is an approximation of wood volume, but it also gives the best results over more complex metrics [2]. The height mask (>1.5 m) was used to account for the possibility of ground and tall grass being misclassified as vegetation. The LiDAR-derived predictor metrics were trained against field-derived biomass for each rangeland as they all exhibit different vegetation structural

patterns, resulting from variable rainfall, different geologies and wood extraction pressures. Not only were these site-specific models able to explain more variation than one general equation; they were also deemed more ecologically valid. Biomass maps were then created by applying the site-specific biomass models to the LiDAR CHM extent (masked at heights >1.5 m) for each rangeland for both 2008 and 2012. Only grid cells that fit the criteria of an average height of >1.5 m (once pixels of <1.5 m were excluded) were used to estimate biomass as this is the vegetation that the fieldwork included. However, the cells that matched these criteria varied in both number and spatial location between 2008 and 2012. For the purposes of biomass change detection, only those cells that met the average height criteria for both years in the same location were considered. Riparian areas adjacent to streams in the rangelands were excluded from the biomass maps as they require separate calibration [2]. Similarly, cultivated fields and built-up areas were excluded.

3.3.5 LiDAR-derived subcanopy analysis

The voxel data (5 m x 5 m x 1 m) were resampled to 25 m x 25 m x 1 m, making the data comparable to the biomass grid cell sizes, and stacked into the following ecologically relevant, vertical height classes: 1–3 m (shrubs and small trees in the 'fire trap' [16]); 3–5 m (trees in the 'elephant trap' [22]); 5–10 m (tall trees contribute to structural diversity and thus to ecosystem function [59]); >10 m (very tall trees, 'keystone structures' [60], are often culturally important trees conserved in the rangelands [61]). These data were used to detect changes in the distribution of the vegetation size classes within the vertical vegetation column. "LiDAR returns" refers the percentage of laser pulses that were emitted from the sensor, hit an object and returned to the sensor. In the results, "Total % LiDAR returns" refers to the returns for the full vegetation column – excluding the ground returns. "% Subcanopy returns" refers to the LiDAR hits within a particular height category. Higher subcanopy returns implies greater density of vegetation in that height class.

3.3.6 Data extraction and analysis

Features of the settlements (e.g. roads, villages, crop fields) and rivers were manually digitised using a combination of SPOT 5 imagery (panchromatic-multispectral merge (480–890 nm), 2.5 m spatial resolution, www.spotimage.com) and aerial photographs (50 cm resolution, www.ngi.gov.za). Biomass estimates were extracted from the maximum number

of randomly distributed points with a minimum enforced distance of 50 m to avoid spatial autocorrelation, based on the results of semivariograms (calculated in ENVI v4.7). All data were analysed in R v3.0 (R Core Team), including descriptive statistics, linear regression models and correlations. Biomass estimates were tested with Shapiro-Wilk Normality tests from the "fBasics" package and all sites in both 2008 and 2012 were found to be non-normally distributed ($p < 0.001$). Thus, a non-parametric Wilcoxon rank sum test was used to analyse differences between means over time within sites.

3.4 Results

3.4.1 Biomass models

A strong relationship existed between the field allometry and LiDAR metrics, although the highly heterogeneous rangeland resulted in high root mean square error (RMSE) values in both high and low use sites on granitic substrates (18.6 and 19.1 Mg ha^{-1}, respectively) (Table 3.1). The increase in variability with increase in biomass indicated (Appendix Figure 3.1) less agreement between the field allometry and LiDAR metrics at higher biomass values. This is a common phenomenon, termed 'heteroskedasticity', of model performance at higher biomass levels where the error variance is not consistent over all the observations [62]. Most typically, modelling the error structure shows a fanning pattern of increasing variance with increasing biomass [62], and this is true of the residual structure for both the high and low wood extraction sites (Appendix Figure 3.1).

3.4.2 Biomass dynamics

Mean biomass ($\pm$ SD) in 2008 at the high, intermediate and low extraction sites was: 26.99 $\pm$ 16.43 Mg ha^{-1} (n = 102 cells), 9.42 $\pm$ 4.13 Mg ha^{-1} (n = 291 cells), and 21.18 $\pm$ 12.04 Mg ha^{-1} (n = 1654 cells), respectively. Biomass increased significantly at all sites between 2008 and 2012 by an average 18.38 Mg ha^{-1} (highest use site: $W = 3036$, $p < 0.001$), 5.45 Mg ha^{-1} (intermediate use site: $W = 16780$, $p < 0.001$), and 11.34 Mg ha^{-1} (low use site: $W = 771641$, $p < 0.001$) (Table 3.2).

Table 3.1 Site-specific biomass models derived from field allometry and LiDAR metric linear regression.

Extraction pressure	Model	R^2	n	RMSE (Mg ha^{-1})
high	y = 2312.3x - 157.14	0.78	16	18.6
intermediate	y = 409.57x + 252.74	0.60	20	4.8
low	y = 913.9x + 127.86	0.68	20	19.1

In the model equations, y refers to the plot-level (25 m x 25 m) biomass estimate (kg/625 m2) and x to the LiDAR-derived H x CC predictor metrics, where H is plot-averaged height (> 1.5 m) and CC is the proportion of canopy cover (> 1.5 m in height) per plot. Root mean square error (RMSE) was reported in Mg ha^{-1} for ease of interpretation and n is number of 25 m x 25 m plots.

Table 3.2. Mean biomass increase (Mg ha^{-1}) at sites under varying wood extraction pressures.

	Extraction pressure		
	High (n = 102)	**Intermediate (n = 291)**	**Low (n = 1654)**
2008 (mean ± S.D.)	26.99 ± 16.43	9.42 ± 4.13	21.18 ± 12.04
2012 (mean ± S.D.)	45.37 ± 28.37	14.87 ± 6.76	32.52 ± 17.60
Absolute increase	+18.38	+5.45	+11.34
Relative increase (%)	+68.08	+57.80	+53.57

n is the number of 25 m x 25 m grid cells in each rangeland.

Variability increased with increased biomass, particularly in the high and low extraction pressure sites (Table 3.2). Represented as a rate of biomass change, the mean annual woody biomass productivity (± 95% spatial confidence interval) translates to 14 ± 1.39% p.a, 12 ± 0.08% p.a. and 11 ± 0.00% p.a for the high, intermediate and low wood extraction sites, respectively. These increases were despite ongoing wood harvesting in these rangelands. Relative to the starting biomass, all mean increases were greater than 50% (Table 3.2). Extreme biomass increases were related to large changes in relative height (Figure 3.2) and relative canopy cover (e.g. >50% increase in canopy cover results in biomass increases of

>20 Mg ha^{-1}, Figure 3.3). However, the extreme biomass changes (i,e. >40 Mg ha^{-1}) predominantly occurred in the 1-3 m height class (Figure 3.2a and Figure 3.3a). Biomass increases of >40 Mg ha^{-1} did not occur in height classes >5 m (Figure 3.2c and Figure 3.3c). The largest increases in biomass occur in the high wood extraction site when compared with the same increases in relative height (Figure 3.2a,b) and canopy cover (Figure 3.3a,b) in the other rangelands. There are no data for the high extraction site for the 5-10m height class as there are no grid cells with an average height >5 m in this rangeland (Figure 3.2c and Figure 3.3c).

3.4.3 Vegetation structural dynamics

Total % canopy returns increased between 2008 and 2012 in all rangelands, but up to 79% of the total change in canopy returns was attributable to the increase in the 1-3 m height category within the subcanopy (Figure 3.4). Losses in subcanopy returns were only found in the high wood extraction rangeland, and only in the 5-10 m height class (Figure 3.4a). There was little contribution to total change in % subcanopy returns from the >10 m height class (Figure 3.4). Although the high and low extraction rangelands had fairly similar overall increases in % total canopy returns, this was not the case with relative change (from 2008), where the highest extraction site was far greater (e.g. relative canopy returns for height class 1-3 m: 425%, 387% and 90% for high, intermediate and low extraction, respectively). Thus, the order of relative change in % canopy returns followed the gradient of wood extraction levels at the different sites.

Another indicator of shrub level increase in the rangelands is the change in the number of cells that remained after an average height mask was applied (i.e. that fulfilled the average height criteria threshold to be included in the biomass analysis), expressed as a percentage of each rangeland. The high extraction rangeland changed from 10% of the rangeland that met the average height (>1.5 m) criteria mask in 2008 to 15.9% of the rangeland in 2012 (χ^2_1 = 107.6; p <0.001); the intermediate use site doubled in the percentage of rangeland that met the average height criteria from 8.5% to 17.4% (χ^2_1 = 780.8; p <0.001); and the low use rangeland increased from 54.2% in 2008 to 63.8% of the rangeland in 2012 (χ^2_1 = 220.7; p <0.001).

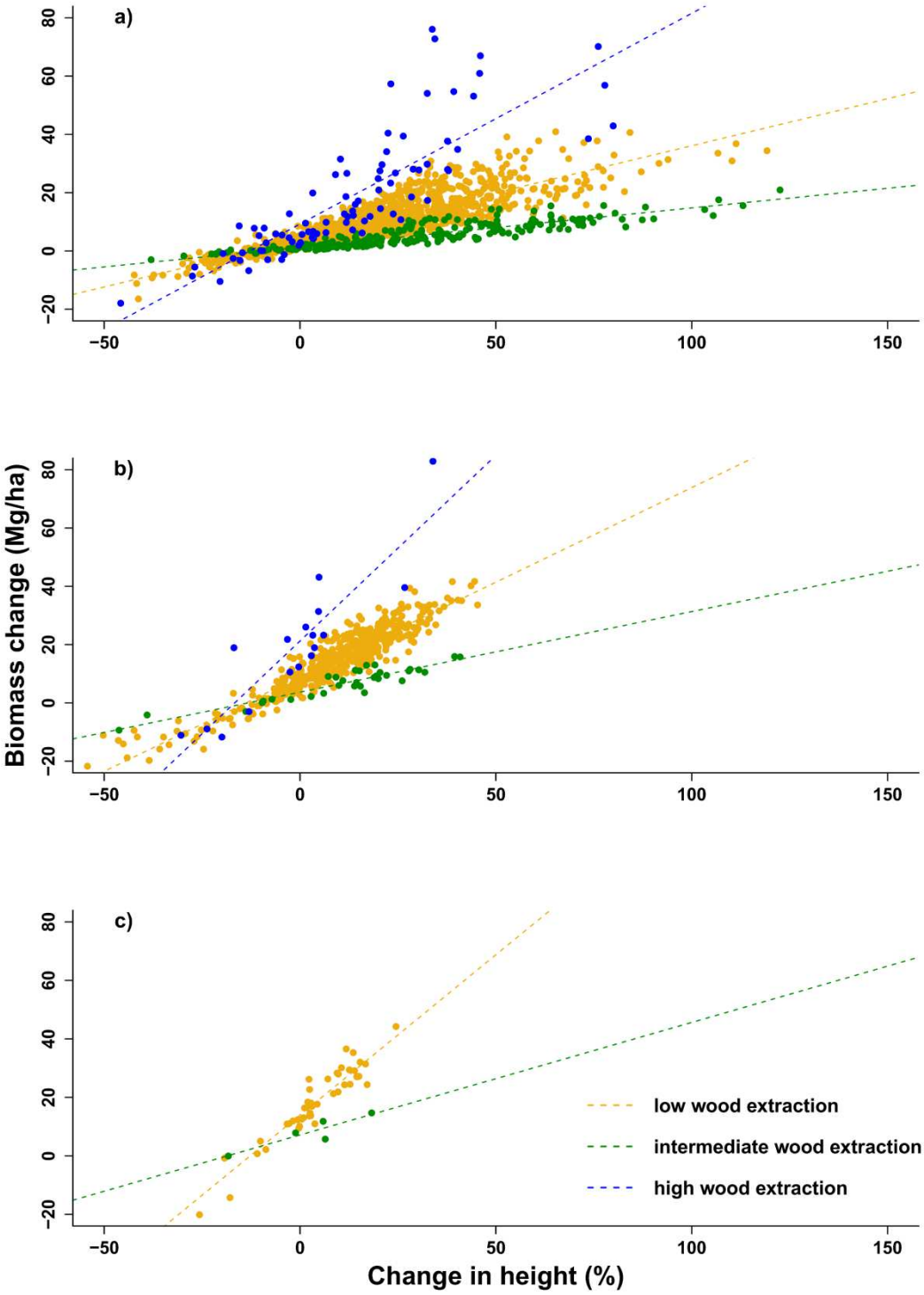

Figure 3.2. Height-specific biomass change as a function of relative height change per grid cell. Height categories are a) 1-3 m, b) 3-5 m and c) 5-10 m for rangelands of high, intermediate and low wood extraction pressure. There were no data for the 5-10 m height class in the high wood extraction rangeland and the >10 m height class for all rangelands as there were no grid cells with an average height over 10 m. Grid cell size: 25 m x 25 m.

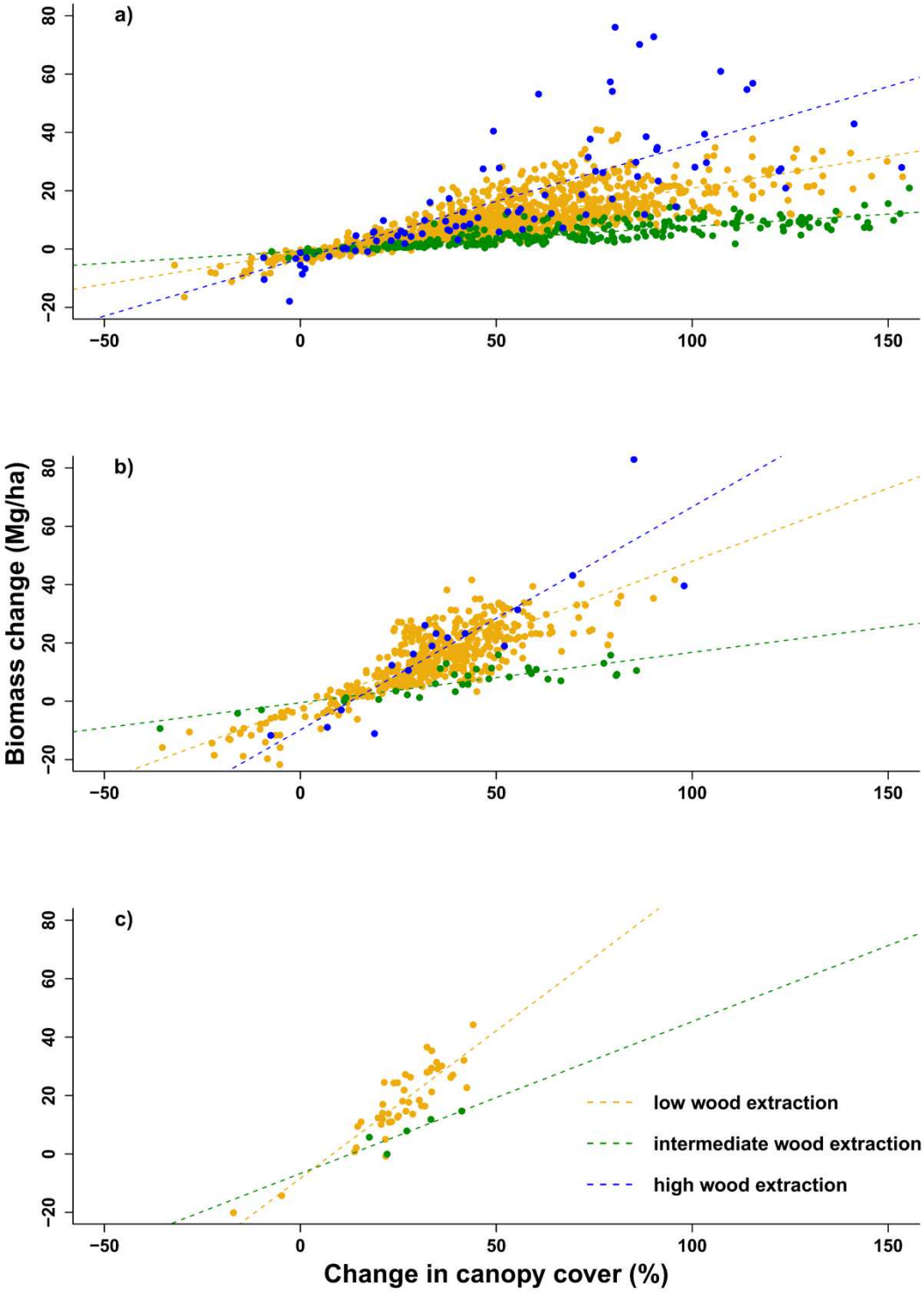

Figure 3.3. Height-specific biomass change as a function of relative change in canopy cover per grid cell. Height categories are a) 1-3 m, b) 3-5 m and c) 5-10 m for rangelands of high, intermediate and low wood extraction pressure. There were no data for the 5-10 m height class in the high wood extraction rangeland and the >10 m height class for all rangelands as there were no grid cells with an average height over 10 m. Grid cell size: 25 m x 25 m.

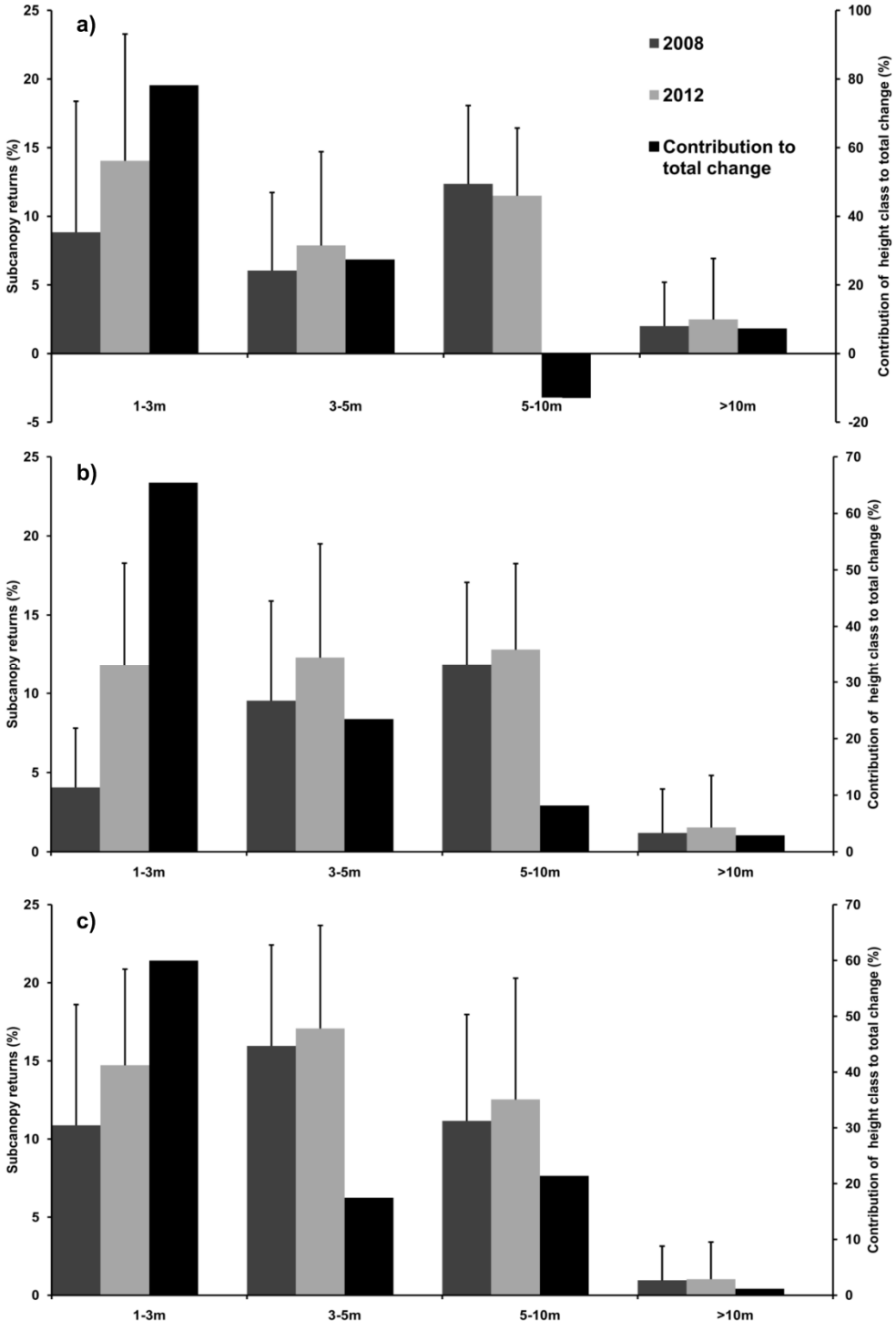

Figure 3.4. Height-specific subcanopy returns (%) (mean ± standard deviation) for 2008 and 2012. Wood extraction levels are: a) high (n = 102 cells), b) intermediate (n = 291 cells), and c) low wood extraction (n = 1654 cells). Contribution of height class change (subcanopy returns) to total change (total vegetation column) (%) is the black bar represented by values on the secondary axis. e.g. In the high wood extraction rangeland, 79% of the change in the total vegetation column was attributable to the 1-3 m height class.

3.4.4 Association between biomass change and vegetation subcanopy returns

There was a positive correlation between change in biomass and change in % subcanopy returns (Figure 3.5); particularly in the 1-3 m height class in the high extraction sites (high extraction: $r = 0.22$, $p < 0.0001$; intermediate extraction: $r = 0.58$, $p < 0.0001$) and the 3-5 m height class (high extraction: $r = 0.62$, $p < 0.0001$; intermediate extraction: $r = 0.64$, $p < 0.0001$; low extraction: $r = 0.56$, $p < 0.0001$). Although this relationship was also present in the 5-10 m height class at all extraction levels ($r > 0.31$), it degraded at heights >10 m ($r < 0.10$) (Figure 3.5). It is interesting to note that the strength of the relationship between change in biomass and change in % subcanopy returns across all height categories was strongest at the intermediate wood extraction site (Figure 3.5).

Changes in biomass and height-specific subcanopy returns were spatially associated (Appendix Figure 3.2). However, these changes were more apparent at <5 m (Appendix Figure 3.2). Almost no change in % subcanopy return for vegetation >10 m is evident (Appendix Figure 3.2). The same biomass values for a given grid cell can manifest as different structural profiles. As such, structural profiles could change in different ways whilst maintaining the same overall biomass value outcome. For example, if the site was dominated by grasses with several trees >5 m, that site could, theoretically, show no change in biomass value by 2012, but the structural profile may have changed to predominant shrub cover and fewer tall trees.

3.5 Discussion

Large increases in biomass at all sites (Table 3.2) are in contradiction to previous fuelwood supply-demand models which predicted biomass depletion [24,32,63]. Biomass increases in Bushbuckridge rangelands were attributable (>80%) to vegetation in the 1-3 m height class within the subcanopy (Figure 3.4), with extreme biomass gains (>20 Mg ha^{-1}) associated with

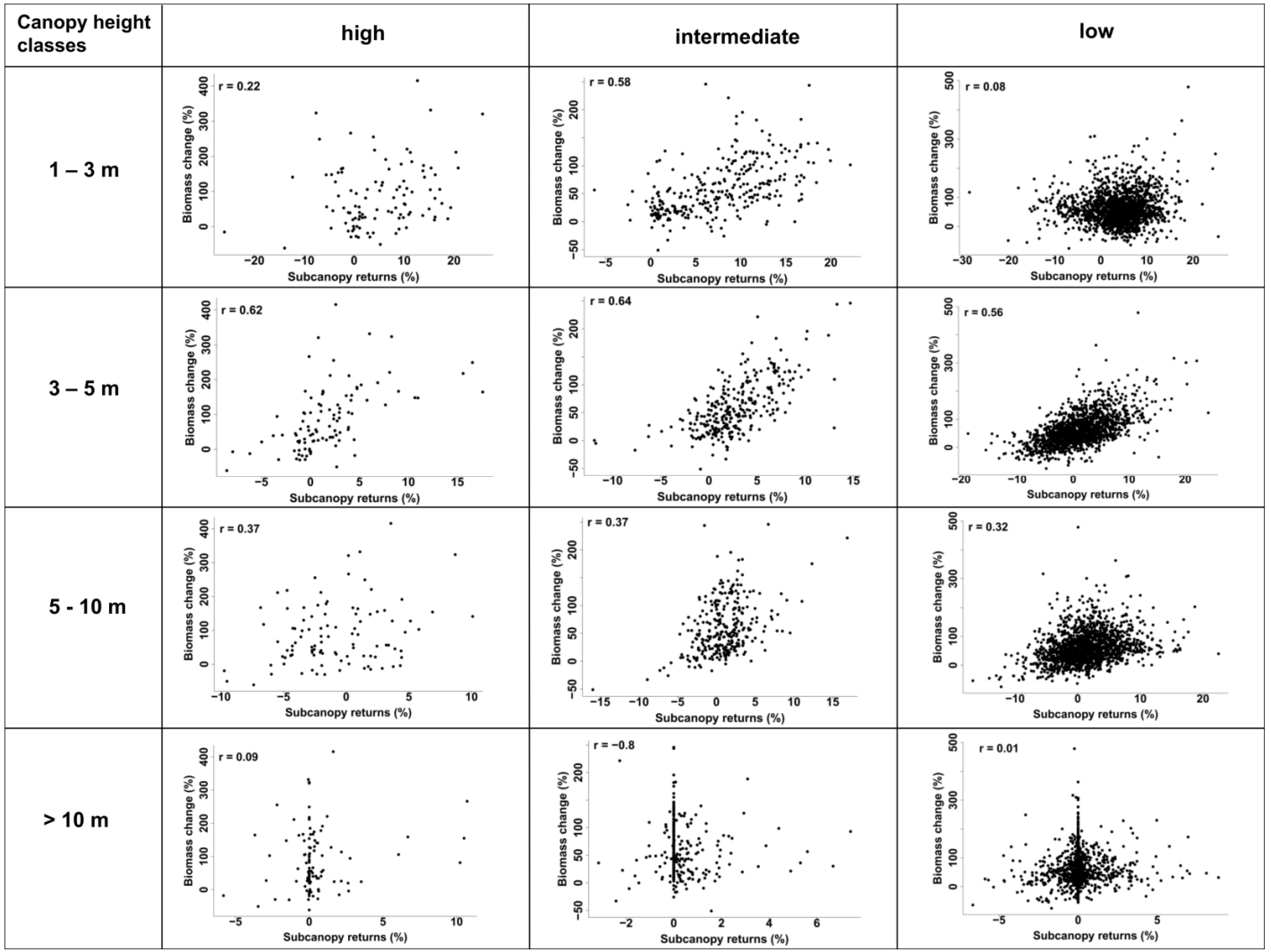

Figure 3.5. Height-specific correlation (p < 0.001) between change in biomass (%) and subcanopy returns (%). Wood extraction levels for each rangeland are listed per column as high, intermediate and low.

vegetation that gained >25% in height (Figure 3.2a) or >50% in canopy cover (Figure 3.3a). This agrees with an observed increase in the number of thinner, taller stems within Bushbuckridge rangelands [35] and more grid cells meeting the average height criteria in each of the rangelands between 2008 and 2012. These low height class increases probably reflect local-scale dynamics of harvesting – more harvesting drives coppicing (resprouting from the stem or roots) in the intermediate and high extraction sites (Figure 3.2a and Figure 3.3a) – but the relationship appears more pronounced in the intermediate site as less of the coppice is harvested. It is likely that wood harvesting is acting as a 'bush thinning' mechanism, changing the size specific growth rates, particularly in resprouting from stumps with fully-developed root systems [64]. Indeed, thick stands of small-stemmed trees can yield more woody biomass than a few, large trees as a result of divergent, size-specific growth rates [65]. However, low height class increases in biomass could also be a result of newly established bush encroachers which characteristically invade overgrazed and degraded rangelands [66-68]. Biomass estimations for different height classes in a savanna woodland reveal, collectively, greater biomass quantities are located below 4.5 m in height than above; a disparity more prominent immediately after a disturbance [69]. Harvesting has been found to increase the density of smaller stems without changing the height structure of the woodland [70]. Unfortunately, there is a dearth of data on the preferred height of harvested species, only preferred diameter size which ranges, location dependent, between 2 - 6.5 cm [26,36]. There are records of stems >1 cm being taken, with preference for those >4 cm and almost no stems harvested >20 cm [71]. Extrapolating 1 cm and 5 cm diameter size into available coppice diameter-height allometry relationships [72] suggests pre-harvested heights of 0.74 m and 2.92 m in *Dichrostachys cinerea*, *0.*63 m and 2.07 m in *Acacia harveyi*, and 0.77 m and 2.44 m for *Combretum collinum*, respectively. Although the relationship between harvested stem diameters and regrowth shoot length is variable, we can infer that stems harvested for fuelwood are generally <3 m. Therefore, preferred 'harvesting heights' coincide with height class with the most subcanopy gains (Figure 3.4).

Subcanopy biomass increases at low heights in a rangeland context are likely a combination of woody regrowth-response (harvesting effects) [71-74] and bush encroachment (overgrazing effects) [15,75-76], here collectively referred to as 'bush thickening'. However, these are not mutually exclusive events and can occur together. Low height-class increases occur in Bushbuckridge both as standalone shrubs as well as occurring underneath the canopies of tall trees [45]. Resprouting rates and the subsequent influence on communal

rangeland dynamics have been underestimated in the earlier research in this region [77]. Although the Wessels *et al.* [32] supply-demand model did include resprouting estimates of 89 kg ha^{-1} yr^{-1} which is significantly higher than the 20 kg ha^{-1} yr^{-1} that the Banks *et al.* [24] model used; these rates are only from one species, *T. sericea,* and thus, may underestimate the growth rates for the other predominant coppicing species, e.g. *D. cinerea*. Previous data suggest that even during a poor rainfall period, in just five months there was coppice of 989 kg ha^{-1} (6.6% of the total post-harvest biomass) and harvested trees recovered two thirds of their preharvest biomass, with no harvest-induced mortality [71]. *T. sericea* coppice shoots from established stumps gained between 1-2 m in height over 3 years [78], whilst coppice stands in Malawi and Kenya gained 3m [79] and 2m [80], respectively, over 4 years. This is evident in the annual productivity suggested by the LiDAR-derived estimates of well over 10% p.a. (especially when we consider that this is over and above the biomass removed for wood energy) which exceeds the previous woodland productivity value of 4% [24,32,81]. The disparity in the growth rates is likely a result of higher productivity in the low height classes [69] and a significant contributor to the Wessels *et al.* [32] underestimation of biomass production rate. Growth rates could also have been affected by the drier than normal conditions in 2007 and, likewise, the high rainfall in 2010 and early 2012. As data collection was subsequent to these events, it is likely that biomass estimates were affected.

Although lower height classes within the subcanopy showed increases across all wood extraction sites (Figure 3.4), this was not true for subcanopy returns in the 5-10 m class in the high wood extraction site (Figure 3.4a). Large, fruiting trees are normally conserved by villagers as they are used for a variety of non-timber uses [82-83]. Despite cultural practices against live-wood harvesting of large fruiting trees, villagers acknowledge that they do cut trees, like marula (*Sclerocarya birrea*), as they feel they have no alternatives in the face of high electricity prices and localised shortages of fuelwood [83]. We observed several felled and pollarded marula trees in the highest wood extraction site and can assume, together with the lack of data for grid cells of average height >5m (Figure 3.2c and Figure 3.3c), that the loss of vegetation returns in the 5-10 m height class reflects a localised lack of fuelwood of sufficient quality and quantity in this rangeland. The reduced number of tall trees and abundance of short subcanopy vegetation in the high use rangeland results in a more homogeneous stand structure (Fig. 4a), a possible explanation for the stronger relationship between field and LiDAR data in this site (Table 3.1). Most fuelwood supply-demand models that predicted loss of biomass are not spatially explicit and did not capture the fine scale

variation at village level [84-85] or the mismatch between the spatial variability in fuelwood supply relative to centres of demand [35], especially considering vehicles are increasingly being used to transport larger amounts of wood from more distant locations [39,86]. Yet, the Wessels *et al.* [32] fuelwood model focused on one "best-case scenario" communal rangeland, exclusively utilised by one village and still predicted losses. However, fuelwood demand is not a linear system and people's responses to changes in their socio-economic and natural resource environment are complex and difficult to quantify [37]; consequently, the community's adaptive responses are not incorporated in these models. Global and national studies highlight the lack of adaptive capacity of people in the developing world [37,87-88]; however, the strategies people adopt on local and regional scales often reveal surprising resourcefulness in response to change [89-91]. Within the fuelwood context in Bushbuckridge and elsewhere in Africa, responses to localised fuelwood shortages have included: changes in the preferred size class of fuelwood [29,35,86]; switching preferred fuelwood species [25,33,91]; more frequent trips or more time spent per trip to collect fuelwood [31,92]; travelling further from home [37]; use of wheelbarrows and vehicles to collect more wood per trip [33,38,86,93]; development of fuelwood markets [33,36]; and collecting from neighbouring private land [35]. Socio-economic factors also play a role in fuelwood demand dynamics. High dependence on government social grants and migrant worker remittances is characteristic of rural areas [33,94-95]; changes in these economic flows will affect household cash flow and, thus, alter household-level demand for natural resources. These adaptive strategies and socio-economic factors are difficult to capture in a supply-demand models and are a contributing cause to the disparity between predicted and measured biomass in communal rangelands.

Biomass values range between 9 Mg ha^{-1} (on gabbro) to 27 Mg ha^{-1} (on granite) which is comparable to the range for field-based allometry studies in the greater Bushbuckridge area (18.9 - 23.1 Mg ha^{-1}) [7], and the LiDAR-estimates for the conserved Lowveld region (11.9 – 92.3 Mg ha^{-1}) [2]. The intermediate wood extraction site has had previous estimates of LiDAR-derived biomass for 2008 of 12 Mg ha^{-1} [32], but this used allometry from Nickless *et al.* [96] and field–LiDAR biomass regression relationships derived from the regional landscape. Most studies on allometry have focused on temperate zone and deciduous forests (e.g. [58,97-98]) or tropical forest monitoring (e.g. [8,99-101]). Very few have focused on savanna systems (e.g. [2,4,96]). Both Chave *et al.* [8] and Colgan *et al.* [9] stress the importance of allometric equation choice on error as even field-allometry had 16% RSE

(Residual Standard Error); these errors often compound with averaging. Although Colgan *et al.*'s [9] plot-averaged LiDAR-derived biomass estimates had 9% more relative error (difference between predicted and measured biomass) than field-harvested biomass, the bias (mean error) was only -3% (compare to Nickless *et al.* [96] allometry with 15% more relative error and 50% bias) [9]. Our study also excluded all cells that were below 1.5 m in average height in both 2008 and 2012, cutting out a large proportion of the area relative to the portion used in Wessels *et al.*'s [32] study. Although our biomass model has fewer field-calibration sites than the Wessels *et al.* [32] study, our calibration sites were specific only to the area the biomass models were applied to.

While we are confident that our biomass estimates are reflecting a true increase, the shortcomings of using this method have the potential to exaggerate increases, particularly error in canopy cover measurements over time. This is of concern when considering leaf area index (LAI) in LiDAR change detection metrics, as both the voxel and the CHM data may be influenced, affecting the biomass estimates as well as the subcanopy LiDAR returns. Although this was controlled for as much as possible by collecting the LiDAR data in the same month each campaign, LAI varies with phenology and with local climatic changes, such as differential rainfall between years, or heavy winds [102]. The relatively high predictive uncertainty (RMSE range: 4.8 - 19.1 Mg ha^{-1}) in the biomass models occur in the high and low wood extraction rangelands, both of which are situated on granitic geology (Figure 3.1) which are more heterogeneous in both topographic relief and stand structure, as well as in the resultant biomass (Table 3.1). In landscape-scale approximations of biomass, errors are introduced and often propagated. The assumption is that individual plant measurement errors will average out over the plot level, provided the plots are large enough and the measurement process is unbiased. There is also an effect of plot size on error; increasing plot size increases the predictive power of the model [10]. However, there is a trade-off between the cost and logistic realities of sampling large plots and the need to sample a large number of plots, as plot number also affects landscape-scale error [9]. Although relative uncertainty in the biomass models was high and may have been reduced by object based image analysis (OBIA) methods applied to single tree crowns to counter vertical structural heterogeneity errors, plot-level averaging methods have a positive trade-off in their simplicity and their ability to average out within-plot variation, particularly the horizontal canopy cover heterogeneity characteristic of savannas.

3.6 Conclusions

Savanna-based biomass studies have considerable scope to rectifying the underestimation of carbon sinks and sources, elucidating the woody encroachment problem in savannas and untangling the interactions between bush encroachment/thickening and wood extraction by rural communities. Without high resolution, 3-D vegetation data covering a large area, the landscape-scale increases in biomass over the Bushbuckridge rangelands could erroneously be interpreted as woodlands recovering to an "unaltered" state. Users of two-dimensional, remotely-sensed biomass estimates should remain aware of structural implications in the landscape to make informed conclusions on vegetation dynamics, particularly in the context of increasing savanna bush thickening in a CO_2 rich environment [103-104]. Indeed, it is the low height class vegetation within the subcanopy which determines future woodland structure. Moreover, most carbon cycle studies in Africa neglect domestic emissions from wood harvesting [105] despite knowing the contribution of deforestation and land degradation to carbon dynamics [106]; a recent carbon model has demonstrated the importance of vegetation increases in the southern hemisphere's semi-arid regions to terrestrial carbon sinks [107]. The repercussions of bush thickening in communal rangelands will have implications for the direct-use values of ecosystem goods and will affect household vulnerability to shocks [39]. Our research suggests that wood harvesting can, paradoxically, exacerbate bush thickening as many of the harvested savanna species have strong regenerative responses [71-72,79-80,108-109]. Not only is coppice an important survival strategy for regenerating woodlands, the resprouted stems may provide a valuable source of future harvestable biomass [74,78,110-112]. There is, however, little information on regrowth rates and response to continued harvesting as well as whether the coppice is of appropriate quality for fuelwood.

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3.8 Data Availability Statement

All data necessary to replicate the results of this study are contained within the paper and its Supporting Information files.

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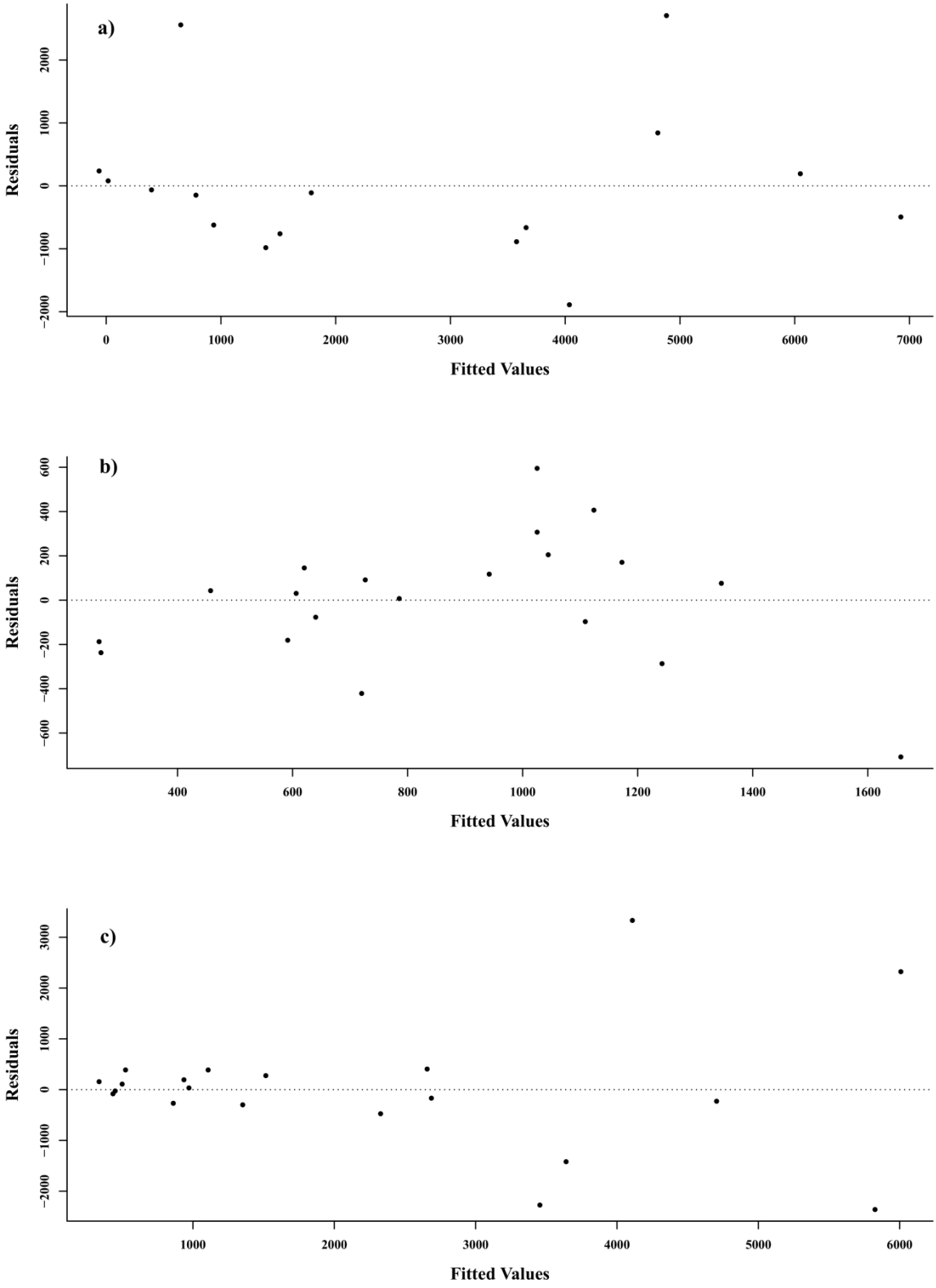
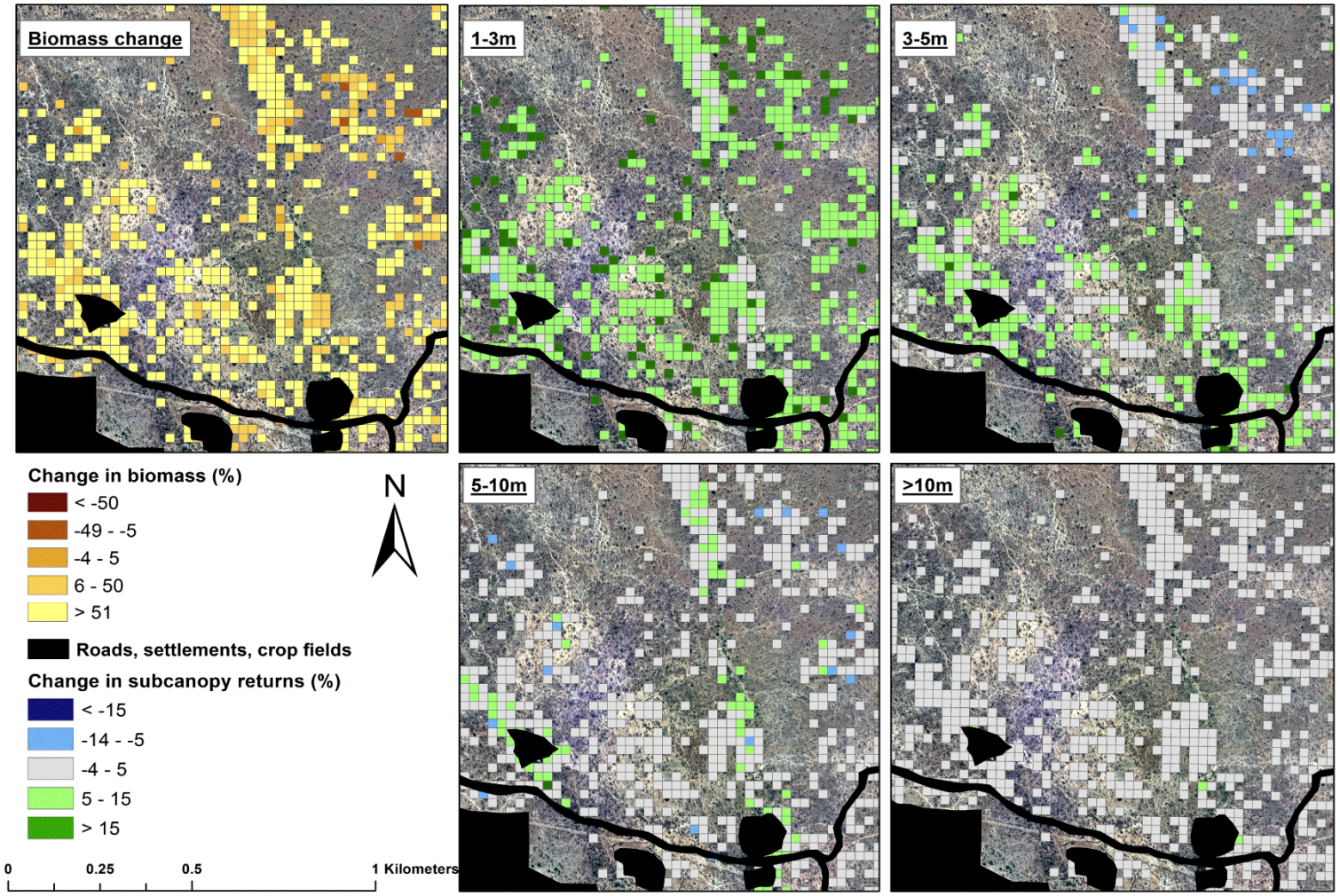
3.11 Supporting Information Captions



Appendix Figure 3.1. Site-specific biomass model residuals. The residual spread demonstrates heteroskedasticity with increasing biomass fitted values for rangelands with a) high, b) intermediate and c) low extraction pressure.



Appendix Figure 3.2. Biomass changes (%) relative to height-specific change in subcanopy returns (%). Height categories are: 1-3 m, 3-5 m, 5-10 m and >10 m.

S1 Dataset. Biomass model data. Data include 2012 LiDAR-derived average height and canopy cover extraction metrics, as well as field-work based allometry. Each line item is per 25 m x 25 m grid cell. Metadata are included in the dataset. [Accessible at http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0127093#sec016.]

S2 Dataset. Biomass and subcanopy data. Data include 2008 and 2012 biomass estimates derived from biomass models as well as % subcanopy returns for voxel data for the height class categories: 1-3m, 3-5m, 5-10m and >10m. Each line item is per 25 m x 25 m grid cell. Data are organized per land extraction category into separate worksheets. Metadata are included in the dataset. [Accessible at http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0127093#sec016.]

S3 Dataset. Biomass changes (Mg ha^{-1}) in relation to relative height and canopy cover change. Data include biomass change estimates (2008-2012), percentage height and canopy cover changes for each 25 m x 25 m grid cell. Each height class (relative to height in 2008) are shown on separate worksheets. Metadata are included in the dataset. [Accessible at http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0127093#sec016.]

Chapter 4: Human-mediated shrub increases in communal lands

4.1 Abstract

Savannas are characterised by growing land-use pressures and this is illustrated by the unsustainable harvesting of fuelwood in South African communal lands. We aimed to establish the spatial extent and intensity of woody biomass and subcanopy vegetation change in relation to anthropogenic and abiotic features of communal lands. Our study sites spanned three communal lands in Mpumalanga, South Africa, across a rainfall and wood extraction gradient. Using light detection and ranging (LiDAR) data, we examined changes in woody biomass and 3-D vegetation structure and demonstrated that bush thickening is exacerbated by anthropogenic factors. Increases in the shrub layer were prevalent in the most accessible portions of the communal lands. A consequence of gains in low vegetation height classes was increased biomass of over 50% between 2008 and 2012. The communal land under low wood extraction pressure had biomass changes occurring spatially as a heterogeneous mosaic at the interactive distances from anthropogenic features, whilst high wood extraction communal lands had 'hotspots' of biomass increases occurring in more easily accessible locations. Lowlands had more bush thickening than uplands, and biomass was three fold greater on granite substrates than on gabbro communal lands. Bush thickening in communal lands is likely a combination of newly established woody encroachers, as well as strong coppice regrowth response in harvested species. The exacerbation of bush thickening in natural resource-dependent communities has implications for sustainable ecosystem service provision and this is explored within the context of a rural, social-ecological system.

4.2 Introduction

In human-utilised landscapes, woody biomass and structure changes may be an expression of natural resource use. Reliance on fuelwood from indigenous woodlands is prevalent in African countries (Soussan 1988; Arnold *et al.* 2003). Despite 66% of South Africa's population having electricity access (Scholes & Biggs 2004), the expected uptake of 'cleaner' energy has not been realised with 54% of South Africans still using wood energy

(Department of Agriculture Forestry and Fisheries 2011). The uptake of fuel-efficient stoves has been low (Williams & Shackleton 2002; Arnold *et al.* 2003) and fuelwood use for cooking can continue for over a decade after initial installation (White *et al.* 1997). It is concerning that household demand for fuelwood in rural areas is relatively inelastic, regardless of the perceived shortages/abundance of fuelwood in the surrounding woodlands (Soussan 1988; Matsika *et al.* 2013). Although the relative contribution of fuelwood to the total household energy pool is expected to decline, absolute growth in population is expected to increase; the FAO (United Nations' Food and Agriculture Organisation) predicted a twenty-five fold increase in wood consumption from 2001 onwards (van Jaarsveld *et al.* 2005). This provisioning ecosystem service is a 'free' service to rural communities, but 93% of current fuelwood demands are no longer met by collection of dead wood (Dovie *et al.* 2004). Thus, live wood harvesting occurs around settlements (Shackleton & Scholes 2011), and various studies have shown that these levels of wood extraction are unsustainable (Banks *et al.* 1996; Wessels *et al.* 2013). Within this context, woodfuel harvesting is a significant driver of woodland degradation in semi-arid ecosystems of southern Africa (Shackleton 1993; Luoga *et al.* 2002; Stringer & Reed 2007). The South African government is aware of the substantial reduction in tree cover in rural woodlands, but this is deemed a 'necessary evil' when woodland utilisation and/or conversion contributes to improved human-welfare; however, in many areas local overharvesting have not led to improvements in human well-being (Ministry of Water Affairs and Forestry 1997; Giannecchini *et al.* 2007), raising concerns on the "poverty-environment trap" where natural resource dynamics are non-linear and the coupled collapse of both human well-being and the natural environment become increasingly likely (World Commission on Environment and Development 1987). Although the use of wood as a predominant energy source is acknowledged in policy and the National Forests Act (Act No. 84 of 1998) stipulates that woodland resources be monitored and managed, there is no landscape-scale data for the status or change in this essential provisioning resource which covers 28 million ha in South Africa (Ministry of Water Affairs and Forestry 1997). Hence, monitoring changes in woody vegetation stocks and structure can thus be considered a viable approach to monitoring the sustainability of rural wood-use.

Bushbuckridge, a former South African 'homeland' is characterised by dense rural population, high unemployment levels, a commensurate reliance on social grants and, despite extensive electrification, dependence on wood energy (Thornton 2002; Kirkland *et al.* 2007). Research from this area has been invaluable in demonstrating that people's socio-economic

status (Twine 2005) and policy decisions (Kirkland *et al.* 2007), as well as fluxes in regional and household level demographics (Twine *et al.* 2003a; Matsika *et al.* 2013) affect vegetation change. These field-based studies revealed that differences were site-specific and often related to population density, land-use intensity and abundance of natural resources (actual as well as perceived) (Shackleton *et al.* 1994; Giannecchini *et al.* 2007).

Here we use repeat airborne, high resolution Light Detection and Ranging (LiDAR) data to explore the change in aboveground woody biomass (hereafter 'biomass') and vegetation subcanopy change in relation to a fuelwood extraction gradient. The LiDAR data span 8 400 ha of communally utilised communal lands across different geologic substrates and a rainfall gradient. We aim to establish the spatial extent and intensity of woody biomass and vegetation change in relation to anthropogenic features (e.g. settlements and roads), as well as the interactions with the abiotic template of the landscape.

4.3 Methods

4.3.1 Study site- political and socio-economic context

The study area is in the north-eastern most portion of the Mpumulanga Province, South Africa (centred on 24.731◦S, 31.181◦E) (Figure 4.1). The three communal lands used in this study are located in Bushbuckridge Municipal District, within the transition zone of the Kruger to Canyons (K2C) Biosphere Reserve (Figure 4.1). Bushbuckridge is surrounded by conservation land (both state-owned and private) with intense pressure for grazing and harvesting occurring outside of these fenced-off conservation concessions (Coetzer *et al.* 2013). Bushbuckridge Municipality is the amalgamation of former South African Apartheid 'homelands' formed under the Native Lands Act (No. 27) of 1913 (Thornton 2002). Although Bushbuckridge is state-owned land, there is customary tenure to the tribal chiefs who determine residential, arable and communal rangeland zoning (Shackleton 2000a). The land-use pattern follows population growth – prior to 1974 there were no patterns to land-use organisation (Matsika *et al.* 2012), but after this, the population increased dramatically to 300 people km^{-2} (Pollard *et al.* 2011). Commensurate with population growth, the spatial footprint of the residential regions have expanded (Giannecchini *et al.* 2007; Coetzer *et al.* 2010), with the previously settlement–specific communal rangeland boundaries coalescing (Coetzer *et al.*

2013). The residential areas are surrounded by a heterogeneous mix of tree-less crop and 'park' land, then a shrubland buffer zone before transition into mixed woodland; as utilisation becomes more intensive and the settlement footprint expands, the land becomes more homogeneous (Matsika 2012).

As over 85% of Bushbuckridge households live below the household subsistence level (Phambili Energy 2009), there is a high level of dependence on the natural resource base. As a result of the dire socio-economic conditions in Bushbuckridge, many households diversify their risk by using a variety of informal activities to supplement their livelihoods, including subsistence-level crop and livestock farming, collection of natural resources (e.g. fuelwood, thatch grass, medicinal plants), casual labour, migrant labour and small-scale ventures (Pollard *et al.* 1998). An increasing activity is commercial harvesting of fuelwood, often with the use of a vehicle to be sold in fuelwood markets (Twine 2005). This has implications for the sustainability of natural resources as it implies that utilisation of the resource is not limited to the region immediately surrounding its source. Much of the natural resource shortages experienced by the local population is being blamed on 'outsiders', especially Mozambican immigrants (Twine *et al.* 2003b). Compounding the problem is that natural resource harvesting used to be restricted by cultural values and tribal authorities, but both these influences have decreased in the context of high demand for woodland products (Higgins *et al.* 1999).

4.3.2 Study site- biophysical characteristics

Bushbuckridge is situated in the savanna Lowveld region and is dominated by Granite Lowveld vegetation, but also contains Gabbro Grassy Bushveld on Timbavati Gabbro outcrops (Rutherford *et al.* 2006). Catenal sequences are distinctive in the area with shallow, dystrophic soils on the uplands and deeper, eutrophic soils on the lowlands (Rutherford *et al.* 2006). The common vegetation species include: *Terminalia sericea, Combretum zeyheri* and *C. apiculatum* on the sandy uplands, and *Acacia nigrescens, Dichrostachys cinerea* and *Grewia bicolor* on the clayey lowlands (Rutherford *et al.* 2006).

Mean annual temperature is 22 °C with, mean daily maxima of 30 °C in summer and 23 °C in winter. Mean annual precipitation (MAP) ranges from > 900 mm in the west to 500mm in the east, falling predominantly in summer (October to May), with a MAP coefficient of variation of 25% (Wessels *et al.* 2011) and decadal drought events (Matsika *et al.* 2012).

Although the tribal chiefs are given tenure of the communal lands and they are predominantly used by their surrounding villages, they are by no means exclusive areas and can be accessed by outsiders, both South Africans from surrounding areas and immigrants from other countries, who do not respect local tribal law (Twine 2005). Natural resource usage between the communal lands can be inferred by the number of people and households utilising each site relative to their communal land extent. These data show that, according to baseline 2008 demographic information, the communal land for Ireagh, Kildare and Liliydale has the highest natural resource usage (9.2 people ha^{-1}, 1.56 households ha^{-1}) (Figure 4.1). The lowest natural resource utilisation is the communal land used by Agincourt and Xanthia (0.21 people ha^{-1}, 0.04 households ha^{-1}) and intermediate usage in Justicia's communal land (1.8 people ha^{-1}, 0.35 households ha^{-1}) (see Fisher *et al.* 2012 for detailed demographic data). The intermediate use communal land is used exclusively by one settlement, Justicia, and is bounded on two sides by a private conservation fence and has a remote location relative to the other settlements. The fences and location of the rangeland ensure local traditional authorities can, as a rule, maintain Justicia's exclusive access (Tuinder 2009; Wessels *et al.* 2013). In contrast, the high use communal land is surrounded by Croquetlawn, Ireagh A, Ireagh B, Kildare A, Kildare B and Kildare C (Figure 4.1) and is utilised in all directions by all of these settlements, hence Fisher *et al.* (2011) found a reduction in disturbance gradients in this relatively small, heavily utilised, site.

4.3.3 Light detection and ranging (LiDAR) data

The Carnegie Airborne Observatory (CAO) (https://cao.carnegiescience.edu/) conducted repeat airborne LiDAR campaigns across savanna woodlands in the South African Lowveld in April 2008 and 2012. The time series data were collected in April to coincide with reduced grass biomass, but before deciduous savanna trees lose their leaves, in order to maximise ground and woody vegetation return accuracy. Ground validation of the vegetation heights was conducted concurrently with the airborne LiDAR campaigns. The 2008 LiDAR data were collected with the CAO Alpha system, using a LiDAR scanner flown 2000 m above ground level, with laser pulse repetition rate of 50 kHz, providing 1.1m laser spot spacing (for technical details, see Asner *et al.* 2007). The 2012 LiDAR were collected with the CAO-2 AToMS (Airborne Taxanomic Mapping System) scanner with a laser pulse repetition of 100 kHz and laser spot spacing of 1m (for technical details, see Asner *et al.* 2012).

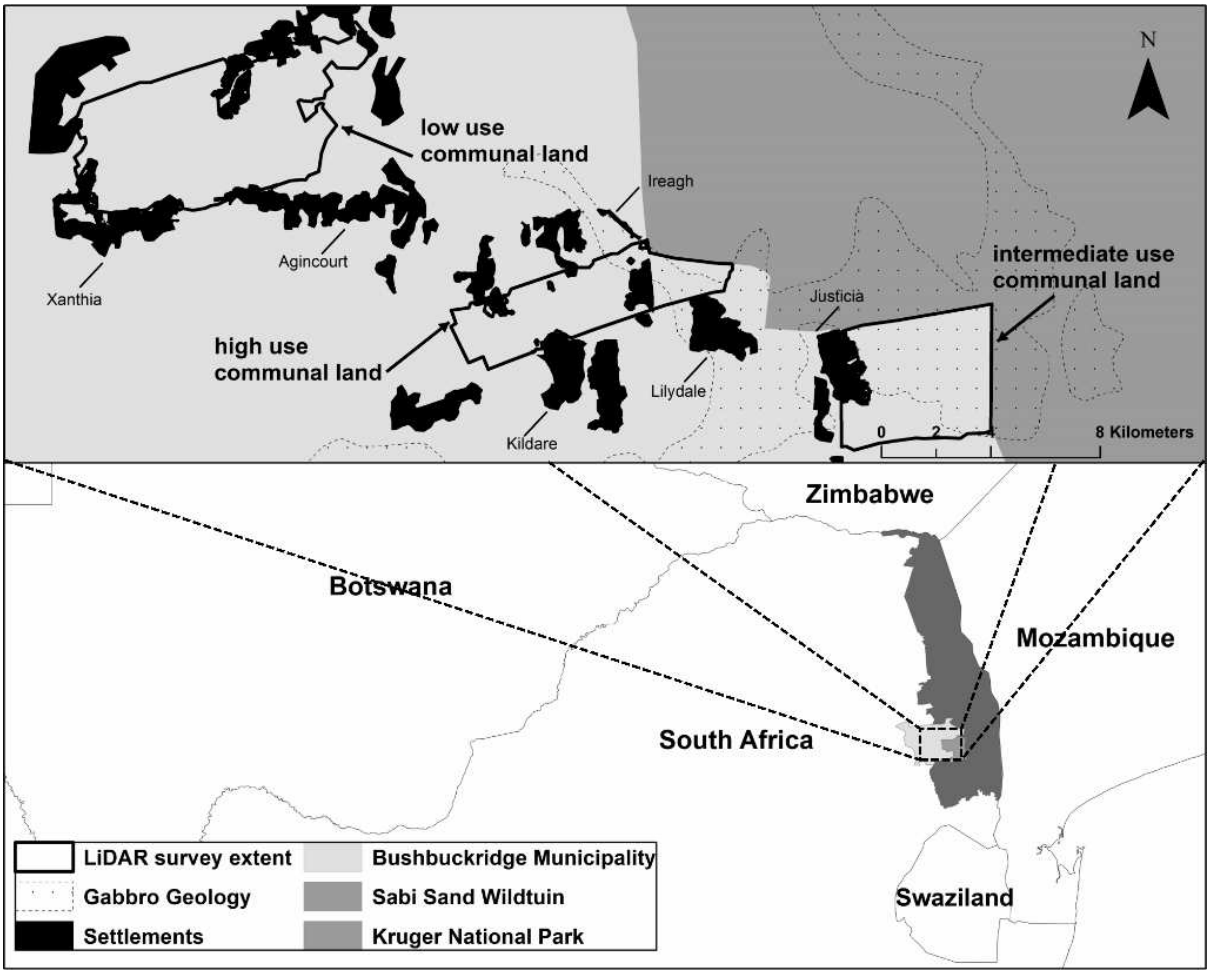


Figure 4.1. Study sites in Bushbuckridge Municipality, west of Sabi Sand Wildtuin (a private reserve) and the Kruger National Park. Settlements use adjacent communal lands. The names of major settlements are included in the map. The geology is predominantly granite, but gabbro outcrops are shown.

The LiDAR scanners contained an integrated Global Positioning System-Inertial Measurement Unit (GPS-IMU), providing precision 3-D location and geographic projection of the laser data. The coarser of the two scanners had a vertical accuracy of <0.20 m vertically and <0.36m horizontally (Asner *et al.* 2009). The LiDAR data provide high resolution three-dimensional mapping of ecosystem structure, as well as high resolution digital terrain models (DTM) at the regional scale. Although different sensors and processing methods were used for the 2008 and 2012 data, errors between corresponding DEMS were < 15cm.

LiDAR data are collected as a dense three-dimensional x-y-z point cloud. DTM's are interpolated from the ground returns, whilst digital surface models (DSM) are interpolated

from the first returns (i.e. the top of the vegetation canopy), using REALM™ (Optech®) and Terrascan/Terramatch (Terrasolid™) software packages. The canopy height model (CHM: 1.12m resolution in 2008 and 1m resolution in 2012) is the difference between the DSM and the DTM. The CHM model provides the highest value (m above the ground) in each pixel and can be used as a representation of the size class distribution of the woodland.

The x-y-z laser point cloud enables quantification of the vertical vegetation structure at landscape scale, through rendering of pseudo-waveform profiles in which vertical returns are aggregated into 1 m bins (Weishampel *et al.* 2000). These then form voxels (volumetric pixels) of 5 m x 5 m spatial resolution, and 1m vertical resolution. The position of each voxel within the vertical vegetation column is defined from the centroid of the voxel relative to the ground. The frequency of LiDAR returns (points) within the voxel were normalised relative to the total number of LiDAR returns in the column, including the ground returns, as a percentage (%).

4.3.4 Field-based biomass and LiDAR-derived biomass models

Field-based biomass was estimated using 25 m x 25 m plots (n = 56) located within the extent of the LiDAR time series collection in the Bushbuckridge communal lands. All woody vegetation > 1.5m in height and > 5cm basal diameter were inventoried. These data were then used in the form of Colgan *et al.*'s (2013) plot-level allometric equations, derived from an extensive biomass harvesting effort in the South African Lowveld; the woody species community composition and structural growth form in our Bushbuckridge study matched those in Colgan *et al.*'s (2013) research, making their allometric relationship form an ideal one for this study. Details on the allometric equations used and the implications for accuracy and bias can be found in Colgan *et al.* (2013) and Mograbi *et al.* (2015).

The methods for LiDAR-derived biomass estimations were based on plot-level H x CC methods (see Mograbi *et al.* (2015)). Briefly, we used the field-derived plot-level biomass to calibrate LiDAR-derived biomass models. A H x CC LiDAR metric was used, where H is mean top of canopy height for each plot and CC is the proportion of canopy cover for each plot, both metrics were derived from the CHM. These models accounted for 78%, 60%, and 68% of the variance for high, intermediate, and low use sites, respectively (Mograbi *et al.* (2015). Site-specific biomass models performed better than a general biomass model and more accurately represents the different environmental and anthropogenic variables that these

communal lands experience. This has the advantage of more ecologically meaningful biomass models as well as maximising the amount of variation explained by the models. The heterogeneity inherent in savannas (Pickett *et al.* 2003) contributes to variation in vegetation structure and environmental variables which affects biomass error values (Colgan *et al.* 2013). The high extraction communal land has the highest amount of biomass explained by the model as the reduction in tall trees and abundance of shrubs result in a more homogeneous landscape that is easier to model (Mograbi *et al.* 2015). The LiDAR biomass models were then applied to LiDAR HxCC maps for 2008 and 2012 to create site-specific extrapolations. A height mask of >1.5 m was applied to the biomass maps to remove the possibility of ground and grass being misclassified as woody vegetation. In addition to the height mask, riparian areas adjacent to rivers were removed from the biomass maps as they require separate model calibration. Similarly, settlement and crop-farming areas were also removed.

4.3.5 Subcanopy structure derivation

Voxel data were resampled from 5 m x 5 m x 1 m to 25 m x 25 m x 1 m. Thus, each bin represents the height-specific structural density of the vegetation subcanopy, hereafter referred to as "subcanopy structure returns" reported as %. The 'total canopy structure' refers to the sum of the stacked 1 m voxels above 1m in height (i.e. excluding ground returns) and represents the structure of the total vegetation column.

4.3.6 Abiotic and anthropogenic variables

In order to relate the biomass and subcanopy structure change to environmental and anthropogenic variables, we selected those based on the data available and whether they had featured in previous studies on woody biomass and vegetation structure in the regional communal rangeland context (e.g. Shackleton & Scholes 2011; Fisher *et al.* 2012) for the purposes of comparison. We also included distance from the nearest road because of the increased access to resources and use of vehicular transport in the communal lands (Luoga *et al.* 2000; Twine *et al.* 2003b) which could have an effect on patterns of natural resource use. Distance classes were created as buffer zones radiating out from settlement areas and roads in classes of 200m until the extent of the communal lands. The high use communal land is

surrounded by settlements, thus the distance classes became circular with the furthest distance class as the midpoint between all the settlements. Upland and lowland sites were manually digitised using a combination of: winter SPOT™ 5 image (2.5 m spatial resolution); a normalised height model (generated from the 2008 DTM using SAGA™ v.2.0.6 (SAGA User Group Association); a relative elevation model (based on a Topographic Position Index (Jenness 2006)); river and drainage lines; and a slope model (Spatial Analyst tool in ARCMap™ v10.1 (ESRI® 2010). The outputs were visually verified by the presence of termite mounds in the 2008 CAO DTM's on uplands (Levick *et al.* 2010). Slope position was not classified on the intermediate use communal land as gabbro has more subdued topographic relief relative to granite. All data analyses were performed in Rv3.0 (R Core Team 2013). Contour plot interpolations were performed using the 'akima' package.

4.4 Results

4.4.1 Regional biomass dynamics

Biomass on gabbro sites was substantially lower (9-15 Mg ha^{-1}) than on granite sites (21-45 Mg ha^{-1}). The intermediate use communal land had the highest standing biomass (2008: 27 Mg ha^{-1}; 2012: 45 Mg ha^{-1}) and was located midway along the rainfall gradient. This was also the site with the highest increase in biomass (Table 4.1). Thus, biomass standing stocks and absolute change were related to geology, and mediated by land-use intensity (Table 4.1). Relative biomass change followed the land-use gradient, with the highest increases in the high use communal land (Table 4.1).

4.4.2 Local biomass dynamics

The communal land-specific trends for biomass were analysed relative to the closest distance from roads and settlements. Overall, biomass increased between 2008 and 2012 regardless of the distance from the nearest settlement (Figure 4.2a). In the intermediate use communal land, biomass increased from 200 m away from the settlement and peaked at 1 km (Figure 4.2a). In the high extraction site in 2008, biomass decreased from 200 m (25 Mg ha^{-1} to 22 Mg ha^{-1}) away from the settlements and then increased gradually; however, in 2012 the initial

standing stocks spiked downward within 200m from the settlements and then gradually increased on a similar trajectory to the 2008 increases (Figure 4.2a).

Table 4.1. Biomass (mean ± SD) (Mg ha^{-1}) and biomass change for the Bushbuckridge study sites, including differences in geology, rainfall and land-use gradients. n refers to number of grid cells.

	Wood extraction level		
	high (n = 102)	**intermediate (n = 291)**	**low (n = 1654)**
Geology	Granite	Gabbro	Granite
Rainfall	semi-mesic	semi-arid	mesic
2008 Biomass	27.0 ± 16.4	9.4 ± 4.1	21.2 ± 12.0
2012 Biomass	45.4 ± 28.4	14.9 ± 6.8	32.5 ± 17.6
Biomass change (absolute)	18.4*	5.5*	11.3*
Biomass change (relative)	68%	58%	53%

*Denotes significant difference ($p<0.001$) between biomass estimates within sites between 2008 and 2012 using a non-parametric Wilcoxon rank sum test.

Biomass distribution trends with increasing distance from the nearest road were different. Although biomass increased in all sites between 2008 and 2012, there were no changes in its distribution relationship to distance from road (Figure 4.2b). Biomass changed the most in the high extraction site where biomass peaked from 1.2 km from the nearest road (Figure 4.2b).

Biomass distribution over time at different hillslope positions showed large biomass increases on the high use site's lowlands, while no clear trends in biomass change were evident in the low use communal land (Figure 4.2c).

4.4.3 Local vegetation structural dynamics

The distributions of the total canopy structure were, initially, similar in the low and intermediate use sites - a slight increase in total canopy returns with increased distance from settlement (Figure 4.3a). However, the total subcanopy returns in the intermediate use communal land decreased from 2.6 km away from the settlement until the boundary of the

rangeland (Figure 4.3a). These two sites were also alike when comparing total vegetation canopy return trends between 2008 and 2012. Both the low and intermediate use sites had largely unchanged distribution shapes with increased distance from settlement, except for the last 600m in the intermediate use communal land where the marked decline matched the 2008 trajectory (Figure 4.3a). The high use communal land showed the most altered total canopy returns gradient over time (Figure 4.3a) – the 2012 total canopy returns increased with distance from settlement at a steeper gradient than the 2008 canopy returns distribution (Figure 4.3a).

Total canopy returns can be deconstructed into the height-specific returns partitioned within the vegetation column (Appendix Figure 4.1-3). Trends in total canopy returns for intermediate and high use communal lands (Figure 4.3a) were explained by increased subcanopy returns in the 1-3m height class (Appendix Figure 4.1a-b). This was less evident in the low use communal land where the increased total canopy returns gradients (Figure 4.3a) were associated with small increases in canopy returns in all subcanopy height classes (Appendix Figure 4.1c). Although total canopy returns increased in all sites with increased distance from roads, there was little change in return gradients between 2008 and 2012 (Figure 4.3b). In 2008, the high use site had increased total canopy returns from 1 km from the nearest road; this distance increased to 1.2 km in 2012 (Figure 4.3b). Most of these increases were attributable to increased subcanopy returns in the 1-3m height class and, to a lesser degree, in the 3-5m height class (Appendix Figure 4.2b). Although the intermediate use site had increased subcanopy returns in the 1-3m height class, and the low use site had increases across all height classes (Appendix Figure 4.2a,c), these changes were not expressed in the gradients of the total canopy returns with increased distance from the nearest road (Figure 4.3b).

The relationship between total canopy returns and hillslope position (Figure 4.3c) was similar to that of biomass and hillslope position (Figure 4.2c); the large increases in biomass in the high use site's lowlands were associated with less pronounced changes in total canopy returns (Figure 4.3c). The increases in total canopy returns in 2012 for the high use site's lowlands (Figure 4.3c) were related to higher subcanopy returns in the 3-5m height class (Appendix Figure 4.3a). There were also noteworthy subcanopy return increases in the 1-3m height class on the high use site's uplands (Appendix Figure 4.3a). In contrast, the low use communal land had an even distribution of subcanopy returns for all height classes and across all hillslope positions (Appendix Figure 4.3b).

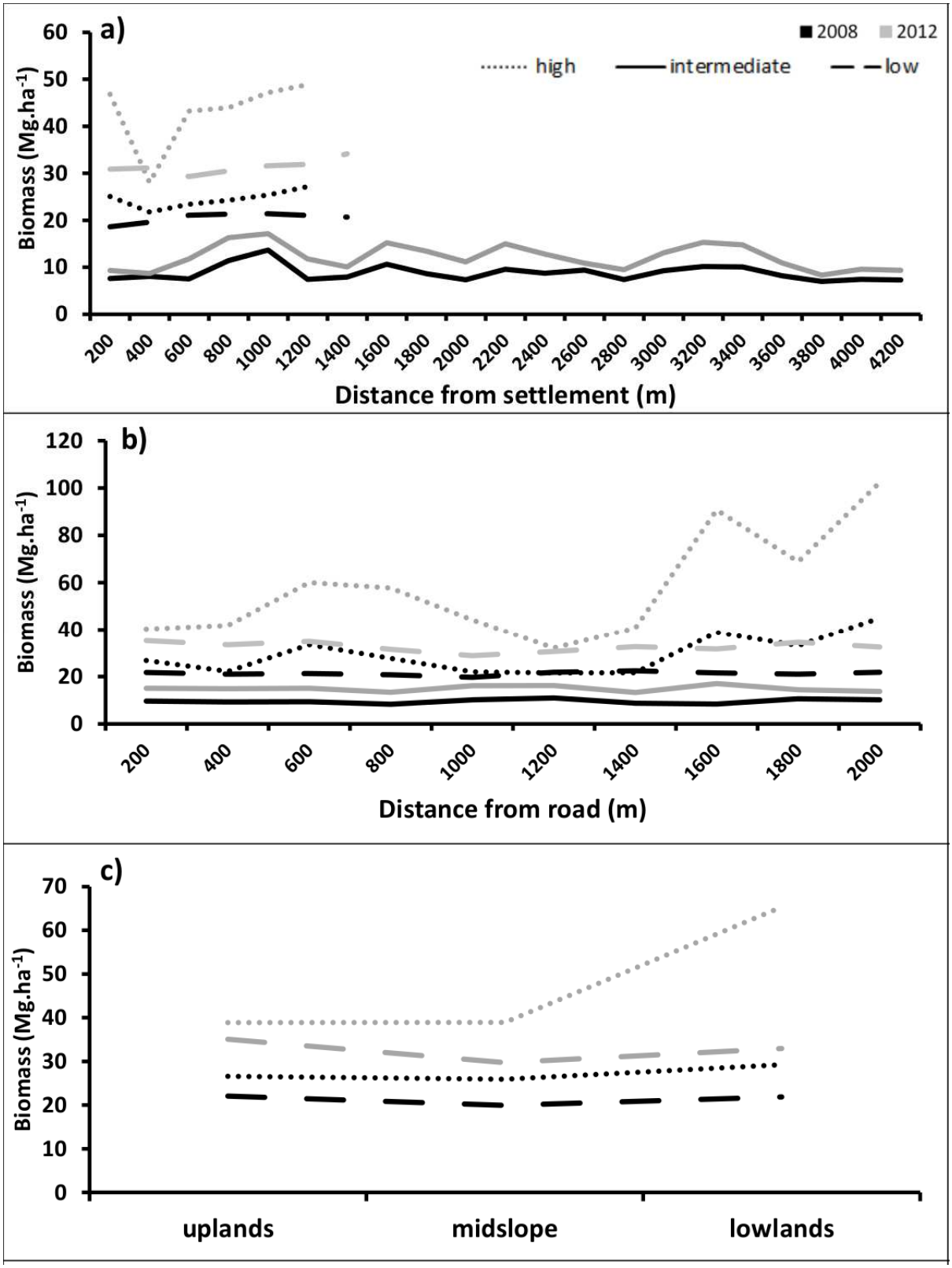


Figure 4.2. Biomass (Mg ha^{-1}) for 2008 and 2012 for three sites in Bushbuckridge along a usage gradient relative to: a) distance from the nearest settlement in 200 m increments, b) distance from the nearest road in 200 m increments, and c) hillslope positions situated on granite (the intermediate wood extraction communal land is on gabbro geology which has less pronounced catenal sequences).

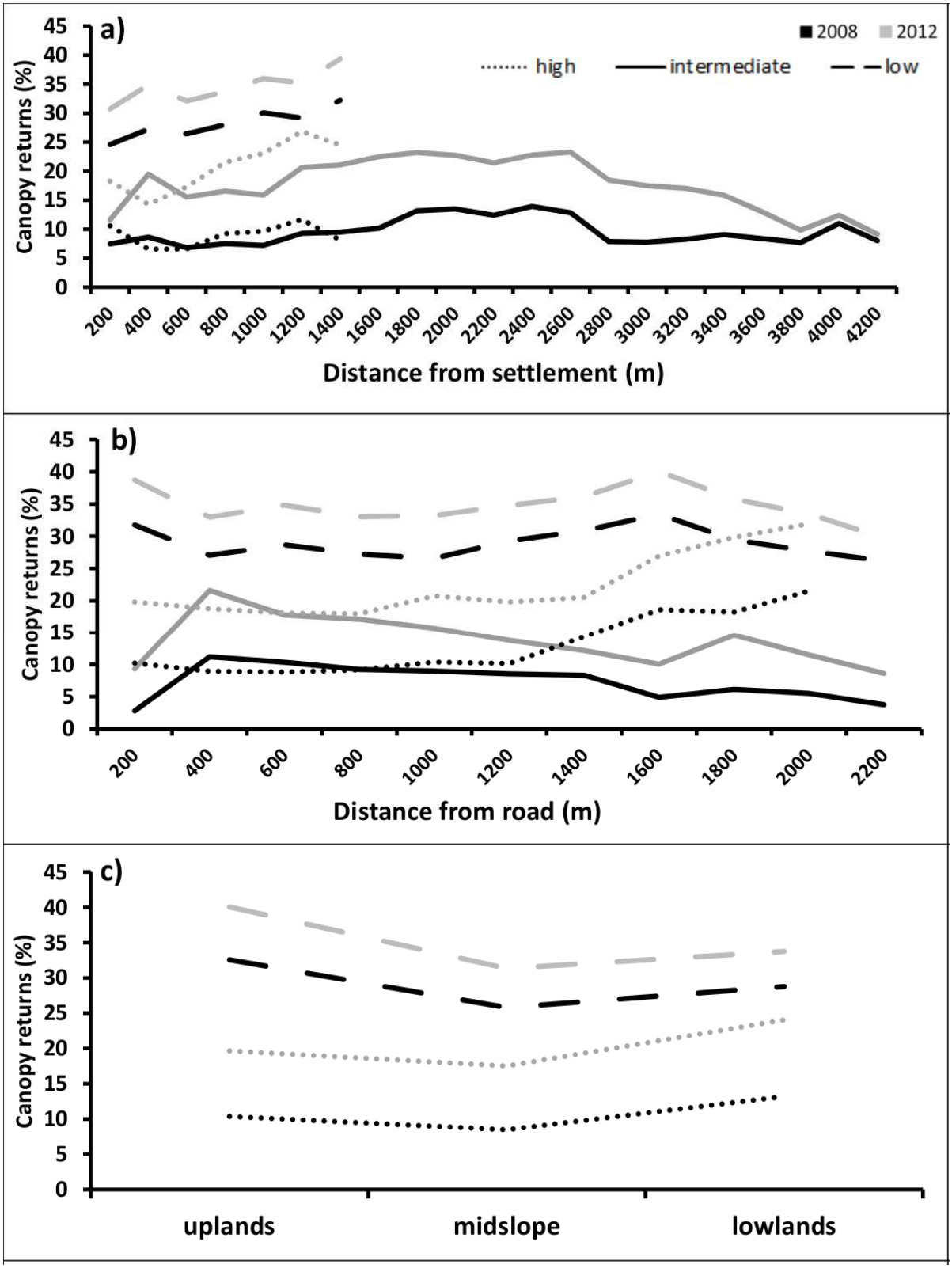


Figure 4.3. Canopy returns (%) for the total vegetation column for 2008 and 2012 for three sites in Bushbuckridge along a usage gradient relative to: a) distance from the nearest settlement in 200 m increments, b) distance from the nearest road in 200 m increments, and c) hillslope positions situated on granite (the intermediate wood extraction communal land is on gabbro geology which has less pronounced catenal sequences).

4.4.4 Biomass and subcanopy structural change were associated

Biomass change was linked to subcanopy returns, such that as biomass increased so did subcanopy returns in all height classes with the exception of >10m (Table 4.2). The association between biomass and subcanopy structure was strongest in the 1-3m and 3-5m height categories in the intermediate use site, and the 3-5m categories in the high and low use sites (Table 4.2). Subcanopy returns >10m in height were not associated with biomass and subcanopy structure change (Table 4.2).

Table 4.2. Correlations between changes in biomass (%) and height-specific subcanopy returns (%) for each communal land ($p < 0.001$ for all correlations). n represents the number of grid cells.

	Wood extraction level		
Height Classes	**high** **r** **(n= 102)**	**intermediate** **r** **(n=291)**	**low** **r** **(n = 1654)**
1-3m	0.22	0.58	0.08
3-5m	0.62	0.64	0.56
5-10m	0.37	0.37	0.32
>10m	0.09	-0.08	0.01

The association between biomass and the spatial intersection of distance from the nearest road and distance from the nearest settlement in the intermediate use communal land showed a 'hotspot' of biomass increase within 1 km of both surrounding settlements and roads (Figure 4.4A). The biomass hotspot in the intermediate use site matched the subcanopy returns hotspot for 1-3m (Figure 4.4B), but less so for the 3-5m and 5-10m height categories (Figure 4.4). There was a prominent spread of biomass increases in the high use communal land within 400 m of the surrounding settlements and at all distances from roads (Figure 4.4C). The high use site's biomass hotspot most closely matched the spatial location of the 3-5m subcanopy return increases (Figure 4.4D) and this was supported by the relatively strong correlation ($r=0.62$; $p<0.001$). Both the biomass and subcanopy structural change across all

height classes were spatially variable for the low use communal land, forming a mosaic of different values without coalescence between patches (Figure 4.4E). An association can be made between the intensity (colour) and the degree of consolidation of biomass increases (spread) of biomass change hotspots and the wood extraction pressure for each communal land (Figure 4.4).

4.5 Discussion

At the communal land-scale, anthropogenic influences on biomass and vegetation structure were evident. This is particularly true for the high use site where the trajectory of biomass and total canopy structure returns increased with distance from settlements in 2012 (Figure 4.2a and Figure 4.3a). The distribution of biomass and total canopy returns for the intermediate use communal land was lower both close to and furthest from the settlement (Figure 4.2a and Figure 4.3a), along the boundary fence with Sabi Sands Wildtuin on the east (Figure 4.1). This trend reflected vegetation clearing for cultivation west of the border, both because villagers believed cultivation along the fence line would reinforce their ownership to land they felt might be incorporated into the eastern conservation areas, as well as because they perceived this area to be good for cultivation (Tuinder 2009). In addition, the north-east corner of the intermediate use communal land has higher abundance of *Acacia nigrescens* than the surrounding land; villagers perceptions are that this location has a high abundance of fuelwood and thicker stems used for construction poles (Tuinder 2009). This section of the communal land is accessible along the fence from the main road in the south and harvesting by outsiders is becoming increasingly common in Bushbuckridge (Twine *et al.* 2003b). As biomass change and vegetation subcanopy structure were positively associated (Mograbi *et al.* 2015), we can relate biomass increases in this context with increasing subcanopy returns in the 1-3m height class. Indeed, 79% of change in the vegetation subcanopy in the high use communal land can be attributed to the 1-3m height class (Mograbi *et al.* 2015). Shrub-level increases, in a communal land context, could be related to coppice-response (from harvesting) (Shackleton 2000b; Kaschula *et al.* 2005a; Neke *et al.* 2006) or bush encroachment (Miller & Wiegand 1994; Archer *et al.* 1995; Scholes & Archer 1997).

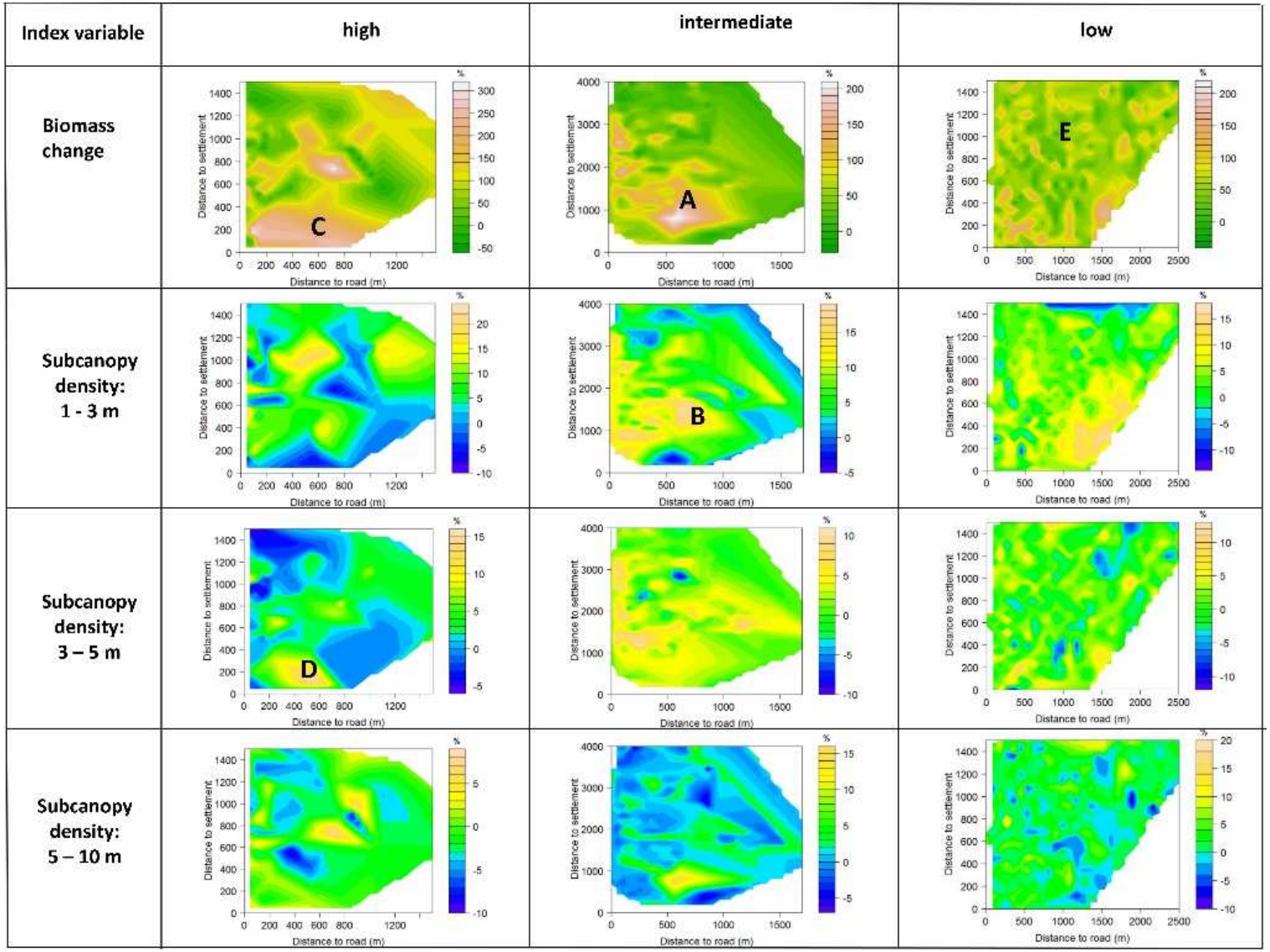


Figure 4.4. Changes in biomass (%) and/or height-specific subcanopy returns (%) along a wood extraction gradient relative to the intersection between distance to the nearest roads and settlements for each communal land. The index bar on the right of each graph provides a gradient of change for each variable. 'Hotspots' of high increases in biomass/subcanopy returns are indicated by warm colours. Letters A-E mark regions of interest that are referred to in-text.

Conclusions based solely on the influence of local anthropogenic variables on rangeland stocks and structure in a pair-wise, univariate manner do not fully reveal the interactive effects between anthropogenic variables. Biomass 'hotspots' were revealed in the spatially-explicit intersection between distance from settlement, distance from road and biomass change (Figure 4.4). In the high use communal land, the biomass 'hotspot' was a large, cohesive area of about 0.4 km^2 within 1km from the settlement and the nearest roads (Figure 4.4C). Thus, vegetation changes were most related to accessibility within the landscape (Soussan 1988; Luoga *et al.* 2002). Spatially-similar hotspots occurred in the subcanopy structure returns of the 1-3m (Figure 4.4B) and 3-5m height classes, reinforcing the association between biomass increases and increases in shrub level vegetation as well as explicitly tying these vegetation changes to proximity to anthropogenic features. Both distance from roads and from settlements affects people's perceptions of distance and representing these interactive processes demonstrates how people make complex trade-offs in their decision-making (Arnold *et al.* 2003; Giannecchini *et al.* 2007). The expanding use of wheel barrows and vehicles to collect fuelwood (Twine 2005; Madubansi & Shackleton 2007) would require people to utilise a combination of distance trade-offs to maximise gain for effort expended.

Comparison of the biomass hotspots between the communal lands reveals their position on the 'coalescence continuum' was in the same order as the utilisation pressure on the rangeland (Figure 4.4). The highly utilised communal land has one, dominant biomass 'hotspot' of 0.72 km^2 very close to the settlement regardless of distance from roads (Figure 4.4C); the intermediate use site has a smaller, cohesive 'hotspot' of 0.4 km^2 within 1km from the settlement and 600 m from a road (Figure 4.4A); whilst the least utilised communal land has a mosaic of different biomass changes scattered across the interactive anthropogenic distance map (Figure 4.4E). These patterns show how highly utilised communal lands functional response becomes homogenised in response to an evenly distributed disturbance. In the case of less (or more recently) disturbed communal lands, the patterns of biomass 'hotspots' could be temporally dynamic, shifting with changing extraction patterns (e.g. introduction of a new road) or as patches recover from previous disturbances. Research on Tanzanian miombo woodlands have demonstrated that woodlands used for wood extraction over a long period (1964-1996) were converted to shrubland, whilst those woodlands under more recent anthropogenic pressure with the construction of the Dar-es-Salaam-Morogoro highway showed different structural characteristics (Luoga *et al.* 2005). It would be

beneficial to track these patterns over time to better understand shifting patterns of utilisation and ecosystem functional response to disturbance.

In Bushbuckridge, disturbance gradients relative to distance from the nearest settlements have been identified with reference to change in community composition, woody size structure and biomass (e.g. Shackleton *et al.* 1994; Higgins *et al.* 1999; Matsika *et al.* 2012). Fisher *et al.* (2011) recorded an example of high utilisation in a small rangeland surrounded by settlements and suggested in situations like these, a decline in disturbance gradients could be construed as a precursor to degradation. Although this theory might hold in special cases, it seems that this particular scenario was temporally dynamic. We also found that the high use communal land had no disturbance gradient in 2008 (Figure 4.3a), but in 2012 the disturbance gradient had clearly steepened with increased distance from settlement (Figure 4.3a). In the absence of subcanopy information (Appendix Figure 4.1-4.3), we could infer that the increases in trajectories of biomass or total canopy change away from settlements and roads were indicative of a reduction in harvesting pressure. The subcanopy information reinforces that the "woodland recovery" is low level shrub gains. This is not an isolated case where more disturbed landscapes have a higher density of woody plants (Skarpe 1990; Archer *et al.* 2001; Asner *et al.* 2003). Bushbuckridge has an extensive land-use history of cattle ranching, from dense colonization in the early 1900's until the 1970's (Shackleton & Scholes 2011), and rural livestock herds after the Promotion of Bantu Self-Government Act of 1959 forced black South Africans to live in 'homelands' (Pollard *et al.* 2003). It is possible that past bush encroachment in Bushbuckridge has been suppressed by woodfuel harvesting. Yet, wood harvesting can paradoxically also exacerbate bush thickening as many of the harvested savanna species have strong regenerative responses (Bond & Midgley 2001; Kaschula *et al.* 2005b). Not only is coppice regrowth an important survival strategy for regenerating woodlands, the resprouted stems may provide a valuable source of future harvestable biomass (Shackleton 2000b; Twine & Holdo 2016). There is, however, little information on coppice regrowth rates and response to continued harvesting as well as whether the regrowth is of sufficient quality for fuelwood.

On a landscape scale, we expected higher biomass distribution on granitic parent material than gabbro (Venter *et al.* 2003); but within that constraint, biomass was anticipated to be greater on the mesic side of the rainfall gradient (Sankaran *et al.* 2005). However, not only did the high use communal land have higher biomass than a site with low wood harvesting intensity despite lower rainfall, the higher use site also showed the greatest increase in

biomass between 2008 and 2012 (Table 4.1). It is unlikely that biomass increases between 2008 and 2012 were driven by rainfall, as the 2008/2009 and 2009/2010 rainy seasons had below average rainfall ('average' here defined as the mean rainfall between 1971 - 2000). Hillslope position influenced biomass stocks and structural change on a local level, but to a far lesser degree than anthropogenic variables. Biomass distribution as a function of hillslope position, in the granitic communal lands, showed very little difference between uplands and lowlands, except in the high use communal land (Figure 4.2c). This is in contrast to previous lowveld studies that found hillslope position had a greater influence on vegetation patterns than distance from settlement (Higgins *et al.* 1999; Fisher *et al.* 2012). We found very little difference in biomass between uplands and lowlands and no change in the trajectory between 2008 and 2012, except for a uniform increase in biomass across the hillslope profile (Figure 4.2c). The exception to this is the high use communal land which had a substantial increase in the lowlands by 2012 (Figure 4.2c), especially in the 1-3m and 3-5 m subcanopy structure classes (Appendix Figure 4.3a). This is suggestive of an interactive influence between hillslope position and unsustainable natural resource use driving bush thickening. An interesting conjecture is that bush thickening occurred evenly on both up- and lowlands in the high use communal land, but as uplands are usually utilised more intensively (Higgins *et al.* 1999), the lowland bush thickening is more evident.

The increased spatial coalescence of biomass and the associated subcanopy structure changes in high wood extraction landscapes are indicative of the expanding footprint of natural resource use. Bushbuckridge landcover change studies have shown that rangeland boundaries are becoming indistinguishable from surrounding landcover (Coetzer *et al.* 2013). The impacts of natural resource use are such that the communal lands are no longer restricted to their associated settlements and are becoming consolidated into a homogeneous area (Matsika *et al.* 2012; Coetzer *et al.* 2013); the likelihood of 'spatial spillovers' increases in amalgamated communal lands as ecosystem functioning in surrounding conservation land is influenced by the unsustainably used adjacent spaces (Barrett *et al.* 2011). Unfortunately, the rural poor are disproportionately affected by the condition of their natural resource base. Although woody stocks appear to have increased, we do not know whether these shrub-level increases would be useful in a natural resource context in the long-term.

Our results suggest that the woody structure dynamics have shifted from a system that previously suppressed bush encroachment, to a system undergoing rapid woody thickening. These results are supported by revised fuelwood supply-demand models that include size-

class specific growth rate data together with dynamic harvester responses (Twine & Holdo 2016). The updated Twine and Holdo (2016) model suggest fuelwood harvesting drives tree resprouting, offsetting losses in extracted biomass and, potentially, maintaining the sustainability of the coupled human-environment system. Tredennick and Hanan (2015) also show that fuelwood harvesting is sustainable except under the most extreme extraction scenarios, mostly as a result of strong regrowth responses of savanna tree species. It is likely that the regrowth responses of certain savanna species will be strengthened in the CO_2-enriched future (Hoffmann *et al.* 2000; Kgope *et al.* 2009; Bond & Midgley 2012).

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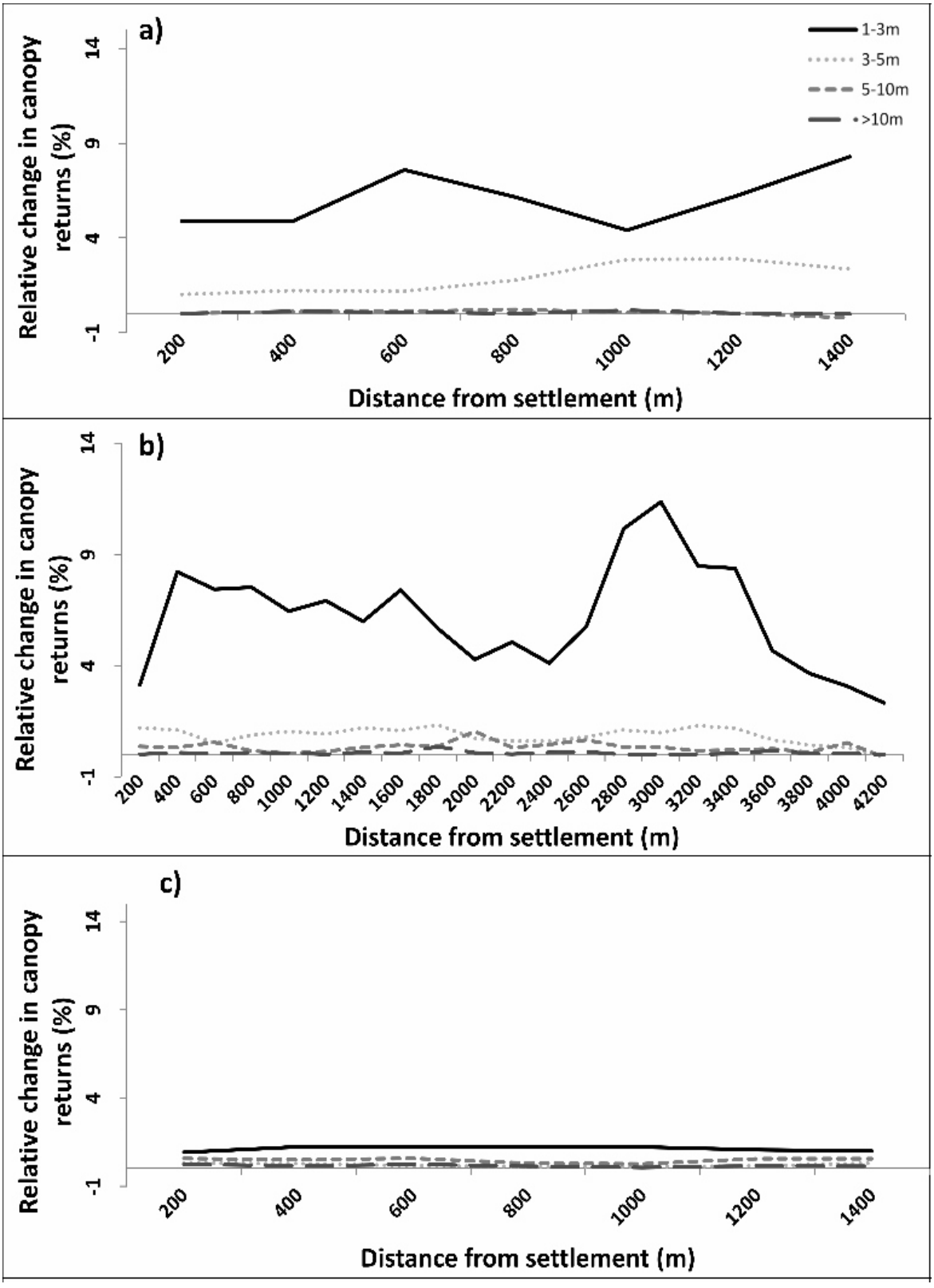
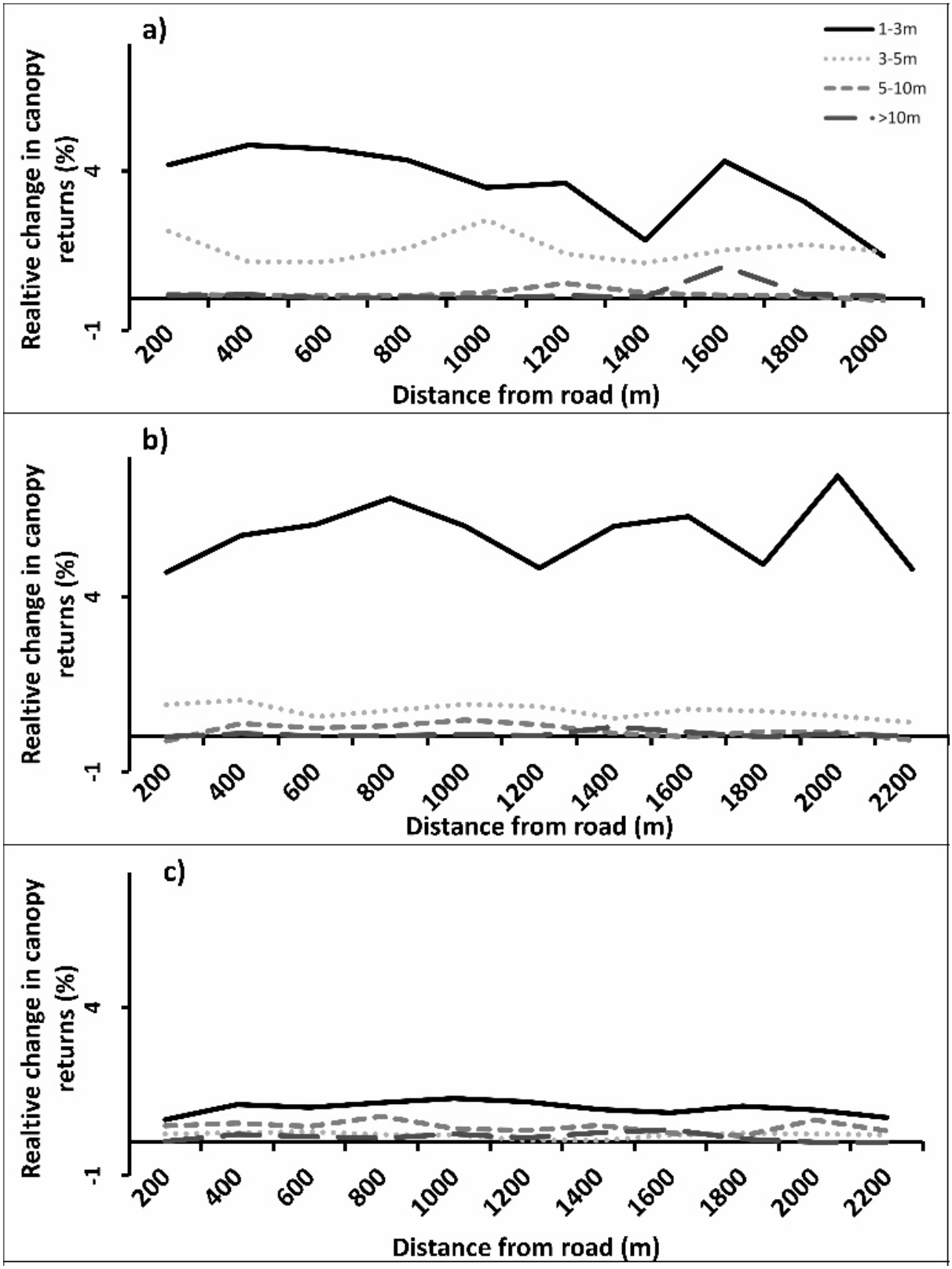
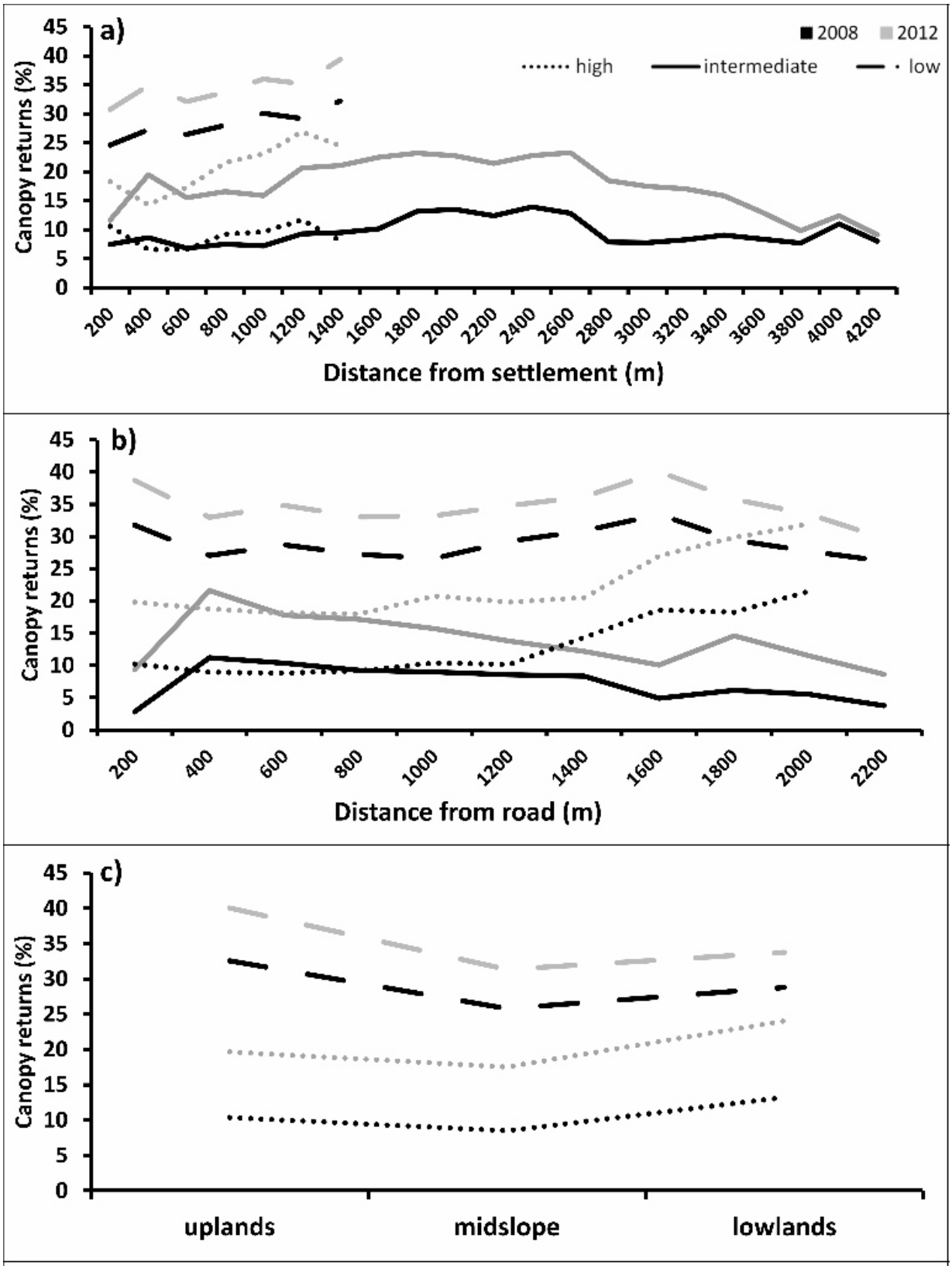
4.7 Appendices



Appendix Figure 4.1. Height-specific relative change in subcanopy returns (%) between 2008 and 2012 with increasing distance from the nearest settlement, for a) high, b) intermediate, and c) low wood extraction communal lands.



Appendix Figure 4.2. Height-specific relative change in subcanopy returns (%) between 2008 and 2012 with increasing distance from the nearest road, for a) high, b) intermediate, and c) low wood extraction communal lands.



Appendix Figure 4.3. Height-specific relative change in subcanopy returns (%) between 2008 and 2012 in relation to hillslope position, for a) high, and b) low wood extraction communal lands.

Chapter 5. Humans and elephants as treefall drivers in African savannas**

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5.1 Abstract

Humans have played a major role in altering savanna structure and function, and growing land-use pressure will only increase their influence on woody cover. Yet humans are often overlooked as ecological components. Both humans and the African elephant, *Loxodonta africana*, alter woody vegetation in savannas through removal of large trees and activities that may increase shrub cover. Interactive effects of both humans and elephants with fire may also alter vegetation structure and composition. Here we capitalize on a macroscale experimental opportunity - brought about by the juxtaposition of an elephant-mediated landscape, human-utilized communal harvesting lands and a nature reserve fenced off from both humans and elephants - to investigate the influence of humans and elephants on height-specific treefall dynamics. We surveyed 6 812 ha using repeat, airborne high resolution Light Detection and Ranging (LiDAR) to track the fate of 453 685 tree canopies over two years. Human-mediated biennial treefall rates were 2-3.5 fold higher than the background treefall rate of 1.5% treefall ha^{-1}, while elephant-mediated biennial treefall rates were 5 times higher at 7.6% treefall ha^{-1} than the control site. Model predictors of treefall revealed that human or elephant presence was the most important variable, followed by the interaction between geology and fire frequency. Treefall patterns were spatially heterogeneous with elephant-driven treefall associated with geology and surface water, while human patterns were related to perceived ease of access to wood harvesting areas and settlement expansion. Our results show humans and elephants utilize all height-classes of woody vegetation, and that large tree shortages in a heavily utilized communal land has transferred treefall occurrence to shorter vegetation. Elephant- and human-dominated landscapes are tied to interactive effects that may hinder tree seedling survival which, combined with tree loss in the landscape, may compromise woodland sustainability.

Keywords: communal land; disturbance; ecosystem engineer; human ecology; LiDAR; South Africa

5.2 Introduction

Humans have been an integral and ancient part of savanna structure and function (Bartlett 1956; Ellis 2011). Currently, savannas contain up to a third of the global human population and the majority of the world's agropastoralism (Safriel *et al.* 2005), and are under immense and growing land-use pressure (Sala *et al.* 2000; Ellis and Ramankutty 2008). Savanna woody cover determinants are frequently considered in terms of abiotic and herbivory factors (Sankaran *et al.* 2005), but human effects can also change the proportion of woody cover both directly, through land-use change (Belsky 1987; Higgins *et al.* 1999), and indirectly, by altering fire regimes (Bird and Cali 1998; Pyne 2001). Human impacts on savanna structure contribute to the emergent properties of tree cover (Bucini & Hanan 2007), highlighting the need to treat humans as ecosystem components (Worm *et al.* 2016).

Humans alter savanna vegetation structure and composition directly through wood removal (House and Hall 2001; Galvin and Reid 2011). In this context, human effects on vegetation can be contrasted to those of the iconic symbol of African savannas, the African elephant (*Loxodonta africana*), dominant in southern and eastern Africa since the late Pleistocene (Coppens *et al.* 1978). As the largest extant land herbivores, elephants are bulk feeders that alter ecosystem structure and composition (Laws 1970; G P Asner *et al.* 2015). This occurs directly through pollarding (Guy 1976) and uprooting (Shannon *et al.* 2008), or indirectly via debarking (Moncrieff *et al.* 2008). Although humans are comparatively smaller in mass to elephants, high human population densities substantially depress woody cover (Bucini & Hanan 2007). Humans and elephants have the potential to affect all vegetation height classes, with cascading effects on ecosystem function and biodiversity (humans: Janzen 1988; elephants: Cumming 1982). For example, humans and elephants facilitate the resprouting response of savanna species through continual harvesting (Luoga *et al.* 2004) and browsing (Jachmann and Bell 1985; Rutina *et al.* 2005) for fuelwood and forage respectively, potentially increasing the availability of a preferred stem size. Both agents are implicated in high rates of tree loss (humans: Ramankutty 2006; elephants: Laws 1970) and shrub layer increases (humans: Archer *et al.* 1988; elephants: Jachmann and Bell 1985).

Both elephant- and human-mediated effects on savannas are confounded by additional factors, including fire, heterogeneous resource distribution, the abiotic context, and land

management and policy. Although associated with more fire ignitions, increased human population density results in greater landscape fragmentation and lower grass fuel loads, with smaller burned areas as a consequence (Archibald *et al.* 2009). Humans intentionally burn savanna vegetation to encourage seasonal growth for livestock grazing or clear vegetation for croplands (Hall 1984). However, widespread fire suppression and overgrazing have been implicated in shrubland encroachment (Archer *et al.* 1995; Roques *et al.* 2001). In contrast, protected areas are the most burned land-use in southern African savannas (Archibald *et al.* 2010). Fire acts synergistically with elephant bark stripping to increase tree mortality (Moncrieff *et al.* 2008; Vanak *et al.* 2012). Elephant-fire contributions to large tree mortality, together with tree seedling suppression in the 'fire trap' (*sensu* Higgins *et al.* 2000) and cascading interactions with seedling herbivores (Rutina *et al.* 2005), have contributed to a reduction in large trees (Barnes 1983; Eckhardt *et al.* 2000).

Elephant foraging varies seasonally (Western and Lindsay 1984; Cerling *et al.* 2006), often centered around resource availability, particularly water (Western 1975; Chamaillé-Jammes *et al.* 2007), but is also mediated at different scales by soil nutrients (Asner, Levick, *et al.* 2009). In contrast, human-associated wood harvesting patterns are affected by the perceived ease of access to wood resources, as well as the fine-scale socio-economic status of each household and "rural production system" context (Soussan 1988; Dovie *et al.* 2004). Nevertheless, despite different drivers of wood resource use, both elephant and human associated effects on woody vegetation are density dependent (humans: Vitousek *et al.* 1986; Bucini & Hanan 2007; elephants: Trollope *et al.* 1998; Skarpe *et al.* 2004).

Woody canopy structure and composition reflect the ecological context of multiple spatial and temporal processes (Watt 1947; Vanak *et al.* 2012; Scholtz *et al.* 2014), complex interactive effects with other species (Dean *et al.* 1999; Sankaran *et al.* 2005), humans (Turner *et al.* 2007; Ellis and Ramankutty 2008), and ecosystem processes (Belsky 1994; Treydte *et al.* 2007). Research on tree canopy dynamics has frequently focused on elephant impacts, but less so on humans as determinants of woody cover resulting from a paucity of data on rates and spatial patterns of human-mediated treefall. In most of African elephants' range, humans and elephants coexist (van Aarde *et al.* 2008), making inferences about treefall drivers unclear. However, in South Africa elephants only exist in fenced conservation areas, often bordered by rural, impoverished communities reliant on local natural resources. South Africa also contains nature reserves fenced off from both elephants and humans, creating a macroscale experimental opportunity for investigating the factors associated with savanna

vegetation dynamics in the exclusive presence and absence of two major disturbance agents. These results will augment valuable field-based research on elephant- (e.g. Shannon *et al.* 2008) and human-mediated treefall (e.g. Luoga *et al.* 2002) by providing a landscape scale geospatial context, especially when combined with detailed tree height specific information.

Here we use 'experimental' landscapes, utilized by either humans, elephants, or neither, combined with repeat high resolution, airborne Light Detection and Ranging (LiDAR) technology to quantify the relative impact of humans and elephants on height-specific treefall rates and to explore the following questions: 1) How do the rates and spatial patterns of treefall differ between human- and elephant-mediated landscapes, and what affects these differences? 2) What is the relative importance of other factors (e.g. fire, geology, hillslope, human-settlement specific differences) in influencing treefall within and between these sites? The insights provided by these questions will improve our understanding of anthropogenic contributions to savanna woody dynamics and have the potential to refocus questions on woodland sustainability.

5.3 Methods

5.3.1 Study area

The study sites were located in Mpumalanga province in the north-eastern portion of South Africa. This area is a multi-use conservation landscape with a graduated scale of land-use intensity across the subregion (Coetzer *et al.* 2014). Summer rainfall averages 750 mm p.a. in the northern study sites and 650 mm p.a in the south eastern extent, with mean daily maxima of 31 °C (minima 20 °C) and 26 °C (minima 8 °C) for summer and winter, respectively. The terrain is gently undulating and the geology is dominated by granite with local Timbavati gabbro intrusions. The vegetation is Granite Lowveld dominated by *Terminalia sericea, Combretum zeyheri* and *C. apiculatum* on the sandy, dystrophic uplands and *Acacia nigrescens, Dichrostachys cinerea* and *Grewia bicolor* on the deep, clayey, high sodium lowlands with dense stands of *T. sericea* delineating the seep zones (M. C. Rutherford *et al.* 2006). Localized Timbavati gabbro intrusions are characterized by Gabbro Grassy Bushveld, a more open savanna with fewer scattered trees on dark clay soils which swell and shrink (M. C. Rutherford *et al.* 2006).

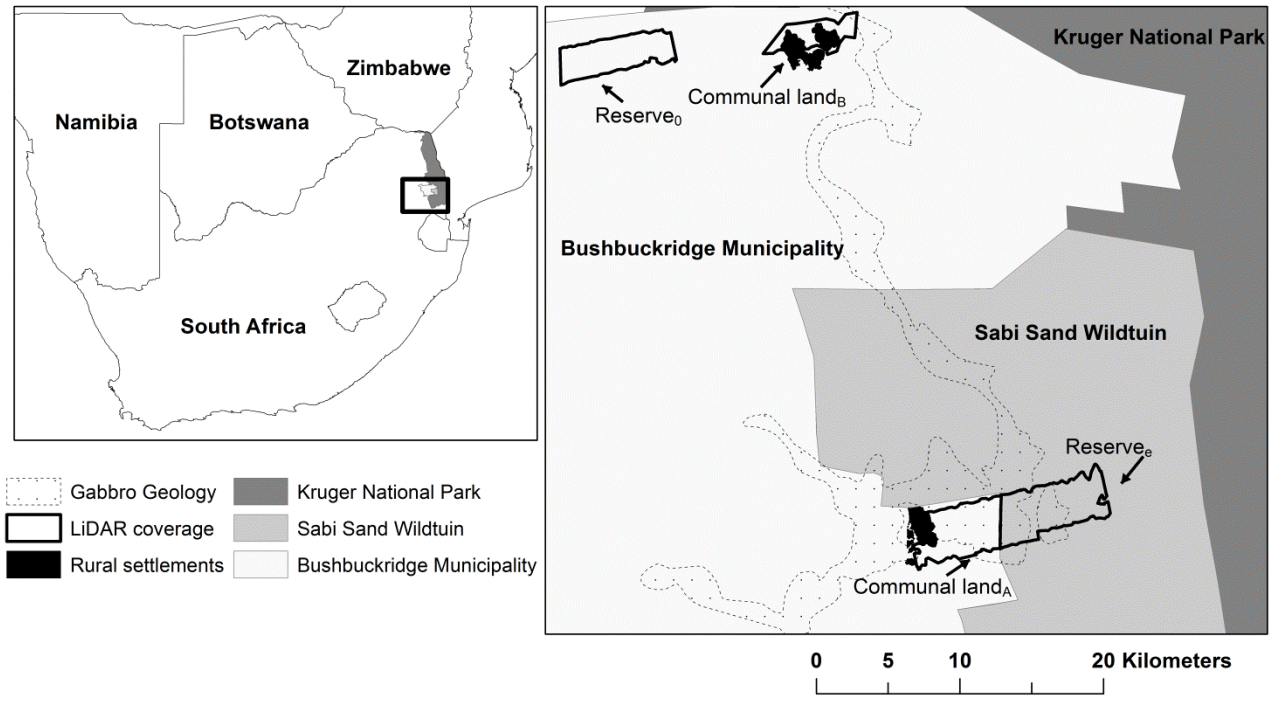

Figure 5.1. Map of Bushbuckridge Municipality and surrounding conservation land showing the locations of the four airborne LiDAR survey areas, monitored in 2010 and 2012. Gabbro outcrop localities are delineated against a granite-dominated backdrop. The inset map shows the location of the Sabi Sand Wildtuin and Bushbuckridge Municipality in South Africa's northeast corner.

Our LiDAR survey sites were two communal lands used by humans (hereafter referred to as Communal land$_A$ and Communal land$_B$), a private nature reserve containing elephants (Reserve$_e$), and a nature reserve fenced off from both humans and elephants which served as a "control site" (Reserve$_0$) (Fig. 1, Table 5.1). The two communal lands had approximately the same human population densities at the time of the surveys ('density' here defined as human population relative to available communal land area) (Table 1) and are state-owned, tribally-managed, former Apartheid 'homelands'. The human settlements that use Communal land$_A$ and Communal land$_B$ have the inherent socio-economic characteristics associated with their former 'homeland' status of extensive unemployment, low education levels, high population densities dependent on migrant labor and social grant remittances (Thornton 2002), coupled with a reliance on natural resources (Twine *et al.* 2003). Communal land$_A$ is communally utilized by the settlement of Justicia (2.0 humans per communal land ha) and Communal land$_B$ is used by Welverdiend (2.2 humans per communal land ha) (Table 5.1). Communal land$_A$ is adjacent to the privately-owned game reserve, Sabi Sand Wildtuin (SSW: Reserve$_e$) established in 1898 (Mabunda *et al.* 2003) with an elephant density of 2.55

elephants km^{-2} in 2011 (de Boer *et al.* 2015) (Fig. 1, Table 5.1). SSW is an association of separately managed farms with a joint focus on tourism-based conservation (http://www.sabisand.co.za). In 1961 a fence was erected between Kruger National Park (KNP) and SSW and removed in 1993, followed by a 17 fold increase (1992-2011) in elephant densities (de Boer *et al.* 2015), entering from KNP during winter (Hiscocks 1999). Communal $land_B$ neighbors state-owned Andover Nature Reserve ($Reserve_0$), a nature reserve with no elephants and fenced off from the adjacent communal land (Fig. 1). Giraffe are present in $Reserve_0$, but have not been implicated in treefall events (Scholes *et al.* 2003).

Table 5.1. Study site details with elephant and human densities.

Site Name	Site Name Abbreviation	Elephant density (individuals km^{-2})	Human density (humans ha^{-1} communal land	LiDAR survey coverage (ha)	Amount of site surveyed (%)
Sabi Sand Wildtuin	$Reserve_e$	2.55[a]	0	2101	61
Justicia communal land	Communal $land_A$	0	2.0[b]	1699	61
Welverdiend communal land	Communal $land_B$	0	2.2[b]	603	20
Andover Nature Reserve	$Reserve_0$	0	0	1674	27

[a] de Boer *et al.* 2015

[b] Population estimates based on the 2011 South African census and the ongoing MRC/WITS Rural Public Health and Health Transitions Research Unit demographic surveillance surveys (see Kahn *et al.* 2007).

5.3.2 Airborne LiDAR mapping

Time series data from airborne LiDAR campaigns was collected in April 2010 and 2012 using the Carnegie Airborne Observatory systems (CAO) at 2000 m AGL with an effective laser point density of 4 laser shots m^{-2} (for technical details see: Asner *et al.* 2007; Asner *et al.* 2012). The CAO LiDAR systems have an integrated Global Positioning System-Inertial Measurement Unit (GPS-IMU) providing accurate locational data for each laser return in the point cloud. The surveys were conducted at the end of the wet, summer season before

deciduous savanna trees lose their leaves to maximize vegetation height return accuracy. LiDAR returns were differentiated between those that reflected off the vegetation canopy or subcanopy and those that penetrated through the vegetation and reflected off the ground surface. The last laser returns (ground returns) were interpolated to create a digital terrain model (DTM); the first returns (top-of-canopy returns) were used for producing a digital surface model (DSM). The difference between the DSM and the DTM provided a canopy height model (CHM) at 1m spatial resolution.

5.3.3 Individual tree identification

Although the LiDAR campaigns were conducted in the same month, variation in phenology between years could compound errors in a pixel-based analysis. In addition, the purpose of the research required monitoring individual trees over time. Thus, we delineated individual tree crowns from the CHM using an object-oriented approach. A crown segmentation method was used with Gaussian kernel smoothed data (to maximize whole-crown detection) and transformed to maximize object identification in multi-crown canopies (for details see: Asner *et al.* 2015). All crowns >1m in height were considered 'trees'. The centre point of each tree was geotagged with coordinates and the changes in the maximum height of each individual tree crown was monitored over time. Here, 'treefall' was said to have occurred if ≥75% of the original object-based crown height in 2010 was lost by 2012. This method does not detect partial canopy and branch loss (like that associated with pollarding and herbivory).

5.3.4 Treefall analysis

As this study was a 'comparative mensurative' experiment on a regional scale with no replicates per 'treatment' (e.g. reserve with/without elephants), the study is inherently pseudoreplicated (Hurlbert 1984). Thus, definitely identifying drivers of differences seen between sites would be irresponsible (Hurlbert 1984); we applied a holistic approach to this landscape study, explicitly acknowledging the underlying heterogeneity and made inductive conclusions, within the bounds of certain assumptions (Hargrove and Pickering 1992). Recognizing the pre-existing confounding variables between treatments (e.g. pre-existing differences in tree density), we reported both absolute and relative change and the combinative analysis of these patterns alludes to drivers of landscape-scale change,

contributing hypotheses which can then be tested empirically in future studies. Treefall was reported as biennial loss in absolute numbers ha^{-1} and as a percentage ha^{-1} relative to the baseline number of standing trees in 2010. Treefall cannot be solely attributable to elephants and humans, but the relative contributions of other agents - such as wind (Spinage and Guinness 1971), frost (Childes and Walker 19987) and other herbivores (e.g. Yeaton 1988) - to treefall and subsequent coppice dynamics were unknown, but were assumed to be equal between sites.

Monthly fire data (2000-2012) were derived from remotely sensed MODIS burned area product (MCD45A1-V051) at 500 m resolution. This product was validated in South African savannas and accurately detected 85% of true burned area (Roy *et al.* 2005), although it is less efficient at identifying smaller burns (<50 ha) (Tsela *et al.* 2014). The data were binned into burned/unburned area and summed per year using the R (R Core Team 2013) packages: sp, rgdal and raster. For the purposes of this study, the data were divided into 'historical burns' (number of times burned p.a. from 2000 to 2010) and 'recent burns' (number of times burned p.a. from 2010 to 2012). Communal land extents were manually digitized using a series of aerial images (50 cm resolution; years: 2009, 2012; www.ngi.gov.za). Upland and lowland locations were generated from relative elevation models generated in SAGA GIS (SAGA User Group Association 2010) using the Terrain Analysis toolset. Ripley's multi-distance spatial cluster analysis was run in SAGA GIS using 100 m distance bands at 40 m intervals, with a boundary correction method to simulate outer values, measuring treefall clustering occurrences as the size of the neighborhood changes (Haase 1995). Ripley's cluster analysis tests the observed spatial homogeneity of fallen trees for departure from completely spatial randomness, expressed as regular or clustered distribution. All spatial analysis was performed in R v3.2.1 (R Core Team 2013). Absolute treefall rates were tested for significant differences using a non-parametric Kruskal-Wallis χ^2 test with a Tukey Kramer (Nemenyi) test (with Tukey distance approximation for independent samples) (R package: PMCMR). Kolmogorov-Smirnov (KS) tests were used to test for differences between sampled treefall height distributions. Treefall height classes were compared using ecologically relevant categories: 1-3m (e.g. Bond and Keeley 2005); 3-5m (e.g. Asner and Levick 2012); 5–10m (e.g. Dean *et al.* 1999); and >10m (e.g. Tews *et al.* 2004). A logistic regression model was used to identify significant variables associated with treefall. The model was run on a randomly selected sample of tree crowns with a distance constraint (40m) to avoid spatial autocorrelation (Legendre & Fortin 1989); the distance constraint was calculated from a

semivariogram run in SAGA GIS. A fully-additive global model was generated from a binary response variable (treefall occurred = 1, treefall did not occur = 0) in sites containing elephants ($Reserve_e$), humans (Communal $land_A$ and Communal $land_B$), or neither ($Reserve_0$), in relation to various abiotic factors and ecologically-relevant interactions. Model selection was based on Akaike's information criteria (AIC) and performed in R (package: MuMIn) using the 'dredge' tool and ranked in increasing values of ΔAIC (Δ_i) (Burnham & Anderson 2002). Tests for multicollinearity and overdispersion of the models (Logan 2010) raised no concerns. We used a model averaging approach to assess the strength of our best-fit model as models with $\Delta_i \leq 2$ can be considered not significantly different from each other (Burnham & Anderson 2002; Burnham & Anderson 2004). Model averaging calculates the relative importance of each variable by calculating each model's contribution in proportion to their Akaike weights (ω_i). Akaike weights can be treated as probabilities that model *i* is the best model for the dataset (Burnham & Anderson 2004). Model results were presented graphically (R package: biology) where odds ratios indicate the change in the odds of treefall occurrence (response variable) per unit increase in a predictor variable whilst holding the other predictor variables constant (Hosmer *et al.* 2013). Odds ratios for each categorical predictor variable were calculated relative to a reference level (see Supplementary material Appendix 1, Table A1).

5.4 Results

5.4.1 Treefall rates

Landscape-scale tree mapping identified 453 685 individual trees >1m in height across the entire area in 2010, of which 11 740 (2.59%) lost ≥75% of their original height, ranging across sites from 1.32% treefall in $Reserve_0$ to 4.18% treefall in $Reserve_e$. Human-mediated treefall rates were 2.29% in Communal $land_A$ and 4.74% in Communal $land_B$, exceeding the elephant-mediated treefall rate. Communal $land_B$ also contained the lowest total number of trees surveyed in 2010 (22 295 trees), compared to Communal $land_A$ (116 498 trees), $Reserve_e$ (135 402 trees), and $Reserve_0$ which had the highest number of trees (179 490). Proportional biennial treefall rates revealed greater disparities between sites than absolute rates as there was no significant difference between $Reserve_0$ and both Communal lands

treefall rates in absolute terms; when controlling for the amount of original standing trees there are significant differences between all sites (Table 5.2).

Table 5.2. Average biennial rate of treefall ha^{-1} ± standard deviation. Reporting is in absolute and relative treefall rates.

Site	Absolute Rate ± SD (treefall ha^{-1})	Relative Rate ± SD (% treefall ha^{-1})	n (ha)
Reserve$_0$	1.32 ± 2.07^{a}	1.45 ± 2. 22^{A}	1674
Communal land$_A$	1.39 ± 2.72^{a}	3.33 ± 7.28^{B}	1699
Communal land$_B$	1.38 ± 3.16^{a}	5.34 ± 11.46^{C}	603
Reserve$_e$	2.33 ± 3.98^{b}	7.59 ± 12.60^{D}	2101

^{a,b} Superscript letters mark significant differences for absolute rates between sites using Kruskal-Wallis $\chi 2$ test ($\chi 2 = 158.85$, $p < 0.001$, $df = 3$) with a Tukey Kramer (Nemenyi) multiple comparisons test.

^{A,B,C,D} Superscript letters mark significant differences for proportional rates between sites using pairwise Kolmogorov-Smirnov tests

Reporting proportional rates averaged per hectare revealed the spatial variability in treefall between sites. Accordingly, Reserve$_e$ had the fastest biennial treefall rate and highest variability at 7.6% ± 12.6 treefall ha^{-1}, followed by Communal land$_B$ with 5.3% ± 11.5 treefall ha^{-1} (Table 5.2).

In Communal land$_A$ treefall occurred relatively evenly (± 3%) across all height classes (Figure 5.2). Communal land$_B$ shows high treefall occurrence (7.03%) in the 1-3 m height class. However, tree height classes >3m in Communal land$_B$ have very low sample numbers and low treefall occurrence (Figure 5.2), an indication that this communal land has been heavily harvested in the past. Elephant-mediated treefall in Reserve$_e$ was concentrated in the >3m height classes (Figure 5.2), peaking at >10% in the 5-10 m height class. However, the 1-3m height class in Reserve$_e$ also experienced considerable treefall of 4.6%.

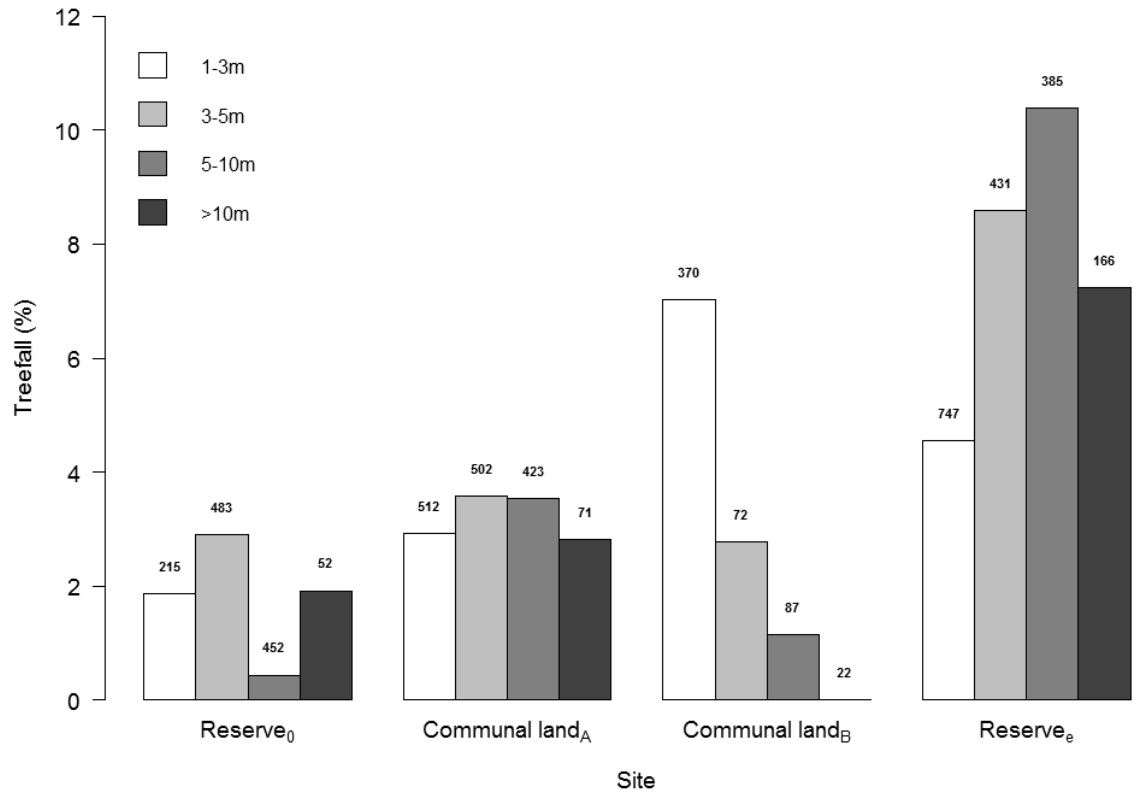

Figure 5.2. Height class of felled trees (2010-2012), reported as a percentage of standing trees in each height class per site in 2010. Data are based on a random subsample of trees in each site. Sample numbers for each height class per site are shown above each bar. The legend denotes height classes of trees in 2010.

5.4.2 Spatial variation in treefall rates

Treefall in Reserve$_e$ and Communal land$_B$ had the most clustered pattern (Figure 5.3). Yet the treefall clusters were more spatially distributed in Reserve$_e$ (Figure 5.4h) relative to the communal lands (Figure 5.4d,f). High treefall rates in Reserve$_e$ were concentrated in 2 large clusters in the eastern portion of the study site (Figure 5.4g), most of which occurred in vegetation <3m in height and were likely related to managed bush clearing. The two smaller red (>21 treefall ha^{-1}) patches of high treefall to the west of Reserve$_e$ were located over permanent water sources and the yellow (11-15 treefall ha^{-1}) patches dotted in the north east were along river courses (Figure 5.4g). Relative treefall patterns revealed higher proportional rates in the western gabbro portion of Reserve$_e$ than in the eastern granite (Figure 5.4h, $D = 0.21$, $p < 0.001$; 13.44 ± 18.19% gabbro treefall ha^{-1}, n = 1029; 4.99 ± 8.34% granite treefall ha^{-1}, n = 1072). The communal lands had discrete clusters of treefall mostly within 1

km of the settlement (Figure 5.4c-f). There were also high treefall rate hotspots on Communal land$_A$'s eastern boundary, adjacent to Reserve$_e$

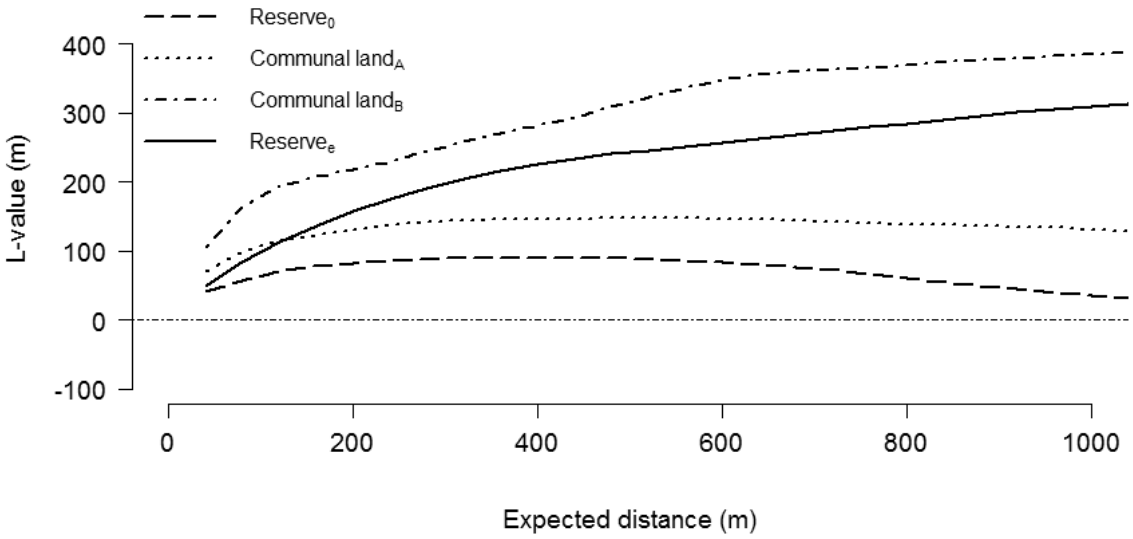

Figure 5.3. Global cluster analysis of sites using Ripley's K statistic. The L-value is the difference between observed and expected differences of treefall (2010-2012) locations. The L-value = 0 m reference line represents complete spatial randomness; L-values >0 m and <0 m represents more clustering or dispersal, respectively, than that expected from a random distribution. Elephant-mediated treefall (Reserve$_e$) shows clustering at a wide range of spatial scales, followed by human-mediated sites (Communal land$_B$ and Communal land$_A$). The site containing no humans or elephants (Reserve$_0$) shows the least clustered pattern of treefall.

(Figure 5.4c-d). Treefall in Reserve$_0$ had the least clustered treefall of all sites (Figure 5.3) and contained no visibly distinct high treefall hotspots (Figure 5.4a-b).

5.4.3 Factors influencing treefall

Treefall was not significantly influenced by historical burns (>10 years), upslope or downslope location or the 2010 tree height (Appendix Table 5.1). However, the odds of treefall occurring were increased ($z = 1.93$, $p = 0.05$) by recent burns between 2010 and 2012 (Figure 5.5). Fires only occurred once in two years in Reserve$_e$ and Reserve$_0$, but occurred more frequently in the communal lands (Appendix Figure 5.1). The burned areas in the communal lands were furthest away from the settlements (Appendix Figure 5.1b-c). It is

worth noting the location of the treefall clusters in $Reserve_e$ were spatially associated with the location of a contiguous burned area (Appendix Figure 5.1d). Of all the sites, the odds of treefall increased most if the trees were in Communal $land_B$ ($z = 4.57$, $p < 0.001$) or $Reserve_e$ ($z = 5.65$, $p < 0.001$), relative to $Reserve_0$ (Figure 5.5), thus treefall was best predicted by the presence of humans or elephants. Treefall occurrence odds decreased on granite geology ($z = -2.62$, $p = 0.01$); the corollary being that treefall odds increased on gabbro geology (Figure 5.5). A synergistic interactive effect of geology and recent burns was also associated ($z = 2.538$, $p = 0.01$) with higher treefall occurrences (Figure 5.5).

5.5 Discussion

Using large-scale, high-resolution LiDAR measurements we tracked the fate of over 450 000 individual trees across 6 812 ha of mixed-used landscapes, quantifying treefall rates and patterns between human- and elephant- mediated sites. Human-mediated treefall was 2.3 to 3.7 times higher than in the control site, $Reserve_0$ (Table 5.2). Thus, human-mediated relative biennial treefall (3 - 5% ha^{-1}) was a significant driver of savanna structural dynamics, approaching that of the elephant-mediated landscape (7% ha^{-1}). Background biennial treefall rates (1.45% treefall ha^{-1}) in areas protected from both elephants and humans were comparable to herbivore exclosure experiments in Kruger National Park (KNP), South Africa, where a site with similar rainfall and geology to the control site, $Reserve_0$, had 1.9% background treefall ha^{-1}over two years (Asner and Levick 2012). Elephant-mediated treefall in $Reserve_e$ was on average 5 times higher than in the control site, $Reserve_0$ (Table 5.2). In comparison, elephants in KNP resulted in 6 times the background biennial treefall rate outside the exclosures (Asner and Levick 2012), with estimated park-wide treefall rates of 12% ha^{-1} (Asner *et al.* 2015). Although elephant-mediated large tree mortality varies from 1-2% yr^{-1} over multi-decadal cycles (e.g. van de Vijver *et al.* 1999), records of up to 20% yr^{-1} mortality have been recorded in some localities (e.g. Beuchner and Dawkins 1961; Pellew 1983). While there are field-based studies (e.g. Shannon *et al.* 2008) and landscape-scale studies (e.g. Asner and Levick 2012) that tracked elephant impacts on individual trees over time, analogous studies for human-mediated treefall exist for field-based methods (e.g.

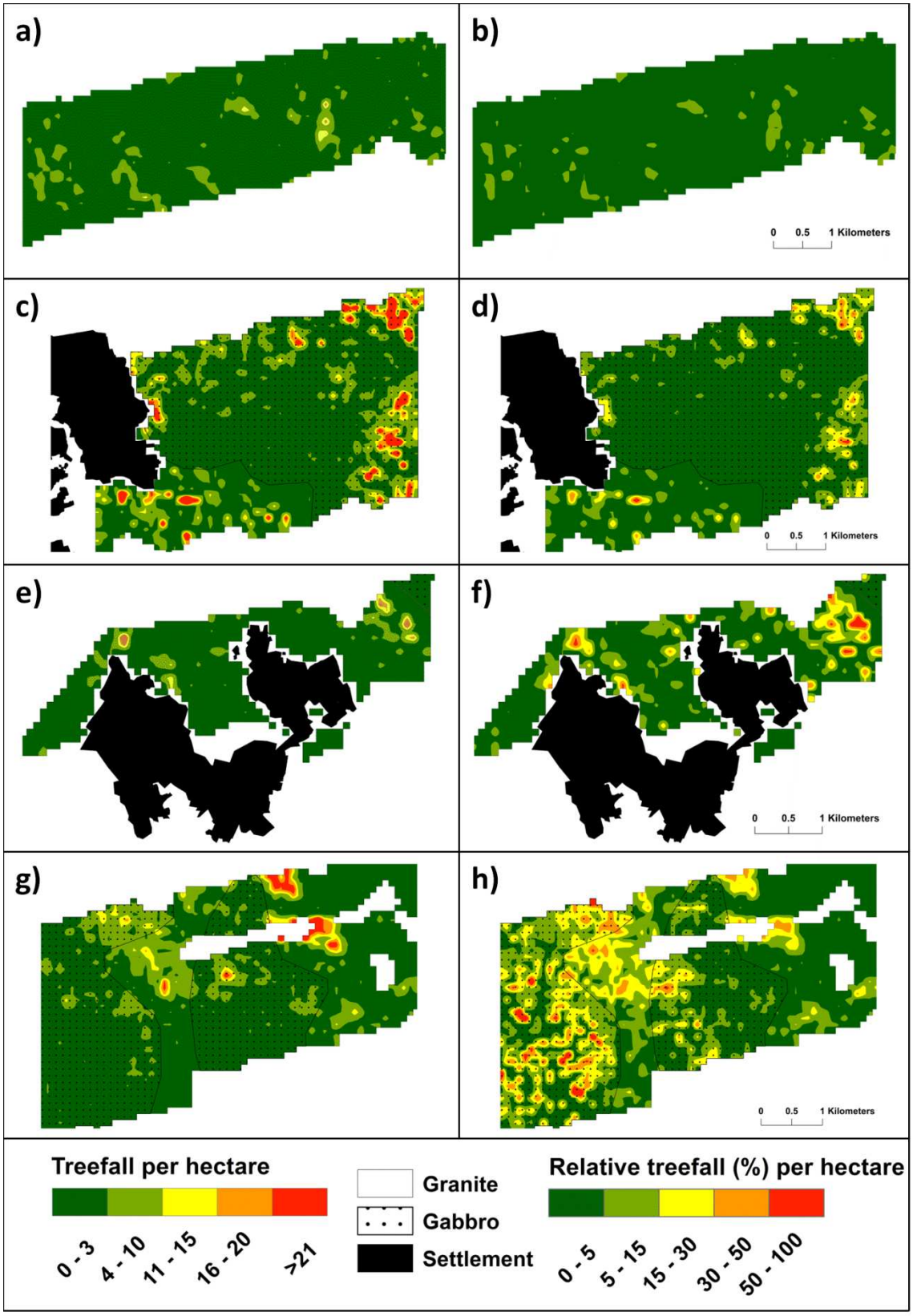

Figure 5.4. Maps of biennial treefall rate expressed in absolute (left column) and relative (right column) treefall ha^{-1} (2010-2012) for: a-b) Reserve$_0$; c-d) Communal land$_A$; e-f) Communal land$_B$; and g-h) Reserve$_e$. Communal land$_A$ and Reserve$_e$ are dominated by gabbro geology.

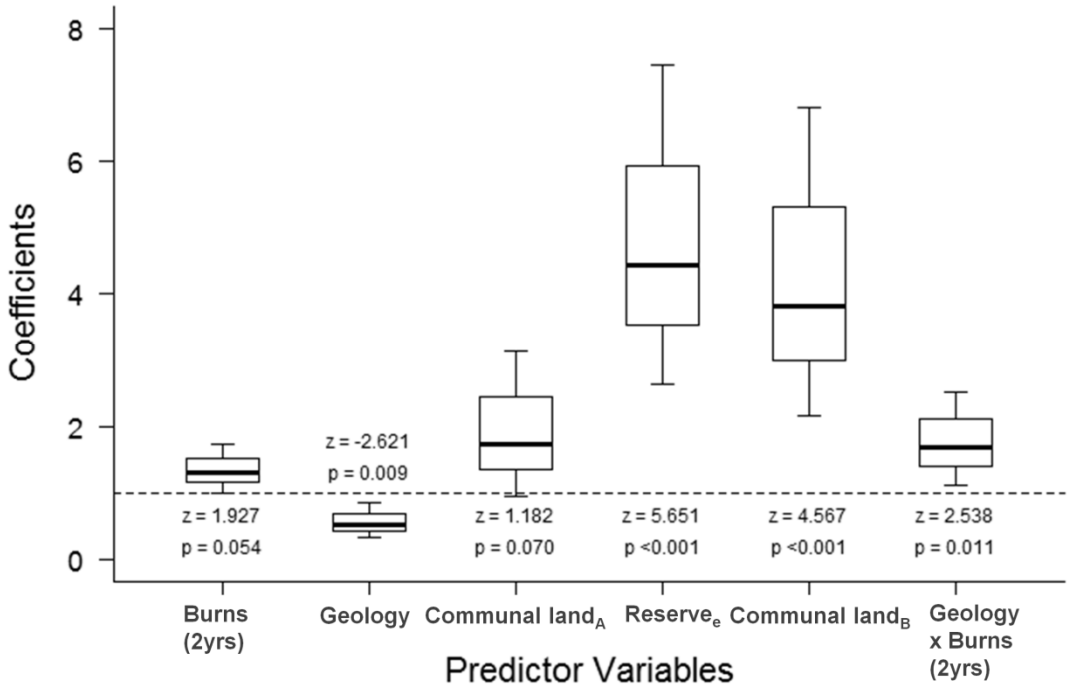

Figure 5.5. Odds-ratio coefficients of the best-fit logistic regression model (Model 1 in Appendix 1, Table A1) of treefall (2010-2012) occurrence. Boxplot whiskers show 95% confidence intervals. Site predictor variables were relative to the reference site, Reserve$_0$. The odds of treefall occurrence increased with more recent burns between 2010 and 2012, as well as in sites containing humans or elephants, i.e. Communal land$_B$, and Reserve$_e$. Decreased treefall occurrence was also associated with geology (i.e. granite as the geology variable is relative to the reference geology, gabbro). Treefall occurrence increased with the synergistic interactive effects of geology and recent burns

Shackleton et al. 2005; Ahrends et al. 2010), but have not been conducted on a broad-scale . Here, we have quantified human-associated treefall in savannas. Elephant- and human-related patterns of treefall differ spatially as they result from divergent functional processes (Watt 1947). We found that elephant-mediated treefall was spatially associated with landscape-scale nutrient distribution. Treefall occurred predominantly on gabbro geology (Figure 5.4-5), corresponding with other studies recording elephant use of vegetation on nutrient-rich soils (Eckhardt *et al.* 2000; Asner and Levick 2012), Shannon *et al.* (2008) also recorded higher rates of pushed over trees on gabbro geology, however Vanak *et al.* (2012) did not find higher levels of large tree mortality on these soils. Our research also shows elephant-associated treefall patterns were highly clustered, centering on surface water (Figure 5.4g). Permanent surface water concentrates elephant effects on the landscape, leading to persistent use of vegetation resources in these areas, ranging from negligible vegetation structural

change in wet years (e.g. Kalwij *et al.* 2010) to severe during droughts (e.g. Napier Bax and Sheldrick 1963). Although treefall in $Reserve_e$ in all height classes was markedly higher than background treefall, the 5-10 m height class was fivefold that in the control site (Figure 5.2). While our results do not show an elephant utilization effect proportional with abundance like that in Shannon *et al.*'s (2008) transect study, we also do not have a clear 'elephant trap' in the 5-9 m height as per Asner and Levick's (2012) findings. However, treefall in all height classes in our study was highest in the elephant-mediated site.

In contrast to elephant-mediated treefall associated with abiotic factors, the rate and pattern of treefall in communal lands was influenced by socio-economic factors and ease of access. Treefall in the communal lands was less clumped than elephant-mediated treefall patterns (Figure 5.3), with high treefall rates (i.e. >15 treefall ha^{-1}) coalescing adjacent to settlements (Figure 5.4c,e) – areas being clear-cut for settlement-associated expansion (Coetzer *et al.* 2013) – or on communal land boundaries to reinforce land ownership under perceived land claim threats. Communal $land_B$'s treefall occurred in the low height class (Figure 5.2), an indication that shortages of trees >3 m are placing disproportionate harvesting pressure on the lower height classes. The high market-share of households purchasing wood in this area (Madubansi and Shackleton 2007) supports this finding. Despite both communal lands having similar human population densities (Table 5.1), Communal $land_B$ is a highly utilized area, accessible to other settlements as it borders a main road and neighbors the more urbanized sections of Bushbuckridge where communal lands have been subsumed by settlement expansion (Coetzer *et al.* 2013). Communal $land_A$ is a rare example of exclusive use by one settlement as it is fenced on two boundaries and the location is, relatively, remote. This is reflected in the height-specific treefall which is spread evenly across all height classes at relatively low levels compared to background rates in the control site, $Reserve_0$ (Figure 5.2).

Fire frequency emerged as an important factor in treefall, but secondary to both elephant and human influence (Figure 5.5). In recent work by Asner *et al.* (2015), fire frequency was also found to be a secondary factor to elephant and abiotic mediation on treefall. Although treefall may be positively associated with higher fire frequency, tree mortality is not necessarily higher under frequent fire conditions (Vanak *et al.* 2012), but large tree mortality is associated with high intensity fires (Bond & Keeley 2005; Smit *et al.* 2016). Savanna woody vegetation is largely fire-resilient: vegetation composition is largely unchanged by fire and individuals rarely suffer mortality, but vegetation structure is fire-responsive (Higgins *et al.* 2007; Pellegrini *et al.* 2015). Lower tree and greater grass biomass on gabbro geology drives

more frequent fire returns in this landscape (Figure 5.5), facilitating treefall in previously damaged trees, which substantially increases tree mortality (Shannon *et al.* 2011). This is particularly pertinent for tree species preferentially targeted by elephants, resulting in large areas with missing size classes of long-lived trees (Helm and Witkowski 2012). Indeed, the association of treefall with a gabbro-fire frequency-elephant nexus supports Vanak *et al.*'s (2012) findings on the strong association between the differential vulnerability of large trees to mortality and a three-way interaction between elephant, fire and landscape type. Though the magnitude of fire's effects are dependent on fire intensity (Smit *et al.* 2010) and tree characteristics, such as stem diameter (Ryan & Williams 2011), due to high spatial variability fire intensity is difficult to measure accurately over large scales (Archibald *et al.* 2013).

Curiously, the presence of recent fires on communal lands was associated with increased treefall (Figure 5.5). Although increased human population densities have been associated with more fire ignitions, but less intense fires over smaller extents (Archibald *et al.* 2009), we can only speculate on possible mechanisms for the association with more frequent burns and increased treefall in the communal lands. Tall trees with hard wood which are difficult to cut by hand are often burned for clearing agricultural fields, which can result in spreading fires and tree mortality (E J Luoga *et al.* 2000). In addition, patch burning to encourage grass regrowth for livestock grazing and cropland clearing is a common phenomenon in African rangeland systems (Hall 1984).

Elephant- and human-associated treefall rates (Table 5.2) represent the "mortality ceiling" of savanna vegetation as fallen trees frequently resprout. For example, in an extensive 30-month field survey in KNP, about 10% of trees in the 5-10m height class were pushed over by elephants, but of these, 60% survived (Shannon *et al.* 2008) through coppicing responses (Jachmann and Bell 1985; Owen-Smith 1998). Repeat damage to large trees over 30 months was reported as 12.5% and 2.6% from elephant and fire, respectively, of which 36.6% died from the damage (Vanak *et al.* 2012), demonstrating substantial resilience of woody vegetation to disturbance. Coppicing responses to human-harvested trees have also been documented (Shackleton 1993; Luoga *et al.* 2004). Fuelwood and charcoal studies in savannas suggest woody vegetation communities shift under high use scenarios to ecosystems dominated by resilient species that coppice readily (Strømgaard 1986; Shackleton 1993). Although this research shows that both elephants and humans are substantial drivers of treefall in savannas and utilize all height classes of woody vegetation, tree loss *per se* does

not result in woodland decline unless accompanied by lack of seedling recruitment (Augustine and McNaughton 1988). This occurs directly through loss of mature, seed-bearing trees and seedling herbivory by elephants or human livestock (e.g. elephants: Western and Maitumo 2004, goats: Hester *et al.* 2006), or indirectly, by rendering the trees 'functionally juvenile' through repeated hedging. Additionally, changes in woodland structure can trigger a cascade of interactions, such as that in Chobe riverfront, Botswana, where elephant-induced shrubland conversion facilitated increased seedling herbivory by expanding impala, *Aepyceros melampus*, habitat (Rutina et al 2005). Similarly, in human-associated woodlands, increased coppice regrowth and bush encroachment favors browsing goats over grazing cattle. To compound issues of tree seedling survival, human presence is associated with more frequent fires, trapping tree seedlings in the fire layer. Here we have shown that both elephants and humans, in combination with fire, can utilize all woody height classes. When large trees disappear from the landscape, more disturbance-related pressure is placed on the lower height classes, reducing structural complexity and compromising ecosystem resilience. Large-scale studies need to be combined with detailed height-class specific information to monitor woodlands to preclude woodland unsustainability.

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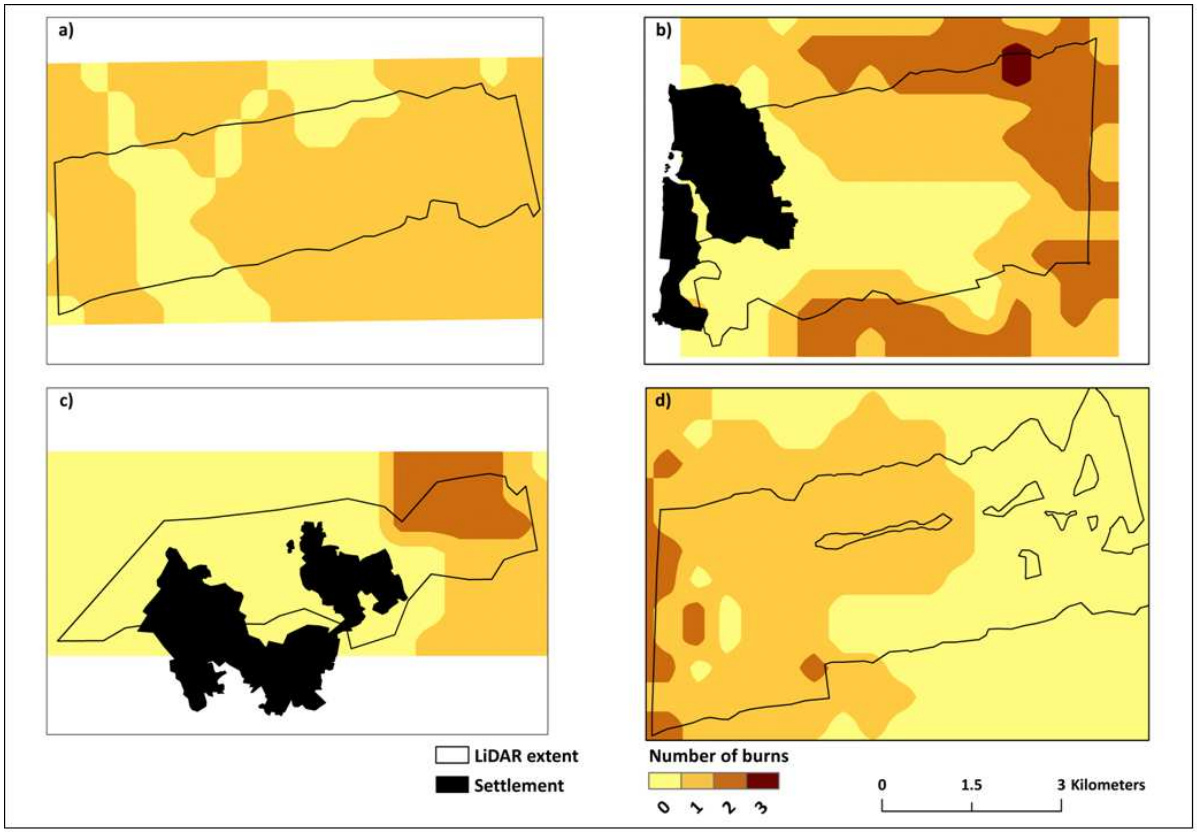
5.8 Appendix

Appendix Table 5.1. Model selection and averaging results of treefall (2010-2012) occurrence in sites containing elephants ($Reserve_e$), humans ($Communal\ land_A$ and $Communal\ land_B$), or neither ($Reserve_0$), in relation to various abiotic factors. Models with AIC differences (Δ_i) ≤2 are ranked in order of increasing Δ_i with Model 1 as the best-fit logistic regression. Variables included in each model have their p-value recorded. Blank cells indicate those variables were not included in the model. Odds ratios of the categorical variables (Site, Geology, and Catena) are calculated relative to a base level ($Reserve_0$, Gabbro, and Lowlands, respectively).

	Logistic Regression Models				**Model Averaging**[**]	
Variables	**1**	**2**	**3**	**4**	**p_{ip}**	**ω_{ip}**
Site: $Communal\ land_A$	0.069	0.045	0.063	0.071	0.063	
Site: $Reserve_e$	<0.001	<0.001	<0.001	<0.001	<0.001	**1.00**
Site: $Communal\ land_B$	<0.001	<0.001	<0.001	<0.001	<0.001	
Burns 2yr	0.054	0.030	0.065	0.056	0.052	**1.00**
Geology: Granite	0.009	0.007	0.008	0.010	0.008	**1.00**
Burns 2yr x Geology	0.011	0.009	0.09	0.011	0.010	**1.00**
Old burns		0.285			0.286	**0.25**
2010 Height			0.362		0.362	**0.21**
Catena: Uplands				0.970	0.970	**0.14**
df	7	8	8	8		
Δ_i	0.00	0.84	1.18	2.00		
ω_i[*]	0.20	0.13	0.11	0.08		

[*] Akaike weights (ω_i) represent normalized model likelihood values where ω_i can be treated as a probability that model *i* is the best model for these data (Burnham & Anderson 2004).

[**] Model averaging relative p values (p_{ip}) and relative weights (ω_{ip}) are with respect to the global model and indicate the relative importance of each variable. Variables are ranked in decreasing ω_{ip}.



Appendix Figure 5.1. Number of burns between 2010 and 2012 for a) Reserve$_0$, b) Communal land$_A$, c) Communal land$_B$, and d) Reserve$_e$.

Chapter 6: Conclusion

6.1 Introduction

The essential problem of 'increasing needs in the face of decreasing means' (Lubchenco *et al.* 1991) is most typified in rural systems where natural resource reliance is the highest, and continued unsustainable use can result in coupled collapse of both people and the ecosystems they rely on (World Commission on Environment and Development 1987; Cervigni & Morris 2016).

As woody vegetation dynamics reflect ecosystem functioning (e.g. primary productivity, biogeochemical nutrient cycling), it is increasingly being used to assess vegetation patterns relative to climatic and topoedaphic gradients (e.g. de Castilho *et al.* 2006; Colgan *et al.* 2012; Dahlin *et al.* 2012) as well as in response to disturbances (e.g. Dayton 1978; Chambers *et al.* 2004; Frolking *et al.* 2009; Shackleton & Scholes 2011). In the context of rural systems where fuelwood extraction is prevalent, measuring vegetation structural change is an underexploited method of inferring both past woodland use and future sustainability.

This thesis presents an explicit view on vegetation structural dynamics and biomass over a landscape utilised communally by a rural/peri-urban population heavily reliant on natural resources. In contrast with traditional biomass studies, I also present concomitant changes of the vertical vegetation subcanopy (voxel data) to reveal three-dimensional dynamics (Section 2). It was in this interaction that I anticipated we could understand any potential changes in biomass. I provide an easily implementable method of unravelling vegetation dynamics in a manner that would allow others in the fields of commons management, sustainable natural resource extraction and bush encroachment trends to relate. Two dimensional remotely-sensed biomass estimates do not capture subcanopy shrub changes, particularly in the context of structurally heterogeneous landscapes and increasing bush encroachment trends in semi-arid environments (Kgope *et al.* 2009; Buitenwerf *et al.* 2012; Secades *et al.* 2014; Fisher *et al.* 2015). We reveal that supply-demand models have consistently underestimated the adaptive capacity of both humans and provisioning ecosystems (Section 6.2). The comparison of vegetation structural dynamics across different land-use gradients and in relation to anthropogenic features provides an understanding of humans as agents of change

in the landscape. By viewing humans as 'functional megaherbivores', we demonstrate that humans are significant drivers of savanna vegetation dynamics and provide a novel lens through which to assess human impacts (Section 6.3). I also present the case for using Bushbuckridge as a model for future African land-use pressure (Section 6.4). Lastly, I present the constraints present in this thesis and opportunities for future work based on, and inspired by, my findings (Section 6.5).

6.2 Underestimated adaptive capacity of social-ecological systems

Woody vegetation structure and structural dynamics are associated to disturbance type (Chapter 5), usage intensity (Chapters 2-5) and spatial location relative to natural and anthropogenic factors (Chapters 2 & 4-5). Vegetation response to disturbance is height-class specific with compensatory growth occurring in low height classes occurring in heavily harvested areas (Chapters 2-3). Thus, woody biomass increased across all the study sites between 2008 and 2012 (Chapter 3), contrary to all previous supply-demand models (de Montalembert & Clement 1983; Banks *et al.* 1996; Wessels *et al.* 2013) and most field-based studies (Madubansi & Shackleton 2007; Shackleton & Scholes 2011; Matsika *et al.* 2013). Biomass increases had a strong relationship to subcanopy increases (Chapter 3), with > 60% of the subcanopy increases attributable to the 1-3m height class and ± 20% to the 3-5m height class (Chapter 3). This relationship was even more defined when looking at the finer-scale patterns of vegetation dynamics with increasing distance from roads and settlements (Chapters 2 & 4). Spatially-explicit representation of biomass and height-specific subcanopy structure revealed that increases in both metrics were concentrated close to roads and settlements in high use landscapes, whilst low use landscapes had patterns of change that were spatially variable (Chapters 2 & 4). These patterns represent the complex trade-offs that people make in their natural resource collection (Giannecchini *et al.* 2007). The adaptive capacity of people to deal with fuelwood shortages has been consistently underestimated (Mortimore & Adams 2001; Thomas & Twyman 2005), but these non-linear responses are difficult to incorporate into fuelwood supply-demand models. The increasing use of vehicles and wheel barrows for fuelwood collection (Dovie *et al.* 2002; Twine 2005; Madubansi & Shackleton 2007) means harvesters will increasingly look to communal lands bordering roads to optimise wood collection gain for effort expended. The LiDAR-based vegetation

monitoring covered a far greater extent than previous field studies and was able to show patterns which would normally be masked by local-scale variation. There have been documented local increases in forest patches in the Eastern Cape of South Africa as a result of villages in the area changing from timber-based to brick-based dwellings (C. Geldenhuys 20th Congress of the Association for the Taxonomic Study of the Flora of Tropical Africa 2014 Stellenbosch, South Africa) and the Makoko communal lands adjacent to Kruger National Park have also had biomass increases (T. Swemmer 12th Savanna Science Network Meeting, Skukuza, Kruger National Park). However, bush encroachment has also been recorded across a span of South African land uses (Buitenwerf *et al.* 2012), with woody plants dominating large parts of what was previously open savanna and grasslands (Stevens *et al.* 2015).

The bush thickening trend in our study area is likely a combination of newly established woody encroachers as well as coppice regrowth from harvested stems. Indeed, previous woodfuel supply-demand models have significantly underestimated the regeneration potential of savanna woodlands through coppice response; in all likelihood, this led to an underestimation of size-specific and annual growth rates, as well as the resultant biomass standing stocks (Chapters 2-3). Shrub level increases were present in all the surveyed communal lands (Chapter 3) which suggests a background bush thickening rate. Increasingly, research is emerging that climate change and atmospheric CO_2 enrichment is driving bush encroachment (Bond & Midgley 2012; Buitenwerf *et al.* 2012; Stevens *et al.* 2015). Usually cattle farming is associated with vegetation changes; the shifting grazing localities also mean that the effects of cattle on the landscape (e.g. increasing soil nutrients through defecation, increasing moisture availability & lowering fire frequency through grass removal, and high grazer selectivity) are widespread (Moleele *et al.* 2002). Bushbuckridge has a historic land use legacy of commercial cattle farming, as well as that of the current subsistence livestock husbandry which serves multiple uses for livelihoods (Dovie *et al.* 2006) could influence vegetation patterns. Although there is a background bush thickening rate, probably related to global drivers (e.g. atmospheric CO_2 fertilisation), the differential rate (Chapter 2) and pattern (Chapter 3) of shrub level increases between and within communal lands suggest bush thickening is enhanced by local level drivers (i.e. the anthropogenic use of the communal lands for harvesting and livestock grazing). In this regard, I concur with Archer *et al.* (1995) and Stevens *et al.* (2015) that woody invasion in semi-arid systems is likely an interactive

combination of both local and global factors, with local effects being the direct cause, but facilitated by global factors.

It is possible that harvesting is acting as a thinning mechanism, reducing the competition for resources between individual plants and fuelling increases in size-specific growth rates, especially in coppice with fully-developed adult root systems. Dense stands with small trees yield more woody biomass than stands of fewer, large trees as a result of size-specific growth rates influencing productivity (Caspersen *et al.* 2011). This has implications for a positive feedback cycle of more fuelwood harvesting driving low-height bush thickening and, potentially, more harvestable wood. However, this has knock-on effects for plant recruitment as the coppice may not reach reproductive maturity before it is harvested. This renders adult trees 'functionally juvenile' (Twine 2005). Fewer seedlings in the population reduces the future population's survival rate (Lykke 1998). Indeed, both fewer reproductively mature plants and fewer seedlings were found in harvested areas relative to protected areas in Bushbuckridge (Neke 2005).

Bush thickening can be seen as a systemic ecosystem ill that is detrimental to ecosystem functioning (Oba *et al.* 2000; Meik *et al.* 2002; Asner *et al.* 2004), but it can also be seen as an opportunity. The use of sustainably managed coppice regrowth as fuelwood has been suggested numerous times (Shackleton 1993; Shackleton 2001; Kaschula *et al.* 2005a). Information has been collected about species response to harvest (Kaschula *et al.* 2005a), methods (Shackleton 2000a) and location (Kaschula *et al.* 2005b) of harvesting. However, there is little information on growth rates of coppice that would inform harvesting frequency and long-term sustainability of the woodlands. There is hope that bush encroachment, the coppice response, and the interactions with changing climate and atmospheric composition, for sustainable coppice harvesting to become the 'cure' for ecosystems under continued wood harvesting pressure. The coppice regrowth could be managed through 'tree thinning' programmes which will provide bush clearing services to maximise grazing, provide fuelwood and, potentially, the establishment of a sustainable, rural, carbon economy which could be geared towards long-term restoration of the landscape. Nevertheless, the repercussions of bush encroachment/thickening in communal lands will have implications for the direct-use values of ecosystem goods and household vulnerability to shocks (Twine *et al.* 2003a). The current realisation is that traditional methods for managing bush thickening (e.g. clearing, fires) may no longer suffice and innovative ways to deal with this problem are

needed. This body of work demonstrates that land-based resource management needs to be more nuanced to co-adaptability of human-environment systems.

6.3 Loss of structural heterogeneity

If the biomass increases reported in this thesis had been interpreted in the absence of detailed three-dimensional data, we would have mistakenly inferred from the biomass increases as well as higher slopes in disturbance gradients (Fisher *et al.* 2012) that the communal lands were recovering. However, I have demonstrated that these biomass increases are solely in the shrub layer, and with the combined influence of loss of large trees in highly utilised landscapes (Chapter 5), are indicative of structural homogenisation of heavily utilised communal lands. Humans can act as 'functional megaherbivores': their impact on savanna vegetation <5m in height exceeds that of both elephants and fire (Wessels *et al.* 2011) and their contribution to tall tree loss is substantial (Chapter 5). Structural complexity reduction has also been recorded in east African miombo savannas where 50% of the woodlands was lost with an accompanying 599% increase in bushlands as a result of communal land use (Luoga *et al.* 2005). Based on the findings in this thesis, I posit a relationship between intensity of natural resource use, vegetation dynamics and structural heterogeneity with repercussions for ecosystem and human resilience, as well as biodiversity and ecosystem function (Figure 6.1). At low levels of natural resource use, both height-specific gains and loss of vegetation structural metrics are low and structural heterogeneity of the vegetation is maintained (Figure 6.1). As usage intensity increases, so do losses in vegetation structural metrics; fairly obvious as vegetation is being extracted. However, there are height-specific gains in some vegetation metrics as compensatory growth occurs with increasing harvesting. Intermediate use scenarios may contain increased biodiversity (Shackleton 2000b; Smart *et al.* 2005). The paradoxical relationship strengthens with increasing usage intensity, resulting in a situation of high growth metrics, predominantly in the shrub layers (Figure 6.1). Under such high intensity, loss metrics decrease as there are less tall trees to remove. Structural heterogeneity collapses and loss metrics decrease as there are fewer trees to harvest (Figure 6.1, 6.3b). This relationship demonstrates the importance of height-specific data collection in vegetation monitoring in social-ecological systems. Exceptions to this hypothesised relationship of vegetation gains and losses exist, depending on the strength of tribal control of

the communal land. Remote, low use intensity communal lands and nature reserves experience hard wood poaching with hand-axes and chainsaws, particularly *Pterocarpus angolensis* (*pers. obs.*), which would affect structural metrics. Conversely, in high use communal lands, culturally important trees, e.g. *Sclerocarya birrea*, may be conserved for non-timber uses (Shackleton *et al.* 2003), which would result in a bi-modal structural profile of a homogeneous shrub layer, and conserved large trees.

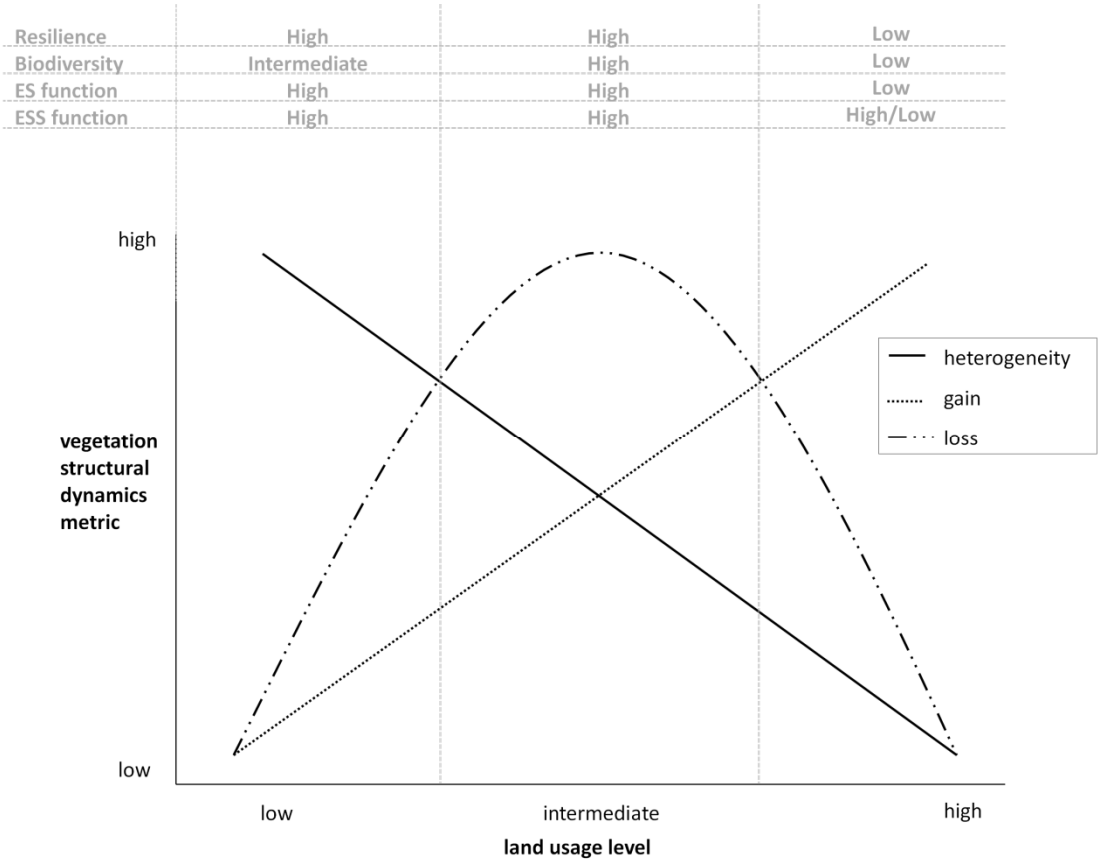


Figure 6.1. Conceptual change in vegetation structural metrics in relation to a natural resource extraction gradient. Increasing natural resource use decreases vegetation structural heterogeneity, but vegetation structural dynamics show varying height-class specific responses. Corresponding conceptual links to resilience, biodiversity, ecosystem (ES) function and ecosystem service (ESS) function are shown in relation to usage intensity.

This paradoxical phenomenon, of high growth under high wood extraction scenarios, contradicts the 'fuelwood crisis' narrative that centres on energy-deforestation links. This thesis demonstrates that the crisis narrative, and its contemporary echoes (e.g. Chambers & Conway 1991), is misplaced and unconstructive when studying natural resource reliant communities. A more nuanced view of sustainability is emerging in the current literature (e.g. Conway et al. 2015) which acknowledges that national and regional resilience to shocks may be compromised, but this manifests unevenly as rural communities and informal sector economies are more flexible and adaptable to shocks. The continued focus on woodfuel extraction driving woodland collapse obscures the real threats (e.g. uncontrolled settlement expansion) behind ecosystem degradation, putting all components of the social-ecological systems at risk, and further delaying constructive engagement on mitigation of the 'real' threats, as well as undervaluing crucial adaptive ecosystem responses to human-mediated disturbance.

6.4 The future of African land-use pressure

Studies on Bushbuckridge Municipality, an electrified area, which maintains extensive reliance on natural resource use, can assist in plotting a way forward for future African land-use pressure. Here, we have examined Bushbuckridge social-ecological systems as part of a rural livelihood framework, but Bushbuckridge is increasingly becoming more urbanised and serves as a snapshot of the future of African land-use pressure (Figure 6.3, 6.4). By 2050, urban sprawl is projected to increase >12 times (Angel *et al.* 2011). Most of these increases will be a reclassification of rural areas as peri-urban as a result of burgeoning human population densities (McHale *et al.* 2013). Not only are rural areas in Africa becoming more urbanised, uncontrolled growth of existing African cities is subsuming previously rural areas. For example, Nairobi's average population density increased from 12 people ha^{-1} in 1979 to 54.4 in 2010 and is predicted to reach 81.1 people ha^{-1} by 2020 (Adebayo 2012). However, localised densities can attain 2000 people ha^{-1} in Kibera, a Nairobi slum (Adebayo 2012). Most sub-Saharan cities have insufficient basic infrastructure. Only 20% of sub-Saharan African's population had access to electricity in 2010, but 53% had access to mobile phones (AfDF 2012). Low-income urban sprawl is characterised by uneducated and unskilled migrants with low or intermittent levels of employment. As a result, these populations are

heavily reliant on natural resources. Cumming *et al.*'s (2014) model describes the rural-urban transition from a sustainable social-ecological system to one which is still dependent on ecosystem services, but de-coupled from awareness of environmental degradation. Increasing industrialisation and human population growth move society from a "green loop" (stable, self-regulating feedbacks between ecosystem use and environmental degradation) into a "red loop" (an economy driven by non-ecosystem services) (Cumming *et al.* 2014). With the increasing human populations (and population densities), many African rural and urban sprawl areas are on a "green trap" trajectory (Figure 6.2) – an unstable system of environmental degradation and erosion of human well-being. The challenge is to transition these areas to "red loop" states, whilst mitigating the effect on ecosystems by maintaining current, or decreasing, consumption patterns (Cumming *et al.* 2014). Maintaining ecosystem service integrity in the face of increasing urbanisation will increase human quality of life and potentially act as mitigation to climate change events. Bushbuckridge, as an increasingly peri-urban area serves as a baseline to how increasing demand for natural resources affects provisioning ecosystem services. Our future African landscape threatens to be a homogeneous layer of impenetrable, low-level shrub: a degraded landscape unable to provide ecosystem services (Figure 6.1, 6.3b) in an increasingly unstable climate (political, social and natural). African slums are already an indictment of state failure. With increasing flows of fuelwood into low-income urban sprawl areas, creating sustainable urban energy solutions might be the most effective environmental management plan for rural areas (Soussan *et al.* 1990). Compounding local need for natural resources is rising global demand for ecosystem goods (Figure 6.4f), where developed countries are effectively outsourcing their own environmental costs. An extreme example is the case of 'blood timber' extraction from the Central African Republic (CAR) to luxury European markets; timber exports during the CAR civil war exceeded diamond exports, funding political strife (Global Witness 2015). Moreover, with decreased state GDP tied to predictions of increased climate change-induced rainfall variability, it is crucial to buffer the capacity of the coupled social-ecological systems to serve as a buffer against the coming water-energy-food crisis (Conway *et al.* 2015). Perhaps management of the Bushbuckridge communal land system could serve as a viable approach for sustainable development in other African cities, one that would buffer the state's capacity to provide basic energy needs and human well-being simultaneously.

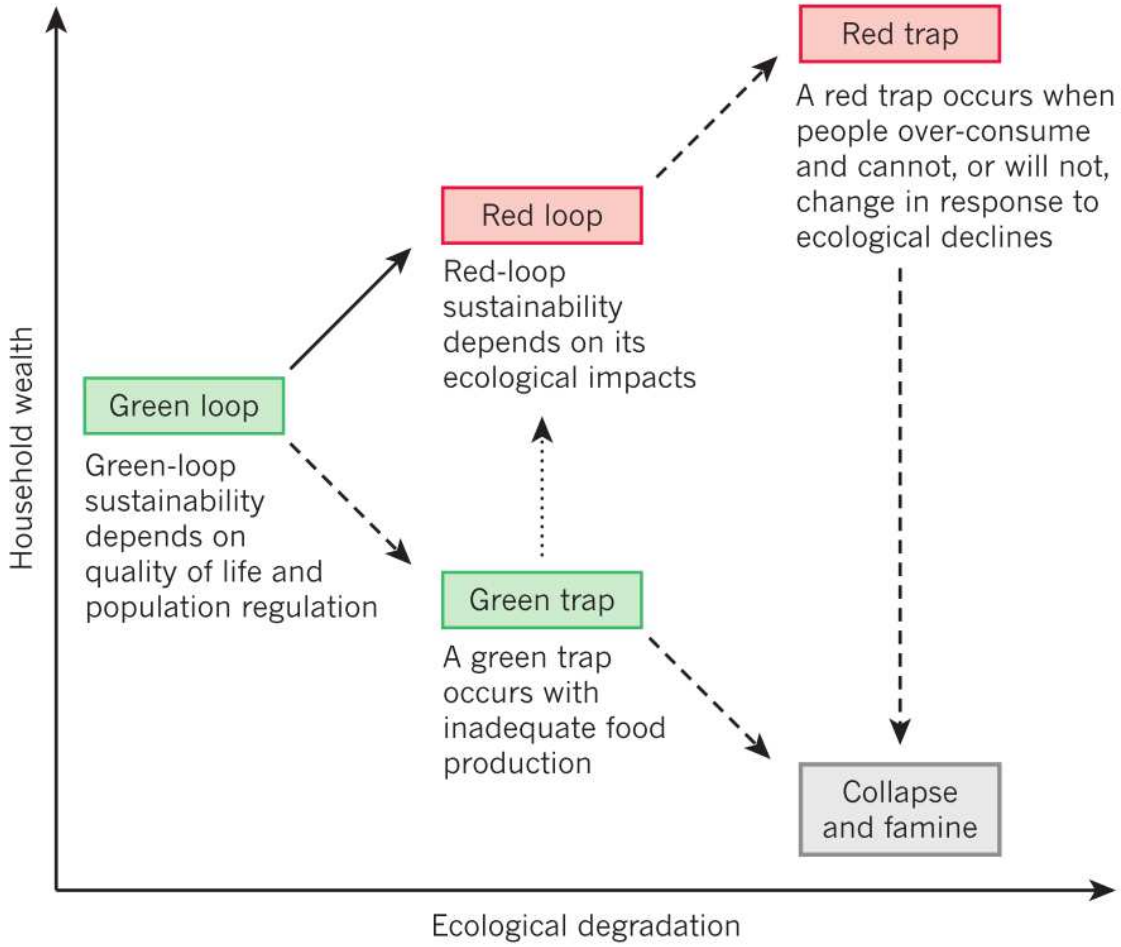


Figure 6.2. Rural-urban transition states and traps. This is a framework for understanding trade-offs between household wealth and ecological degradation. Societies exist in a 'green loop' when a sustainable relationship exists between ecosystem use and human population size. This is possible when society is directly linked to their ecosystem service use and social-ecological feedbacks are clear. If the population increases without restructuring the social-ecological relationship, societies fall into a 'green trap', a cycle of rural poverty and environmental degradation. If technological advances industrialise society, it exists in a "red loop" – an economy based on non-ecosystem service based products where environmental costs are often externalised – here sustainability depends on ecological impacts. A "red loop" society falls into a "red trap" when unsustainable use precipitates ecosystem decline. Dashed lines indicate avoidable transitions, while the dotted line is the challenge facing African societies – moving from a "green trap" into a "red loop" whilst maintaining sustainability and awareness of environmental dependence. This is the ideal scenario of improving human well-being and quality of life without compromising that of future generations. [taken from Cumming *et al.* (2014)].

Figure 6.3. a) Bushbuckridge Municipality is increasingly becoming a peri-urban landscape. b) High intensity wood harvesting has reduced the structural complexity in the communal lands. This has implications for continued ecosystem service provisioning and ecosystem functioning and compromises the resilience of the ecosystem and the communities reliant on it. Photo credits are the author's own.

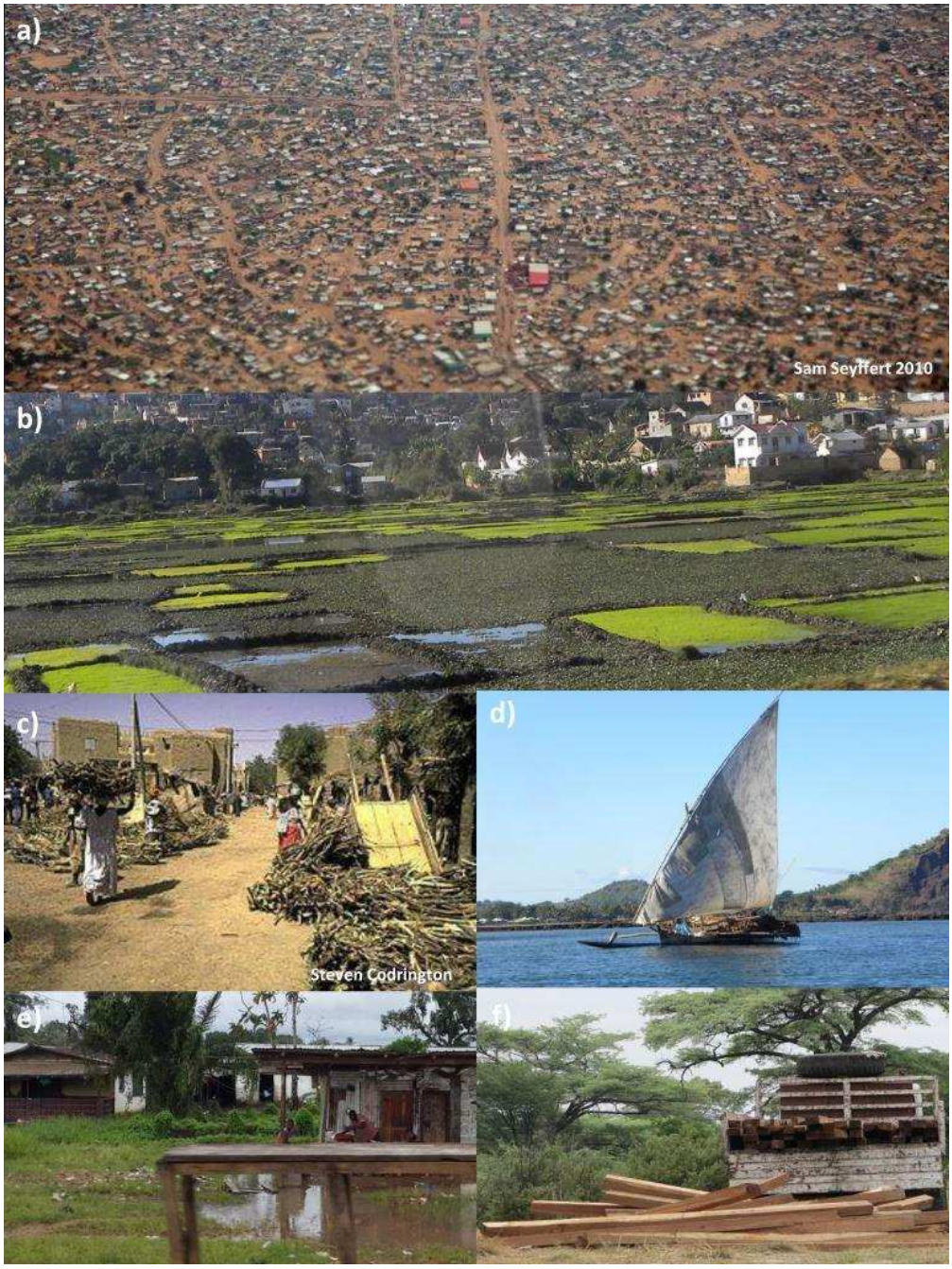


Figure 6.4. The future of African development is in sprawling urban landscapes, with compromised social-ecological systems. a) Uncontrolled development in Luanda, Angola has subsumed remaining natural land. b) Major African cities have become combinations of urban business districts, slums and degraded commons, such as in Antananarivo, Madagascar and e) Monrovia, Liberia. The loss of ecosystem provision in urban areas drives the commodification of fuelwood, expanding the harvesting footprint in other areas and transported to fuelwood markets. c) A fuelwood market in the Democratic Republic of Congo and d) transportation of fuelwood in Nosy Be, Madagascar. Developed countries will often outsource local ecosystem services. e) Illegally traded *Pterocarpus angolensis* timber is being transported from a sawmill in Zambia, destined for China. Unless otherwise stated on the image, photo credits are the author's own.

6.5 Opportunities and constraints

6.5.1 Technical constraints

While it is not unprecedented to base LiDAR-derived models calibrated against corresponding field data on subsequent or previous LiDAR-campaigns with no corresponding field work (Dubayah *et al.* 2010; Huang *et al.* 2013; Meyer *et al.* 2013), ideally the models would perform better and be more ecologically meaningful if separate predictive models were based on temporal matching of LiDAR data and fieldwork. This is potentially a method to mitigate change in leaf area index (LAI) error introduced when comparing canopy cover change over time. LAI and phenology are under researched in the LiDAR change detection literature, but the frequency of LiDAR hits through the vegetation canopy will be affected by leaf presence, as well as orientation. These influences were accounted for as far as possible by collecting the LiDAR data in the same month during each campaign. However, LAI can also be affected by differential rainfall between years or even strong winds (Ryu *et al.* 2012). It is also likely that vegetation in the shrub layer has a higher LAI than tall trees, making LAI complex across three-dimensional space. There has been a record of higher numbers of thinner, taller stems in the study area over time (Matsika *et al.* 2012).

The main data set in this thesis is based on the canopy height model (CHM) which is in turn derived from the difference between the digital terrain model (DTM) and the top-of-canopy digital surface model (DSM). Thus, errors in the DTM and DSM are propagated through the CHM. Most DSM and DTM errors are derived from either filtering points into terrain and non-terrain points (Kraus & Pfeifer 1998), particularly in LiDAR with low hits m^{-2} (Wagner *et al.* 2004), and interpolation of filtered points into DSM and DTM's. The CAO LiDAR has an achieved laser spot spacing of 4 shots m^{-2} and up to 4 returns per pulse, ensuring high accuracy of both point filtering and interpolation. Although different LiDAR sensors were used between successive surveying campaigns, the pre- and post-processing methods remained consistent, ensuring that we could compare like with like by controlling for algorithmic and processing errors. Errors in the CHM would manifest in the tree height validation, which was highly accurate ($r^2 = 0.92$, $p < 0.01$ for the coarsest CHM; Asner *et al.* 2009). An additional limitation of using two different sensors is the reset time – the minimum distance between vertical returns that the sensor can discriminate between. Thus, a sensor with a shorter reset time will resolve vertically clumped vegetation more accurately than a sensor with a longer reset time. This difference is partially mitigated by the voxel

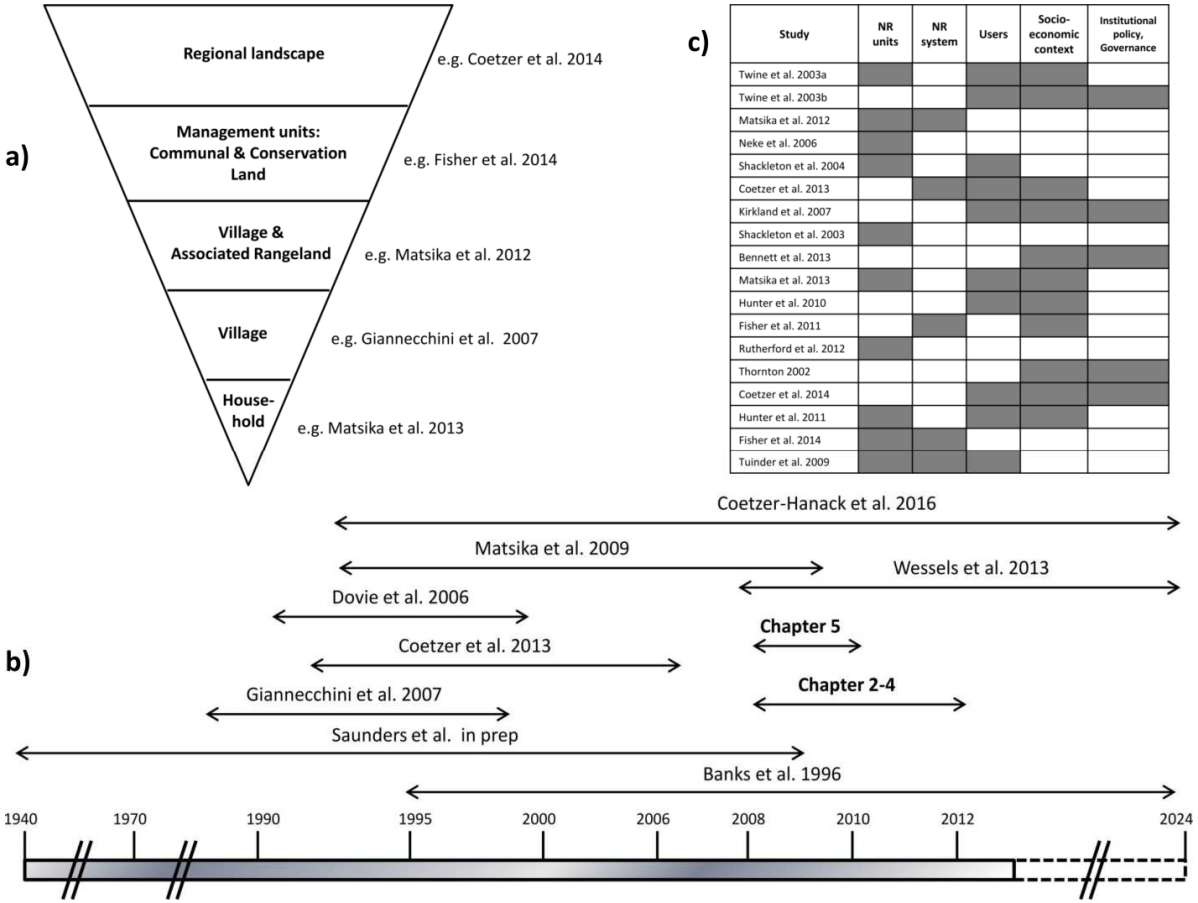
normalisation process, but can pose a difference in comparing fine-scale height changes between years. The difference in sensor reset times between the CAO-Alpha and CAO-2 AToMS sensors was ~0.72m – any change ≤0.72m could be considered sensor noise. Hence, the threshold of height change at ≥1m in Chapters 2 and 4 was a conservative one in order to detect 'real' change. In addition, this is less of a concern in Chapters 2 and 5 as maximum vertical height change per tree object is considered rather than a per pixel approach. Ideally, vegetation structure monitoring should be conducted with the same sensors, but we mitigated potential error where possible and have faith in the results considering the extremely accurate outputs of both sensors.

6.5.2 Recommendations

I have identified a number of research gaps and prospective opportunities, both stemming from my literature search on relevant topics and for the subregion in general. In addition, the outcomes of my research have posed more questions, particularly around the potential implications of biomass increases in heavily-used landscapes. I put forward the following recommendations:

a) Although this thesis contributes significantly to the body of knowledge of woody vegetation dynamics in human-modified landscapes, there is still a dearth of synthesised information for these social-ecological systems (SES) in order to implement effective strategies to deal with the reality of fuelwood use, despite access to electricity. There are a number of studies, many by our larger research group, in the Bushbuckridge region that span various spatial and temporal scales, as well as across a number of disciplines (Figure 6.5). These studies are comprehensive in their specific foci, but have not been integrated in a meaningful manner to make future policy interventions effective in these coupled systems. We do not know if trends occur consistently through the scale hierarchy (both temporally and spatially), or whether a comprehensive transdisciplinary synthesis would reveal causality of the patterns seen through the lens of other disciplines (Figure 6.5). This, yet unexploited, synthesis opportunity of the Bushbuckridge SES would provide an invaluable case study for understanding other systems under similar pressures.

b) Bush thickening in human-utilised systems provides a number of concerns (and potential opportunities) that need further investigation:



Study	NR units	NR system	Users	Socio-economic context	Institutional policy, Governance
Twine et al. 2003a	■		■	■	
Twine et al. 2003b			■	■	■
Matsika et al. 2012	■	■			
Neke et al. 2006	■				
Shackleton et al. 2004	■		■		
Coetzer et al. 2013		■	■	■	
Kirkland et al. 2007			■	■	■
Shackleton et al. 2003	■				
Bennett et al. 2013				■	■
Matsika et al. 2013	■		■	■	
Hunter et al. 2010			■	■	
Fisher et al. 2011		■		■	
Rutherford et al. 2012	■				
Thornton 2002				■	■
Coetzer et al. 2014			■	■	■
Hunter et al. 2011	■		■	■	
Fisher et al. 2014	■	■			
Tuinder et al. 2009	■	■	■		

Figure 6.5. A selection of examples of research, associated with our greater research group, in Bushbuckridge covering: a) various spatial scales from the household level to the regional landscape, b) different temporal scales based on long-term aerial and LANDSAT imagery from the 1940's and 1990's, respectively, as well as repeat household and fieldwork studies from the 1970's onwards and fine-scale, 3-D LiDAR research. There is research which includes future predictions on woodfuel supply-demand and land-use change. c) The studies also span various disciplines and have different foci from the social-ecological system to those that focus on one or more of the following components: natural resource units (NR units, such as timber and non-timber products), the natural resource systems (NR systems, such as communal land ecosystems), those that focus on various aspects of the natural resource users themselves as well as their socio-economic context; and the institutional governance and policy frameworks they exist within.

- A recent carbon model has shown that vegetation increases in the southern hemisphere's semi-arid systems was the reason for the record 2011 terrestrial carbon sink; the implications being that El Niño–Southern Oscillation (ENSO) swings, could shift importance from tropical forests to semi-arid systems with regard to carbon sinks (Poulter *et al.* 2014). Moreover, above-ground biomass fluxes in savannas were associated with vegetation response to rainfall variability in water-limited systems (Liu *et al.* 2015). Thus, knowledge of the carbon storage dynamics of semi-arid systems becomes more urgent in the face of increasing uncertainties of global change. Additionally, feedbacks between global and local drivers of bush thickening are not understood well enough to provide meaningful knowledge to terrestrial carbon sinks in semi-arid systems.
- The heterogeneity paradigm emphasises that biodiversity and ecological systems function across the full spectra of biotic and abiotic constituents, as well as across the complete spatio-temporal hierarchy (Pickett *et al.* 2003). Thus, heterogeneity is not an easily defined measurement. However, the Kruger National Park is managed for acceptable levels of heterogeneity using the Thresholds of Potential Concern (TPC's) model (Biggs & Rogers 2003). Fisher (2013) in her comparison of management effects on woody vegetation structure across both private and public protected areas and communal lands suggested that the success of TPC's for management strategies could be applied to the communal lands through user-identified thresholds. Whilst this is a valuable method of monitoring and managing for heterogeneity, in the context of woody vegetation heterogeneity, different height classes operate on different temporal scales. That is, managing for heterogeneity in the present period does not mean managing for heterogeneity in the future. To effectively predict future woodland structure, we need to add fine-scale data over broad extents on stage-class survival, from germination level. For example, differential germination and seedling survival success has been recently explored across a rainfall (Stevens 2014) and temperature gradient (Stevens *et al.* 2014) in key savanna woodland species. The low height classes are crucial to monitor as they determine the future structure and composition of the woodland.
- Following on from the above, there is a need for information on size-class specific growth rate data at different usage levels. Experimental plots to test density-dependent species and size-class specific growth and mortality (Schmitt *et al.* 1987) would be a valuable contribution to the implications for bush thickening effects, the sustainability

of harvesting different size-classes and potential feedbacks on landscape (and global) scales. These results could then be upscaled with LiDAR to provide a monitoring strategy for long-term sustainable management. Currently, bush thickening monitoring over large areas is only possible with LiDAR (Secades *et al.* 2014).

- The opportunities of utilising the increasing vegetation in the lower height classes for sustainable fuelwood are exciting. As mentioned earlier, the sustainability of continued harvesting of this vegetation would need to be studied. However, we also need to ascertain whether the 1-5m height classes provide fuelwood of the appropriate quality or time-efficiency – multi-stemmed coppice may have more wood in total biomass, but it requires more effort to extract and more stems are needed to cook with to derive the same energy. Our study is also not species specific and we cannot observe species-specific changes, i.e. if the increases are occurring in the preferred fuelwood species (e.g. *Combretum collinum* is a preferred fuelwood species over *Lantana camara* (Shackleton 1993)). In addition, identifying the species which are flourishing at the heights this research has identified could determine if these increases are newly established woody encroachers, a coppicing response from harvested species, invasive alien plants in these communal lands, or various combinations of these.
- Previously, I raised concerns with the effects of LAI on LiDAR change detection data and suggested that differently calibrated biomass models could possibly mitigate some of the differences in LAI. However, I found very little useful information during my search on the LiDAR-LAI interaction. There is considerable need for LAI comparisons between field and remote sensing products, between the products themselves and over time.

c) Poverty-traps are shaped by the interactive relationship between people and the social-ecological environment (Clark & Dickson 2003; Folke *et al.* 2010), often resulting in a causal loop of "fixes that fail" (Senge 1990; Cumming 2011). These result from immediate 'fixes' to the challenges NR-dependent societies face, leading to unintended consequences on the social-ecological system (SES) that supports them. In this case, communities' inelastic demand for fuelwood (Matsika *et al.* 2013) and resistance to switching to electricity (White *et al.* 1997; Madubansi & Shackleton 2007) have driven them to harvest live wood from communal resources unsustainably and led to the development of a fuelwood economy (Twine *et al.* 2003b). However, the accompanying bush thickening and structural

homogenisation (Chapter 2) with attendant land degradation and reduction in ecosystem service provision are a slow variable feedback. Slow dynamics are particularly important in SES as they are responsible for the maintenance of resilience and are involved in SES regime shifts (Cumming 2011). Moreover, the most important variables in SES interactions should show some degree of quantifiable decay as proximity or connectivity decreases (Cumming 2011) which can be seen in the biomass and vegetation structure disturbance gradients around roads and settlements (Chapter 2,4). Although this research demonstrates the slow dynamics consequences of the "fixes that fail", we do not fully understand the form of this bush thickening (e.g. coppice response, newly germinated woody species), likely interactions and consequences between different types of land-use (e.g. livestock grazing and wood harvesting interaction), the relative contribution of global drivers (e.g. CO_2 fertilisation) and the buffer capacity of the ecosystem (e.g. woodland regeneration rates, functionally juvenile coppice stands). Considering the fundamental importance of slow dynamics on ecosystem functioning, the answers to these questions are likely all linked in complex, interactive feedback systems, but need to be understood if intervention and mitigation strategies are to be effective. Understanding the slow dynamics in an ecosystem characterised by fuelwood harvesting could contribute to operationalising resilience. In this case, the ecosystem's 'identity' can be defined by the nature of the fuelwood-harvesting interactions and components, and the resilience of the SES can be defined by quantifying this 'identity' (Cumming & Collier 2005). This approach could be developed to ascertain the Bushbuckridge SES's potential to change its fuelwood-harvesting/supplying identity to a different identity, such as one where woodland regeneration above 5m in height ceases, providing reduced fuelwood services and grass biomass. This system could be classified as a novel ecosystem with a different functional suite (Hobbs *et al.* 2014). For example, goat herding becomes more profitable than cattle herding in such a scenario.

d) Although fuelwood is acknowledged as a predominant energy source in South Africa, despite electrification, and that dependence on fuelwood is actually expected to grow in the future, there is little real action from the policy level to address this. The South African government deems unsustainable fuelwood harvesting a "necessary evil" if it contributes to human well-being (Ministry of Water Affairs and Forestry 1997); but not enough emphasis is being placed on the increasing vulnerability of natural-resource dependent people in the face of ecosystem service failure in which both people/communities and the environment face a coupled-collapse. Although the National Forests Act (No. 84 of 1998) specifies monitoring

and management of woodland resources, there is a lack of landscape scale data (let alone detailed 3-D data for bush thickening monitoring) for the current or future status of the woodlands. These are significant challenges which require considerable attention from national and provincial government, and more importantly, discernible action.

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