The biomass and biodiversity of African savanna woodlands: spatial patterns, environmental correlates and responses to land-use change

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Declaration

The candidate confirms that the work submitted in his own, except where indicated otherwise. No part of this thesis has been submitted for any other degree or qualification.

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Abstract

Tropical savannas and woodlands are the dominant vegetation cover in Southern Africa covering 4 million km^2. Their large spatial extent means they are potentially a globally important store of biomass carbon with implications for global climate, and an area of high biodiversity value. They provide natural resources such as food, fuel and timber that help sustain the livelihoods of over 100 million people. The ability of these savanna woodlands to maintain these important ecological functions is under question due to increases in land use and land cover change. This thesis addresses a set of science questions aimed at (i) improving our knowledge of the amount of carbon and biodiversity stored in these ecosystems and how they co-vary, (ii) how these variables are spatially distributed at landscape scales and the factors which underlie these patterns, and (iii) how they respond over time to human disturbance.

In Chapter 2 I examine how patterns in aboveground woody carbon storage (AGC) are linked to differences in forest structure, tree species diversity and floristic composition across a recently established network of 25 permanent sample plots in south-east Tanzania. Large stems were a significant contributor to plot-level AGC stocks with the top 3% of individuals (>40cm) in terms of size containing 35% of the total measured C. This data can potentially be used to simplify future measurements of biomass in these systems. Tree species diversity was positively related to AGC indicating the potential to align forest conservation efforts. The linear relationship suggests a functional relationship between the variables and is consistent with ecological theory on niche complementarity and selection effects, however based on the available data the mechanisms underlying this relationship can only be theorised. Changes in tree species composition were also noted across plots with differences in vegetation structure between plots explaining 16% of the variation in composition, with environmental differences related to climate and soils explaining only 3%.

In Chapter 3, the focus shifts to understanding larger-scale spatial patterns in AGC. Field plots are spatially limited in this regard, therefore radar remote sensing data was used to generate a map of AGC in order to improve our knowledge on what principally controls its spatial variability at landscape scales. Results showed that factors related topography, climate and soils explained very little of the variation in C stocks across the landscape (r^2 = 15 – 20%). Differences in slope angle and topographic position were important in discriminating between low biomass savannas and moderate biomass woodlands, while differences in annual precipitation were more important in separating woodlands and denser forests. A large proportion of the variation in C stocks (~80%) was unexplained highlighting the role of unmeasured variables. It is suggested that fire may play a key role in shaping patterns in tree species composition and C stocks across these landscapes. This data has important implications for a local REDD+ project which is aiming to generate carbon credits through improved fire management.

In the second part of the thesis the attention shifts to understanding the long-term ecological impacts of shifting cultivation and the sensitivity and resilience of these woodlands to anthropogenic change. In Chapter 4 I examined how carbon stored in trees and soils recover across a 40-year chronosequence of abandoned agricultural land, and how this patchy disturbance impacts spatial pattern in tree species composition and diversity. I show that re-growing woodlands can act as carbon sinks through the accumulation of woody biomass (0.83 tC ha^{-1} yr^{-1}), with soil texture having no clear impact on accumulation rates. Re-growing woodlands were also found to contain considerable biodiversity value by promoting novel species assemblages. Bulk soil carbon stocks appeared to be largely unaffected by the full cycle of shifting cultivation. However in Chapter 5 I show evidence of a previously unquantified legacy effect of land clearance on soil CO_2 production with more recently abandoned fields (c. 6 years) exhibiting significantly higher efflux rates than the older abandonments (15 -25 years) and mature woodlands. Total soil nitrogen was the most important predictor of soil respiration across the plots (r^2 = 0.3) followed by fine root density (r^2 = 0.12). Soils in the younger sites were found to be more nitrogen rich which was used to explain the greater CO_2 fluxes in these areas, however, it is still unclear why this pattern exists.

The thesis concludes by discussing the wider implications of the results, as well as outlining further work needed to solidify some of the conclusions drawn in this thesis.

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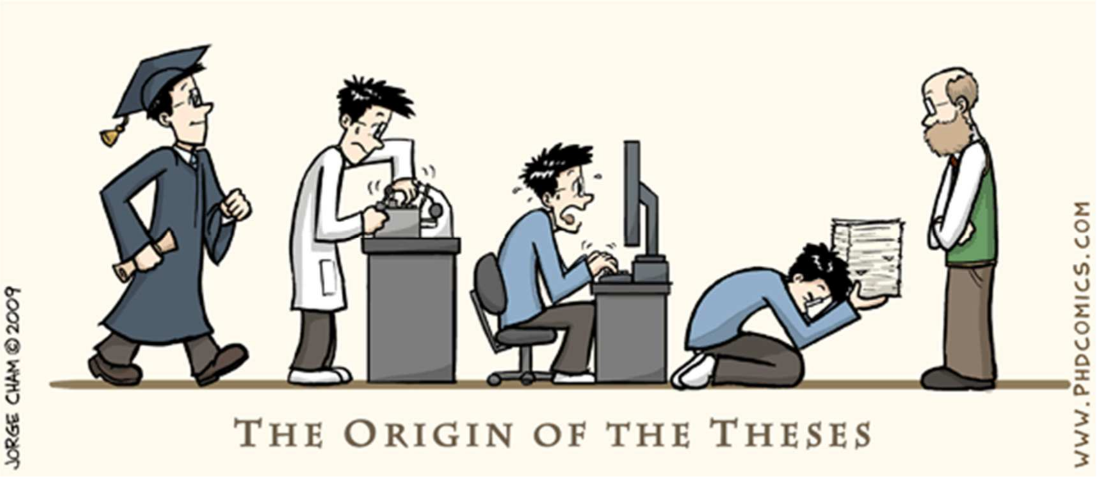
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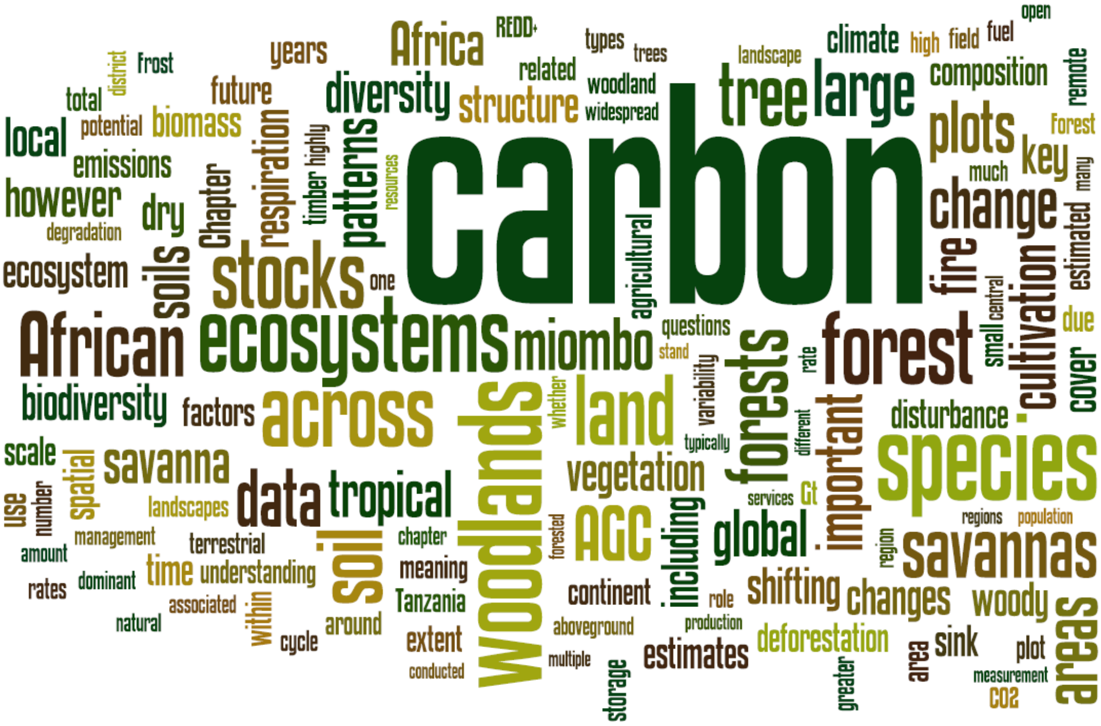
Chapter 1

Introduction to the thesis



1.1 Setting the scene

The most important scientific challenge facing human society in the 21st century is to improve our understanding of how global environmental change will affect the Earth system and the people who inhabit it. Global mean temperatures are now rising at an unprecedented rate, with anthropogenic emissions of greenhouse gases linked to fossil fuel burning and land use change known to be largely responsible for these observed changes in global climate (IPCC 2013). Forest ecosystems occupy a central position in the debate over the future evolution of climate change, having the potential to dampen or dramatically amplify climatic warming (Lenton et al. 2008; Bonan 2008). A considerable proportion of the world's forested ecosystems are spread across the tropical regions of South America, Africa, South-East Asia and Australia (Bonan 2008). They are defined by the United Nations Food and Agricultural Organisation (FAO) as any area with a tree canopy cover of >10% and that span more than 0.5ha (FAO 2010). Within the bounds of this definition, the actual tree cover across tropical forests can be highly variable, ranging from closed canopy systems at the woodier and wetter end of the spectrum, through seasonally dry forests and open woodlands, down to woody savannas with a continuous grass layer. The latter are sometimes considered as 'non-Forest' ecosystems as they often have canopy cover of <10%. In fact, the term 'Savanna' is often used instead by many ecologists to describe any ecosystem where there is a coexistence of grasses and trees that do not form a fully closed canopy (Scholes & Archer 1997; Ratnam et al. 2011). This ambiguity in terms of classification reflects a long standing debate among tropical ecologists over how to categorise these seasonally dry ecosystems (White 1983; Putz & Redford 2010; Ratnam et al. 2011). For the purpose of this section I will sometimes refer to the savannas within the broader spectrum of tropical 'forested' ecosystems, however where a distinction between vegetation types is required they are explicitly named.

However they are defined, the tropical forest and savanna biomes are globally important on multiple levels. From an ecological standpoint, they are the most biologically diverse ecosystems on the planet, accounting for at least 50% of plant species with many of these endemic to the particular habitats in which they occur (Frost 1996; Myers et al. 2000; Howell & Msuya 2012; Platts 2012). The diversity of species they support help to provide a myriad of ecosystem services such as food, fuel and construction materials which help to support the livelihoods of an estimated 1.4 billion people (FAO 2008).

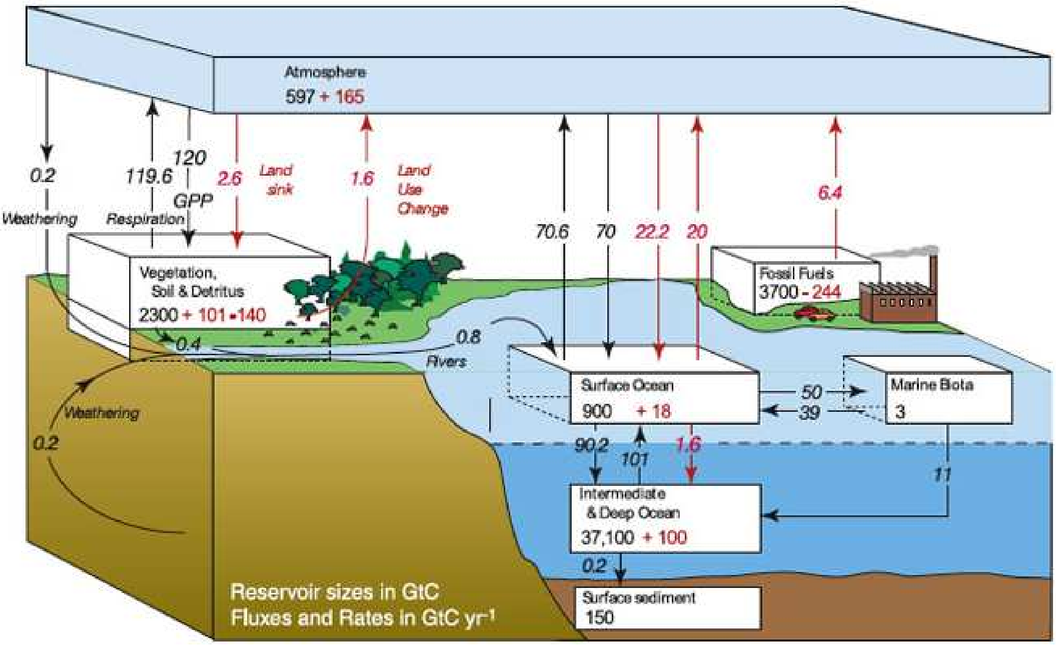


Figure 1.1 – The global carbon cycle showing estimated sizes of the atmospheric, ocean and terrestrial carbon pools in **black** (Gt) and the net annual fluxes between them in **red** (Gt C yr^{-1}). Note that the component pools and fluxes differ slightly from those reported in the text. Source: Climate Change 2007: The Physical Science Basis, IPCC (2007)

They also form an integral component of the global carbon (C) cycle by absorbing vast amounts of carbon dioxide (CO_2) from the atmosphere into living biomass via photosynthesis, a flux known as gross primary production (GPP) (Beer et al., 2010; Figure 1.1). Nearly 50% of all terrestrial biomass is located in tropical forests (Bonan 2008) approximately half of which is carbon (Schlesinger & Bernhardt 2013). The rainforests of Amazonia, Central Africa and SE Asia are the most carbon dense of all tropical forest ecosystems, storing around 200 – 225 tC ha^{-1} (Slik et al. 2010; Quesada et al. 2012; Lewis et al. 2013) Seasonally dry forests and savannas are considerably less carbon dense – typically storing between 2 - 80 tC ha^{-1} in living biomass (Grace et al. 2006). The lower carbon storage capacity of savanna ecosystems highlights the key role of fire and other anthropogenic disturbances that suppress the accumulation of biomass carbon (Murphy & Bowman 2012). Yet despite these large differences in standing C stocks, at the global scale they are similar in terms of total GPP which is attributable the greater spatial extent of savanna biome (Grace et al. 2006; Beer et al. 2010). The productivity of these forested systems is unparalleled and has traditionally been explained by extrinsic factors such as the greater precipitation, higher temperatures and greater amount of solar energy that these equatorial regions receive (Beer et al. 2010). However over the last twenty years, there has been increasing ecological interest in understanding whether or not the high biodiversity of these forests also contributes to their high levels of productivity (Naeem et al. 2011; Conti & Díaz 2013). A plant's ability to acquire carbon strongly depends on how well it is able to capture limiting resources such as nutrients and light, particularly in dense, highly competitive environments. At the ecosystem or stand level, a combination of species with divergent resource acquisition and growth strategies is likely to result in greater woody productivity through the effective partitioning of resources, and result in a greater resilience to small change in their supply (Thompson et al. 2009). Empirical support for this diversity-productivity relationship has now been observed in tropical forest ecosystems (Vilà et al. 2007; Thompson et al. 2009; Maestre et al. 2012; Ruiz-Jaen & Potvin 2010; Ruiz-Benito et al. 2014). The aim of this branch of terrestrial ecology to better understand whether losses of biodiversity or certain keystone species due to climate or land use change will impair the future functioning of natural ecosystems by reducing the amount of carbon they can sequester (Cardinale et al. 2012).

At present, the size of the tropical carbon sink is estimated at 2.4 ± 0.4 Gt C year^{-1}, equivalent to around a quarter of fossil fuel emissions meaning they represent an important natural buffer on anthropogenic climate change (Pan et al. 2011). The strength of this sink is not constant over time due to annual fluctuations in rainfall and solar radiation leading to considerable inter-annual variability in the global carbon balance (Le Quéré et al. 2009). The location and size of the terrestrial carbon sink is also highly uncertain being reliant on region-specific estimates of aboveground carbon density and it's changes over time which are bias towards temperate regions and wetter tropical forests (Pan et al. 2011; Wright 2013).

Not all of the carbon captured by forests is fully sequestered in the biosphere; approximately 30 - 60% of the carbon that is assimilated by plants is subsequently released back to the atmosphere via autotrophic respiration from roots and stems, with the remainder used to construct new tissues, otherwise referred to as Net Primary Production (NPP; GPP – plant respiration)

(Chambers et al. 2004; Chapin III et al. 2011). Over time, a significant fraction of NPP is then delivered to the soil through litter-fall and root exudates which form the substrate for soil microbes, bacteria and fungi which break down the soil organic matter, thus constituting the heterotrophic component of respiration (Figure 1.2). A significant proportion of the carbon deposited in the soil is not readily accessible to microbes, especially woodier material which is often much harder to decompose (Chapin III et al. 2011). Tropical soils are therefore capable of sequestering large amounts of organic carbon and can comprise up 60 – 70% of the total ecosystem carbon stock (Ryan et al. 2011), mostly in wetter, more clay rich areas where conditions for decomposition are less favourable (Bruun et al. 2010; Saiz et al. 2012; Woollen et al. 2012).

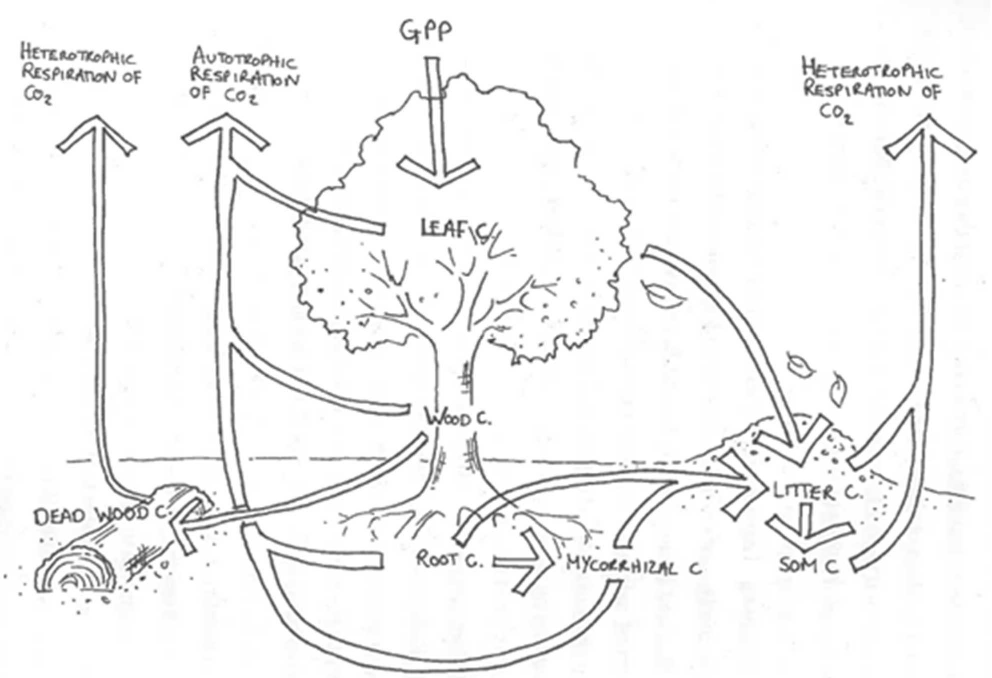


Figure 1.2 – Schematic diagram of the forest carbon cycle showing major pathways through which carbon is cycled through forest ecosystems. The illustration was produced by Veronica Fleming and was obtained with permission from the thesis of Theresa Meacham (University of Edinburgh).

There is often a fine balance between the amount of carbon entering the ecosystem through photosynthesis, and the amount leaving through respiration, with the net difference between the two fluxes often determining whether an ecosystem is a net sink or net source of CO_2. Soil respiration, being the outcome of both root respiration and heterotrophic metabolism of soil organic matter, typically accounts for between 50 – 80% total ecosystem respiration meaning it constitutes an important natural flux to the atmosphere (Schlesinger & Andrews 2000; Metcalfe et al. 2007; Bond-Lamberty & Thomson 2010). Our understanding of soil respiratory fluxes is limited for tropical regions, compared to the large numeric of studies that have been conducted temperate agricultural and forested ecosystems (i.e. Harmon et al. 2011; Giasson et al. 2013). The paucity of available data arises due to a number of challenges in deriving reliable estimates soil gas exchange at large scales, including; (1) the inherent spatial variability of soil carbon stocks and fluxes necessitating intensive sampling (i.e Rossi et al. 2009) and (2) the need for a regular power supply with which to run measurement equipment, which is difficult in remote areas with poor infrastructure (Bahn et al. 2010). Improving our knowledge of soil gas fluxes is crucial given that both the autotrophic and heterotrophic components of respiration will be highly sensitive to future changes in climate, specifically increases in temperate and moisture (Davidson & Janssens 2006); and to changes in land cover and land use, through changes to plant community structure and composition (Barlow et al. 2007; Feeley et al. 2013).

The sensitivity of the carbon cycle to human perturbations is of particular concern given that rising human populations are rapidly transforming the tropical land service (Hansen et al. 2013). Increasing demands for food and fuel are resulting in high rates of deforestation and forest degradation across the tropics. Carbon emissions from tropical deforestation are estimated to be ~1.0 ± 0.5 Gt C yr^{-1} for the period between 2000 - 2007, equivalent to 6 - 17% of global anthropogenic CO_2 emissions, second only to fossil fuel burning in magnitude (van der Werf et al. 2009; Harris et al. 2012). This loss partially offsets the terrestrial carbon sink but also reduces its future effectiveness.

The main driver of these changes is thought to be related to agricultural expansion for the commercial production of both food and income cash crops (Gibbs et al. 2010). These large areas of deforestation are generally well delineated via earth observation (Hansen et al. 2008), however quantifying changes associated with more small scale shifting cultivation is often more challenging (Hett et al. 2012; Ryan et al. 2014). As with terrestrial carbon sink, the magnitude of the carbon losses from tropical deforestation is highly uncertain (~ 50% of the mean) and is largely based on combining already poorly resolved estimates of forest cover change with local carbon stock estimates that are derived from national forest inventories, which typically rely on a handful of plots, many of which are poorly resourced, have inconsistent methods, or the data from which is simply out of date (Grainger 2008; Houghton 2010). Therefore knowing how much carbon is stored in the area that was cleared becomes one the key barriers to constraining carbon losses from deforestation. Improving field based measures of carbon stocks are limited by the high costs of setting up plots in the typically remote and inaccessible environments. In recent years, aboveground carbon estimates based on space-borne remote sensing data linked to field plots for calibration have led to significant advancement's in our ability to map large scale patterns in forest carbon stocks

(Saatchi et al. 2011). However there are still large uncertainties associated with these pan-tropical carbon maps, particularly in areas where there is a paucity of field data (Mitchard et al. 2013). Improvements in carbon mapping and monitoring, particularly for data deficient parts of the world is therefore necessary if we are to reduce the uncertainties in the both the land use change flux, and the terrestrial carbon sink.

1.2 Why is the African continent important in the context of global environmental change?

Over the last decade, the scientific community have started to understand in more detail the complex and unique nature of the African continent in terms of its internal carbon cycle and its significance within the broader context of global environmental change. This is unsurprising given that Africa comprises 20% of the earth's surface, contains around one-sixth of the world's population and has the highest annual population growth rate in the world at ~3% in 2012, three times the average rate of other tropical regions such South America and South-East Asia (UN, 2012). One of the standout features of the African continent is its relatively small contribution to global fossil fuel emissions (~0.2 Gt C yr^{-1}; 4% of global total). However recent estimates have highlighted that African ecosystems contribute 40% (~1.03 Gt C yr^{-1}) of global fire emissions mostly from savanna burning, and 20% of global land use CO_2 emissions (~0.32 Gt C yr^{-1}), the majority of comes from small-scale shifting cultivation (Silva et al. 2011). In Africa, the relative contribution of land use change and deforestation to global CO_2 emissions (35%) is greater than in any other region of the globe and is likely to increase further with expanding human populations (Bombelli et al. 2009; Valentini et al. 2014).

Despite its vast extent, the African continent remains one of the weakest links in our understanding of the global carbon cycle. The component fluxes of the African carbon balance have so far not been adequately determined with any precision. Depending on the methods and source data used, recently published estimates vary from a maximum sink of about 3.2 Gt C year^{-1} (Bombelli et al. 2009), to a much smaller sink of around 0.2 Gt C year^{-1} (Ciais et al. 2009). In contrast, an atmospheric inversion study by Williams et al. (2007) suggested that the continent has a neutral decadal-scale carbon budget. It is now generally accepted that Africa constitutes a net sink of CO_2 somewhere in the region of 0.61 ± 0.58 Gt C year^{-1} (Valentini et al. 2014). This masks the large regional variations across the continent, with the dense tropical forests of central Africa acting as a large sink (Lewis et al. 2009), while the savannas and woodlands of central, eastern and Southern Africa are estimated to be a small source of CO_2, attributable to regular fires, and to a lesser extent agricultural activities (Valentini et al. 2014).

Efforts to better constrain the carbon balance of the African continent is hindered by a lack of permanent forest plots or a network of eddy covariance flux towers in the dominant ecosystems which would allow a better characterisation of the spatial and temporal variations in both C stocks and fluxes. Although the recent CarboAfrica and AfriTRON projects have gone some way to reducing this knowledge gap (see Merbold et al. 2009; Lewis et al. 2009; Fauset et al. 2012), their coverage is still relatively restricted to the forests of central and western Africa meaning there is still a distinct absence of detailed field data from the more spatially dominant savannas and woodlands. An improved understanding of their carbon stocks and productivity of these areas is therefore an important step if we are to better understand the role that Africa plays in the global carbon cycle (Ciais et al. 2011)

1.3 The ecology of African savannas and woodlands

Sub-Saharan Africa contains the largest extent of savanna globally, covering an estimated 15 million sq km^2, or 50% of the African land surface (Grace et al. 2006). The term 'Savanna' is variously used by tropical ecologists to describe a range of vegetation types that vary markedly in their woody structure and composition but which ultimately fall within the broad spectrum of savanna type ecosystems due to the coexistence of trees and C_4 grasses (Scholes & Archer 1997; Ratnam et al. 2011). The savanna climate is characterised by distinct wet and dry seasons with 95% of the annual rainfall falling within a period of 3 – 7 months (Frost 1996). Regular dry season fires are a characteristic feature of all tropical savannas which are fuelled by the senescing grass layer. They are largely started by humans for agricultural clearance and for hunting; however these can often burn out of control leading to widespread degradation.

The most widespread 'savanna' type ecosystem in Africa are the miombo woodlands which extend over 2.7 million km^2 of southern, central and eastern Africa, spanning some of the world's poorest countries, including Tanzania, Malawi, Mozambique, Zimbabwe, Zambia and Angola and the Democratic Republic of Congo (Campbell et al. 2007; Figure 1.3).

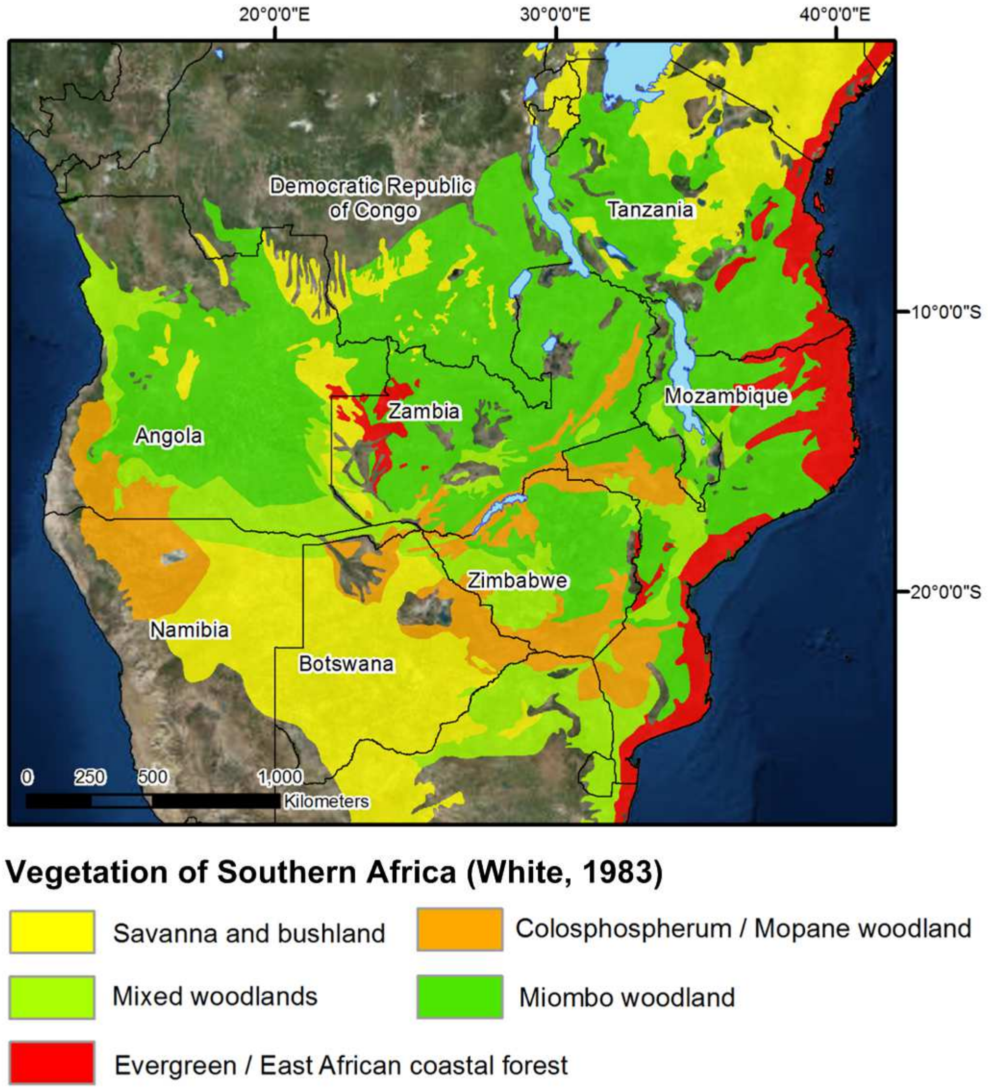


Figure 1.3 – The dominant vegetation types in Southern Africa based on floristic composition. Adapted from White (1983)

They are defined by the widespread dominance of species in the subfamily Caesalpinioideae (family Fabaceae) with 'miombo' the vernacular name for a number of species in the associated genus *Brachystegia*, which along with *Julbernardia* and *Isoberlinia* are endemic to the region. They are highly diverse ecosystems, harbouring an estimated 8500 species of higher plants of which over 50% are endemic, including nearly 350 tree species (White 1983; Frost 1996). The underlying soils are typically highly weathered oxisols and ultisols, which have a low nutrient status and are often well drained and acidic (Scholes 1990; Frost 1996). To persist in these otherwise infertile soils the dominant species utilise ectomychorrizae to obtain phoshorous (Hogberg & Nylund 1981; Högberg 1992) while several others in the Fabaceae have nitrogen fixing nodules. The trees vary in their phenologcal behaviour, ranging from evergreen, fully deciduous and brevi-deciduous, with the latter dropping their leaves late in the dry season to allow a new flush of leaves to come through (Ryan et al. 2013). In terms of tree cover, miombo occupies the midpoint between more open savannas (< 10 – 20%) and denser forests (>60%) (Scholes & Archer 1997). However, spatial variations in soil characteristics and frequent disturbances by fire and herbivory can lead to large differences in tree between areas meaning miombo has been variously described as mesic savanna, open woodland or seasonally dry forest (Menaut et al. 1995; Frost 1996).

Figure 1.4 – Examples of three of the dominant vegetation types found in Southern Africa.

At the woodier end of the savanna spectrum, miombo woodlands eventually grade in to more closed canopy ecosystems, which in Tanzania, Kenya and Mozambique take the form of the East African Coastal Forests (Burgess & Clarke 2000; Figure 1.4). These ecologically important ecosystems once covered large tracts of the coastline but have been greatly reduced in area due to human disturbances. The remaining fragments are global hotspots of diversity and endemism and are considered a priority for conservation due their rapidly diminishing extent and their inclusion of extremely rare and threatened species, some of which are close to extinction (Howell & Msuya 2012; Myers et al. 2000). These forests are considered by some as a climax community to miombo due to the occasional presence of *Brachystegia* in these otherwise floristically distinct habitats (Burgess & Clarke 2000). However this assertion is challenged by others who suggest that these forests exist on more nutrient rich and/or deeper soils and therefore current areas of miombo are unlikely to succeed to denser forests in the absence of fire (Frost 1996; Timberlake 2011).

The processes that drive this landscape-scale (10s km) heterogeneity in vegetation types are poorly defined (Bond 2008). Disturbance by fire is key component of savanna ecosystems and has a strong limiting influence on woody biomass in the savannas and woodlands, however fire is largely absent from the denser forests as they suppress the flammable grass layer (Furley et al. 2008; Ryan & Williams 2011; Hoffmann et al. 2012). At more localised scales, soils exhibit bottom up controls through effects on soil water holding capacity and nutrient availability, both of which are closely linked to local topography,. Miombo appears to favour well drained sandy soils over more clay rich depressions where grasses, and thus fire proliferate (Woollen et al. 2012). At regional to continental scales, the relative abundances of trees versus grasses become gradually more influenced by climatic factors such mean annual precipitation and the length of the dry season (Sankaran et al. 2005; Lehmann et al. 2011). This combination of factors means that deciphering the key determinants is a difficult task, yet understanding *why* certain vegetation types and carbon stocks are *where* they are now is important for predicting how changes in climate or land management (i.e. fire suppression) will influence the distribution of these different vegetation types in future.

1.3.1 Savanna woodlands as human-dominated ecosystems

Humans have had an astonishingly long relationship with the savanna woodlands of Southern Africa, having lived in and extracted resources form these ecosystems for thousands of years (Ekblom et al. 2014). Today, they directly sustain the livelihoods of over 100 million urban and rural dwellers, many of whom live in acute poverty and strongly depend on the substantial natural resources and ecosystem services that the woodland provide (Campbell et al. 2007; Syampungani et al. 2009). The growing demand for food, timber and wood fuels is currently leading to widespread deforestation and degradation, particularly around rapidly expanding urban centres and road networks (Ahrends et al. 2010; Ryan et al. 2014). Current rates of woodland loss are not well established being largely a result of country level statistics which are considered to be unreliable (Dewees et al. 2011), however recently derived estimates via remote sensing indicate that in some regions carbon stocks are decreasing at a rate of around 3% per year (Ryan et al. 2012).

The African continent differs from the rest of tropics in that much is of this change is driven by the expansion of small scale, shifting cultivation, which often forms the main source of income for rural communities (Mertz 2009). This practice involves clearing a small patch of land with the aid of the fire, then cultivating for around 2 - 5 years until soil fertility is depleted, after which the land is abandoned and allowed to regrow (Fisher 2010; Ryan et al. 2014). The constant turnover of land in and out of crop production gives rise to complex mosaic landscapes, with mature, old-growth woodlands interspersed with land parcels at different stages of cultivation and abandonment. At the continental scale, this cycle is estimated to release 0.2 ± 0.14 Gt C year^{-1} to the atmosphere

(Silva et al. 2011), although this loss is partially offset by the subsequent regrowth meaning that secondary reforestation are considered as a means of carbon sequestration (Chidumayo & Gumbo 2010).

Due the widespread usage of shifting agriculture, areas recovering from land clearance are now becoming an increasingly dominant vegetation cover in the tropics meaning they potentially have an important role in terms of carbon and biodiversity storage (Hett et al. 2012). Theories such as the intermediate disturbance hypothesis posit that diversity should peak in mid-successional stands when species coexistence between ruderals and canopy dominants is maximised (Sheil & Burslem 2003). Support and rejection of this hypothesis have been reported with almost equal frequency (Kershaw & Mallik 2013), however affirmation is generally more common among studies conducted in dry forest ecosystems (Kalacska et al. 2004; Bongers et al. 2009; Mwampamba & Schwartz 2011). The extent to which the carbon lost during deforestation recovers depends on how long the field is left fallow and the rate at which carbon accumulates in vegetation and soils. Fallow lengths appear to be decreasing more land is required for cultivation, thus limiting the extent to which re-growing stands can act as carbon sinks (Pan et al. 2011; Grogan et al. 2013). However there is still limited data on how fast carbon accumulates following agricultural abandonment, and the impact that this patchy disturbance has on other ecosystem services such as biodiversity (Williams et al. 2008; Mwampamba & Schwartz 2011) .

Traditionally, these woodlands have been of little commercial value to farmers due to the relatively infertile soils and the prevalence of Tsetse flies which largely prevent the keeping of cattle (Frost 1996). This is changing with shifting cultivation systems gradually being replaced by more intensive farming practices across many tropical regions indicating a shift to more export-oriented activities (van Vliet et al. 2012). In Africa, most of these changes are being driven be external investments from countries such Japan, Brazil and China with aim of establishing large industrial farms in order to produce low cost commodity crops such as soybeans for export. There is general perception that shifting cultivation is a destructive and degrading land use practice (Mertz 2009). The expansion of commercial agriculture is seen as a way improving agricultural yields and financial returns for farmers and is considered a more sustainable route for development in African woodlands (Jones and Tarp, 2012). Given the close dependence of people on woodland resources, and the importance of shifting cultivation for local livelihoods, there is concern that removing this practice from the landscape will reduce the provision of key ecosystem services such as biodiversity, which may have important consequences for local well-being (Padoch & Pinedo-Vasquez 2010).

1.4 Thesis rationale: the need for an improved understanding of biomass and biodiversity patterns in African savanna woodlands

There is now an increased awareness of the adverse environmental and socio-economic effects of deforestation and forest degradation on both climate and the provision of ecosystem services (Cardinale et al. 2012). However landholders across the developing world have historically had few economic or policy incentives to change management practices and thus reduce the emissions that stem from land use change. As such, in 2010 the UN Framework Convention on Climate Change (UNFCCC) adopted the methodological text on 'Reduced Emissions from Deforestation and Forest Degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks', otherwise referred to as REDD+. This approach is a means of translating global interest in tropical forest conservation into financial compensation to nations and local communities for the opportunity cost of avoiding deforestation and forest degradation. Based around a Payment for Ecosystem Services (PES) scheme, the REDD+ mechanism aims to provide financial incentives to landholders to reduce deforestation by allowing the carbon sequestered in forests to be traded on international carbon markets. These carbon credits are then bought by polluters in order to justify continued emissions elsewhere.

Since then there has been a strong push to ensure that management activities aimed at promoting carbon sequestration should have the benefit of maintaining key ecosystem services (the '+' in REDD+), such as the continued provision of both timber and non-timber products as well as biodiversity. If biodiversity benefits from carbon sequestration projects can be demonstrated, REDD+ has the potential draw in more support from stakeholders and can increase the value of the carbon credits (i.e. through the Climate Community & Biodiversity Alliance standard) with some people will be willing to pay more for the preservation or enhancement of biodiversity (Venter et al. 2009). For progress to be made, it is necessary to quantify how carbon stocks and biodiversity co-vary over space, and how they are both likely to respond over time to reforestation initiatives.

There is now a key economic justification for measuring, mapping and monitoring carbon stocks in savanna woodlands which will go on to help to reduce some of the key uncertainties in the African carbon cycle. However, quantifying carbon storage and biodiversity in these largely remote and poorly resourced environments represents a formidable scientific and technical challenge. The establishment of a network of permanent forest inventory plots is necessary step to monitor stocks and is required to help calibrate remote sensing technologies which can be used to decipher large scale patterns in AGC storage. Given the high costs associated with even preliminary plot measurements, knowing how much carbon is stored in different stem sizes classes is important for developing cost effective and standardised measurement protocols to facilitate rapid sampling. The associated collection of species data will allow co-variation between AGC and diversity to be explored in the context of forest conservation, but can also permit an exploration of whether a functional relationship exists between the two variables.

A secondary data requirement is to better understand how these woodlands respond to disturbance, specifically from shifting cultivation, the dominant driver of land use change in Africa. Carbon credit programs including REDD+ rely upon estimates of vegetation growth to calculate the carbon sequestration potential of conserving 'degraded' forests. There remains considerable uncertainty over how fast woody carbon stocks accumulate in re-growing stands, and how the initial land clearance impacts soil carbon stocks, the largest carbon pool in miombo ecosystems (Williams et al. 2008; Ryan et al. 2011). When viewed at large scales, the cyclical nature of shifting cultivation creates spatial patters in tree species composition and diversity which can have consequences for the ecology of shifting cultivation landscapes (Barlow et al. 2007). It is of interest to understand whether these disturbed habitats allow species not commonly found in mature woodlands to flourish, thus increasing landscape diversity. These questions are important in determining the ecological value of these recovering forests, but also in the context of conservation initiatives that reward land holders for improved carbon storage and biodiversity (CBD 2011).

1.5 Thesis objectives and key questions

The carbon cycle and biodiversity of forested ecosystems are now a topic of immense interest in the context of global environmental change. However as the preceding sections have highlighted, there still exists a large degree of uncertainty over role of African savannas, including the spatially dominant miombo woodlands in the global carbon cycle. Despite their obvious importance, they have failed to attract the scientific attention they deserve (Bond and Parr, 2010), and as such, there remain a number of fundamental questions related to the ecology and functioning of these ecosystems that need to be resolved. The analytical chapters of this thesis will help to address some of the key questions and data requirements raised in the previous sections. The fieldwork for this PhD was undertaken in south-eastern Tanzania, a region that has so far escaped some of the widespread forest degradation occurring in other parts of the miombo eco-region (Milledge et al. 2007; Ahrends et al. 2010; Ryan et al. 2012). It contains a floristically and structurally diverse mosaic of vegetation types including open savannas, miombo dominated woodlands and patches of east African coastal forest. A common theme throughout this thesis is to better understand spatial and temporal processes in these diverse landscapes, including a quantification of the amount of carbon and biodiversity stored in these ecosystems, how both of these variables are spatially distributed across the landscape and the factors which underlie these patterns, and finally their response to anthropogenic disturbance over time. Specifically, the objectives of this PhD will be to:

1) Quantify aboveground woody carbon stocks (AGC) across the different vegetation types and examine how these patterns in AGC storage are linked to differences in stand structure and to tree species diversity
2) Determine what principally controls patterns in tree species composition and AGC stocks across these heterogeneous landscapes
3) Determine the rate and extent to which aboveground woody carbon stocks (AGC), soil carbon, floristic composition and tree species diversity recover over four decades of succession following abandonment of sites cleared for shifting cultivation
4) Determine whether there is long-term residual effect of cultivation on soil respiration across the chronosequence of abandoned farmland and which abiotic and biotic factors are most important in controlling its variability across these landscapes

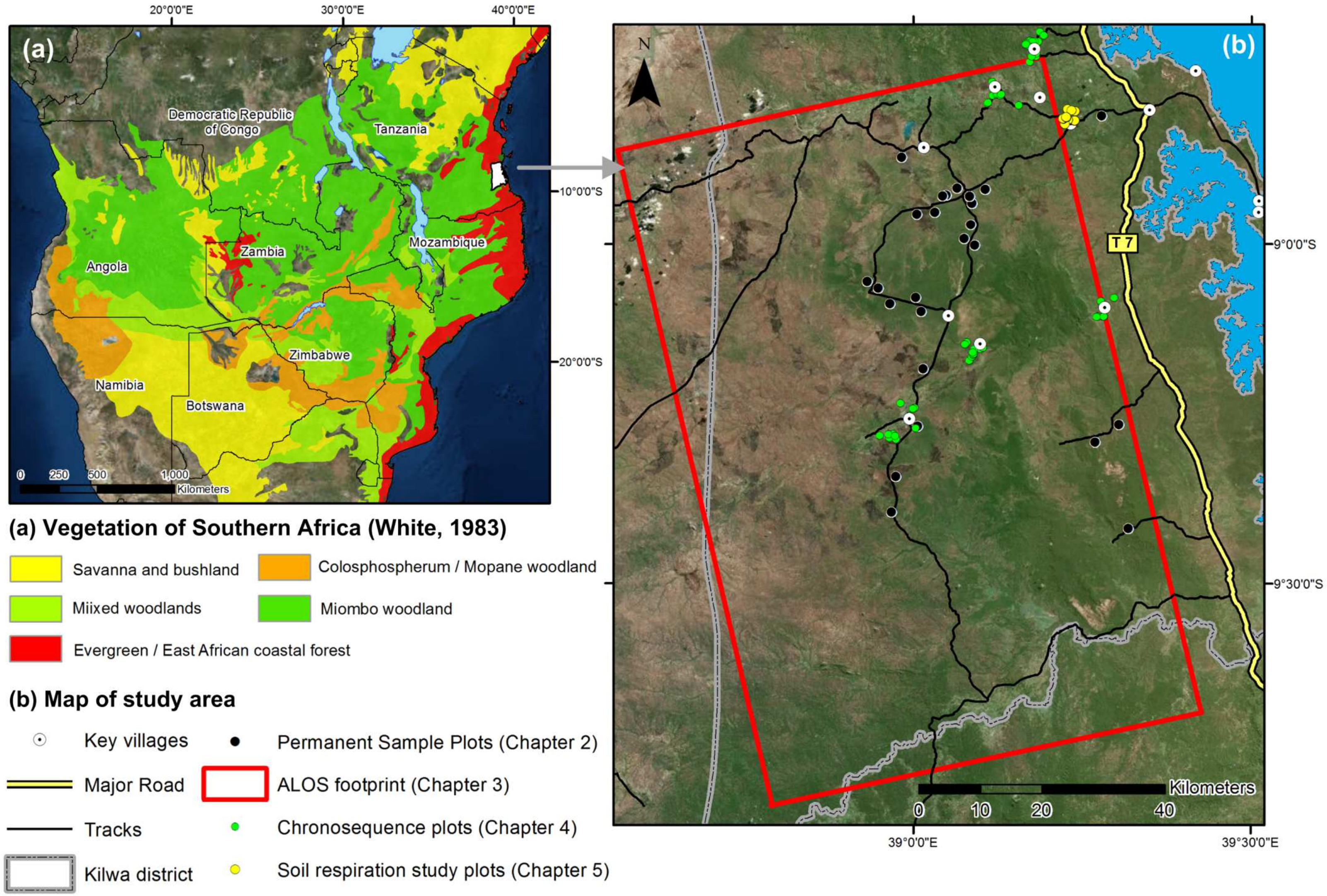


Figure 1.5 – (a) Location of Kilwa district in south-eastern Tanzania and (b) the distribution of the various forest inventory plots sampled as part of this thesis (Chapters 2, 4 & 5), along with the radar footprint (Chapter 3)

1.5.1 Background to the thesis

1.5.1.1 Study area

Tanzania, which is estimated to have lost 7% of its coastal forest and 13% of its miombo woodlands between 1990 and 2000 (Burgess *et al.*, 2010) was one of five countries targeted for REDD+ pilot projects. The country still retains significant forest cover which was recently estimated at ~35 million ha, or 38% of the land surface (Burgess et al. 2010). However like many other African countries, Tanzania's forests and woodlands are coming under greater pressure from local populations which currently sit at ~40 million having increased four-fold since independence in 1960 and are projected to reach 70 million by 2025 (Platts 2012). Hence, there is a very real potential for a long term degradation of these locally important ecosystems.

Our study area is located in Kilwa district in the south-east of the country and covers approximately 12,000 km^2. It is one of the most highly forested parts of the country, and also one of the poorest with the median household income below $1 per day (MCDI 2009). As of 2010 the district had a population of 190,744 people, many of whom live in rural communities dotted down the centre of the district and along the main road (Figure 1.5). The majority of the rural population make their living from small-scale agriculture and are largely dependent on the local woodlands for fuel wood and timber (Miya et al. 2009).

The principle vegetation type in the area is miombo woodland, with areas of more open savanna occurring to the west and scattered patches of Eastern African Coastal Forest concentrated largely along the coastal plans and hills to the east. Most of the vegetation is regularly burned with an average fire return interval of around 2 -3 years (MCDI 2009). Population densities are amongst the lowest in Tanzania, while the absence of commercial agricultural or logging enterprises means the area remains relatively undisturbed, particularly in the hinterlands in the central and west of the district. Tsetse fly prevents widespread livestock production, however, in recent years pastoralists from the north have been moving in to the local woodlands. The completion of the Mkapa Bridge across the Rufiji River in 2005, approximately 50km north of Kilwa district, has potentially opened up the region to new urban markets such as Dar Es Salaam (DES). Forest inventories conducted by Milledge et al (2007) revealed that Kilwa district has one of the highest densities of timber resources in southern Tanzania (10.5 m^3/ha) meaning it is attractive area for commercial loggers (i.e. Ahrends et al. 2010)

1.5.1.2 Mpingo Conservation and Development Initiative

The research was conducted in collaboration with the Mpingo Conservation and Development Initiative (MCDI), a Tanzanian non-governmental organisation based in Kilwa. Since 2004 they have been developing an approach to Participatory Forest Management (PFM) that focuses on helping communities to sustainably manage a number of high value timber species in local village forest land reserves (VLFRs), including the flagship Mpingo tree (*Dalbergia melanoxylon*) which is commercially extinct in many parts of Tanzania. Since 2010, they have been implementing a new REDD+ pilot project, the money from which will be used to expand areas of conservation. The project aims to generate carbon credits through improved fire management which involves reducing fire intensity and frequency in the VLFRs through a programme of community-based fire management focused on early burning. By removing the grass layer early in the dry season, MCDI aim to prevent the ignition of more intense and destructive fires later in the dry season when temperatures are hotter and the grass has had longer to cure (Ryan & Williams 2011).

Under the original project proposal, the University of Edinburgh's role was to develop the methodology for carbon assessment and monitor the changes over time under a project scenario. A number of permanent sample plots (PSPs) were set up across the district as part of the University of Edinburgh's original commitment to provide MCDI with baseline carbon stock estimates against which future changes in carbon stocks would have been measured (Figure 1.6). Monitoring is now taking place in the VLFRs where fire management is being undertaken; however the network of PSPs still forms an important part of the project being used to calibrate earth observation data that is being used to monitor large-scale change in AGC storage. The plots are also being used to monitor natural changes in tree populations such as the growth rates of selected important timber species which will help to determine sustainable extractions plans.

1.6 Data collection

1.6.1 Permanent sample plots and radar remote sensing (Chapters 2 & 3)

The establishment of the permanent sample plots was initiated in 2010 at twenty-five sample locations stratified between three major vegetation types chosen to represent the known variability in vegetation structure and biomass found in the study area. The network of plots is one of the densest and most detailed in Africa, the data from which forms the basis of Chapter 2 of this PhD. Plot measurement is being undertaken with a nested plot design that includes a

1 ha PSP in which all stems >5cm DBH are tagged and measured, 4 x 0.2 ha circle plots in which all stems >10cm DBH are recorded but not tagged, and a 9 ha large permanent sample plot (LPSP) in which all stems are tagged and measured (Figure 1.6).

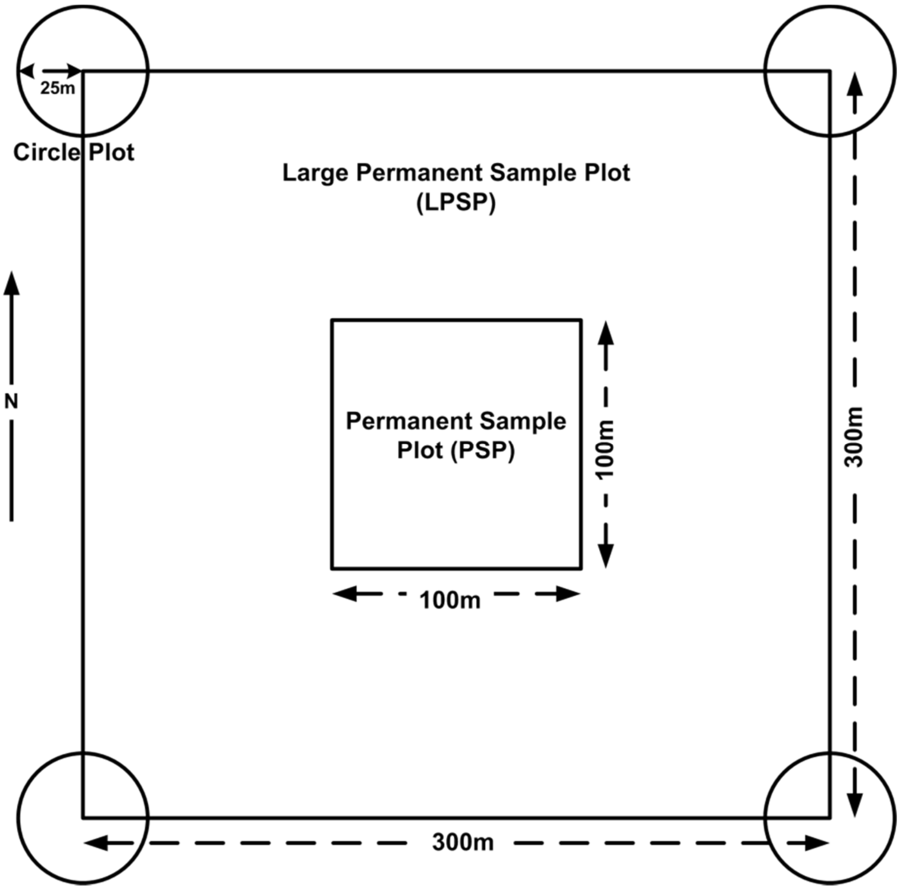


Figure 1.6 - The plot design used at each sample location

The 1-ha plots were split in to 10 x 100m strips for easier enumeration and to allow x,y co-ordinates to be calculated for each stem. In the 9-ha plot the location of each tree was noted with a GPS. A total of 18,562 trees were measured and identified according to their local species name by a field guide knowledgeable in botany. Most of these subsequently translated to their botanical names based on a combination of field identifications and comparing names to existing local and national species lists (Appendix A). An examination of both carbon and species dynamics over time, including growth rates, recruitment rates and mortality rates will be obtained through repeat inventories, the first of which was completed in late 2013, two years after the initial measurement of each plot.

Remote sensing data was used to extrapolate the plot level carbon stock data and map regional patterns in AGC storage (Chapter 3). Optical remote sensing is limited in its capacity derive estimates of AGC as essentially what is being seen is the colour of the leaves, rather than the woody stems from which ground based measurements of AGC are derived. Radar imagery has multiple advantages over optical imagery for this purpose; firstly, it can operate independently of atmospheric inference and cloud cover which persists over much of the tropics. Secondly, it is not sensitive to the seasonal grass layer and inter-annual variability in tree leaf phenology, which further complicates the interpretation of optical imagery (Ryan et al. 2013). Instead, satellite-based radar sensors such ALOS PALSAR have been shown to be sensitive to woody structure up to a signal-saturation point of between 60 - 100 t C ha^{-1} (Lucas et al. 2010); values which encompass African woodlands and dry forests. When integrated with local field plots for calibration radar is capable of estimating AGC distributions at a high spatial resolution (25m). This approach has been widely used to produce maps of AGC across African savannas and woodlands, and have been useful in the large scale quantification of AGC stocks, and developing our understanding of the location and drivers of land use change (Mitchard et al. 2009; Ryan et al. 2014). The unprecedented spatial resolution of these maps is sufficient to capture small-scale patterns in AGC, and when compared against ancillary climatic and soil data, can help to improve our understanding of what principally determines patterns in AGC across these complex landscapes. An additional legacy of the plot network will be to provide ground truth data for future radar sensors such as the European Space Agency's BIOMASS mission (Quegan et al. 2012)

1.6.2 Post-disturbance chronosequence (Chapters 3 & 4)

Assessing long-term changes in C stocks in trees and soils and tree species composition following disturbance is complicated by fact that recovery occurs over decades, considerably longer than the duration of most projects. Therefore, recovery trends are necessarily based on establishing chronosequences where time, i.e. long-term monitoring of forest re-growth, is replaced by space, i.e. multiple stands of different ages but similar disturbance histories, soils and climate (Figure 1.7). Previous studies using this approach have yielded valuable insights into ecosystem responses to shifting cultivation (Williams et al. 2008). However uncertainty still exists over the role of soils on recovery trends, something which previous studies fail to control for. In this study plots were located on both sandy and more clay rich soils in order to examine associated effects of recovery rates and patterns. . Sampling was undertaken in 6 village areas spread across the district measuring a total of 67 sites including areas currently under cultivation, areas that had been under cultivation but have been abandoned for between 1 – 40 years, and areas of mature miombo woodland for comparison purposes. Site ages and land-use histories were determined through semi-structured discussions with local village councils and then cross checked with independent local guides and a time-series of Landsat images spanning the past 30 years to verify the information provided by local informants. At each site a 0.2 ha circle plot was set up within which all trees with a DBH >5cm were measured and identified according to their local name by the same guides used to measure the PSPs. Soil sample were also extracted from two depths (topsoil & subsoil) at 7 locations spread across the plot (Figure 1.7).

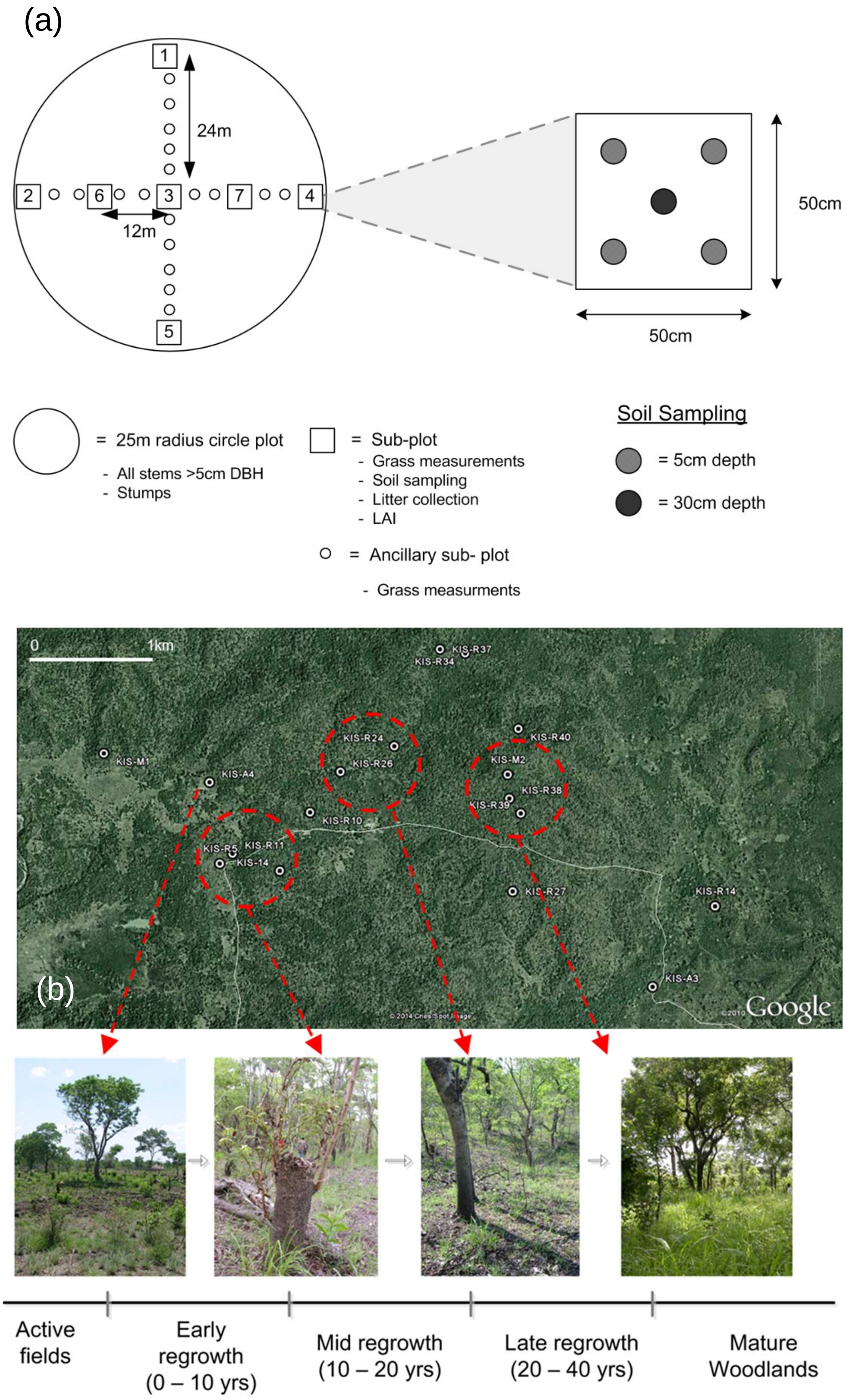


Figure 1.7 – (a) Sampling strategy employed at each site and (b) the distribution of plots around Kisangi village - the most northerly group of plots in Figure 1.5 - showing how the chronosequence was constructed. Source imagery: Google Earth, 2013

1.7 Outline of research chapters

The core chapters of this thesis are presented in the style of a scientific journal articles as they are intended for rapid publication post-submission. As such, there exists some overlap between introductory and methodological sections in order for each chapter to stand alone. Chapters 2 through 5 address the key aims and objective of the thesis, while Chapter 6 provides a summary of the results, their wider implications and potential avenues for future research.

Chapter 2 – Spatial patterns in aboveground woody biomass and its links to forest structure, tree species diversity and floristic composition in south-eastern Tanzania. In the first analytical chapter of the thesis, I present the data from the first forest inventory conducted between 2010 and 2011. I assessed how aboveground woody carbon densities varied across the 25 PSPs and how these patterns are linked to differences in (a) stand structure (b) tree species diversity and (c) floristic composition. The data from each of these mini-studies is combined in to an integrated assessment of the structure and functioning of these complex mosaic landscapes. The key questions in Chapter 2 are:

- How are spatial patterns in AGC stocks related to differences in stand structure/ stem size distributions and how can this information be used inform future sampling methodologies in these areas?
- How is tree species diversity within plots (α-diversity) related to AGC storage? Based on the available can we decipher a functional relationship between the two variables?

- How does tree species composition vary between plots (β-diversity) and what does this tell us about the processes that create these patterns across the landscape?

Chapter 3 – What determines spatial patterns in aboveground woody biomass across a heterogeneous African woodland landscape? The aim of Chapter 3 was to assess which factors are most important in controlling vegetation structure at the landscape scale (10s km) using a radar-derived map of AGC stocks that was calibrated using the local network of field plots. The fine resolution (1-ha) of the maps means they are able to capture small scale patterns and when compared with ancillary GIS data related to climate, soils and topography can help to improve our knowledge of what promotes or limits AGC storage in these ecosystems. The key questions in Chapter 3 are:

- Is the amount of AGC an area supports fixed within clear biophysical limits?
- To what extent do factors related to topography, soils and climate explain spatial variations in biomass across these complex landscapes?

Chapter 4 – How resilient are African savanna woodlands to disturbance from shifting cultivation? This chapter provides a comprehensive analysis of the long term ecological impacts of shifting cultivation by examining how carbon stored in trees and soils recover across a 40-year chronosequence of abandoned agricultural land. The chapter also details how this patchy disturbance impacts spatial patterns in tree species composition and diversity through the creation of multiple areas that differ in their time since abandonment. Additional novelty is provided through the analysis of whether recovery trends differ depending on soil texture. Specific questions include;

- What is the rate of recovery in AGC and does it vary depending on soil mineralogy?
- What is the impact of land clearance on soil carbon stocks and are there any changes in these stocks with increasing time since abandonment?
- Does tree species composition differ between re-growing and mature woodlands?
- Does land-use change alter patterns of tree species diversity at both the stand and landscape scale?

Chapter 5 - Spatial variation and magnitude of total soil respiration across a post-disturbance chronosequence. The objectives of this, the final data chapter of the thesis are to further advance our understanding of soil CO_2 production and its controlling factors, and explore the potential residual effects of disturbance on the magnitude of the respiration flux across a chronosequence of abandoned agricultural land used in Chapter 4. A small number of the plots used in the previous chapter were selected for analysis including 6-, 15-, 25-year old stands, and mature woodlands. I examined the potential role of multiple variables which I hypothesized would have a strong influence over respiration and would change over successional time, including (i) micro-climatic factors, i.e. soil temperature and soil moisture, (ii) edaphic drivers, i.e. soil organic carbon, nitrogen and phosphorous, and (iii) plant drivers, i.e. fine root biomass and cumulative tree size within a zoned proximity of each measurement point. The questions asked in Chapter 5 include:

- Which biophysical factors are most important in driving respiration across plots varying in their time since abandonments?
- Is there a significant difference in the rate of soil respiration across the chronosequence?

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Chapter 2

Spatial patterns in aboveground woody biomass and its links to forest structure, tree species diversity and floristic composition in south-eastern Tanzania

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Author contributions
MW, CMR and SJB developed the experimental design for plot establishment while CMR produced the vegetation classification upon which plot location was based. Forest inventory data was collected by IMM, CMR and partners at Mpingo Conservation and Development Initiative (SJB). Richard Lamprey from Flora and Fauna International, a project partner of MCDI provided estimates of canopy cover based on aerial photographs taken over the permanent sample plots. IMM compiled the species list. IMM, MW and CMR conceived the research questions. IMM collated and analysed the data, and wrote the manuscript.

2.1 Introduction

Seasonally dry tropical forests and woodlands are the dominant vegetation cover in Southern Africa, extending over 4 million km^2 across 10 countries (Mayaux et al., 2004; Figure 1.3). Across its range, variations in climate, soils and disturbance maintain a structurally and floristically diverse mosaic of habitats, covering a spectrum from open savanna with a dominating grass layer and scattered trees, through open canopy woodland with an understory of grasses and shrubs, to denser woodlands and dry forest (White 1983). The most extensive of these formations are the miombo woodlands, a typically open canopy ecosystem that is distinguishable from the surrounding vegetation types by the presence of the endemic genera, *Brachystegia* and *Julbernardia* (Fabaceae, subsp. *Caesalpinioideae*) (Chidumayo, 1997). Levels of biodiversity and endemism are thought to be high, with the miombo woodlands alone harbouring an estimated 8500 species of higher plants including over 300 tree species (Frost, 1996). The diversity of species the system supports helps to underpin the livelihoods of an estimated 100 million people rural and urban dwellers who rely heavily on the timber, food, medicine and construction materials that the woodlands and forests provide (Campbell *et al.*, 2007; Syampungani *et al.*, 2009).

However despite their scale, the ecology and functioning of these seasonally dry ecosystems remain poorly studied in comparison with the more carbon dense and diverse tropical forests of Central Africa (e.g. Bond & Parr 2010; Lewis et al. 2013). Tropical savannas and woodlands thus represent a potentially large, but poorly quantified store of biomass carbon, biodiversity and species endemism (Platts *et al.*, 2010; Ryan *et al.*, 2012). Forest inventory plots with which to quantify these patterns are both few in number and spatially uneven, typically favouring certain geographic regions (Zambia; i.e. Chidumayo 2013), and biodiversity hotspots (Eastern Arc Mountains; Platts et al. 2010), while other habitats remain distinctly understudied (i.e. Eastern African Coastal Forests; Prins & Clarke 2007; Timberlake 2011). Thus, many important ecological questions remain poorly resolved, for example: what is the magnitude and distribution of aboveground woody carbon stocks (AGC) across these heterogeneous landscapes? How are these patterns linked to differences in vegetation structure and to tree species diversity? What principally determines floristic variation and species distributions?

Understanding these questions is important on multiple counts. Firstly, increasing human pressure linked to resource extraction is currently driving widespread, but uncertain losses of AGC, as well the localised extinction of important tree species (Ahrends *et al.*, 2010; Ryan *et al.*, 2012). It is therefore of paramount importance to directly quantify, and therefore reduce uncertainty in our estimates of AGC storage in order to better understand future losses, and to underpin carbon sequestration and storage practices (e.g. REDD+) aimed at mitigating this loss. Plot level estimates of AGC storage are also necessary for calibrating earth observation data from which we can decipher larger scale spatial and temporal patterns in AGC (i.e. Saatchi et al. 2012; Chapter 3). From a measurement perspective, knowing which stem size-classes contain most of the carbon may help improve our knowledge of how best to capture these patterns and thus design effective data collection protocols (Marshall *et al.*, 2012).

Measuring and managing ecosystems based on their carbon stocks can also have benefits for biodiversity accounting and conservation, with premium carbon credit price suggested for conservation initiatives that help to maintain or enhance biodiversity (i.e. through the Climate Community & Biodiversity Alliance standard; Venter *et al.*, 2009). It is therefore of interest to quantify how diversity measures such as species richness co-vary with AGC storage to highlight important trade-offs and thus help inform mutually beneficial conservation schemes (Miles & Kapos, 2008; Díaz *et al.*, 2009). From an ecological perspective, such information may also be useful in elucidating a potential functional relationship between tree species diversity and AGC (Conti & Díaz, 2013). Debate has typically centred on the applicability of diversity/compositional driven controls, where the number and/or identity of species present within a forest patch control ecosystem function (i.e. C storage or woody productivity), or the more traditional viewpoint of habitat driven controls, where structural variables such as vegetation cover and/or density determine the number and diversity of species able to colonise a given area. Prominent ecological theories have postulated that areas of high biomass should coincide with high tree species diversity. This may occur due the effective partitioning of resources among species (i.e. Niche Complementarity Hypothesis; Tilman et al., 1996), or by the greater chance in denser areas that one particularly rare, or a few highly productive or large species are present within the stand (i.e. Sampling/Selection Effect Hypothesis; Fargione et al. 2007). Other studies have suggested a 'hump-shaped' relationship, where diversity is maximised at some intermediate level of productivity/biomass, declining towards more productive and/or denser habitats. This pattern fundamentally assumes that environmental conditions drive species diversity. Proposed mechanisms for this pattern postulate that fewer species will be adapted to extreme ends of the gradient (Species Pool Hypothesis; Eriksson 1993). Here, increased competition for resources in denser forest for example, may effectively exclude sub-dominant species, while the increased moisture stress and frequency of disturbance in savannas means only a few tolerant species can persist. Thus, areas of more open woodland, with a more moderate disturbance regime, and therefore greater niche differentiation, will be the most diverse (i.e. Intermediate Disturbance Hypothesis; Connell, 1978). Each theory predicts an ecologically distinct mechanism, however testing the applicability of each these hypotheses remains out with the scope of this study due to a lack of information on functional traits (Díaz et al. 2004; Chave 2008; Thompson et al. 2009). However, the form of the relationship may provide insights into the processes that create and maintain patterns of tree diversity and biomass across these patchy landscapes.

The collection of species data also allows us to perform one of the first explorations in to the mechanisms that principally determine mesoscale (10s km) patterns in tree community assembly. In miombo, the widespread dominance of species in the subfamily *Caesalpinioideae* have led some to suggest that community composition is largely homogenous (uniformity hypothesis) and largely dominated by a small number of competitively dominant species (Frost, 1996), such as those which utilise ectomycorrhizae or have N-fixing abilities allowing them to compete on the poor soils (Högberg, 1992). However, spatial variations in vegetation structure related to environmental influences and fire disturbance may encourage species with different niches, and so create differences in species composition between areas (β-diversity) (Whittaker, 1977). At smaller spatial scales, tree species distributions may therefore be spatially patchy due to a combination of niche assembly and dispersal assembly. Under the theory of niche assembly, species are deterministically filtered by environmental conditions and via competitive displacement (i.e. Phillips & Vargas 2003), whereas under dispersal assembly theory, floristic differences between areas is related to the distance between these sites, with areas that are closer together likely to be compositionally similar, and areas that are far apart more likely to contain different species (Hubbell, 2001). The degree to which each of these factors shape species patterns is a fundamental question in plant community ecology and been widely explored in Neotropical forests (Tuomisto *et al.*, 2003; Linares-Palomino & Kessler, 2009; Dexter *et al.*, 2012; Kristiansen *et al.*, 2012). Due to a general lack of detailed field data, few attempts have been made to assess the spatial distribution of tree species and their underlying determinants in African savannas and woodlands. Those which have point to environmental controls such as soils and fire as having a key role in miombo woodlands (Backéus *et al.*, 2006; Woollen *et al.*, 2012; Flack, 2013). However, neither of these studies acknowledged the potential and combined role of dispersal assembly, or how these processes influences patterns across broader gradients in vegetation, such as savannas and forests.

In this study, I examine spatial patterns in tree community structure, tree species diversity and floristic composition, and their links to aboveground woody carbon storage (AGC) across 25 forest inventory plots in Kilwa District, South-Eastern Tanzania that span a range of vegetation types and biomass densities. Published data from permanent sample plots (PSPs) across the region are sparse. Our network of plots represents one of the densest and most detailed in African networks allowing us to improve our understanding of how species and forest structure co-vary with AGC across landscapes.

The specific questions I will address in this study are: (1) how are spatial patterns in AGC stocks related to differences in stand structure/ tree size distributions? (2) How is tree species diversity within plots (α-diversity) related to AGC storage? (3) How does tree species composition vary between plots (β-diversity) and what does this tell us about the mechanisms that create these patterns across the landscape?

2.2 Methods

2.2.1 Study area and sampling strategy

The study area is located in Kilwa District in the Lindi Region of south-eastern Tanzania (8°21’ - 9°56’ S; 38°40’ - 39°39’ E; Figure 2.1), and covers approximately 12,000 km^2. Terrain varies in altitude from 0 to 740m a.s.l. with a steep escarpment running north to south dissecting the centre of district (Prins & Clarke, 2007). The estimated mean annual precipitation is 821 ± 350 mm (±SD), with a distinct gradient between the east and west with the east generally receiving >1000 mm and the west <1000 mm (Chapter 3; Figure 3). From October 2010 – October 2011 permanent sample plots were established at 25 locations and stratified between three major vegetation types qualitatively based on structure; savanna (grass dominated sparse woodland), through woodland (tree-grass mix) to denser woodland and forest (closed canopy). A supervised classification of Landsat 5 imagery based on visual interpretations of vegetation type at 300 ground reference points was initially used to stratify the area (Figure 2.1) Ground classifications were compared to reflectance values from Landsat (30m resolution), which expanded the classification to the rest of the study area.

However, the classification only proved to be only partially accurate once plots were measured. After visiting the sites, I re-classifed the plots again based on structure with plots grouped in to more open 'savannas' (canopy cover <10%), moderate density 'woodlands' (10 – 50%), or denser 'forests' (canopy cover >50%). Canopy cover estimates were derived from aerial photographs collected over the plots (Richard Lamprey, personal communication; Table 2.1).

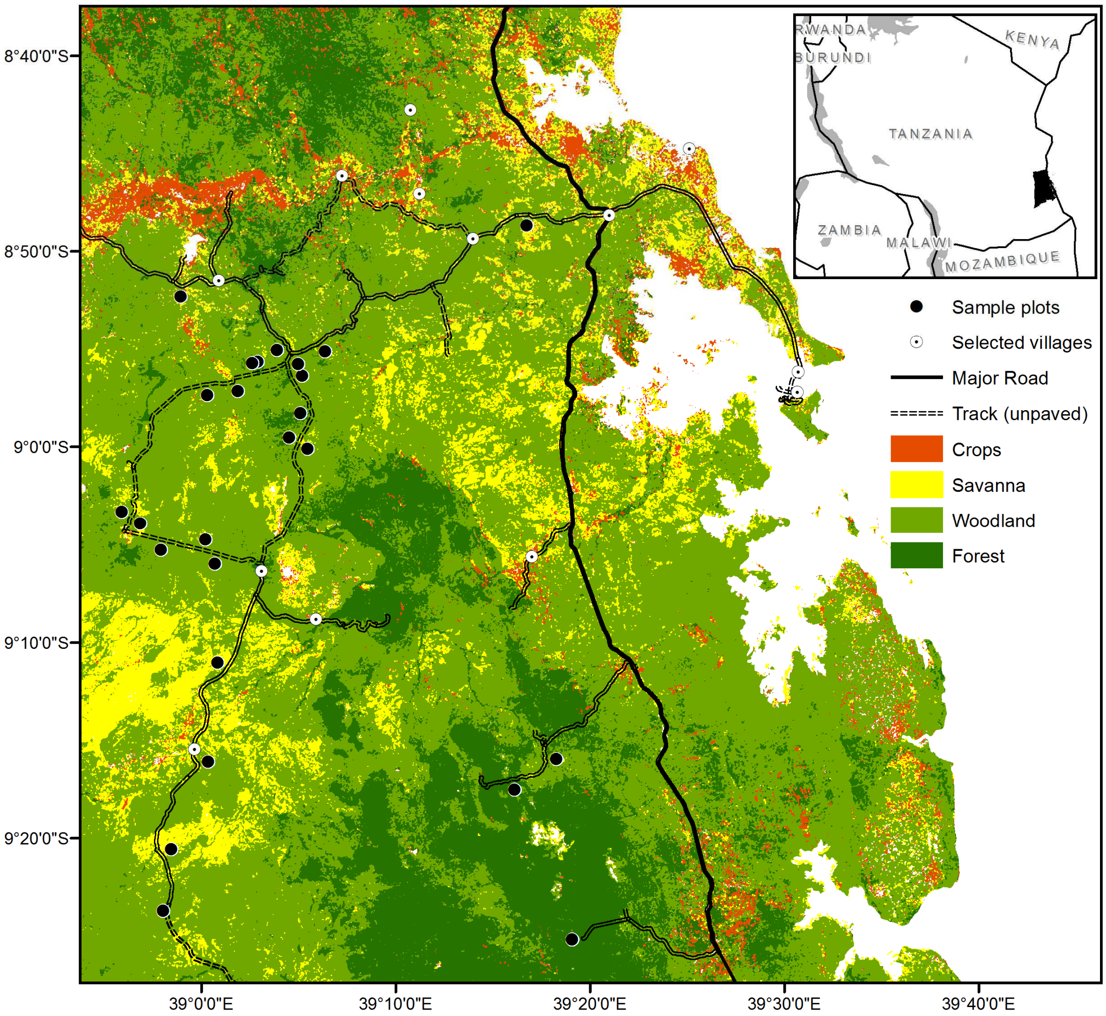

Figure 2.1 – Land cover map used to locate the PSPs. The land cover classification was derived from Landsat (30m resolution) using 300 ground truth points as a guide for a supervised classification.

Plots were proportionally allocated to each land cover based on their spatial extent over the study region to ensure the preferential sampling of the most dominant land cover. On this basis, 12 sample locations were allocated to woodland areas, 6 to forest, and 7 to savanna. Pragmatism played a role in site location, with plots located randomly along the track network; however a 1 km buffer from roads was enforced to reduce the likelihood of intense human disturbance. For sampling, we utilised a 1 ha (100 x 100m) sized permanent sample plot (PSP) in which all trees with a stem diameter ≥5 cm were recorded along with spatial co-ordinates. These PSPs, upon which most of the analyses in this study are conducted, were nested within a larger 9-ha (300 x 300m) sample plot in which all stems > 40cm were recorded. Tree diameter was measured at 1.3m along the stem from the ground and if the tree forked below 1.3m each stem was measured and counted as one individual. Stem carbon stocks were estimated using a miombo-derived allometric equation produced by Ryan et al. (2011). In the field, we also recorded the local name of each measured stem, and where possible, identified each by their species botanical name using a range of local and national species lists (NAFORMA, 2011), and by comparing specimens to published reference guides (Appendix A; Coates-Palgrave 2002).

2.2.2 Data analysis

All data analyses were performed using R statistical software version 3.0.2 (R Core Team 2014, http://cran.r-project.org) and associated packages where stated.

2.2.2.1 Patterns in tree structure, composition and diversity

To determine how differences in stand structure are related to differences in AGC (Q1), stems were separated in to discrete size classes of 5cm ($n = 19$). The proportional contribution of each size class to the total measured AGC in each plot was calculated and then averaged for all plots in each vegetation type. I used Chi-square goodness-of-fit tests to test whether the average proportion of AGC in different size classes differed between vegetation types. We tested for significant differences in stem density and AGC storage among size classes using ANOVA and Tukey's HSD tests.

To assess spatial patterns in species composition and diversity, we used the species botanical names or genus where known; where this was not possible, the species local name was used instead. We acknowledge that this can result in a potential overestimate of diversity where unidentified species are more common as we assume these morphospecies are all unique whereas multiple names were sometimes used for the same species. However on average, unidentified species contributed no more than 5 of the species measured in each plot, thus we consider the likelihood that our diversity measures are subject to extreme bias to be minimal (Dexter *et al.*, 2010). The small numbers of individuals not identified to any taxonomic level (0.07% of total inventory) were excluded from the analysis.

All of the subsequent analyses were performed using various functions in the 'vegan' package (v. 2.0-10; Oksanen 2013) unless otherwise stated. Tree species diversity (Q2) was calculated for each of the 25 1-ha plots using four metrics; species richness, family richness, and Fisher's alpha, which is less sensitive to the number of individuals than species richness. To further control for this potentially confounding effect, I also calculated rarefied species richness using Mao-Tao individual-based rarefaction analysis. Diversity measures were calculated for all measured stems (>5cm) in each 1-ha plot, then again for small trees (5 – 15cm), medium sized trees (15 – 40cm) and large canopy dominants (>40cm) separately, with the simple aim of understanding where most of the diversity occurs in these systems. For the analysis of large stem diversity (>40cm), I include the inventory data from the 9-ha plots to allow a suitable number of stems for analysis. When comparing diversity and AGC, I treated diversity as the independent variable, in order to test the hypothesis that diversity has a deterministic effect on AGC (due to niche complementarity and selection effects), rather than if axis were reversed which would assume environmental/ disturbance controls on diversity. In order to test this alternative scenario, I also performed the analysis with AGC as the independent variable to test of the relationship differed. Multiple models were fitted to each dataset using a variety of functional forms based on ecological theory with aim of characterising the link between different diversity indices and AGC storage, including a linear relationship ($y = ax + b$), saturation ($y = ax/(b + t$), quadratic ($y = ax^2 + bx + c$), and a hump shaped ricker curve ($y = axe^{-bx}$) (Crawley, 2007). Model selection based on minimising the Akaike Information Criterion (AICc), corrected for small sample sizes.

I used both the number of individuals and the mass of carbon contributed by each species as separate measures of species dominance. Quantitative differences in species composition between plots (ß-diversity) were calculated using the Bray-Curtis Index of Species Dissimilarity (Q3). Overall compositional patterns were visualised using Non-Metric Multidimensional Scaling, which was performed using the 'metaMDS' function. Permutational multivariate analysis of variance (PerMANOVA) was used to test the alternative hypothesis that there are no significant differences in tree species composition among different vegetation types (Uniformity Hypothesis) (Anderson 2001). PerMANOVA uses randomisations of the data to generate the p-value for the hypothesis test, and was implemented using the 'adonis' function. The analysis was repeated separately for small, medium and large trees to test whether composition differed among size classes. Prior to analysis, the raw species abundance data was square root transformed and site standardised to account for the number of trees sampled at each site, and to reduce the influence of the most common species (sensu Barlow et al., 2007)

2.2.2.2 Determinants of floristic variation among plots

To answer the final question on what drives floristic variation across the landscape, I collated data on vegetation structure, environmental/climatic conditions and the distance between plots which I hypothesised would have a deterministic effect on species composition across the landscape. As above, quantitative differences in community composition among plots were calculated using the Bray-Curtis Index. Spatial distance was calculated as the geographic (linear) distance between the centres of each plot in ArcGIS10.1 (ESRI, 2013). Data analysis was separately performed using the linear distance and log-transformed distance, in keeping with Hubbell's neutral theory (Hubbell, 2001). Variables related to vegetation structure were included as a proxy for competition for resources such as light and nutrients (Fortunel *et al.*, 2014), but also for fire disturbance with denser, higher stature habitats likely to be less disturbed than more open ones (Ryan & Williams, 2011). Based on the forest inventory data, I included 6 explanatory variables in the analysis: total basal area (m^2/ha), stem density (ha), the number of small (5 - 15cm), medium (15 – 40cm) and large stems (40cm+) (ha) and canopy cover (%). Four variables were included related to the physical environment for which I could obtain reliable data: soil type (factor), which was extracted from the Harmonized World Soil Database (Nachtergaele *et al.*, 2009), mean annual precipitation (MAP), based on data from the Tropical Rainfall Measurement Mission (TRMM; Huffman et al. 2007), and plot elevation and slope angle which were based on Shuttle Radar Topography Mission (SRTM) data (Farr *et al.*, 2007). Throughout this study, I refer to these simply as the environmental variables. Other potentially descriptive factors such as rainfall seasonality, a proxy for dry season length; soil carbon content, a proxy for soil fertility (Lehmann et al. 2014); and soil texture did not vary significantly across the plots to warrant inclusion. I acknowledge the limitations with using both topographic proxies (i.e. De Cáceres *et al.*, 2012) and modelled estimates to represent edaphic conditions, rather than taking samples directly from the plots (see discussion section 2.4.3), although field data is forthcoming.

Principal Component Analysis (PCA) was used to remove collinearity among explanatory variables, using plot PCA axis scores instead of the raw data to calculate environmental and structural dissimilarities between each plot-pair. Species abundance data were Hellinger transformed prior to analysis to permit the use of linear ordination methods on heterogeneous datasets (Lepš & Šmilauer, 2003; Borcard *et al.*, 2011). For both groups of explanatory variables, the first PCA axis accounted for most of the total structural variation (80%) and the environmental variation (55%) between plots, with a 10% cut-off for inclusion. Environmental and structural dissimilarity between plots was calculated as the Euclidian distance spanned by the PCA axis. Distance decay plots and Mantel correlations were used to assess how well environmental, structural or spatial distance alone could explain patterns in species turnover across the landscape.

Canonical redundancy analysis (RDA; Borcard et al., 2011) was then used to partition variation in community composition between each group of explanatory variables. In short, RDA combines multiple regressions with PCA and is ideally suited for modelling multivariate response data. I used forward selection on the raw environmental and structural data to extract the most important variables shaping patterns and remove potentially strong linear correlations among the explanatory variables in the RDA model ('packfor' package; Dray et al., 2007). The aim of variance partitioning based on RDA is to assess how much of the observed compositional variation between sites can be explained purely by environmental heterogeneity, purely by structural differences, purely by spatial distance, by some combination of each (i.e. spatially structured environmental variation), and unexplained variation (Legendre et al. 2005).

Table 2.1 – Metadata for each 1-ha permanent sample plot. The plot ID's reflect their original designation in terms of vegetation type with stars (*) indicating plots that were reclassified based on their canopy cover and aboveground woody carbon stocks

	Plot centre (UTM)		Vegetation structure						Environment				
Plot ID	Eastings	Northings	AGC (t C ha$^{-1)}$	Stem density	Stems 5 - 15 cm	Stems 15 - 40 cm	Stems 40 cm+	Canopy cover (%)	MAP	Soil type	Soil texture	Slope (°)	Elevation (m)
F12	533406	8975717	33.81	270	158	86	26	52.0	1506	Cambisol	Sandy Clay	4.5	268
F13	529495	8972831	44.87	1511	1299	192	20	90.5	1573	Cambisol	Sandy Clay	1.3	380
F15	534907	8958771	58.21	1185	963	201	21	92.5	998	Cambisol	Sandy Clay	6.9	326
F5	504782	9013010	37.14	1506	1293	200	12	59.1	697	Cambisol	Sandy Clay Loam	1.9	127
F6	509325	9008315	33.40	450	283	153	14	51.2	628	Cambisol	Sandy Clay Loam	1.3	151
F7*	508276	9006030	28.38	665	551	93	21	41.4	874	Acrisol	Sandy Clay	2.9	144
S3	511675	9014077	3.56	536	519	17	0	7.6	792	Cambisol	Sandy Clay Loam	1.1	152
S4	509518	9011808	6.90	72	51	19	2	10.7	799	Cambisol	Sandy Clay Loam	0.8	138
S5*	500394	8996420	29.04	610	477	118	15	42.6	663	Acrisol	Sandy Clay	1.1	190
S7	501549	8984788	2.47	206	191	14	1	6.7	817	Fluvisol	Silt Loam	0.9	133
S9*	497160	8967214	16.39	275	177	92	6	22.0	847	Lixisol	Loam	0.7	194
W1*	530619	9026004	3.34	554	547	7	0	7.5	828	Vertisol	Silty Clay	0.5	107
W11	509127	9012908	29.30	470	361	86	22	43.1	799	Cambisol	Sandy Clay Loam	1.3	148
W12	503456	9010353	18.82	397	300	80	14	25.5	841	Acrisol	Sandy Clay	0.5	94
W13	500568	9010008	18.00	602	236	119	5	24.3	841	Acrisol	Sandy Clay	1.7	119
W14	509991	9004949	12.30	220	170	45	5	16.7	936	Cambisol	Sandy Clay Loam	1.0	142
W16	492514	8999043	16.53	431	337	89	4	22.2	599	Acrisol	Sandy Clay	1.9	206
W17	494266	8997929	33.93	703	549	128	26	52.3	599	Acrisol	Sandy Clay	1.4	190
W18	501266	8994109	23.72	352	273	54	24	33.2	486	Acrisol	Sandy Clay	2.3	168
W19*	496201	8995409	1.93	77	66	10	1	6.3	459	Acrisol	Sandy Clay	0.6	163
W26	500662	8975430	25.73	873	721	143	9	36.6	881	Acrisol	Sandy Clay	0.6	182
W29	496408	8961422	15.49	361	276	77	8	20.8	718	Lixisol	Loam	2.3	249
W6*	498084	9019296	4.74	165	148	16	1	8.7	816	Acrisol	Sandy Clay	0.7	68
W7*	507125	9014242	5.20	256	216	38	0	9.1	568	Cambisol	Sandy Clay Loam	3.2	165
W9	505295	9013127	18.00	360	532	62	8	24.3	697	Cambisol	Sandy Clay Loam	2.2	131

2.3 Results

2.3.1 Patterns in aboveground woody carbon stocks and stand structure

In total, we surveyed 13098 stems (>5cm) across the 25 1-ha plots, including 10694 small trees (5 -15cm), 2139 medium sized trees (15 – 40cm) and 265 large trees (>40cm). The surrounding 9-ha plots contained an additional 2069 large trees, highlighting the importance of large plots for the analysis of large trees. AGC stocks in the 1-ha plots ranged from 1.9 tC ha^{-1} in an area of open savanna (W19) to 58.2 tC ha^{-1} in an area of dense forest (F15) (Figure 2.2). AGC stocks were normally distributed across the landscape (Shapiro-Wilk test; $P = 0.3$), with an overall landscape mean of 20.9 ± 14.6 t C ha^{-1} (± indicates one standard deviation throughout).

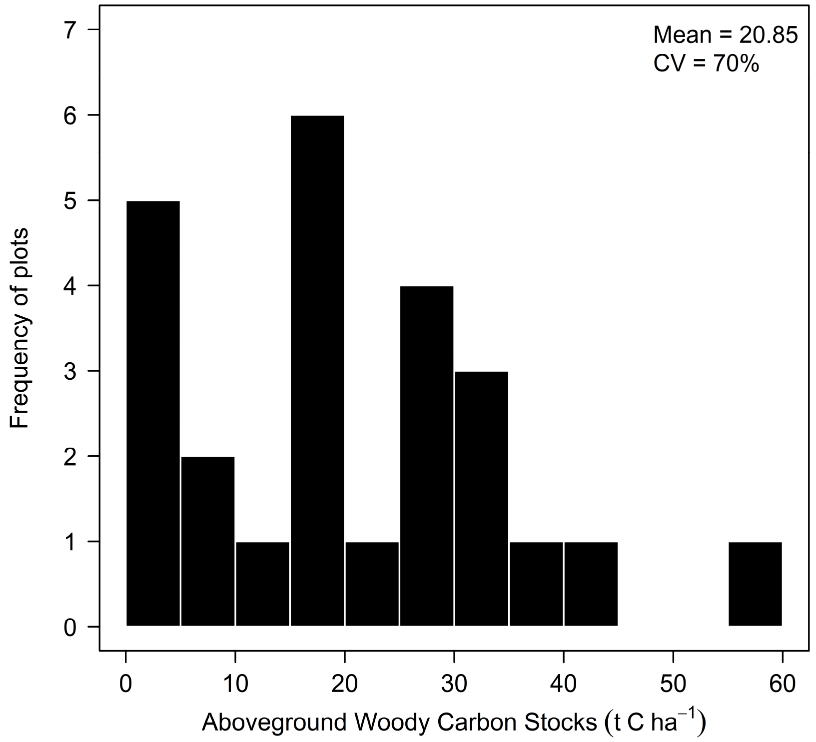

Figure 2.2 – Histogram of the AGC of the 1-ha plots (*n* = 25). CV refers to the Coefficient of Variation and is used as a measure of the heterogeneity in stocks

The classification of vegetation types based on canopy structure was concomitant with a gradient in AGC with plots in savanna storing <10 t C ha^{-1}, woodlands 10 - 30 t C ha^{-1} and forest >30 t C ha^{-1}. Stem densities ranged from 72 – 1511 stems/ha and were positively correlated with AGC stocks (Spearman's rho, $p < 0.001$). The average stocking density (ha) of large canopy trees across the 9-ha plot was variable ranging from 1 – 22 stems ha^{-1}. In the 1-ha plots, the a large proportion of AGC stocks were attributed to these large trees (>40cm), contributing between 18 - 73% (mean 35 ± 19%) of plot AGC where large trees were present, with some savanna plots containing no large trees. The distribution of AGC among stem-size classes differed significantly between savanna and woodland plots (Chi-square test; $\chi^2 = 54.98$, $P = <0.001$) and between savanna and forest plots ($\chi^2 = 52.15$, df = 18, $P = <0.001$). In savannas, the majority of AGC (42%) was contributed by the smallest diameter classes (5 - 15cm) (Figure 2.3; Table S1). In the woodland and forests, a smaller proportion of AGC was in these small stems (14%) despite their greater density in these areas (Figure 2.3). Overall, there were no significant differences in the proportion of AGC allocated to different size classes between the woodland and forest plots ($\chi^2 = 7.41$, df = 5, $p = 0.89$), despite there being a clear trend towards greater stature in the forests as evidenced by the higher maximum tree size. Woodlands contained a slightly greater proportion of AGC in medium sized trees than forests (47 – 42%) with the same true for larger (40 – 80cm) trees (39% - 35%). The greatest structural difference between woodlands and forests was the presence of stems >80 cm DBH in the forests which also had a disproportionate contribution to plot AGC (~10%) relative to their abundance (1 ± 1 ha^{-1}) (Figure 2.3).

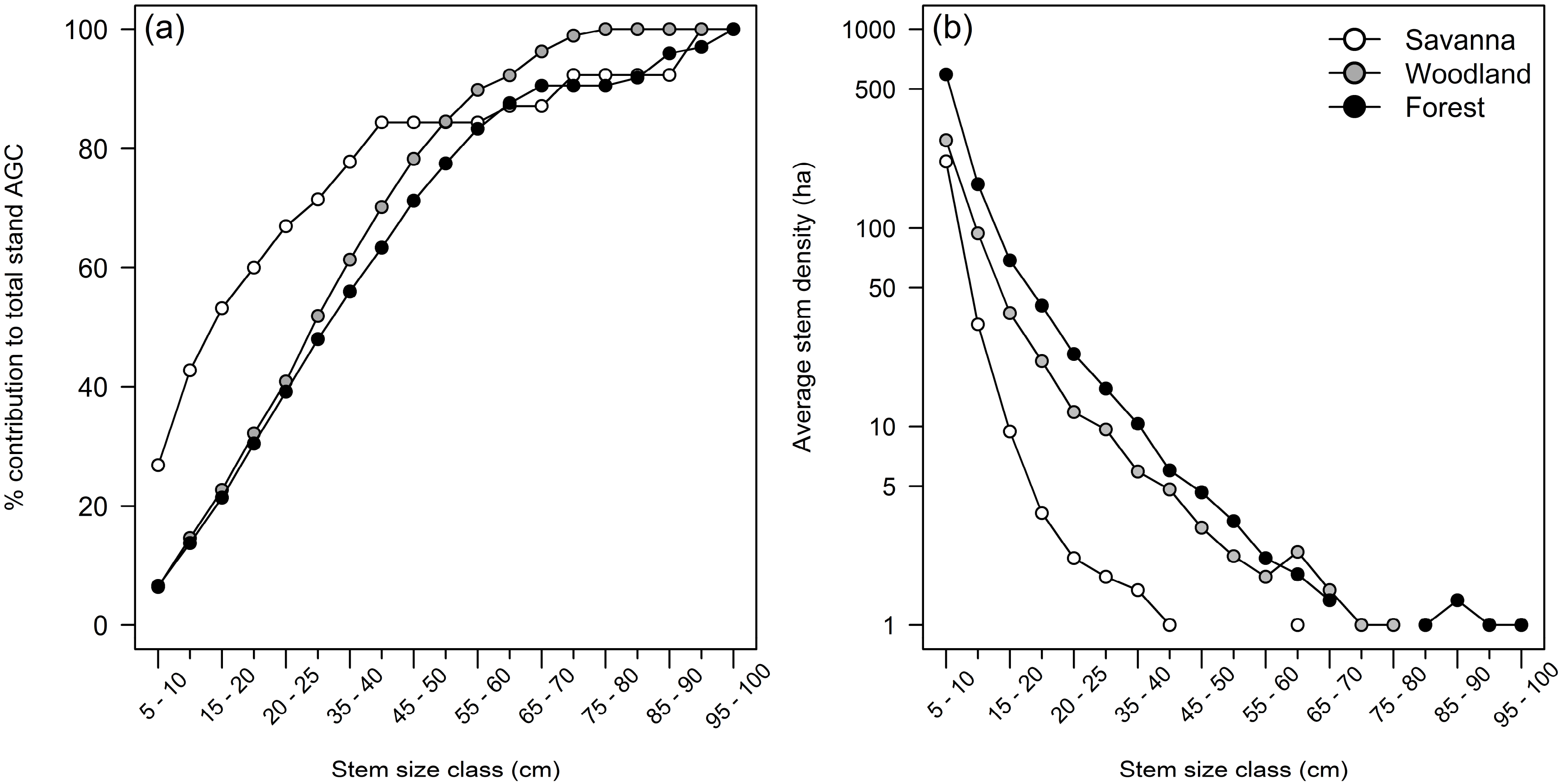

Figure 2.3- (a) Fraction of total stand biomass (cumulative distribution) contributed by different stem size classes within different vegetation types; (b) the average number of stems within each size class. Each data point represents the mean contribution of all the plots within each vegetation type. The variability among plots is highlighted in Table S1.

2.3.2 Patterns in tree species composition and diversity

2.3.2.1 *Floristic survey*

Across the 25 1-ha plots,157 morphospecies were recorded and identified according to their local species name, of which 90 were fully identified to species level (58%) and a further 18 to genus (11%), with 32 families represented. The fully and partially identified species contributed 96% of the total measured stems and AGC across all sites. In the surrounding 9-ha plots (>40cm), an additional 29 morphospecies were identified, of which 9 were identified to species level and 1 to genus, with a further 3 families represented. The data presented in the following sections is largely from the 1-ha plots, with the data from the 9-ha plots only included in the analysis of large stem diversity (Table 2.3)

2.3.2.2 *Relationship between tree species diversity and AGC (Q2)*

The number of species per plot ranged from 8 - 43 ha^{-1} with both richness and Fisher's alpha diversity found to be significantly higher in the woodlands and forests compared to the savannas (ANOVA, $P < 0.01$). The results were the same when considering small, medium and large trees separately (Table 2.3). Species richness, Fisher's alpha, and number of families represented all exhibited a positive linear relationship with AGC storage ($P <= 0.002$ in all cases) (Figure 2.4). The trend was maintained when controlling for stem density (rarefied richness) however the relationship was slightly weaker ($P = 0.01$) (Figure 2.4). Switching the axis (diversity – dependent, AGC – independent) did not alter fact that linear models performed better than any of the quadratic models (data not shown).

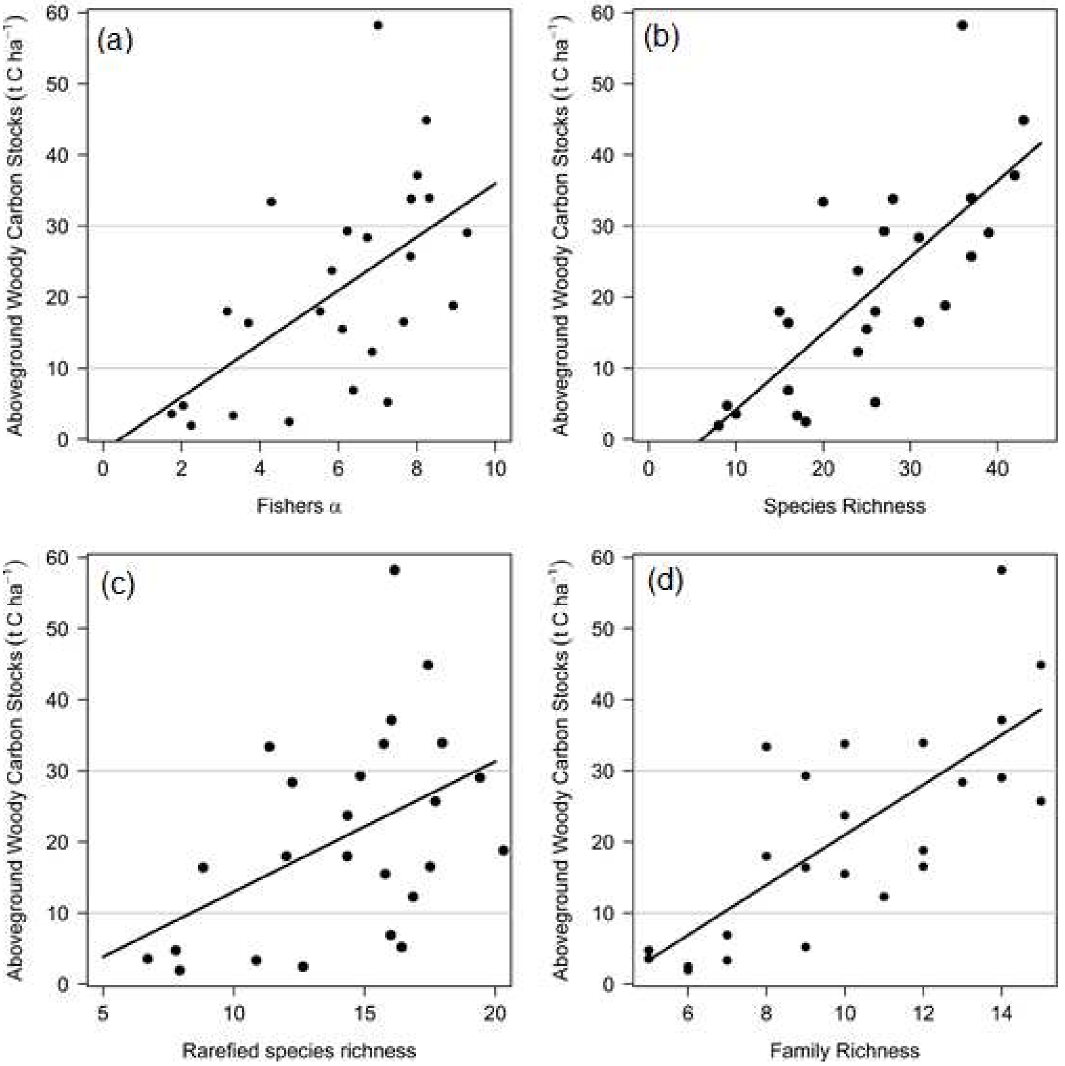

Figure 2.4 - Relationships between various measures of tree diversity and aboveground woody carbon stocks. OLS regression models are fitted to the data; (a) Fisher's α (y = 3.75 – 1.55, $r^2 = 0.3$, $p = 0.002$), (b) tree species richness (y = 1.07 – 5.55, $r^2 = 0.55$, $p = <0.001$), (c) rarefied richness (y = 1.83 – 5.3, $r^2 = 0.19$, $p = 0.01$), and (d) the number of families represented (y = 3.52 - 14.24, $r^2 = 0.55$, $p = <0.001$). Switching the axis did not alter the form of the relationship. For clarity, the division between vegetation types is shown by the horizontal lines.

2.3.2.3 Patterns in tree species composition and β-diversity between plots

Euphorbiaceae was the dominant family (39% of total AGC; 17% of total stems) followed by both Combretaceae and Fabaceae (~21%; ~11%), and Apocynaceae

(12%; 17%). Familial dominance differed among vegetation types with trees in the family Euphorbiaceae more common in the forests (39%; 24%), while species in the family Fabaceae were proportionally more dominant in the savannas and woodlands (39%; 21%), compared to the forests (25%; 6%) where they were few in number but large in stature. Consequently, the dominant species also differed between vegetation types (Table 2.2). A small number of species were both abundant and widespread, including *Combretum apiculatum, Diplorhynchus condylocarpon* and *Hymenocardia ulmoides*. Together these three species comprised 36% of the total stems and 19% of the total AGC measured.

The majority of species were less abundant, with 49 species contributing fewer than 50 individuals. Many of the recorded species were endemic to particular vegetation types, with 9 species only recorded in savanna plots, 36 in woodland plots and 41 in areas of denser woodland and forest (Figure 2.3). Savannas were characterised by a range of species, among which *Spirostachys africana* and *Burkea africana*, and fruit trees such as *Sclerocarya birrea* were common, along with the key timber and priority conservation species, *Dalbergia melanoxlyon*, which was also widely found in the woodlands. The wider sub-dominance of species common to more open habitats (i.e. *Acacia sp.*) meant that the savanna plots were found to be floristically distinct from the surrounding woodlands and forests, both when considering all stems together (>5cm) (PerMANOVA, $P < 0.001$; Figure 2.5) and when considering small, medium and large trees separately (Table 2.3); refuting the hypothesis that composition is uniform across the landscape.

Table 2.2 – The top 5 dominant species ranked by their total carbon stock and stocking density within each vegetation/ AGC class. Additional information included the mean species richness, fisher's α and evenness per plot (±SD) and the total number of species recorded in each class

Order	**Savanna (0 – 10 t C ha^{-1})**	**Woodlands (10 – 30 t C ha^{-1})**	**Forests (>30 t C ha^{-1})**
AGC (tC ha^{-1})			
1	*Diospyros quiloensis*	*Julbernardia globiflora*	*Julbernardia globiflora*
2	*Sclerocarya birrea*	*Brachystegia spiciformis*	*Hymenocardia ulmoides*
3	*Combretum apiculatum*	*Dalbergia melanoxylon*	*Hymenaea verrucosa*
4	*Dalbergia melanoxylon*	*Pseudolachnostylis maprouneifolia*	*Combretum apiculatum*
5	*Burkea africana*	*Combretum apiculatum*	*Burkea africana*
% of total	55.8	46.5	41.3
Stocking density (n/ha)			
1	*Combretum apiculatum*	*Diplorhynchus condylocarpon*	*Hymenocardia ulmoides*
2	*Spirostachys africana*	*Combretum apiculatum*	*Suregada zanzibariensis*
3	*Acacia nilotica*	*Pseudolachnostylis maprouneifolia*	*Diplorhynchus condylocarpon*
4	*Burkea africana*	*Dalbergia melanoxylon*	*Combretum apiculatum*
5	*Bauhinia petersiana*	*Hymenocardia ulmoides*	*Combretum molle*
% of total	62.8	58.3	44.8
n plots	7	12	6
Species richness	15 (7)	27 (8)	34 (9)
Fisher's α	3.5 (2.1)	6.5 (1.7)	7.3 (1.5)
Total species richness	54	102	103
Evenness	0.69 (0.05)	0.65 (0.06)	0.66 (0.07)

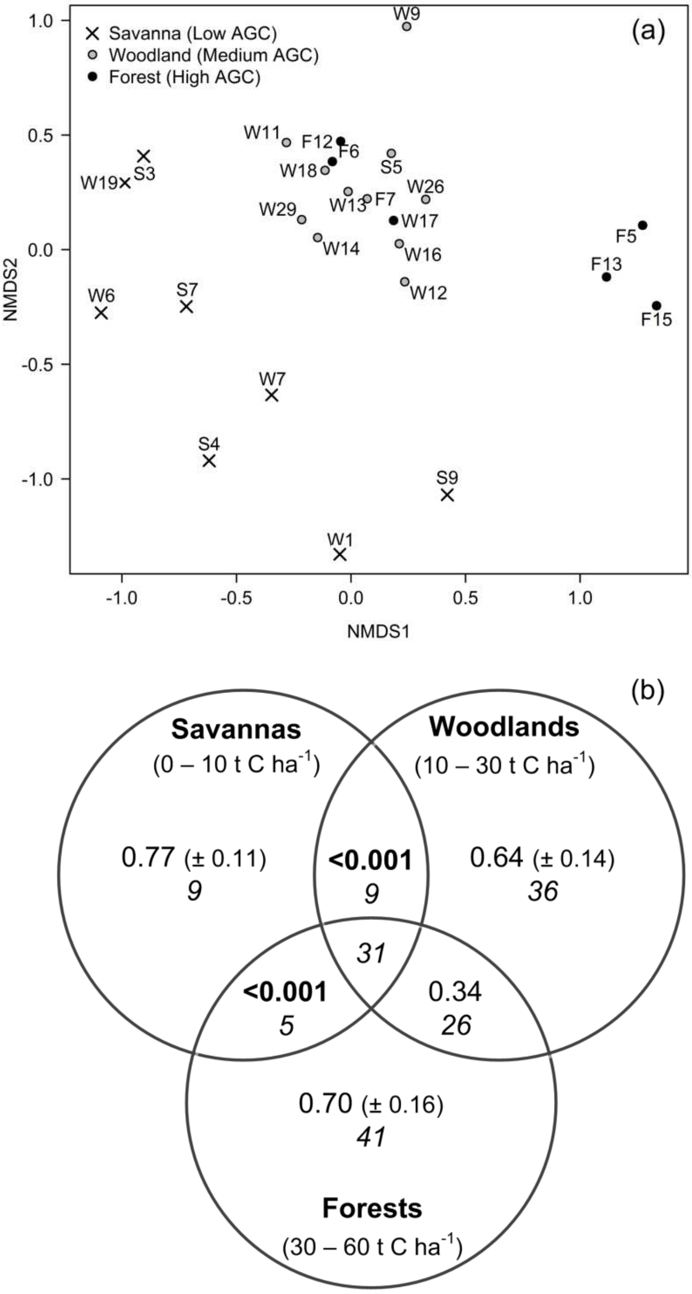

Figure 2.5 – (a) NMDS ordination based on the Bray-Curtis index which is used to uncover the main compositional patterns across the plots; (b) Venn diagram illustrating the compositional dissimilarity (mean ± SD; Bray-Curtis Index) between plots of similar AGC. The scale of the Bray-Curtis index is from 0-1, with 0 representing plots that have the same species and 1, areas that share no species. PerMANOVA was used to test for significant differences in composition between groups of plots with the test P-values shown in the shared space between vegetation classes with significant differences highlighted in bold. Numbers in italics indicate the number of species that are unique and shared (interactions) between vegetation types.

Species turnover (ß-diversity) among savanna plots was also relatively high as evidenced by the NMDS ordination plot, with some plots of similar AGC and structure found to contain entirely different species assemblages (Figure 2.5). Species dissimilarity between plot-pairs, measured using the Bray-Curtis index, was significantly higher (ANOVA; $F = 14.98$; $P < 0.001$) among savannas (range = 0.55 - 1.0), than both the woodlands (0.41 - 0.87) and forests (0.37 to 0.81) The comparatively low species dissimilarity and tight clustering between woodlands plots in the NMDS indicates that these areas are largely homogeneous in composition. Here, plots were dominated in terms of AGC storage by two of the defining miombo species – *Julbernardia globiflora* and *Brachystegia spiciformis* – which also dominated in the forests although were relatively few in number indicating the typically large size of these stems (Table 2.2). At the upper end of the AGC gradient, species characteristic of wet miombo woodland and coastal forest, including *Suregada zanzibariensis* and *Hymenaea verrucosa* were more common. This apparent shift in species composition was reflected in the NMDS plot with three of our highest AGC forest plots ($\geq$ 37 tC ha^{-1}) showing clear differences in composition to others (Figure 2.4). Based on the initial classification of vegetation types, both woodlands and forests appeared be floristically similar based on the analysis of all stems (PerMANOVA; $P = 0.34$), however the composition of small stems differed between habitats (Table 2.1; $P = 0.02$). When the three highest AGC plots (>37 t C ha^{-1}) were analysed separately to the other forest plots and woodlands, a clearer distinction in terms of composition became apparent for all size classes (PerMANOVA; $P < 0.001$).

Table 2.3 – Diversity indices for each vegeation class but this time separated by size class. As with Table 2.2 information includes the mean species richness, family richness and fisher's α (±SD) for different size classes within each plot. The Bray-Curtis index is used to highlight difference in floristic composition within plots. The letters in superscript indicate the results of the PerMANOVA which tested whether the composition of small, medium and large trees significantly varied between vegetation types.

Size class	Small trees (5 - 15cm DBH)	Medium trees (15 - 40cm DBH)	Large trees* (40cm+ DBH)
Savanna			
Species richness	14 (7)	6 (3)	7 (4)
Family richness	6 (2)	3 (1)	3 (2)
Fisher's α	3.2 (2.0)	3.8 (3.7)	3.4 (2.0)
Bray-Curtis Index	0.77 (0.11) ^{a}	0.89 (0.12) ^{a}	0.77 (0.12) ^{a}
Woodland			
Species richness	22 (6)	15 (5)	15 (5)
Family richness	9 (3)	6 (2)	5 (1)
Fisher's α	5.5 (1.7)	6.0 (2.3)	4.9 (1.6)
Bray-Curtis Index	0.66 (0.14) ^{b}	0.67 (0.13) ^{b}	0.64 (0.17) ^{b}
Forest			
Species richness	28 (9)	19 (4)	17 (4)
Family richness	11 (3)	8 (3)	6 (2)
Fisher's α	6.2 (1.1)	5.6 (1.7)	5.0 (1.1)
Bray-Curtis Index	0.73 (0.14) ^{c}	0.74 (0.15) ^{b}	0.74 (0.16) ^{b}

* Includes the measured stems from the 9-ha plot

2.3.2.4 Explaining patterns in tree species composition

Mantel tests used to compare differences in species composition between all plot-pairs indicated that geographic distance, both in standard form and log-transformed, explained little of variability in species composition between sites (Figure 2.6). Species β-diversity tended to be high at small spatial scales and did not increase significantly with increasing geographic distance. In comparison, gradients in vegetation structure were strongly correlated with gradients in species composition (Mantel, $P<0.001$), while environmental dissimilarities between plot-pairs were also significantly correlated with species turnover (Mantel, $P = 0.02$), however the strength of the relationship was weaker. Yet even sites that were environmentally or structurally similar differed widely in their composition alluding to the potential effects of unmeasured environmental variables, whereas some sites that were highly dissimilar in terms of structure and environment typically shared less than 40% of their species (Figure 2.6). Both sets of explanatory variables were not correlated with geographic distance (data not shown) indicating that neither was spatially structured.

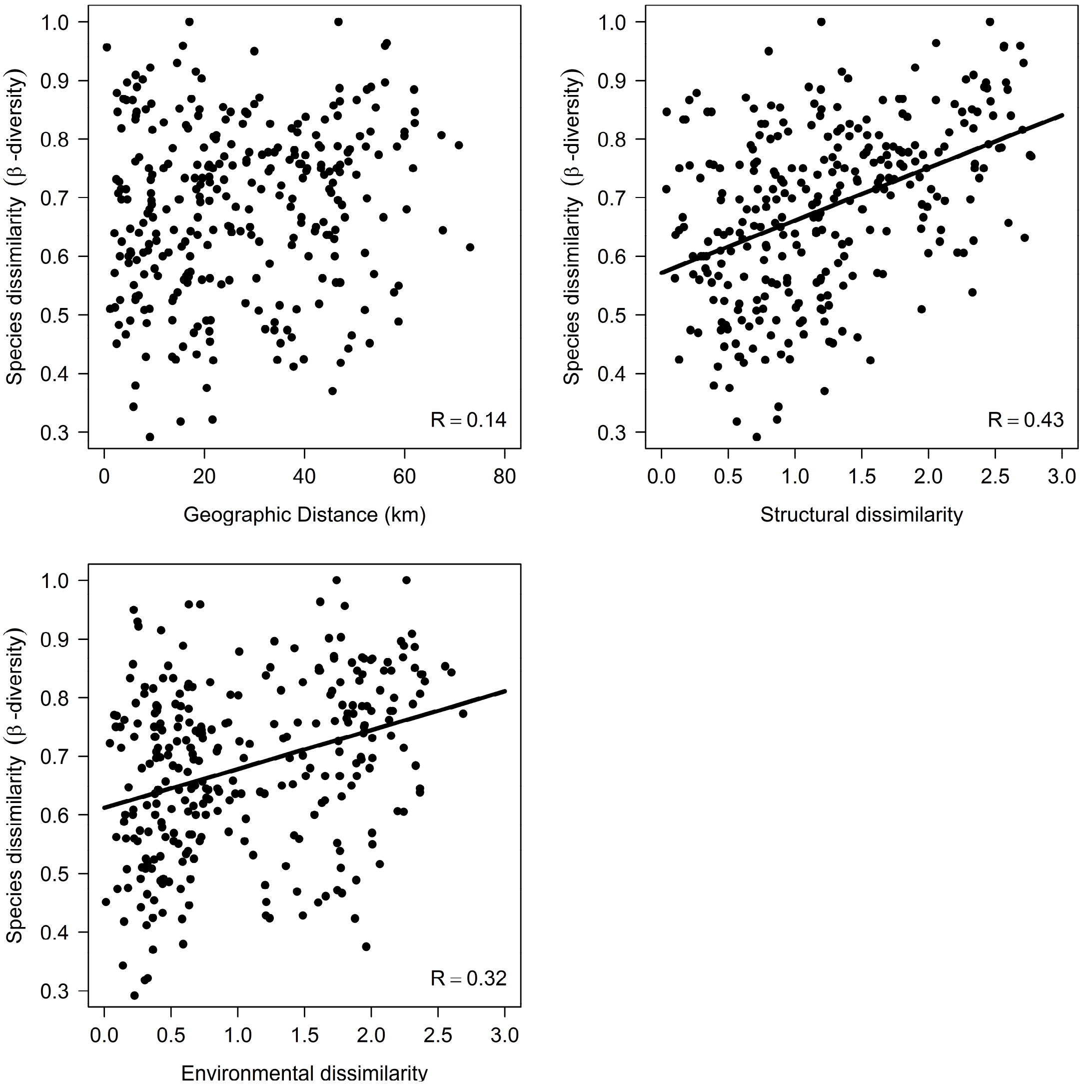

Figure 2.6 – Distance decay plots showing the changes in species similarity between each plot with increasing geographic distance, structural dissimilarity and environmental dissimilarity. Solid lines indicate significant Mantel correlations along with the associated correlation statistic (R). Ordinary least squares regression models are used to illustrate the correlations between β-diversity each dissimilarity/distance metric

Because of its lack of explanatory power spatial distance was excluded as an independent variable in the RDA, focussing instead on the effect of environment and structure. Results of the variance partitioning analysis revealed that the total explained variation was just 19%, the majority of which (16%) was attributable purely to differences in stand structure (Figure 2.7). Forward selection retained two explanatory variables that were significant; total stem density (10.3%) and the number of small stems DBH (5%). The environmental variables used in this analysis explained virtually none of the variation in composition between sites, nor was there a significant interaction between these environmental factors and stand structure, suggesting that vegetation structure is not influenced by the environmental factors included here.

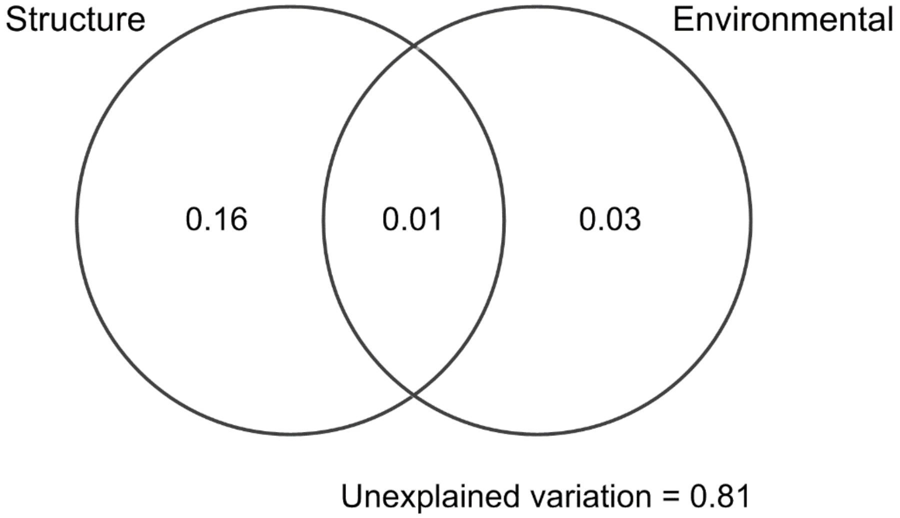

Figure 2.7- Venn diagram showing the results of the variance partitioning analysis. The reported values are adjusted R^2 statistics representing the proportion of the variation in species composition explained by each component.

2.4 Discussion

2.4.1 Question 1: Links between vegetation structure and aboveground carbon storage

Our landscape level estimates of aboveground carbon (AGC) stocks (20.9 tC ha^{-1}) are similar to those recorded using similar approaches in Mozambique by Ryan et al. (2011) (21.2 tC ha^{-1}) and Woollen et al (2012) (20.7 tC ha^{-1}). Here, our forest inventory incorporated two additional vegetation types based on vegetation structure in the analysis, allowing us to investigate how AGC stocks co-vary with stand structure and to assess which stem sizes contain most of the carbon with the aim of understanding how best to measure these areas in future.

As would be expected, savannas were characterised by lower stem densities and lower AGC stocks (<10 tC ha^{-1}) (Figure 2.3; Table S1). The majority of stems (80%), and thus AGC (42%), were attributable to the smallest stem size classes (5 - 15 cm DBH), as is consistent with systems that are highly disturbed (Marshall *et al.*, 2012). Larger trees were rare in the savannas further distinguishing them from the woodlands and forests, however on the one plot (S4) where a very large tree was present (>94.9cm, *Diospyros quiloensis*), its contribution to the total measured AGC was considerable (50%) (Table S1). The results highlight the obvious importance of maintaining a low DBH threshold in areas of savanna in order to capture the majority of AGC.

In both the woodlands (10 – 30 tC ha^{-1}) and forest plots (>30 tC ha^{-1}), a greater proportion of AGC was typically found in larger trees, with stems >40cm contributing ~41% of the plot AGC but only 3% of the stems. The proportion of AGC stored in different size classes was statistically similar for both woodlands and forests (Figure 2.3). Our results complement those of Ryan (2009) and who found similar proportion (50%) of plot AGC in the same size classes in miombo woodlands in Mozambique suggesting this is widespread structural characteristic of miombo dominated ecosystems. We stress this distinction as our results contrast those of Marshall et al. (2012) who found that in forests of the Eastern Arc Mountain, stems >40cm stored between 75 - 80% of plot AGC.

Due to the similar tree size distributions in woodlands and forests it is concluded that differences in the average stem density is what causes differences in AGC stocks between plots (Figure 2.3). However, there was evidence to suggest that differences in AGC may also reflect the greater density of very large trees (≥ 80cm) in the forests, which typically numbered only 1 per plot, yet contributed on average 8% of the measured AGC. The tendency towards greater stature in forests may be due to the fact that our highest AGC stands were typically, although not exclusively, found at high elevations and away from human populations. It can therefore be speculated that historically lower levels of disturbance in these areas has allowed larger trees to persist and AGC to accrue over longer periods (Lewis *et al.*, 2013).

In the 12 1-ha woodland plots, no stem exceeded 75cm, yet in surrounding 9-ha plots many stems surpassed this limit (max. 112cm) questioning how representative these 1-ha plots are of the surrounding woodland matrix (Anderson *et al.*, 2009), which in turn may lead to errors when scaling these estimates across the landscape (Fisher et al. 2008). This again highlights the importance of sampling on a sufficiently large scale to account for the inherent patchiness of these ecosystems and presence of rarer larger stems which we know can have disproportionate impact on AGC estimates. Such information may also be important in calculating the uncertainties in using these plots as calibration sites for earth observation sensors operating at coarser resolutions that the plots here, such as the European Space Agency's BIOMASS mission, which will operate at a resolution of 4-ha.

The need to acquire data on AGC stocks has taken on added significance due to the rise in carbon sequestration initiatives such as REDD+. Given the potentially high costs associated with even preliminary measurements of AGC stocks, a standardised methodology based on existing datasets is crucial in order to rapidly facilitate the establishment of new plots in the region and to allow cross project comparisons to take place. Limited resources often mean that field surveys need to be conducted in a credible and cost effective manner yet information on how best to sample these areas is lacking, a fact which is evidenced by the variety of methodologies used to measure carbon stocks (i.e. NAFORMA 2010). In the discussion section of the thesis I go into more detail on the trade-off between time and effort of different stem measurement thresholds for different vegetation types and the effects that this has of the measurement of biodiversity.

2.4.2 Question 2: Relationship between AGC storage and tree species diversity

The inclusion of biodiversity as a necessary co-benefit in carbon sequestration projects necessitates an assessment on how the two co-vary to assess trade-offs. Our finding of a pervasive positive relationship between tree species diversity and AGC has clear implications for conservation management, highlighting that more carbon dense areas also harbour the greatest tree species diversity (Figure 2.4). It is predicted that a diverse tree community will also lead to greater diversity across multiple trophic levels, however it unclear whether these communities also increase the ecosystem services provided to humans such as timber resources and medicinal products (Maestre *et al.*, 2012; Gamfeldt *et al.*, 2013). Among the recorded species in forests were a number of species that appear to be largely restricted to the remaining fragments of coastal forest in the region; including *H. verrucosa* and *Uvaria kirkii*, which is recorded as Near Threatened on the IUCN red list (http://www.iucnredlist.org/). The other vegetation types, particularly the woodland areas, also harboured significant levels of diversity and local endemism (Figure 2.5) and included a large number of high value, and thus locally important timber species including *Julbernardia globiflora* and the priority conservation species *Dalbergia melanoxylon* which is commercially extinct in many parts of Tanzania.

Aside from the implication for conservation management, the collection of species diversity data also permitted us to explore a widely debated topic in ecology; what is the relationship between species diversity and ecosystem function, measured here as AGC storage? In this study, I examined how tree species diversity varied across our AGC gradient and used the form of this relationship to evaluate which mechanisms based on ecological theory most likely contribute to the observed pattern.

As noted above, there was strong positive linear relationship between and AGC storage and all four measures of diversity – species richness, Fisher's alpha, family richness and rarefied richness (Figure 2.4). The results are consistent with other observational studies from tropical forests which typically note a positive effect of multiple species on either C storage and/or woody productivity (Vilà *et al.*, 2007; Thompson *et al.*, 2009; Ruiz-Jaen & Potvin, 2010; Maestre *et al.*, 2012; Ruiz-Benito *et al.*, 2014). The positive linear relationship found here is consistent with ecological theory on niche complementarity and selection effects (Fridley, 2001). In this study, I used simple indices related to species abundances as indicators of tree species diversity (see also Maestre et al., 2012). However as many of the studies that have shown similar relationships highlight, it is the diversity of functional traits within the community that shed more light on the mechanisms underlying the relationship between diversity and AGC storage (Conti and Díaz, 2013). The dominant species in our plots are poorly represented in trait databases (i.e. TRY; http://www.try-db.org) which prevented this from being incorporated into the analysis. Therefore, I can only theorise based on the the form of the relationship as to what causes the positive relationship between diversity and AGC.

Under complementarity, AGC is predicted to be maximised in areas that contain more functionally diverse species due to reduced interspecific competition for limiting resources leading to a related increase in productivity (Tilman, 1996). I included family richness as a proxy for complementarity effects based on the assumption that species in different families will have different methods of resource acquisition and growth strategies, and so will occupy separate niches. On this basis, the positive relationship between family richness and AGC storage would suggest that niche complementarity is a key factor in allowing this pattern to arise.

Selection effects on the other hand consider the greater probability that in an already diverse or structurally dense habitat that one or a number of highly productive species are present within the community. This concept is similar to the Mass Ratio Hypothesis (Grime, 1978) as it predicts that ecosystem function is largely influenced by the traits of the dominant competitors in the system.

Testing for selection effects is more challenging in the absence of trait data (Lavorel *et al.*, 2007); however, I did find a strong statistical difference between woodlands and the three high AGC forest plots in the composition of both medium and large trees (Table 2.3), which we can assume will have the largest impact on ecosystem function (Grime, 1998). On this basis it may be possible that higher AGC forests are dominated by species with traits related to greater productivity or a large mature size. An alternative may be that both variables are positively correlated to stem density (Figure 2.4c), however the significant relationship between rarefied richness and AGC also provides strong evidence that high diversity is not simply related to differences in stem density (i.e. Hubbell, 1999)

A key caveat in this interpretation of complementarity effects is that it assumes areas with high AGC stocks are also areas of high woody productivity. Whilst this may a reasonable assumption, Malhi et al. (2006), found no correlation between AGC and productivity in Amazonian forests, opening up the possibility that the same is true in our study area. Under this scenario, the relationship between diversity and AGC storage should be explained more by environmental factors, such as variations in soil characteristics or disturbance regime. Indeed, Chisholm et al., (2013) showed that niche-based factors principally operate at smaller spatial grains than the plots sampled here; and at larger scales, environmental conditions ultimately prevail.

When including diversity as the dependent variable, there was no evidence for the classic 'hump-shaped' pattern predicted by theories such as the Intermediate Disturbance Hypothesis; instead all four measures of diversity again increased linearly with increasing AGC. Therefore in the absence of any saturation in the relationship which would be suggestive of competitive exclusion, it appears that patches of dense forest are still capable of efficiently utilising available resources to allow many species and high AGC stocks to co-exist, suggesting some form of complementarity or facilitation. A caveat to this interpretation is the greater diversity of tree species at higher AGC densities may reflect more heterogeneous environmental conditions within these areas, leading to greater species turnover related to habitat specialisation in certain patches. They may also just be areas that have so far escaped major disturbances, as highlighted in the previous section allowing that less adapted to disturbance to persist.

The results highlight the potential role of multiple processes in shaping the diversity-AGC relationship and therefore causation cannot be strictly determined based on the available data. Future research endeavours should focus on collecting trait data for the key species in the region, particularly those traits related to resource acquisition and growth (i.e. leaf nitrogen, leaf mass per area, wood density, leaf phenology) in order to explicitly test the hypotheses related to niche complementarity (functional trait diversity) and selection effects (functional identity). The collection of soils data will also aid in this interpretation to see whether there is any edaphic differences between the savannas, woodlands and forests (i.e. habitat heterogeneity hypothesis).

2.4.3 Question 3: Drivers of floristic variation across the landscape

The final question was to assess how species composition varies across these structurally heterogeneous and patchy landscapes and to try and explain *why* certain species assemblages occur *where* they do. As above, the analyses were based on ecological theory and centred around three unique views; the idea of uniformity, where species composition is largely homogeneous over large areas; environmental determinism, where species are filtered by edaphic or other environmental conditions; and dispersal assembly, which places emphasis on seed dispersal processes (fecundity and spatial distribution) and the ability of a particular species to reach a certain area. I used mantel tests to assess the relationship between β-diversity and both spatial distance and physical factors individually, and variance partitioning to decompose and test the relative importance of each of these processes in shaping tree community structure across the 25 1-ha plots.

The uniformity hypothesis gained little support with plots in savannas found to floristically distinct from the surrounding woodland and forest plots (Figure 2.5). In comparison, the woodland areas were relatively homogenous and dominated by species in the defining miombo genera *Brachystegia* and *Julbernardia* giving credence to the assertion that miombo are uniform over large areas (Frost, 1996). The results of the NMDS and PerMANOVA analyses also revealed a compositional shift at the upper end of the AGC gradient related to the presence of species more indicative of coastal forest (Prins & Clarke, 2007; Timberlake, 2011).

Spatial distance between plots, often used as a proxy for dispersal processes, did not result in a concomitant increase in species turnover between plots. The idea that communities are predominantly spatially structured is based on the hypothesis that all species are competitively equal meaning any one can dominate by chance, but also that they are poor dispersers meaning that a species is likely to be present in nearby stands but not ones that are far away. Instead a small number of apparently competitively dominant species were found to be present across multiple plots and abundant in those areas, resulting in similar patterns of composition for some plots that were relatively far apart (Figure 2.6). This is not surprising given the comparatively small scale of this study (i.e. Tuomisto and Ruokolainen, 2003). However, sites that were close together also exhibited strong compositional differences, both of which give a strong indication that in this area species are not ecologically equivalent, as proposed by (Hubbell, 2001), and the importance of niche assembly in shaping species patterns across the gradient.

Indeed, we found that differences in forest structure, which we used here as a proxy for both resource competition and fire disturbance, was the primary determinant, yet alone this only explained 16% of the compositional variation between sites (Figure 2.7). Structural patterns were not environmentally controlled (i.e. by soils or precipitation) alluding to the role of fire in shaping this gradient. Total and small stem density were the only two variables retained in the RDA model suggesting that differences in composition are largely due to inter-specific competition with higher density forests perhaps favouring species that are more fire sensitive and more competitive in light limited and denser environments.

Although environmental conditions are predicted to act as a filter on species distributions in other parts of the miombo region (Backéus *et al.*, 2006; Woollen *et al.*, 2012), in this study compositional differences were poorly related to the environmental proxies used in the analysis, explaining only 3% of the variability. Here, I used topographic proxies and modelled estimates to represent the impact of soils. These data are most often utilised in studies examining larger scale distributions of vegetation types where the collection of field data is impractical (Lehmann et al., 2011), however they provide only basic information on soil properties at coarse resolution (1km). Soils are known to vary over small spatial scales (Woollen *et al.*, 2012) therefore it is unlikely that these data are representative of the actual conditions at each plot. We therefore predict that the environmental influence will be underestimated contributing to a large proportion of the unexplained variation (Baldeck *et al.*, 2013). Patches of coastal forest, for example, have been linked to the presence of more nutrient rich and/or deeper soils (Frost, 1996; Timberlake, 2011). This assertion is given extra weight by the relatively low abundance within high AGC communities of trees in the family Fabaceae, many of which have N-fixing capabilities, or in the case of *B. spiciformis* (not N-fixing), utilise mychorrhizae in their root networks allowing them to compete on poorer soils (Hogberg and Nylund, 1981). This leads to speculation that the soils underlying the forest are not nutrient limited, as is predicated to common across savanna woodlands (Frost 1996). Accumulations of aluminium and iron in the subsoil leading to the formation of laterite hardpans have also been mooted as determinants of vegetation cover across topographic gradients (Frost 1996). Soil data is forthcoming (texture, total nitrogen and extractable phosphorous) and it is expected that by incorporating field measured soil data in to the analysis there will be an increase in the overall explanatory power of the environmental component in driving patters in tree community assembly.

2.5 Summary

Question 1: Tree carbon stocks were highly variable across the study area ranging from a minimum of 1.9 tC ha^{-1} in an area of open savanna, up to 58.2 tC ha^{-1} in a patch of East African Coastal Forest. Large stems had a significant contribution to plot-level AGC stocks (35%) especially in the miombo dominated woodlands and coastal forests where they were greater in number. Averaged across all plots the top 3% of individuals (>40cm) in terms of size contained 41% of the carbon. Ecosystem carbon stocks are therefore highly sensitive to losses of these very large trees which may occur through selective logging given that many of these stems were highly valued timber species (i.e. *J. globiflora* + *D. melanoxylon*). Field measurement campaigns that focus on sampling slightly larger stems than the 5cm diameter threshold used here may provide a more cost/time efficient method of measuring and monitoring AGC stocks, however this will differ depending on the vegetation type. This issue will be discussed in more detail in the final chapter of this thesis.

Question 2: Tree species diversity was positively correlated with AGC storage with more carbon dense areas also harbouring the greatest tree species diversity, a 'win-win' scenario for forest conservation. Lower biomass areas, particularly the miombo woodlands, still contained relatively high levels of tree species diversity. A large number of species were also found to be constrained to either woodlands or forests thus creating localised patterns of species endemism. The positive relationship between diversity and AGC suggests the importance of a functionally diverse assemblage of tree species. An increase in family diversity was used to suggest that complementary effects may be an important determinant of higher AGC. However, causation cannot be strictly determined based on the available data with selection effects also potentially important (functional ‘identity’ over ‘diversity’). Results are further confounded by the fact that carbon dense stands are not necessarily more productive. Future research endeavours should therefore focus on collecting trait data for the key species in the region, particularly those traits related to resource acquisition and growth. Repeat measurement of the plots will also be required in order to test whether the biodiversity-productivity relationship holds true in these ecosystems.

Question 3: The uniformity hypothesis gained no support with the savannas found to be floristically distinct from the surrounding woodland and forest plots. The original plot classification based on forest structure also largely coincided with differences in tree species composition. The top 3 highest biomass plots were also marked out as floristically different from the more miombo dominated areas and indicating the presence of coastal forests. Results also showed that these patterns in tree communities could not be explained by neutral processes such as dispersal limitation. Instead the results suggest that tree community assembly is more strongly driven environmental factors. However a combination of both environmental and structural determinants explained only 19% of the variability in species composition. Fire is known to be a key component of savanna ecology, the effects of which were partially vectored through differences in stand structure with denser plots assumed to favour more disturbance intolerant species. The role of soils should not be discounted as they were poorly represented in this study.

2.6 Chapter 2 references

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Table S1 - Mean (±1SD) stem density and AGC stock per stem diameter size class for each 1-ha plot, for different forest types. Percentage contributions are given in italics

	Stem density (ha^{-1})						**AGC stocks (tC ha^{-1})**					
	Savanna (*n* = 7)		Woodland (*n* =12)		Forest (*n* = 6)		Savanna		Woodland		Forest	
	Total #	% of total	Total #	% of total	Total #	% of total	Total	% of total	Total	% of total	Total	% of total
5-10	217 (190)	*74.2 (14.0)*	276 (138)	*57.0 (9.8)*	594 (408)	*57.6 (12.9)*	0.92 (0.77)	*26.8 (23.0)*	1.36 (0.68)	*6.4 (2.6)*	2.74 (1.87)	*6.6 (4.3)*
10-15	33 (18)	*14.9 (5.3)*	94 (38)	*20.6 (4.7)*	166 (92)	*18.2 (1.6)*	0.58 (0.33)	*15.9 (8.3)*	1.71 (0.71)	*8.2 (2.6)*	2.93 (1.55)	*7.2 (3.5)*
15-20	9 (7)	*6.0 (5.5)*	37 (16)	*8.4 (3.0)*	69 (28)	*8.2 (1.9)*	0.41 (0.29)	*10.4 (6.3)*	1.67 (0.77)	*8.1 (3.3)*	3.09 (1.25)	*7.6 (2.8)*
20-25	4 (2)	*1.9 (1.5)*	21 (7)	*5.1 (2.2)*	41 (12)	*5.7 (3.5)*	0.31 (0.20)	*6.8 (4.3)*	1.88 (0.58)	*9.5 (3.4)*	3.55 (1.03)	*9.0 (3.0)*
25-30	2 (2)	*1.1 (0.8)*	12 (3)	*2.8 (1.1)*	23 (7)	*3.2 (1.7)*	0.31 (0.21)	*7.0 (4.9)*	1.74 (0.43)	*8.7 (2.6)*	3.46 (1.04)	*8.7 (2.5)*
30-35	2 (2)	*0.6 (0.9)*	10 (4)	*2.3 (1.0)*	16 (5)	*2.4 (1.8)*	0.37 (0.33)	*4.5 (6.6)*	2.25 (1.06)	*11.0 (4.7)*	3.50 (1.13)	*8.8 (2.7)*
35-40	2 (1)	*0.6 (0.6)*	6 (3)	*1.3 (0.6)*	10 (6)	*1.4 (0.8)*	0.46 (0.29)	*6.3 (7.4)*	1.95 (0.97)	*9.5 (4.0)*	3.35 (1.86)	*8.0 (2.7)*
40-45	1 (0)	*0.3 (0.5)*	5 (4)	*1.0 (0.8)*	6 (3)	*1.0 (0.9)*	0.50 (0.05)	*6.6 (11.5)*	2.22 (1.62)	*8.9 (6.3)*	2.76 (1.50)	*7.4 (4.2)*
45-50	--	--	3 (2)	*0.7 (0.6)*	5 (4)	*0.9 (1.0)*	--	--	1.91 (1.27)	*8.0 (5.4)*	2.83 (2.56)	*7.9 (7.9)*
50-55	--	--	2 (1)	*0.4 (0.3)*	3 (3)	*0.5 (0.5)*	--	--	1.81 (0.81)	*6.3 (4.9)*	2.67 (2.01)	*6.3 (3.4)*
55-60	--	--	2 (1)	*0.3 (0.3)*	2 (1)	*0.5 (0.7)*	--	--	1.78 (0.86)	*5.3 (4.6)*	2.14 (1.47)	*5.8 (4.6)*
60-65	1 (0)	*0.2 (0.5)*	2 (1)	*0.1 (0.2)*	2 (1)	*0.1 (0.1)*	1.33	*2.8 (7.3)*	2.82 (1.38)	*2.5 (4.9)*	2.28 (1.37)	*4.3 (2.9)*
65-70	--	--	2 (1)	*0.1 (0.3)*	1 (1)	*0.2 (0.3)*	--	--	2.31 (0.97)	*4.0 (7.7)*	2.01 (1.04)	*2.9 (3.8)*
70-75	1 (0)	*0.1 (0.2)*	1 (0)	*0.1 (0.1)*	--	--	1.73	*5.2 (13.8)*	1.84 (0.11)	*2.6 (4.8)*	--	--
75-80	--	--	1 (0)	*0.0 (0.1)*	--	--	--	--	2.12	*1.1 (3.7)*	--	--
80-85	--	--	--	--	1 (0)	*0.1 (0.2)*	--	--	--	--	2.75	*1.4 (3.3)*
85-90	--	--	--	--	1 (1)	*0.1 (0.1)*	--	--	--	--	3.91 (1.66)	*4.1 (4.6)*
90-95	1 (0)	*0.2 (0.5)*	--	--	1 (0)	*0.0 (0.0)*	3.69	*7.6 (20.2)*	--	--	3.71	*1.1 (2.6)*
95-100	--	--	--	--	1 (0)	*0.1 (0.1)*	--	--	--	--	3.81 (0.14)	*3.0 (4.8)*

Chapter 3

What determines spatial patterns in aboveground woody biomass across a heterogeneous African woodland landscape?

Iain M. McNicol, Yaqing Gou, Mathew Williams and Casey M. Ryan

Aerial photograph showing the sharp transition between open savanna and miombo woodland
Latitude: -8.97, Longitude: 39.07
Image courtesy of Richard Lamprey, Flora and Fauna International, October 2010

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Author contributions
The idea for this study was contrived by IMM, MW and CMR. IMM sourced and submitted the application for the radar imagery. YG obtained and processed the data with assistance from CMR. IMM sourced and processed the relevant environmental data layers, performed the data analysis and wrote the paper

3.1 Introduction

Tropical savannas and woodlands occupy 20% of the global land surface, a large proportion of which are found in sub-Saharan Africa where they are the dominant land cover (Menaut *et al.*, 1995; Grace *et al.*, 2006). Their vast spatial extent means they constitute a large, but poorly quantified store of organic carbon with potentially important implications for global carbon cycling (Ciais *et al.*, 2011; Pan *et al.*, 2011; Willcock *et al.*, 2014). They provide a range of ecosystem services to local populations such as food, timber and fuel, as well as containing a large diversity of flora and fauna, many of which are endemic to the region (Bond & Parr, 2010; Platts *et al.*, 2010). Unlike wetter tropical forests, these ecosystems are densely populated and human pressures linked to resource extraction and agricultural activities are now known to be resulting in significant, but poorly constrained losses of CO_2 to the atmosphere (Silva *et al.*, 2011; Ryan *et al.*, 2012). Areas of deforestation are generally well delineated via earth observation (Ryan *et al.*, 2014), therefore the critical uncertainty is knowing the amount of carbon stored in the area that was cleared (Houghton & Hackler, 2006; Houghton, 2010). Improvements in carbon mapping will help to reduce this uncertainty in the African carbon balance, and can facilitate an improved understanding of what determines biomass variability in these heterogeneous ecosystems. There are economic incentives as well with conservation efforts such as REDD+ aiming to reduce rates of land cover change by placing a monetary value on the woodlands based on the carbon they contain. Positive relationships between tree species diversity and woody carbon stocks have also been recorded in the region (Chapter 2); therefore knowing where most of the biomass is located can also inform areas of high biodiversity value.

The term ‘Savanna’ is widely used to encompass a broad range of vegetation types found in the region, ranging from the characteristic open grasslands with scattered trees, through open canopy *Combretum* and the regionally dominant ‘miombo’ (*Brachystegia – Julbernardia*) woodlands before finally grading in to closed canopy dry forest at the end of the spectrum (not-‘Savanna’). The result is a mosaic of patches of varying floristic composition, density and AGC stocks (Chapter 2). Most of the recent discussion has focused on what controls large scale shifts between biomes (i.e. 'Savanna' vs 'Forest'; Staver et al. 2011; Lehmann et al. 2011), yet there is less information on what constrains these different savanna vegetation types and coastal forests as alternative states.

The inherent variability in tree cover and thus AGC storage across these complex landscapes reflects the interacting effects of multiple abiotic and biotic factors, the relative influence of which is often difficult to disentangle. At the regional level (100s km), mean annual precipitation imposes a maximum limit on woody cover (Sankaran *et al.*, 2005) however other factors often act to maintain tree cover well below its climatic potential (see Bucini and Hanan, 2007, Sankaran et al. 2008). Due to their intense human utilisation, regular fires linked to agricultural clearance and hunting are often considered to be the main limiting factor to woody growth (Furley *et al.*, 2008; Staver *et al.*, 2009). Herbivory also imposes top-down controls on woody biomass through grazing and browser pressure although over large scales the impacts of these are difficult to quantify. At the same time, soils impose bottom up controls on AGC through controls on nutrient availability and water holding capacity, both of which directly affect woody productivity. High soil fertility would be expected to promote denser forest by lessening growth constraints in these generally nutrient and base poor substrates (Scholes, 1990; Bond, 2008), however this pattern is not always evident (Sankaran *et al.*, 2008; Lehmann *et al.*, 2011) with some finding the opposite relationship (Bell, 1982). Soil texture has direct effects on soil moisture availability and vertical drainage, both of which are closely linked to topographic factors such as slope angle and position (Frost *et al.*, 1986; Menaut *et al.*, 1995). Roots can also penetrate to lower depths on more coarse-textured substrates and so access deep water reserves, potentially leading to greater productivity. This pattern was noted by Woollen et al. (2012) who found higher AGC stocks on coarse textured, well-drained ridges compared with lower-lying depressions in a miombo dominated landscape in Mozambique supporting earlier observations that seasonal waterlogging or the presence of hardpans prevent trees establishing (Tinley, 1982). Similar patterns were noted by Colgan et al. (2012) on granitic soils in the more open savannas of Kruger National Park, with the opposite relationship found on basalts. Thus, while regional biomass patterns linked to climate and disturbance are relatively well established, there is little consensus of what factors, or combinations thereof, principally determine AGC stocks at landscape scales, where local climate, disturbance, topography and substrate all interact to create patterns (Bond, 2008).

This study builds upon the rich history of research into 'savanna' biogeography by examining the extent to which the aforementioned factors influence landscape scale (10s km) patterns in AGC storage in a part of South-Eastern Tanzania containing a range of vegetation types including savannas, woodlands and coastal forests (Chapter 2). The scale of this study is of special interest as it occupies the boundary between coarser scales, where precipitation and seasonality are shown to be significant (Sankaran *et al.*, 2008), and finer scales where clear topographic and edaphic trends are evident (Colgan *et al.*, 2012; Woollen *et al.*, 2012). Understanding the current environmental determinants of woody biomass is crucial for predicting how potential changes in climate (i.e. precipitation, dry season length, increasing atmospheric CO_2 concentrations), or land use (i.e. fire management and herbivory) will influence these patterns in future (Bond, 2008; Mitchard *et al.*, 2011; Buitenwerf *et al.*, 2012; Higgins & Scheiter, 2012). This study has implications for a local REDD+ project aiming to generate carbon credits through improved fire management by quantifying how much of the variation in AGC storage by environmental factors, and how much is explained by disturbances.

Field plots provide the most reliable estimates of AGC stocks, as well as detailed information on soil conditions, micro-topography and species diversity which allow co-variation to be explored (Chapter 2; Sankaran et al. 2005; Quesada et al. 2012). However, restraints on time and resources mean that it is often not possible to capture the full range of environmental conditions present within the landscape, particularly areas that are remote or inaccessible, such as steep slopes, or marginal areas such as riverine habitats. Satellite remote sensing, linked to field plots for calibration, thus constitutes the only practical means of gaining synoptic biomass data across large areas (Mitchard *et al.*, 2009; Asner *et al.*, 2010). Space-borne radar imagery is ideally suited for this purpose as the transmitted radar signal from current instruments (ALOS-PALSAR) has been shown to be sensitive to woody structure up to a signal-saturation point of between 60 - 100 t C ha^{-1} (Lucas *et al.*, 2010). The fine spatial resolution of these maps (10s m) is sufficient to capture small-scale patterns in

AGC stocks which when compared with ancillary data related to climate, soils and topography can be used to improve our understanding on what principally controls spatial variability in AGC at landscape scales. Using these datasets as a basis, the questions I aim to address in this study are;

(Q1) What is the environmental distribution of AGC and is the amount of AGC an area supports bound within clear biophysical limits?

(Q2) To what extent do factors related to topography, climate and soils explain spatial variations in AGC across these complex landscapes?

This study is novel in its assessment of large-scale patterns in above ground woody biomass. Previous studies have used estimates of woody cover derived from optical imagery and field data as measures of vegetation density (i.e. Sankaran et al. 2008; Bucini & Hanan 2007), which do not capture potentially important variation in tree vegetation structure below the canopy, and is also sensitive to patterns in phenology (Ryan *et al.*, 2013). The ability to map woody biomass at landscape scales has wider implications in the context of the global carbon cycle by helping to reduce the uncertainties in the deforestation flux (van der Werf *et al.*, 2009), and the sink strength of these dry-land ecosystems (Pan *et al.*, 2011)

3.2 Study area

The study area covers 7788 km^2 and encompasses large parts of Kilwa district and the eastern edges of Liwale district in Lindi region, South-Eastern Tanzania (Figure 3.2). It has a seasonally wet-dry climate averaging ~865 ± 361 mm rain yr^{-1} (Tropical Rainfall Measuring Mission – TRMM; Huffman et al. 2007) with the majority of the precipitation falling in two distinct periods – the short rains between November and January, and the longer rains between February and May. Topography is gently undulating over most of the study area (mean slope = 2.0 ± 1.9°), and has an elevation range of 21 – 493m a.s.l (Shuttle Radar Topography Mission - SRTM), 90m resolution). The dominant vegetation type is miombo woodland, the most widespread 'savanna type' in southern Africa. Isolated patches of floristically important East African coastal forest are scattered across the region and are concentrated on a dissected plateau/ escarpment that runs along the eastern edge of the study area (Chapter 2; Prins & Clarke 2007). Towards the centre and west, the vegetation grades in to more open savannas and woodlands. The proximity to Selous Game Reserve means that wildlife numbers are estimated to be greater in western parts with large browsers such as elephant being common. There are several small village communities spread across the study area which have populations ranging from ~ 500 – 3000 persons with a total estimated population of ~12,000 (2012 Tanzanian census, Mitole, Likawage and Kikole wards; www.nbs.go.tz). The majority of the population make their living from small scale subsistence agriculture and are largely dependent on the local woodlands and forests for other provisions such as fuel and timber (Miya *et al.*, 2009). Large scale commercial agriculture is non-existent which is likely due the fact that none of the roads are surfaced and so the majority of the area is not easily accessible in the wet season. The distance from large population centres (Dar es Salaam, c. 300km) has also meant that the area has so far been spared the extensive degradation occurring in other parts of the region, such as along the main road (Milledge *et al.*, 2007; Ahrends *et al.*, 2010). As a consequence, extensive anthropogenic disturbances are considered to be low out with the immediate vicinity of villages and the track networks making it an ideal location to examine environmental controls without the confounding effects of widespread disturbance (see section 3.5).

3.3 Data

3.3.1 Field biomass estimation

Field inventories of biomass were conducted between 2010 and 2011 with the location of sample sites chosen to capture the known variability in vegetation structure and biomass found in the study area (Chapter 2). Plots were established at 25 sample locations using a stratified random sampling strategy and a nested plot design that encompassed three difference plot sizes - 0.2ha, 1ha and 9ha – all of which are separately used to calibrate the remote sensing imagery. All stems above a specified diameter threshold at breast height (1.3m) were measured and converted in to estimates of aboveground woody carbon using an regionally derived allometric equation (stem only) by Ryan et al (2011). In the 1ha plots, the DBH threshold was set at 5cm, increasing to 10cm in the 0.2ha circle plots, and 40cm in the larger 9ha plot.

3.3.2 Generation of biomass maps from radar imagery *(see footnote)*

Regional maps of AGC stocks were generated using radar imagery obtained from the Phased Array L-Band Synthetic Aperture Radar sensor on-board JAXA's Advanced Land Observation Satellite (ALOS-PALSAR). Synthetic aperture radar (SAR) is an example of an active sensor in that it emits a pulse of

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The construction of the biomass-backscatter relationships and the subsequent biomass map was done by Yaqing Gou and Casey Ryan radiation towards the earth's surface and then detects the intensity of the signal that returns to the sensor, a value known as the radar 'backscatter'. L-band (23cm wavelength) radar is sensitive to woody structure (branches and tree boles), with more woody biomass resulting in more backscatter. The processing steps used to generate the AGC maps is described in detail in Ryan et al. (2012), however a summary is provided here. The study area encompassed two ALOS scenes (each ~35 x 35km). The radar signal is highly sensitive to soil and canopy moisture therefore all images are from the dry season with monthly rainfall data from the TRMM (3B43) used to ensure that precipitation did not exceed 10mm in the month preceding data acquisition. Four images, two for each original scene, were subsequently acquired from separate dates (10th July and 10th October) and were then mosaicked into one image to produce an average backscatter value. All imagery was obtained through a European Space Agency Category-1 proposal in the name of the author. Twenty-four of the twenty-five field plots were located within the mosaicked scene and so were used in the calibration of the radar imagery (Figure 3.1; Figure 3.2). Ordinary least squares regressions were used to relate backscatter values to the field derived AGC stocks and were performed separately for each plot size to see which size performed best, something which up to now has not been assessed within the same landscape (Figure 3.1).

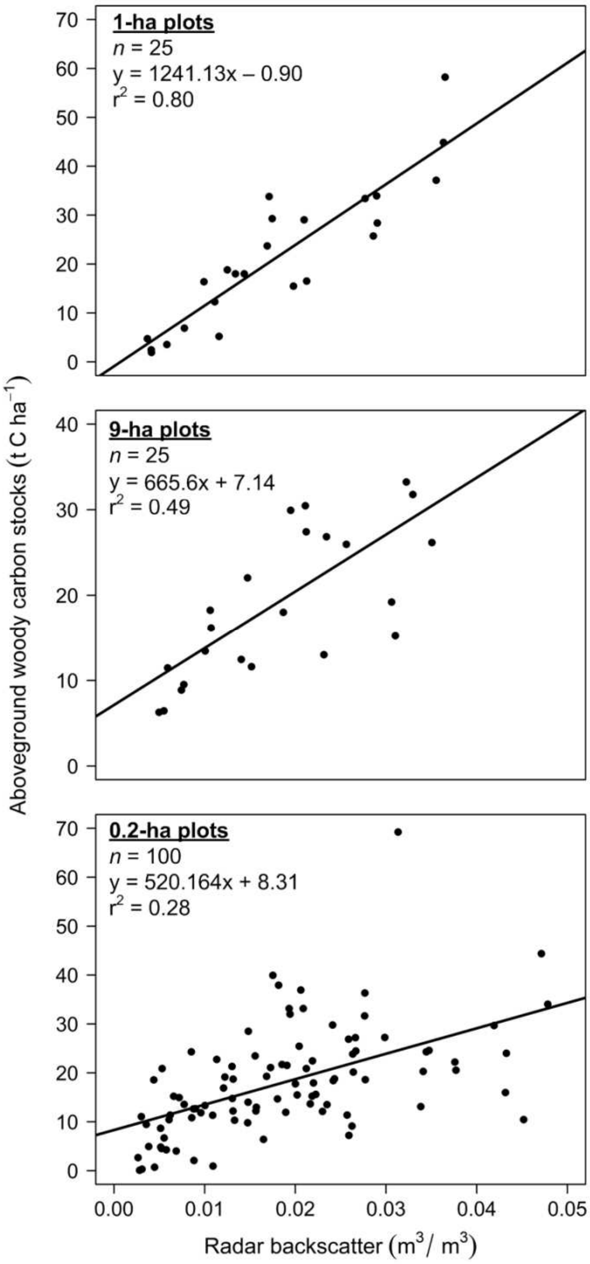

Figure 3.1 - Regression of the radar backscatter from ALOS PALSAR and field derived AGC stocks from each of the three plot sizes sampled. Note the different scales on the y-axis for the large plots.

The regression equation generated from the 1ha plots had by far the highest r^2 (0.80) and so was used to covert backscatter values to AGC. The estimated root mean square error (RMSE) on the prediction from the regression was 6.57 tC

ha^{-1} with a mean absolute bias of 0.1 t C ha^{-1}. The resultant map had a resolution of 25m but was subsequently aggregated to 100m (1 ha), the same scale as the field plots used to calibrate the map. Both negative and anomalously large AGC values were present which is due to random noise in the imagery related to speckle and soil moisture, therefore a maximum threshold of 70 tC ha^{-1} was applied to the to the dataset to mask out these areas (Figure 3.2).

3.3.3 Assessing the biophysical limits of AGC stocks

To understand what limits or promotes AGC storage in these systems, it is important to identify the ecological thresholds within which current stocks exist and to see at which point savannas give way to woodlands and then on to forests at the upper end of the woody spectrum. The processes driving the transition from open savanna to woodlands, and from woodlands to denser forests are unlikely to be similar, therefore I separately assessed the drivers of AGC variability across the transition between savanna and woodlands (0 – 35 t C ha^{-1}) and between woodlands and forest (10 – 70 t C ha^{-1}) to determine what prevents denser vegetation from establishing. The classification system used is the same as in Chapter 2 with the region stratified to low carbon density 'savannas' (< 10 tC ha^{-1}), moderate density 'woodlands' (10 – 35 tC ha^{-1}), and high density forests (>35 tC ha^{-1}). The stratification based on AGC storage also conforms with more formal definitions of these 3 different vegetation types related to canopy cover and floristic composition with the savannas dominated by species in the genera *Combretum* and *Acacia*, the woodlands by species in the keystone miombo genera *Brachystegia*, *Julbernardia* and *Diplorhynchus,* and the forests by species characteristic of East African coastal forests, such as *Suregada zanzibariensis* and *Hymenaea verrucosa*. Here, the threshold between woodland and forest is set at 35 tC ha^{-1} (instead of 30 tC ha^{-1} in Chapter 2) in order to better distinguish between miombo dominated woodlands and coastal forests (Figure 2.5).

3.3.4 Environmental correlates

Building upon the large number of observational studies which have examined linkages between vegetation and environmental factors in African savannas, I collated data related to climate, topography and edaphic conditions which I hypothesised would have a deterministic effect on AGC stocks at the relevant scale, and for which I could obtain credible and easily interpretable data. All environmental layers were processed in ArcGIS 10.1 (ESRI, 2013) a subset of which are visualised in Figure 3.3.

Rainfall and seasonality: Estimates of mean annual precipitation were derived from TRMM (2B31) and are based on average measurements from 1998 – 2009. The original data is provided at 4 km resolution and was interpolated to 1 km resolution - the same resolution as the seasonality and soils data - using the natural neighbour technique in the Raster Interpolation toolset in ArcGIS. Variations in MAP across the study areas were surprisingly large, ranging from 358 – 1846 mm year and shows strong spatial variability with the more coastal eastern edges of the study area typically receiving >1000mm year and the hinterland to the west <1000mm. Rainfall seasonality was downloaded from the WorldClim database and gives an indication of how evenly distributed rainfall is throughout the year expressed as the coefficient of variation (CV, %) (Bioclim variable 15; Hijmans et al. 2005). Lower values indicate a more even distribution of rainfall across the year, while the higher values indicate a more patchy distribution. As nearly all of the rainfall falls within a distinct wet season, a higher variability in rainfall indicates a longer dry season which in turn is linked to increased moisture stress and a longer period of grass curing leading to more intense fires later in the dry season. Greater rainfall seasonality is expected to favour savannas over denser forests (Staver *et al.*, 2011) Other climatic factors not included such as mean annual temperature were more uniform ranging from 23 – 27°C (Bioclim variable 5) and based on visual inspection appeared to be linked to elevation.

***Soil fertility and textural properties*:** Soil data was obtained from the International Soil Reference and Information Centre (ISRIC; www.isric.org/data/) which provides continuous maps of soil properties at 1km resolution and so was favoured over the frequently used Harmonised World Soil Database which only provides rough estimates of soil conditions within broad soil mapping units and is not spatially explicit. The ISRIC soil maps are created by interpolating (kriging) sample data from 12,000 points spread across the African continent to provide a continuous surface. Soil data from across Africa is sparse with one measurement used to predict an average of 1500 pixels so these maps are unlikely to capture subtle differences in soil conditions, however they represent the best estimates of soil properties at large scales. All data are from the top 30cm (topsoil) and were created by combining and averaging information from three depths: 0 - 5cm, 5 – 15cm and 15 - 30cm. Cation-exchange-capacity (CEC) was used as the primary proxy for soil fertility where high values are associated with high soil fertility. This dataset was favoured over the more reliable soil carbon dataset, another proxy of soil fertility (Lehmann et al. 2014) as the inclusion of the latter would have likely produced circularity in the analysis of what drives variability in AGC. Using the same data source, I extracted information on soil textural properties (sand, silt and clay content, %). As at least two of the properties are certain to co-vary, I principally chose %Sand as an easily interpretable proxy of drainage conditions, and as a secondary proxy for soil fertility given lower capacity of sandy soils to physically retain both nutrients and organic matter (Baldock & Skjemstad, 2000). Combining the sand, clay and silt datasets into categorical soil textural classes based on the USDA textural classification system highlighted that landscape was characterised by a narrow range coarser textured soils including Sandy Clay Loams, Clay Loams, and to a lesser extent, Loamy Sands.

Topographic and hydrological conditions: Topographic information is based on the 90m resolution SRTM data from which we directly derived two variables; absolute elevation (m) and slope angle (°). A measure of topographic or soil wetness index (SWI) was also developed to summarise landscape level soil moisture conditions and was calculated using the method of Beven & Kirkby (1979):

$$\mathrm{SWI} = \ln(A_s/\tan\beta)$$

Where A_s is the local upslope or catchment area of a given pixel, and β is the slope angle of the pixel in radians and was calculated using the Hydrology toolbox in ArcGIS The scale of the output dataset is both unit-less and relative with higher index scores associated with wetter sites. Based on the DEM, I also calculated the relative topographic position of each pixel (i.e. the height of an individual pixel in relation to those around it) using the Topographic Position Index extension in ArcGIS (http://www.jennessent.com/arcview/tpi.htm). The analysis proceeds by comparing the elevation of each pixel to those in a user-specified neighbourhood around it. Positive values are assigned to areas that are on average higher than their surroundings, values around zero are given to flatter areas, with negative values given to areas that are lower lying than their surroundings. Two measures of topographic prominence were determined using both a local (TPI_750m) and large (TPI_3000m) neighbourhood size. A detailed description of the processing chain is located in supplementary material along with a procedure for classifying the landscape in to discrete landform classes (Figure S1).

There exists some cross over in the terms of which processes each variable is describing. For example, slope angle and the SWI can both used as predictors of soil moisture content/drainage, however slope angle also includes information on soil stability (i.e. Ferry et al. 2010), while the SWI considers the upslope conditions and indicates areas where water is likely to pool within the landscape. Topographic position can also be used as an indirect proxy for localised variations in soil moisture and will also retain some information regarding soil textural properties (Woollen *et al.*, 2012); however it also encompasses information on the roughness of the local terrain, which has been used to describe natural barriers to fire spread (*sensu.* Archibald et al. 2009). Methods on accounting for this potential co-variation between predictor variables are described in section 3.4.

***Accounting for disturbance*:** Fire and herbivory are common disturbance agents and thus key determinants of woody biomass (Saito & Luyssaert, 2014).

Directly including such data in our analysis is complicated due to the difficulties in quantifying both of their effects. Estimates of fire frequency can be derived from various satellite products (i.e. MODIS active fire and burned area products) and have been widely used in studies linking vegetation cover to disturbance (Lehmann *et al.*, 2009; Staver *et al.*, 2009, 2011). However these datasets struggle to detect smaller sub-canopy fires, which may have a significant impact on AGC storage. Furthermore, Ryan and Williams (2011) showed that in miombo, tree populations and biomass are more sensitive to fire intensity than to fire occurrence per se, which is more challenging to determine via remote sensing. I therefore focus purely on ecological and physical controls over AGC stocks. It is certain that some of residual variation in AGC not explained by the ecological model ($1 - R^2$) will be attributed to these disturbance effects. However to try and account for this, it was necessary to remove areas of high human impact as it creates patterns not related to the prevailing environmental conditions. It is assumed that particularly intense disturbances will mostly occur in areas that are easy to access (Rideout *et al.*, 2013; Wessels *et al.*, 2013). I therefore excluded all areas within a zoned proximity of villages (4km) and tracks (1km). Google Earth was used to map the local track networks and to verify whether the chosen buffers were sufficient to capture clearly observable disturbances. Even after excluding areas likely to be heavily disturbed, the map still retained ~600,000 valid points for analysis, therefore it is expected that any small scale human impacts occurring outside the buffer zones, such as those related to logging or charcoal production are likely to be averaged out.

3.4 Data analysis

3.4.1 Statistical modelling

All statistical analyses were conducted in the open source statistical software R (R Core Team, 2014) and associated packages. Multiple linear regressions were used to model the relationship between AGC stocks and the explanatory variables detailed above across each of the vegetation transitions. Model diagnostics were performed following the guidance provided by Zuur et al. (2010). First, relationships between each of the continuous explanatory factors were tested for collinearity using Spearman's rank correlation tests with a threshold correlation coefficient of r >0.6, and a Variance Inflation Factor of <2 used indicate variables that were strongly collinear; if detected, the variable with the strongest relationship to AGC was retained. This pre-screening step of the analysis was to ensure that there was no overlap in terms of explanatory power for datasets describing similar, but subtly different processes in the landscape. In addition to the co-variation between soil textural properties, results indicated that the two measures of topographic prominence were correlated with the large scale measure (TPI_3000m) chosen for inclusion. Elevation was also correlated with soil fertility, the ecological reasons for which are not obviously apparent; therefore soil fertility was retained as the strongest predictor of AGC, and because it has the clearest theoretical effect on AGC. The elimination procedure resulted in 7 predictor variables; MAP, seasonality, slope angle, topographic prominence, SWI, CEC, and %Sand. I used both forward and backward selection using the stepAIC function (Venables & Ripley, 2002) to extract the most parsimonious set of environmental variables that best explain the variability in AGC based on minimising the Akaike Information Criterion (AIC), using $P < 0.05$ as a cut-off for variables to enter or leave the model. The bivariate relationships between biomass and each of the explanatory variables indicated that over both transitions linear terms were appropriate representation of the relationship between the dependent- independent variables (data not shown). Linear and quadratic models were compared using analysis of variance tests (ANOVA) and AIC. The relative contribution of each explanatory variable (i.e. a partial/pseudo r^2) was estimated by dividing the regression sum of squares for each variable and the residuals by the total sum of squares of the final model (i.e. Marín-Spiotta & Sharma 2013). Examination of the residual plots indicated that a square root transformation of AGC was needed to ensure heterogeneity of variance and the presence of normality in the residuals.

3.4.2 Accounting for spatial dependency in the dataset

A key assumption of regression is that the model residuals are both identically and independently distributed. In the case of the continuous datasets used here, this assumption is likely to be breached given that both AGC (response) and the predictor variables are highly likely to be spatially auto-correlated (SAC), i.e. points which are geographically close together have the same underlying environmental conditions and therefore cannot be considered as independent samples (Tobler, 1970; Woollen *et al.*, 2012). This violates the principle assumption of the multiple regression analysis resulting in an overestimation of the effective degrees of freedom and increasing the chances of obtaining a Type I error (i.e. the probability of finding a statistically significant result when in fact none exists - a false positive) (Dormann et al. 2007). An exploratory analysis of the AGC map revealed significant positive SAC in the data (Moran's $I = 0.68$, $P < 0.001$; ArcGIS 10.1). There are a variety of methods for accounting for SAC varying in their statistical complexity (Beale *et al.*, 2010). I adopted a simpler approach of subsampling the dataset at a scale where autocorrelation is no longer detected in order to partial out any spatial dependency in the data. This method has the additional benefit of thinning the otherwise large dataset, thus easing data processing. Semi-variograms were used to quantify the spatial dependence in the data and were produced using the 'variog' function is the 'geoR' packages. The AGC map was subset in three locations in order to better capture localised patterns of SAC within largely homogeneous areas of savanna, woodland and forest (Figure 3.4). The empirical variograms were constructed by averaging the squared differences in AGC between all paired pixels that lie within a set number of increasing distance intervals, or lags. The number of lags was chosen to ensure at least 30 data pairs per distance with the final separation distance set at half the maximum possible distance between points. All variograms assumed isotropy, that is, the spatial correlation structure was only defined in one geographic direction. A spherical model was fitted to each variogram (Woollen *et al.*, 2012) meaning that the semi-variance eventually becomes constant at a certain lag distance, denoted as the variogram 'range' and highlights the scale at which AGC is no longer auto-correlated, thus points separated by less than this distance cannot be considered as independent samples. The maximum range encountered across all three areas was used to randomly subsample points this fixed distance apart (Figure 3.5).

When randomly sampling any dataset there is an increased likelihood of under sampling or even missing extreme or rare values, therefore the full dataset was repeatedly sub-sampled 30 times in ArcGIS to test for stability in the results (mean *n* pixels per subsample = 1205 ± 7). Subsampling the data in R was not possible due to its inability to construct a distance matrix for more 4000 pixels. It is acknowledged that there are more elegant methods available for accounting for SAC; an improvement to this method would be to randomly subsample the data to a manageable size in R following which the regression model (non-spatial) is then run using all points independent of geographic location then checking for spatial dependency in the model residuals (Moran's I). Variograms are again used to quantify the spatial structure of the data, which is then used to define a spatial weights matrix which places less emphasis on points that lie with within the autocorrected range. The model is then run again with the spatial weights matrix included and then compared to the results of the non-spatial model. Any future publication will incorporate this method, perhaps as a comparison to the one used here.

3.5 Results

3.5.1 Spatial patterns in AGC storage

Aboveground woody carbon stocks averaged 23.81 ± 15.0 tC ha^{-1} across the landscape with 20% of the study area categorised as low carbon density savannas (<10 tC ha^{-1}), 55% as moderate density woodlands (>10 & <35 tC ha^{-1}), with 25% classed as high density forests (>35 tC ha^{-1}). Stocks were highly spatially variable with a large block of high AGC (mean ~ 50 ± 8 tC ha^{-1}; Figure 3.3) occurring along the relatively high elevation escarpment to the east of the study area where precipitation is also considerably higher than average (>1000mm year^{-1}; Figure 3.4). Scattered patches of denser forests were also found in the more low-lying areas to the centre and south where they were interspersed with moderate density woodlands (Figure 3.2). Carbon stocks were lower to the west of the region where elevations were still relatively high, but where precipitation was lower (<700mm). Small dendritic stream networks were visible as discontinuous sections of higher AGC in otherwise sparse landscapes (Figure 3.2).

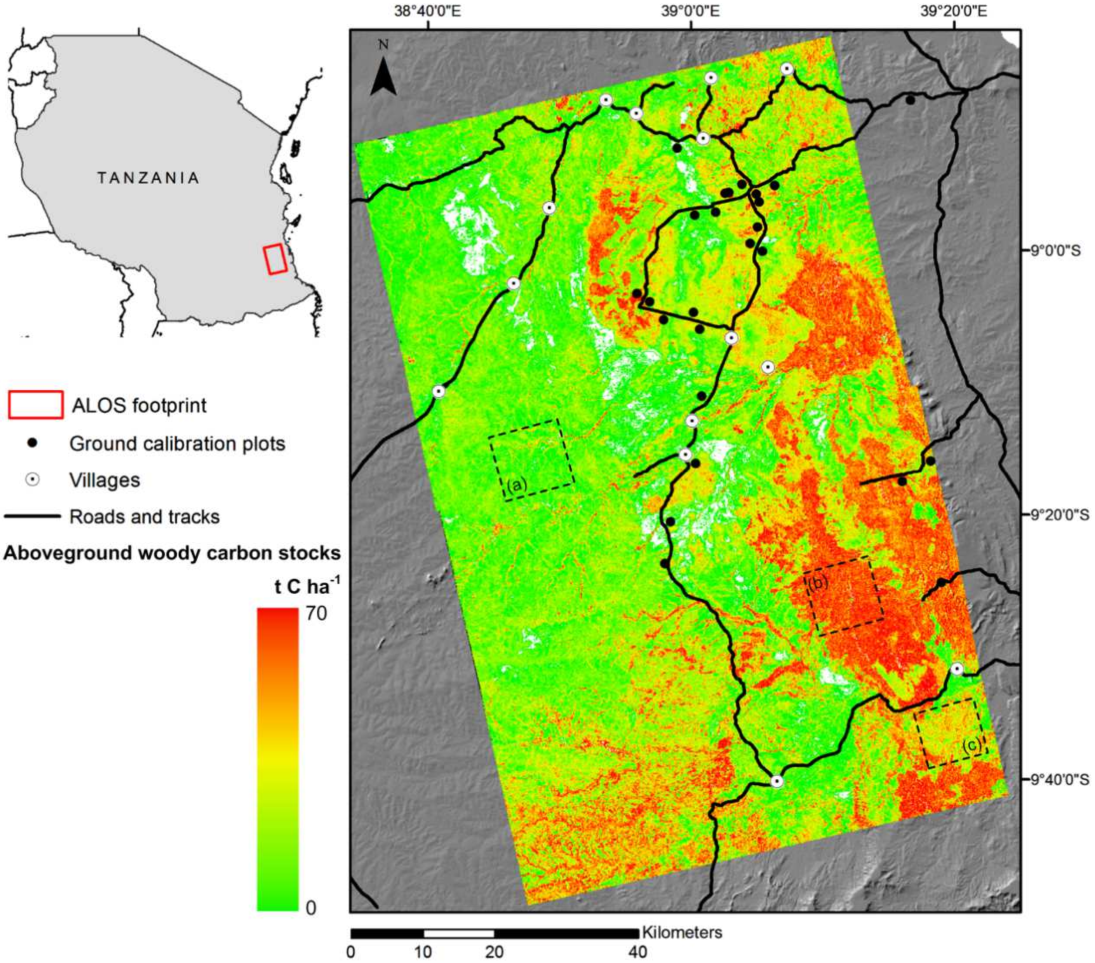

Figure 3.2– The map to the top-left shows the location of the study area within Tanzania as delineated by the footprint of the radar imagery. The main map shows the estimated AGC stocks across the study area. Areas with AGC density < 0 & > 70 tC ha^{-1} were removed as they represent noise in the data. The road running north to south along the eastern edge of the map is the only paved road in the area. The hatched boxes indicate the sub-areas used described in section 3.4.2 and in Figure 3.5.

There were no obvious patterns related to human activities with patches of relatively high AGC occurring close to village centres and along the main track networks. There was a strong spatial correlation in AGC in as indicated by the semi-variograms for each of the three sub-areas (Figure3.2; Figure 3.3). AGC stocks were auto-correlated up to maximum distance of ~2km in an area of denser woodland to the south (c); hence this was the distance at which the map was subsampled for the statistical analysis. The areas dominated by savannas (a) and forests (b) were more spatially variable with AGC auto correlated up to 1250m and 1707m, respectively.

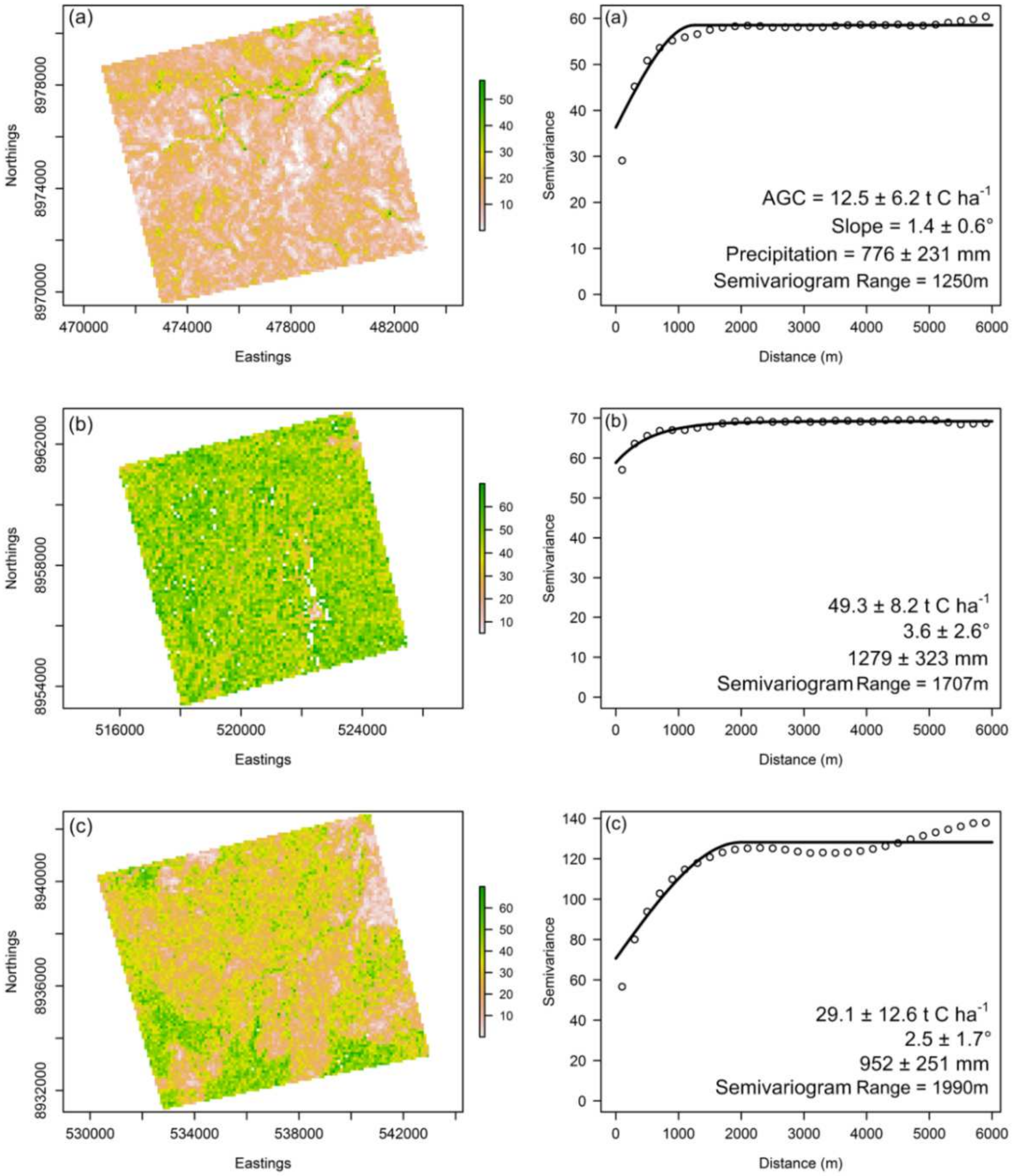

Figure 3.3– Semi-variograms of the AGC stocks extracted from within boundaries of each sub-area shown in Figure 3.2. The sub-areas were chosen to capture variability in different vegetation types including areas dominated by (a) savannas (b) forests and (c) woodlands. The pixel values denoted in the colour bar are in tC ha^{-1}

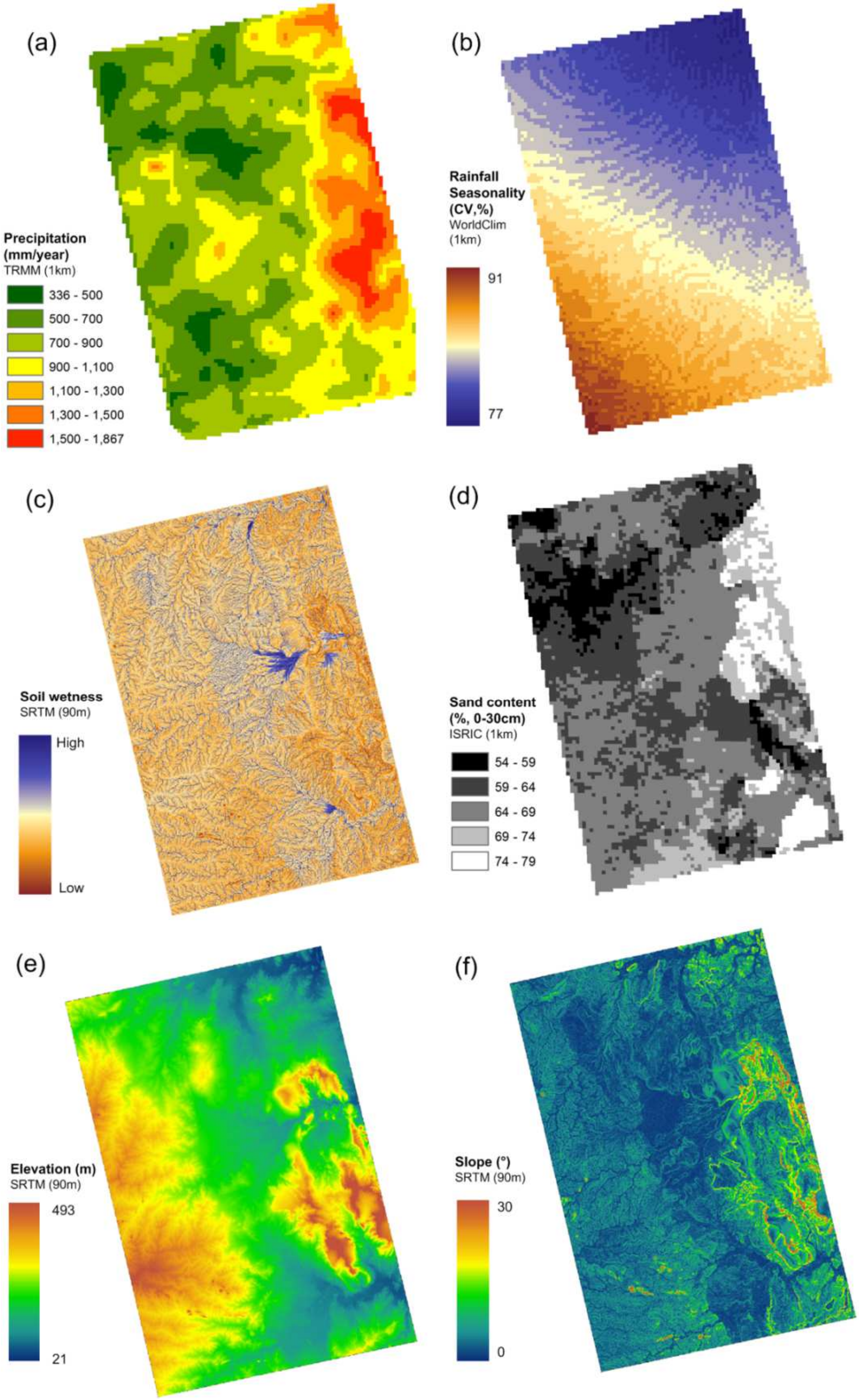

Figure 3.4- Maps of environmental factors used as predictors of AGC: (a) mean annual precipitation (mm), (b) rainfall seasonality (CV,%), (c) Soil Wetness Index, (d) sand content (%), (e) absolute elevation (m), (f) slope (degrees)

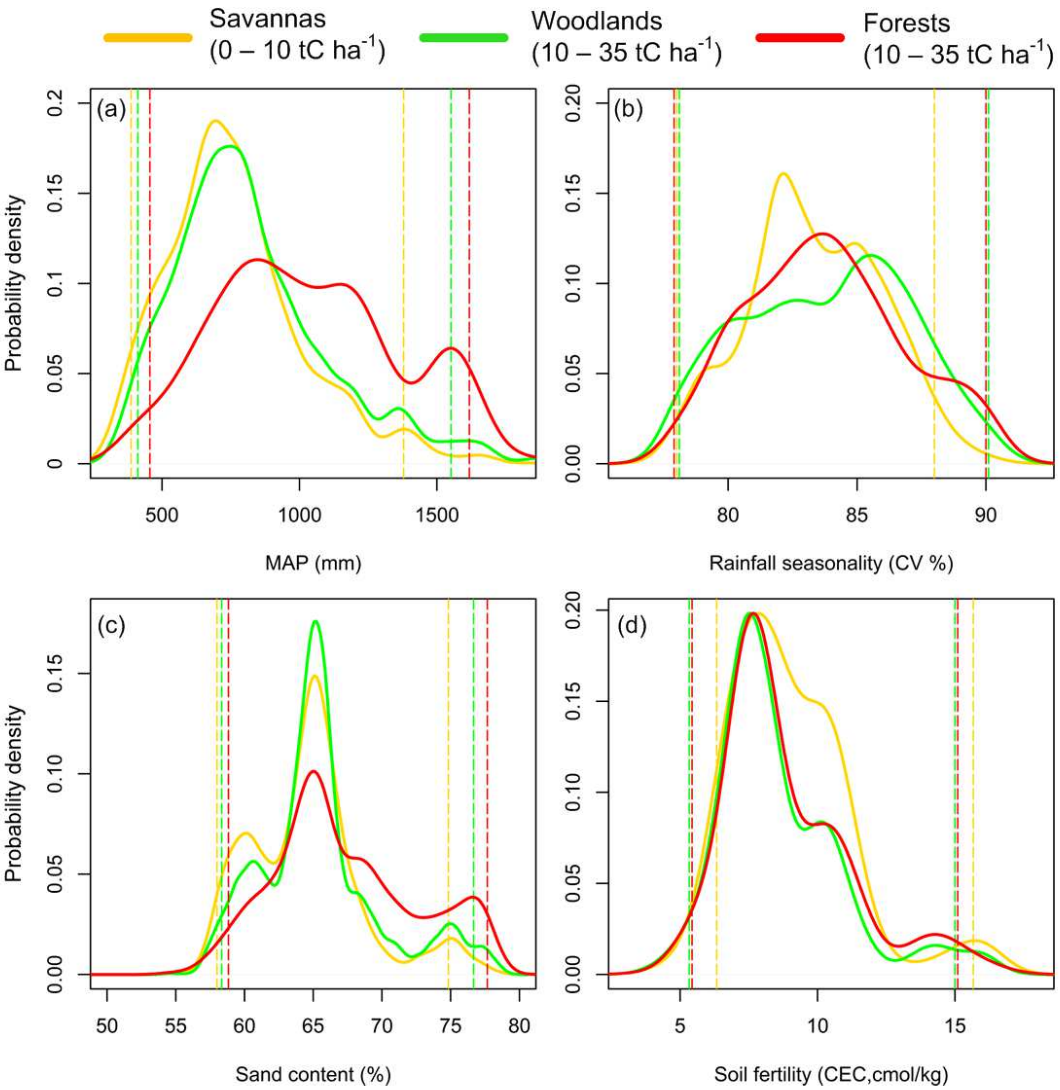

Figure 3.5 – Frequency distribution of savannas (**gold**), woodlands (**green**) and forests (**red**) across a range of environmental gradients. Histograms are represented using probability density curves to ease comparisons between AGC classes. The numbers of bins used to create the histograms are the same for all classes in each of the figures. Frequencies are standardised so that the area under the curve is equal to one. Shown here are the climatic factors, (a) mean annual precipitation and (b) rainfall seasonality, and the edaphic factors; (c) sand content and (d) soil fertility. The topographic predictor variables are shown on a following page. For all variables, the 'environmental envelope' occupied by each AGC class was determined using the 2.5% (lower limit) and 97.5% (upper limit) percentiles of the data meaning that 95% of the pixels within each class are constrained within the vertical lines.

3.5.2 Spatial distribution and limits of savannas, woodlands and forests along environmental gradients

An initial comparison of the frequency distributions of the three AGC classes across the various environmental gradients indicated potentially significant co-variation between AGC stocks and environmental conditions (i.e. Figure 4a, e, f, h). However there were also considerable overlaps in the environmental space occupied by each AGC class for all 7 predictors indicating that no single factor can adequately explain differences in AGC across the landscape. Savannas and woodlands had a similar distribution across the rainfall gradient mostly occurring in areas receiving <900mm MAP , yet both were found to persist up to a MAP of 1300mm – 1500 mm. Similarly, a substantial proportion of high density forests occurred in more arid areas (<650mm) despite principally being found in areas receiving over 1000mm MAP, however this is likely due to the presence of riverine areas which are not dependent on local rainfall for moisture (Figure 3.2). An effect of rainfall seasonality was less apparent while soils also appeared to have limited effects on AGC storage with data showing that each vegetation type occurs with almost equal frequency across the soil gradients; although savanna did appear to persist in areas of greater soil fertility, whilst the forests tended to persist on sandier soils.

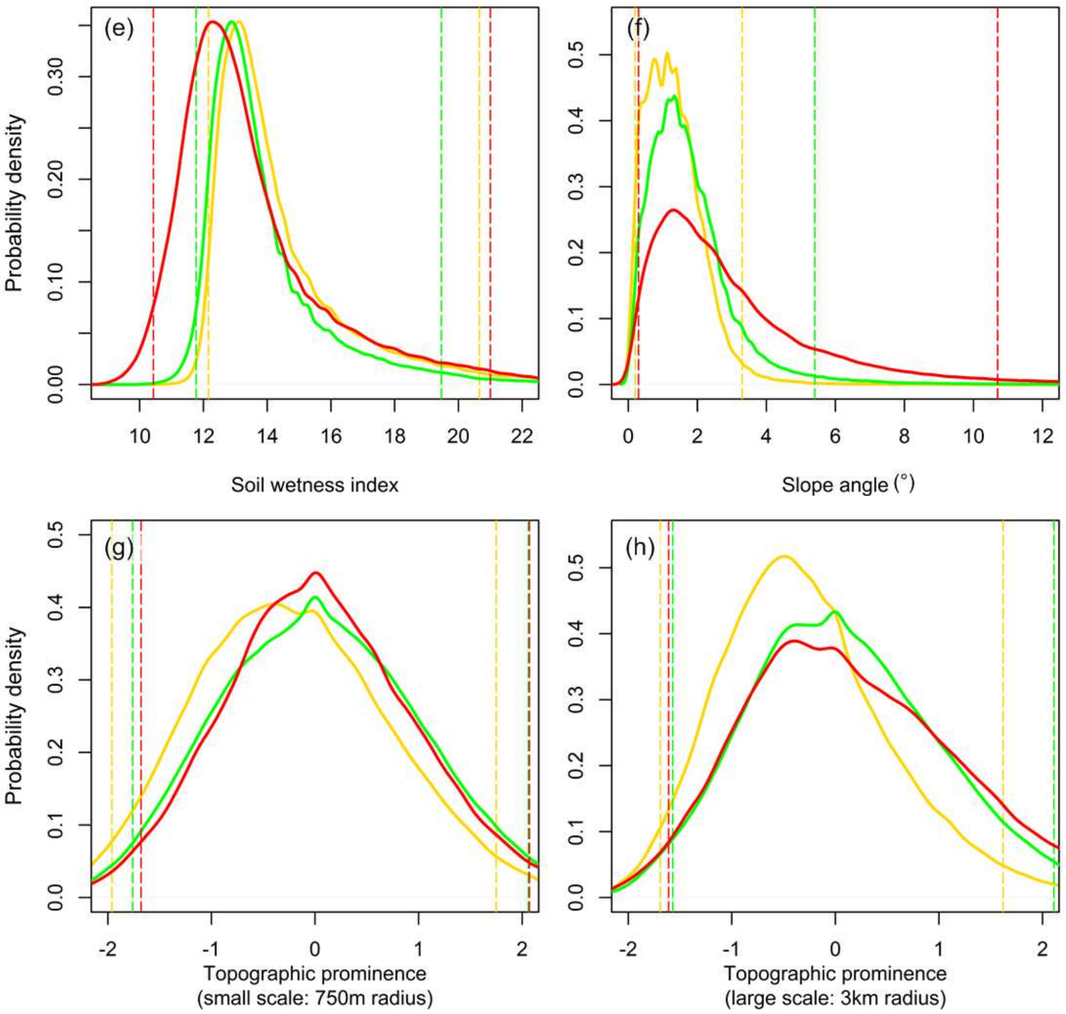

Figure 3.5 (cont.) – Extended from previous Figure but now showing topographic variables; (e) soil wetness index (f) slope angle, (g) small scale prominence (750m), which is not included in the ecological models due to its correlation with (h) large scale prominence (3km). For the two measures of topographic prominence, note that the x-axis reflects scaled values (mean = 0, SD =1, see supplementary material for more information). Areas that are typically low lying are represented by negative values, and areas that are typically higher than their surrounding are given positive values.

Patterns related to topography were generally better defined, the combined effects of which are also illustrated in Figure S2 where the landscape has been classified in to 10 discrete topographic positions to see where in the landscape AGC is typically concentrated. Relatively low lying areas such as flat open plains and depressions had the lowest average AGC stocks across the landscape (~18.7 tC ha^{-1}), with 30% of savanna pixels occurring in these low-lying areas, however they were also found to support denser woodlands and forests. Other relatively low-lying areas such as riverine habitats and drainage lines had slightly higher AGC stocks indicating the importance of being near to water, even though most of these streams will be ephemeral.

Savannas were also largely constrained to relatively shallow slopes of <3° suggesting that a combination of poor drainage conditions and seasonal waterlogging is a strong limiting factor to woody growth (Figure 3.5f). This was partially reflected in the SWI scores with savannas occurring on marginally wetter soils than more carbon dense areas. The majority of woodland patches occurred on slopes of up to ~6° with forest almost exclusively on steeper slopes. Indeed, the highest AGC stocks across the landscape were located at relatively higher elevations such as on ridge tops and the upper reaches of slopes (~27.2 tC ha^{-1}), with 32% of all forest patches and 27% of all woodland areas found in these more topographically prominent landscapes positions (Figure 3.5; Figure S2).

3.5.3 What principally determines AGC variability across both transitions?

The multiple regression models (n = 30) indicated that environmental factors had a weak impact on AGC stocks at the scale considered, cumulatively explaining an average of 14% (range = 10 -16%) of the variability between savannas and woodlands, and 20% (16 – 23%) of the variation across the transition from woodland to forest (Figure 3.6). When all other variables were held at a constant mean value, topographic factors including slope angle and topographic position accounted for most of the explained variation (~9%) in AGC stocks between savannas and woodlands. Climatic factors have a limited effect at the savanna-woodland transition with precipitation explaining just 2% of the variability. However climate effects were much stronger across the transition from woodland to forests, where MAP explained ~12% of the deviance. Slope angle was again retained as an important predictor across all model runs although its explanatory power was low (Figure 3.6). As expected based on the data shown in Figure 3.5, edaphic factors including fertility, sand content and SWI had no clear influence on AGC patterns across the landscape.

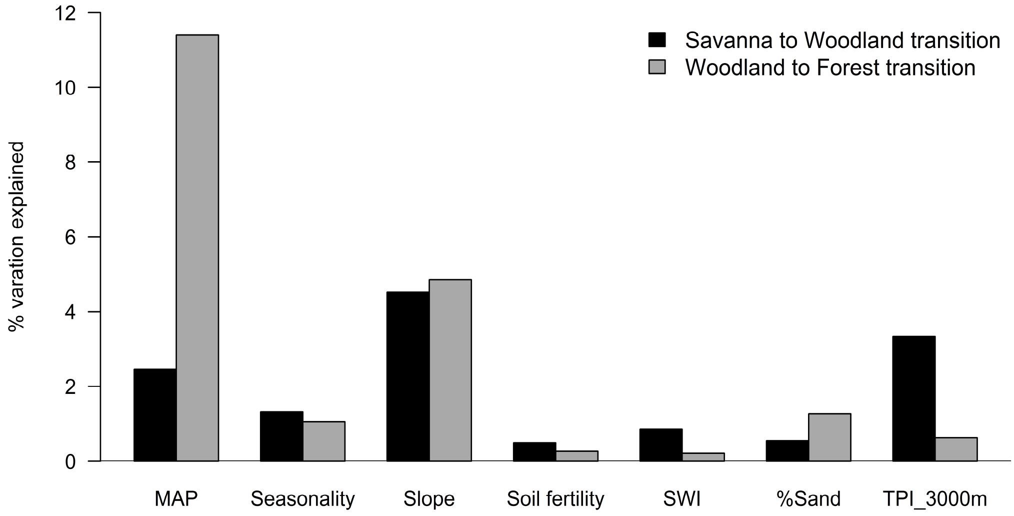

Figure 3.6 – Variation in AGC explained by each predictor variable across both of the transitions. Values indicate the average variance explained across the 30 sub-sampled datasets. Deviations from the mean were low for all variables and so are not shown.

3.6 Discussion and conclusions

3.6.1 The use of radar remote sensing for mapping AGC stocks

Radar remote sensing has provided a step change in our ability to map large-scale patterns in aboveground woody carbon stocks (AGC) having previously been shown to have a strong positive relationship with AGC across African savannas and woodlands (Mitchard *et al.*, 2009; Ryan *et al.*, 2012). The unique nature of the field inventory encompassing three distinct plot sizes and measurements thresholds (Figure 1.6) meant it was possible to assess which plot size provided the best correlation between the radar backscatter and the field – derived AGC estimates. Results indicated that the small 0.2-ha circle plots were the least useful for calibrating radar data having the lowest r^2 (0.28) of all three plot sizes (Figure 3.1). Other studies have also noted a weak correlation between radar backscatter and AGC when using relatively small plot sizes such as these (<0.25-ha) (Cassells, 2012; Carreiras *et al.*, 2013). This is likely to be attributable to geolocation errors between the field plots and the radar imagery, which in the case of Ryan et al (2012) was around 1 – 2 pixels, or 25 -50m and therefore of similar in size to the plots (25m radius). This information is not available for our study area, however assuming similar errors as Ryan et al (2012) there is the potential that the biomass-backscatter values that are being compared are not be from the same area. These differences will be further exacerbated where there is small-scale heterogeneity in vegetation structure between neighbouring points.

The regression coefficients improved markedly when using larger plot sizes with the 1-ha plots providing the strongest correlation ($r^2 = 0.82$; Figure 3.1). Increasing the plot size to 9-ha did not result in an improvement to the biomass-backscatter relationship; instead the r^2 was considerably lower at 0.49. Here, AGC stocks were only determined for stems >40cm DBH whereas the radar backscatter includes information on stems smaller than this. The density of stems <40cm is shown to vary strongly between plots (Table 2.1) and therefore will result in greater variability in the biomass-backscatter relationship. The results indicate the need for larger plots (> 0.2ha) in order to enable a more accurate calibration of remote sensing data (see also Réjou-Méchain et al. 2014), but also the use of an appropriate DBH threshold in order capture all of the AGC that the sensor is 'seeing'. It is still unclear as to exactly what characteristic of the vegetation the sensor is more strongly related to, i.e. is it stem density or stem size? Improving this knowledge is necessary in order to know whether field calibration campaigns should focus on measuring slightly larger trees or if the measurement of all stems (i.e. >5cm) is required.

The generally weak correlation between small plots and the radar backscatter has wider consequences in terms of the usefulness of the recently established Tanzanian National Forest Inventory Network (NAFORMA) which utilised a nested plot design with a maximum plot size of 0.07ha (NAFORMA, 2010). A combination of their small size and the relatively large DBH threshold (20cm) used in the largest of these plots (15m radius), it is unlikely that this extensive network (32,660 plots across 3,419 locations) will be of any use in the future generation of larger-scale carbon maps based on ALOS PALSAR data. It is therefore of interest to understand whether existing biomass-backscatter relationships can be applied to areas with no ground data, and the uncertainties associated with this approach.

3.6.2 Landscape-scale controls over AGC distributions

Aboveground woody carbon stocks averaged 23.1 ± 15.0 tC ha^{-1}, similar to the estimates derived from the field plots (20.7 tC ha^{-1}) highlighting that these were successful in capturing the variability in vegetation structure across the study area (Fisher *et al.*, 2008). It was assumed that AGC stocks would vary in a predictable manner across the landscape with wetter, more elevated areas supporting greater AGC stocks through increases in productivity and better drainage (Sankaran *et al.*, 2005; Bucini & Hanan, 2007). In contrast, the more arid and relatively low-lying parts of the study area would contain the lowest AGC stocks with drought stress in the dry season and seasonal waterlogging in the wet season both acting to inhibit woody growth (Woollen *et al.*, 2012). Small scale patterns related to topography were clearly observable, including the sharp transition in AGC along the edges of the escarpment that runs down the east of the district which suggests a topographic or even geological influence. The presence of high AGC stocks along dendritic stream networks in western areas where vegetation is typically sparse also shows the localised importance of topographic position and hydrology.

However at the landscape scale (10s km) the breadth of environmental space occupied by each biomass class indicated that these smaller scale trends were far from universal with low biomass savannas persisting in areas where environmental conations suggested forests should dominate and vice versa (Sankaran *et al.*, 2005). Overall, the predictor variables accounted for only 14% of the variation in AGC stocks between savannas and woodlands, and 20% of the variation between woodland and forests. The reasons for this lack of explanatory power are likely to be manifold, including (i) the importance of unmeasured variables such as fire and herbivory (Ryan & Williams, 2011; Saito & Luyssaert, 2014), (ii) interacting effects between predictor variables in shaping patterns, such as between absolute elevation and precipitation (Lehmann *et al.*, 2014), and (iii) deficiencies in the datasets used to describe environmental conditions, particularly those representing edaphic conditions, and to a lesser extent, topography.

Slope angle and topographic prominence accounted for most of the variation in AGC stocks (9%) between low AGC savannas and moderate AGC woodlands (0 - 35 tC ha^{-1}). Both predictors were interpreted as indirect measures of soil moisture content and drainage. Savannas were more prominent in relatively flat, low lying parts of the landscape such as in depressions and on flat lowland plains whereas woodlands (and forests) tended to occur in more elevated positions and on steeper slopes (Figure 3.5; Figure S2). The results complement those of Woollen et al (2012) who noted that miombo woodlands – which dominated most of our study area – tend to favour drier, more elevated positions in the landscape (Frost, 1996) Similar patterns in C stocks have been noted in other tropical regions with suggested mechanisms for this pattern including (i) the seasonal waterlogging of low-lying areas (Ferry *et al.*, 2010; Colgan *et al.*, 2012),and (ii) the greater variability in water uptake strategies in deeper soils leading to more complex vegetation structure through greater niche differentiation (Jackson *et al.*, 1999; Rossatto *et al.*, 2012). A more slightly more tangential explanation may be that at relatively high elevations such as on ridge tops or interfluves, the greater complexity of the local terrain provides a natural barrier to fire spread meaning these areas are less disturbed (Archibald et al. 2009). However the low explanatory power of topographic prominence shows that the localised topographic trend observed by Woollen et al. (2012) is not pervasive and at larger scales other factors supersede these natural patterns.

Interestingly, mean annual precipitation (MAP) explained almost none of the variation in AGC between savanna and woodland with both principally occurring within a similar climatic space (Figure 3.5). At the woodier end of the spectrum, higher AGC stocks were more strongly associated with a greater MAP, which accounted for 12% of the variation between woodlands and forests (Figure 3.6). Forests almost completely replaced woodlands and savannas at MAP of >1500mm which conforms with the climatic limits of savannas and woodlands across the African continent (Lehmann *et al.*, 2011). The seasonal distribution of rainfall, which was used as a proxy of dry season length, did not have any influence, which is likely attributable to the lack of any clear variation at the scale considered.

Soils also explained little of the variation in AGC stocks with results showing that different AGC classes can occur on any soil type (Menaut *et al.*, 1995). This is surprising given that soils are undoubtedly an important factor in shaping fine scale patterns in vegetation structure (Scholes, 1990; Bond, 2008). The results contradict several observational studies which have opined that the Coastal Forests found in this part of Tanzania are largely confined to relatively deeper, well-drained sandy soils on fertile coral rag substrates suggesting edaphic or even geological controls (Timberlake, 2011; Howell & Msuya, 2012).

The absence of any clear relationship may be attributable to our reliance on modelled estimates of soil characteristics which are unlikely to be representative of actual conditions. These data have a low resolution meaning that soils are unlikely to correlate well with AGC with up to 100 pixels occurring in each 1km cell. It is therefore hypothesised that some of the residual variation in the ecological model will be explained by soils. Testing this assumption will require improvements to these modelled datasets, however it unlikely that these will ever be able to capture subtle small-scale changes that occur in soils meaning that plot-based soil sampling alongside forest inventories may be required to help fully understand edaphic controls over AGC storage (Quesada *et al.*, 2012; Lewis *et al.*, 2013).

Even if we do assume some unquantified edaphic controls, the large amounts of unexplained variation (~80 - 85%) in each of the datasets indicate the importance of unmeasured variables in determining spatial patterns AGC storage. For example, localised differences in tree species diversity or composition may result in hotspots of increased woody productivity, while the spatial distribution of rare large stems may also generate small scale differences in AGC between areas, neither of which may be associated with the prevailing environmental conditions (Chapter 2). However the most likely factor shaping these patterns is fire (Staver *et al.*, 2009). Results from fire exclusion experiments highlight that fire is key process preventing woody biomass from reaching its climatic potential across African savannas and woodlands (Furley *et al.*, 2008). Miombo woodlands have often been viewed as a seral community to denser forest with fire determining their existence as alternative states (Frost, 1996). Biomass is likely to be even more sensitive to disturbances than woody cover as even small intensity fires can remove a significant proportion of the understory but are less likely to remove large canopy dominants (Ryan & Williams, 2011). The apparently anthropogenic origin of current AGC patterns is perhaps surprising given that areas where intense disturbances is likely to have occurred were removed from the analysis. However hunters naturally operate independently of the tracks networks and are known to set uncontrolled fires to flush out animals which then spread over large areas (Miya *et al.*, 2009). Historical disturbances such as land clearance for shifting cultivation may also have a long-term residual effect on AGC storage (Chapter 4; Willcock et al., 2014) however these are difficult to account for without multi-temporal earth observation data (i.e. Lehmann et al. 2008). The proximity to Selous game reserve means that herbivory may also exert a top-down control on woody biomass through grazing and browser pressure, although in the absence of any data on the density of range of large mammals in our study area, these effects are difficult to quantify.

The hypothesised strong dependence of fire on AGC stocks suggests that changes in the local fire regime could result in a rapid gains in woody biomass, particularly in more mesic savannas and woodlands (> 700mm year) where there is likely to be enough rainfall to support more closed canopy systems, except on the more low-lying, seasonally inundated soils. Mitchard et al. (2011) also noted the expansion of denser forest into more mesic savannas in Cameroon in response to a decrease in human disturbance, supporting the idea that similar reductions in our study area may result in large scale vegetation shifts in a short period of time. The results suggest that similar reductions in fire intensity and frequency will result in similarly significant changes in AGC storage. This information has major implications for land management in African woodlands and gives further weight to the achievability of a recently approved REDD+ project operating in the local area who are seeking to generate carbon credits through improved fire management (Fehse & Ball, 2014).

3.7 Chapter 3 references

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3.8 Chapter 3 - Supplementary material

3.8.1 Calculation of topographic prominence and landscape position

At local scales, topographic position, or relative prominence, has been mooted a key determinant of woody biomass in African savannas and woodlands with more elevated areas appearing to result in greater standing biomass stocks (Menaut et al. 1995; Woollen et al. 2012). To assess to whether these small scale patterns are consistent at larger scales, and to visualise how AGC stocks are spatially distributed across topographic gradients, I used the Topographic Position Index tool within the Land Facet Analysis extension in ArcGIS (Jenness, 2006) to classify the landscape in to discrete topographic positions based on a DEM (Figure S1 & S2). The analysis proceeds by comparing the elevation of each pixel to those in a user-specified neighbourhood around it. Positive values are assigned to areas that are higher than their surroundings, with negative values given to areas that are lower lying. Values near to zero indicate either a flat plain, or a shallow slope, therefore slope angle can be added to the analysis to distinguish between the two. The calculation is inherently scale dependent; for example, a small neighbourhood (100s m) will better capture micro-topographic features such as small hills and ridges whereas larger neighbourhoods (1,000s m) reveal broad topographic features such as flat plains and large hill chains. Combining the two scales allows nested landforms to be distinguished, i.e. a high TPI value in a small neighbourhood, combined with a moderate TPI value in a large neighbourhood is classified as a local ridge or hill in a wide flat plain, while a low TPI value in a small neighbourhood coupled with a high TPI are the larger scales would be classed as a depression. I examined a number of possible combinations of neighbourhood sizes (Small: 500m, 750m, 1000m; Large; 2000m, 3000m and 4000m), selecting 750m and 3000m as being the ideal combination for highlighting known small and large landscape features respectively and were put forward as predictors of AGC in the regression analysis. Small scale spatial correlation in elevation means the range of TPI values increases with the scale of analysis. To allow the same classification procedure to be used, results of both layers were standardised to mean of 0 and SD of 1. As before, highly positive values are indicative of elevated areas and negative values for low lying areas. From this we identified 10 topographic position classes using a modified version of the approach by (Weiss, 2001) (Figure S1).

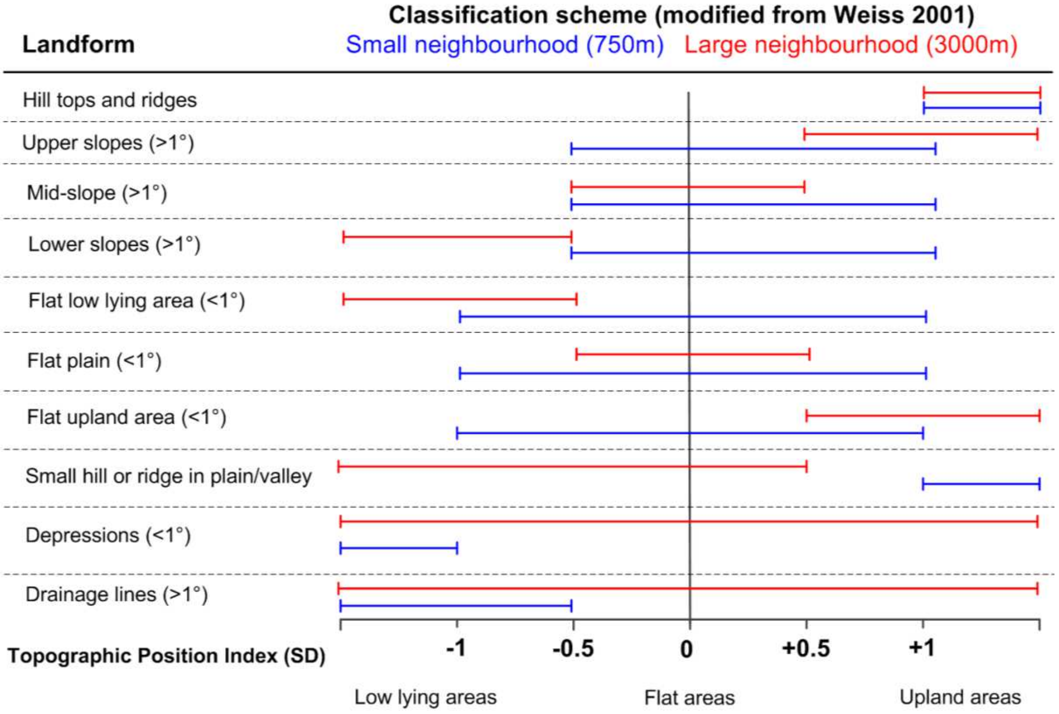

Figure S1 - Classification scheme used to separate the landscape in to discrete topographic positions. Areas with a high TPI at the small scale, but a low TPI at the large scale, which can be interpreted as a hill within a broader valley, were not included in the classification as we do not consider this to be a valid or widespread landform (0.1% of total study area).

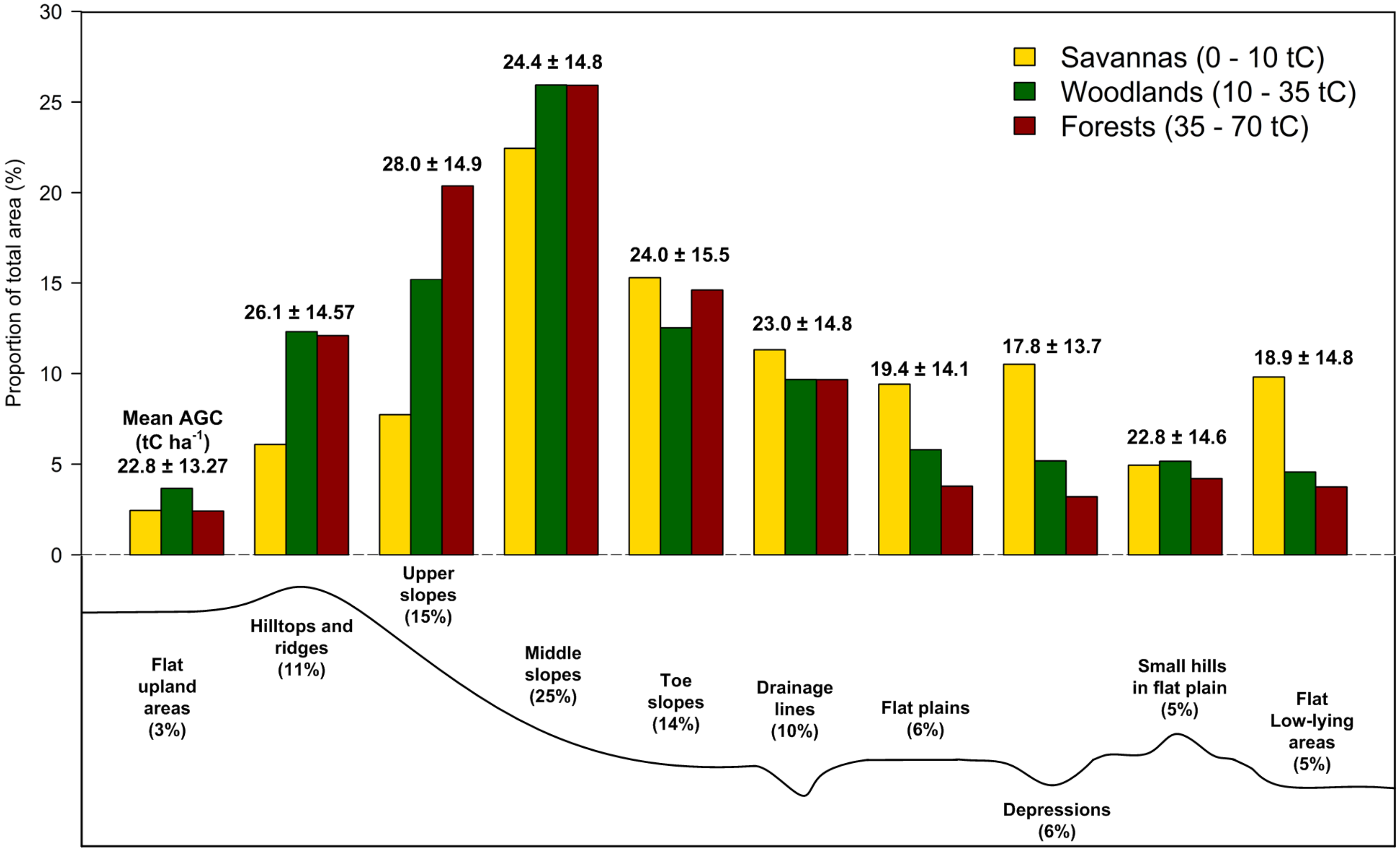

Figure S2 – Spatial distribution of savannas, woodlands and forests along an idealised topographic gradient. For each topographic position class (*n* = 10) the proportion of each vegetation type found at that position is indicated, i.e. 2.3% of all savanna points are located in flat upland areas. The average AGC stocks ± 1SD for each position are noted at the top each set of bars while the numbers in brackets indicate the proportion of the landscape covered by each landform.

Chapter 4

How resilient are African woodlands to disturbance from shifting cultivation?

Iain M. McNicol, Casey M. Ryan and Mathew Williams

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Author contributions

The idea for this study and experimental design was developed by IMM, MW and CMR. IMM designed the sampling strategy, collected and analysed the data. IMM and CMR contributed to the botanical database, which was then further compiled and cleaned by IMM. IMM wrote the manuscript with inputs from MW and CMR

4.1 Introduction

Seasonally dry tropical woodlands are the dominant vegetation cover in Southern Africa extending over large parts of Tanzania, Malawi, Mozambique, Zimbabwe, Zambia and Angola and the Democratic Republic of Congo (Campbell *et al.*, 2007). Poverty and a lack of economic development have led to a heavy reliance on the woodlands for local livelihoods across the region (Ahrends *et al.*, 2010). Increasing demand for resources means the woodlands are currently undergoing extensive deforestation and forest degradation (Ryan *et al.*, 2012), the majority of which is being driven by the small scale production of food and income cash crops (Fisher, 2010). Shifting cultivation is the traditional method of agriculture in these areas and is often the main source of income among local communities. This practice involves the almost complete removal of the surface vegetation using a mixture of cutting and fire, followed by a period of manual cultivation, before eventually shifting to a new patch of land once soil fertility is depleted, allowing the abandoned field to regenerate. To understand the long term ecological impacts of this practice, and its effects on ecosystem services (CBD 2011; Barlow et al. 2007), it is necessary to examine the rate and extent to which both ecosystem carbon stocks and biodiversity develop in abandoned fields.

In African woodlands, there are no long-term studies with which to observe changes in both carbon stocks and biodiversity following agricultural clearance (although see Ando et al. 2014). Consequently, our understanding is necessarily based on establishing chronosequences (Martin *et al.*, 2013). In this case, long-term monitoring is replaced by multiple plots that vary in their time since abandonment, but have similar environmental conditions (Johnson & Miyanishi, 2008).

Comparisons to a nearby patch of relatively undisturbed woodland are required to gauge the extent to which ecosystem carbon stocks and biodiversity 'recover' in re-growing woodlands. Several studies have used this approach to predict recovery trends following land clearance in African woodlands (Williams et al., 2008; Mwampamba & Schwartz, 2011; Kalaba et al., 2013), yet there still remains a number of critical issues which limit our ability to generalise about the wider ecological impacts of shifting cultivation, namely the uncertainty over the role of soil texture on carbon dynamics in plants and soils. Few chronosequences explicitly control for this, yet differences in texture can significantly affect the water holding and nutrient retention capacity of the soil, potentially creating marked differences in aboveground productivity (Wright et al., 2013), and species composition (Backéus *et al.*, 2006). Adsorption to mineral particles is a key mechanism through which soil organic carbon (SOC) is stabilised and protected from decomposition (Bird et al., 2000; Bruun et al., 2010). Coarser textured sandy soils exhibit only weak bonding affinities to SOC, leaving a significant proportion in a physically unprotected, labile form. Moderate to fine textured clay soils, however, provide a larger surface area and numerous reactive surfaces with which SOC can bind and stabilise (Baldock & Skjemstad, 2000). Unlike sandy soils, clay rich soils may be relatively resistant to change when soil structure is not severely disrupted. Therefore it is thought that soils with different mineralogies will vary in their direct and longer term response to land clearance (Marín-Spiotta & Sharma, 2013). However few studies have examined associated changes in soils, yet they store up to 70% of the total ecosystem carbon meaning they represent a potentially large source of CO_2 (Ryan *et al.*, 2011).

Aside from its impact on ecosystem carbon storage, the patchy nature of shifting cultivation may also have an impact on spatial patterns of species composition and diversity, which in turn can have consequences for the ecology of shifting cultivation landscapes. Studies comparing secondary and mature forests suggest that re-growing areas can harbour greater tree species diversity by maximising the co-existence of both fast-growing pioneers and more competitive canopy species (Bongers *et al.*, 2009; Mwampamba & Schwartz, 2011), a pattern that is supported by ecological theory (i.e. Intermediate Disturbance Hypothesis: Connell, 1978), while others highlight that disturbance has minimal long-term effects on localised patterns of diversity (Robertson 1984; Stromgaard 1986; Williams et al. 2008). Although tree species diversity tends to reach levels similar to old-growth forest relatively quickly after disturbance, tree species composition is predicted to take much longer to recover (Dent *et al.*, 2013; Martin *et al.*, 2013), although these conclusions are typically based on data from the neo-tropics and wetter tropical forests (Chazdon *et al.*, 2007). Given the long history of shifting cultivation in African woodlands, and the frequency of other disturbance processes such as fire (Furley *et al.*, 2008; Ryan & Williams, 2011) we hypothesise that tree communities will be more resilient to land use change (Cole *et al.*, 2014). Many of the common species in these woodlands are known to regenerate from stumps and substantial root stocks following the removal of above-ground parts (Frost, 1996; Luoga *et al.*, 2004), a life-history trait that allows them to persist in these regularly disturbed environments, leading to speculation that the original composition may recover relatively quickly (Chidumayo, 2004; Clarke *et al.*, 2012). This hypothesis is congruent with the initial floristic composition model of succession (Egler, 1954) which posits that all species are present at the start of succession (i.e. as roots or in a persistent seed bank) with compositional change occurring due to interspecific differences in growth rate, longevity and competitiveness. Other models of succession suggest that change occurs in an ordered sequence, with faster growing species being gradually replaced by denser, larger stature species typical of the preceding woodlands ('relay floristics'; Egler 1954; Connell & Slatyer 1977). However, differences in land management both during and after cultivation, and the composition/ proximity of the local species pool may instead result in sites following divergent successional pathways, with additional species being recruited by chance into the abandoned fields over time, thus creating differences in species composition (ß-diversity) between similarly aged stands. Therefore through impacts on ß-diversity, this patchy disturbance may increase the number of species the landscape supports (γ-diversity) without necessarily creating large differences in plot α-diversity (Berry *et al.*, 2010).

In this study we provide an integrated examination of how ecosystem structure - aboveground woody carbon stocks (AGC), soil carbon, trees species composition and diversity - change over four decades of succession following abandonment of sites cleared for shifting cultivation in SE Tanzania. To study the effect of soil type on temporal trends, sample plots were stratified between those on coarse textured soils (<18% clay), and those on more medium textured soils (>20% clay) (FAO, 2006). The key questions we will address and their associated hypotheses are as follows:

1) What is the rate of accumulation in AGC and does it vary depending on soil mineralogy?

H_1: There will be a significant difference in the rate of AGC accumulation between soil types, with AGC accruing faster on the more clay rich soils due to their greater nutrient and moisture retention capacity.

2) What is the impact of land clearance and the subsequence regrowth on soil carbon stocks?

   H_2: Soil carbon stocks in more clay rich soils will be less impacted by clearance, losing proportionally less organic carbon than sandier soils, while also accumulating carbon faster in abandoned fallows, due to their greater capacity to physically protect organic matter.

3) Does tree species composition differ between re-growing and mature woodlands?

   H_3: Tree species composition will return to that of undisturbed woodland within the timeframe of the chronosequence, and with no effect of soil type

4) Does land-use change alter patterns of tree species diversity at both the stand and landscape scale?

   H_4: Areas of re-growing woodland will contain greater localised diversity due to their inclusion of both fast growing ruderal species and larger canopy dominants. The potential for a diverse range of species to recruit in these re-growing areas means that at the landscape scale re-growing woodlands will support a greater number of species than mature woodlands.

4.2 Materials and Methods

4.2.1 Study area

This study was conducted in Kilwa District, South-Eastern Tanzania which covers approximately 12,000 km^2 and is bounded between 38°40’ - 39°42’ East and 8°16’ - 9°56’ South (Figure S1). The terrain is flat to generally undulating across most of the district (mean slope = 1.9°, elevation = 21 – 492m a.s.l; SRTM 90m resolution). It has a seasonally wet/dry climate with a mean annual precipitation of 600 - 800 mm (Tropical Rainfall Measurement Mission; Huffman et al. 2007). The dominant vegetation type is *miombo* woodland, the vernacular name for species in the genus *Brachystegia*, which along with *Julbernardia,* is endemic to the region. Areas of open savanna and patches of East African Coastal Forest are also present in the landscape.

The estimated human population of the district in 2010 was 182,000, with 85% living in rural communities. Shifting cultivation is the primary method of agriculture among local communities with no inorganic fertiliser input or mechanisation. Fields are typically small (c. 0.5 - 1 ha) with clearance normally taking place towards the end of the dry season. Plots are rarely clear-felled, and a few large trees are often left due to difficulties removing these stems. Cultivation lasts for between 3 – 5 years with fields often burned at the end of each cropping season to remove weeds and provide fresh inputs to the soil to sustain productivity. The main food crops include maize, sorghum, cassava and cowpeas, with sesame widely grown as a cash crop. Re-growth occurs primarily through natural regeneration, although in some areas a small number of trees were found to have been coppiced.

4.2.2 Site Selection

Sampling was undertaken in 6 village areas spread across the district (Figure S1). Site ages and land-use histories were primarily determined through semi-structured discussions with local village councils and then cross checked with independent local guides. To further validate the information provided by local informants, true colour images of the study areas were produced across a time series of Landsat scenes (1989, 1991, 1993, 2008) to assess whether clearance was evident close to the proffered age of the site, and to check for evidence of re-clearance post abandonment. Our oldest sites (38 – 40 years) coincided with a period of socio-economic change in Tanzania known as '*Ujamma*', a key part of which was the centralisation of all forms of local production into administratively determined villages, resulting in the relocation of many small communities and the abandonment of their surrounding fields. The dates of these relocations in our study area were well remembered amongst village elders.

In space-for-time studies there is a need to control for both environmental and management differences between sites, which if not accounted for can introduce significant variation in ecosystem structure that is unrelated to site age. Sites were grouped *a posteriori* according to whether they were located on "sandy" soils (7 – 18% clay, $n = 42$), or "clay" soils (20 – 31% clay; $n = 25$) (FAO, 2006). Our dataset includes active fields, re-growing woodlands of various age (1 – 40 years), and areas of mature woodlands which are used for reference purposes in the absence of any information on the pre-disturbance conditions at each site (Table 4.1; Table S1).We use the term mature woodland to refer to areas that have not been cultivated in living memory (>60 years), although the exact ages of each site are unknown.

Additional selection criteria included; (i) vegetation type, sampling only in areas where mature woodlands associated with that soil type would grow; (ii) site accessibility and the proximity (<3km) of suitable reference sites in the local areas, and (iii) disturbance history, ensuring that all sites had not been subject to any major cutting or burning post abandonment.

4.2.3 Sampling strategy and field measurements

Sampling was undertaken within a 25m radius (0.2 ha) circle plot, the size of which was chosen to fit comfortably within the fields to minimise edge effects. The diameter of all live standing trees ≥5cm at 1.3 m above ground level was measured, counting multiple stems from a single base as separate trees. The local species name was recorded for each tree and where possible, translated to species botanical name using existing local (http://www.mpingoconservation.org/), and national species lists (NAFORMA, 2011), with nomenclature and additional species information derived from Coates-Palgrave (2002). Aboveground carbon stocks (AGC) were calculated using a allometric model developed in the same region ('Lindi' model: Mugasha et al. 2013) with biomass assumed to be 47% carbon.

Soil carbon stocks were measured within 7 x 0.25m^2 quadrats located at specified locations within the plot. Soil samples of known volume were extracted from the top 5cm and top 30cm using a metal soil corer (diameter = 10cm) and bagged separately. Bulk density (g/cm^3) was determined for each sample based on the core volume and the dry weight of the soil. The soil was sieved at 2mm and subsampled using a riffle splitter. Stones and gravel >2mm were weighed and the bulk densities of samples containing stones were corrected accordingly.

Subsamples from each core (5cm and 30cm separate) were sent to Sokoine University of Agriculture, Tanzania, with each sample tested for organic carbon content (%). For the analysis of soil texture, samples were bulked to produce one sample per depth per plot. Organic carbon was determined using the Walkley – Black Wet Combustion Method (sulfochromic oxidation titration) (Nelson & Sommers, 1996) with soil texture estimated using the Bouyoucos hydrometer method (Day, 1965).

4.2.4 Data analysis

Remnant trees (i.e. trees not removed when cultivation started) were a common occurrence in active fields, and thus are likely to be present in regrowing sites. To account for their presence, I estimated the average annual growth rate of each tree in the regrowing woodlands by dividing its DBH by the plot age and comparing it to a theoretical growth model which predicted the maximum possible tree DBH for given period of regrowth. I assumed that tree growth would be rapid following agricultural abandonment, steadily decreasing with increasing tree size / stand age. The rationale is that younger trees will grow quickly to try and attain a fire resistant size which will lower their chance of being top-killed by subsequent fires. As tree size increases the amount of energy required to maintain this rapid rate of growth becomes prohibitive and the annual DBH increment subsequently decreases. I subjectively assumed a liberal DBH increment of 4 cm yr^{-1} in the first 5 years following abandonment, slowing to 2 cm yr^{-1} after 6 – 10 years, 1 cm yr^{-1} between 10 – 20 years, and then 0.5 cm yr^{-1} thereafter. It is acknowledged that growth rates are species specific, however for simplicity the model is applied to all trees independent of species. A saturation curve was fitted to the theoretical growth data: $D = \alpha t / (\beta + t)$, where t is plot age (years), D is the maximum predicted tree size for that fallow age, with $\alpha = 59.9$ and $\beta = 11.9$ as the best fitting parameters that minimise the RMSE. If the measured DBH was greater than its maximum predicted DBH then it was classed as a remnant tree ($n = 106$; 1.4%). According to the model, no tree in the chronosequence should have exceeded 46cm DBH, even after 40 years of abandonment. To test for significant effects, we first conducted all analyses on the full inventory data and then again with remnant trees excluded. The results of both analyses are reported when differences were substantial, however the data presented in the Figures and Tables are based on the initial analysis of all measured stems. All data analyses were performed using R statistical software version 3.0.2 (R Core Team, 2014).

4.2.4.1 Changes in above and below ground carbon stocks

To account for the impact of outlier plots in our analysis of AGC storage we performed both ordinary least squares (OLS) regression and robust regression to describe changes over time on both groups of plots. Robust regression is done by iterated re-weighted least squares assigning a lower weighting to points with large residuals on the initial model fit, and was implemented using the ‘rlm’ function in the ‘MASS’ package (v. 7.3-29; Venables & Ripley 2002). Analysis of Covariance (ANCOVA) was used to test our hypothesis of significant differences in the rate of AGC accumulation between soil types. Generalised Linear models were also used with clay content as a continuous co-variate to test for associated effects. Soil carbon stocks were calculated using the standard fixed depth approach (Anderson & Ingram, 1993);

$$\text{tC ha}^{-1} = D_b \text{ x (depth/100) x \%C x } S_f \text{ x } 100$$

where D_b is the bulk density (g cm^{-3}) of each sample, depth is in cm and S_f is the soil fraction. We again assessed whether soil clay content had any effect on the results by including clay content (%) as a second covariate in our models used to describe changes with time since abandonment. Because the initial C stock at the start of the re-growth phase is likely to affect both the rate and pattern of change in the abandonments, the active fields were included in model fitting; however the mature woodland sites were not due to uncertainties over their age.

4.2.4.2 Species composition and diversity

We used both species richness and Fisher's α as measures of tree species diversity, with the latter included as it is theoretically less sensitive to the number of individuals at each site (Table 4.1). To describe changes in species composition and dominance over time, we calculated each species' abundance and basal area as a % of the total within each plot. The relative dominance of each species was then calculated as the midpoint of these two values to produce a combined value ranging from 0 – 100%. NMDS ordination was used to visually assess patterns in species composition between plots with compositional differences based on the Bray-Curtis dissimilarity index with species abundance data site standardised prior to analysis to account for differences in the number of individuals recorded at different sites. We used this measure of similarity to assess the extent to which the species composition in each re-growing woodland plot resembled that of nearby mature woodlands, i.e. those sampled in the same village area. Evidence for a distance-decay in community similarity has been recorded in many tropical forests across the globe (Condit *et al.*, 2002; Tuomisto & Ruokolainen, 2003), including in the absence of environmental variation (Linares-Palomino & Kessler, 2009; Dexter *et al.*, 2010), meaning we expect similar trends will also occur in our study area. Hence, when comparing the species composition of re-growing and mature woodlands it is difficult to decipher what is a disturbance effect, and what is simply natural variation related to spatial turnover in species composition between sites (Ramage *et al.*, 2013). Therefore, in order to assess the extent to which species composition has 'recovered' across the chronosequence, we examined whether the compositional similarity of re-growing woodlands to their nearest mature woodland plots reached levels equal to, or greater than the similarity among nearby pairs of mature woodland plots (Dunn, 2004; Dent & Wright, 2009; Dent *et al.*, 2013). Spatial autocorrelation is an often unavoidable problem when using space-for-time approaches, potentially biasing comparisons of community similarity. We managed to avoid some of the extreme issues of pseudo-replication and spatial auto-correlation found in other studies (see Ramage et al. 2013) by sampling across 6 different village areas. Within these, re-growing plots of similar age and mature woodland plots were largely spatially interspersed with sites of different ages meaning any spatial auto-correlation effects are likely to be minimal (Figure S1, Table S2). Re-growing plots were also a similar distance to a patch of mature woodland, as comparable mature woodland plots were to one another meaning distance-decay in community similarity is likely to be similar (Table S2).

Age-related trends in tree species diversity and community similarity were evaluated using various model forms (linear, quadratic, logarithmic, unimodal-ricker or saturation) with the most parsimonious model selected on the basis of ANOVA tests where models were nested (linear vs. quadratic), or the minimisation of the Akaike Information Critetion (AICc), corrected for small sample sizes, and the residual standard error (RSE) when comparing models fit using linear ('lm' function in R) and non-linear ('nls') methods. Patterns of total species richness between re-growing and mature woodlands were compared using Mao-Tao individual-based rarefaction analysis in order to account for differences in sampling intensity (Table 4.1). Rarefaction curves were first compared at the sample size of the smallest reference sample thus giving a minimum estimate of the difference in total species richness, and then after extrapolating rarefaction curves to the size of the most intensively sampled group to generate maximum estimate of the difference, with curves constructed using EstimateS (version 9; Colwell et al. 2012). We also used permutational multivariate analysis of variance (PerMANOVA; Anderson 2001) to test for significant differences in tree community composition between mature woodlands on different soil types, and was implemented using the 'adonis' function in the 'vegan' package (v. 2.0-10; Oksanen 2013).

4.3 Results

4.3.1 Recovery of aboveground woody carbon stocks

We measured 7638 stems ≥5cm DBH across the 67 plots. AGC stocks in mature woodlands were similar between soil types (Mann-Whitney, $P = 0.6$), both averaging ~ 38± 11(SD) tC ha^{-1}. Active fields typically retained very little woody biomass, although a few large remnant trees resulted in plots with AGC densities of > 10 tC ha^{-1}. AGC steadily increased with time since abandonment on both soil types (Figure 4.1) with models fit using both OLS and robust regression having similar slope coefficients (max. Δ0.05 tC/ha/yr^{-1}); therefore we based our interpretation on the simpler OLS regression models. Soil type had no clearly significant effect of on C accumulation rates (ANCOVA; slope, $P = 0.42$, intercept, $P = 0.11$), though AGC accrued slightly faster on clay soils (0.93 ± 0.15 (±SE) tC ha^{-1} yr^{-1}; $r^2 = 0.65$) compared to sandier sites (0.75 ± 0.14 tC ha^{-1} yr^{-1}; $r^2 = 0.50$). When grouping plots together, the average accumulation rate was 0.83 ± 0.10 tC ha^{-1} yr^{-1} ($r^2 = 0.56$). We initially assumed that each fallow plot had a similar number of remnant trees, whereas the number of trees left varied among the active fields (range 0 – 39 tC ha^{-1}). In some instances, this will lead to an overestimate in stand-level (ha) AGC stocks where large trees were more common, potentially altering the rate and pattern of re-growth. We therefore re-ran the analysis with remnants removed, yet again we found no statistical difference in accumulation rates between soil types ($P = 0.54$; $r^2 = 0.84$ (sand) & 0.75 (clay)), however AGC was now estimated to accumulate at slightly slower rate of 0.72 ± 0.05 tC ha^{-1} yr^{-1} ($r^2 = 0.81$).

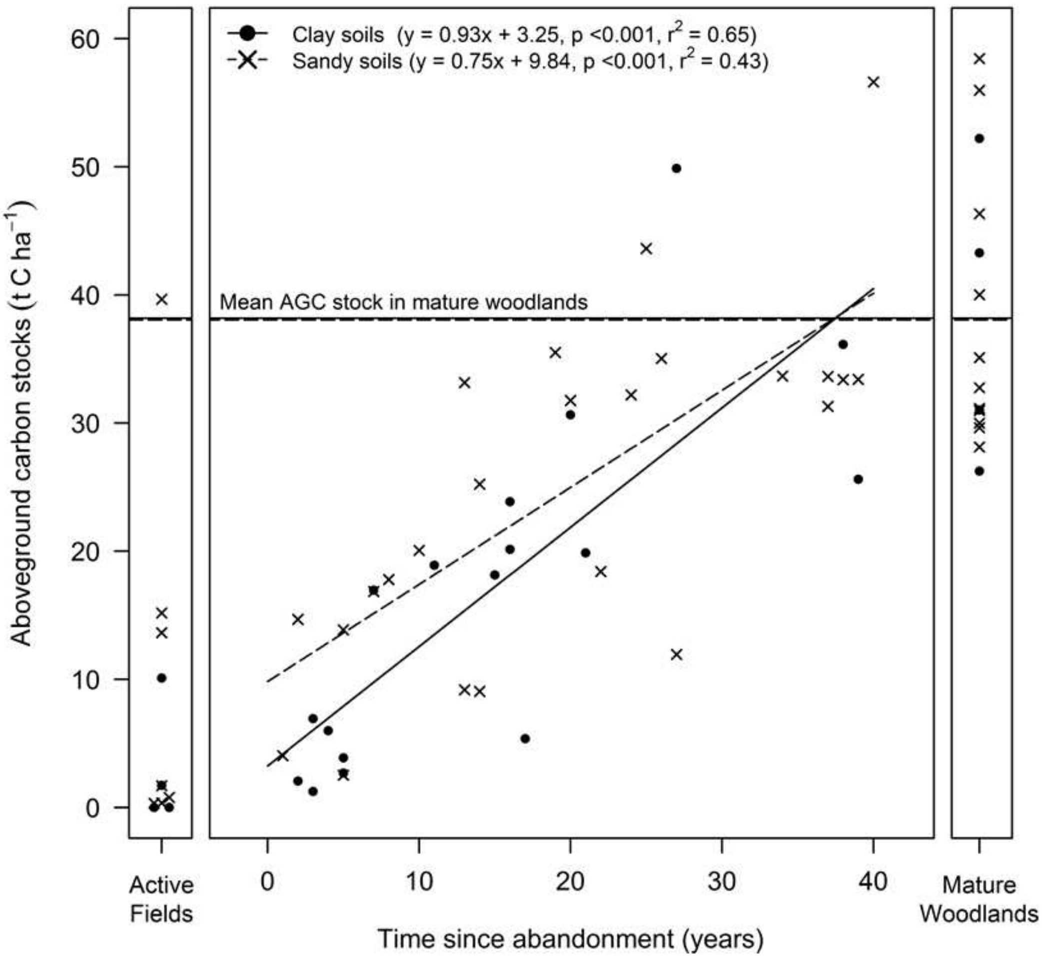

Figure 4.1 - Ordinary least squares (linear) regression models are used to describe changes in AGC with time since abandonment. The regression coefficients for models fit to the data from each soil type are indicated at the top of the figure, with plots on sandy soils (<18% clay) represented by crosses and a thick dashed line, with plots on clay soils (>18% clay) represented by black dots and soil lines. The active fields were included in the regression model (age = 0) although they are plotted separately for clarity. Horizontal lines show the average AGC stock of mature woodlands plots on clay (solid) and sandy soils (hatched).

4.3.2 Impacts of land clearance and re-growth on soil carbon stocks

Despite clear changes in AGC stocks along the chronosequence, soil carbon stocks exhibited an idiosyncratic response to the full cycle of shifting cultivation (Figure 4.2). Under mature woodlands there were clear differences in SOC stocks between plots on different soil types with the more clay-rich soils containing significantly higher SOC stocks in both the topsoil and subsoil than on sandy soils (Mann-Whitney, $P<0.05$). SOC stocks under woodlands were also well constrained (CV = ~15%) in contrast to SOC stocks among active fields which were more variable (CV = ~30%). SOC stocks were greater on average in active fields than in mature woodlands on both clay (+14%) and sandy soils (+7%), with subsoil C stocks also found to be greater under agriculture (+5% clay and +19% sandy), although the differences were not statistically significant at either depth on both soil types (two sample t-test, $P>0.1$). Comparisons of SOC stocks between re-growing woodlands and active fields revealed similar patterns with stocks consistently greater under agriculture, but not significantly so ($P> 0.1$). Both the subsequent period of cultivation (max. 5 years) and the recovery phase following abandonment resulted in no statistically significant changes in SOC at either depth on both soil types, even after fitting both linear and negative exponential models (clay soils only) to the data (Figure 4.2).

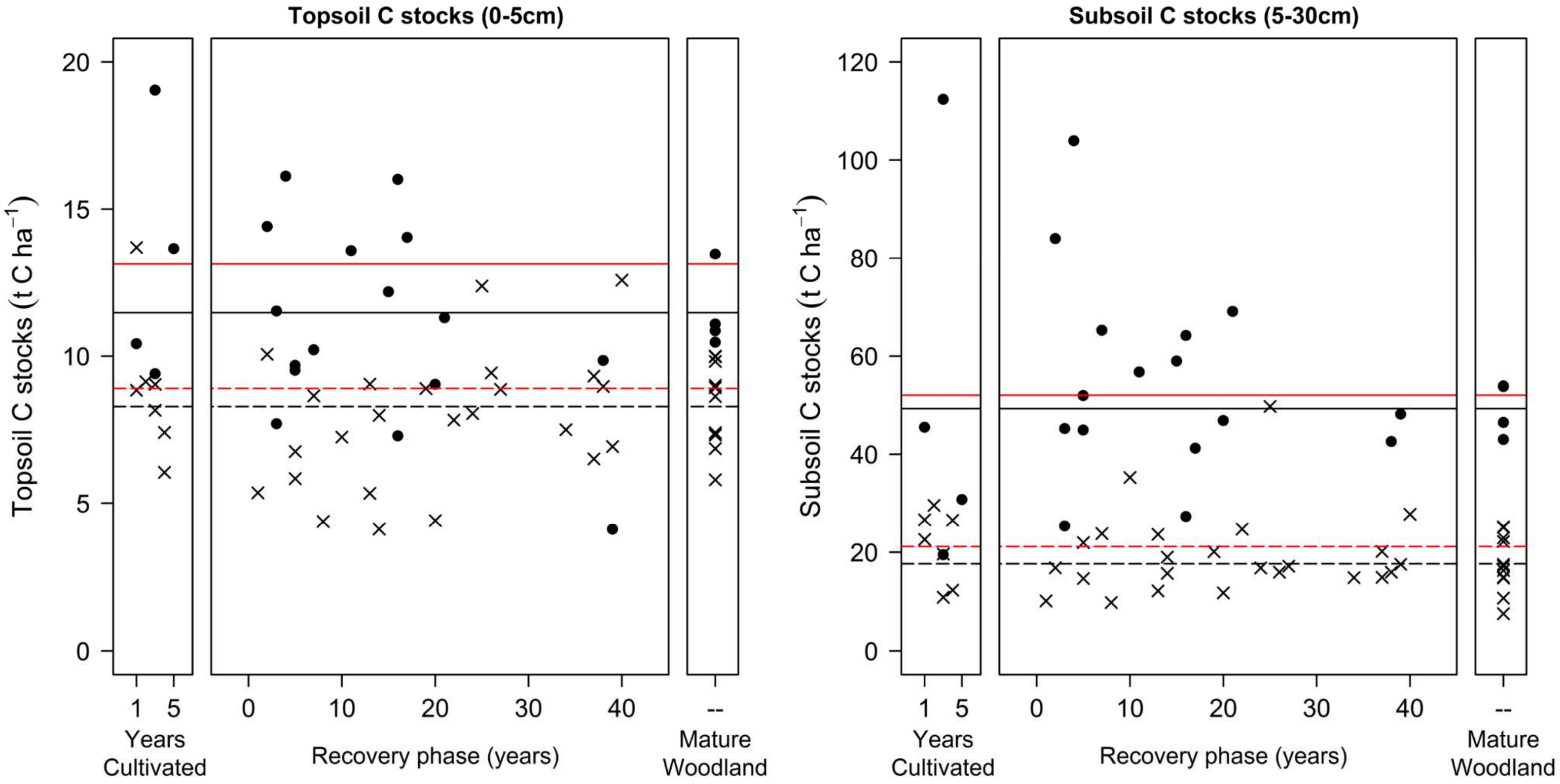

Figure 4.2 - Soil carbon stocks in active fields, secondary woodlands and mature woodlands. Solid lines indicate the mean C stocks in active fields (red) and woodlands (black) for clay soils with the hatched line showing the same but for sandy soils. Our estimate of subsoil C stocks (5 - 30cm) was generated by subtracting the SOC stocks in the top 5cm (topsoil) from the C stock estimate from top 30cm as they were taken directly next to one another. The one active field with a high silt content (Appendix A; Figure A2) appeared as an outlier, however removing the plot did not affect our conclusions.

4.3.3 Tree species composition and diversity

Across the 67 plots we identified 200 morphospecies by their local name, of which 98 were identified by their species botanical name and a further 17 to genus level. Nearly 80% of all recorded species had fewer than 50 individuals while 55% had 10 individuals or less. Together, the 115 identified species contributed 91% of the total measured basal area and 87% of the total number of stems measured across all plots, with similar levels of taxonomic identification when separating plots by soil type. On all subsequent analyses we use the species botanical name or genus where known, and where this is not possible, the species local name is used instead.

4.3.3.1 Patterns of species α-diversity within plots

Species richness and Fisher's alpha diversity increased rapidly following agricultural abandonment with patterns in species richness on both soil types best represented by a unimodal (ricker) curve, which also best captured the trend in Fisher's alpha diversity on clay soils, whereas a saturation (Michaelis-menton) function performed better on the sandy soils (Table S4). Both diversity measures reached levels equivalent to that of mature woodland after 6 - 12 years of abandonment (Figure 4.3). The best-fit models highlighted a tendency towards greater plot-level diversity in the mid to later stages of re-growth (15 – 30 years), although some plots of similar age also exhibited some of the lowest diversity values across the chronosequence (Figure 4.3).

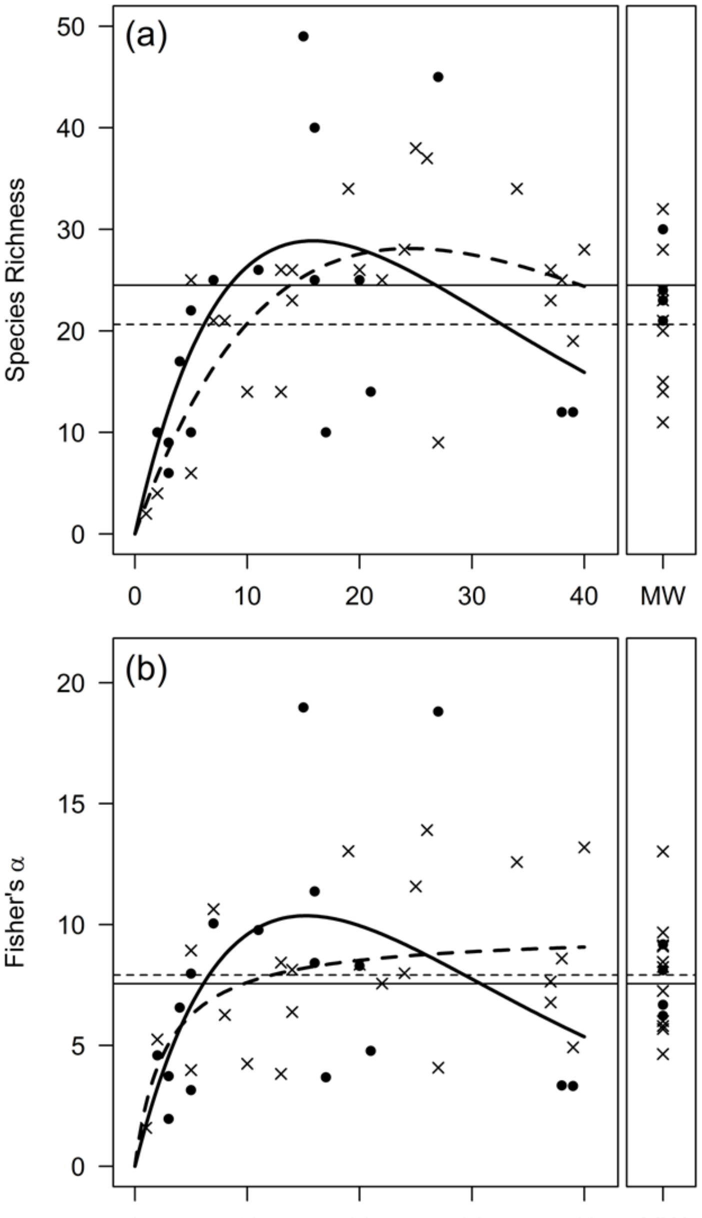

Figure 4.3 – Changes in plot-level (a) species richness and (b) Fisher's alpha diversity across the chronosequence, with mature woodlands (MW) as the reference point. Again, black circles and solid lines represent plots on clay soils with the crosses and dashed lines representing plots on sandy soils, with horizontal lines indicating the average species richness and Fishers alpha values for mature woodlands on clay (solid) and sandy (hatched) soils.

Table 4.1. Comparisons of the mean (±SD) tree community structure and diversity among re-growing plots of similar age, and plots in mature woodlands

Soil type	Sandy soils (7 - 18% Clay)						Clay soils (20 - 31% Clay)					
Stage	Active fields	Abandoned fallows				Woodland	Active fields	Abandoned fallows				Woodland
Age class	n/a	0 - 10	11 - 20	21 - 40	All fallows	n/a	n/a	0 - 10	11 - 20	21 - 40	All fallows	n/a
Number of plots	7	7	6	11	24	11	4	7	6	4	17	4
Vegetation structure												
Stem density	n/a	71 (69)	181 (28)	184 (54)	150 (79)	103 (54)	n/a	70 (34)	182 (109)	127 (43)	122 (84)	202 (69)
Total # stems	n/a	500	1084	2027	3611	1131	n/a	490	1093	506	2089	807
Stems 5 - 10cm	n/a	55 (62)	129 (36)	107 (49)	98 (57)	53 (39)	n/a	59 (29)	122 (80)	69 (20)	83 (57)	111 (42)
Stems 10 - 30cm	n/a	14 (12)	49 (20)	71 (33)	48 (34)	40 (17)	n/a	10 (14)	58 (32)	50 (18)	36 (31)	82 (29)
Stems 30+	n/a	2 (1)	3 (2)	6 (5)	4 (4)	10 (4)	n/a	1 (1)	2 (2)	7 (7)	3 (4)	9 (4)
Tree species diversity												
Bray-Curtis Index	n/a	0.93 (0.09)	0.69 (0.12)	0.74 (0.13)	0.81 (0.14)	0.76 (0.10)	n/a	0.76 (0.11)	0.82 (0.10)	0.83 (0.10)	0.83 (0.10)	0.66 (0.09)
Plot species richness	n/a	12 (10)	25 (6)	26 (8)	23 (10)	21 (6)	n/a	14 (6)	29 (14)	20 (17)	21 (14)	23 (4)
Total recorded number of species	n/a	61	73	109	137	102	n/a	55	112	61	141	63
Rarefied richness	n/a	71	76	109	n/a	115		66	112	68	n/a	69
Fisher's α	n/a	4.8 (4)	8.0 (3.0)	8.9 (3.4)	8.0 (3.4)	8.0 (2.5)	n/a	5.6 (2.5)	10.2 (5.2)	7.3 (7.7)	7.9 (5.5)	7.1 (1.3)

4.3.3.2 Patterns in tree community composition

There were clear trends changes in tree composition and dominance over time with the 12 most dominant species accounting for between 13% of all stems (clay plots) to 35% (sandy plots) in plots <10 years old, increasing to 70% and 59% respectively in mature woodlands (Figure 4.4). A comparison of the floristic composition between soil types revealed two distinct vegetation communities (PerMANOVA; Table S3) with miombo (*Brachystegia – Julberndardia*) dominated woodlands occurring on the sandy soils, with the clay soils tending to support undifferentiated savanna woodlands where the keystone miombo species are present, but not dominant (Figure 4.4) (White, 1983). On clay soils, the species *Acacia polyacantha*, *Dombeya rotundifolia* and *Annona senegalensis* were commonly observed in re-growing woodlands and decreased in dominance with increasing stand age (Figure 4.4), with the latter two species absent from mature woodlands, whereas *A. polyacantha* was only rarely found. *A. senegalensis* showed similar patterns on sandy soils where it was common in re-growing woodlands, but less so in mature habitats. *Millettia stuhlmanii* and *Pteleopsis myrtifolia,* which are typically harvested for timber, or used for charcoal production, were frequently found across the chronosequence on both soil types, as was *Combretum apiculatum* which tended to dominate the understory meaning all three were considered habitat generalists.

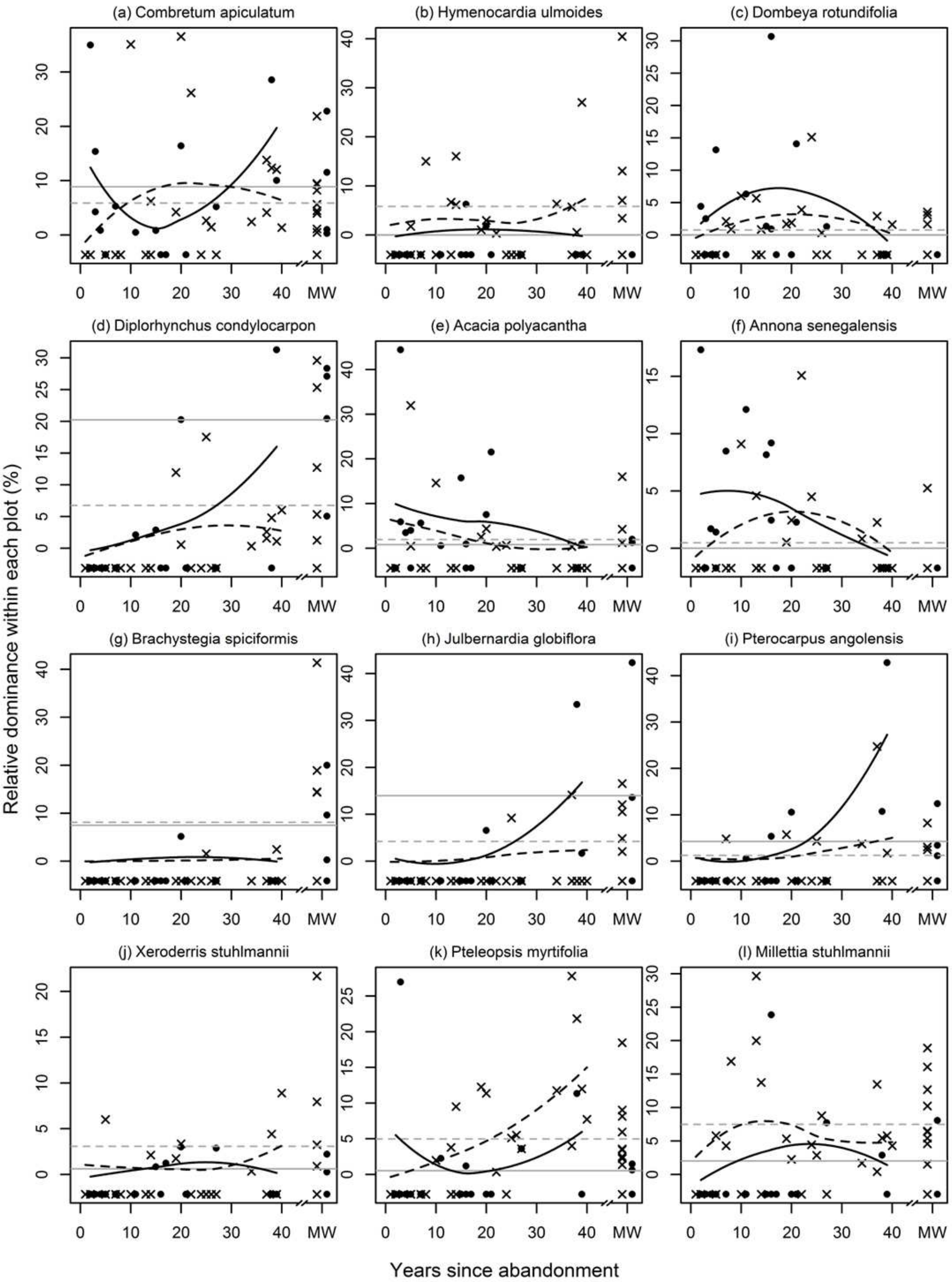

Figure 4.4 - Changes in the relative dominance of 12 tree species found to be among the most dominant across the 67 sites. Plots (a-f) are species that were principally dominant in the re-growing stands, and/or can be considered as species which are typically small in

stature and common to the understory, whereas plots (g-l) are species that are more characteristic of mature woodland, and/or typically exist as larger canopy dominants (Coates-Palgrave 2002). Changes in relative dominance over time are represented by a LOESS (locally weighted scatterplot smoothing) curve with a span value of 1.5. The average dominance of each species in mature woodlands is shown by the grey horizontal lines with hatched lines and crosses again representing plots on sandy soils and solid points and lines representing clay sites. Sites where the species was not recorded are plotted separately in the negative space at the bottom of each plot.

Species similarity among re-growing plots (β-diversity) was typically low (Bray-Curtis Index > 0.6) with some plots of similar age sharing no species (Table 4.1; Figure S3). Sites <20 years old were generally distinguishable from the latter stages of abandonment by the increasing presence of larger stature tree species common to mature woodlands, including *Pterocarpus angolensis*, *P.myrtifolia*, and those in the defining miombo genera - *Brachystegia spiciformis* and *Julbernardia globiflora* – which first appeared after ~20 years of abandonment (Figure 4.4).

The overall similarity in species composition between re-growing and mature plots clearly increased with stand age and were best represented by a logarithmic relationship on sandy soils (ΔAICc = 2.46), with a linear model preferred instead on clay soils (ΔAICc = 1.44; $r^2 = 0.31$) (Table S3, Figure 4.5). On sandy soils, the similarity in composition between proximate mature woodland plots ranged from 0.11 – 0.54 with a mean of 0.31, whereas for clay soils the midpoint was 0.46. Neither model reached levels equal to the average background similarity among pairs of mature woodland plots within the 40-yr timespan, with convergence instead predicted to occur after 57 years on sandy soils, and 66 years on clay soils. There were only two mature, and two re-growth plots > 25 years old on clay soils meaning we have less confidence in our model predictions after this time-point.

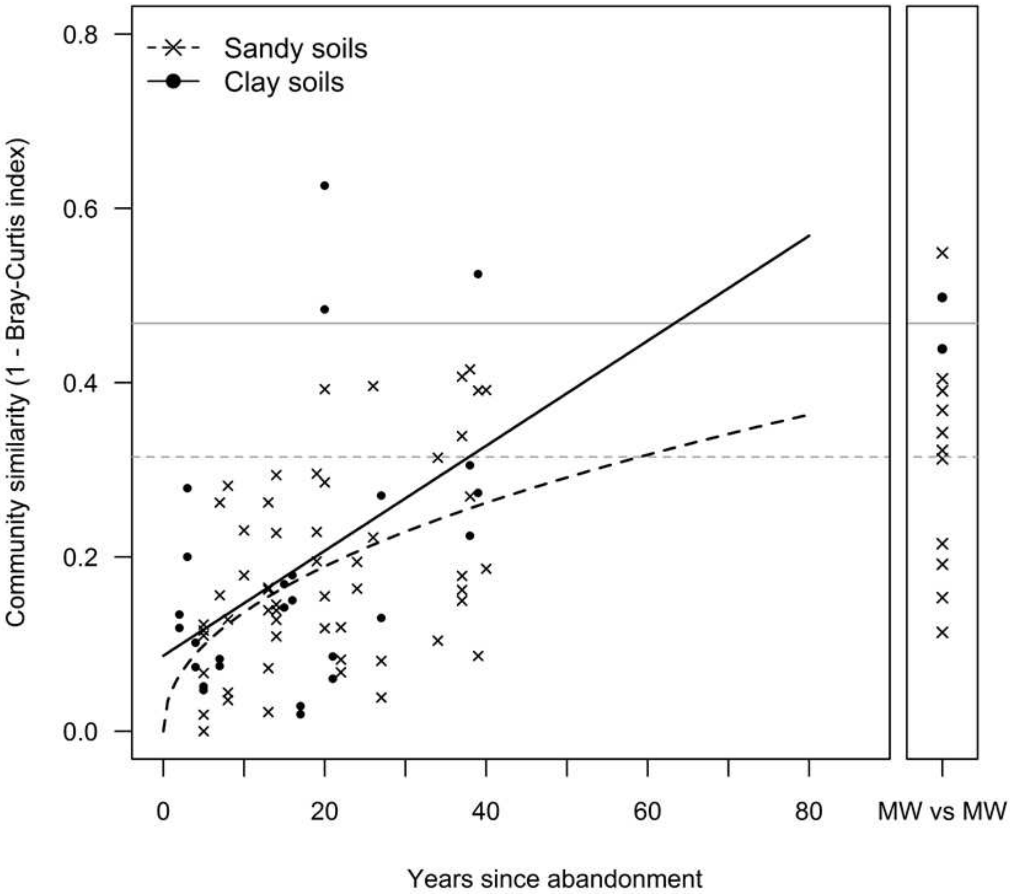

Figure 4.5. Changes in tree community similarity with increasing time since abandonment. Each point represents the similarity between each re-growing woodland plot and of its associated mature woodland plots sampled in the same village area. The horizontal lines represent the average similarity between nearby pairs of mature woodland plots.

One 20-yr old plot exhibited a relatively high similarity to re-growing woodlands (Figure 4.5), although this site had an idiosyncratic composition compared to other similarly aged plots (see section 4.4.3). Removing this site from the analysis still resulted in a linear model being preferred over a log-model (ΔAICc = 4.02), however convergence was now reached at 78 years. Results of the model fitting were robust to the exclusion of pre-defined remnant trees (59 years (sand) & 63 years (clay); Table S4); however our interpretation is complicated by the fact we had no way of identifying, and thus removing smaller stems which propagated from these larger remnants.

4.3.3.3 Landscape scale patterns in tree diversity and endemism (γ-diversity)

When combining all re-growing plots together (0 – 40 years), the total species richness in these secondary habitats was significantly higher than in mature woodlands, ranging from a minimum difference of 20% (7 – 34%, 95% CI; 28 species), to a maximum of 30%: (13 – 46%; 51 species) after extrapolating rarefaction curves (Figure 4.6). Both of the extrapolated curves appeared close to asymptote suggesting our maximum estimate of the difference in total species richness between habitats is accurate for this landscape.

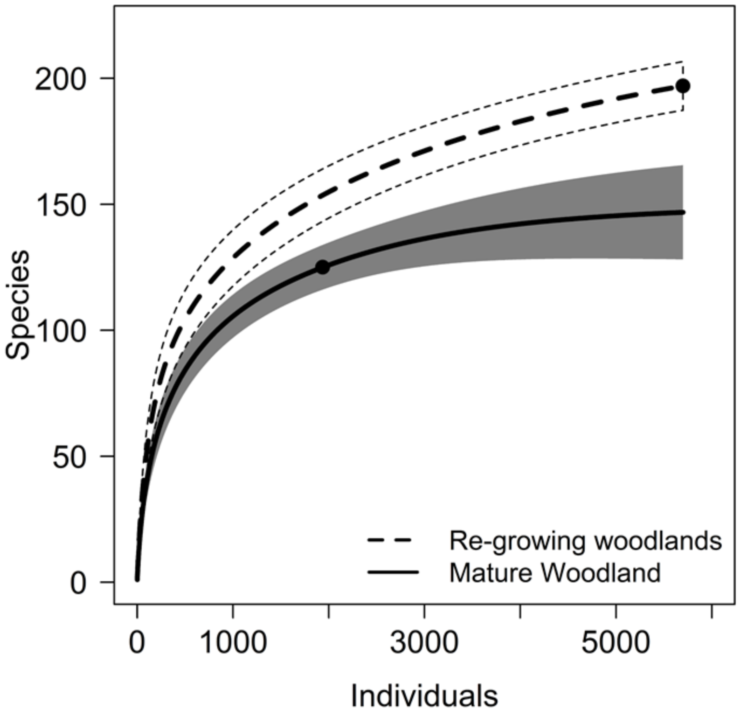

Figure 4.6. Individual-based species accumulation curves showing the estimated total species richness in re-growing woodlands (0 – 40 years) and mature woodlands. Plots are not separated by soil type in order to highlight broader trends. Shading indicates 95% CI on the predictions. The points on each curve are the *observed* species richness. The significance of the observed differences in species richness between habitats (α = 0.05) is assessed by comparing rarefaction curves and their associated 95% confidence intervals to see if they overlapped. If the 95% CI of a given habitat type fell outside the 95% CI of another, then we inferred that the two groups differed in their species richness.

We found no evidence of our mature sites plots being more clustered in space than the re-growing woodlands which may have resulted in more species being unique to these sites simply because of greater spatial turnover in species (Table S2). Of all the species recorded, 84 (42%) were only found in re-growing woodlands, of which

19 had an abundance ≥10, while only 25 species (12%) were unique to mature woodland (1 species >10) (Figure 4.7).

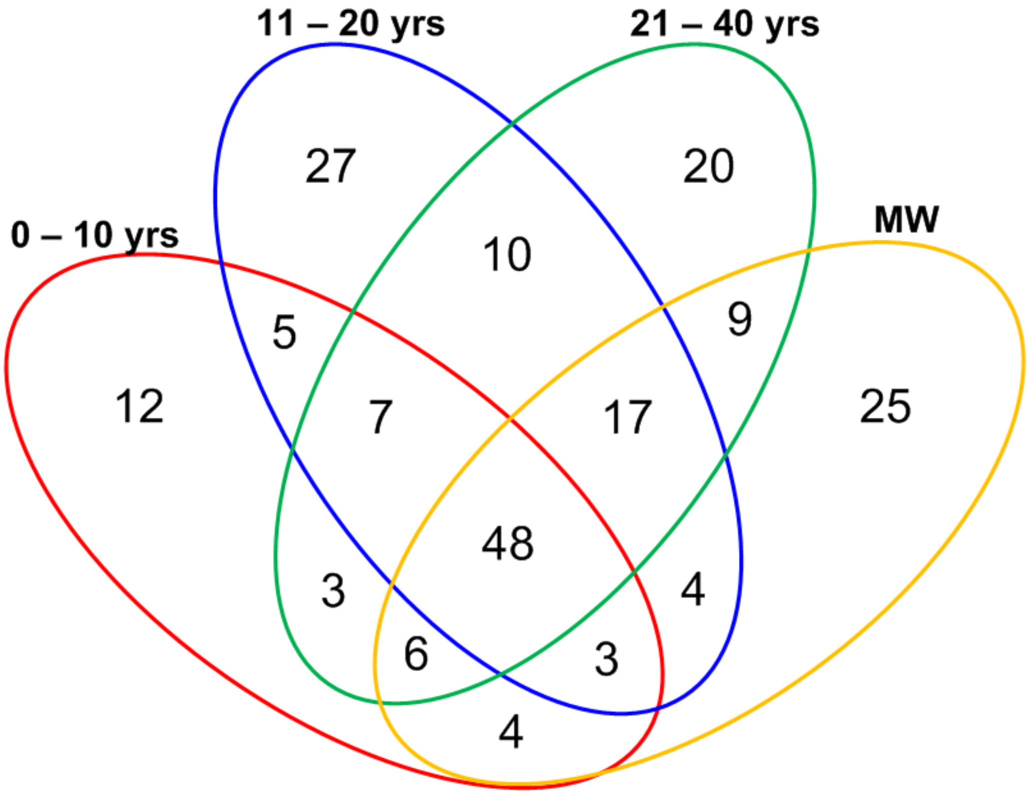

Figure 4.7. Venn-diagram showing the number of species recorded in different stages of succession, with interactions showing the number of species shared between successional stages.

4.4 Discussion

In this study we examined how carbon stocks in trees and soil developed following agricultural abandonment, and whether soil texture had a significant effect on the rate and pattern of recovery. We also examined whether the altered vegetation structure of secondary habitats had a long term impact on patterns of species composition and diversity, both at the plot and landscape scale. Our results highlight that African woodland ecosystems can be highly resilient to disturbance by shifting agriculture, attaining many of the key characteristics of mature woodlands in a relatively short period of time. Our results are of known relevance to carbon sequestration projects by helping to inform the carbon benefits of restoring disturbed habitats (REDD+), but also for understanding the biodiversity value of these created landscapes in the face of pressures to shift to more intensive/commercial forms of cultivation (Lambin & Meyfroidt, 2011) .

4.4.1 Recovery of aboveground carbon stocks

Re-growth was characterised by clear changes in woody structure (Table 4.1) and significant increases in tree AGC stocks (Figure 4.1). We hypothesised that soil texture would be a critical control on aboveground productivity, with carbon accumulation rates higher on more clay rich soils due to their potentially greater moisture and nutrient retention capacity. Despite plots on clay soils exhibiting a marginally faster rate of re-growth (0.93 vs 0.75 tC ha^{-1} yr^{-1}), the difference between soil types was not significant, even when excluding potential remnant trees from the analysis (Figure 4.1). Our results suggest that soil texture has a limited impact on aboveground productivity, despite many reasons to expect an influence. Indeed, Bucini & Hanan (2007) found that finer textured soils supported more woody cover across African savannas (including savanna woodlands), while Woollen et al (2012) observed the opposite in miombo dominated woodlands, showing greater biomass on well drained, coarse textured sites, both of which suggested some form of textural controls. A caveat in this interpretation is that high biomass does not necessarily imply high productivity (Keeling & Phillips, 2007). The finding of clear differences in species composition between similarly aged stands on different soil types (Appendix B, Table B4) means that similar rates of re-growth may be a response to species-specific adaptations to different edaphic conditions.

Combining plots of both soil types revealed an average accumulation rate of ~0.83 tC ha^{-1} yr^{-1} with carbon stocks predicted to reach equivalent values to mature woodlands after 35 years on both soil types. Removing remnant trees reduced accumulation rates to 0.72 tC ha^{-1} yr^{-1} giving a lower bound on our productivity estimates. Our carbon accumulation rates are marginally higher than the previous estimate of Williams et al. (2008) (0.7 tC ha^{-1} yr^{-1}) from a similar site in Mozambique also with ~800 mm rainfall, where plots were sampled over a range of soil textures. Chidumayo (1990; 1993) reported similar accumulation rates (0.6 – 1.0 tC ha^{-1} yr^{-1}) with slightly faster recovery rates observed in areas receiving >1000mm rainfall (1.0 tC ha^{-1}; Kalaba et al. 2013).

4.4.2 Land use change effects on soil carbon stocks

Conversion of forest to agriculture is typically associated in a reduction in SOC stocks due to a reduction in litter inputs, increased erosion and enhanced microbial respiration as a result of burning and soil disturbance (Walker & Desanker 2004; Williams et al. 2008; Don et al. 2011). In this context, we hypothesised that soils would be negatively impacted by land clearance, but that the more clay rich soils would lose proportionally less SOC, and recover stocks at a faster rate than sandier soils due to their greater capacity to physically protect and store organic matter

(Baldock & Skjemstad, 2000). Sites on the more clay rich soils were marginally more resilient to land clearance, however the manner in which soils responded differed from expectations with stocks marginally greater under active fields compared to re-growing and mature woodlands, although the differences were not statistically significant. We attribute the lack of any clear changes to limited soil disturbance (i.e. mechanisation or furrowing) associated with agricultural practices in our study area.

Subsequent regeneration of the woodlands also resulted in no significant changes in bulk SOC stocks, which combined with the lack of any obvious effect of land clearance, refutes the second part our hypothesis that stocks would 'recover', but supports arguments that time is often a poor predictor of bulk SOC stocks, particularly over the timescale sampled here (Marín-Spiotta & Sharma, 2013). Some early re-growth plots did exhibit relatively high SOC stocks which we attribute to incorporation of burned residues during cultivation.

Our results strongly suggest that soils are comparatively resistant to the full cycle of shifting cultivation, despite the clear changes in aboveground biomass. However, detecting changes in bulk soil C pools is difficult without very intensive sampling (Poussart *et al.*, 2004). Soil carbon stocks were found to be patchy at small spatial scales, with SOC densities varying by up to a factor of 5 within plots making change detection difficult. The lack of any clear positive trend in SOC has previously been attributed to both fire and termite activity decoupling above and below ground stocks via the removal of the surface litter layer (Williams et al. 2008; Ryan et al. 2011). Soil carbon stocks are also strongly impacted by the intensity and length of cultivation, which was poorly known in our older plots (Zingore *et al.*, 2005; Ando *et al.*, 2014). In some plots, the residence time of both crop (C_4) and woodland derived (C_3) SOC may outlast the period of cultivation making trends more difficult to observe (Bruun *et al.*, 2013). Indeed, despite also finding no clear trend in bulk soil samples across an 80-yr chronosequence of abandoned pasture land, Marin-Spiotta et al. (2009) found that the SOC pool was not static and that increases in woodland derived carbon was offset by losses in physically unprotected pasture-derived C, resulting in no net change over time. Soil export issues prevented us from conducting similar analyses along these lines, which may be required to fully understand the effects of land use change on soils.

4.4.3 Changes in tree species composition and diversity

Our results highlight that re-growing woodlands recover many of the compositional and diversity characteristics of mature woodland within the timeframe of the chronosequence, highlighting the resilience of these tree communities to shifting agriculture. We found that tree species diversity at the plot-level (α-diversity) reached levels equivalent to that of mature woodlands after ~6 -12 years of abandonment. This relatively rapid increase in tree species diversity is consistent with similar studies carried out across the miombo region (Williams et al. 2008; Kalaba et al. 2013), and in other tropical forests (Guariguata & Ostertag, 2001; Marín-Spiotta *et al.*, 2007; Dent *et al.*, 2013; Martin *et al.*, 2013). Our prediction that α-diversity would eventually peak in re-growing woodlands was based on the Intermediate Disturbance Hypothesis which posits that diversity should maximise at a point when disturbance is not so recent that only a few pioneer species exist, but before large canopy trees competitively exclude subdominant species (Connell, 1978). Our best-fitting statistical models indicated a tendency towards greater species richness mid-abandonment, a pattern also found in Williams et al. (2008); however the variance between plots of similar age and the saturation in Fisher's alpha diversity on sandy soils suggests this is not a pervasive pattern in our study area.

As African savanna woodlands are characterised by frequent disturbances (Furley *et al.*, 2008; Ryan & Williams, 2011), we also hypothesised that tree community composition would also be resilient to land clearance. This is in contrast to observations from wetter tropical forest which generally show that species composition in secondary habitats tends to remain distinct from old-growth forests, even after 80 years of re-growth (Marín-Spiotta *et al.*, 2007; Dent *et al.*, 2013; Martin *et al.*, 2013), although Piotto et al. (2009) used the same method to infer 'recovery' when comparing 40-year old fallows to patches of old-growth Atlantic forest in Brazil.

Many studies have criticised the use of chronosequences as a method for predicting long-term compositional changes following disturbance (Chazdon *et al.*, 2007; Johnson & Miyanishi, 2008), particularly as each site is assumed to have the same history, and that the pre-disturbance composition of each site is unknown leading to a reliance on reference woodlands which suffer from distance related turnover in species composition (Ramage *et al.*, 2013). Despite these potential issues, our data did capture some general changes in species composition and dominance over time, with plots in the earlier stages of abandonment (0 – 20 years) distinguishable from the latter stages of abandonment by a reduction in the dominance of early successional, fire resistant species (*A. polyacantha,, D. rotundifolia, A. senegalensis*; Coates-Palgrave 2002; Higgins et al. 2012) and an increase in the presence of slower-growing, fire tender tree species commonly associated with old-growth habitats (*J. globiflora, B. spiciformis*) (Figure 4; Appendix B, Figure B2). Elements of the initial floristic composition (IFC) model of succession were more prevalent among sites on sandy soils, as evidenced by NMDS plots with some of the younger plots appearing more compositionally similar to mature woodlands than older abandonments (Figure B2); however this was not a pervasive pattern. Changes in species composition occurred in a more ordered manner for plots on clay soils, with sites of similar age tending to cluster together with re-growing sites on both soil types becoming more similar to mature woodlands with increasing stand age (Figure B2).

This transition was reflected by an overall increase in the compositional similarity between re-growing woodlands and their nearest patch of mature woodland with increasing time since abandonment, eventually reaching levels equivalent to the background variation among mature patches after ~ 57 - 66 years (Figure 5). We have more confidence in the model fit to data for sandy soils than the clay plots where sample size was smaller, particularly for older abandonments and mature woodlands. Log-models are considered more ecologically plausible than the linear models used as it's unlikely that species will be added at a similar rate as stands reach maturity meaning time to convergence may be under-estimated. However, both pairs of mature woodland plots on clay soils were also relatively close together (Villages 3 & 6, Appendix A, Table A2) meaning that compositional similarity between plot-pairs may be biased higher. The results partially validate our third hypothesis that composition would approach similarity to mature woodlands over time, although not within the timeframe of the chronosequence as predicted. Previous studies conducted in African woodlands show that species composition remains distinct after 25 years of re-growth

(Williams et al. 2008; Stromgaard 1985), however none of these evaluated the compositional similarity between habitat types in the context of old-growth similarity, or noted the distances between re-growing and mature sites. Kalaba et al. (2013) concluded that after 44 years of abandonment that species compositon in re-growing woodlands still differed from mature woodlands, despite many of the dominant miombo species being present in their re-growing fallows. In this study, the plots which showed the strongest similarity to nearby mature woodlands also contained species in the genera *Brachystegia* and *Julbernardia,* along with other canopy dominants such as *Pterocarpus angolensis*, contrasting the results of Williams et al. (2008) and Stromgaard (1986) who found these flagship miombo species to be completely absent from re-growing woodlands. However, their relatively high dominance in some plots was due to the presence of only a few large individuals which given their slow growth rates means they are likely to be remnants, although our liberal growth model did not class these as such (Chidumayo & Gumbo 2010 and refs. therein). Smaller individuals of these species were recorded in some younger fallows, but only where a larger remnant (>30cm) of the same species was also present. These species have low dispersal ability with seed dispersal occurring from an explosive pod rather than through wind or animal dispersal suggesting that these keystone species and are not readily recruited when a viable seed source is not in close proximity (Frost, 1996; Caro *et al.*, 2005). This suggests recovery in floristic composition is likely to be controlled by the proximity and composition of local species pools, and the number and composition of remnant trees left over (Guariguata & Ostertag, 2001; Dent & Wright, 2009; Mwampamba & Schwartz, 2011). Removing likely remnant trees from the analysis did not significantly alter the results; however this approach fails to account for smaller conspecifics which have propagated from these larger trees meaning their influence is likely to be under-estimated. We therefore speculate that the 60-80 years predicted by our models may be the minimum time required for species composition in re-growing stands to converge with that of mature woodlands.

Changes in species composition did not follow a predictable pattern with some large differences in tree community composition among some similarly aged plots (Appendix B, Figure B1) and only a few species shared across successional stages (Figure 7). We attribute the generally low compositional similarity between sites to the different species that are recruited into the re-growing woodlands, creating this patchiness in species composition across the landscape. Indeed, when considering all re-growing woodland plots together we found them to be considerably more species-rich (20 - 30%) than mature woodland habitats after correcting for differences in sampling effort, thus indicating that re-growing woodlands promote high beta and gamma diversity in these landscapes (Figure 6). Supporting evidence comes from the fact that a relatively large number (42%) of the recorded species were only sampled in re-growing woodlands with most only appearing at certain points in the recovery phase, though the majority of these species were rare (Figure 7). Of the 116 species recorded in mature woodlands, 78% were also found in re-growing stands, with the majority of these appearing in the first 20 years of abandonment suggesting most species common to mature woodland can tolerate a wide range of conditions, further supporting our conclusions that tree communities are relatively resilient to land clearance. Mature woodlands still supported a significant number of species not common to secondary woodlands, which we expect to be the more disturbance intolerant and/or slow growing species. Therefore the extra time taken for similarity in species composition to ‘recover’ most likely reflects the time required for species adapted to old-growth habitats to colonise and begin to dominate. These results clearly indicate the importance of maintaining a mosaic of land-cover types across the landscape to allow some certain specialist species to persist.

4.4.4 Implications for land management and policy

Despite the various criticisms of this approach, chronosequences remain the only way of estimating long-term woody productivity in African woodlands and the biodiversity value of secondary habitats. As such, our data are of clear relevance to current REDD+ projects that wish to estimate the financial and ecological benefits associated with the natural regeneration of previously disturbed lands. Our results provide further evidence of the extent to which re-growing woodlands act as carbon sinks, but also the consistency at which this occurs across these heterogeneous landscapes (Williams et al. 2008; Kalaba et al. 2013). AGC stocks reached values similar to those in mature woodlands after 35 - 40 years of abandonment, considerably slower than the decade or so required for tree species diversity to reach equivalence. Many of species common to mature woodlands re-appeared relatively quickly after abandonment, although species composition is expected to take considerably longer to recover fully with results suggesting that maintaining a small number of remnant trees from the previous woodlands may be critical factor in facilitating woodland recovery (Mwampamba & Schwartz, 2011). Despite the common, but misplaced, perception that shifting cultivation is a destructive and degrading land use practice (Mertz, 2009), the patchiness in vegetation cover that it creates also appears to increase the number of species present in the landscape, potentially by allowing those that are otherwise rare or sub-dominant to proliferate. Our results therefore suggest a win-win scenario for carbon sequestration projects focussing on woodland regeneration as this is also likely to encompass strong biodiversity benefits.

More data is needed to verify the generality of these results; however our data does raise important questions in the current debate over REDD+ and the proposed shifts to more intensive, commercial focused agricultural practices which is considered by many to be a more sustainable route for development in African woodlands (Jones & Tarp, 2012; van Vliet *et al.*, 2012). Instead, we suggest that mitigating against the rapid and extensive land-use change occurring in African woodlands could be achieved by channelling funds to support improved land-management in areas of shifting cultivation, principally by extending farm life and maintaining soil organic matter status through organic fertiliser inputs (i.e. Kimetu et al. 2008), excluding, or limiting mechanisation and/or tillage to maintain SOC stocks and thus productivity (i.e. Mujuru et al. 2013), and maintaining long enough fallow lengths to offset the carbon that was originally lost, without jeopardising potentially important reserves of biodiversity.

Given the close dependence of people on woodland resources, there is justifiable concern that removing this practice from the landscape will potentially reduce the provision of key ecosystem services, which may have important consequences for local well-being (Padoch & Pinedo-Vasquez, 2010). Chazdon and Coe (1999) showed that secondary forests Costa Rica were important sources of non-timber forest products, however the extent to which local communities depend on and utilise the resources from secondary habitats is not well documented for African woodlands (although see Coates-Palgrave (2002) for a general overview).

An important area for further research is therefore to establish whether disturbance is necessary process in allowing certain locally important species to establish and/or flourish, including in the herbaceous and sapling layer which was not sampled in this study. Studies from other parts of the tropics have also noted that some species of bird, insect and mammal are only found in patches of disturbed forests (Barlow et al., 2007), however it is unclear as to whether similar associations are found in African woodlands.

4.5 Conclusions

- Following agricultural abandonment, aboveground woody carbon stocks recover at an average rate of 0.83 tC ha^{-1} yr^{-1} with soil texture having no significant impact on recovery rates. Our results are also congruent with other studies from African woodlands (0.6 – 1.0 tC ha^{-1} yr^{-1}) suggesting this value can be applied across different regions.
- Soil carbon stocks were largely unaffected both by the initial land clearance and the recovery phase suggesting that soils are resilient to small-scale shifting cultivation.
- The compositional similarity between re-growing and mature woodlands increased with time since abandonment and after 60 – 80 years is expected to be similar to levels of similarity among old-growth sites. It is suggested that local site factors (i.e. local seed sources or number of remnant trees) strongly determine the rate and extent to which African woodlands, and the keystone species which dominate mature habitats recover over time.

- Tree species diversity recovers within the first decade after agricultural abandonment with a slight peak in diversity in 15 – 30 year old stands, although this pattern was not ubiquitous. Re-growing woodlands appear to support a large number of species not found in more mature habitats highlighting the importance of these human created ecosystems for biodiversity.

4.6 Chapter 4 references

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4.7 Supplementary material

Table S1 – Metadata for the 67 sites sampling in this study. UTM zone is 37S.

Village	Plot ID	UTM_X	UTM_Y	Age	Class	Sample year	Soil type	%Clay	%Silt	%Sand
Kikole (1)	KikoleA0	517165	9027717	0	Active Field	2011	Sand	10.84	6.2	82.96
Kikole (1)	KikoleA2	512993	9029704	0	Active Field	2011	Sand	15.76	5.28	78.96
Kikole (1)	KikoleA3	512883	9029308	0	Active Field	2011	Clay	23.76	7.28	68.96
Kikole (1)	KikoleM1	513124	9028956	50	Mature	2011	Sand	11.76	1.28	86.96
Kikole (1)	KikoleM2	513673	9029563	50	Mature	2011	Sand	15.76	2.28	81.96
Kikole (1)	KikoleM3	512009	9028023	50	Mature	2011	Sand	15.76	3.28	80.96
Kikole (1)	KikoleR16	513166	9029725	16	Abandoned	2011	Clay	21.76	3.28	74.96
Kikole (1)	KikoleR19	514267	9029510	19	Abandoned	2011	Sand	13.76	1.28	84.96
Kikole (1)	KikoleR22	514163	9029329	22	Abandoned	2011	Sand	15.76	3.28	80.96
Kikole (1)	KikoleR3	513015	9030601	3	Abandoned	2011	Clay	22.76	2.28	74.96
Kikole (1)	KikoleR37	512126	9028193	37	Abandoned	2011	Sand	11.76	1.28	86.96
Kikole (1)	KikoleR5	512796	9031536	5	Abandoned	2011	Sand	9.76	1.28	88.96
Kisangi (2)	KisangiA3	521187	9039105	0	Active Field	2011	Sand	13.76	1.28	84.96
Kisangi (2)	KisangiA4	519230	9035644	0	Active Field	2011	Sand	13.76	3.28	82.96
Kisangi (2)	KisangiM1	518914	9034781	50	Mature	2011	Sand	7.76	3.28	88.96
Kisangi (2)	KisangiM2	519377	9038094	50	Mature	2012	Sand	11.04	5.28	83.68
Kisangi (2)	KisangiR10	519549	9036456	10	Abandoned	2012	Sand	9.04	3.28	87.68
Kisangi (2)	KisangiR11	519834	9035797	11	Abandoned	2012	Clay	21.04	2.28	76.68
Kisangi (2)	KisangiR14	520586	9039671	14	Abandoned	2011	Sand	11.76	3.28	84.96
Kisangi (2)	KisangiR24	519060	9037188	24	Abandoned	2011	Sand	9.76	1.28	88.96
Kisangi (2)	KisangiR26	519235	9036729	26	Abandoned	2011	Sand	7.76	3.28	88.96
Kisangi (2)	KisangiR27	520329	9038050	27	Abandoned	2011	Sand	9.76	1.28	88.96
Kisangi (2)	KisangiR34	518332	9037837	34	Abandoned	2011	Sand	9.4	2.92	87.68
Kisangi (2)	KisangiR37	518282	9037631	37	Abandoned	2011	Sand	8.48	1.28	90.24
Kisangi (2)	KisangiR38	519575	9038089	38	Abandoned	2011	Sand	12.48	2.28	85.24
Kisangi (2)	KisangiR39	519704	9038171	39	Abandoned	2011	Sand	11.4	2.92	85.68
Kisangi (2)	KisangiR40	519004	9038217	40	Abandoned	2012	Sand	9.04	3.28	87.68
Kisangi (2)	KisangiR5	519907	9035690	5	Abandoned	2012	Clay	27.04	3.28	69.68
Likawage (3)	LikawageA1	500209	8978445	0	Active Field	2012	Clay	20.04	4.28	75.68
Likawage (3)	LikawageA3	499382	8977165	0	Active Field	2012	Clay	31.04	27.28	41.68
Likawage (3)	LikawageM1	496669	8974163	50	Mature	2012	Clay	29.04	3.28	67.68
Likawage (3)	LikawageM2	496137	8973544	50	Mature	2012	Clay	21.04	5.28	73.68
Likawage (3)	LikawageR17	494529	8973943	17	Abandoned	2012	Clay	21.04	5.28	73.68
Likawage (3)	LikawageR2	495943	8974142	2	Abandoned	2012	Clay	21.6	6.56	71.84
Likawage (3)	LikawageR20	497208	8973327	20	Abandoned	2012	Clay	20.6	4.56	74.84
Likawage (3)	LikawageR21	497901	8979216	21	Abandoned	2012	Clay	29.04	5.28	65.68

Likawage (3)	LikawageR3	499644	8977919	3	Abandoned	2012	Clay	25.04	7.28	67.68
Likawage (3)	LikawageR38	497029	8973879	38	Abandoned	2012	Clay	31.04	5.28	63.68
Likawage (3)	LikawageR39	500350	8975157	39	Abandoned	2012	Clay	27.04	5.28	67.68
Likawage (3)	LikawageR4	499925	8978326	4	Abandoned	2012	Clay	25.04	9.28	65.68
Liwiti (4)	LiwitiA3	511326	8988206	0	Active Field	2011	Sand	13.76	1.28	84.96
Liwiti (4)	LiwitiA4	509060	8986095	0	Active Field	2011	Sand	11.76	0.28	87.96
Liwiti (4)	LiwitiM1	508678	8989093	50	Mature	2011	Sand	9.76	1.28	88.96
Liwiti (4)	LiwitiM2	508392	8988769	50	Mature	2011	Sand	11.76	1.28	86.96
Liwiti (4)	LiwitiM3	509896	8988008	50	Mature	2011	Sand	9.76	1.28	88.96
Liwiti (4)	LiwitiM4	509629	8987456	50	Mature	2011	Sand	9.76	1.28	88.96
Liwiti (4)	LiwitiR1	511317	8988341	1	Abandoned	2011	Sand	9.76	3.28	86.96
Liwiti (4)	LiwitiR13	509723	8987062	13	Abandoned	2011	Sand	9.76	1.28	88.96
Liwiti (4)	LiwitiR14	509741	8987218	14	Abandoned	2011	Sand	11.76	1.28	86.96
Liwiti (4)	LiwitiR20	509500	8986751	20	Abandoned	2011	Sand	7.76	1.28	90.96
Liwiti (4)	LiwitiR5	510855	8988020	5	Abandoned	2011	Sand	17.4	2.92	79.68
Liwiti (4)	LiwitiR8	510993	8988127	8	Abandoned	2011	Sand	9.76	1.28	88.96
Mchakama (5)	MchakamaA0	529792	8993256	0	Active Field	2011	Sand	10.84	6.2	82.96
Mchakama (5)	MchakamaA5	529984	8993271	0	Active Field	2011	Clay	26.84	10.2	62.96
Mchakama (5)	MchakamaM1	530492	8995749	50	Mature	2011	Sand	12.84	8.2	78.96
Mchakama (5)	MchakamaM2	532659	8996327	50	Mature	2011	Sand	10.84	8.2	80.96
Mchakama (5)	MchakamaR13	530793	8993283	13	Abandoned	2011	Sand	8.84	4.2	86.96
Mchakama (5)	MchakamaR2	530980	8993378	2	Abandoned	2011	Sand	10.84	4.2	84.96
Mchakama (5)	MchakamaR7	530950	8993291	7	Abandoned	2011	Sand	8.84	4.2	86.96
Migeregere (6)	MigeregereM1	524866	9025765	50	Mature	2012	Clay	21.6	2.56	75.84
Migeregere (6)	MigeregereM2	525696	9026889	50	Mature	2012	Clay	20.6	3.56	75.84
Migeregere (6)	MigeregereR15	526209	9025218	15	Abandoned	2012	Clay	21.6	3.56	74.84
Migeregere (6)	MigeregereR16	525123	9025335	16	Abandoned	2012	Clay	20.6	2.56	76.84
Migeregere (6)	MigeregereR25	525046	9027058	25	Abandoned	2012	Sand	18.6	2.56	78.84
Migeregere (6)	MigeregereR27	526276	9026765	27	Abandoned	2012	Clay	TEXTURE ESTIMATED BY HAND		
Migeregere (6)	MigeregereR5	524566	9024680	5	Abandoned	2012	Clay	23.6	10.56	65.84
Migeregere (6)	MigeregereR7	524355	9025523	7	Abandoned	2012	Clay	23.6	8.56	67.84

Table S2 – Geographic (Euclidean) distance between plot-pairs (metres; mean ± SD)

Village area	Average distances between pairs of mature woodland plots	Average distances between re-growing plots and nearby mature woodlands	Average distance between pairs of re-growing plots			
			All	0 - 10	11 - 20	21 - 40
Kikole (1)	1513 (726)	1376 (663)	1816 (852)	960	1121	2332
Kisangi (2)	3345	3119 (2201)	1690 (881.5)	845	3945	1134 (485)
Likawage (3)	817	2975 (559)	3991 (1939)	3853	2748	4568
Liwiti (4)	1343 (644)	1745 (800)	1236 (784)	375 (194)	355 (186)	n/a
Mchakama (5)	2243	2066 (933)	153 (58)	93	n.c	n/a
Migeregere (6)	1398	1718 (1042)	1657 (593)	868	1092	1264

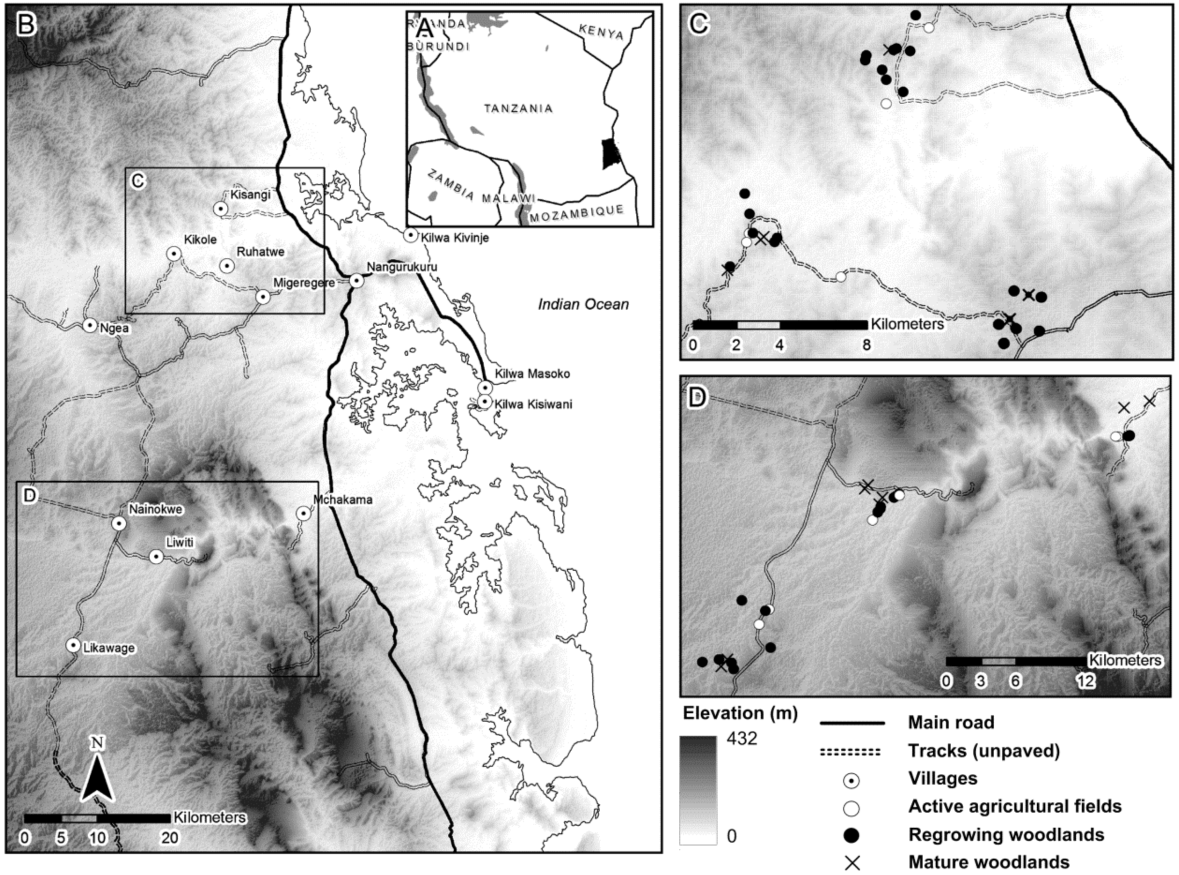

Figure S1. (A) Location of our study region (Kilwa District) in Tanzania and (B-D) the distribution of plots within each of the village areas where sampling was undertaken. Dark patches show areas of high eleveation. Plot co-ordinates are provided in Table S1

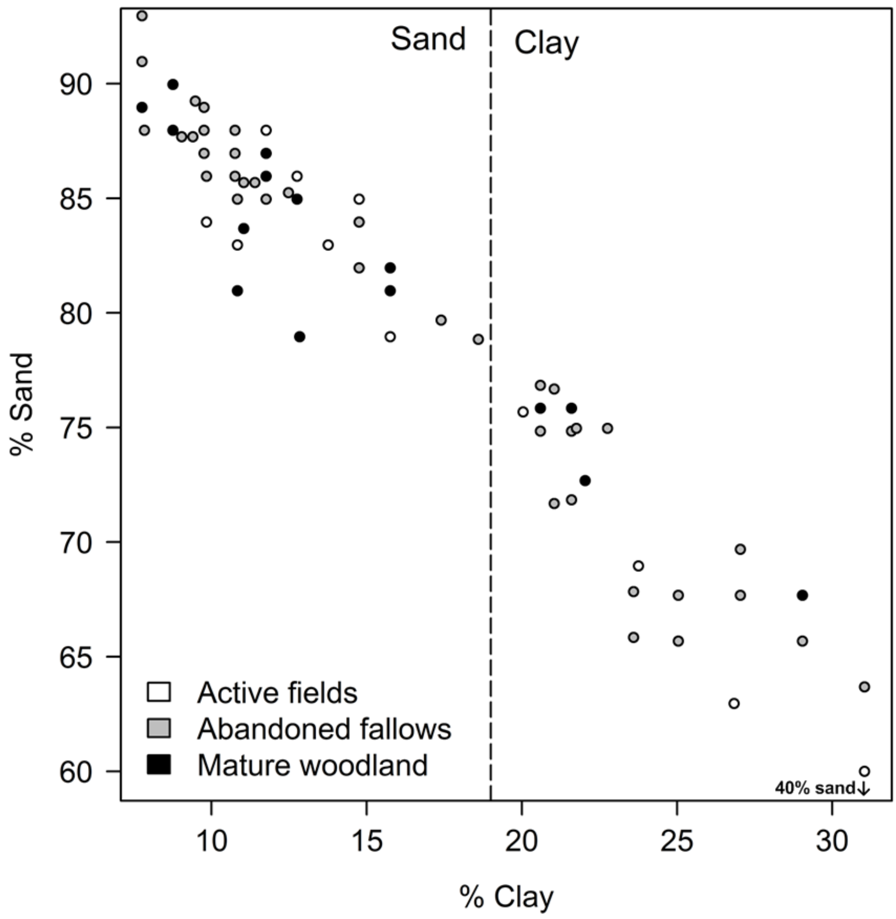

Figure S2. There was considerable variation in soil texture across our sample plots, ranging from 91% sand and 8% clay on our most coarse textured sites, to 63% sand and 31% clay. Plots were separated 18% clay content threshold (FAO, 2006). The mean (±SD) clay content in plots classified as sandy was 11.5 (2.7) %, and 24.0 (3.5) % on the sandy clay (loam) soils. Clay contents were non-normally distributed within both groups, with plots clustering at around 8 – 10% for sandy soils and 20 – 22% sandy clay loams, but with a tail of increasingly fine textured soils in both groups. On one plot classified as being on a clay soil, texture was estimated by hand instead. On the sandy soils, some plots had similar soil textures meaning there is some overlap in the points

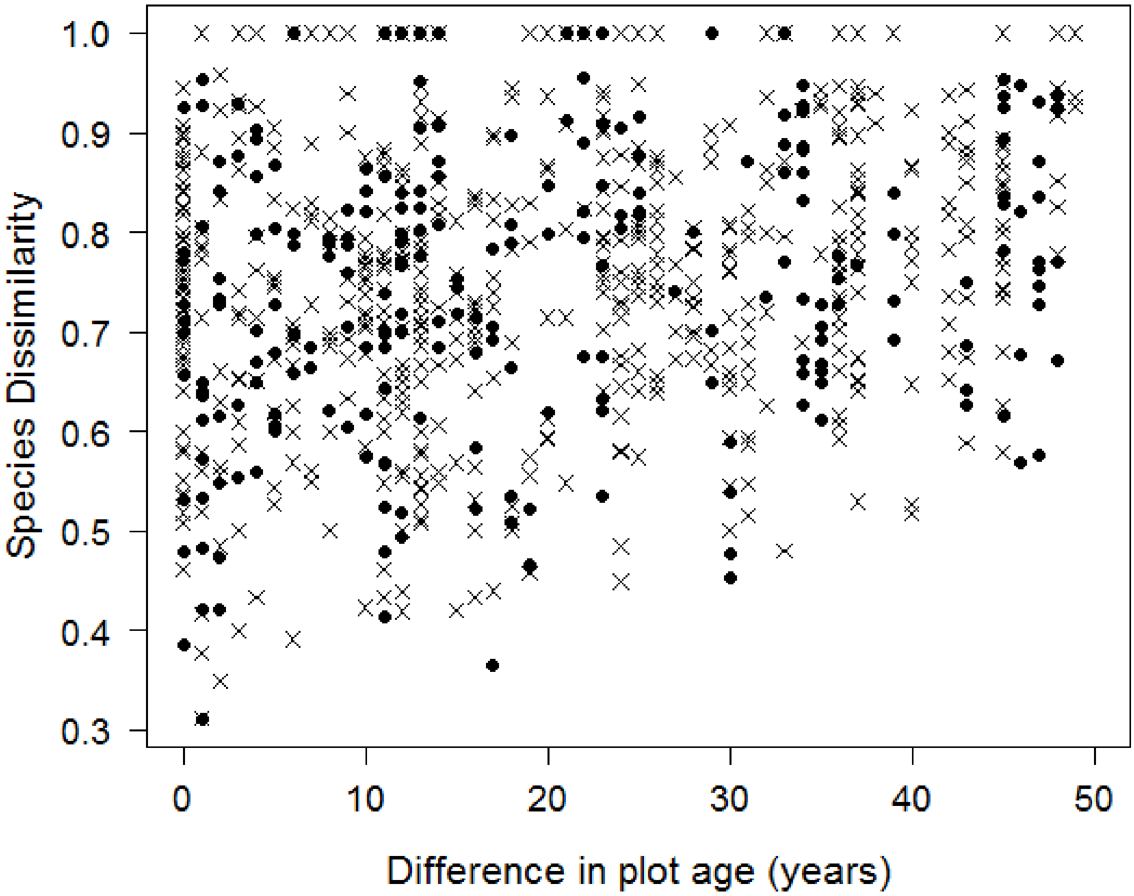

Figure S3. Plot-pair differences in species composition based on the Bray-Curtis Dissimiliarity Index with differences in site age.

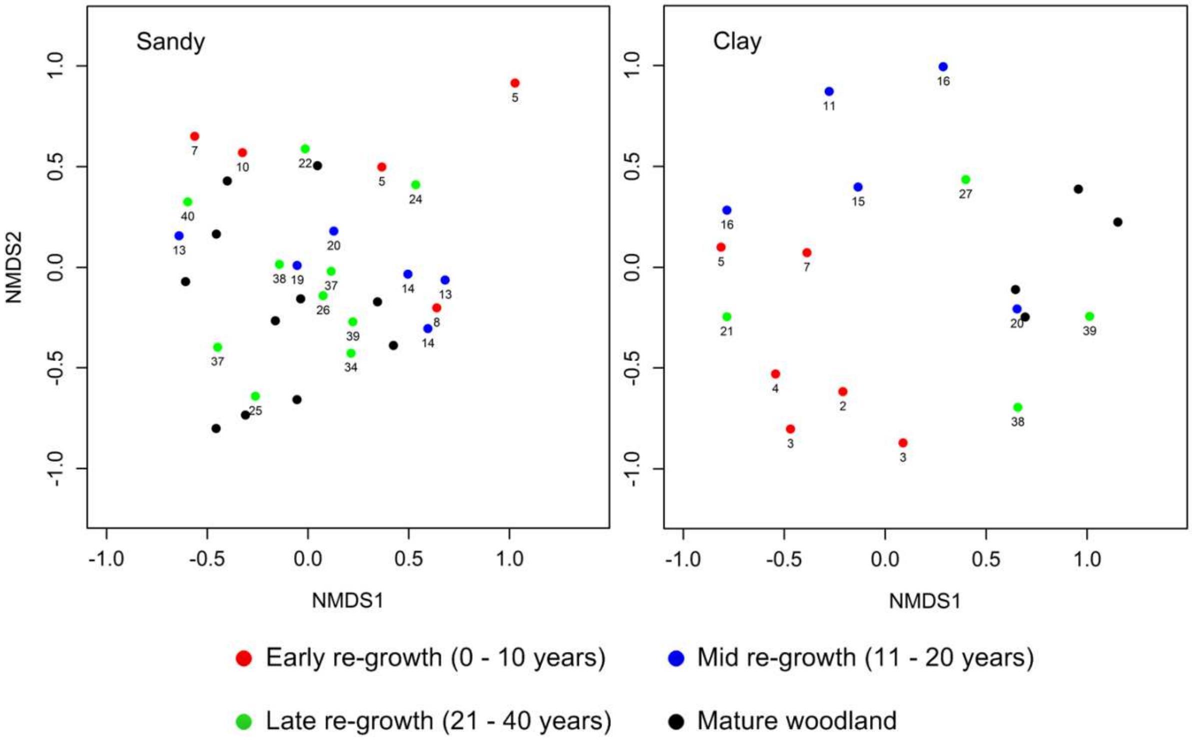

Figure S4. NMDS plot based on Bray-Curtis distances among the plots sampled on both soil classes. Plots are grouped in to age classes purely to aid interpretation. Plot age is located directly below each point. Composition is shown to differ among similarly aged plots, however some general trends can be observed with the younger sites generally mapping our differently from the older plots, with regrowth plots beginning to converge with those in mature woodlands as recovery proceeds. On sandy soils, two early re-growth plots (LiwitiR1 & MchakamaR2) that contained only remnant trees are not shown.

Table S3. (a –b) The unshaded cells show the mean (± SD) species similarity (1 – Bray Curtis) between plot-pairs from groups of plots of similar age. The shaded cells summarise the results of the PerMANOVA test for significant pairwise differences in composition between age classes, with an additional comparison (c) which shows compositional differences between equivalent age classes on different soil. PerMANOVA is a permutation-based version of the multivariate analysis of variance and uses randomisations or permutations of the data to produce the p-value for the hypothesis test. Shown are the p-values derived from the pairwise comparisons between age classes. Significant differences in species composition between groups of plots are highlighted in bold. *P* = * <0.05, ** <0.01, ***<0.001. The results suggest that convergence in composition occurs after 20 – 40 years on both soil types, despite few plots in these age classes, particularly on clay soils, exhibiting a strong similarity to mature woodlands, thus highlighting the different conclusions which can be drawn when using an ANOVA type approach to study successional trends.

(a) Sandy plots

Age class	0 - 10 (7)	11 – 20 (6)	21 – 30 (5)	31 - 40 (6)	Mature (11)
0 - 10	----	0.15 (0.15)	0.10 (0.10)	0.11 (0.11)	0.11 (0.10)
11 - 20	0.14	----	0.21 (0.11)	0.27 (0.10)	0.22 (0.09)
21 - 30	0.14	0.19	----	0.24 (0.10)	0.20 (0.08)
31 - 40	**0.001****	**0.02***	0.21	----	0.27 (0.09)
Mature	**0.003****	**0.03***	0.35	0.33	----

(b) Clay plots

Age class	0 – 10 (7)	11 – 20 (6)	21 – 40 (4)	Mature (4)
0 - 10	----	0.14 (0.07)	0.17 (0.10)	0.11 (0.06)
11 - 20	**0.02***	----	0.16 (0.12)	0.17 (0.13)
21 - 40	0.12	0.36	----	0.24 (0.13)
Mature	**0.004****	**0.04***	0.44	-----

(c) Sandy vs. Clay

<0.001***
0.002**
0.001**
0.001**

Table S4. Goodness of fit statistics for each of the statistcal models fit to each dataset. Model selection was based on ANOVA tests where models were nested (linear vs. quadratic), or the minimisation of the Akaike Information Critetion (AICc), corrected for small sample sizes, and the residual standard error (RSE) when comparing models fit using linear ('lm' function in R) and non-linear ('nls') methods. R-sqaured values are provided where it is an acceptable goodness of fit measure. Model forms followed by the letters 'n.s' are those which had insignificant parameter estimates and so were excluded from consideration

Ecosystem component	**Soil type**	**Remant trees**	**Fitting method (R command)**	**Model form**	***n***	**df**	**ANOVA (*F*, *p-value*)**	**AICc**	**Residual sum of squares (**10⁴*)**	**RSE**	**r²**
Aboveground carbon stocks											
	Sand	Yes	OLS (lm)	**Linear**	**31**	**29**	0.19; *0.74*	**238**	**n/a**	**10.4**	**0.5**
		Yes	OLS (lm)	Polynomial	31	28		240.53	n/a	10.57	0.48
		Yes	Robust (rlm)	Linear	31	29	…	239.2	n/a	10.31	…
	Clay	Yes	OLS (lm)	**Linear**	**21**	**19**	2.64; *0.12*	**151.99**	**n/a**	**7.95**	**0.66**
		Yes	OLS (lm)	Polynomial	21	18		152.2	n/a	7.63	0.68
		Yes	Robust (rlm)	Linear	21	15	…	152.019	n/a	5.836	…
	Sand	No	OLS (lm)	**Linear**	**31**	**29**	…	**185.19**	**n/a**	**4.44**	**0.84**
	Clay	No	OLS (lm)	**Linear**	**21**	**19**	…	**129.95**	**n/a**	**4.706**	**0.74**
Soil carbon stocks											
-> *Topsoil (0 - 5cm)*	Sand	…	OLS (lm)	Linear (n.s)	31	29	…	144.64	n/a	2.308	0
	Clay	…	OLS (lm)	Linear (n.s)	20	18	…	109.48	n/a	3.266	0.13
		…	NLR (nls)	Negative exponential (n.s)	20	18	…	109.73	n/a	3.286	…
-> *Subsoil (5 - 30cm)*	Sand	…	OLS (lm)	Linear (n.s)	31	29	…	224.85	n/a	8.415	0
	Clay	…	OLS (lm)	Linear (n.s)	20	18	…	190.39	n/a	24.68	0.01
		…	NLR (nls)	Negative exponential (n.s)	20	18	…	190.39	n/a	24.68	…
Tree species diversity											
-> *Species richness*	Sand	Yes	OLS (lm)	Polynomial	24	21	…	170.12	*28.52*	7.25	0.46
		Yes	NLR (nls)	Saturation	24	22	…	168.57	*29.34*	7.29	…
		Yes	NLR (nls)	**Unimodal (ricker)**	**24**	**22**	…	**166.79**	***28.32***	**7.02**	…

	Clay	Yes	OLS (lm)	Polynomial	17	14	…	137.68	*12.74*	10.96	0.30
		Yes	NLR (nls)	Saturation	17	15	…	138.93	*13.16*	12.17	…
		Yes	NLR (nls)	**Unimodal (ricker)**	**17**	**15**	…	**134.49**	***13.66***	**10.68**	…
-> Fisher's alpha	Sand	Yes	OLS (lm)	Polynomial	24	21	…	128.69	*3.53*	3.06	0.16
		Yes	NLR (nls)	**Saturation**	**24**	**22**	…	**125.53**	***3.53***	**2.97**	…
		Yes	NLR (nls)	Unimodal (ricker)	24	22	…	128.06	*3.09*	3.13	…
	Clay	Yes	OLS (lm)	Polynomial	17	14	…	107.39	*1.66*	4.50	0.23
		Yes	NLR (nls)	Saturation	17	15	…	108.20	*1.69*	4.93	…
		Yes	NLR (nls)	**Unimodal (ricker)**	**17**	**15**	…	**104.66**	***1.74***	**4.44**	…
Tree species composition											
	Sand	Yes	OLS (lm)	Linear	62	60	1.01; *0.316*	-109.02	108.37	0.096	0.29
		Yes	OLS (lm)	Polynomial	62	59		-107.79	108.37	0.096	0.29
		Yes	NLR (nls)	**Logarithmic**	**62**	**60**	…	**-111.48**	**110.39**	**0.095**	**…**
	Clay	Yes	OLS (lm)	**Linear**	**26**	**24**	0.49; *0.486*	**-22.71**	**24.485**	**0.142**	**0.16**
		Yes	OLS (lm)	Polynomial	26	23		-20.46	24.485	0.143	0.15
		Yes	NLR (nls)	Logarithmic (n.s)	26	24	…	-21.26	22.81	0.146	…
	Sand	No	OLS (lm)	Linear	56	54	0.13; *0.71*	-94.73	100.87	0.099	0.21
		No	OLS (lm)	Polynomial	56	53		-92.54	100.87	0.1	0.19
		No	NLR (nls)	**Logarithmic**	**56**	**54**	…	**-95.29**	101.26	**0.093**	…
	Clay	No	OLS (lm)	**Linear**	**26**	**24**	0.24; *0.62*	**-23.35**	**23.33**	**0.14**	**0.19**
		No	OLS (lm)	Polynomial	26	23		-20.81	23.33	0.142	0.16
		No	NLR (nls)	Logarithmic (n.s)	26	24	…	-22.29	21.76	0.143	…

Chapter 5

Spatial variation and magnitude of total soil respiration across a post-disturbance chronosequence

Iain M. McNicol and Mathew Williams

This chapter is intended for submission to ***Biotropica***

Author contributions

The idea for this study was conceived by IMM and MW. IMM designed the experiment and sampling strategy with inputs from MW. IMM conducted the fieldwork, analysed the data and wrote the chapter with advice from MW.

5.1 Introduction

Soil respiration (Rs) forms a major component of the global carbon cycle transferring an estimated 98 ± 12 Gt carbon (C) to the atmosphere annually, an order of magnitude greater than emissions from fossil fuel burning (Bond-Lamberty & Thomson, 2010). This efflux accounts for a significant proportion of total ecosystem respiration (Giasson *et al.*, 2013) yet this natural loss is often counterbalanced by carbon fixation via photosynthesis resulting in an almost neutral long term carbon balance in many regions (Valentini *et al.*, 2000; Williams *et al.*, 2007; Malhi, 2010). Therefore, even relatively a small proportional change in the strength of the Rs flux could determine whether an area becomes a net sink or source of CO_2 (Valentini et al. 2000; Metcalfe et al. 2007). This sensitivity is of particular importance given that human activities are rapidly transforming the land surface (Hansen *et al.*, 2013) resulting in potentially significant changes to the Rs flux across large areas through alterations to the abiotic environment (i.e. temperature and moisture) and through changes in plant abundance and composition (i.e. substrate quality and quantity) (Chapter 4). Understanding the physical factors regulating soil CO_2 fluxes and how these fluxes respond to environmental change has therefore become central to the understanding of feedback mechanisms between ecosystems and the climate system (Heimann & Reichstein, 2008)

In Africa measurements of soil gas fluxes are particularly sparse (Nouvellon *et al.*, 2008; Mapanda *et al.*, 2010; Merbold *et al.*, 2011), leading to considerable uncertainty in their magnitude and dynamics. Savannas and open woodlands cover approximately half of the African continent (Mayaux *et al.*, 2004) however there is a distinct lack of information regarding the magnitude of soil CO_2 fluxes in these areas, it's spatial variability, drivers, and its potential response to environmental change. Interest in the carbon cycle of African savannas is increasing, stimulated largely by an awareness that these ecosystems are both highly productive (Grace et al. 2006; *sensu* Högberg et al. 2001), and are undergoing amongst the most rapid rates of land use change globally, contributing 20% of global land use CO_2 emissions (Ciais *et al.*, 2011). A major driver of these land use changes is small scale, shifting agriculture, the cyclical nature of which produces complex landscapes with a mosaic of patches in different stages of recovery from clearance (Williams et al. 2008; Hett et al. 2012; Ryan et al. 2012; Chapter 4). These transitional ecosystems now cover large areas, yet despite their increasing prevalence no studies have examined how the resultant changes in forest structure and species composition impact Rs. Such information is crucial to better understand land use impacts on carbon cycling, to help constrain the potential sink strength of re-growing woodlands (Chapter 4), and to improve models of soil processes.

The release of CO_2 from the soil is the combined result of heterotrophic respiration through the decomposition of plant detritus and root exudates by soil organisms, and autotrophic respiration by live roots and their associated mycorrhizae. Across large spatial and temporal gradients, soil temperature and soil moisture are the main physical factors driving Rs (Fang & Moncrieff, 2001; Davidson & Janssens, 2006). At smaller spatial scales (1 – 10 m), respiration is partly decoupled from climatic variables, with biogeochemical factors such as nutrient supply (Teklay *et al.*, 2006; Lovelock *et al.*, 2014), fine root mass (Metcalfe et al. 2007), plant production (Högberg *et al.*, 2001) and the quantity and quality of the available substrate (Merbold et al. 2011; Saiz et al. 2006) all shown to exhibit strong controls on Rs. Since both root and microbial respiration are dependent on below ground allocation from trees and other herbaceous vegetation, it is expected that changes in forest structure and species composition following disturbance (Chapter 4) will result in significant differences in both the magnitude and spatial pattern of Rs both within and between plots of different ages (Saiz et al. 2006; Metcalfe et al. 2011).

Studies from temperate forests have highlighted the potentially variable long term responses to reforestation, with some showing increases in respiration with stand age related to increased litter inputs (Litton *et al.*, 2003; Wiseman & Seiler, 2004), others a peak in respiration in younger stands, decreasing over time due to a reduction in fine root biomass and stand productivity (Saiz et al. 2006), while others have observed no net change (Klopatek 2002; Wang et al. 2010). Comparable studies from African savannas are rare, although Merbold et al. (2010) detected no difference in respiration rates between a single logged area, and comparatively undisturbed woodlands in Zambia, with soil carbon content highlighted as the main factor driving within-plot heterogeneity of Rs. The generality of these results is therefore unclear, and uncertainty still exists over the potential role of plant drivers and nutrient concentrations in regulating gas fluxes. For example, in savannas, the presence of both trees and grasses means that differences in fine root biomass could have a major impact in determining spatial patterns of Rs, but so far this has not been explicitly explored. The role of nutrient availability is also of particular interest given the generally nutrient poor status of the highly weathered and old savanna soils (Frost, 1996; Okin *et al.*, 2008) leading us to speculate that respiration processes will be strongly nutrient limited and so will respond strongly to changes in nutrient concentrations.

The objectives of this paper are to further advance our understanding of soil respiration and its controlling factors, and explore the potential residual effects of disturbance on the magnitude of the respiration flux across a chronosequence of abandoned agricultural land in Kilwa District, SE Tanzania (Chapter 4). Specifically, the questions this study aims to answer are: (Q1) which biophysical factors are most important in driving Rs across plots varying in their time since abandonments? and (Q2) is there a significant difference in the soil respiration rate between plots of different age?

I examine the potential role of multiple driving variables, including (i) micro-climatic factors, i.e. soil temperature and soil moisture, (ii) edaphic drivers, i.e. soil organic carbon, total soil nitrogen (N) and extractable phosphorous (P), and (iii) plant drivers, i.e. fine root biomass and distance to nearest tree. It was hypothesised that (H1) spatial variability in the magnitude of Rs both within and between plots of different ages will be positively correlated with biotic factors including soil carbon and nitrogen contents and the availability of phosphorous. I also anticipate (H2) that respiration rates will be higher in the most recently abandoned sites, decreasing as succession proceeds.

The rationale for expecting these patterns is manifold; firstly (H1), due to the almost complete ground cover of shrubs and/or grasses across the plots, spatial variations in soil temperature are likely to be small. In the wet season, trees will typically concentrate water uptake and increase interception around trunks – however in the dry season little water uptake is occurring leading to a more even distribution of any available soil moisture. The patchiness in vegetation cover and composition within regrowing stands will mean that biological factors such as the quantity of available substrate and the concentration of potentially limiting nutrients such as nitrogen and phosphorus will result in hotspots of respiration where their concentrations are higher, such as close to trees or shrubs. It is anticipated that the most recently abandoned sites will contain the greatest soil carbon contents due to the incorporation of burned residues such as charcoal during cultivation (Chapter 4; Figure 4.6). This will result in a greater number of negatively charged organic surfaces to which nutrients such as phosphorous can bind increasing its availability to microbes (Kimetu *et al.*, 2008). It is also expected that the younger stands will be dominated by faster growing plant species that are re-sprouting from root stocks which will allocate a significant amount of assimilated C to growth to allow them to reach a size that limits the probability of top-kill in a returning fire (Hoffmann *et al.*, 2012). The dominance of non-woody species in the younger plots - compared to the large woodier species that occur later in succession - will also result in more leaf litter production that is richer in nitrogen and has lower lignin contents (i.e. low C:N ratio) and so is more available to microbes thus enhancing mineralisation and increasing respiration (Wardle *et al.*, 2004; Metcalfe *et al.*, 2011).

Due to logistical constraints sampling was only undertaken in the dry season (see also Mapanda et al. 2010 for a similar aseasonal study). Autotrophic respiration is likely to be lower at this time of year as the majority, but not all of the trees drop their leaves leading to a reduction in gross primary production and the supply of sugars to the roots for respiration (Högberg et al. 2001; Ryan et al. 2013) . Therefore our hypotheses strongly reflect the more likely contribution of heterotrophs to the observed fluxes (Hanson *et al.*, 2000). However, the combination of trees and grasses in savannas means that fully interpreting the drivers of Rs is highly complex. Despite these uncertainties, given the paucity of available flux data from African savannas and woodlands the results generated in this study represent an important step in better understanding the carbon cycle of these poorly studied ecosystems and the residual effects that land use change has on this process.

5.2 Methods

5.2.1 Study sites

The study was conducted across the Migeregere village area within Kilwa District, south-eastern Tanzania (-8°49' S, 39°14' E) in August 2012. The sites were located ~125 m above sea level and 24 km inland from the coast, with all stands located within a 3 km radius of the village centre. Mean annual precipitation is 890mm (derived from Tropical Rainfall Measurement Mission (TRMM) 2B31 data, 1998 – 2009; Huffman et al. 2007), the majority of which falls during the wet season between November/December and May with a subsequent 5 - 6 month dry season within which the monthly precipitation is on average 14mm (TRMM monthly product, 3B43, 1998 - 2012). Precipitation during the month of sampling was 4mm, none of which fell during the period of field sampling. The average air temperature in the dry season is around 25°C (WorldClim database variable 9; data 1950 – 2000; Hijmans et al. 2005). The dominant vegetation type is miombo woodland, which is characterised by species in the endemic genera *Brachystegia* and *Julbernardia* with 'Migeregere' being the local name for *Brachystegia bussei*, which is commonly found in the local area.

The effect of stand age on Rs was studied across a chronosequence of abandoned agricultural land composed of 6-, 15-, 25-year old stands, and mature woodlands which were used for reference purposes (Figure 5.1). The sample sites comprise a subset of the plots used in Chapter 4 and so detailed methods for site selection are outlined in that chapter, however in short, we ensured that all sites were (i) located on soils with a similar soil texture (18 – 22% Clay, 65 – 79% Sand), (ii) were cultivated using the traditional 'slash-and-burn' method, and (iii) would support miombo woodland (i.e. not coastal forest, or open acacia savanna). The plots have not been actively managed post abandonment, although evidence of minor disturbances by fire and logging was observed at all sites through the presence of charred tree stems and occasional stumps. Two sites were sampled in each of the four age classes, with the exception of the 25-year age class as the second replicate site was burnt the day prior to gas sampling. Evidence of both elevated and reduced CO_2 fluxes directly following fire has been detected in African savannas (Andersson *et al.*, 2004; Castaldi *et al.*, 2010) therefore the site was excluded from the study.

Figure 5.1 – Photographs of four of the sites sampled along the post-disturbance chronosequence. The vegetation characteristics of each of the sample site are shown in Table 5.1.

5.2.2 Sampling strategy

Within each forest stand, a 30 x 30 m plot was set up within which Rs measurements were taken at thirty-three points using a cyclical sampling strategy aligned on an irregularly spaced grid, each separated by 1m, 2m, 4m and 8m separation distances (Figure 5.2). The strategy was designed to capture the expected large spatial variability in measured variables within each site and to allow geo-statistical analyses to be conducted by maximising the number of possible pairwise distances between samples (Burrows *et al.*, 2002). Surrounding the respiration plot, a 50 x 50 m plot was established to measure forest structure and composition and allow for its effects on Rs to be examined. All live, rooted trees with a diameter at breast height (DBH; 1.3m) ≥ 5cm were measured along with the species and precise location (x,y co-ordinates) within the plot. The number of saplings (1 – 5cm DBH) and seedlings (<1cm DBH) were recorded along two 50m x 1m perpendicular strips running across the central axis of the plot. The total number of saplings and seedlings recorded were divided by the area covered ($100m^2$) in order to estimate the density of each per m^2.

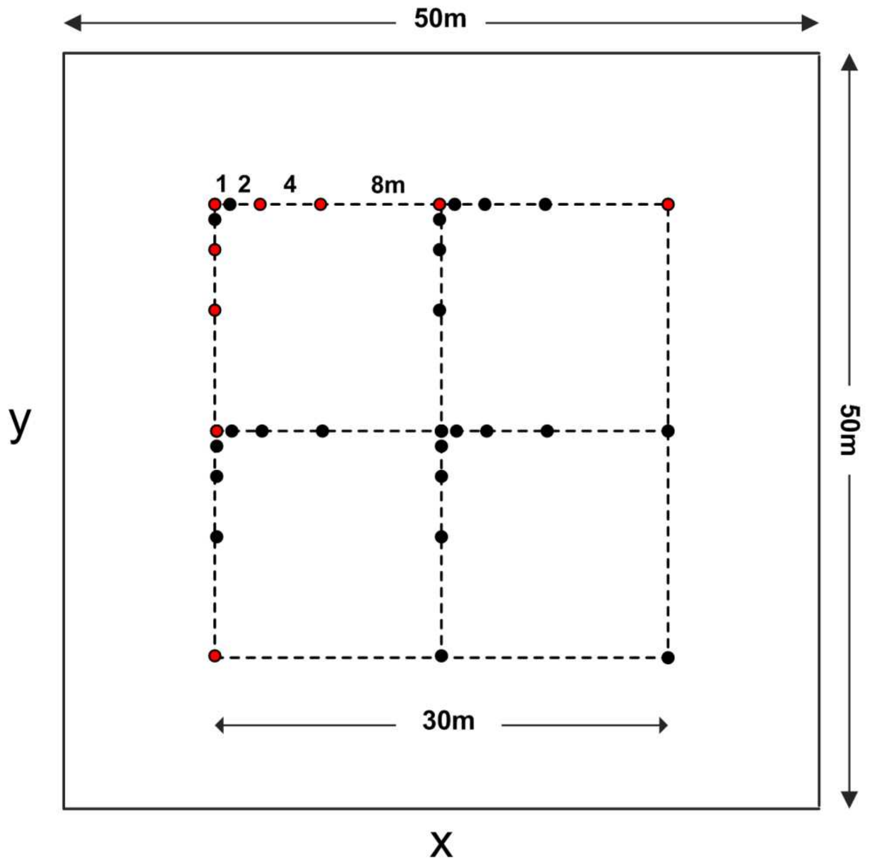

Figure 5.2 – Soil respiration measurements were taken along with soil temperature and moisture at each of the 33 marker points (**red** + **black**). Soil measurements, including organic C, total N, ext. P, bulk density and fine root biomass, were made only at the **red** markers (*n* = 9).

5.2.3 Soil respiration measurements

Total soil respiration was measured at each site over a 5 day sampling period during August 2012, around the peak of the dry season. Measurements were made using a portable infra-red gas analyser attached to a soil respiration chamber with an internal diameter of 10cm and headspace volume of 1143cm^3 (EGM-4 and SRC-1: PP-Systems, Hitchin, UK). The chamber was inserted 1.5cm into the soil, creating a seal with the soil surface, which based on visual inspection caused minimal damage to fine roots. Surface litter was cleared prior to sampling. Similarly, if the measurement location was directly above the base of a grass sward the chamber was moved slightly to the side although not too far to avoid jeopardising the cyclical sampling strategy. The Rs flux was measured as the linear CO_2 increase (4s readings) over a 2 minute chamber closure period. Measurements were made between 10am and 4pm to avoid diurnal effects. Since temperature changes throughout the day, I measured one site from each age class in the morning and one in the afternoon, and on separate days. At all measurement points, soil temperature (digital thermometer) and soil moisture (m^3 m^{-3}) (handheld SM200 probe; Delta-T devices, Burwell, Cambridge, UK) were measured at 5cm depth at three points adjacent to the chamber and then averaged.

5.2.4 Soil, fine root and forest structural measurements

Following gas sampling, at nine of the thirty-three markers, also aligned in a cyclical pattern across the plot, soil samples were extracted from the top 5cm and top 30cm soil layers and analysed for organic carbon content and particle size (soil texture). Only the data from the top 5cm layer is used for further analysis as most decomposition, and thus CO_2 production, will occur near the soil surface where organic inputs are likely to be concentrated. The 30cm sample was taken as part of the larger chronosequence study in Chapter 4. The bulk density (g cm^{-3}) of each core was determined by dividing the dry weight of the soil by the core volume. Samples were thoroughly homogenised by hand and sieved at 2mm to remove stones. Each sample was passed through a riffle splitter with one half prepared and analysed for organic carbon (%) content (Walkley – Black Wet Combustion Method) at Sokoine University of Agriculture (SUA) in Tanzania. The other half of the sample from each core was then pooled on a per plot basis and assessed for particle size.

Directly beneath the chamber, an additional core of the top 10cm was collected in order to quantify fine root biomass (<2mm) and nutrient content. Samples were immediately stored in a cool bag and transported back to base where they were processed within 6 days of collection. Roots were extracted using a rapid sampling technique devised by Metcalfe et al. (2007). For each soil sample, coarse roots were extracted by sieving the soil at 2mm before fine roots were picked out of the sieved soil at 1 min, 3 min, 5 min and 7 min intervals for a total time of 16 minutes. The initial plan was to predict the total mass of fine roots within each core by plotting saturation curves of cumulative root extraction over time. However after the 16-min extraction period nearly all of the roots had been picked from each core, therefore the collected mass is used instead for further analysis. Roots were washed clean of soil particles and dried before being weighed. The remaining soil was analysed at SUA for total nitrogen content (%; Kjeldahl method) and extractable phosphorous (mg/kg; Olsen method). In order to assess the potential effects of stand structure on respiration rates, the total dbh of trees within a 4m (dbh-4), 6m (dbh-6) and 8m (dbh-8) radius of the measurement location was calculated and used as a proxy for substrate availability (Søe & Buchmann, 2005). The analysis was performed using the 'spatstat' package (Baddeley & Turner, 2005) in the statistical package R, version 2.14.0 (R Core Team, 2014). Stem biomass was determined using a regionally derived allometric equation (stem only) by Ryan et al. (2011). The key vegetation and soil characteristics for each of the seven study sites are presented in Table 5.1 and Table 5.2 respectively.

5.2.5 Data analysis

All data were initially checked for normality using Shapiro-Wilk tests after which all non-normal data which had a positive skew were log-transformed while outliers which contributed to non-normality were also removed in order to satisfy the assumptions of parametric statistical tests. Welch's t-tests were used to compare soil characteristics between pairs of similarly aged sites, while analysis of variance (ANOVA) and Tukey HSD tests was used to test for significant differences in the same variables between age classes (Q2; H2). Multiple linear regression was used to investigate which of the explanatory variables were significantly correlated with soil respiration across the landscape (Q1; H1). An analysis of how the relative influence of these driving variables changes across the chronosequence was not possible due both the small number of measurement points in each age class (max. $n = 18$) and the large number of potential explanatory variables available ($n = 11$), which would result in over-parameterised models (Crawley, 2007). Therefore for simplicity, all plots are grouped together to assess which predictors are the dominant controls across the landscape (n points = 63). Statistical models were refined and validated using procedures outlined by Zuur et al. (2010). First, I checked for potential spatial autocorrelation in the dataset to validate the use of non-spatial regression models. Failure to account for auto-correlation (i.e. pseudo-replication) can potentially lead to false interpretations on the significance of any effects by artificially lowering the error estimate on the model, thus increasing the likelihood of committing a Type 1 error (see Chapter 2).

Table 5.1 – Geostatistical analysis used to examine spatial structure in the respiration data. Analyses were performed separately for all measurement points and for the points for which we have the full set of predictor variables. A positive Moran's *I* statistic coupled with a *P*-value <0.05 indicates significant positive autocorrelation in soil respiration within the plot. When autocorrelation was detected, semi-variograms were used to quantify the spatial structure of the data (see Chapter 3 for information on how these are constructed) and were fitted using a spherical model. The semi-variogram range highlights the scale at which respiration is auto-correlated.

Plot	All measurement points (*n* = 33)			Soil points (*n* = 9)		
	Moran's *I*	P-value	Semi-variogram range (m)	Moran's *I*	P-value	Semi-variogram range (m)
5-yr	0.12	0.002**	9.4	-0.14	0.90	n/a
7-yr	0.01	0.25	n/a	-0.11	0.83	n/a
15-yr	-0.003	0.48	n/a	-0.15	0.96	n/a
16-yr	0.1	0.005**	3.18	-0.14	0.84	n/a
25-yr	0.19	<0.001***	7.1	-0.15	0.66	n/a
Mature 1	-0.01	0.65	n/a	-0.06	0.36	n/a
Mature 2	-0.01	0.76	n/a	-0.22	0.09	n/a

The soil respiration data were tested for spatial autocorrelation using Moran's *I* statistic ('ape' package; Paradis *et al.*, 2014), the results of which indicated significant auto-correlation in 3 of the plots when analysing all measurements points (black markers in Figure 5.2; Table 5.1), however this pattern disappeared after repeating the analysis only on the measurement points where the full set of biophysical variables (red markers) is available. Consequently, each point can be treated as an independent sample in the following analyses, negating the need for more complicated spatial regression models. An exploratory analysis of the individual relationships also indicated that linear terms outperformed more complex quadratic models. To test for co-linearity among explanatory variables, Spearman's rank correlation tests were calculated to identify variables that were highly correlated with one another based on threshold correlation coefficient of $r > 0.6$, and a Variance Inflation Factor of <3 in the final model (Table 5.2). When significant correlations were detected, the variable with the strongest linear relationship with the response variable was retained as a predictor in the analysis. The most parsimonious models containing significant variables ($P < 0.05$ for inclusion) were derived using backward-forward stepwise selection based on minimising Akaike's Information Criterion (AICc), corrected for the small sample size. The relative importance of each predictor variable was calculated by dividing the sums of squares for each variable and the residuals by the total sums of squares of the model. Model residuals were checked for normality and homogeneity of variance.

Table 5.2 – Spearman's rank correlations between the 11 explanatory variables. Significant correlations (r > 0.6) are highlighted grey and in bold. Non-significant but potentially ecologically meaningful correlations (r > 0.5) are in bold.

	Soil temp.	Soil moisture	Bulk density	% Carbon	% Nitrogen	P	C:N ratio	Fine roots	dbh_4	dbh_6
Soil moisture	-0.1									
Bulk density	0.36	-0.21								
% Carbon	0	0.42	-0.09							
% Nitrogen	-0.19	**0.55**	-0.44	0.28						
Phosphorus	-0.21	-0.38	-0.06	0.03	-0.06					
C:N ratio	0.3	-0.32	0.38	0.33	**-0.75**	0.04				
Fine roots	0.14	-0.31	0.15	-0.1	-0.24	0.04	0.16			
dbh_4	0	-0.31	0.17	-0.23	-0.29	-0.02	0.22	0.41		
dbh_6	0.02	-0.4	0.23	-0.14	-0.28	0	0.26	**0.53**	**0.82**	
dbh_8	0.04	-0.43	0.29	-0.23	-0.43	-0.08	0.34	**0.5**	**0.78**	**0.89**

Table 5.3. Summary of the key vegetation characteristics and dominant species at each of the seven study sites.

Successional stage	Age	Stem density (trees ha^{-1})	Mean DBH (cm)	Stem basal area (m^2 ha^{-1})	Stem biomass (t C ha^{-1})	Sapling density (stems/m^2)	Seeding density (seedlings/m^2)	Dominant species (by abundance)
Early	5	468	6.2	2.0	1.91	1.39	1.55	*Ficus spp., Blighia unijugata, Markhamia spp., Dombeya shupangae, Tabernamontana spp.*
Early	7	384	10.9	6.3	10.23	1.97	1.51	*Bauhinia petersiana, Annona senegalensis, Ficus spp., Acacia camplyacantha, Tabernamontana spp.*
Mid	15	872	9.2	9.7	13.81	0.09	0.41	*Annona senegalensis, Acacia camplyacantha, Croton dichogamus, Acacia reficiens, Hugonia castanefolia*
Mid	16	1384	9.1	13.8	17.96	0.21	0.53	*Millettia stuhlmanii, Markhamia obtusifolia, Pseudolachnostylis maprouneifolia, Hymeocardia ulmoides, Croton dichogamus*
Late	25	1100	10.8	18.1	32.18	0.17	1.14	*Diplorhynchus condylocarpon, Ochna holstii, Pseudolachnostylis maprouneifolia, Margaritaria discoides, Pteleopsis myrtifolia*
Mature (1)	n/a	908	11.4	15.5	24.49	0.15	0.22	*Julbernardia globiflora, Diplorhynchus condylocarpon, Crosspteryx febifuga, Pseudolachnostylis maprouneifolia, Pterocarpus angolensis*
Mature (2)	n/a	820	12.1	17.7	33.01	0.39	1.25	*Diplorhynchus condylocarpon, Margaritaria discoides, Pseudolachnostylis maprouneifolia, Julbernardia globiflora, Unknown (Mserekete)*

Table 5.4. Soil characteristics at each of the seven study sites (Mean (±SD)). Superscripts indicate significant differences in the mean value of each variable between plots of similar age, based on two-sample t-tests. Comparisons between age classes are shown graphically in Figure 3 and Figure 4. To facilitate comparisons with other published studies, I also report respiration rates in µmol m^2 s^{-1}

Stage	Age	Rs rate (g CO$_2$ m^2 hr^{-1})	Rs rate (µmol m^2 s^{-1})	CV (%)	Soil temp. (°C)	Soil moisture (m^3/m^3)	Bulk density (g/cm^{-3})	Soil C content (%)	Soil N content (%)	C:N ratio	Ext. P (mg/kg)	Fine root biomass (g/ core)
Early	5	0.29 (0.09)	1.83 (0.60)	32.7	26.1 (2.0) ^{a}	0.06 (0.02)	1.37 (0.14)	1.75 (0.42)	0.16 (0.04)	11.4 (4.8)	1.56 (1.1)	2.82 (0.42)
Early	7	0.30 (0.11)	1.91 (0.72)	37.9	28.4 (1.2) ^{b}	0.07 (0.03)	1.46 (0.14)	2.19 (0.83)	0.18 (0.02)	12.0 (4.1)	1.47 (0.6)	3.02 (0.83)
Mid	15	0.13 (0.05)^{a}	0.82 (0.32)	39.8	29.8 (3.0) ^{a}	0.02 (0.01)	1.60 (0.24)	1.24 (0.45)	0.08 (0.01) ^{a}	16.6 (8.7) ^{a}	2.77 (2.2)	3.07 (0.46)
Mid	16	0.19 (0.06)^{b}	1.22 (0.39)	31.9	26.6 (0.7) ^{b}	0.02 (0.005)	1.49 (0.18)	1.39 (0.44)	0.05 (0.01) ^{b}	30.2 (12.0) ^{b}	3.43 (1.7)	2.80 (0.44)
Late	25	0.22 (0.07)	1.45 (0.46)	31.7	29.6 (1.4)	0.02 (0.01)	1.53 (0.26)	1.62 (0.42)	0.07 (0.02)	25.9 (11.4)	1.96 (0.1)	3.95 (0.42)
Mature 1	n/a	0.19 (0.04) ^{a}	1.23 (0.24)	19.9	31.6 (1.8) ^{a}	0.02 (0.007) ^{a}	1.83 (0.33) ^{a}	1.46 (0.31)	0.05 (0.01) ^{a}	30.6 (12.2) ^{a}	0.96 (0.6) ^{a}	4.0 (0.31)
Mature 2	n/a	0.25 (0.04) ^{b}	1.62 (0.30)	19.0	27.6 (1.8) ^{b}	0.01 (0.005) ^{b}	1.52 (0.16) ^{b}	1.27 (0.63)	0.08 (0.03) ^{a}	16.4 (9.1) ^{b}	2.63 (1.6) ^{b}	3.89 (0.63)

5.3 Results

5.3.1 Changes in vegetation structure and composition over time

Increasing time since abandonment was generally associated with greater stem densities, greater mean tree size, and a compositional shift from typically small stature species (i.e. *Tabernaemontana spp.* & *Bauhinia petersiana*) and fruit trees such as Fig (*Ficus spp.*) towards larger stature woody species typical of mature miombo woodlands such as *J. globiflora* and the common understory dominant *D. condylocarpon* (Chapter 4). The younger abandonments also contained a relatively dense layer of saplings and shrubs (Table 5.1) resulting in there being less grass biomass in these areas compared to the older abandonments (personal observations). Two large remnant trees were present in the Early-7 plot resulting in a higher mean DBH and plot level AGC stock than the Early-5 plot.

5.3.2 Spatial variability and drivers of soil respiration

The measured soil respiration rates ranged from 0.05 – 0.49 g CO_2 m^2 hr^{-1} with an overall landscape mean of 0.22 ± 0.08 (1 SD) g CO_2 m^2 hr^{-1}. Stand structural variables and plant drivers including fine root biomass, as well as soil C content did not appear to have a significant effect on respiration rates (Table 5.5). Instead respiration was most closely related with total nitrogen (%) which alone explained between 27 – 38% of the between point variability (Table 5.5; Figure 5.3). Contrary to general trends (Fang & Moncrieff, 2001), Rs exhibited a significant negative relationship with soil temperature, both within mature woodland plots, and across all plots combined (Table 5.5; Figure 5.3a), and was not correlated with any other environmental variables (i.e. soil moisture) which may have explained this idiosyncratic pattern (Table 5.2).

Table 5.5 - Bivariate relationships between the predictor variables and soil respiration fitted using OLS regression models. Data are calculated using only the 9 points from each plot where there is data on the full set of biophysical variables. Relationships within successional stages are shown however I did not perform a separate multiple regression analysis for each stage due to a lack of data points. Data are illustrated in Figure 5.3. Significance level: #0.1, *0.05, **0.01, ***0.001

	OLS regression model slope (adj. r^2)				
Variable	All plots	Early succession (6-yr)	Mid Succession (15-yr)	Late Succession (25-yr)	Mature Woodlands
Forest structure					
dbh-4	-0.0001 (0.0)	-0.0005 (0.00)	0.0004 (0.0)	-0.0006 (0.0)	0.004 (0.0)
dbh-6	-0.0004 (0.0)	-0.06 (0.00)	0.0003 (0.04)	-0.0005 (0.0)	0.0003 (0.16) #
dbh-8	-0.0007 (0.0)	-0.05 (0.00)	0.0001 (0.01)	-0.0002 (0.0)	0.004 (0.0)
Soil					
Soil temperature	**-0.009 (0.10)****	-0.01 (0.13) #	-0.0004 (0.0)	0.005 (0.0)	**-0.01 (0.73)*****
Soil moisture	0.56 (0.04) #	-0.4 (0.0)	-1.02 (0.01)	0.19 (0.0)	**-4.03 (0.42)*****
Bulk density	**-0.09 (0.09)****	-0.16 (0.05)	-0.07 (0.06)	-0.14 (0.22)	-0.07 (0.14) #
Soil C content	0.02 (0.01)	0.002 (0.0)	-0.0008 (0.0)	-0.005 (0.0)	-0.03 (0.02)
Soil N content	**0.72 (0.29)*****	**1.35 (0.29)***	0.26 (0.0)	**2.30 (0.38)***	**0.97 (0.28)***
Soil C:N ratio	**-0.002 (0.12)****	-0.006 (0.07)	-0.0002 (0.0)	-0.002 (0.12)	-0.001 (0.17) #
Extractable P	-0.005 (0.0)	-0.0008 (0.0)	0.002 (0.0)	-0.007 (0.0)	**0.02 (0.47)****
Fine root biomass	0.02 (0.0)	0.02 (0.0)	-0.0006 (0.0)	0.04 (0.02)	0.02 (0.0)

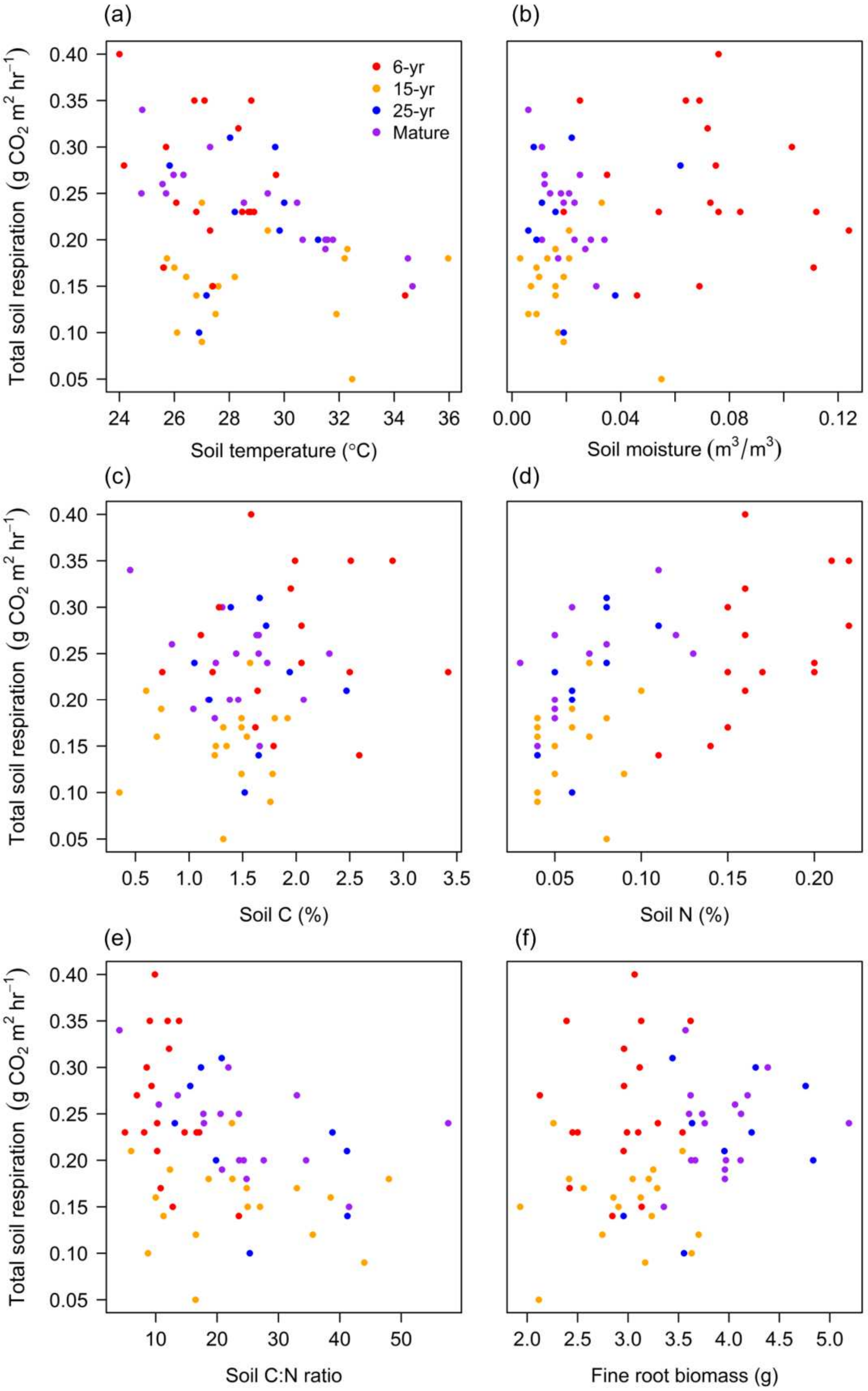

Figure 5.3 - Relationships between key soil chemical and physical properties and soil respiration; (a) soil temperature (°C) at 5cm, (b) soil moisture (m^3/m^3) at 6cm, (c) soil organic carbon content (%), (d) total nitrogen (%), (e) soil C:N ratio, and (f) the mass of fine roots underlying the respiration chamber. Regression statistics are presented in Table 5.5.

Multiple regression models were fitted to the respiration data pooled across all plots to identify the main driving variables of Rs across the landscape, and to examine whether the trends noted in Table 5.5 and Figure 5.3 were consistent after statistically controlling for the effects of other variables. Soil C:N ratio was omitted from the analysis due its negative correlation with nitrogen content, while dbh-6 was used as the structural parameter (Table 5.2). The minimum adequate model explained 42.3% of the variability in respiration ($F = 21.95$, $P < 0.001$) with %N retained as the most significant explanatory variable (standardised coefficient, ß = 0.67) explaining 30% of the total explained variance. Fine root biomass was revealed to be significant predictor of Rs when the other variables were held constant and explained the remainder of the variability (12%) in the data (ß = 0.67). This was despite finding no clear bivariate relationship between fine root biomass and Rs (Table 5.5) highlighting complex interactions among different biophysical factors in regulating patterns in soil respiration. These interactions are best visualised using regression tree models (De'ath & Fabricius, 2000), which repeatedly partition the independent variables into dichotomous groups along the values of an explanatory variable that explains the majority of the variance in the response to the left and right of the split (Figure 5.4). It is clear that %N is the most important predictor (Figure 5.4); however at higher levels of %N, the amount of Extractable Phosphorous appears to have a subtle but positive effect on respiration. At lower levels of N, fine root biomass appears as an important predictor with areas with higher root densities (>3.4g) exhibiting greater fluxes. The lowest respiration rates were generally associated with low N concentrations, low fine root biomass and low extractable P.

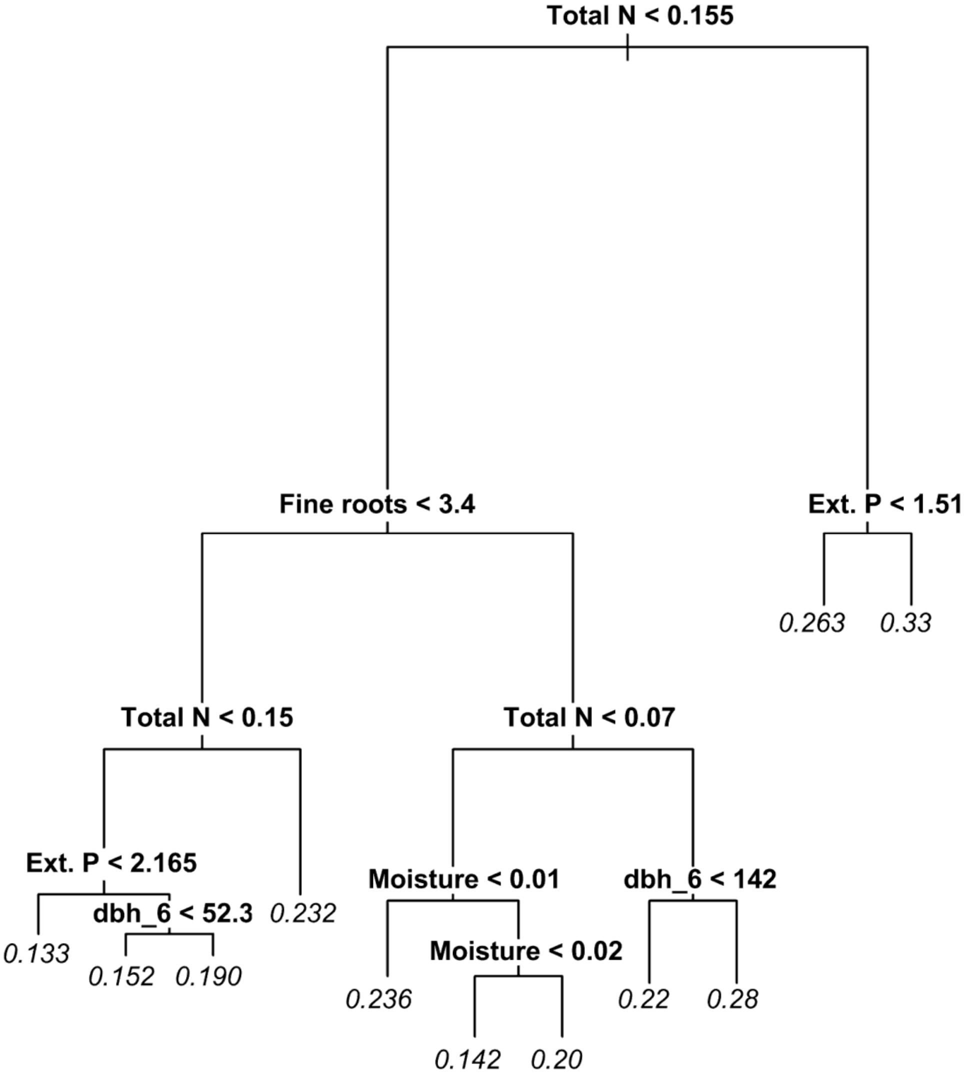

Figure 5.4. Regression tree model used to visualise more complex interactions among the explanatory variables, constructed using the 'tree' package in R. Values in italics indicate the average rate of soil respiration for a given combination of predictors and their values.

5.3.3 Changes in soil respiration over time

Soil respiration rates were significantly higher in the youngest abandonments (0.3 g CO_2 m^2 hr^{-1}) than each of the older stands (ANOVA + Tukey HSD; $P < 0.01$). Respiration rates were lowest in the mid-successional sites (0.15 g CO_2 m^2 hr^{-1}), before increasing in the older abandonments and mature woodlands (~0.22 g CO_2 m^2 hr^{-1}) (Table 4; Figure 5.5 top-left panel). Interestingly there was no significant difference in Rs between the Mature-2 plot and Early-5 stand indicating that younger abandonments do not consistently have greater fluxes and that this pattern may be an artefact of the plots chosen. There were also significant differences in respiration between pairs of similarly aged stands in the mid-successional stage and the mature woodlands (T-tests; Table 5.4). Spatial variability in Rs within plots was greater in the secondary woodlands (CV = 32 – 39%) with 'hotspots' of high and low respiration present (Table 5.4), whereas respiration in mature stands which was comparatively homogeneous (CV = 19%).

The strong positive effect of %N, and by extension the C:N ratio of the soil, on soil respiration may explain why fluxes were higher in the younger abandonments, with both variables shown to be significantly greater and lower respectively in these areas (Figure 5.5). The younger sites were also characterised by greater soil moisture, and generally greater soil carbon contents, however they also exhibited the lowest soil temperatures and lower fine root densities and C:N ratios than both the older abandonment and mature plots (Figure 5.5). Indeed, given the general similarity in soil conditions between the older abandonments and mature woodlands, it is predicted that lower fine root biomass in the mid-successional sites may explain the significantly lower efflux rate in these areas.

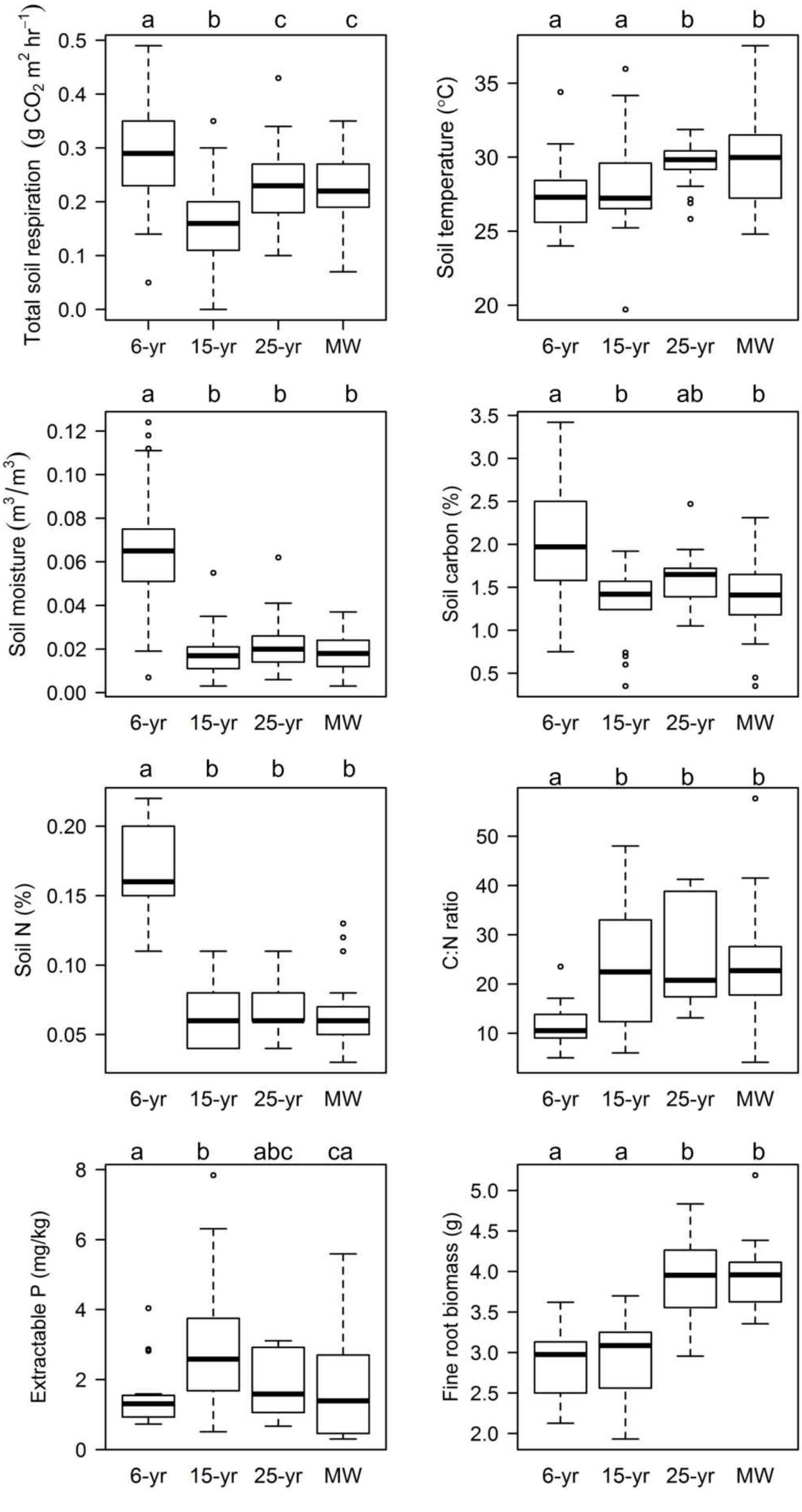

Figure 5.5 – Comparison of soil respiration and soil characteristics in each age class. Significant differences ($P < 0.05$) were tested with one-way ANOVA followed by Tukey's HSD tests, the results of which are indicated by different superscript characters above each boxplot

5.4 Discussion and conclusions

The objectives of this study were to (1) quantify spatial variation in soil respiration and its controlling factors, and (2) outline the effects of disturbance on the respiration flux across a chronosequence of plots previously cleared for agriculture. This is one of only a few studies to have measured soil respiration in semi-natural, unmanaged miombo woodlands. Further novelty is provided through its exploration of whether there is a residual effect of shifting cultivation – the main driver of land use change in the region - on soil respiration, the largest natural efflux of CO_2 to the atmosphere in terrestrial ecosystems.

5.4.1 Spatial patterns and drivers of soil respiration across the landscape

Respiration was found to be spatially variable at the scale of just a few metres as evidenced by the lack of any widespread positive auto-correlation between points (Table 5.1), thus indicating that small scale controls on Rs are operating in these systems and that intensive sampling would be required to capture potentially important variability in Rs within stands (Saiz et al. 2006). Respiration was more spatially variable within the secondary woodlands (CV = 30%) with hotspots of high respiration detected, which was principally linked to higher nutrient availability (Figures 5.4 and 5.5). In contrast, respiration in mature Miombo woodlands was more spatially homogenous perhaps reflecting the denser vegetation and greater canopy cover in these plots (Table 5.3).

It was hypothesised that this spatial variability in respiration would strongly reflect similar variations in soil carbon content, as well as the relative availability of phosphorous and nitrogen due to their important role in controlling the quantity and quality of soil organic matter and thus microbial activity. The results largely supported our hypothesis with soil N content shown to correlate most strongly with soil respiration, however neither soil carbon content or phosphorus could successfully predict respiration either within successional stages, or when including all plots together (Table 5.5; Figure 5.3).

Patterns in CO_2 fluxes were also not readily attributable to changes in soil moisture (Figure 5.5), but were negatively related to soil temperature both within mature plots, and across the landscape as a whole (Table 5). Contrary to expectations, spatial variability in Rs both within and across plots was not related to differences in soil organic carbon (SOC) content, strongly suggesting that respiration is not limited by the quantity of the available substrate. This result contrasts those of Merbold et al (2010) who suggested SOC to be a key driving variable, despite the low explanatory power of the correlation (~6%). The SOC stocks measured in this study are similar in magnitude to those of Merbold; therefore the absence of any relationship here could be due to the chemical composition of the organic carbon within different samples. The bulk soil carbon pool is not homogeneous, but in fact represents a mix of substrates with different turnover rates, stabilities and decay behaviours (Schlesinger and Bernhardt, 2013). The degree to which respiration is affected by organic carbon content depends on how much is in a labile form that is readily decomposable by soil microbes (Luan *et al.*, 2011; Whitaker *et al.*, 2014) and how much is in a chemically recalcitrant or mineral associated form, such as charcoal, which is more stable and harder to break down (Cross & Grace, 2010; Mujuru *et al.*, 2013). The potential range of organic compounds in the soil could have masked any effect and it is hypothesised that a clearer pattern will emerge when only labile carbon is considered. The lack of any relationship may also be due to the way sampling was performed; instead of taking intact cores and freezing soil samples to stop the microbial decomposition, samples were extracted, immediately bagged and then air dried for at least 6 days. The potential for a continued mineralisation of the labile soil C pool post sampling may have affected the results.

Instead, the results of the multiple regression analysis indicated that total nitrogen and fine root biomass were the strongest predictors of soil respiration, together explaining 42% of the observed spatial variation in total soil CO2 efflux. When all other variables were equal, fine root density was revealed as a key predictor explaining 12% of the variability despite finding no clear relationship when compared in isolation (Figure 5.3). This result suggests an autotrophic contribution to the measured fluxes. However at the time of sampling most of the grasses from which the fine roots are likely to come from were found to be dead, therefore areas with greater root mass may in fact be hotspots of heterotrophic respiration with microbes decomposing the dead material.

Soil nitrogen content was found to have the strongest relationship with Rs explaining 30% of the total variability across the plots. Soil %N was also positively correlated with respiration within similarly aged stands, with the exception of the mid-successional sites which had comparatively smaller range of total N concentrations. It is important to note that total N is not necessarily indicative of available N (NH_4 and $NO3^-$) as some of this could be bound to clay minerals or held in organic structures that are recalcitrant (Templer *et al.*, 2012), however it is considered a reasonable assumption that increases in total N will linearly scale with microbial N-availability. Soil %N was not correlated with SOC content suggesting the latter is not a critical factor in maintaining greater nutrient concentrations which is surprising given the most N in the system is derived from organic matter (Vitousek & Howarth, 1991; Table 5.2). The increase in respiration with increasing nitrogen content indicates the nitrogen limitation of respiration processes and microbial growth in these soils, but also alludes to the presence of significant stores of labile carbon, backing up the earlier suggestion that these soils are not limited by the quantity of the available substrate (Hartley et al. 2010).

Instead the results suggest that the quality of the available substrate may partially determine the strength of the flux, as suggested by the negative correlation between Rs and the soil C:N ratio (Figure 5.3). The total amount of nitrogen is closely associated with the quality of organic matter present within the soils (i.e. Sjögersten & Wookey 2005) with substrates with a higher C:N ratio generally decomposing slower than more N rich material (low C:N ratio). Soil microbial biomass typically has a lower C:N ratio than the surrounding litter - around 8:1 - and so there is a greater demand for nitrogen to support metabolic processes than exists in most soils (Schlesinger & Bernhardt, 2013). This means microbes must absorb additional inorganic nitrogen from the soil to meet their growth demands. Therefore unless nitrogen is available from outside the system, or incorporated via root exudates from N-fixing trees, microbes are unable to decompose the litter as effectively leading to less CO_2 production.

5.4.2 Changes in soil respiration across the post-disturbance chronosequence

The second question I set out to answer was whether the previously noted changes in forest structure and species composition that are known to occur across the chronosequence (Chapter 4) would result in significant differences in the magnitude of Rs flux between different aged stands. It was hypothesised that respiration would be higher in the most recently abandoned plots due to a combination of greater soil carbon and nutrient contents in these soils and the prevalence of faster growing species and non-woody plants and shrubs resulting in more and better quality litter being delivered to the soil (Metcalfe *et al.*, 2011). The results validate this hypothesis with respiration rates found to be greater in the youngest abandonments (~0.3 g CO_2 m^2 hr^{-1}), decreasing to a low point in the mid-successional sites (~0.15 g CO_2 m^2 hr^{-1}), before increasing and levelling out in the older abandonments and mature woodlands (~0.22 g CO_2 m^2 hr^{-1}). The finding of elevated carbon fluxes well into the early stages secondary succession highlights a previously unquantified legacy effect of land use change in miombo woodlands. More plots will need to be sampled in order to test to whether this is a pervasive pattern given the similar flux rates between the Early-5 and Mature-2 sites (Table 5.4).

Soil moisture was found to be significantly higher in the younger stands (Figure 5.5) but was not retained as a clearly significant factor in the multiple regression analysis, although it's P-value was close to the threshold for inclusion (P = 0.09) meaning it cannot be fully discounted. Instead, the positive correlation between soil N% and Rs noted in the previous section is used to explain why the most recently abandoned plots had significantly higher Rs rates, with the younger sites containing significantly greater soil N contents and lower soil C:N ratios than the older sites (Figure 5.5; Table 5.4).

The reasons for this difference are unclear although potential reasons may include; (1) the cultivation or inter-cropping of nitrogen fixing crops such as cowpeas in these fields, (2) the greater litter quality (low litter C:N) of the dominant species as originally hypothesised, or (3) the decomposition of residues and roots from trees removed during cultivation. There is no information on which crops were cultivated in each area so this cannot be excluded as a possibility, however field observations and farmer interviews from other areas suggests that maize and sesame are the main crops, neither of which are known to have N-fixing capabilities. The second explanation is that a difference in the initial litter quality is the key factor resulting in the observed differences in respiration between different aged stands. Data on the leaf quality of the dominant species found in the plots (Table 4.3) is limited and generally restricted to the dominant keystone species (Mtambanengwe & Kirchmann, 1995). The senesced leaves from two of these species – *J. globiflora* and *D. condylocarpon* – have lower leaf N content than mature leaves, attributable to the reabsorption of nutrients before leaf-fall to compensate for the nutrient poor soils. The resultant litter of *J. globiflora* therefore has a high C:N ratio (30-45:1) while the woody material is also known to contain relatively high concentrations of substances such as lignins and polyphenols (Mtambanengwe & Kirchmann 1995; Frost, 1996). Thus, the potential accumulation of relatively recalcitrant organic matter low in nitrogen suggests that initial litter quality may be a highly limiting factor to respiration in the older sites. Of the species that were dominant in the early successional sites only *Acacia camplyacantha* and the sub-dominant *Albizia amara* are known to be N-fixing and therefore are found to have higher leaf N contents than those noted above (Frost, 1996 and references therein). The potential input of a more N rich litter is congruent with general soil characteristic data displayed in Figure 5.5 and Table 5.4, where the soil C:N ratio can be taken as proxy for the substrate quality and N-availability (see also Wang et al. 2010). In the early stages of abandonment the C:N ratio was on average 12:1 and thus considerably lower than the typical 20:1 threshold required to instigate N mineralisation from organic matter (assuming 40% growth efficiency and a microbial C:N ratio of 8:1; Manzoni *et al.*, 2012). As decomposition proceeds the soil C:N ratio decreases as the carbon is respired and instead of being immobilised for further use, inorganic nitrogen is released into the soil from the decomposing organic matter leading to a greater concentration of soil N, as is found here. This nitrogen can then be used to break down more recalcitrant substrates. In contrast, soils in the older abandonment and mature woodlands had much lower nitrogen contents and variable but typically higher soil C:N ratio (> 20:1), again suggesting that nitrogen limitation and low litter quality are the proximal reasons for the lower recorded fluxes in these areas (Table 5.4; Figure 5.5). None of the other dominant species in the younger stands were in the family Fabaceae which tends to contain species with N-fixing abilities. Therefore, it is unclear as to whether the theorised difference in litter/ substrate quality between young and old stands exists in reality and so is in need of further investigation.

In the absence of any difference in substrate quality, an alternative explanation for both the greater fluxes and the increased nitrogen contents in the younger sites could be due to the continued decomposition of dead tree roots left over from prior to cultivation the nitrogen from which is then be used by microbes to break down the organic matter. A potential side effect of the greater nitrogen contents in the soils could be a similarly greater efflux of nitrous oxide (N_2O) as found by Mapanda et al. (2010) in a recently cleared patch of miombo woodland. This is something which warrants further investigation if we are to fully understand disturbance impacts on greenhouse gas fluxes in these systems. This N enriched soil is also predicted to result in greater aboveground productivity as plants take up the available nutrients, thus increasing the supply of photosynthate to the roots which could also be contributing to the observed fluxes (Schlesinger & Bernhardt, 2013). This data also gives extra weight to an assumption in the previous chapter that trees in the early stages of regrowth will grow faster than older ones (Chapter 4, section 4.2.4).

The seasonality of the soil respiration flux is still a source of uncertainty in our conclusion that there exists a legacy effect of disturbance on soil CO_2 fluxes. Further work is required to assess whether these patterns are consistent in the wet season given the predicted large seasonality in the autotrophic flux (Hanson *et al.*, 2000). Sampling was performed only in the dry season due to difficulties in reaching the sample sites in the wet season. As such both the original hypotheses and the subsequent discussion about which factors principally regulating respiration strongly reflected the more likely contribution of the heterotrophic component to total soil respiration due to the assumption that plant photosynthetic rates would be lower in the dry season (Woollen 2012), limiting the supply of sugars to the roots for respiration (Högberg *et al.*, 2001). Increases in tree biomass with stand age combined with the greater fine root biomass in the older plots (Figure 5.5) suggests that during the growing season the magnitude of the autotrophic component will be much higher in these areas than in the younger sites, and may counterbalance the greater dry season fluxes observed here.

Disentangling the relative contribution of heterotrophic and autotrophic respiration is impossible without using root exclusion collars (Saiz *et al.*, 2006b), or isotopic labelling to partition the component fluxes, neither of which were possible here. Future work should therefore focus on quantifying the seasonal pattern of soil respiration in Miombo woodlands, and partitioning the fluxes in order to better understand the key drivers and the effect of disturbance on these fluxes. An investigation into the potential N limitation in the in whether there is a dormant heterotrophic capacity, and possible priming effects on organic material.

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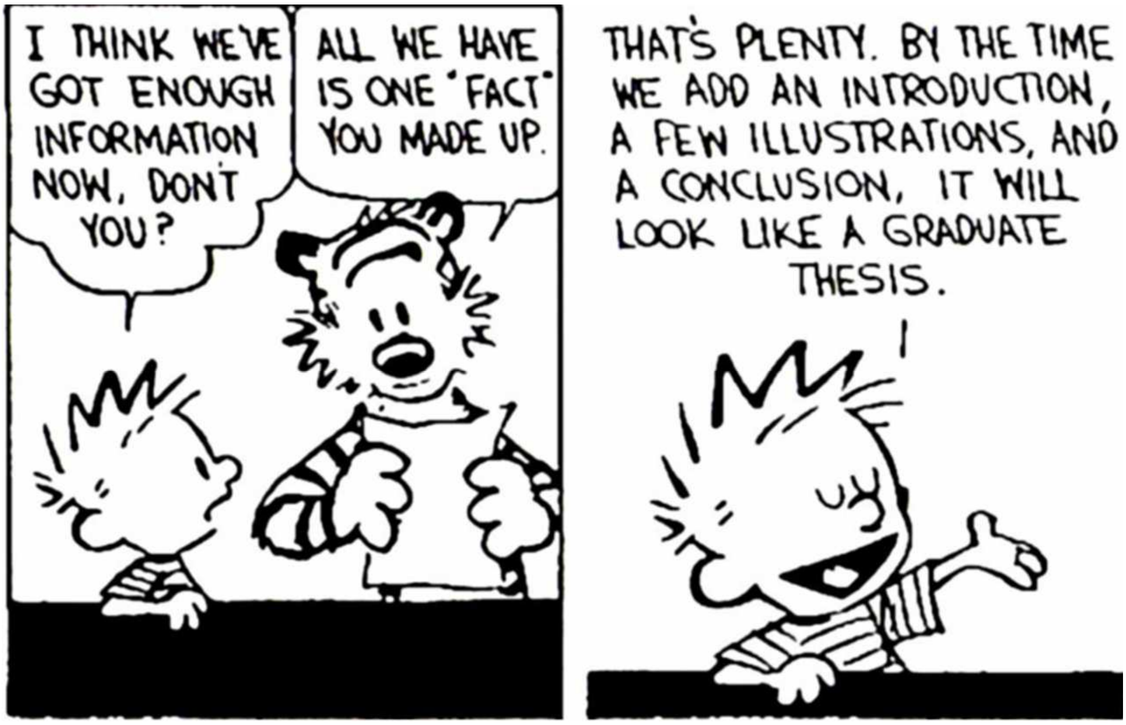
Chapter 6

General discussion and conclusions



6.1 Summary

The aim of this thesis was to improve our knowledge of carbon dynamics and biodiversity patterns in the poorly studied African savannas, woodlands and seasonally dry forests. A common theme throughout this PhD has been to better understand spatial-temporal patterns and processes in these landscapes with each of the questions in the data chapters incorporating at least one of these elements. The specific objectives of this thesis were as follows:

Section 1 – Understanding spatial patterns in woody carbon stocks, tree species diversity and composition

1) To quantify aboveground woody carbon stocks (AGC) across the different vegetation types found across the study region and examine how these patterns were linked to differences in stand structure (stem size distributions) and to tree species diversity
2) To determine the main controls over spatial variations in floristic composition and AGC stocks across the landscape

Section 2 –Quantifying the long-term ecological impacts of shifting cultivation

3) To determine how aboveground woody carbon stocks (AGC), soil carbon, floristic composition and tree species diversity change over four decades of succession following the abandonment of sites previously cleared for shifting cultivation
4) To investigate whether the strength of the soil CO_2 flux also changes during secondary succession, and to assess which biotic and abiotic factors are the most important in controlling it's spatial and temporal variability

In this, the final chapter of the thesis, I summarise the key results from each of the four data chapters which were aimed at achieving the objectives listed above. I go on to discuss some of the wider implications of the results and outline some key areas for further research.

6.2 Key findings from Chapters 2 & 3

The first two chapters were dedicated to understanding spatial patterns and processes in our study area. In Chapter 2 I examined how differences in aboveground woody carbon storage (AGC) were linked to changes in forest structure and tree species (α-) diversity across a recently established network of 25 permanent sample plots in south-east Tanzania. In the same chapter, I went on to assess to what degree tree species composition varied between the plots (β-diversity) and tried to decipher the mechanisms underlying species distributions. Chapter 3 was conducted along similar lines, however this time I examined the spatial distribution and environmental determinants of AGC stocks at the landscape scale. For this, I utilised a new radar-derived map of AGC stocks, calibrated against the data from the local plot network, and compared it against spatial data on climate, soils and topography. I assessed whether AGC stocks were fixed within clear environmental limits, and to what degree these biophysical factors explain the observed patterns. The results and conclusions from Chapters 2 and 3 were:

1) Tree carbon stocks averaged 20.8 ± 14.6 tC ha^{-1} across the network of 1-ha permanent sample plots, ranging from 1.9 tC ha^{-1} in an area of open savanna up to 58.2 tC ha^{-1} in a patch of East African Coastal Forest.

2) Large stems were a significant contributor to plot-level AGC stocks with trees >40cm diameter containing on average 35% of the carbon, yet only 2.5% of the stems measured. Ecosystem carbon stocks are therefore likely to be highly sensitive to losses of these very large trees
3) Tree species diversity was positively correlated with AGC storage, a 'win-win' scenario for forest conservation. A large number of species were also found to be constrained to areas of woodland or forest creating localised patterns of species endemism.
4) The positive relationship between tree diversity and AGC storage suggested the importance of a functionally diverse assemblage of tree species in creating patterns of biomass. An increase in family level diversity was used to suggest that complementary effects may be an important determinant of higher AGC. However, causation cannot be strictly determined based on the available data with selection effects also potentially important (functional 'identity' over 'diversity').
5) Tree species composition was not evenly distributed across the landscape with the lower biomass savannas found to be floristically distinct from the surrounding woodland and forest plots meaning the uniformity hypothesis was rejected. The top 3 highest biomass plots were also marked out as being floristically unique indicating the presence of coastal forests.
6) The observed differences in tree species composition could not be explained by dispersal processes. Instead the results suggest that tree community assembly is more strongly driven by physical factors/niche partitioning, however a combination of both environmental (3%) and structural (16%) determinants explained little of the variability. Fire is known to be a key

component of savanna ecology, the effects of which were partially vectored through differences in stand structure with denser plots assumed to favour more disturbance intolerant species. Environmental controls had a weak influence; however the effect of soils should not be discounted as they were poorly represented in this study, although data is forthcoming and will be incorporated in to the analysis to test for significant effects.

7) Factors related topography, climate and soils also explained very little of the variation in C stocks across the landscape (r^2 = 15 – 20%). Differences in slope angle and topographic position were important in discriminating between low biomass savannas and moderate biomass woodlands, while differences in precipitation were more important in separating woodlands and denser forests. As with the analysis of floristic patterns, a large proportion of the variation in C stocks (~80%) was unexplained. This led to speculation that are C distributions are more strongly determined by disturbances such as fire and herbivory. The results have important implications for a local REDD+ project who are seeking generate C credits through reductions in fire intensity. Environmental factors were again poorly characterised, particularly the effects of soil nutrient status (nitrogen and phosphorus), soil texture and topography. Improvements to the methodology may involve including a higher resolution DEM such as the forthcoming TanDEM-X data (12x12m horizontal, 4m vertical resolution) which will better capture topographic trends.

8) Smaller plots (0.2ha) performed poorly in the calibration of ALOS PALSAR data indicating the need for larger plots.

6.2.1 Implications for stem measurement and monitoring

Measuring and monitoring aboveground woody carbon stocks across sub-Saharan Africa is critical for reducing uncertainties in the global carbon cycle, and for implementing conservation policies such REDD+ that are targeted at stemming rapid rates of forest loss. The collection of species data also needs to be included in any future measurement campaign to allow co-variation between AGC and biodiversity to be explored in the context of forest conservation (Venter *et al.*, 2009). Expanding the current network of permanent forest inventory plots is a necessity, however these are expensive to implement. The inventory process usually involves measuring the diameter at breast height (DBH) of every tree above specified threshold - usually 5 or 10cm – in plots of 1-ha in size. Yet there appears to be a degree of disconnectedness between groups conducting forest inventories across the miombo eco-region, which is evidenced by the wide variety of sampling methodologies used to sample tree carbon stocks (Ribeiro *et al.*, 2008; NAFORMA, 2010; Chidumayo, 2013). To date, no studies have presented a clear view on the most appropriate and efficient strategy (i.e. sample size, plot size, appropriate DBH threshold) for accurately measuring carbon stocks and/or biodiversity in savanna woodlands (i.e. Baraloto et al. 2013). The RAINFOR manual has provided some consistency based on data collected in Amazonia (Phillips *et al.*, 2009), however there is no equivalent methodology for the dry tropics which are very different in terms of their structure and floristic composition. The results here provide some insights into how sampling could be tailored in future to suit the aims of a given project and its financial resources.

For example, in both the woodland and forests (>10 t C ha^{-1} 10% canopy cover), measuring only those stems >10cm DBH would have captured on average

93% of the total AGC in each plot, yet would only have required measuring 40% of the stems. Such an approach would have been considerably quicker, excluding an average of ~600 stems ha^{-1} in denser forests (> 30 tC ha^{-1}) and ~275 stems ha^{-1} in the miombo dominated woodlands. Raising the threshold to 15cm would still have captured 86% of the total AGC stocks in only 20% of the stems. Such an approach would be ideal for conducting rapid inventories of AGC, such as for the calibration of earth observation data.

Measuring for biodiversity and species composition would have very different requirements with 50% of the species sampled here likely to be missed when measuring at 10cm. These species are likely to be amongst the rarest; therefore sampling at a higher DBH threshold will have little value when assessing the biodiversity or conservation value of these areas. Furthermore, the use of smaller plots (i.e. <1-ha), which are ideally suited for rapid sampling are considered to be inappropriate for species measurement as they are more likely to exclude rare species and are sensitive to species clustering (Tuomisto & Ruokolainen, 2003; Baraloto *et al.*, 2013). They are also more likely to either overestimate, or completely miss the presence of rare, large stems which can create significant small scale variations in AGC stocks. In Chapter 3, it was shown that smaller plots are also poorly suited to the calibration of radar data from ALOS PALSAR due to the larger relative geo-location errors, with larger 1-ha plots found to exhibit much stronger relationship (Carreiras *et al.*, 2013; Réjou-Méchain *et al.*, 2014). It is still unclear what the optimal plot size is for the calibration of EO data in terms of balancing field effort and data quality; however subsampling the PSPs could allow for the effect of different plot sizes on the biomass-backscatter relationship to be tested in more detail (Robinson *et al.*, 2013)

Another issue to the future of remote mapping of AGC stocks is the mismatch in spatial scale between many of the current field inventory plots and larger pixels of future sensors such as the European Space Agency's BIOMASS mission which has a resolution of 4-ha (Quegan *et al.*, 2012). This has the potential to introduce considerable errors when scaling plot AGC values to the size of the radar pixel (Réjou-Méchain *et al.*, 2014). The use of higher DBH thresholds would allow for larger areas to be sampled in a more time and cost efficient manner, as was achieved in this study with the 9-ha plots which were typically sampled in 2/3 of the time taken to sample the 1-ha plots. However as previously noted, this would be at the detriment of biodiversity accounting.

The development of a standardised field protocol that appropriately incorporates measurements of both tree species diversity and aboveground carbon stocks, but is also suitable for the calibration earth observation data is needed to make the best use of time and resources, and to facilitate cross-plot comparisons. In view of the preceding discussion, this may involve some form of nested sampling strategy as was used in this study in order to account for the different data requirements. I hope to fully address these issues and trade-offs in a follow up paper using data from this inventory and from a network of identically sampled 1-ha field plots in Mozambique (Ryan *et al.*, 2011).

6.2.2 An empirical test of the biodiversity-ecosystem function relationship

In Chapter 2, I began to examine a widely debated topic in ecology; what is the relationship between tree species diversity and ecosystem function, measured here as AGC storage? This question was motivated by both a theoretical and applied interest in understanding how these ecosystems function, and to see whether the positive relationships observed in other areas of tropical forest existed in our study area (Díaz *et al.*, 2004; Chave, 2008; Thompson *et al.*, 2009; Chisholm *et al.*, 2013). Ecological theory presented a number of explanations for the positive linear relationship found here between tree diversity and AGC storage, including niche complementarity and selection effects (Fridley, 2001; Fargione *et al.*, 2007; Chisholm *et al.*, 2013). It is important to remember the maxim that correlation does not necessarily imply causality, and whilst the relationships observed here may be useful is descriptive sense they fail to explicitly answer the question of whether there is a functional relationship between the two variables. An increase in family richness was used to suggest that niche complementarity is the key process through which diversity, and thus carbon stocks are maximised, based on the assumption that species in different families will have different ecological niches and traits. However based on the available data, we cannot exclude the possibility of selection effects, which are best explained by through the Mass Ratio Hypothesis (Grime, 1998) which posits that in an already dense stand there is a greater chance of there being one, or a few highly productive species present.

Species-based diversity indices were used in this study due to the ease of calculation (i.e. Chisholm et al. 2013), however it is the diversity of functional traits within the community that better explain the mechanisms underlying the relationship between diversity and AGC storage (Conti and Díaz, 2013). The dominant species in our plots were poorly represented in trait databases such as the TRY initiative (http://www.try-db.org). Future research endeavours aimed at answering this question need to focus on collecting trait data for the dominant species, particularly those related to life history strategies, resource acquisition and growth (Conti and Diaz, 2013). There are a number of traits commonly recognised in the literature as being important, and for which data can be easily gathered, including; maximum tree height, wood density, leaf nitrogen content, specific leaf area and leaf phenology (Díaz & Lavorel, 2007; Baker & Phillips, 2009; Siefert *et al.*, 2013; Ruiz-Benito *et al.*, 2014)

Species-specific data on tree height and phenology was partially gleaned from Coates-Palgrave (2002), however information was unavailable for ~45% of the identified species, most of which were in the coastal forests, which were the most carbon dense and species diverse parts of the landscape and so of greatest interest in the context of this study. Wood density data was also partially derived from Zanne et al. (2009) and Williams et al. (2008) yet was only available for 34% of the identified species. The collection of these data is important if we are to empirically test whether high carbon storage and/ or productivity is associated with a greater functional diversity, thus supporting the idea of niche complementarity, or whether the functional identity of species traits is more important, thus supporting the idea of selection effects and the mass-ratio hypothesis. The repeat inventory data can also be incorporated to test whether areas of high carbon storage are also more productive which will provide a more robust test of the biodiversity-ecosystem function relationship (Chisholm *et al.*, 2013).

6.3 Key findings from Chapters 4 & 5

In the second part of the thesis, I examined the rate and extent to which carbon stocks in trees and soils recover after cultivation, and detail how this disturbance and regrowth affect tree species composition and diversity over 40 years of succession in miombo woodlands. Further novelty was provided through the analysis of whether the rate and pattern of recovery differed depending on soil texture, something which previous studies fail to account for (Williams *et al.*, 2008; Kalaba *et al.*, 2013). Measurements of soil respiration were also made across a subset of these plots in order to test whether the observed temporal changes in vegetation structure and species composition following agricultural abandonments chronosequence had any effect on the strength of the soil CO_2 flux. The key results found in Chapters 4 and 5 were:

- Following agricultural abandonment, aboveground woody carbon stocks recover at an average rate of 0.7 tC ha^{-1} yr^{-1} with soil texture and the inclusion/ exclusion of potentially remnant trees having no significant impact on recovery rates. Accumulation rates are consistent with other studies in the region (0.6 – 1.0 tC ha^{-1} yr^{-1}) suggesting this value can be applied over large areas.
- Tree species composition within regrowing plots was found to be similar to that of mature woodlands in groups of plots aged between 20 – 40 years on both soil types. There was, however, large variance in composition among

similarly aged plots, highlighting the range of species that are recruited in to and dominate these regrowing woodlands. It was concluded that local site factors (i.e. local seed sources or number of remnant trees) strongly determine the rate and extent to which these woodlands, and the keystone species which characterise it, recover over time.

- Disturbance did not result in an increase in localised patterns of diversity as predicted by the intermediate disturbance hypothesis, with plots >10 years old containing similar numbers of species to mature woodland. Species endemism within age classes was high, and together, plots in regrowing woodlands supported more species that mature miombo woodland. This was due to secondary woodlands containing a large number of species that were not found in more mature habitats highlighting the importance of these human created ecosystems for biodiversity.
- Bulk soil carbon stocks appeared to be largely unaffected by land use changes. There were no significant differences in SOC between mature woodlands and active fields on either soil type which was used here to represent to effects of deforestation. The recovery phase also resulted in no clear changes in stocks
- In contrast to the results noted above, soil respiration rates were found to vary significantly across the chronosequence with more recently abandoned fields (c. 6 years) exhibiting significantly higher efflux rates than the older abandonments (15 -25 years) and mature woodlands. The 15-yr old sites were also found to exhibit significantly lower respiration rates that the older stands.

- Soil nitrogen (N) content explained the largest proportion of the variation in soil respiration rates across the plots ($r^2 = 0.3$) followed by fine root density ($r^2 = 0.12$). The results indicate that nitrogen may be a limiting nutrient in the system. Soils in the younger stand were found to be more nitrogen rich which was therefore used to explain why CO_2 fluxes were higher in these sites. However the reasons for this apparent increase in N-availability are still unclear

The results highlight that miombo ecosystems are highly resilient to land clearance, recovering many of the key characteristics of mature woodlands in a relatively short period of time (Martin et al. 2013). The results are known to be of direct relevance to a number carbon sequestration projects operating in the region under the umbrella of REDD+ by helping to inform the potential future carbon and biodiversity benefits of restoring disturbed habitats (Campbell *et al.*, 2007). However there are a number of questions that warrant further investigation in order to better understand the effects of shifting cultivation of carbon stocks and biodiversity.

6.3.1 The effect of disturbance on soil carbon stocks and cycling

Despite finding clear and consistent changes in vegetation structure across the chronosequence, there still remains a large degree of uncertainty over how belowground processes are affected by the full cycle of shifting cultivation. In Chapter 4 it was suggested that soils are largely resilient to land use change with soils under active agricultural fields found to contain similar SOC stocks to mature miombo woodlands. This was surprising given that several studies have noted a reduction in SOC stocks following land clearance, which was attributed to the loss of significant litter inputs and increases in microbial respiration as a result of burning and soil disturbance (Andersson *et al.*, 2004; Walker & Desanker, 2004; Williams *et al.*, 2008; Don *et al.*, 2011). A suggested reason for the lack of any observable change was the absence of any mechanisation or tilling during cultivation resulting in minimal disturbance to the SOC pool (Mujuru *et al.*, 2013). However, detecting changes in bulk soil C pools over time is also very challenging due to the high spatial variability and slow rates of changes in stocks (Marin-Spiotta *et al.*, 2009; Bruun *et al.*, 2013). Intensive sampling is often required in order to obtain precise enough stock estimates to detect any differences, which is often impractical and too expensive to implement (Poussart *et al.*, 2004; Berry & Ryan, 2013). The residence of soil organic matter may also outlast the period of cultivation making changes even more difficult to quantify (Marin-Spiotta *et al.*, 2008). This can lead to the potentially erroneous conclusion that the soil C pool has not responded to land use change (Marin-Spiotta et al. 2009; Orihuela-Belmonte et al. 2013). However the carbon stored in soils are not homogenous, but in fact represents a combination of carbon pools that vary in their stability and turnover rates (von Luetzow *et al.*, 2007). The degree to which soil carbon stocks respond to land use change depends on how much of the carbon is in a form that will readily respond to land use and land cover change (labile carbon, i.e. fresh litter or roots), and how much is in a form that will not (stable or recalcitrant carbon, i.e. charcoal and/or carbon protected in soil aggregates) (Cross & Grace, 2010; Mujuru *et al.*, 2013). Separating these different soil pools can be achieved via methods such density fractionation (see Sohi et al. 2010) or hydrogen pyrolysis (i.e. to specifically quantify black/pyrogenic carbon; see Meredith et al. 2012) and was considered in this thesis as a way of examining how carbon was distributed across these different soil fractions across the chronosequence. Quantifying changes in these SOC fractions over time, particularly the more sensitive labile pool, is now widely used as an indicator of human induced change in SOC stocks (Sohi *et al.*, 2010; Bruun *et al.*, 2013). In this study, this could have been used to help answer questions such as why we observed no significant changes in SOC stocks with deforestation, i.e. were losses of more labile carbon compensated by an increase stable pyrogenic carbon due to increased burning leading to no net change (Lehmann *et al.*, 2008)? Also, following agricultural abandonment is there an increase in labile SOC stocks with increases in vegetation cover, particularly after accounting between plot differences in black carbon? Soil export issues prevented me from performing similar analyses along these lines which will likely be required if we to fully understand the effects of shifting cultivation on soils.

Although we were unable to detect clear changes in bulk soil carbon stocks, measurements of soil respiration did reveal the presence of elevated CO_2 fluxes well into the early stages of secondary succession. The results suggested that greater soil nitrogen contents in the younger sites were the main reason for this pattern; however it is unclear why these sites were more nitrogen rich with explanations ranging from the greater litter quality of the dominant species to the continued decomposition of the root structures of tree cleared during cultivation. The collection of leaf quality data (C: N ratio) from the dominant species will help to address the question of whether the changes in soil properties and respiration are linked to changes in initial substrate quality. The seasonality of this flux is also still a major source of uncertainty in our interpretation and is in need of further investigation.

The finding that increases in soil nitrogen content typically resulted in a concomitant increase in soil respiration was used to indicate the nitrogen limitation of microbial growth and decomposition in these soils. The potential for soil respiration to respond to increases in nutrient availability is something which warrants further investigation, particularly in light of a potential shift to more intensive agricultural practices which use synthetic fertiliser (Giller *et al.*, 2009), or via increases in N-deposition. This trend has been found in other African dry-land ecosystems where soil amendments of labile substrates such as glucose and nutrients such ammonium nitrate have been shown to cause increases in Rs above the basal respiration rate (Fontaine *et al.*, 2004; Teklay *et al.*, 2006). Studies that have found evidence of elevated carbon effluxes following these soil amendments have also found evidence for changes in the decomposition rate of existing, or old, organic matter, which is generally referred to as 'priming effects' (Kuzyakov *et al.*, 2000; Heimann & Reichstein, 2008). Priming theory suggests that positive priming effects should be most pronounced in soils characterised by low nutrient availability, especially nitrogen due its limiting effects on microbial growth and decomposition. These nutrient enrichments may also lead to increases in NPP thus increasing the autotrophic component of respiration (Lovelock *et al.*, 2014). Large-scales shifts to commercial agriculture could therefore result in a large increases is soil respiration across the miombo eco-region and thus have a major effect of the carbon balance of these ecosystems (Heimann & Reichstein, 2008). Comparing soil respiration rates under different land management systems will allow for this hypothesis to be tested and should be considered as a future study.

6.3.2 Impacts of shifting cultivation on biodiversity in miombo woodlands

Despite the common, but misplaced, perception that shifting cultivation is a destructive and degrading land use practice (Mertz, 2009), the patchiness in vegetation cover it creates has been shown here to increase the number of species the landscape supports.   However it is important to remember that it is the trees themselves that help underpin local livelihoods through the provision of medicines, construction material, timber and food (Dewees *et al.*, 2011; Thobega, 2014). The extent to which local communities depend on and utilise the resources from secondary woodlands is not well documented, therefore, an important area for further research is to establish whether disturbance is necessary process in allowing certain locally important species to establish. This will be important step in better understanding the value of these created landscapes to local livelihoods in the face of potential changes to more permanent agricultural practices. It is also unknown how this patchy disturbance affects the diversity and composition of plant species in the herbaceous and sapling layer, or whether they are an important habitat for certain animal species. Studies from other parts of the tropics have noted that some species of bird, insect and mammal are only found in patches of disturbed forests (Barlow *et al.*, 2007; Berry *et al.*, 2010), however it is unknown as to whether similar associations are found in the miombo woodlands.

In terms of land management, the results of this study suggest that the intensification of this shifting cultivation, i.e. cultivating the land for a greater number of years through weeding or the addition or organic mulches, may provide a more sustainable route for development in African woodlands by reducing the amount of land required for cultivation without jeopardising the creation of potentially important reserves of biodiversity.

6.4 Chapter 6 references

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Appendix A – Species list

Local name	Other names	Species botanical name	Family	Sub-family
Cashew		***Anacardium occidentale***	Anacardiaceae	
Kalanganjiwa		***Diospyros cornii***	Ebenaceae	
Kiguruka		***Elaeodendron stuhlmannii***	Celastraceae	
Kigwaya		***Philenoptera wankieënsis***	Fabaceae	Papilionoideae
Kilimandembo		***Rhus natalensis***	Anacardiaceae	
Kingonogo		***Combretum apiculatum***	Combretaceae	
Kiruma		***Acacia senegal***	Fabaceae	Mimosoideae
Kitonya		***Acacia toetzei***	Fabaceae	Mimosoideae
Lugoe		***Glycine wightii***	Fabaceae	Papilionoideae
Malala	Mtete	***Hymenocardia ulmoides***	Phyllanthaceae	
Mango		***Mangifera indica***	Anacardiaceae	
Mbalika		***Hura crepitans***	Euphorbiaceae	
Mbarubaru		***Croton dichogamus***	Euphorbiaceae	
Mbinji		***Flacourtia indica***	Flacourtiaceae	
Mbubudu	Mkolyongo	***Grewia conocarpa***	Tiliaceae	
Mbula		***Parinari curatellifolia***	Chrysobalanaceae	
Mchecheta		***Ormocarpum kirkii***	Fabaceae	Papilionoideae
Mchenamila	Mkarati	***Burkea africana***	Fabaceae	Caesalpinoideae
Mchenga		***Julbernardia globiflora***	Fabaceae	Caesalpinoideae
Mcherenje	Mchelenje	***Bridelia scleroneura***	Euphorbiaceae	
Mchikichi		***Elaeis guineensis***	Arecaceae	
Mchonda		***Acacia sieberiana***	Fabaceae	Mimosoideae
Mchongoma		***Acacia nilotica***	Fabaceae	Mimosoideae
Mchumbu		***Diospyros sp2.***	Ebenaceae	
Mchungwapori	Mchungwa	***Citrus sinensis***	Rutaceae	
Mchuyo	Mpululu	***Terminalia sericea***	Combretaceae	
Mdaa		***Diospyros fischeri***	Ebenaceae	
Mdimumwitu		***Teclea nobilis***	Rutaceae	
Mdimupori	Mdiumpole	***Suregada zanzibariensis***	Euphorbiaceae	
Mdomolomo		***Diospyros quiloensis***	Ebenaceae	
Mfupa wa kuku		***Phyllanthus sp.***	Euphorbiaceae	
Mfuru		***Vitex Payos***	Lamiaceae	
Mfurudume		***Vitex sp.***	Lamiaceae	
Mgamba		***Cremaspora triflora***	Rubiaceae	
Mgeregere	Mgelegele	***Brachystegia bussei***	Fabaceae	Caesalpinoideae
Mgongo		***Sclerocarya birrea***	Anacardiaceae	
Mgongoro	Mnungamo	***Ochna holstii***	Ochnaceae	
Mgulugai		***Multidentia crassa***	Rubiaceae	
Mgunguti		***Combretum adenogonium***	Combretaceae	
Mgwe		***Olea sp.***	Oleaceae	

Mjabu		***Xylotheca tettensis***	Flacourtiaceae	
Mjanda		***Acacia reficiens***	Fabaceae	Mimosoideae
Mjengaua	Mjengana	***Ekebergia capensis***	Meliaceae	
Mjombo		***Brachystegia boehmii***	Fabaceae	Caesalpinoideae
Mjongoo		***Kigalia pinatta***	Bignoniaceae	
Mkaa		***Heeria reticulata***	Anacardiaceae	
Mkakatale		***Hugonia castaneifolia***	Linaceae	
Mkala		***Heeria reticulata***	Anacardiaceae	
Mkambakamba		***Cleistochylamys kirkii***	Annonaceae	
Mkandaa		***Ceriops tagal***	Rhizophoraceae	
Mkangazi		***Khaya anthotheca***	Meliaceae	
Mkaniki		***Dalbergia spp***	Fabaceae	
Mkarati		***Burkea africana***	Fabaceae	Caesalpinoideae
Mkasili		***Phyllanthus maderaspatensis***	Euphorbiaceae	
Mkiu		***Dombeya shupangae***	Sterculiaceae	
Mkokobara		***Lamprothamnus zanguebaricus***	Rubiaceae	
Mkokonaimba		***Tabernaemontana sp.***	Apocynaceae	
Mkolora		***Commiphora pilosa***	Burseraceae	
Mkolyongo		***Grewia conocarpa***	Tiliaceae	
Mkonge		***Psychotria sp.***	Rubiaceae	
Mkongo		***Afzelia quanzensis***	Fabaceae	Caesalpinoideae
Mkongo myzewa	Mpumbe	***Hymanaea verrucosa***	Fabaceae	Caesalpinoideae
Mkulakula		***Diospyros sp1.***	Ebenaceae	
Mkulo		***Spirostachys africana***	Euphorbiaceae	
Mkumbi	Mkanga nangu	***Trachylobium verrucosum***	Fabaceae	Caesalpinoideae
Mkunda	Mkunde	***Vigna unguiculata***	Fabaceae	Papilionoideae
Mkundekunde		***Cassia abbreviata***	Fabaceae	Caesalpinoideae
Mkungu		***Uvaria lucida***	Annonaceae	
Mkunya		***Sterculia appendiculata***	Sterculiaceae	
Mkuruti	Mkuluti	***Flueggea virosa***	Euphorbiaceae	
Mkuya		***Ficus sp.***	Moraceae	
Mkuyakuya	Mkuya	***Ficus sp.***	Moraceae	
Mkuyu		***Ficus sur***	Moraceae	
Mkwaju		***Tamarindus indica***	Fabaceae	Caesalpinoideae
Mkwanga		***Acacia polyacantha***	Fabaceae	Mimosoideae
Mkwichimbi	Mkwichimbo	***Manilkara discolor***	Sapotaceae	
Mlamakoa		***Combretum molle***	Combretaceae	
Mlandege		***Ficus ingens***	Moraceae	
Mlewelewe	Mkundekunde	***Cassia abbreviata***	Fabaceae	Caesalpinoideae
Mliawali		***Senna singueana***	Fabaceae	Caesalpinoideae
Mlondondo		***Xeroderris stuhlmannii***	Fabaceae	Papilionoideae
Mmangangoi		***Pericopsis angolensis***	Fabaceae	
Mmbinji		***Flacourtia indica***	Flacourtiaceae	

Mnanawele		***Combretum sp1.***	Combretaceae	
Mnangu	Mtandarusi	***Hymenaea verrucosa***	Fabaceae	Caesalpinoideae
Mndundu		***Cordyla africana***	Fabaceae	Papilionoideae
Mnepa		***Pteoleopsis myrtifolia***	Combretaceae	
Mng'odoka		***Xeromphis obovata***	Verbenaceae	
Mngomele		***Bridelia cathartica***	Phyllanthaceae	
Mnġomele		***Bridelia cathartica***	Phyllanthaceae	
Mngonogo		***Sclerocarya birrea***	Anacardiaceae	
Mngulunguya		***Vangueria infausta***	Rubiaceae	
Mnindila	Muhindila	***Combretum binderianum***	Combretaceae	
Mninga		***Pterocarpus angolensis***	Fabaceae	
Mningabonde		***Pterocarpus tinctorius***	Fabaceae	
Mningajangwa		***Pterocarpus angolensis***	Fabaceae	
Mnungamo		***Ochna holstii***	Ochnaceae	
Mnungu		***Zanthoxylum spp***	Rutaceae	
Mnunji		***Grewia holstii***	Tiliaceae	
Mnuwili		***Balanites maughamii***	Balanitaceae	
Mnyenye	Mchongoma	***Acacia nilotica***	Fabaceae	Mimosoideae
Mpalanganga		***Margaritaria sp.***	Euphorbiaceae	
Mpalapala		***Margaritaria discoides***	Euphorbiaceae	
Mpande		***Strychnos sp1.***	Loganiaceae	
Mpangapanga		***Millettia stuhlmannii***	Fabaceae	
Mperapa		***Psidium sp1.***	Myrtaceae	
Mperapori		***Psidium sp3.***	Myrtaceae	
Mperema		***Psidium sp2.***	Myrtaceae	
Mpilipili		***Sorindeia spp.***	Anacardiaceae	
Mpingi		***Ximenia americana***	Olacaceae	
Mpingo		***Dalbergia melanoxylon***	Fabaceae	
Mpinji		***Ximenia caffra***	Olacaceae	
Mporoto		***Ficus sansibarica***	Moraceae	
Mpucha	Mpuche	***Coffea eugenioides***	Rubiaceae	
Mpugumaoka		***Deinbollia borbonica***	Sapindaceae	
Mpugupugu		***Markhamia obtusifolia***	Bignoniaceae	
Mpupulu		***Tragia brevipes***	Euphorbiaceae	
Mpwekapweka		***Blighia unijugata***	Sapindaceae	
Mpweke		***Diospyros squarrosa***	Ebenaceae	
Mpwipwi		***Lannea stuhlmannii***	Anacardiaceae	
Msagawi	Mkulo	***Spirostachys africana***	Euphorbiaceae	
Msakala		***Fluggea virosa***	Euphorbiaceae	
Msekese		***Bauhinia petersiana***	Fabaceae	Caesalpinoideae
Msekeseke		***Bobgunnia madagascariensis***	Fabaceae	Papilionoideae
Msekeseke dume		***Bobgunnia madagascariensis***	Fabaceae	
Msenjele		***Acacia nigrescens***	Fabaceae	Mimosoideae
Msimbasi		***Uvaria sp.***	Annonaceae	

Msofu		***Uvaria kirkii***	Annonaceae	
Msolo	Mtanga bonde	***Pseudolachnostylis maprouneifolia***	Euphorbiaceae	
Msosonga	Msongasonga	***Euphorbia nyikae***	Euphorbiaceae	
Msufi		***Ceiba pentandra***	Malvaceae	
Msufi pori		***Bombax rhodognaphalon***	Bombacaceae	
Mswaki		***Salvadora persica***	Salvadoraceae	
Mtachi		***Diospyros mespiliformis***	Ebenaceae	
Mtalala		***Acacia polyacantha***	Fabaceae	Mimosoideae
Mtamba		***Ficus stuhlmannii***	Moraceae	
Mtandandumbili		***Markhamia sp1.***	Bignoniaceae	
Mtandawala		***Markhamia sp2.***	Bignoniaceae	
Mtandi		***Brachystegia tamarindoides***	Fabaceae	Caesalpinoideae
Mtanga		***Albizia amara***	Fabaceae	Mimosoideae
Mtangatanga		***Albizia sp.***	Fabaceae	Mimosoideae
Mtao		***Swartzia madagascariensis***	Fabaceae	Papilionoideae
Mtatu		***Allophylus africanus***	Sapindaceae	
Mtau		***Swartzia madagascariensis***	Fabaceae	Papilionoideae
Mtawa		***Polyalthia stuhlmannii***	Annonaceae	
Mteja		***Margaritaria discoides***	Euphorbiaceae	
Mtele		***Maytenus senegalensis***	Celastraceae	
Mtene	Mteno	***Ricinodendron gracilior***	Euphorbiaceae	
Mtete		***Hymenocardia ulmoides***	Phyllanthaceae	
Mtomoni		***Diplorhynchus condylocarpon***	Apocynaceae	
Mtomoni dume		***Holarrhena pubescens***	Apocynaceae	
Mtondo		***Julbernardia paniculata***	Fabaceae	Caesalpinoideae
Mtondoo	Mtondoa	***Brachystegia spiciformis***	Fabaceae	Caesalpinoideae
Mtonga		***Strychnos sp2.***	Loganiaceae	
Mtongatonga		***Strychnos cocculoides***	Loganiaceae	
Mtopetope		***Annona senegalensis***	Annonaceae	
Mtukuli		***Boscia salicifolia***	Capparaceae	
Mtumbitumbi		***Ximenia americana***	Olacaceae	
Muhani		***Dodonaea viscosa***	Sapindaceae	
Muhiru	Muhilu	***Vangueria acutiloba***	Rubiaceae	
Muhungo		***Acacia campylacantha***	Fabaceae	Mimosoideae
Mvule		***Milicia excelsa***	Meliaceae	
Mwalita		***Ehretia sp.***	Boraginaceae	
Mwambala		***Vangueriopsis lanciforia***	Rubiaceae	
Myombo	Miombo	***Brachystegia spiciformis***	Fabaceae	Caesalpinoideae
Mzambarau pori		***Syzygium guineense***	Myrtaceae	
Mzigozigo		***Isolona sp.***	Annonaceae	
Nakapweo		***Crosspteryx febifuga***	Rubiaceae	
Uwindi		***Acacia sp.***	Fabaceae	Mimosoideae

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Appendix B

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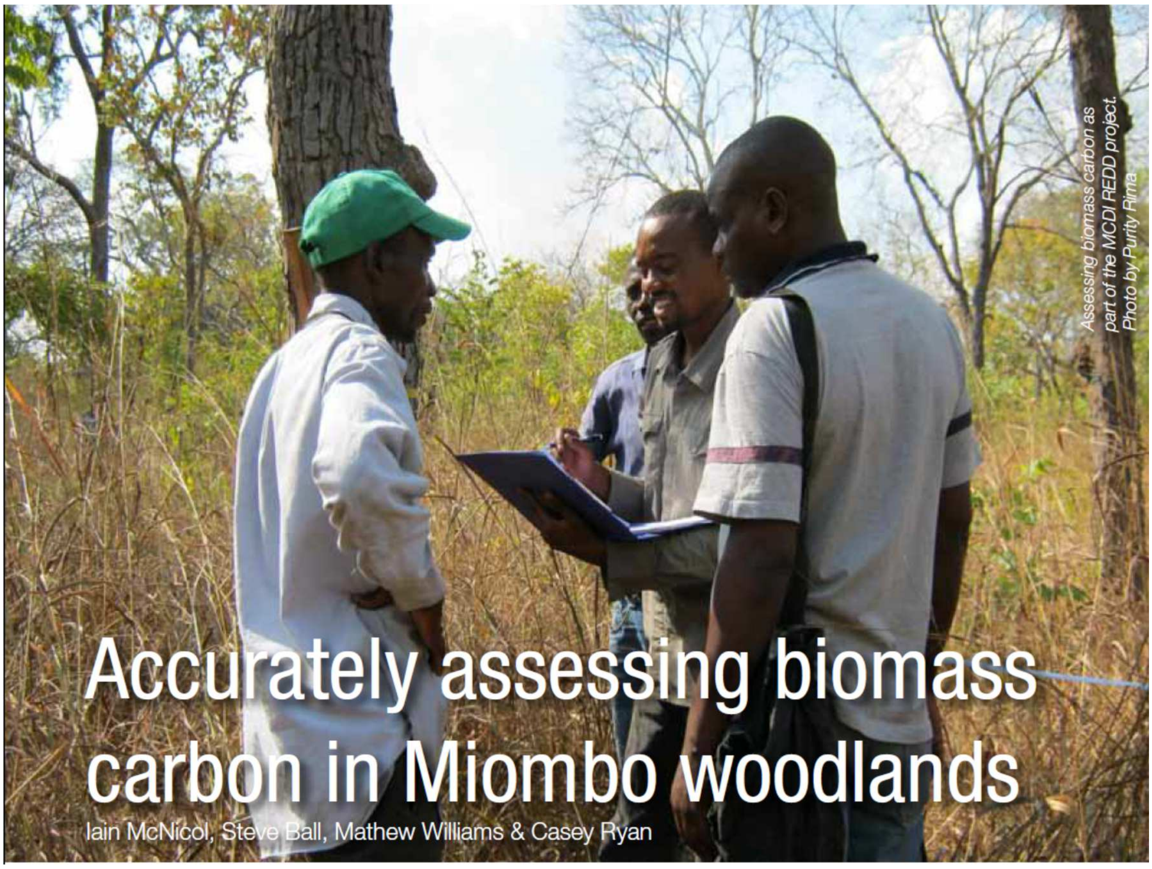

Assessing biomass carbon as part of the MCDI REDD project. Photo by Purity Rima

Accurately assessing biomass carbon in Miombo woodlands

Iain McNicol, Steve Ball, Mathew Williams & Casey Ryan

The Mpingo Conservation and Development Initiative's (MCDI) REDD pilot project is unusual. Most REDD projects assume a static area of forest. However, MCDI are more interested in the timber values of the forests in Kilwa in south-east Tanzania (a patchwork of Miombo Woodlands and East African Coastal Forest), which, we calculate, could yield substantially higher revenues than carbon, so long as the timber can be properly differentiated in the market which forest certification does.

MCDI holds the first and so far only certificate from the Forest Stewardship Council for community-managed natural forest in the whole of Africa. However, MCDI needs to expand the area of certified forest in order to achieve the economies of scale which will make the certification scheme self-sufficient in the long run. MCDI has found it hard to raise from donors all the funds it needs to do this. In the language of the carbon markets, MCDI faces an 'investment barrier' to expanding a proven, effective means of sustainable forest management, and if carbon savings can be demonstrated, then carbon offsets can be generated using a REDD+ model, and sold on the global market to cover the costs of expanding PFM and FSC certification.

In the remote forests in which MCDI is working, there are relatively few pressures from the traditional drivers of deforestation in Tanzania: agriculture and charcoal production. Uncontrolled timber extraction is a problem, but is highly selective and thus the carbon losses are relatively low. MCDI is thus focusing on the degradation caused by regular bush fires. These often occur during the middle of the dry season, when farmers are clearing new land, but also the windiest time of year. The combination of high winds and abundant dry grasses lead to hot, extensive fires. MCDI aims to reduce the damage this causes the forest by embarking upon an ambitious programme of early burning in partnership with the communities with whom it is working. This improved fire management is expected to lead to annual carbon savings of the order of 0.5tCha^{-1} or about 2.5% of above-ground biomass. These small changes require an extremely effective monitoring regime to detect.
In collaboration with the University of Edinburgh, MCDI is therefore pioneering new methods of carbon assessment in order to provide scientifically

robust estimates of both above and below ground carbon stocks, and monitoring their change over time. To achieve this objective, MRV activities have been broken down into three stages:

1) Forest area pre-assessment to locate potential plot locations and to assess spatial variability,
2) Field measurements from a representative sample of the project area, and
3) Extrapolation of carbon stocks across the district and monitoring changes over the project lifetime.

Viewed at a project level scale, Miombo woodlands are spatially extremely heterogeneous, encompassing open grassland areas (*dambos*), savannah woodland and thicker riparian forest. Stratification is the usual solution to land cover heterogeneity, but the scale at which Miombo varies is too small to be accurately determined by analysis of satellite imagery. Thus instead we need a solution which manages extremely localised variation; large plot size is one answer. Previous fieldwork by the University of Edinburgh in Mozambique shows sample plots need to be at least 1ha in size if the resulting data set is to be approximately Normal (required for most statistical analyses) (Ryan *et al.*, 2011).

We adopted a nested 'super' plot design, not dissimilar to the cluster plots used by NAFORMA. Thus our sample plots consist of 1 x 1ha Permanent Sample Plot (PSP), 1 x 9ha Large Sample Plot (LSP) and 4 x 0.2ha circle plots (one at each corner of the LSP). A large fraction of Miombo biomass is found in large trees. This fact allows us to increase the efficiency of surveying such large plots; only stems >40cm DBH are surveyed in the LSP (except where it overlaps with the smaller sub-plots). Nonetheless this survey design requires a lot of effort per plot, so the total sample size must be reduced; in our case to 25 super plots. For the circle plots plus PSPs, however, that delivers an *n* of 225. So long as the plots are not biased in their location, the width of the confidence interval on carbon stocks will primarily be driven by the number of trees measured and area surveyed. We surveyed a total of 225ha which compares very well with an expected project size of approx. 30,000ha.

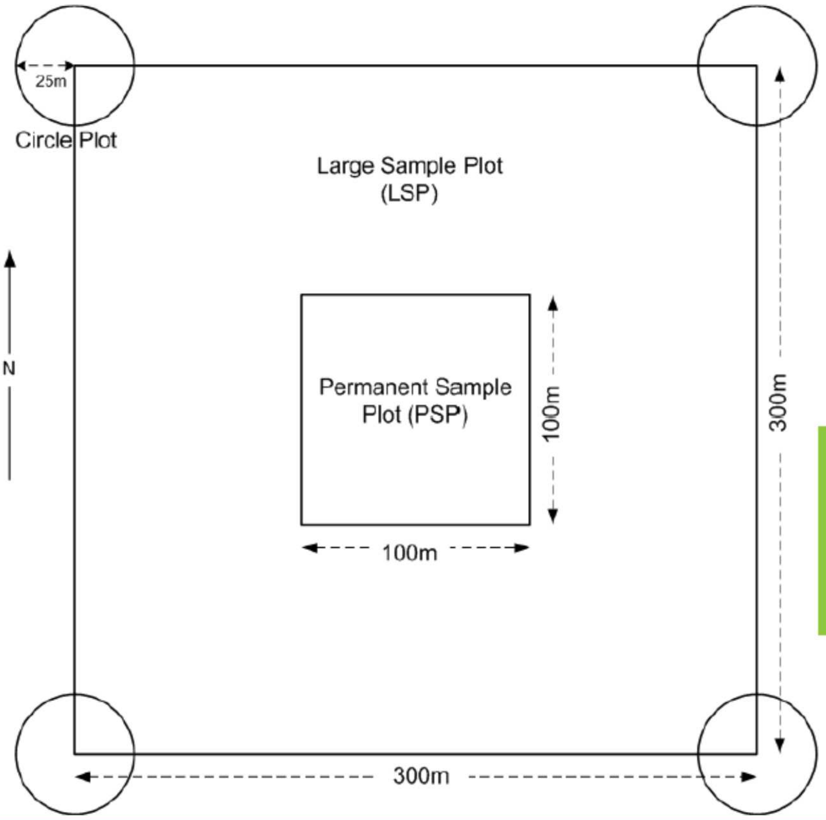

Figure 1. Plot layout showing arrangement of permanent, large and circle plots.

Super plots were located through an initial (experimental) stratification of the landscape based on LandSat imagery. Three discrete strata – Forest, Woodland and Savanna – were mapped based on >100 ground reference points. To maximise surveying efficiency we preferentially sampled the spatially dominant communities. Thus of the 25 sample locations, 14 were situated in woodland, 6 in forest and 5 in savannah. Pragmatism naturally played a role in site selection as it is easier to survey sites close to the road network; however a minimum 1km buffer from the road was implemented in order to reduce the effects of disturbance (as per Williams *et al.*, 2008).

The 25 super plots were established and subject to baseline surveys from October 2010 to October 2011. These were complemented with an additional 43 plots (0.2ha each) that were set up across the district, encompassing a chronosequence of active and abandoned farmland which is being used to quantify losses associated with conversion to agriculture and to analyse how the woodlands recover over time.

To estimate biomass carbon stocks we used the standard approach for a forest inventory, determining the species, and the diameter at breast height (DBH) for each stem using specified DBH thresholds for each plot type. The project employed local guides knowledgeable in botany to assist MCDI field technicians with species identification and to take DBH measurements. To convert DBH into aboveground biomass, the project used a new regionally derived allometric model, obtained from the destructive harvest of 29 trees in Mozambique, which relates tree diameter to stem and root biomass (Ryan *et al.*, 2011a).

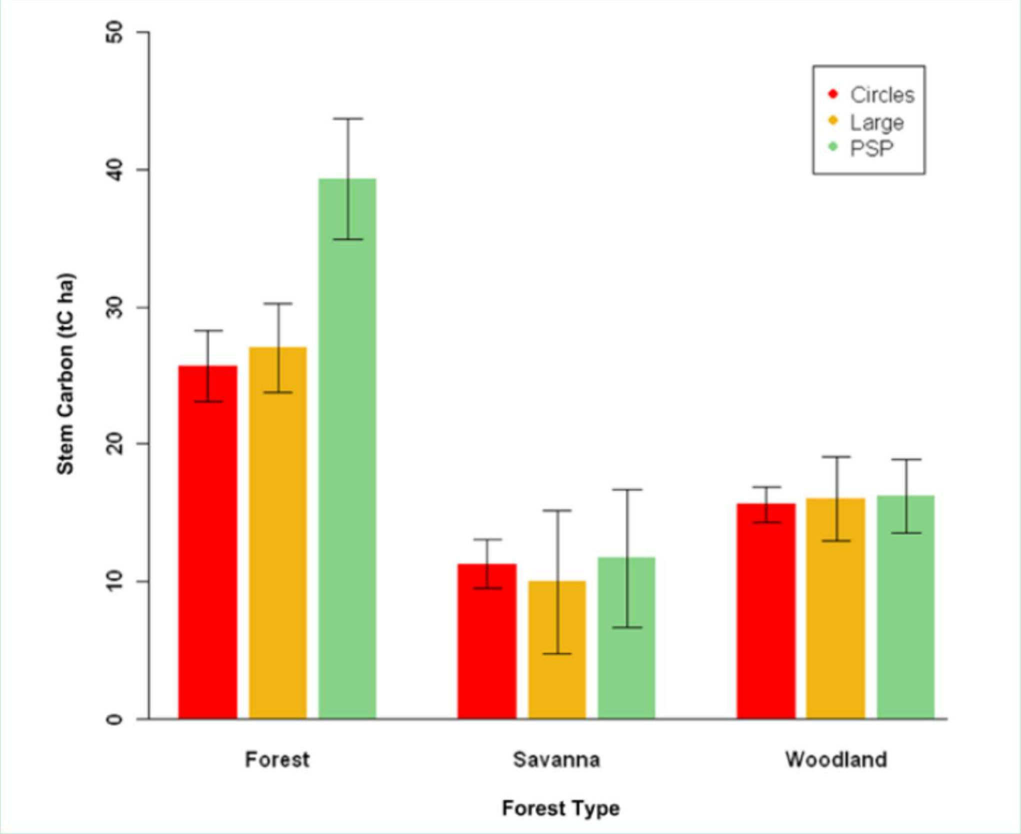

Figure 2. Mean carbon density (tC ha^{-1}) of each land cover type separated by plot typeError bars indicate standard error of the mean (SEM)

The results of the baseline were further processed to align the data from the three different plot types. This showed that across the central Kilwa Landscape the following carbon densities apply:

	Mean stem C density ($t\ ha^{-1}$)	*Area (000 ha)*	*Total stem C (000 tonnes)*
Forest	28.4	428	12,155
Woodland	15.7	824	12,937
Savannah	11.5	262	3,013
Farmland	9.4	236	2,218
TOTAL		1,750	30,323

Analysis, also showed that, as expected, the biomass figures for the smaller circle plots, and even the 1ha PSPs, were non-Normal, the data for the LSPs are indeed normally distributed.

The final steps in MRV will be to extrapolate the ground based measurement across the project area and to monitor changes over time. Repeat inventories of the 1 and 9ha plots only are scheduled for 2013 and will allow the project to record and monitor natural and anthropogenic changes in C stocks at a high spatial resolution and with careful error assessment.

However, due to constraints on time, effort and resources, it is not possible to directly sample a sufficient number of plots across the district in order to be able to use ground based data alone to directly estimate relatively small changes in carbon stocks. Instead remote sensing data will be used to extrapolate the plot data across the landscape. By combining the field based inventory data with information derived from ALOS PALSAR, an L-Band radar satellite sensor, the project will generate carbon density maps at 25m resolution using the method of Ryan et al. (2011b). The ability to combine the plot based measures with more extensive EO data will ultimately enhance our understanding of the carbon balance of the district as a whole. The inclusion of both relatively undisturbed as well as degraded areas in the sampling strategy will provide extra calibration and validation capacity for the remote sensing data.

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