A scaled, contextual perspective of woody structure and dynamics across a savanna riparian landscape

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August 5, 2008

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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Abstract

Sound understanding of the influence of scale and context on ecological pattern-process relationships is lacking in many systems. The hierarchical patch dynamics paradigm (HPDP) provides a framework for addressing spatio-temporal heterogeneity, but the range of systems in which, and scales at which, its principles apply are largely unknown. Furthermore, it does not explicitly account for the influence of spatial context. Recent developments in remote sensing science show potential for bridging this gap by enabling the exploration of landscape heterogeneity at multiple scales and across a wide range of systems and contexts, but the ecological application of these new techniques is lagging. The savanna riparian landscapes of the northern Kruger Park, South Africa, provided a unique platform in which to explore the influence of spatial context, and to test the pattern-process-scale and metastability principles of the HPDP, to further its potential as a unifying framework in landscape ecology.

LiDAR and high-resolution aerial imagery were integrated through object-based image analysis to create spatial representations of woody structure (canopy height, canopy cover, canopy height diversity and canopy cover diversity) across a portion of the savanna landscape (60 000ha). Temporal change in woody cover and heterogeneity (number and size of woody patches) was assessed from a historical aerial photography record, that spanned 59 years from 1942 to 2001. Spatial relationships between environmental variables and patterns of woody structure and dynamics were tested at broad (100ha), medium (10ha) and fine-scales (1ha) through canonical correspondence analysis (CCA). The relative contribution of different categories of environmental variables, to the total explained variation in woody structure, was assessed at each scale through partial canonical correspondence analysis (PCCA). Spatial variation in environmental variables, and the influence of spatial context on

woody structure-environment relationships, was explicitly tested through geographically weighted regression (GWR).

LiDAR results provided an unprecedented basis from which to explore spatial patterns of woody structure in an African savanna. Standard approaches to generating normalized canopy models (nCM) from LiDAR suffered interpolation artifacts in the heterogeneous landscape, but an object-based image analysis technique was developed to overcome this shortfall. The fusion of LiDAR with aerial imagery greatly enhanced the structural description of the landscape, and the accuracy of canopy height estimates varied between different vegetation patch types.

Woody structure and dynamics displayed distinct spatial trends across the landscape with high diversity and variability occurring in the alluvial riparian zones. Woody canopy height, canopy cover and cover dynamics exhibited scale variance in their relationship with environmental variables, but woody structural diversity-environment relationships were scale invariant across the analysis patch hierarchy. These findings from different woody attributes both support and contradict the pattern-process-scale principle of the HPDP, which hypothesizes that ecological processes shift with scale, but that spatial variance measures exhibit stepwise patterns of change with scale, along a patch hierarchy.

Percentage woody cover was stable over time across the landscape, despite high variability at smaller scales. However the metastability principle cannot be considered generally applicable in this system, as a broader view of the woody component revealed a marked decline in woody heterogeneity over time. Although losses of woody cover on the diverse alluvial substrates were countered by increases of cover in the uplands, analysis of current woody structure in the context of historical change revealed that the increases took place in the form of shrub encroachment and not the replacement of tall trees. The vertical structure of woody vegetation, and therefore both the biodiversity and ecological functioning of the system, has changed over time across the landscape. The metastability principle of the HPDP may not be applicable in spatially heterogeneous systems, where ecological processes act differentially across the landscape, but may apply within specific patch types at certain temporal scales.

Spatially localized analysis models revealed significant spatial non-stationarity in the majority of processes correlated with woody structure, and showed that both the magnitude and direction of woody structure-environment relationships varied in different spatial contexts across the landscape. These results have fundamental implications for the manner in which both science and conservation measures are conducted in heterogeneous systems. Global analysis models, that assume stationarity, are widely accepted and employed in ecological research but may greatly misrepresent ecological relationships that are context-dependent. These findings question the level of system understanding that field studies can provide, by revealing the dangers of inferring patterns and relationships from measurements of limited spatial representation. Leveraging the latest remote sensing technologies, that provide large-extent but fine-grain coverage, in a scaled and context conscious manner, will enhance ecological understanding by spatially quantifying the full spectrum of system heterogeneity.

The heterogeneous patterns, scaled relationships and context-dependent patterns identified in this study are challenging from both ecological research and biodiversity conservation points of view. Traditional approaches to science and conservation are ill equipped to address these issues. The HPDP provides an excellent conceptual construct for meeting such challenges, but the influence of spatial context needs to be more explicitly incorporated within the framework.

A catchment-based hierarchy is suggested for guiding future research and conservation efforts in heterogeneous landscapes, where context-dependency of ecological processes may be the norm.

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Chapter 1

The structure and dynamics of ecological systems

1.1 Introduction

Paradigms of equilibrium and homogeneity dominated ecology and natural resource management for most of the past century. These balance of nature principles assume that natural systems are ordered, predictable and stable (Egerton, 1973). Such age old myths limit our understanding of the natural world as well as our ability to solve environmental problems (Botkin, 1990). Furthermore, the theories and models built around equilibrium principles have often misrepresented the foundations of resource management and nature conservation (Wu and Loucks, 1995).

Recently the complexity of natural ecosystems in both space and time has been recognized, and ecological paradigms have shifted toward hierarchical patch dynamics and heterogeneity (Wu and Loucks, 1995). Such concepts are beginning to be incorporated into conservation and management policies, but a sound understanding of the spatial and temporal heterogeneity of ecological systems is still lacking in many areas. Recent developments in remote sensing hold great potential for furthering understanding of heterogeneity and aiding biodiversity conservation, through their ability to measure fine-scale ecological properties over large spatial areas (Kerr and Ostrovsky, 2003; Turner et al., 2003; Chambers et al., 2007), but greater integration of these technologies with ecological research is needed (Wu and Hobbs, 2002).

Although landscape ecology has emerged as a science dealing explicitly with spatial pattern and scale in landscapes, its principles are often neglected in ecological research and natural resource management (Liu and Taylor, 2002). Consequently it has been criticized for producing few theoretical generalizations to guide research and management (Wu and Hobbs, 2002; Haines-Young, 2005). The hierarchical patch dynamics paradigm (HPDP) (Wu and Loucks, 1995) is an exception to this, but its applicability across a broader range of systems needs exploration for it to develop further as a unifying framework in landscape ecology.

Furthermore, Wiens (1995) regards the fundamental premise of landscape ecology, that spatial context influences ecological patterns and processes, as "more an article of faith than an empirically validated fact". Sound understanding of context-dependency in vegetation pattern is lacking, although it may be the norm in most ecological systems (Jones and Callaway, 2007). Whilst the influence of context is implicit within the HPDP, as hierarchical patch structuring gives rise to constraint (O'Neill et al., 1986), explicit understanding of contextual influences on pattern-process relationships is needed. The range of scales and systems in which these landscape ecology principles are applicable must be empirically tested, as it is only through the explicit exploration of these ideas, across different systems, contexts and scales, that the science will develop and successful integration with biodiversity conservation will take place.

The savanna riparian landscapes of the northern Kruger Park, South Africa, with their high levels of spatial heterogeneity (Venter et al., 2003; Saah, 2004), provided a useful basis from which to address these issues.

1.2 Background literature

1.2.1 Spatio-temporal heterogeneity in ecological systems

Landscape ecology is primarily concerned with the ecological effects of the spatial patterning of landscapes. It addresses the development and dynamics of spatial heterogeneity, interactions and exchanges across heterogeneous space, the influences of spatial heterogeneity on biotic and abiotic processes, and the management of spatial heterogeneity (Risser et al., 1984; Turner, 1989; Wiens, 2002).

The term landscape ecology was initially coined in the late 1930s by Carl Troll, a German biogeographer, whilst interpreting aerial photographs of an East African savanna (Bastian, 2001). Gleason (1939) was the first to argue that spatially heterogeneous patterns were important, and suggested that they be interpreted as individualistic species responses to spatial gradients in the environment. These ideas later led to the development of gradient analysis (Whittaker, 1956). Clements' (1936) work on successional dynamics highlighted the temporal variability of the plant community, but it did not recognize the importance of spatial patterning. It was not until Alex Watt's seminal work that space and time were explicitly linked for the first time at the landscape level. Watt's (1947) conceptualization of spatio-temporal vegetation patterns later led to the formation of the pattern-process paradigm (Turner, 1989) which is still a central theme in landscape ecology today (Pickett and Cadenasso, 1995; Wu and Hobbs, 2002).

The landscape ecology approach is conceptually very different from the standard ecology approach, as it assumes that spatial context affects the ecological processes within a patch and the interaction between patches (Figure 1.1). Fundamental to the landscape ecology approach is the recognition of heterogeneity in both space and time at multiple scales, and the consideration of ecological systems in a hierarchical manner.

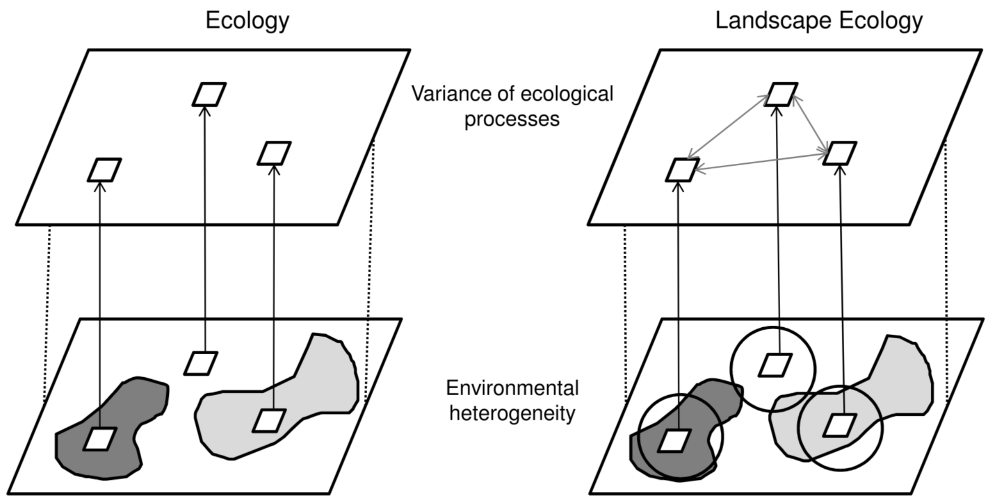


Figure 1.1: Schematic representations of the conceptual framework of ecological and landscape ecological analysis. In the ecological framework, the ecological process (upper graph) observed in a set of plots (white squares) depends on the level of the environmental factor (polygons in lower graph) measured at the plot location. Patches/plots are internally homogeneous, plot context does not matter, and observations are spatially independent. In the landscape ecological framework, patches/plots may be internally heterogeneous, plot context may affect local processes, and observations may not be independent due to spatial interaction between local processes. After Wagner and Fortin (2005).

Hierarchical structure of ecological systems

Hierarchy theory is a framework for examining scale in systems (O'Neill et al., 1989). It was initially developed in the 1960s and 1970s through a framework of general systems theory, mathematics and philosophy (Pattee, 1973). Allen and Starr (1982) and O'Neill et al. (1986) introduced these principles to ecology and argued that they could be applied to ecosystems and used to determine ecological phenomena at multiple spatio-temporal scales. An ecological hierarchy can be viewed as a series of organizational levels that are constrained within a nested vertical structure (O'Neill et al., 1986). Levels within the hierarchy can be distinguished on the basis of functional process rates or structural spatial criteria. Higher levels of an ecological hierarchy occur at larger spatial scales and have slow process rates while the lower levels occur at smaller scales and have faster process rates (O'Neill and King, 1998).

Ecological hierarchies can therefore be described as "decomposable" since each level of organization responds at a characteristic spatial and temporal scale (Bergkamp, 1995), and the analysis and understanding of the system can be enhanced by organizing their numerous components into fewer discrete, interactive units (O'Neill et al., 1986; Wu and Loucks, 1995). Certain properties of higher organizational levels, termed emergent properties, cannot be inferred from the functioning of their parts, but arise through the average, filtered or smoothed properties of the lower organizational levels (Allen and Starr, 1982; O'Neill et al., 1989, 1986). The greater the separation between two organizational levels within an ecological hierarchy, the greater the difficulty in deducing the influence of the faster process rates of lower levels on the levels above them in the hierarchy (Kotliar and Wiens, 1990). This nested vertical arrangement gives rise to the concept of constraint, which is the single most important consequence of hierarchical structuring (O'Neill et al., 1989). An ecological hierarchy is constrained or limited by the behaviours of its components and by the environmental constraints imposed by higher levels in the hierarchy. These hierarchical constraints provide the platform for context-dependent relationships to emerge in spatially heterogeneous systems.

Spatial heterogeneity and context-dependency of vegetation pattern

Heterogeneity may be defined as the uneven, non-random distribution of objects and is perceived at any scale (Farina, 2000). Quantification of pattern and scale enables assessment of the controls and consequences of heterogeneity (Ettema and Wardle, 2002), as landscape patterns and ecological processes are tightly coupled in a reciprocal relationship (Turner, 1989; Pickett and Cadenasso, 1995; Wu and Loucks, 1995). Heterogeneous landscapes are best considered as mosaics that comprise patches, gradients and boundaries (Forman, 1995).

A patch is a relatively discrete spatial unit that may vary in size, internal homogeneity and discreteness (Pickett and White, 1985). Patches differ from their surroundings in nature or appearance and have definable boundaries (Kotliar and Wiens, 1990). An important aspect of patchiness is that it is scale and organism dependent. Any given patch forms part of a larger patch and is itself comprised of smaller patches. The finest scale of patchiness is referred to as the grain and the coarsest scale of patchiness is termed the extent. Ranges of grain and extent differ for different organisms (Figure 1.2) as they see the environment from their own perspective and therefore recognize and respond to patchiness across a different range of scales. Likewise, ranges of grain and extent may differ for different studies, disturbances and ecosystem drivers (Rogers, 2003).

Recognition of patches in a landscape infers the recognition of boundaries between those patches. The concept of boundaries refers to areas of transition, contact, or separation between the contrasting elements of a mosaic (Cadenasso et al., 2003a). Although they occupy a relatively small proportion of the total mosaic, boundaries are important control points as they mediate the interaction of mosaic elements by modulating the connecting flows (Wiens et al., 1985; Pickett and Ca-

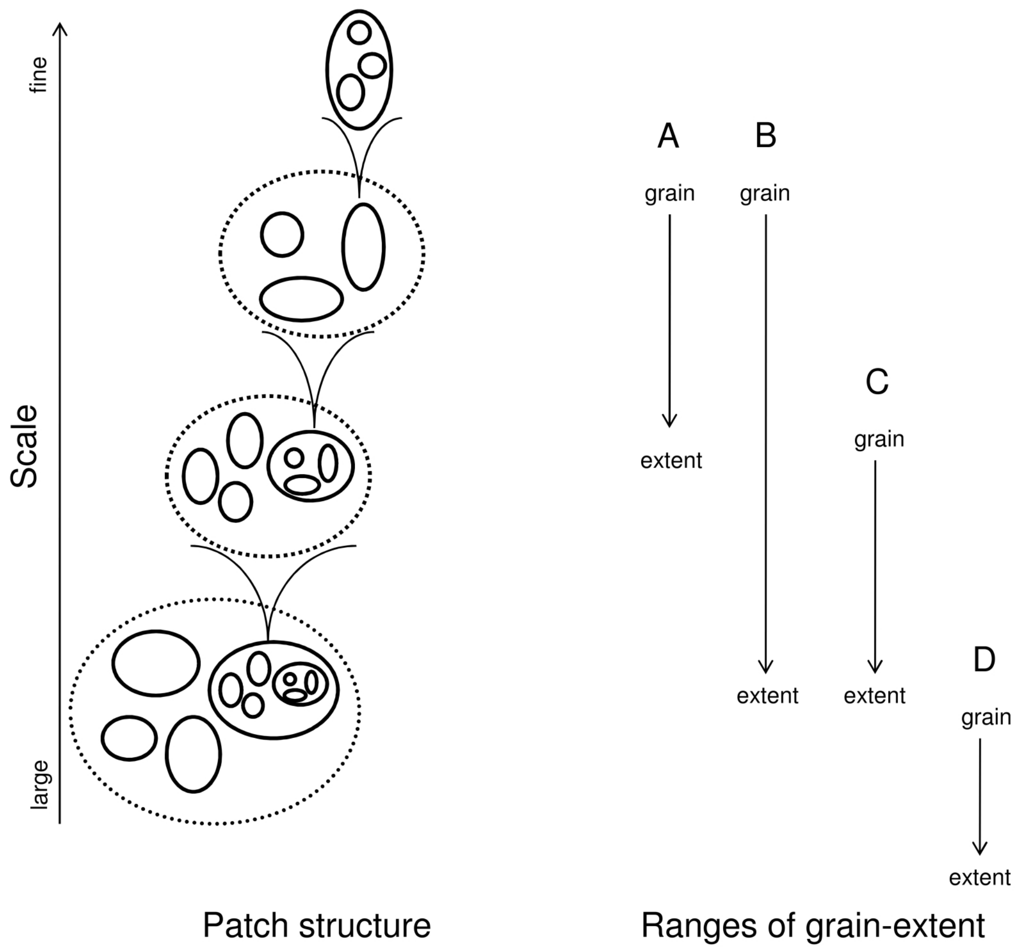


Figure 1.2: Hierarchical patch structure and grain extent ranges for four types of organisms (A-D).One organism (B) may have the same grain as another (A), but a larger extent. The grain of one organism (C) may be the extent of another (A). After Kotliar and Wiens (1990).

denasso, 1995; Cadenasso et al., 2003b). Riparian/upland boundaries in particular are regarded as being important control points in the landscape which mediate flow between the aquatic and terrestrial environments (Forman, 1995; Naiman and Decamps, 1997).

The structure of a mosaic can be quantified in terms of both patch composition and patch spatial configuration. The types and relative abundances of patches constitute patch composition whereas the spatial configuration of patches refers to patch shape, juxtaposition, contrast and boundary characteristics (Farina, 1997). Forman (1995) suggests that patch context is more important than patch content in regions and landscapes, and that the surrounding mosaic should have a greater effect on patch functioning and change than do present characteristics within the patch. Context in this sense incorporates three components – adjacency, neighbourhood, and location within a landscape. Although the importance of temporal context in understanding stream diversity has been illustrated (Harding et al., 1998), and landscape position has been found to be an important determinant of temporal variability (Kratz et al., 1991), comprehensive empirical evidence of the importance of context in ecological systems is still lacking and Forman's prediction remains untested. This issue has emerged as a key challenge in ecology, demanding an explicit, comprehensive and integrative attack on the problem of context-dependency in vegetation pattern (Jones and Callaway, 2007).

Temporal heterogeneity of vegetation pattern

Vegetation is not a static feature of the landscape but is continuously changing. The first explicit consideration of the role of heterogeneity in vegetation dynamics is attributable to Alex Watt (1925; 1947), who recognized that the processes that determine the relative proportions of individuals and species within the plant community, and their spatial and temporal relations to each other, were largely unknown. The plant community had previously only been identified and classified with no attempt to formulate laws according to which it maintains and regenerates itself. Watt (1947) considered the plant community as a dynamic mosaic of patches in upgrading and downgrading seral stages. The spatial arrangement of patches provided an insight to the temporal sequence of patch succession and therefore system dynamics. Watt's ideas, however, received little attention until Bormann & Likens (1979) expanded on his work and developed the shifting steady-state mosaic hypothesis.

Their studies of disturbance and gap phase succession, in forested ecosystems, led them to propose the landscape as a shifting steady-state mosaic of differing seral stages. The vegetation present at individual points in the landscape changed, but if averaged over a sufficiently long time or large area, the proportion of the landscape in each seral stage remained relatively constant (Bormann and Likens, 1979). Although the shifting steady-state mosaic, otherwise termed metastability, has been difficult to test empirically (Turner et al., 1993), it has been found to apply in various Northern Hemisphere systems, but has exhibited scale-dependency in some cases (Zackrisson, 1977; Sprugel and Bormann, 1981; Romme, 1982; Romme and Despain, 1989; Sprugel, 1991). Turner et al. (1993) found the concept to be problematic as a general property of landscapes as it requires factors influencing disturbance frequency or recovery to be averaged across the landscape, which is an inappropriate assumption in some systems. Therefore, the shifting steady-state mosaic may only be applicable when disturbances are small and frequent in large areas of homogeneous habitat (Pickett and White, 1985). Turner et al. (1993) considered defining the sufficiently broad temporal and spatial scales over which to consider the aggregate mosaic to be problematic, but suggested that it is conceivable to find a shifting steady-state mosaic in certain landscapes where feedback mechanisms influence disturbance frequency. Furthermore, different degrees of metastability may arise in a landscape as a function of disturbance/recovery interval and disturbance/landscape extent (Figure 1.3). This model is backed by multi-scaled ecological research in northern forested systems (Turner et al., 1993), but the concept

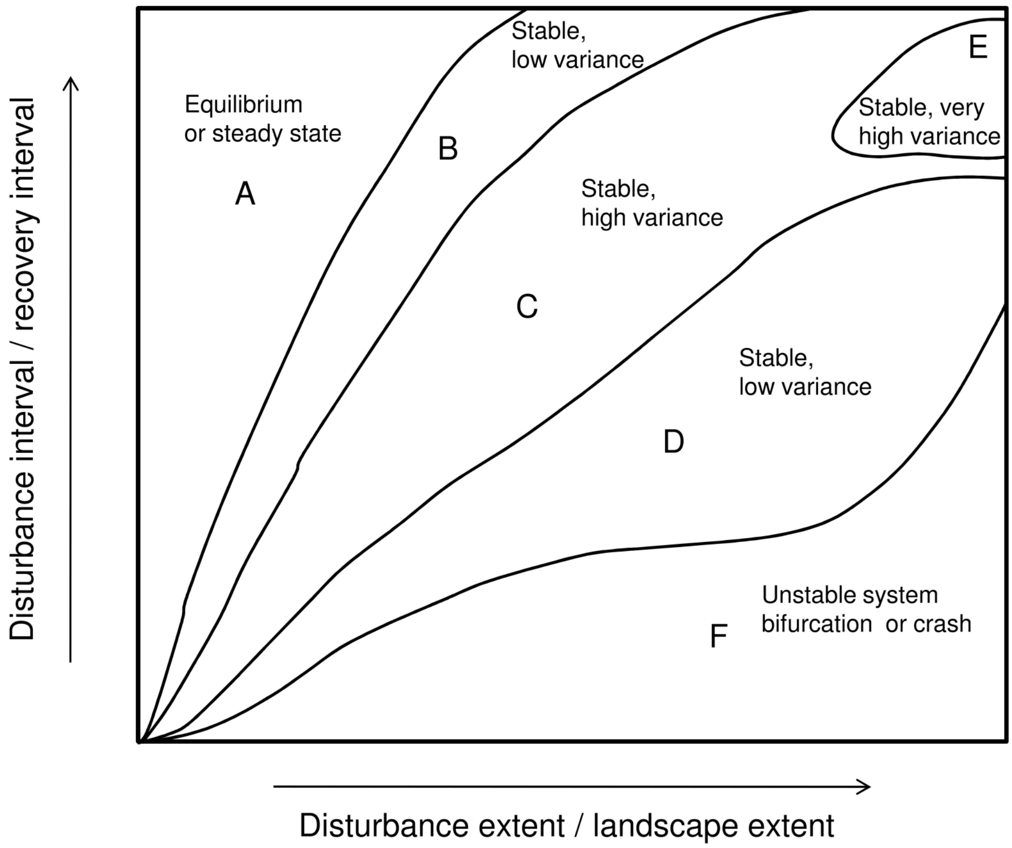


Figure 1.3: A range of landscape equilibrium scenarios as a function of disturbance/recovery interval and disturbance/landscape extent. After Turner et al. (1993).

has not been explored in more heterogeneous systems, such as savannas, with large extent but selective disturbances such as megeherbivores.

1.2.2 Emergence of the hierarchical patch dynamics paradigm

A hierarchical perspective of ecological systems, that recognizes spatio-temporal heterogeneity, provides a strong theoretical basis for elucidating the problem of scale in ecology (Levin, 1992). Wu and Loucks (1995) argued that it is the integration of hierarchy theory with a patch dynamics perspective that holds the greatest value for ecology, by emphasizing multiple-scale properties of pattern and dynamics in ecological systems. Wu and Loucks integrated much of the theory discussed above to formulate the hierarchical patch dynamics paradigm (HPDP) which explicitly acknowledges the causes and mechanisms of heterogeneity, and can be considered in terms of five major elements (Wu and Loucks, 1995):

1. **Ecological systems as nested, discontinuous hierarchies of patch mosaics**. Ecological systems can be viewed as hierarchical systems of patches that differ in size, shape and successional stage at particular scales. The fundamental unit is the patch, unlike the traditional ecological focus on the individual organism, population, community or ecosystem. *The delineation of a patch is scale dependent*.

2. **Dynamics of ecological systems as a composite of patch dynamics**. Emergent properties are important as the dynamics of ecological systems are composed of the dynamics and interactions of constituent patches on different scales, thus the sum is greater than the whole. *Better understanding of the dynamics of ecological systems can be achieved by considering a few adjacent levels in the patch hierarchy, in addition to the focal one.*

3. **The pattern-process-scale perspective**. Pattern and process operate on a wide range of scales. A variety of processes can create, maintain, modify, and destroy pattern. Pattern can in turn either facilitate or constrain ecological processes. *Ecological processes and environmental controls shift with scale along a patch hierarchy*. Whilst certain descriptors of spatial pattern may change considerably with scale, *spatial variance can exhibit a staircase or stepwise pattern of change over a range of scales*.

4. **The nonequilibrium perspective**. Nonequilibrium and stochastic processes are important elements of system dynamics. Abiotic and biotic disturbances often introduce local transient dynamics into ecological systems. *Spatio-temporal scale influences what is perceived as nonequilibrium, transient or unstable dynamics*.

5. **Metastability and incorporation**. Incorporation and metastability are dependent on the types of processes and their spatio-temporal scales in the system under consideration. *Nonequilibrium patch processes at one level may translate to metastability at a higher level and variation is likely to decrease with increasing spatial scale as it becomes incorporated through the levels.*

The HPDP is appealing from both theoretical and applied points of view as it provides a framework for considering spatio-temporal heterogeneity in ecological systems and draws together the key concepts of landscape ecology. Despite its potential, however, the HPDP is yet to emerge as a unifying framework in landscape ecology, as it currently suffers two key shortcomings.

Firstly the paradigm is largely theoretical, through its adoption of some of the key assumptions of landscape ecology, and lacks empirical validation for the manner in which the two central elements of scale and context influence pattern-process relationships. Secondly, the paradigm stems mostly from understanding gained in northern temperate systems, so its applicability to a broader range of systems, particularly heterogeneous ones, is largely unknown. It may hold value for understanding heterogeneous systems like savannas, but this has not been validated. Savanna landscapes, with their high levels of spatio-temporal heterogeneity (Belsky, 1995; Pickett et al., 2003) and wide range of driving processes (Coughenour and Ellis, 1993; Gillson, 2004a), may provide a useful setting in which to not only test, but also to further develop this paradigm.

A hierarchical patch dynamics perspective of savanna systems

The exploration of landscape ecology principles in savannas is extremely limited (Belsky, 1995; Gillson, 2004a). Heterogeneity of savanna vegetation has been attributed to a host of drivers including rainfall, substrate variation, topography, fire, herbivory, nutrients and competition (Dublin et al., 1990; Coughenour, 1991; Scholes and Walker, 1993; Higgins et al., 2000; van Langevelde et al., 2003; Sankaran et al., 2005). Most theories of savanna structure and dynamics have been scale free and there have been few attempts to integrate these processes across spatio-temporal domains of scale (Gillson, 2004a). Coughenour and Ellis (1993), however, suggested a hierarchy of constraint in savannas in which: (1) climatic patterns determine the extent of the biome at the continental scale; (2) rainfall, hydrology and topography influence savanna structure at the regional to landscape level; and (3) local scale structure is determined by variations in water availability and disturbances. Gillson (2004a) built on these ideas and eloquently condensed published theories, and insight gained from her own work, into a hierarchical spatio-temporal framework of the processes governing density of woody plants in savannas (Figure 1.4). This framework has potential to enhance both the understanding and management of savannas as it illustrates the range of spatio-temporal scales over which processes operate, and integrates both bottom-up processes, such a geology and soil type, with top-down process such as fire and herbivory. By considering the spatio-temporal domains of driving processes, the manner in which, and the scales at which "large and slow" or "small and fast" variables interact becomes evident (O'Neill and King, 1998), and provides a platform for understanding ecological complexity (Gunderson and Holling, 2002).

Despite the potential that this hierarchical framework shows, it has not yet been applied to other components of woody vegetation, such as height, cover and structural diversity, and its transferability across different spatial contexts has not been explored. Addressing these gaps will not only provide a much needed broader perspective of woody vegetation-environment relationships in savanna ecology, but will provide the empirical evidence and cross-system research needed to advance the HPDP in landscape ecology.

Historically, technological limitations have made it difficult or even impossible to obtain a large-extent and fine-grain perspective of savanna vegetation. Recent developments in the remote sensing field, however, provide the potential to fill these

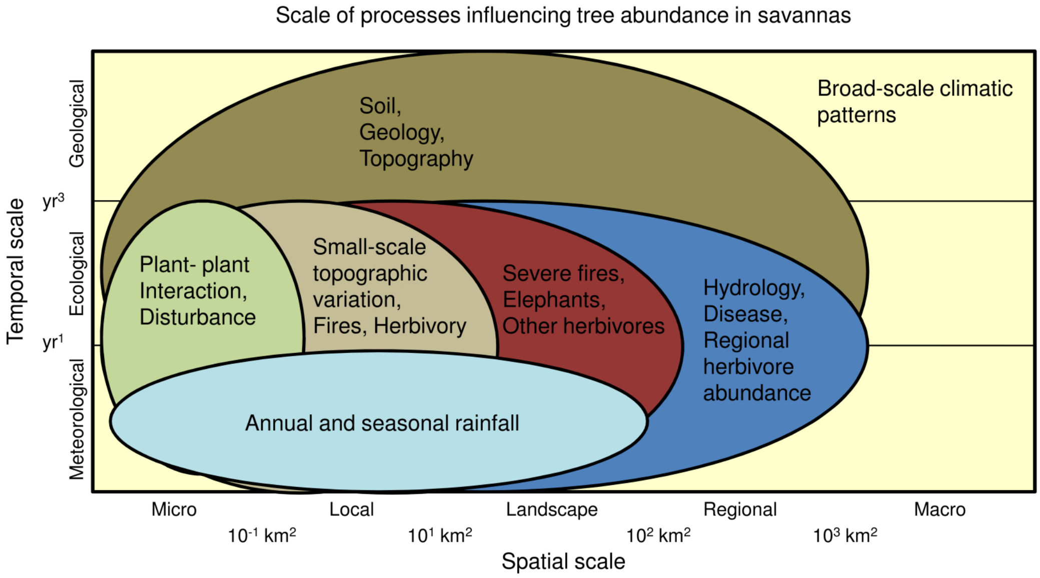


Figure 1.4: A spatio-temporal framework of processes that govern savanna tree density. After Gillson (2004a).

gaps in knowledge and greatly advance current understanding of ecological spatio-temporal patterns and processes in heterogeneous systems.

1.2.3 Developing multi-scaled, spatio-temporal understanding of ecological systems through remote sensing

Remote sensing has typically focused on the coarse-scale representation of landscape features. This focus stems from limitations of sensor spatial resolution, but recent improvements in the spatial and spectral resolutions of sensors have enabled the fine-scale representation of landscapes over large spatial areas (Turner et al., 2003). Whilst certain very high resolution (VHR) sensors, such as QuickBird and IKONOS, hold great potential for mapping vegetation cover, they suffer similar constraints as traditional aerial photography, in that they can only provide a two-dimensional representation of vegetation. Whilst cover is an important constituent of vegetation, the vertical component is increasingly being recognized as critical to ecosystem functioning (Diaz et al., 2004) and biodiversity (Noss, 1990). The presence of specific organisms, and the overall richness of wildlife communities, is highly dependent on the vertical structure of vegetation (MacArthur and MacArthur, 1961; Cumming et al., 1997; Fenton et al., 1998).

The vertical representation and description of woody vegetation has historically relied on field surveys that are time intensive and impractical over large spatial areas. Developments in the forestry industry led to the use of range finder technology that can greatly aid the field based description of vegetation structure, but it is still spatially limited and time intensive. Synthetic Aperture Radar (SAR) and laser altimetry have emerged as solutions to these problems as they have the ability to return vegetation height information remotely over large areas. SAR holds much potential for monitoring vegetation communities in savanna landscapes as it has the ability to penetrate cloud cover, which is often present in tropical and sub-tropical regions (Menges et al., 2001). SAR can therefore provide valuable insight into temporal changes in ecosystems by enabling monitoring at all times of the year. The sensitivity and accuracy of SAR devices have, however, been shown to fail with increasing above ground biomass and leaf area index (Waring et al., 1995).

Laser altimetry, or Light Detection and Ranging (LiDAR), is an alternative laser-based technology that is beginning to show great promise for ecological applications (Lefsky et al., 2002b).

Light Detection and Ranging (LiDAR)

LiDAR devices measure the distance between their sensor and a target. Distance is determined by measuring the elapsed time between the emission of a laser pulse and the arrival of the returned reflection of that pulse. Dividing the time traveled by two, and multiplying by the speed of light, returns the distance between sensor and target surface (Bachman, 1979; Wehr and Lohr, 1999). LiDAR sensors therefore have the ability to directly measure the horizontal and vertical distribution of plant canopies, as well as sub-canopy topography, providing high-resolution topographic maps and highly accurate estimates of vegetation height, cover, and canopy structure (Lefsky

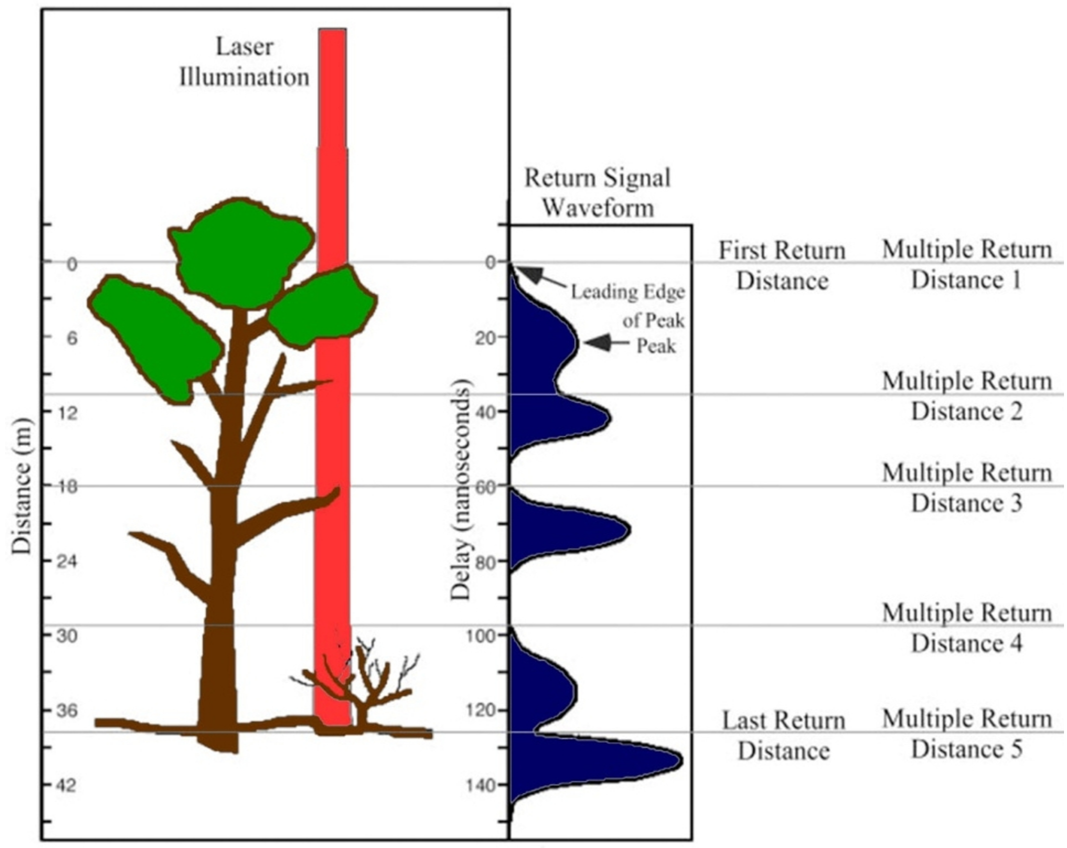


Figure 1.5: LiDAR measurement of vegetation canopies. After Lefsky et al. (2002).

et al., 2002b).

LiDAR systems differ primarily in terms of the nature of the laser pulse (Figure 1.5). Discrete return systems can return ground elevation as well as the above ground height of the first layer of vegetation that the laser strikes. Waveform LiDAR, however, operates at much higher frequencies and can distinguish the full above ground vegetation profile. Discrete return LiDAR has been utilized extensively in forestry applications and has been shown to reliably return ground elevation and tree height data in forested systems (Lefsky et al., 2002a,b). LiDAR has experienced limited use in semi-arid areas, however, and there is no empirical evidence of its reliability in African savannas. Assessing the true value of LiDAR to ecological studies and biodiversity conservation requires the explicit testing of its reliability across a broad range of environments, particularly in heterogeneous systems like savannas.

The integration of remote sensing science with ecology and conservation has often lagged due to a mismatch in scales between the disciplines (Turner et al., 2003). Although recent advances in sensor technologies have addressed this separation, the increased resolutions of remote sensing products present new challenges to ecologists and conservationists. Extracting meaningful information from increasingly large, fine-resolution datasets is a difficult task with traditional pixel-based classification procedures, but the field of object-based image analysis shows promise for addressing this issue (Blaschke, 2003).

Object-based image analysis (OBIA)

Object-based image analysis (OBIA) arose through the realization that image objects hold more real world value than pixels alone (Blaschke and Strobel, 2001). OBIA provides a platform for incorporating contextual and ancillary data in image classification which can greatly enhance the reliability of classification results. OBIA follows a hierarchical segmentation approach, and should therefore be well suited to the analysis of heterogeneous systems. The first step in the analysis is the multiresolutional segmentation of an image into areas of homogeneity. Homogeneity criteria utilize both colour and shape properties. A bottom-up region merging technique merges smaller objects into larger ones based on the criteria set by the researcher. The approach enables segmentation at different scales, which is used to construct a hierarchical network of image objects representing the image information at different spatial resolutions simultaneously (Laliberte et al., 2004). The image objects have relationships to both adjacent objects on the same level and objects on different hierarchical levels. Classification is then performed on the image objects at the desired scale, not the pixels.

The hierarchical object-based approach is appealing for applications in heterogeneous systems, where classification criteria need not remain constant across an image but may vary in different patch contexts. However the potential for OBIA to enhance the interpretation of remotely sensed data in savannas has not been explored. Empirical evaluation of these benefits in heterogeneous savanna systems would greatly benefit both ecological research and biodiversity conservation planning by providing a bridge between remotely sensed and ecologically meaningful data.

1.3 Research aim, objectives and layout of thesis

The primary aim of this work is to advance current understanding of scale and context in heterogeneous systems, in a manner that contributes to the theory of landscape ecology. Central to this aim is the applicability of the hierarchical patch dynamics paradigm (HPDP) in a savanna system. The role of remote sensing in advancing ecological understanding and aiding biodiversity management is also an underlying theme in the thesis. The broad objectives of this research therefore fall into three categories:

1. Remote sensing objective
   - Assess the potential for LiDAR remote sensing to provide a spatially explicit representation of vegetation structure in savanna landscapes (addressed in Chapter 2).
2. Hierarchical patch dynamics objectives
   - Evaluate the pattern-process-scale perspective in a savanna setting (addressed in Chapter 3).
   - Assess the applicability of metastability or shifting mosaic concepts in a savanna setting (addressed in Chapter 4).

3. Broader landscape ecology objective

    - Evaluate the influence of spatial context on ecological pattern-process relationships in savanna landscapes (addressed in Chapter 5).

The introduction of each chapter links back to the key literature discussed thus far and further develops these broad objectives. The key findings in each chapter are first discussed separately, and are then drawn together to explore the implications of scale and context for understanding heterogeneous systems (Chapter 6).

1.4 Study area

The Kruger Park, South Africa, is one of the largest conservation areas in the world and spans over 2 million hectares. High levels of substrate and vegetation heterogeneity (Venter et al., 2003), and the presence of large mammalian herbivores (du Toit, 2003) and fire (van Wilgen et al., 2004), make it a suitable location in which to tackle scientific questions of spatio-temporal pattern. The Shingwedzi Catchment in the northern Kruger is one of the most remote areas in the Park and is one of the few areas left in which to study natural ecological patterns and processes (Figure 1.6). The broader catchment is drained by the Mphongolo, Phugwane, Bububu and the Shingwedzi rivers, across granitic substrates in the west and basaltic substrates in the east (Figure 1.7). The granite substrates have weathered to give rise to sandy soils whilst the basalts have predominately weathered to dark clay soils. Mean annual rainfall for the area is 400mm pa but it can range from 50-600mm pa. All of the rivers of the Shingwedzi catchment are ephemeral as a result of the low and erratic rainfall patterns. The four major rivers flow in most but not all years, and only in the summer months.

The influence of geological substrate and soil type on savanna vegetation is well documented (Scholes and Walker, 1993; Belsky, 1995; Venter et al., 2003) and provides a heterogeneous template which is reflected in vegetation characteristics. The

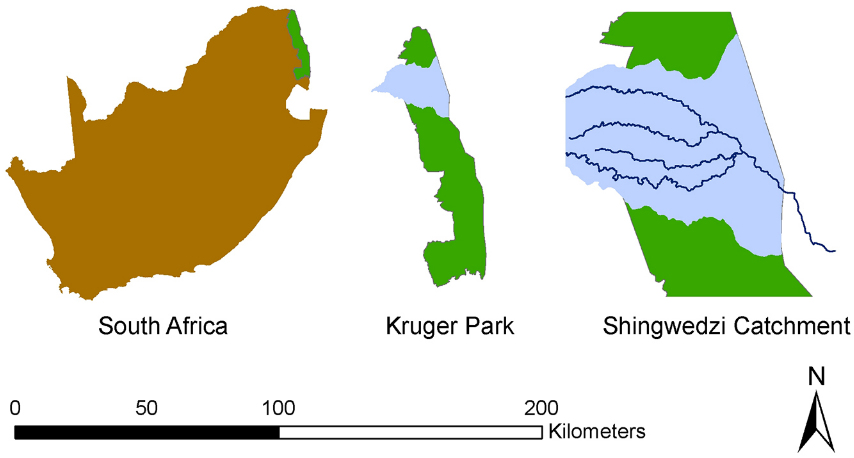


Figure 1.6: Study location. Shingwedzi Catchment, Northern Kruger Park - South Africa.

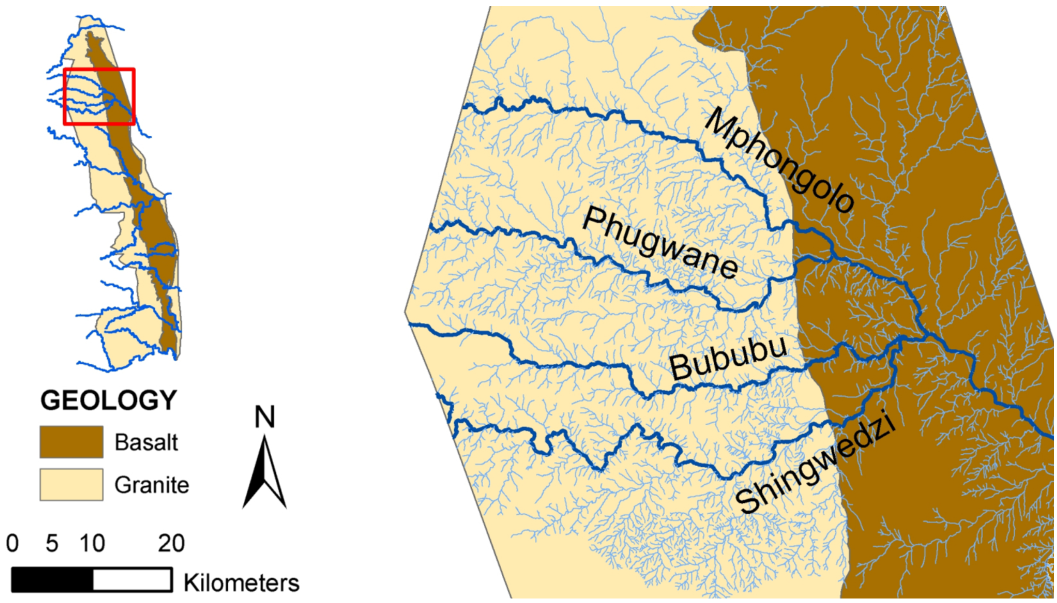


Figure 1.7: Four main rivers of the Shingwedzi Catchment that cross the primary geological divide between granite and basalt.

rivers are all flanked by extensive paleo alluvial deposits which are granitic in origin (Venter, 1990; Khomo and Rogers, 2005). The alluvium is predominately present in the inner bends of rivers and on the upstream side of a tributary confluence. The river channels are deeply (15-30m) incised within the alluvium and flood events are confined within the macro-channel. These alluvial zones form boundaries between the terrestrial upland and the rivers themselves (Figure 1.8). The upland areas are dominated by *Colophospermum mopane* ((Kirk ex Benth.) Kirk ex J. Leonard) trees on the basalts and by both *C. mopane* and *Combretum apiculatum* (Schinz) on the granites. *Salvadora australis* (Scweick) and *C. mopane* are prominent in the alluvial zones. Vegetation within the alluvial zone is distributed in an irregular mosaic pattern and is structurally diverse.

Bare areas within the alluvial zone have a heterogeneous micro-topography where small vegetated islands of different sizes and species composition are raised slightly above harder impermeable soils (Figure 1.9), which are often sodic in nature (Jacobs et al., 2007). The heterogeneity of the Shingwedzi Catchment at multiple scales (Saah, 2004) made it an ideal study location to address the aim and objectives of this work.

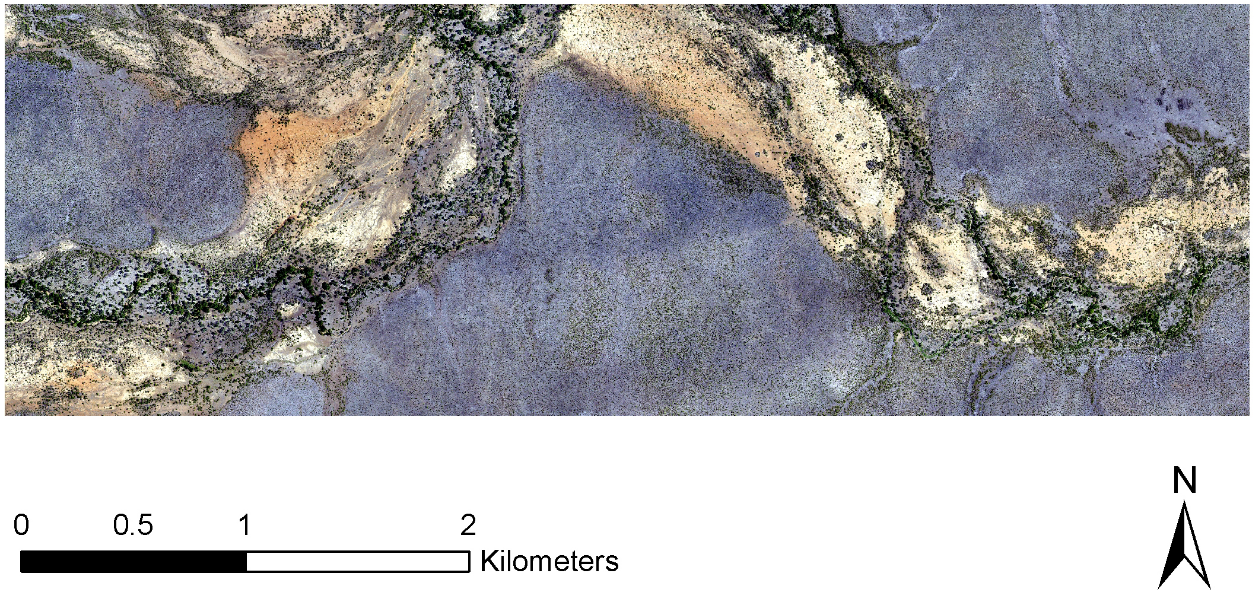


Figure 1.8: Alluvial lowlands and basaltic uplands of the heterogeneous savanna landscape.

Figure 1.9: Heterogeneous micro-topography and vegetation distribution in a sodic site of the alluvial zone.

Chapter 2

Integrating LiDAR and aerial imagery for the spatial representation of savanna woody vegetation structure

2.1 Introduction

The three-dimensional structure of vegetation is vital to both ecological functioning (Belsky and Canham, 1994; Diaz et al., 2004) and biodiversity conservation (Noss, 1990), as the horizontal and vertical components provide diverse habitat for organisms and influence ecological processes such as moisture retention, nutrient cycling and herbivory. Current understanding of the vertical dimension of woody vegetation structure is severely limited in savanna systems, as means of quantifying canopy height over large spatial areas have been lacking. Field-based sampling has long provided site-specific measurements of woody structure, but it is time intensive and impractical over large areas in heterogeneous landscapes. Remote sensing is the only feasible avenue for providing detailed information of system structure and composition over large spatial areas, and LiDAR (section 1.2.3 on page 29) has emerged as the key technology for the fine level mapping of vegetation horizontal and vertical structure (Lefsky et al., 2002b).

LiDAR has experienced extensive use in Northern Hemisphere temperate systems, but its applicability in African savannas has not been explored. The transferability of the technology needs to be tested as the heterogeneous canopy structure of savanna woody vegetation may be problematic for LiDAR measurements and post-processing techniques. Typically, ground returned LiDAR points are interpolated to create a digital terrain model (DTM) representing ground elevation above sea level. Both the ground and vegetation returned LiDAR points are then interpolated into a digital surface model (DSM) representing total elevation above sea level. By subtracting the DTM from the DSM, a normalized canopy model (nCM) is created that represents vegetation height above ground level. Whilst this standard approach produces good results in systems with continuous canopy cover (Maier et al., 2006; Tiede et al., 2006), the discontinuous nature of savanna woody cover is likely to cause interpolation artifacts in the DSM model and lead to substandard results. The fusion of LiDAR with aerial imagery, through object-based image analysis (OBIA) (section 1.2.3 on page 31), has the potential to enhance the structural description of savanna woody vegetation by masking the DSM with a woody coverage layer derived from image objects.

In this chapter I assess the potential of LiDAR to provide a spatially explicit structural description of savanna woody vegetation, and explore the extent to which object-based image analysis may enhance this structural description in heterogeneous landscapes.

The object-based approach used in this chapter, in combination with the one described in Chapter 4 (section 4.2.1 on page 87), has been peer-reviewed and accepted for publication in the first book on object-based image analysis of remotely sensed imagery (Levick and Rogers, *in press*).

2.2 Methods

The outlined objective was addressed by first creating a standard normalized canopy model of savanna woody vegetation from discrete return LiDAR. An object-based normalized canopy model of savanna woody vegetation was then constructed through the fusion of LiDAR and aerial imagery. Both standard and object-based canopy models were statistically compared with ground validated data, and LiDAR canopy height estimates were statistically compared with ground validated data across two dominant vegetation patch types with different canopy architectures.

2.2.1 Standard normalized canopy model (nCM) construction from LiDAR

Acquisition of LiDAR data and aerial imagery

Discrete return LiDAR data and high resolution RGB imagery were acquired for a 1-2km wide strip (60 000ha) along the length of all four rivers of the Shingwedzi Catchment in November 2003 (Figure 2.1). The survey was conducted as part of the River Savanna Boundaries Programme (RSBP), and the flight path was selected to allow comparisons to be made between the alluvial riparian zones and the adjacent upland hillslopes, which are both integral components of savanna landscapes. The aerial scan was conducted by Airborne Laser Solutions, South Africa. An ALTM 1225 (Optech, Canada) sensor with an operational frequency of 25 kHz was used. Average height of the fixed-wing aircraft housing the sensor was 500m above ground level and 15cm vertical accuracy was achieved. Digital RGB imagery was simultaneously recorded at a resolution of 30cm. Raw processing was conducted by ALS in Microstation SE/J™ (Bentley Systems) with the TerraModeler™, TerraScan™ and TerraPhoto™ add-ons (Terrasolid).

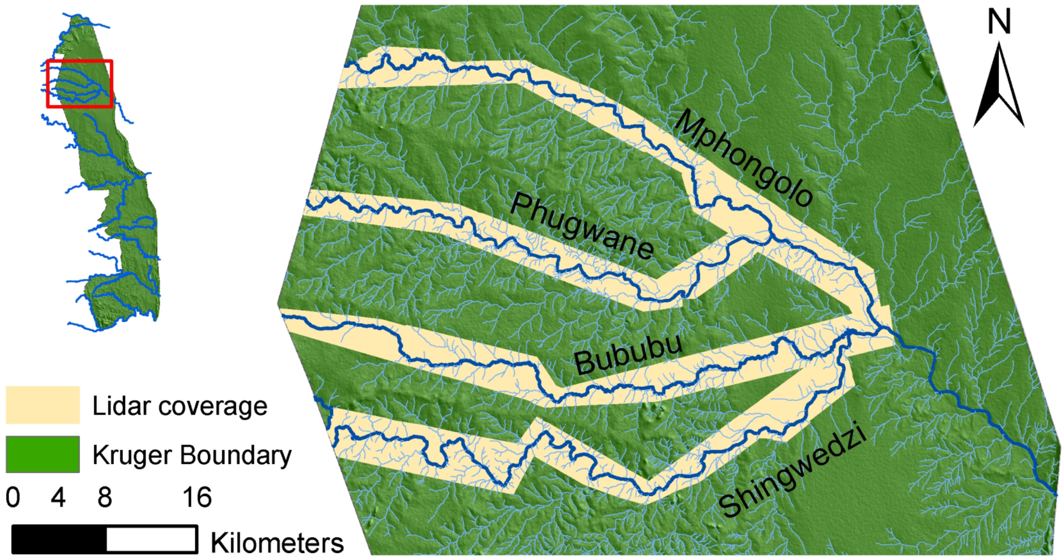


Figure 2.1: Aerial coverage of the LiDAR survey that focused on the major alluvial riparian zones and portions of their adjacent upland hillslopes (two integral components of savanna landscapes).

Construction of a standard normalized canopy model (nCM)

The LiDAR ground points were interpolated to create a high-resolution (1m) digital terrain model (DTM) (Figure 2.2). The interpolation was performed with the inverse distance weighting function in ArcInfo 9.2 (ESRI) . A digital surface model (DSM) was constructed in the same manner through the interpolation of the combined sets of ground and vegetation points (Figure 2.3). A normalized canopy model (nCM) was then created through standard DSM-DTM subtraction (Figure 2.4).

2.2.2 Construction of an object-based normalized canopy model (nCM) through the fusion of LiDAR and aerial imagery

Object-based image analysis (OBIA) was conducted in eCognition 4.0 (Definiens Imaging) and a segmentation and classification procedure was developed to integrate the LiDAR derived nCM with high-resolution aerial colour photography. The segmentation processes utilized the red, green and blue layers of the aerial imagery in conjunction with the nCM. All layers were filtered with a 3 X 3 low pass filter,

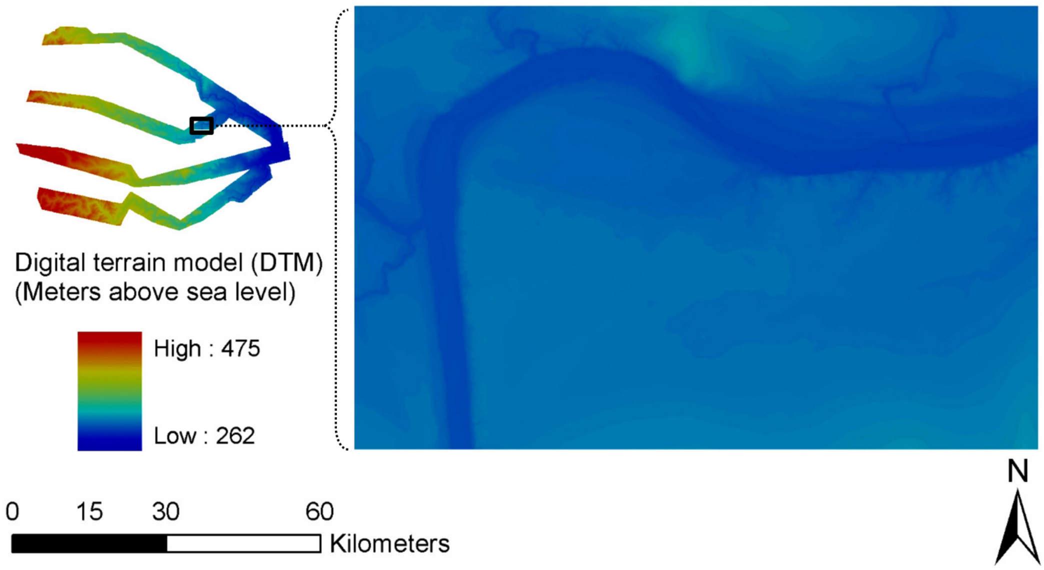


Figure 2.2: Subset of the digital terrain model (DTM) generated from discrete return LiDAR.

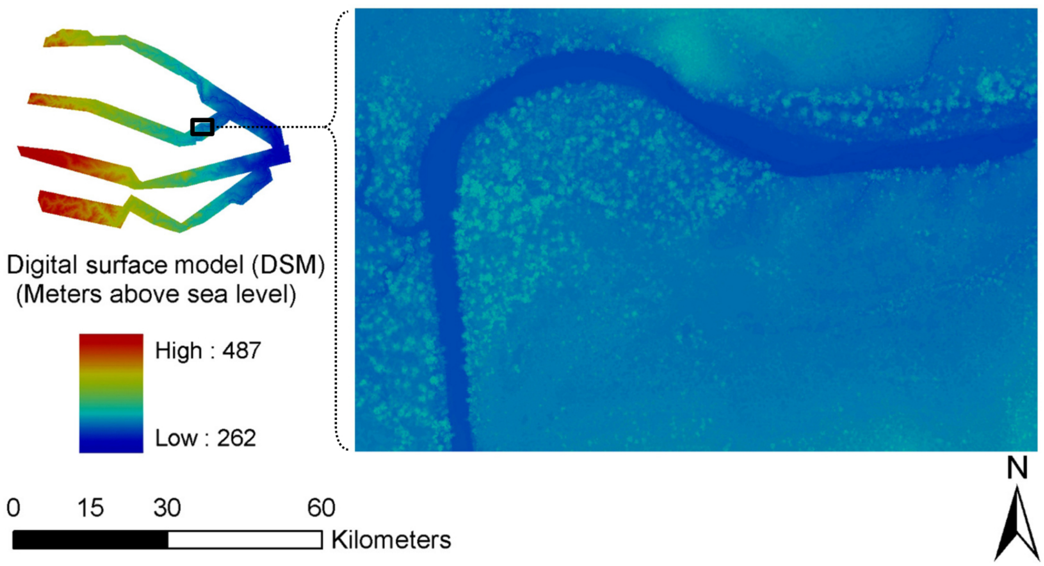


Figure 2.3: Subset of the digital surface model (DSM) generated from discrete return LiDAR.

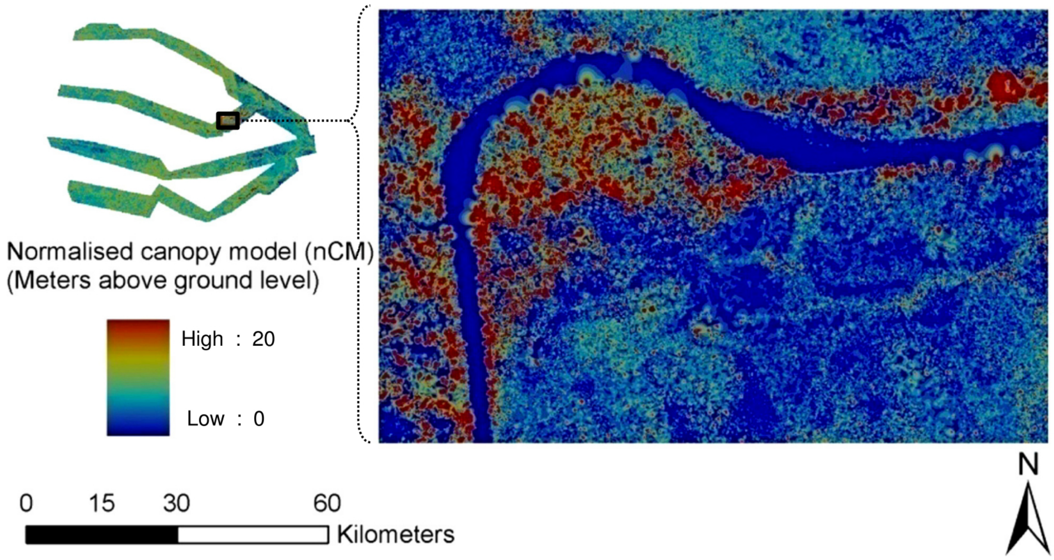


Figure 2.4: Subset of the standard normalized canopy model (nCM) constructed through DSM-DTM subtraction.

prior to segmentation, to remove noise in the data. Segmentation was conducted at two different scales (Table 2.1). A fine-scale, first level segmentation (Figure 2.5a) ensured that even the smallest tree was represented by a single image object. The second level segmentation (Figure 2.5b) aimed to create broader-scale objects that represented similar vegetation patch types within the landscape. The larger scale objects were created to provide context for the smaller objects. The nCM was weighted twice as heavily as each of the colour image layers in the segmentation process.

Table 2.1: Segmentation parameters used to derive the woody canopy mask.

Segmentation	Scale	Colour	Smoothness
Level 1	3	0.8	0.2
Level 2	250	0.7	0.3

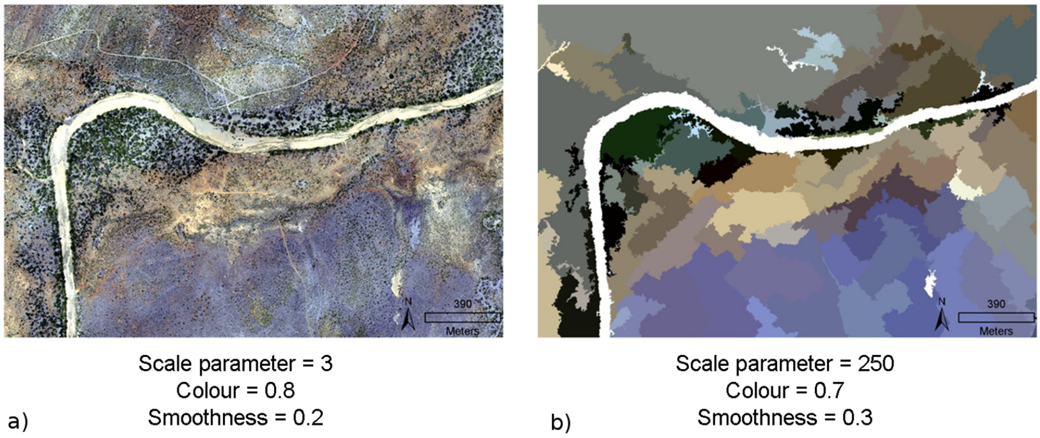


Figure 2.5: Subset of the segmentation results from the fusion of an nCM and imagery at (a)fine and (b) broad scales. The broad scale segmentation provided context for the classification of the finer scale objects.

A classification hierarchy was then constructed to separate out woody cover from that of bare ground and grasses. As a first step, all fine scale objects with a mean above ground elevation of less than 1 meter were considered non-woody. The ratio in spectral properties between the fine and broad scale objects, of the remaining woody objects, was then used to refine the classification by distinguishing small shrubs from dark coloured or wet soils. The resulting classification (Figure 2.6) proved 98% accurate against manual classifications of smaller subset areas.

The woody classification layer was then used to mask the original nCM and ensure that only actual woody coverage was represented in the elevation layer and that potential interpolation artifacts were removed (see Figure 2.7 for full workflow).

2.2.3 Comparison of normalized canopy models and ground validated data

Ground truthing was conducted on 16 sites across the total data set. Sites were selected to cover the main geological divide in the landscape and to ensure that riparian zone, alluvial plains and upland areas were sampled. One hundred ground validation points (50 woody trees and 50 bare ground/grass points) were randomly selected within each site to ensure a high level of confidence in the classification er-

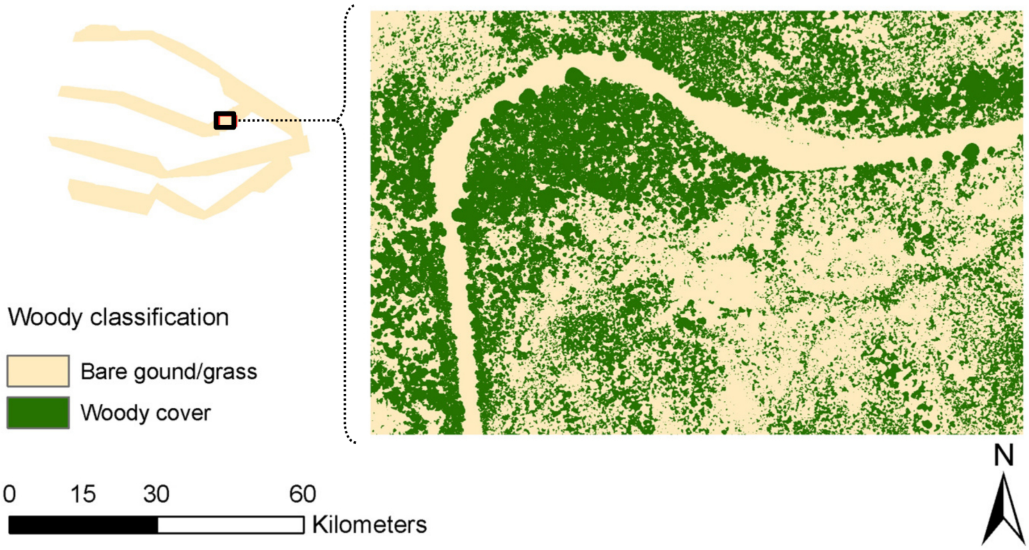


Figure 2.6: Subset of the woody layer mask derived from the nCM and colour imagery classification.

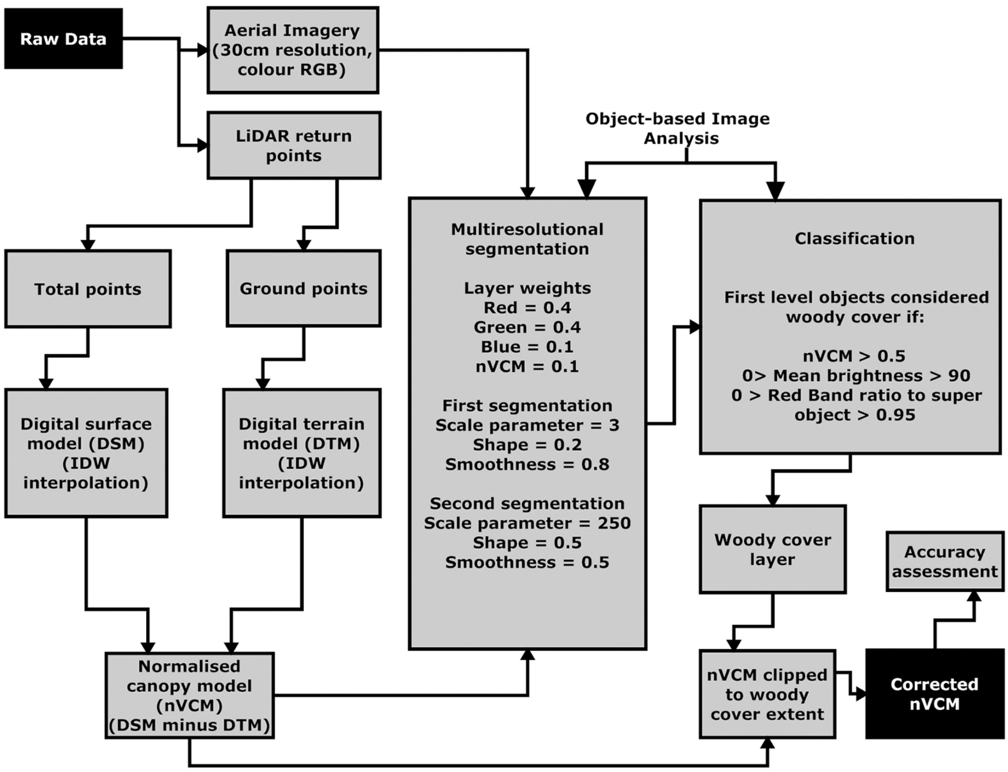


Figure 2.7: Segmentation and classification workflow used to integrate LiDAR with aerial imagery.

ror matrix. Points were located in the field with a Trimble differential GPS and tree height and species, or the presence of bare ground, were recorded at each point. Tree height was measured with a Vertex III hypsometer that was calibrated each morning before sampling. Bare ground/grass points were recorded as inter-gap points with an above ground elevation of zero. Ground measured tree heights were compared against the LiDAR derived heights by means of ordinary least squares regression.

The standard normalized canopy model was compared against the object-based model by means of least squares regression and a 250m cross-sectional profile comparison to test for predicted interpolation artifacts, and to assess if the object-based fusion of LiDAR and imagery improved the structural description of savanna woody vegetation.

2.2.4 Comparison of LiDAR canopy height estimates across different vegetation patch types

LiDAR height estimates were compared against ground-validated data for the two prominent but contrasting woody patch types in the study site. These were patches of riparian forest adjacent to the large rivers with dense canopies, and more sparsely vegetated patches of *Salvadora australis* and *Colophospermum mopane* scrub. Comparisons were made by ordinary least squares regression.

2.3 Results

2.3.1 The object-based fusion of LiDAR and aerial imagery produced accurate structural descriptions of savanna woody vegetation

Ordinary least-squares regression of field measured tree height against the standard nCM indicated that LiDAR returns good estimates of tree height in savanna sys-

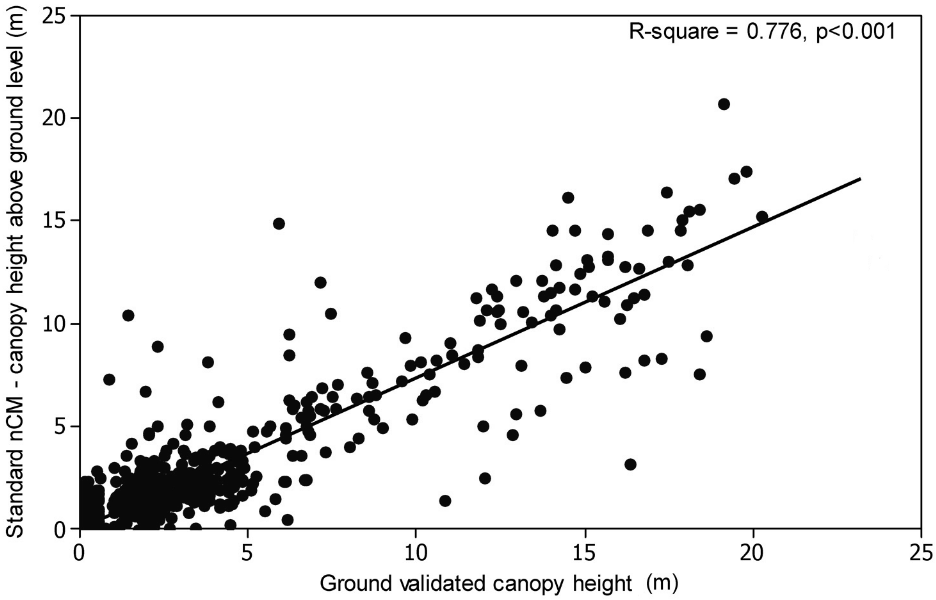


Figure 2.8: Regression of field measured tree height against the standard nCM derived from discrete return LiDAR.

tems (Figure 2.8). The regression was skewed however by a large number of bare ground points in the field data, which were attributed above ground height values in the nCM. This discrepancy is a result of the predicted interpolation artifacts present around the edges and in the gaps of the savanna tree canopies (Figure 2.9). Repeating the regression against the object-based nCM showed a substantial improvement in results (Figure 2.10).

A cross-sectional profile running through both the standard nCM (brown) and the corrected nCM (green) highlighted the differences between the two approaches (Figure 2.11). Very little difference was apparent between the standard and corrected nCM in areas where trees were present, but differences were found in the bare gaps between trees. The cross-section through the standard nCM returned a mean canopy height of 5.17m with a coefficient of variation equal to 78.975. The corrected nCM, however, returned a mean of 3.74m and a coefficient of variation equal to 121.16.

This has important implications for the monitoring of vegetation structure and diversity. Without applying the object-based approach in savannas, remotely sensed

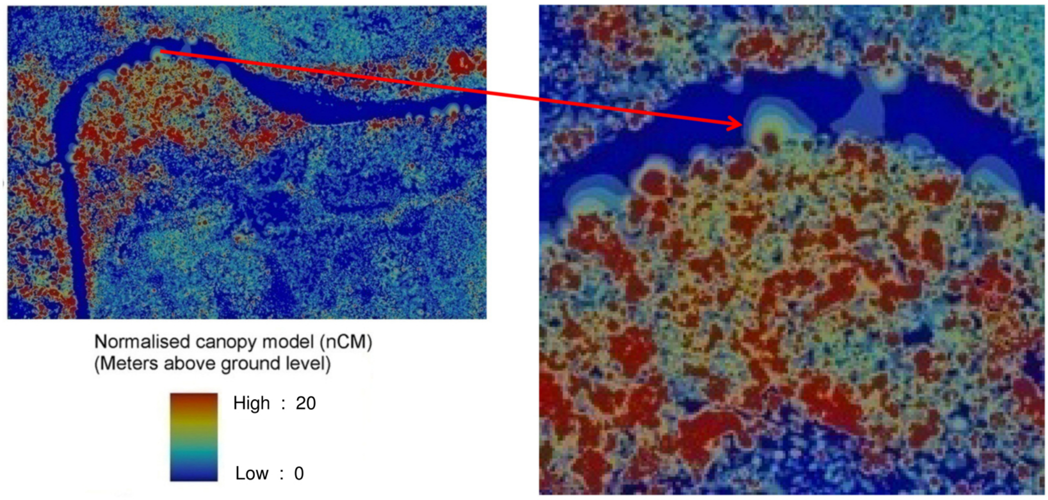


Figure 2.9: Visible interpolation artifacts in the nCM that arose from the discontinuous nature of the woody canopy layer.

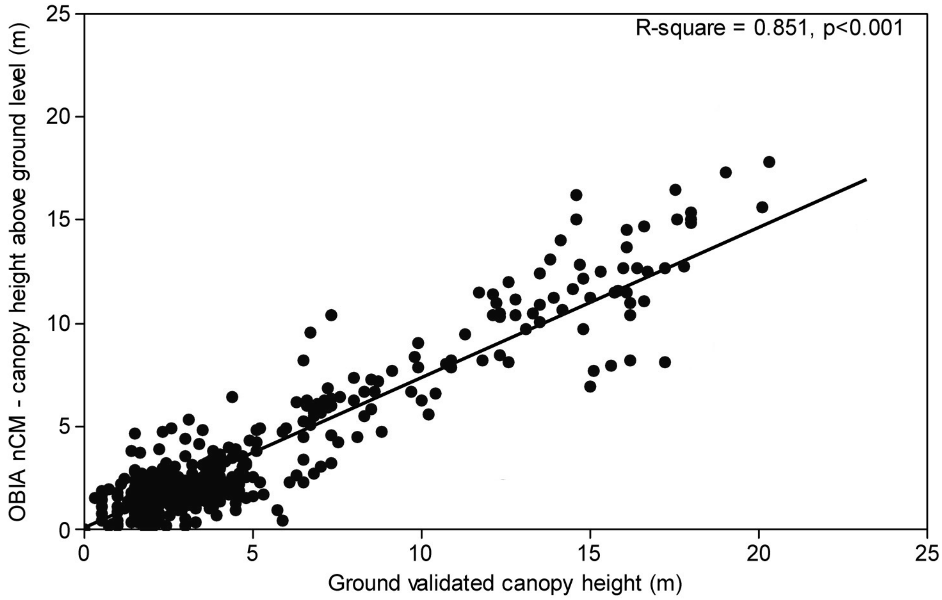


Figure 2.10: Regression of field measured tree height against the nCM derived from discrete return LiDAR and object-based image analysis.

results may greatly overestimate the average above ground canopy height and standing biomass of the system, and underestimate the level of structural diversity. The standard approach depicts the system as being more homogeneous by smoothing over the heterogeneous arrangement and patchy structure of savanna woody vegetation. These results highlight the degree to which the fusion of LiDAR with imagery, through object-based image analysis, can enhance the structural description of savanna woody vegetation by overcoming the nCM interpolation artifacts.

Furthermore, the stratified random approach adopted for ground point selection enforced the sampling of both trees and the bare ground between them. This was important, as if sampling had only been conducted at locations where trees were present, as is often the case, then ground-validation would not have detected the interpolation artifacts and overestimation errors that were present. At the same time, it should be noted that the high R-squared values achieved in this study were partly due to the high number of ground points sampled, as there was very little error associated with the bare ground height estimates in the corrected normalized canopy model.

2.3.2 The accuracy of discrete return LiDAR varies between different vegetation patch types in savanna landscapes

The pattern of residuals versus estimated values, for the corrected nCM and ground-validated data, indicated a spatial influence in the fit of the model (Figure 2.12). Separation of regression points into riparian forest (Figure 2.14) and *Salvadora* / mopane scrub (Figure 2.13) patch types revealed different correlations between LiDAR derived height and ground validated data. The riparian forest model showed an increase in the R-squared value over the global model (R^2= 0.873 compared to 0.851), whilst the *Salvadora* / mopane scrub model showed a decrease (R^2= 0.63 compared to 0.851). Patch type and canopy architecture therefore strongly influence LiDAR results as reliability decreased in the patch type where canopy cover

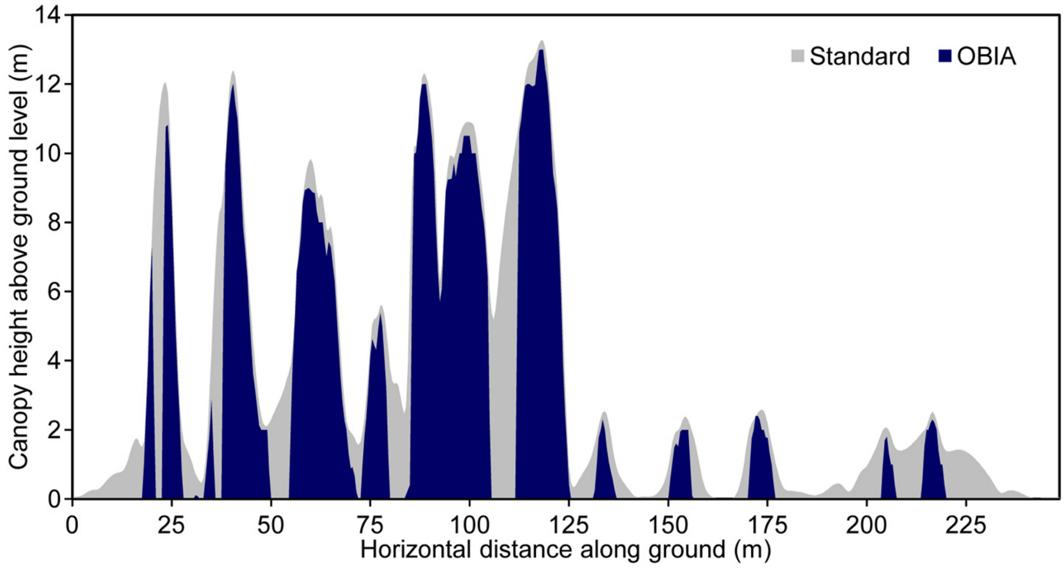


Figure 2.11: Cross-sectional profile of the woody canopy layer illustrating the difference between standard and object-based image analysis normalized canopy models. Standard approaches overestimate average woody height and underestimate structural biodiversity.

was sparser and leaf area index (LAI) was lower. These differences should be considered in future LiDAR based work in savannas where sparse woody coverage is the norm.

2.4 Discussion

Combining elevation data from LiDAR with high-resolution digital colour imagery, through object-based image analysis, greatly enhanced the structural description of a landscape by adding the third-dimension of canopy height. This holds significant implications for vegetation research and biodiversity conservation in savannas by providing a tool for understanding and monitoring vegetation structure remotely.

Developing a sound understanding of the spatial patterns of vegetation structure is an important step in determining the processes that create those patterns (Turner, 1989). If the description of pattern in the landscape is limited or flawed, then so too will be the interpretation of processes operating in that landscape. The fusion of LiDAR and imagery in an object-based image analysis environment, however, pro-

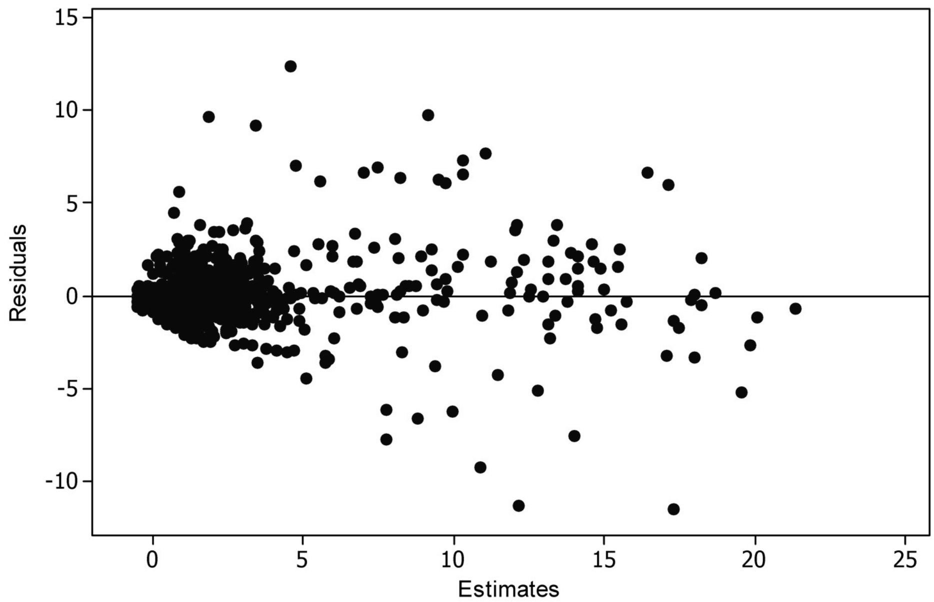


Figure 2.12: Spatial aggregation in the plot of residuals versus estimates for the LiDAR derived height and ground validated data.

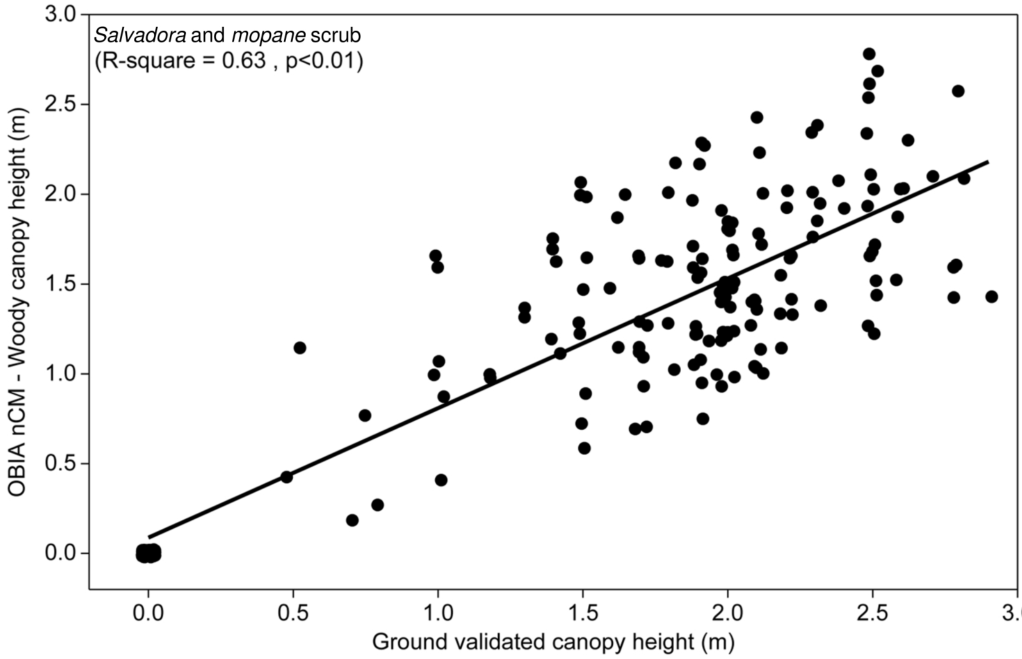


Figure 2.13: LiDAR derived height versus ground-validated data in the *Salvadora* / mopane scrub patch type.

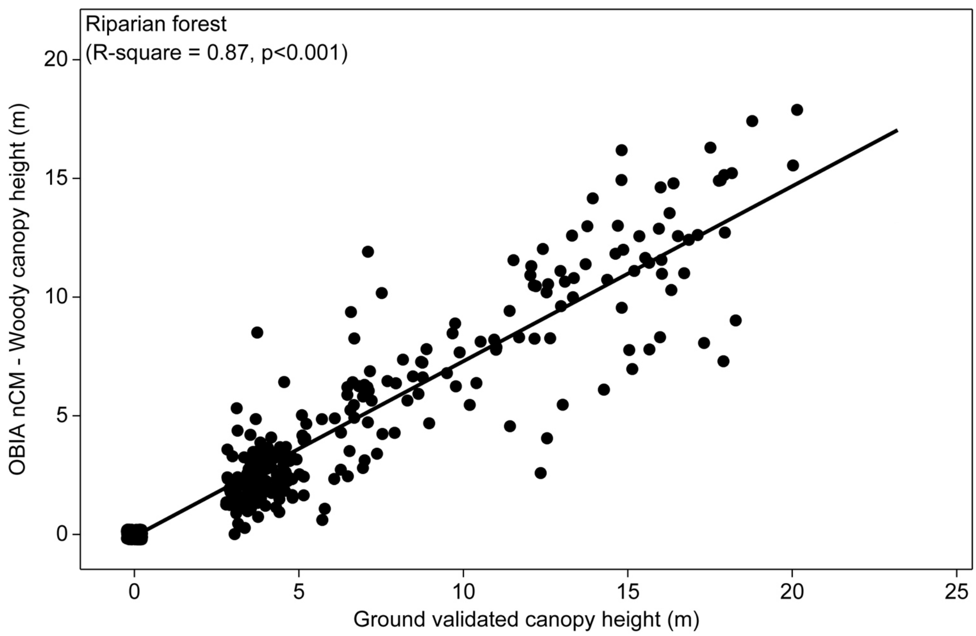


Figure 2.14: LiDAR derived height versus ground-validated data in the Riparian forest patch type.

vided an excellent means of generating spatial representations of woody structure across the savanna riparian landscape.

A primary goal of this thesis was not to simply classify and describe the spatial patterns, but to explore them in a manner that provides ecological insight into the processes driving them. Much contemporary work on pattern has focused on the analysis or description of spatial geometry, but has failed to provide any understanding of the significance or meaning of those patterns (Haines-Young, 2005). This has been exacerbated by the availability of high resolution landscape data in recent years, which provides such a tempting platform for pattern exploration. The multi-scale, contextual approach inherent in object-based image analysis, however, provides both researchers and managers with the potential to gain greater insight into processes driving patterns than single scale descriptions.

The discrete return LiDAR used in this study was not of a high enough frequency to enable individual tree crown extraction (Tiede et al., 2006), but as LiDAR technology progresses and return frequencies increase, individual tree crown extraction will become feasible. Furthermore, the recent fusion of waveform Li-

DAR (wLiDAR) and imaging spectroscopy (Asner et al., 2007), makes it possible for the all three components of biodiversity (structure, function and composition) to be monitored over large areas, as structural measurements from the wLiDAR can be linked to species and chemistry data inferred from the hyperspectral imagery. Individual crown extraction, species level classification and functional linkages are key areas of future research that will greatly enhance current understanding of savanna landscapes. However, the canopy height and canopy cover layers produced in this chapter currently represent an unprecedented dataset of savanna woody vegetation structure over a large spatial area.

The advances in ecological understanding presented in following chapters stem from further analysis of these two datasets.

Chapter 3

Scale variance of woody pattern-process relationships across a savanna riparian landscape

3.1 Introduction

A fundamental assumption of landscape ecology is that reciprocal relationships exist between ecological patterns and processes (Turner, 1989; Pickett and Cadenasso, 1995; Wu and Loucks, 1995). Most ecological processes are inherently spatial as they operate within and between adjacent units (Levin, 1992), therefore quantification of landscape spatial pattern should lead to a better understanding of ecological processes operating within landscape mosaics. A multi-scaled, hierarchical approach is needed to achieve this goal, as patterns at one scale may influence, or result from, processes acting at higher or lower scales (Wu and David, 2002).

Most studies of savanna landscapes have ignored scale and have provided limited insight into both the processes driving vegetation pattern and the scales at which they operate (Gillson, 2004a). It was not until Gillson's (2004a) review of processes influencing tree abundance in savannas that a broad range of driving processes was explicitly linked to specific spatio-temporal scales (Figure 1.4 on page 28). This framework integrated current knowledge of processes operating in savannas, but remains a hypothesis, as many of these pattern-process relationships are yet to be empirically tested. Gillson's (2004a; 2004b) paleo-ecological work did, however, infer that different processes dominate tree abundance at micro (10^2m^2), local (10^{-1}km^2) and landscape scales (10^2km^2), which suggested that principles of the hierarchical patch dynamics paradigm (HPDP) may apply in savanna systems. Current HPDP theory (section 1.2.2 on page 24), developed in northern temperate systems, may therefore benefit greatly from further multi-scaled explorations of heterogeneous savanna landscapes. The HPDP suggests that ecological processes shift with scale along a patch hierarchy (Wu and Loucks, 1995), but the manner in which a broad range of driving processes changes across scales, and the pattern of these changes with scale, have not been empirically explored in many systems, including savannas.

Furthermore, previous studies of pattern-process relationships in savannas have primarily focused on woody cover and tree abundance, but there has been no consideration of the controls on woody vertical structure and structural diversity. The HPDP theory predicts that measures of spatial variance display stepwise patterns of change with scale (Wu and Loucks, 1995), so woody structural diversity should respond differently to other attributes of woody structure over a range of scales, but such differences have never been tested. Pattern-process-scale relationships need to be assessed from a broader perspective of woody vegetation, that considers height and structural diversity, to further develop the HPDP as a unifying framework in landscape ecology.

Lastly, savanna ecology has traditionally shown a strong bias towards the terrestrial environment, despite both the recognition of the importance of water in shaping savanna landscapes (Coughenour and Ellis, 1993), and the recognition of riparian zones as important control points in the landscape (Forman, 1995; Cadenasso et al., 2003b). Although riparian areas are widely regarded as zones of high structural diversity (Naiman and Decamps, 1997), this assumption has also not been validated over large areas in savanna systems, and the biodiversity contribution of stream networks to the landscape mosaic has been ignored altogether.

In this chapter I assess the applicability of the pattern-process-scale perspective of the HPDP in savanna landscapes, by exploring how pattern-process relationships change with scale along a patch hierarchy. I approach this question from a broad perspective of woody structure that considers the horizontal component, vertical component, and structural diversity components, across both riparian and upland patch types.

3.2 Methods

Direct measures of ecological processes are difficult to obtain over large heterogeneous landscapes, which means that processes are usually inferred from pattern (Turner, 1989; Wu and Loucks, 1995; Underwood et al., 2000). As such, the manner in which ecological pattern-process relationships changed with scale was assessed by exploring changes in pattern at different scales. The processes underlying the patterns were then inferred through multivariate analysis techniques.

3.2.1 Spatial representation of woody structure

Spatially explicit quantification of system structure is an elementary step towards addressing questions of how pattern-process relationships may vary with scale. The object-based fusion of LiDAR data and aerial imagery (Chapter 2) provided this quantification, and formed the first high-resolution, large-scale representation of woody structure in a savanna landscape. The structural representation comprised both horizontal canopy cover (Figure 3.1) and vertical canopy height (Figure 3.2).

Although canopy cover and canopy height are two key components of woody

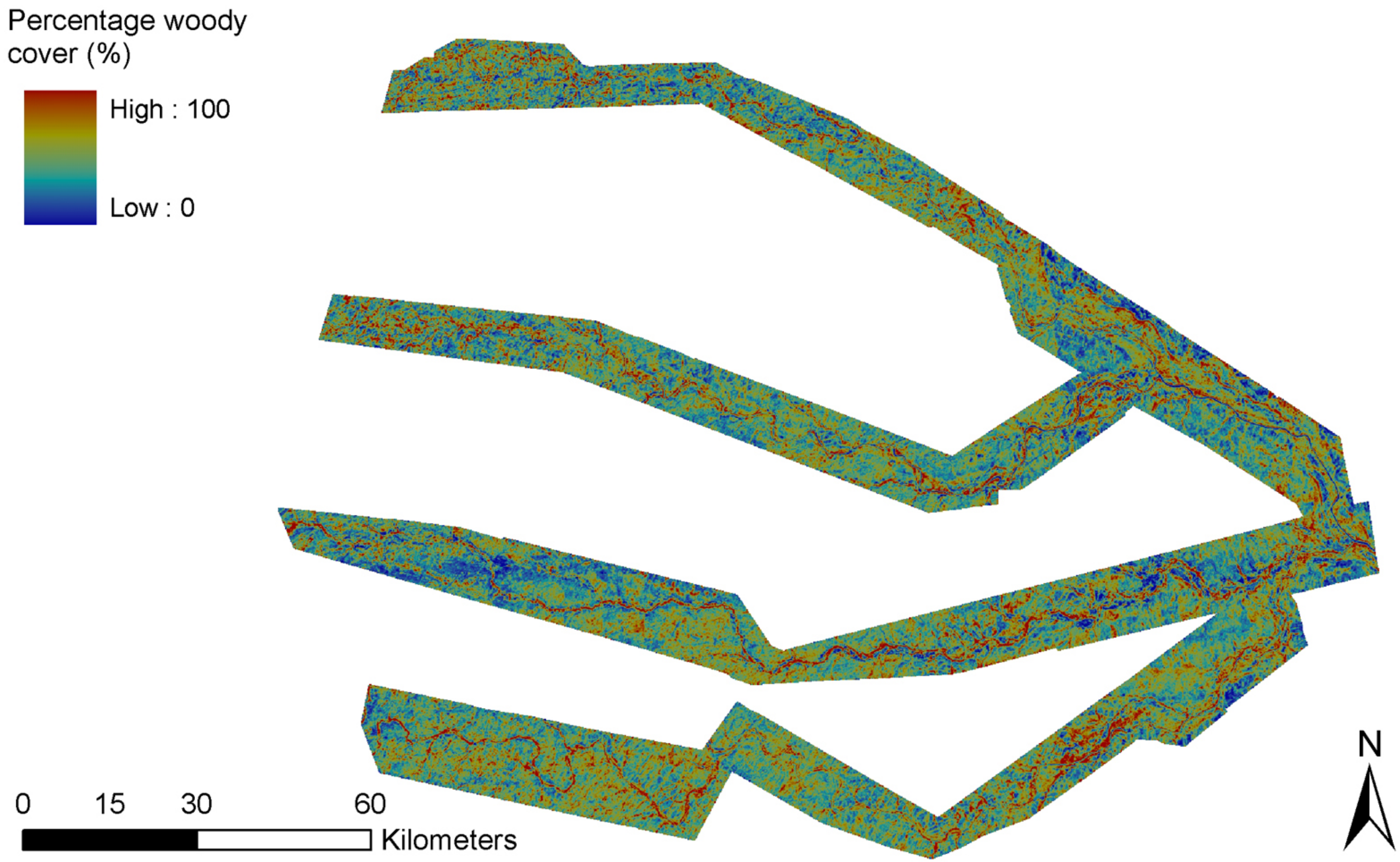


Figure 3.1: Large-scale, fine resolution representation of percentage woody canopy cover (%) across the study site. 60 000ha coverage at 1m resolution.

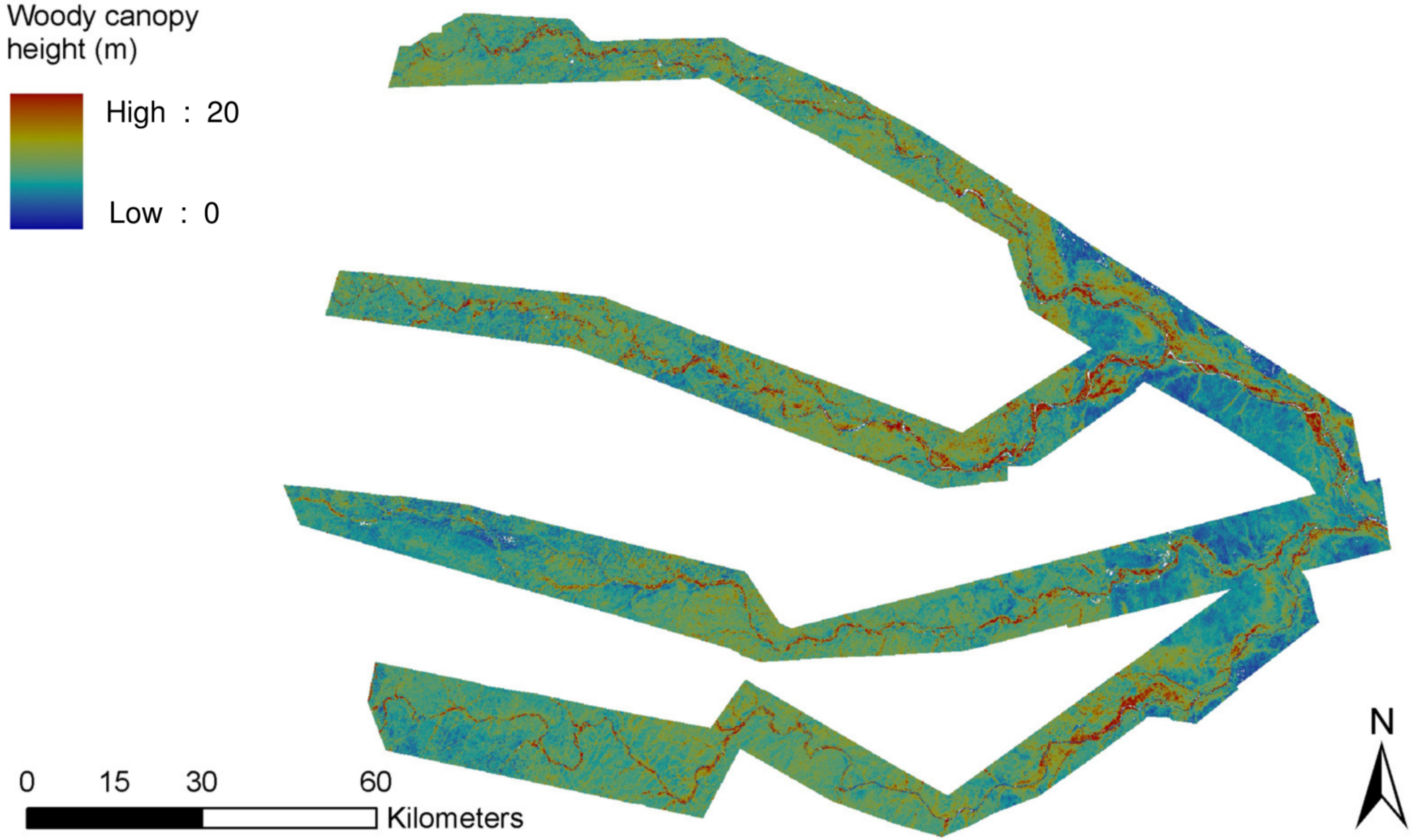


Figure 3.2: Large-scale, fine resolution representation of woody canopy height (m) across the study site. 60 000ha coverage at 1m resolution.

structure, I wished to consider a broader perspective of woody structure, and therefore explored means of evaluating cover diversity and height diversity from the base layers of canopy height and canopy cover. Methods of quantifying structural diversity are poorly established as biodiversity research has primarily focused on species diversity. As such, a broad range of indices exists for the characterization of species diversity, but none have been specifically developed for structural diversity. The Shannon-Weiner diversity index stems from information theory (Shannon and Weaver, 1962) and is widely used to characterize species diversity within a community and accounts for both abundance and evenness of the species present (Magurran, 1988, 2004). The index is calculated according to the following equation:

$$H = -\sum_{i=1}^{s} p_i ln p_i$$

whereby p*i* is the proportion of individuals found in the *i* th species and *ln* is the natural logarithm.

The principle of this index is transferable to structural data in categorical format, and it is a commonly used metric of landscape spatial pattern (O'Neill et al., 1988; Turner, 1990). Here, the index was applied to categories of woody canopy height and canopy cover. As the canopy height data ranged from 0-20m, the height layer was reclassified into 20 classes of 1m intervals, and the woody canopy cover layer was also reclassified into 20 categories (5% intervals) for consistency.

This application of the diversity index to the woody canopy cover (Figure 3.3) and canopy height (Figure 3.4) data provided the first spatial representation of woody structural diversity over such a large area.

The four layers (canopy cover, canopy height, cover diversity, height diversity) formed a unique set of response variables from which to address questions of woody structure. No previous study has been able explore these components of structure over such a large spatial extent, or at such a fine resolution.

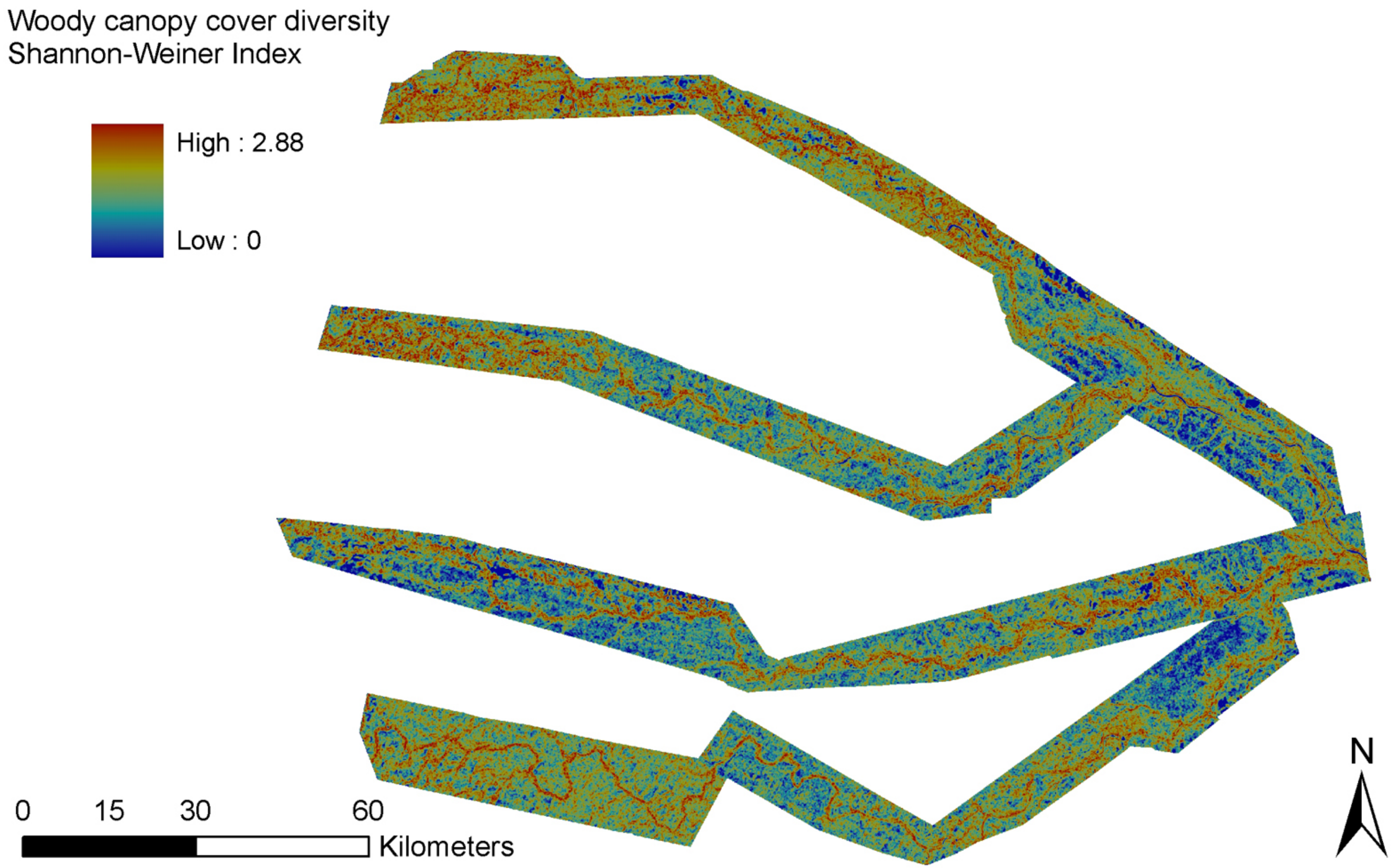


Figure 3.3: Large-scale, fine resolution representation of woody canopy cover diversity (Shannon-Weiner Diversity Index) across the study site. 60 000ha coverage at 1m resolution.

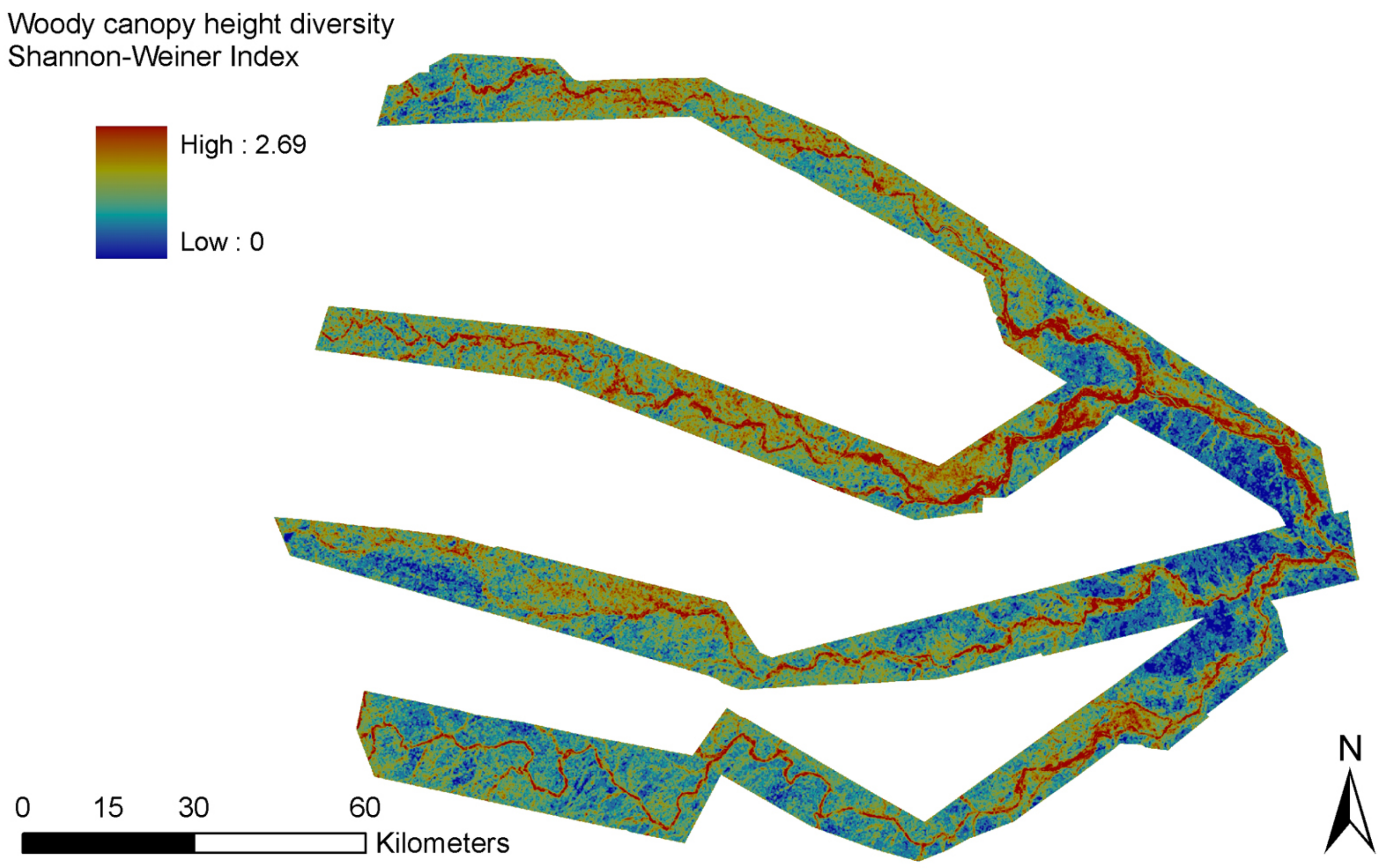


Figure 3.4: Large-scale, fine resolution representation of woody canopy height diversity (Shannon-Weiner Diversity Index) across the study site. 60 000ha coverage at 1m resolution.

3.2.2 Relationship between spatial patterns of woody structure and environmental variables at different scales

Selection of environmental variables

The four response variables described above were evaluated against a wide range of environmental variables to draw inference of the ecological processes underlying woody structure. The environmental variables were selected according to both their deemed importance in published literature, and their suitability to explore the outlined questions by accounting for "large and slow" and "small and fast" processes, which would be expected to act at different scales (Gillson, 2004a). The 22 explanatory variables fell into five broader categories of substrate, hydrology, topography, landscape position and management (Table 3.1 provides description and justification for selected variables).

The majority of the variables were derived directly from the source data using the Spatial Analyst function in ArcInfo 9.2 (ESRI), but aspect was first cosine and sine transformed to create continuous representations of north-south and east-west orientation (Kupfer and Farris, 2007). The spatial records of fire history were reanalyzed to calculate the fire return interval at different spatial locations across the study area, and I custom built the relative elevation model (REM), which represents elevation above the nearest major river channel, in ArcGIS Model Builder (ESRI).

This set of environmental variables predominantly represented bottom-up processes, but top-down processes were accounted for through the inclusion of fire return interval, and the measures of proximity to rivers and water points which can act as proxies for the intensity of herbivory in semi-arid landscapes (Brits et al., 2002; Gaylard et al., 2003).

Table 3.1: Five broad categories of environmental variables selected for their potential to influence woody structure and dynamics.

Category	Variable	Reasoning/references	Data sources
Substrate	Geology (Granite, Basalt)	The importance of substrate material in shaping savanna vegetation is well established in the literature (Coughenour and Ellis, 1993; Scholes and Walker, 1993; Belsky, 1995; Scholes et al., 2003).	KNP GIS repository Digitised from 1:50 000 geological maps and South African defence-force soil maps
	Soil type (Alluvium, sand, clay)		
Hydrology	River catchment (Mphongolo, Phugwane, Bububu, Shingwedzi)	These variables reflect differences in water availability across the landscape, which strongly influences vegetation structure in savannas (Coughenour and Ellis, 1993; Belsky, 1995; Ludwig and Tongway, 1995; Ludwig et al., 2005).	Defined and calculated from CGIAR-CSI 90m SRTM data.
	Contributing area (CTA)		
	Flow length		
Topographic	Elevation above sea level (DTM)	Topographic variables affect woody structure through their influence on soil properties (Milne, 1935; Scholes and Walker, 1993) and water movement (Tongway and Ludwig, 1989; Aguiar and Sala, 1999; Ludwig et al., 1999).	DTM derived from LiDAR data, interpolated at 1m resolution. The other topographic variables were calculated from the DTM.
	Slope		
	Aspect		
	Run-on/run-off zones		
Position	Relative elevation above river channel (REM)	Elevation above the river channel influences woody vegetation in savanna riparian landscapes (van Coller et al., 1997; 2000).	Custom model derived from the LiDAR DTM.
	Distance to large rivers	Riparian zones may experience higher levels of herbivore utilization than other parts of the landscape (Naiman and Rogers 1997, Levick and Rogers 2008a).	KNP GIS data repository Digitised from 1:50 000 topographic maps
	Distance to small rivers		
Management	Fire return interval	The influence of fire on woody plant structure in savannas is well established (Dublin et al., 1990; Bond and van Wilgen, 1996; Trollope et al., 1998; Eckhardt et al., 2000; van Langevelde et al., 2003). Fire return interval has impacted woody structure in the Kruger Park (Higgins et. al., 2007).	KNP GIS fire records (1970 – 2001).
	Distance to water points	Artificial water point provision can impact woody structure by concentrating herbivore utilization around the water source (Brits et al., 2002)	KNP GIS data repository
	Distance to roads	Road construction can influence woody structure by disturbing soil and increasing water run-off along the verges (Lamont et al., 1994; O'Farrell and Milton, 2006).	KNP GIS data repository

Multi-scaled sampling design

Woody structure-environment relationships were explored through a hierarchically nested sampling procedure, which considered three spatial scales, to test for scale variance along the patch hierarchy. Scale selection was determined by a combination of: (1) the spatial extent of different soil-types within the LiDAR coverage, and (2) the consideration of vegetation distribution patterns previously recorded within the broader Shingwedzi Catchment (Khomo, 2003; Saah, 2004), (3) the maintenance of a consistent scaling relationship between the three scales.

The largest spatial scale of analysis was determined by both the extent of the LiDAR coverage and the distribution of soil-types within the landscape. The largest circular plot that could adequately cover the different soil-types, without overlapping different substrates, was 100ha in area. The broad-scale plots were distributed across the study area in a stratified random manner, using proportional allocation (Manly, 1992), which resulted in the distribution of 362 plots across the LiDAR coverage. Five 10ha plots were then randomly placed with each of the 100ha plots, and five 1ha plots were randomly placed within each of the 10ha plots, to produce a multi-scaled sampling design which maintained a constant scaling relationship (Figure 3.5). The random placement of plots was achieved with Hawth's Analysis Tools for ArcGIS (Beyer, 2007). This sampling design ensured proportionate, multi-scaled coverage of the alluvial soils of the riparian zones and of the sand and clay soils of the upland areas.

Exploring woody structure-environment relationships

Woody structure-environment relationships were explored, at each of the three scales of analysis, through canonical correspondence analysis (CCA), which is a constrained multivariate technique to expose the relationships between biological assemblages and their environment (ter Braak, 1987). The method is designed to extract synthetic environmental gradients from ecological datasets, which form the

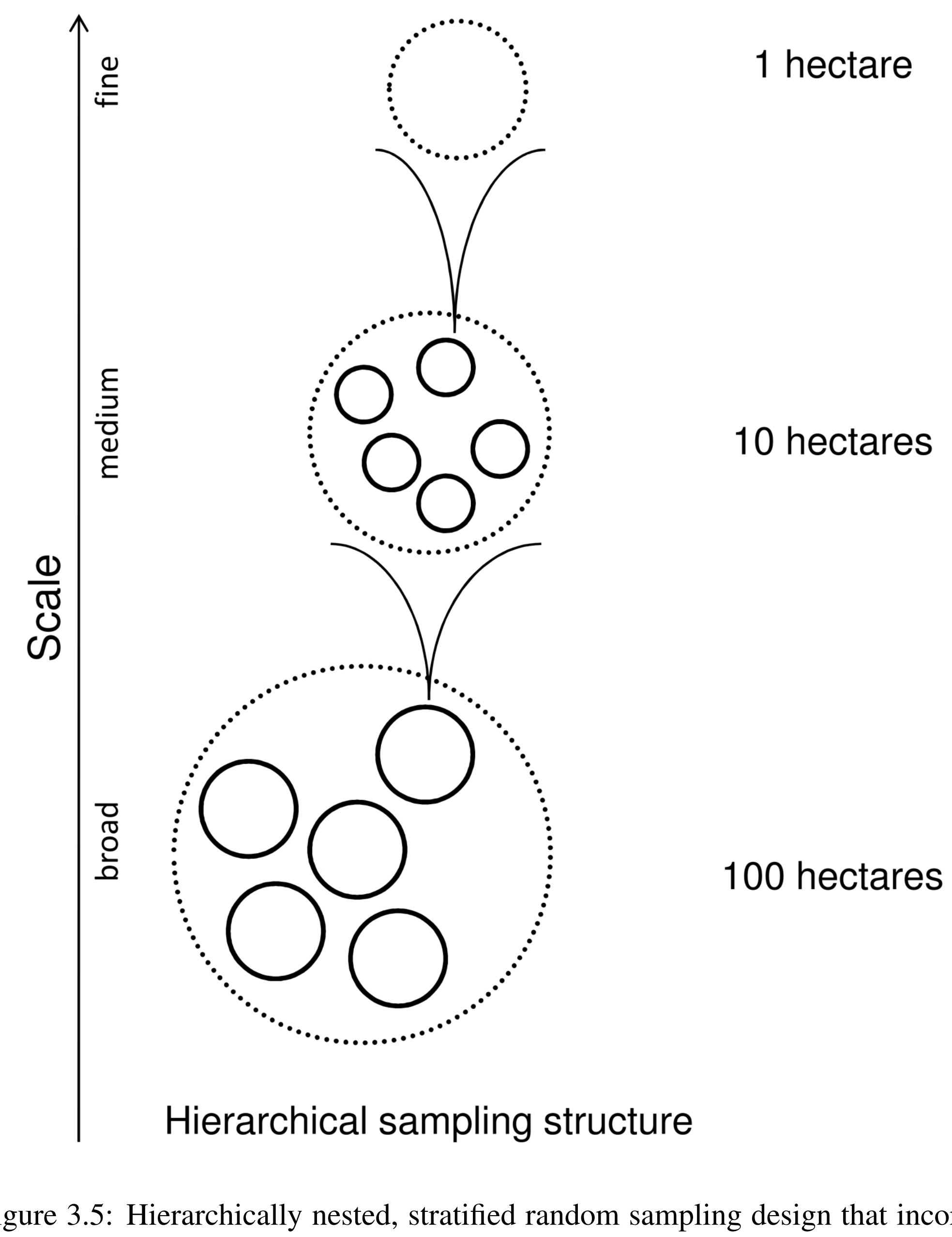


Figure 3.5: Hierarchically nested, stratified random sampling design that incorporated three scales: 100ha (broad-scale), 10ha (medium-scale) and 1ha (fine-scale).

basis for describing and visualizing habitat preferences through ordination diagrams (ter Braak and Verdonschot, 1995). All CCA procedures were conducted in CANOCO version 4.5 (ter Braak and Smilauer, 1998) and Brodgar version 2.0 (Highland Statistics). Environmental variables were tested for normality prior to inclusion in the model, and non-normal variables were log transformed and retested to satisfy the assumptions of the technique. Environmental variables were subjected to forward selection by Monte Carlo tests (999 permutations) and only variables that significantly contributed to the explained variation were retained ($p<0.05$).

CCA analysis requires categorical response variables for analysis, so the four response variables were reclassified into ten classes of woody canopy height, canopy cover, height diversity and cover diversity. The number of size classes was limited to ten to enable clearer interpretation of the resulting ordination diagrams. The abundance of each height, cover, height diversity and cover diversity size class was recorded in each plot at the three scales of analysis. Categories or mean values of the environmental variables were also recorded in each plot, at the three scales of analysis, to provide a basis from which to explain the spatial distribution of the response variables.

3.2.3 Scale variance in woody structure-environment relationships

The manner in which woody structure-environment relationships changed with scale was assessed through partial correspondence analysis (PCCA), which is a modification of standard CCA (explained in detail by Borcard et al. 1992). Evaluation of the total unconstrained inertia in a dataset, against the sum of the canonical eigen values, provides a measure of how much of the response variable variation can be explained by the environmental variables (Borcard et al., 1992). As such, PCCA is being increasingly utilized to understand the contributions of different explanatory variables to the total explained variation in a dataset (Anderson and Gribble, 1998;

Pozzi and Borcard, 2001; Stave et al., 2005; Campagne et al., 2006).

The procedure involves the stepwise running of a series of CCAs in which at each step, a focal group of environmental variables is retained and the remaining environmental variables are treated as co-variables. By repeating this process for all possible combinations of environmental variable groups, the contribution of each group of environmental variables to the total explained variation can be partitioned out. The PCCA procedure was conducted in CANOCO 4.5 and Brodgar 2.0 to partition the total explained variation in woody structure and structural diversity among the five broad categories of environmental variables used in the analysis (Table 3.1). Variance partitioning was conducted at each of the three scales of analysis to determine how the contribution of the different categories of environmental variables, to the total explained variation in woody structure-environment relationships, changed with scale.

The extraction of these patterns provided a means of exploring whether or not ecological processes had shifted with scale along a patch hierarchy, and if spatial variance measures (structural diversity) exhibited stepwise patterns of change with scale, as predicted by the HPDP.

3.3 Results

3.3.1 Changes in woody structure-environment relationships with scale

The explanatory power of the environmental variables decreased with scale of analysis for all four woody structural attributes (Figure 3.6). The environmental variables explained more of the variation in woody height attributes than they did for canopy cover attributes across all scales, suggesting that different components of the woody layer respond differentially to environmental processes.

The contribution of substrate variables dominated the total explained variation

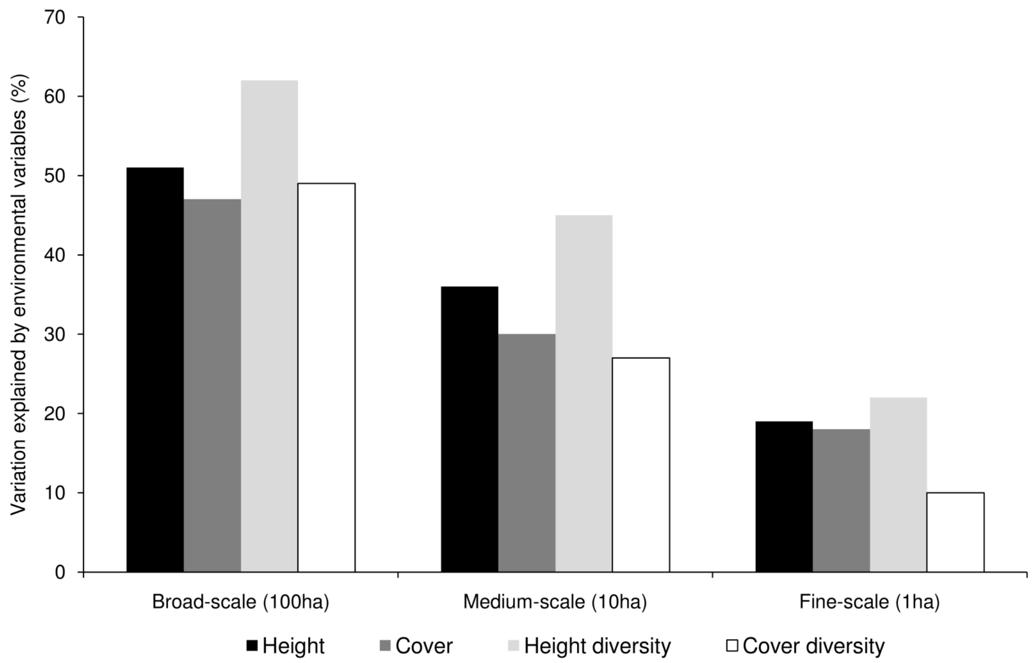


Figure 3.6: The influence of scale on the proportion of the variation in woody structural attributes that was explained by all the environmental variables. Total explained variation was determined by comparison of constrained and unconstrained Eigen values.

in the distribution of all four woody structural attributes (Figure 3.7, Figure 3.8, Figure3.9 and 3.10), highlighting the strong association between geology/soil-type and woody vegetation. Categories of environmental variables displayed scale variance in their relationship with woody canopy height (Figure 3.7) and with woody canopy cover (Figure 3.8). The contribution of substrate variables decreased with scale of analysis, while landscape position and topography variables became more prominent in both cases. Hydrology variables contributed a large proportion of the explained variation in woody canopy height, but not canopy cover, at the broad-scale (100ha), with the reverse being true at the fine-scale (1ha). Likewise, the contribution of management variables, to the total explained variation, showed opposite scale relationships with woody canopy height and woody canopy cover. These patterns highlight the importance of considering multiple attributes of woody structure, as woody height and cover responded differentially to environmental variables across the range of scales. Therefore, studies that only explore one component of

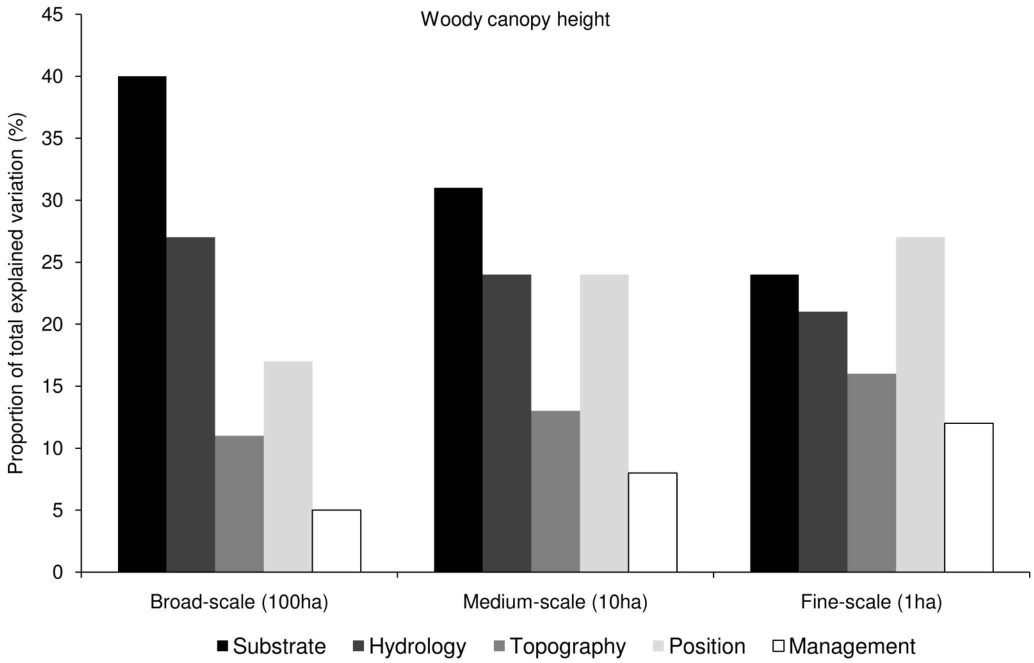


Figure 3.7: Contribution of different categories of environmental variables to the total explained variation in woody height class distribution at different scales.

woody vegetation, or one scale of analysis, will fail to gain full understanding of the processes that influence woody structure as a whole, and may provide misguided insight into pattern-process relationships.

The value of considering multiple attributes and scales was emphasized by the patterns shown in woody height diversity (Figure 3.9) and cover diversity (Figure 3.10). The contribution of different environmental variable categories, to the total explained variation in structural diversity attributes, differed very little with scale of analysis. To ensure that these scale invariant relationships were not an artifact of the diversity index calculation, the co-efficient of variation of both woody canopy height and canopy cover was evaluated through exactly the same procedure, and displayed the same scale invariance as the Shannon-Weiner diversity index.

The scale variant patterns shown by woody height and cover validate the pattern-process-scale predictions of the HPDP in a savannas setting, as pattern-process relationships shifted with scale along the patch hierarchy. However the scale invariant patterns displayed by woody structural diversity contradict the HPDP prediction

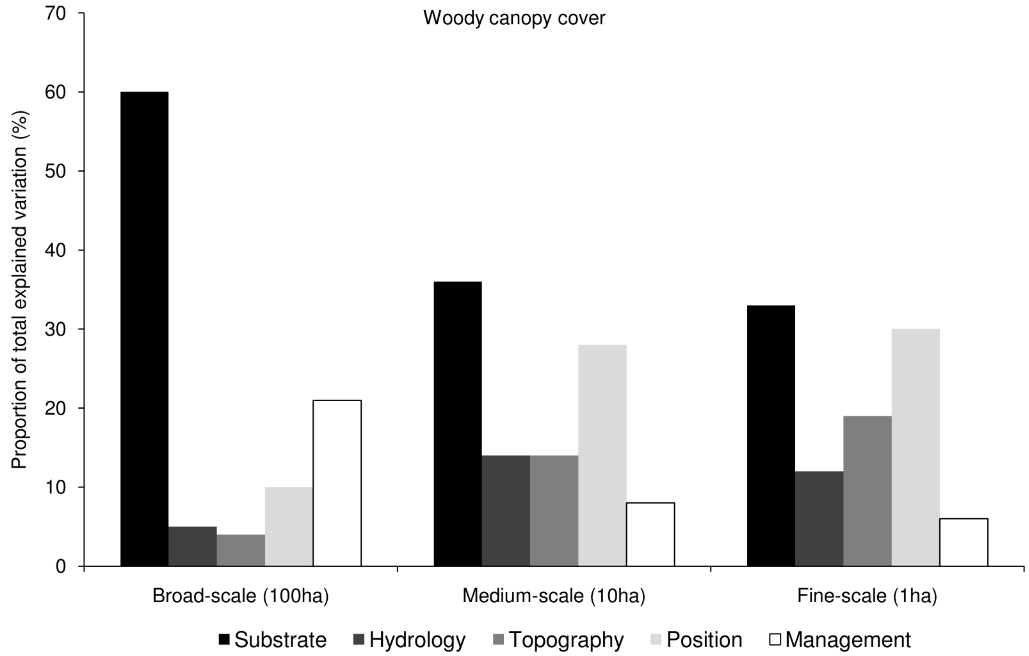


Figure 3.8: Contribution of different categories of environmental variables to the total explained variation in woody cover class distribution at different scales.

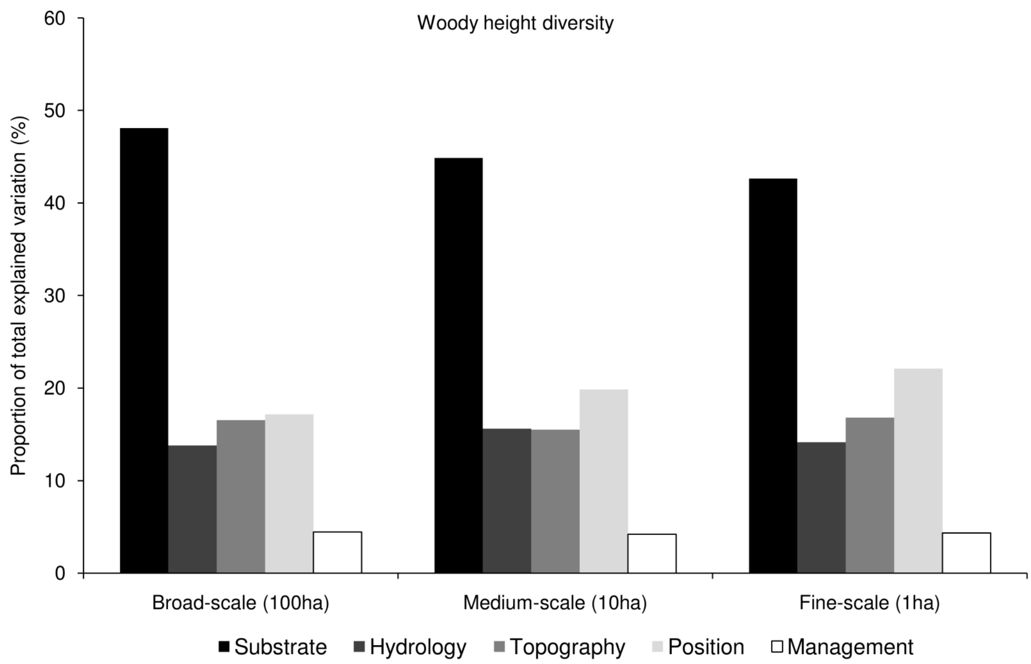


Figure 3.9: Contribution of different categories of environmental variables to the total explained variation in the distribution of classes of woody height diversity (Shannon-Weiner Index) at different scales.

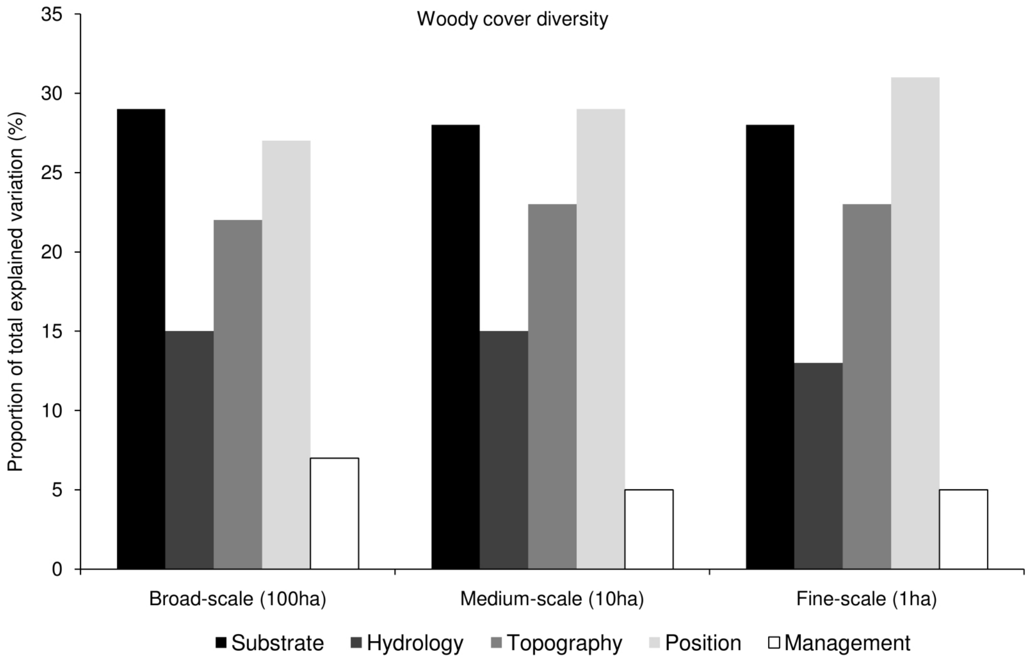


Figure 3.10: Contribution of different categories of environmental variables to the total explained variation in the distribution of classes of woody cover diversity (Shannon-Weiner Index) at different scales.

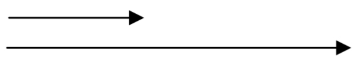
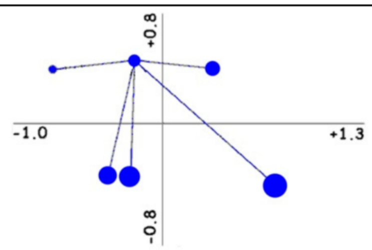
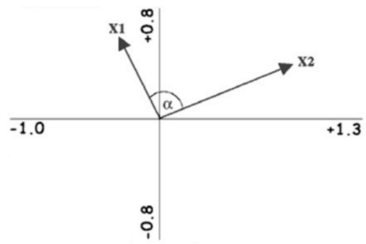
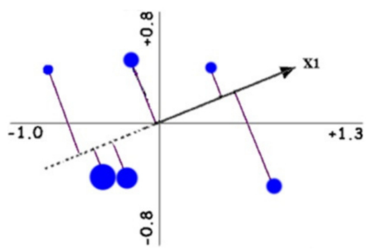
that spatial variance measures exhibit stepwise patterns of change with scale.

3.3.2 Woody structure-environment relationships at different spatial scales

The spatial nature of the differential responses shown by the woody structural attributes was explored further through ordination diagrams, to draw inference of potential underlying processes (Table 3.2 outlines the interpretation of ordination diagrams).

Woody height distribution (Figure 3.11a), cover distribution (Figure 3.11b), height diversity distribution (Figure 3.11c) and cover diversity distribution (Figure 3.11d) displayed strong spatial trends at the broad-scale (100ha). Tall, dense and structurally diverse woody vegetation was positively correlated with the presence of alluvium (riparian zones) and steep slopes (macro-channel banks within the riparian zones), but was negatively correlated with sand and clay soil-types, dis-

Table 3.2: Interpretation of woody structure-environment variable relationships from CCA multivariate plots. After ter Braak and Smilauer (1998).

Graph objects	Interpretation
	Each arrow represents an environmental variable. The length of the arrow corresponds to the degree of influence that the variable exerts on the distribution of woody structure categories. Long arrows indicate strong influences.
	Each dot represents a size class of woody structure. The size of the dot relates to the size class category, so larger dots represent larger size classes.
	The distance between dots in the diagram approximates the dissimilarity of distribution of relative abundance of those size classes across the samples, measured by Chi-squared distance. Points in close proximity correspond to size classes often occurring together.
	Each arrow points in the expected direction of the steepest increase in value of the environmental variable. The angles between arrows indicate correlations between individual environmental variables. Small angles indicate positive correlations between the environmental variables, right-angles indicate little or no correlation whilst large angles (90°-180°) represent negative correlations between variables.
	When size class dots are projected perpendicularly onto the arrow of a particular environmental variable, these projections approximate the optima of individual size classes in respect to values of that environmental variable. The closer a dot to an arrow head, the stronger the positive correlation between size class and environmental variable. Arrows can be projected backwards (dotted line) to explore negative correlations between size classes and environmental variables. Size classes clustered around the origin indicate that the environmental variables have limited explanatory power for the distribution of those size classes.

tance from river, elevation above river channel (REM) and hydrological flow length (upland areas adjacent to the riparian zones). The contrast in woody structure between the alluvial and upland zones highlights the importance of riparian areas in the broader savanna system, as they provide the only template in this landscape for the establishment of tall, structurally diverse woody vegetation.

Only environmental variables that exerted a significant ($p<0.05$) correlation with woody structure were plotted in the ordination diagrams, but fire was the only driver widely regarded at being a strong determinant of woody structure, that was not significantly correlated with woody height and cover at the broad-scale (100ha). These patterns also reveal the dominance of substrate-type and water availability, rather than top-down processes, in influencing broad-scale spatial patterns of woody structure across savanna landscapes.

The composition of the significant environmental variables, however, differed at both the medium-scale (10ha) (Figure 3.12) and at the fine-scale (1ha) (Figure 3.13). The importance of "large and slow" variables diminished and "small and fast" variables become more prominent as scale decreased. Variables that showed stronger correlations with decreasing scale of analysis primarily included ones that would be expected to have a patchy, rather than a homogeneous, influence on woody structure, such as fire return interval, distance to roads, and run-on/run-off zones.

Although the composition of the significant variables differed with scale, the spatial arrangement of woody structure classes remained relatively constant in environmental space. Woody height class distribution (Figures 3.11a, 3.12a and 3.13a), showed strong spatial delineation at all scales, with height class values increasing continuously away from the origin, suggesting that environmental processes structure woody height in a uniform manner. Woody cover class distribution (Figures 3.11b, 3.12b and 3.13b), on the other hand, displayed mixed distribution patterns with different classes of woody cover clustered around each other at all scales, indicating that cover is less environmentally constrained than woody height. For exam-

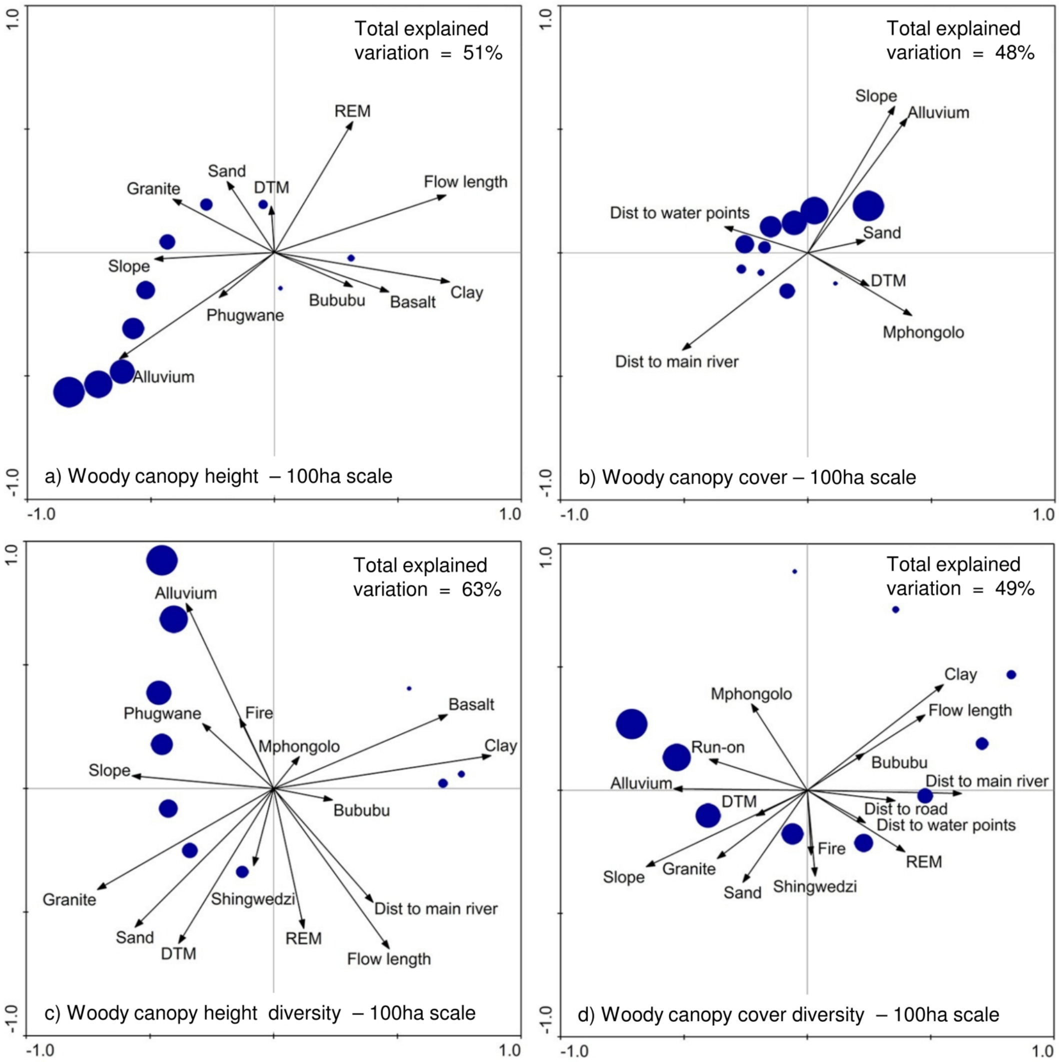


Figure 3.11: Broad-scale (100ha) patterns of woody structure in relation to environmental variables. Blue dots represent size class categories for the different woody structural attributes. Larger dots represent larger size classes. (a) Woody canopy height categories ranged from 0 to 20m in 2m increments. (b) Woody canopy cover categories ranged from 0 to 100% in 10% increments. (c) Woody canopy height diversity categories ranged from 0 to 2.69 on the Shannon-Weiner diversity index in 0.269 increments. (d) Woody canopy cover diversity categories ranged from 0 to 2.88 on the Shannon-Weiner diversity index in 0.288 increments. Total explained variation was determined by comparison of constrained and unconstrained Eigen values.

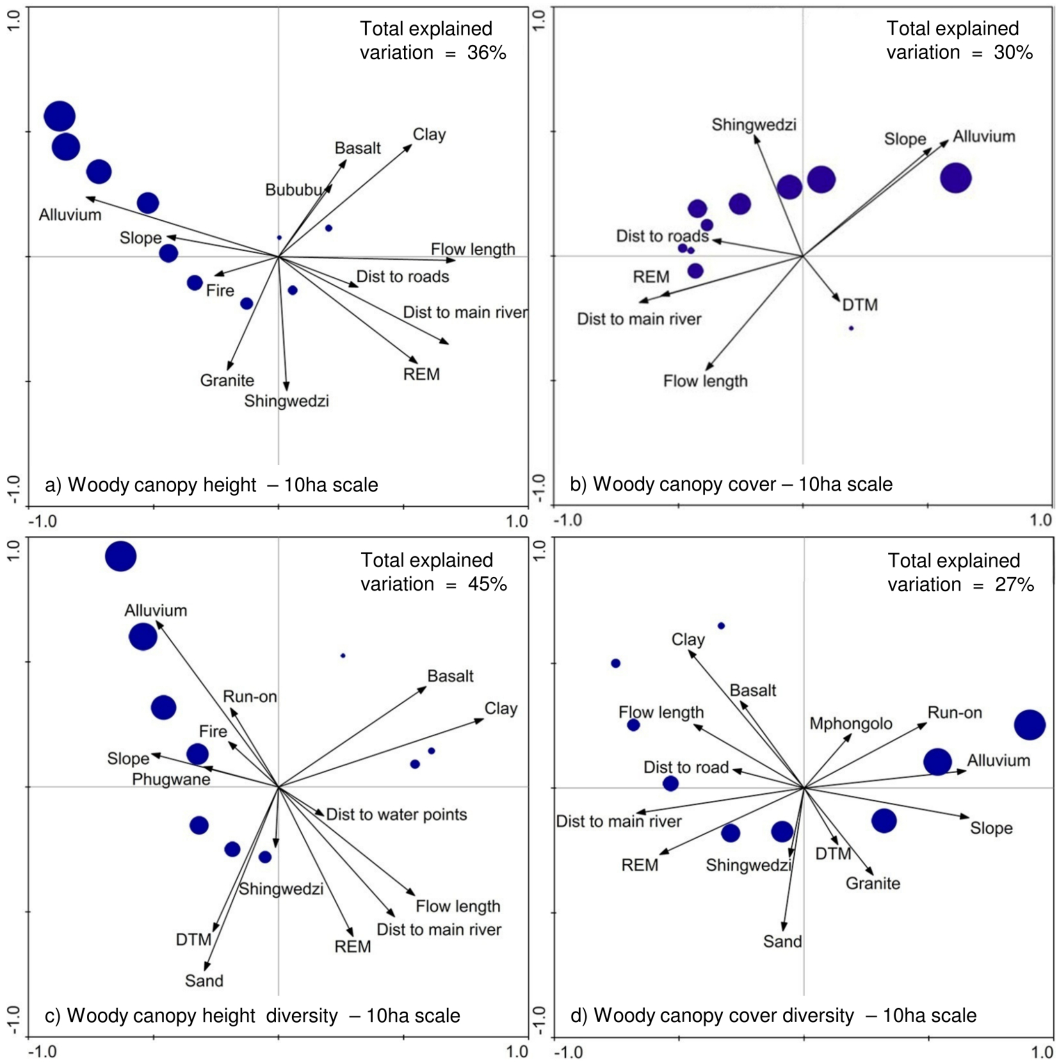


Figure 3.12: Medium-scale (10ha) patterns of woody structure in relation to environmental variables. Blue dots represent size class categories for the different woody structural attributes. Larger dots represent larger size classes. (a) Woody canopy height categories ranged from 0 to 20m in 2m increments. (b) Woody canopy cover categories ranged from 0 to 100% in 10% increments. (c) Woody canopy height diversity categories ranged from 0 to 2.69 on the Shannon-Weiner diversity index in 0.269 increments. (d) Woody canopy cover diversity categories ranged from 0 to 2.88 on the Shannon-Weiner diversity index in 0.288 increments. Total explained variation was determined by comparison of constrained and unconstrained Eigen values.

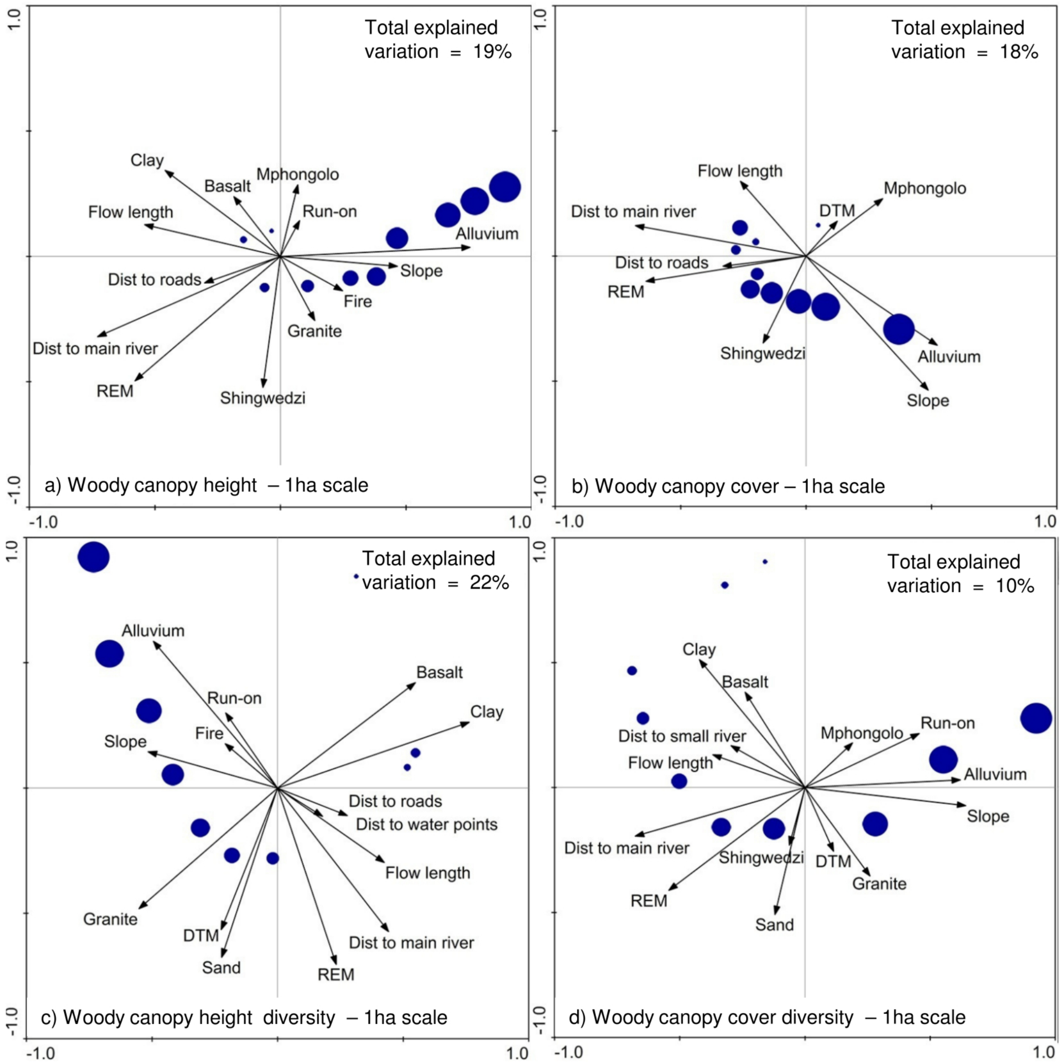


Figure 3.13: [Fine-scale (1ha) patterns of woody structure in relation to environmental variables. Blue dots represent size class categories for the different woody structural attributes. Larger dots represent larger size classes. (a) Woody canopy height categories ranged from 0 to 20m in 2m increments. (b) Woody canopy cover categories ranged from 0 to 100% in 10% increments. (c) Woody canopy height diversity categories ranged from 0 to 2.69 on the Shannon-Weiner diversity index in 0.269 increments. (d) Woody canopy cover diversity categories ranged from 0 to 2.88 on the Shannon-Weiner diversity index in 0.288 increments. Total explained variation was determined by comparison of constrained and unconstrained Eigen values.

ple, whilst alluvial substrates supported both the tallest and densest woody classes, dense woody cover classes were also strongly associated with some upland soils-types, but these soils only supported the shortest of the woody height classes. Tall trees were therefore spatially restricted to the alluvium, but dense cover arose from both tall trees and short shrubs, so woody cover distribution was less strongly coupled with a particular substrate.

Woody height diversity (Figures 3.11c, 3.12c and 3.13c) and cover diversity (Figures 3.11d, 3.12d and 3.13d) displayed similar spatial restrictions to woody canopy height, whereby diversity increased steadily with increasing alluvial influence, but the pattern broke down for the lower diversity classes. This disjunction likely stems from the diverse nature of the alluvial zones that support both tall trees and bare sodic soils with sparse and short trees. The general trend is for structural diversity to increase with increasing proportions of alluvium, but bare patches with low height diversity are also found within the alluvial zone. Therefore, patches of low structural diversity may occur in close proximity to patches of high diversity, and not at the opposite ends of the prominent alluvial gradient. This gives rise to the spiral pattern in the distribution of diversity classes in the ordination diagrams.

3.4 Discussion

Savanna woody vegetation is shaped by a broad range of bottom-up and top-down drivers. Over long time scales, the physical and biological components of systems provide the context within which biological heterogeneity arises (Venter et al., 2003). In savannas, fire and herbivory have received disproportionate attention as top-down controllers of system structure, and the influence of bottom-up controls have often been neglected (Scholes et al., 2003b; Venter et al., 2003). This emphasis on fire and herbivory (Dublin et al., 1990; Dublin, 1995; Ben-Shahar, 1996; Higgins et al., 2000; van Langevelde et al., 2003) is a consequence of their influences being more apparent at the scale at which humans perceive landscapes, than are bottom-up processes, and both are readily manipulated by managers. For too long, scale has been ignored in the debate between bottom-up and top-down controls. The scale specific pattern in woody structure-environment relationships in this landscape reveal that the top-down versus bottom-up debate is irrelevant without the explicit consideration of scale.

3.4.1 A scaled understanding of woody-structure environment relationships

Multi-scaled exploration of woody structure-environment relationships revealed the importance of substrate-type for the spatial distribution of all four woody attributes. The prominence of soil-type in these patterns appears to contradict the HPDP (Wu and Loucks, 1995), as underlying geology would be expected to explain more of the variation in woody structure at large scales. However, the broadest scale tested in this analysis was relatively small (100ha) and the dominant influence of geology may only become evident at larger scales. Even though geological control is not directly evident in the results, its influence emerges in the data, as the distribution of alluvium is not consistent across geological substrates (Venter, 1990). Less alluvium is present in the granitic setting where the longitudinal profile of the river is steeper than on the flatter basalts. The sinuosity of the rivers is greater on the flat basalts, and as such, gives rise to greater alluvial flood-outs and depositions (Saah, 2004). Although woody structure appears to be proximally controlled by soil-type, it is ultimately determined by geology through its influence on geomorphology and water movement in the landscape (Figure 3.14).

High levels of unexplained variation in woody structure at finer-scales suggest that disturbances, feedbacks and contingency become increasingly important at local scales within a particular soil-type . The full impact of disturbances on woody vegetation, such as large mammalian herbivory, is difficult to establish, as highly

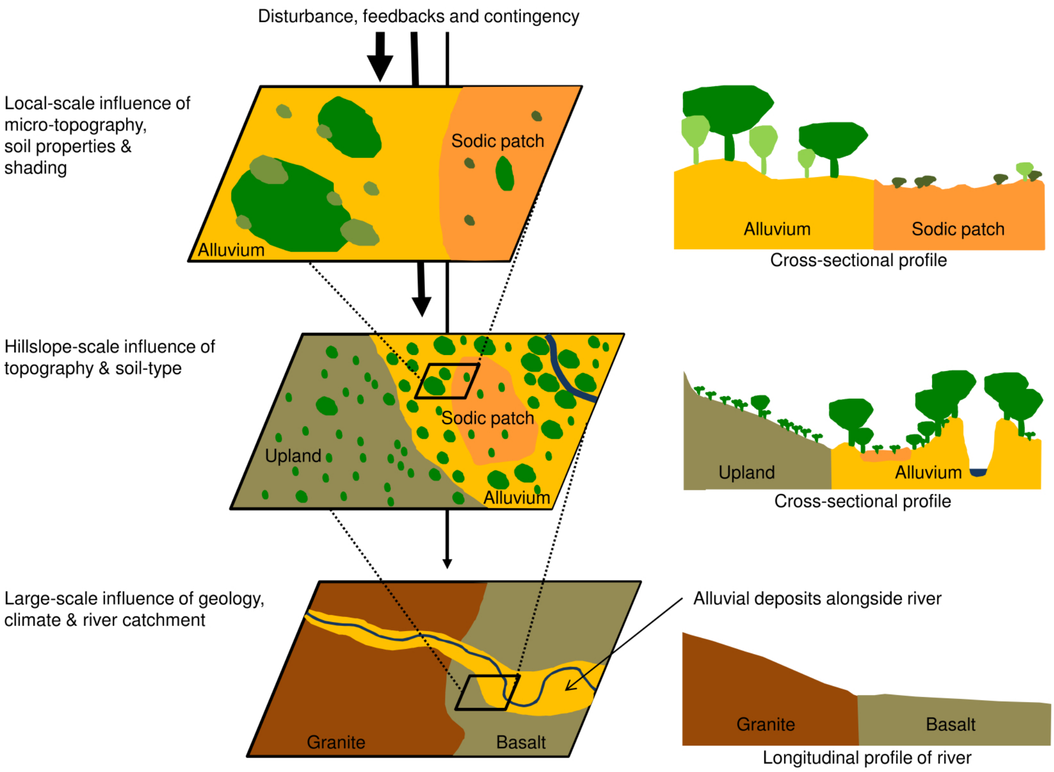


Figure 3.14: Schematic conceptualization of the scales at which different processes influence vegetation structure. Vegetation pattern is strongly controlled by soil-type at the hillslope scale. The patterns at this scale are ultimately determined by the influence of geology and climate, at the large scale, which influence the distribution of different soil-types at the hillslope scale by constraining the movement of water through the landscape. Local scale variation in vegetation patterns stem from disturbances, interactions and feedbacks. The influence of these local scale factors is emergent at larger scales, but the degree of influence diminishes with increasing vertical separation in the hierarchy.

mobile animals are capable of first choosing a large patch of suitable foraging conditions (e.g. alluvial lowlands) and then making additional decisions at finer and finer scales (e.g a sodic patch within the alluvium), eventually to position individual foraging efforts (e.g. on an specific woody species within the sodic patch) (Turner et al., 1997). The scale of these choices is bounded by the movement capability of the organism and by the spatial and temporal extent of an individual foraging event (Kotliar and Wiens, 1990).

Distance to water-points provides a proxy for herbivory in semi-arid landscapes, as herbivore impacts are often greatest in close proximity to water-points (Brits et al., 2002; Gaylard et al., 2003; Ryan and Getz, 2005), but piosphere effects did not emerge in the results. Although the study site covered both riparian lowland and upland patch types, most of the water-points were located in close proximity to the major rivers, so piosphere effects are likely to have been masked by the stronger proximity to river gradient. Similarly, the full impact of fire disturbance on woody structure was not well accounted for in this study. Although fire return interval was included in the analysis, the data were coarse scale and gave no indication of fire intensity which strongly influences woody structure (Higgins et al., 2007). Given the heterogeneous distribution of vegetation within the savanna riparian setting, fire occurrence and intensity are likely to be patchy in nature (van Wilgen et al., 2003). Gaining a better understanding of the spatio-temporal distribution and intensity or fire, and explicitly quantifying the full range of scales and extents at which different herbivores utilize the landscape, will contribute greatly to understanding the finer-scale variation in woody structure.

Woody structure and woody diversity were addressed in this analysis at the vegetation community level at a single point in time. A large proportion of the unexplained variation in woody structure may stem from biological constraints and/or species, temporal and spatial variation. Temporal dynamics of woody structure and heterogeneity are explored in Chapter 4, and spatial variation in woody structure-environment relationships are explicitly dealt with in Chapter 5. The consideration of biological constraints and species variation was beyond the scope of this thesis, but are avenues of research that should be pursued in future work. A sound understanding of the feedbacks and interactions between species remains a key gap in ecology (Agrawal et al., 2007).

The importance of riparian zones in the savanna landscape mosaic

The high levels of woody structural diversity in the riparian zones are likely to provide habitat for a wide range of other species and make a significant contribution to the biodiversity of the savanna landscape as a whole. The influence of habitat heterogeneity on species diversity is well documented in different landscapes (Simpson, 1949; Bazzaz, 1975; McCoy and Bell, 1991) and vertical foliage structure, rather than plant species composition, is an important determinant of species diversity (MacArthur and MacArthur, 1961; MacArthur, 1964). In savannas, tall and dense woody patches create micro-habitats and islands of fertility for numerous species (Belsky and Canham, 1994; Cumming et al., 1997; Fenton et al., 1998). In this system, such patches only occurred in the riparian zone. Therefore while these zones occupy a relatively small proportion (15-20%) of the broader savanna landscape (Saah, 2004), their potential influence on biodiversity and ecological functioning is disproportionate to their areal extent.

High levels of heterogeneity do not always lead to an increase in biodiversity, however, and depending on the taxonomic group, the structural parameter of vegetation and the spatial scale, animal species diversity may also decrease with an increase in vegetation diversity (Tews et al., 2004). Now that LiDAR has enabled the detailed structural description of savanna vegetation over large areas (Chapter 2), greater research attention needs to be given to the linkages between structure, biodiversity and ecological functioning in savanna landscapes.

3.4.2 Implications for the pattern-process-scale perspective of the HPDP

Woody structure-environment patterns revealed the complex influence of scale on pattern-process relationships. The HPDP predicts ecological processes to shift with scale along a patch hierarchy (O'Neill et al., 1986; Wu and Loucks, 1995). Scale variant patterns shown by woody height and cover demonstrate that the principle is applicable in two contrasting systems, from relatively homogeneous temperate forests to event driven heterogeneous savannas. However the scale invariant patterns shown by woody structural diversity highlighted the importance of considering multiple attributes of vegetation in ecological analyses, and contradict the HPDP prediction that variance measures exhibit stepwise patterns of change with scale (O'Neill, 1995; Wu and Loucks, 1995). Stepwise changes with scale may still emerge across a different range of scales, or with a different set of environmental variables, to those tested in this study. The scale invariant patterns shown here could simply represent the horizontal portion of a larger scale "step", but exploration across a broader range of scales is need to validate this.

Abrupt changes in pattern with scale indicate the presence of scale-breaks in a system which mark the boundaries of the domains of scale (Wiens and Milne, 1989; Allen and Holling, 2002). Explicit delineation of such scale-breaks would provide a means for explicitly quantifying the spatial scales proposed in Gillson's (2004a) framework. Assessing woody structure-environment relationships over a much larger range of scales, to identify scale-breaks in the processes correlated with woody structure, is an important avenue of future research. The scale variant and invariant patterns found here necessitate the consideration of multiple attributes of woody vegetation in future explorations, as they respond differentially to changes in environmental variables and to changes in scale.

Chapter 4

Metastability of woody structure across a savanna riparian landscape

4.1 Introduction

Vegetation is not a static feature of the landscape, it changes continuously through time and over space. Long-term temporal studies are few but the spatial arrangement of patches can provide insight into the temporal sequence of patch succession, and therefore system dynamics (Watt, 1947). Although the vegetation present at individual locations in a landscape may change over time, in some systems the proportion of the landscape in each vegetated stage may remain relatively constant, if averaged over a sufficiently long time or large area (Bormann and Likens, 1979). Such shifting steady-state mosaic patterns (section 1.2.1 on page 23) gave rise to the metastability component of the hierarchical patch dynamics paradigm (HPDP), which hypothesizes that nonequilibrium patch processes at one level of a patch hierarchy may translate to metastability at a higher level (Wu and Loucks, 1995). Metastability ideas have been validated in northern temperate systems (Zackrisson, 1977; Sprugel and Bormann, 1981; Sprugel, 1991; Turner et al., 1993), the concept has only recently been considered in a savanna setting (Gillson, 2004a,b).

Gillson's paleo-ecological work showed that whilst tree density fluctuated considerably at small spatial scales (10^2m^2), it remained relatively constant at broader scales (10^2km^2) over the long term (1400 years). Savanna woody plant cover and density, however, have shown high levels of variability over much shorter time scales (15-40 years) in many African landscapes (Beuchner and Dawkins, 1961; Barnes, 1985; van de Vijver et al., 1999; Western and Maitumo, 2004; Western, 2007). These changes have largely been attributed to the combined influence of fire and large herbivore browsing (Laws, 1970; Barnes, 1985; Dublin et al., 1990; Ben-Shahar, 1996; Eckhardt et al., 2000), but these studies have considered change at single spatial scales and have not considered the heterogeneous structure of savanna landscapes. When scale and space are ignored, temporal changes are averaged across different patch types within the landscape mosaic, and are likely to poorly reflect processes operating in a particular patch. Patch and scale specific exploration of woody dynamics should provide greater insight into the processes driving change (Levick and Rogers, 2008), as different processes act at different scales (section 3.3.1 on page 67) and their influence may vary in different contexts (Jones and Callaway, 2007).

Furthermore, most research on woody dynamics has focused on woody cover and density and there is currently no broader understanding of woody dynamics that also considers heterogeneity and vertical structure, despite their importance for both ecosystem functioning (Diaz et al., 2004) and biodiversity conservation (Noss, 1990; Cumming et al., 1997; Pickett et al., 2003).

In this chapter I assess the metastability principle of the HPDP in a savanna riparian landscape, by exploring spatio-temporal patterns of woody structure and heterogeneity at different scales.

4.2 Methods

Assessment of the metastability principle of the HPDP required spatially explicit understanding of woody vegetation dynamics at different scales. This understanding was gained through object-based analysis of the historical aerial photography record. Patterns of woody dynamics were explored in relation to environmental variables to draw inference about the underlying processes. Spatio-temporal variation in woody cover and heterogeneity was then assessed within a patch hierarchy, and current woody structure was explored in relation to patterns of historical dynamics.

4.2.1 Spatial representation of woody dynamics

Site selection and data acquisition

Sixteen sites were selected within the LiDAR coverage to explore spatio-temporal patterns of woody structure and heterogeneity (Figure 4.1). Sites were placed within the LiDAR coverage to enable the use of high-resolution imagery and terrain data for orthorectification purposes, and were distributed across the riparian and upland zones of both the granitic and basaltic substrates, to assess spatial patterns of change. Certain gaps were present in the spatial coverage of the historical aerial photography record so site location and size selection took temporal and spatial continuity of the data record into account. The available aerial photography record spanned a 59 year period from 1942 to 2001 (Table 4.1). Photographs were also available for 1963 and 1977 but were of too poor a quality for use in this analysis.

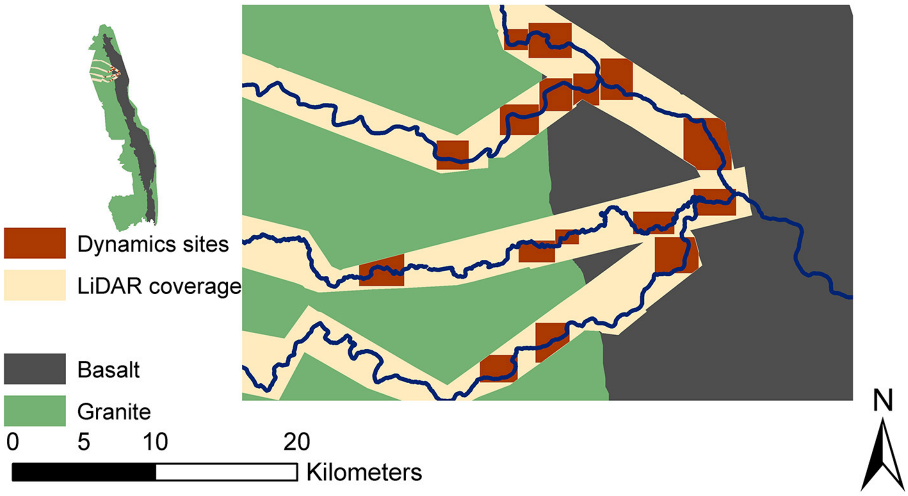


Figure 4.1: Distribution of sites that were used for woody spatio-temporal analysis. Sites covered the dominant geologies and soil-types, and encompassed both the alluvial lowlands and their adjacent uplands.

Table 4.1: Aerial photography used in the woody spatio-temporal analysis.

Year	Resolution	Acquisition	Quality
1942	0.8m	May	Good
1971	1m	June	Poor
2001	0.8m	April	Good

The 1942 and 2001 datasets were the most comparable in terms of image quality and date of acquisition. The 1942 aerial photography survey was conducted in March, whilst the 2001 survey took place in April, therefore both sets were obtained shortly after the wet season when the majority of woody vegetation would still have been in leaf. The historical imagery was scanned at 3200dpi with an Epson Perfection 3200 flatbed scanner. The scanned imagery was georeferenced and orthorectified in ArcGIS 9.2 (ESRI) with the colour aerial imagery (30cm) and DTM (1m) derived from the LiDAR survey.

Object-based extraction of woody vegetation cover from historical aerial photographs

Black and white aerial photographic records provide valuable evidence of changes in woody vegetation cover over time, but accurately extracting the woody layer has proved difficult in semi-arid landscapes where cover is sparse and sometimes difficult to distinguish from the heterogeneous substrate (Laliberte et al., 2004). Figure 4.2a, for example, depicts an aerial view of the riparian fringe adjacent to the Phugwane river in the broader Shingwedzi Catchment. A split between dark basaltic soils (top left-hand corner) and white alluvial soils (bottom right-hand corner) runs diagonally through the image. This variation in soil colour presented challenges in extracting woody cover from the image as the dark soils were similar in brightness values to some of the woody vegetation types. A visual comparison showed that traditional pixel-based classification of woody cover failed to extract only the woody plants, and overestimated woody coverage, as large areas of dark soil as classified as woody canopy (Figure 4.2). Object-based image analysis was therefore explored as an alternative as it has been shown to produce superior classification results to pixel-based analysis (Blaschke and Strobel, 2001).

Multiresolutional segmentation and classification were conducted on the historical imagery in eCognition 4.0 (Definiens Imaging). Prior to segmentation, the imagery was filtered with a 3 X 3 low-pass filter to remove excessive variation (Figure 4.3a). Smoothing of layers prior to segmentation helps produce fewer, and more homogeneous image objects, so that individual trees are represented by fewer polygons (Laliberte et al., 2004). A fine level of segmentation was initially chosen to ensure that image objects were small enough to represent individual trees (Figure 4.3b). Larger scale segmentation was then conducted to group areas of similar vegetation/soil-type units together (Figure 4.3c). The primary aim of this broader segmentation was to provide some spatial context for the smaller ‘tree’ objects at the lower level. Segmentation parameters are provided in Table 4.3.

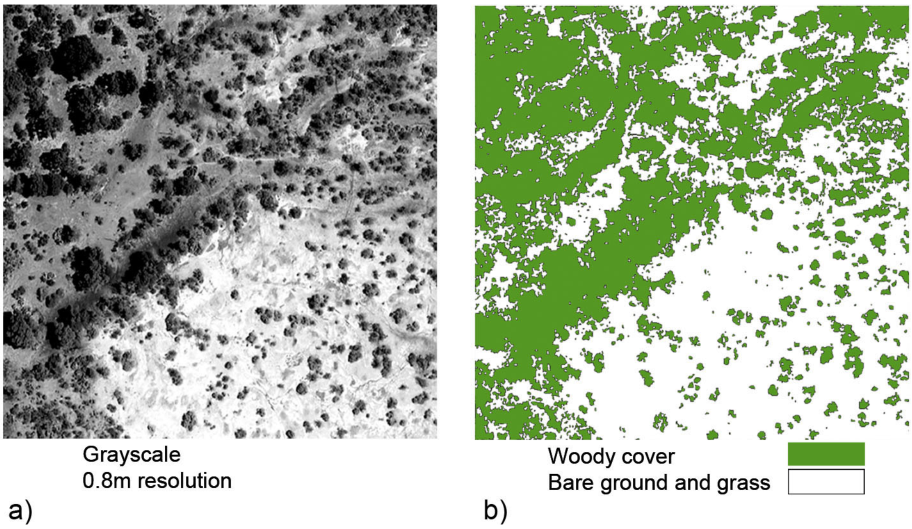


Figure 4.2: Overestimation of savanna woody coverage through pixel-based classification. Woody plants often have similar brightness values to background soils and are difficult to extract with traditional techniques.

Table 4.3: Segmentation parameters used for extracting woody coverage from back and white aerial photography.

Segmentation	Scale	Colour	Compactness
Level 1	3	0.8	0.2
Level 2	250	0.5	0.5

Classification rules in object-based analysis are context-dependent and can vary across the different patch types within an image. Therefore, although there was little difference in image brightness values between woody trees and basaltic soils (Figure 4.3a), the ratio between the mean of the smaller image objects (Figure 4.3b) and the larger image objects (Figure 4.3c) was used to differentiate trees from soil (Figure 4.3d). The entire workflow is presented in Figure 4.4.

Classification accuracy assessment

Classification results could not be tested against ground validated data in the traditional manner, as a consequence of the historical nature of the photographic record. Instead, 50 points were randomly distributed in each of the 16 spatio-temporal study

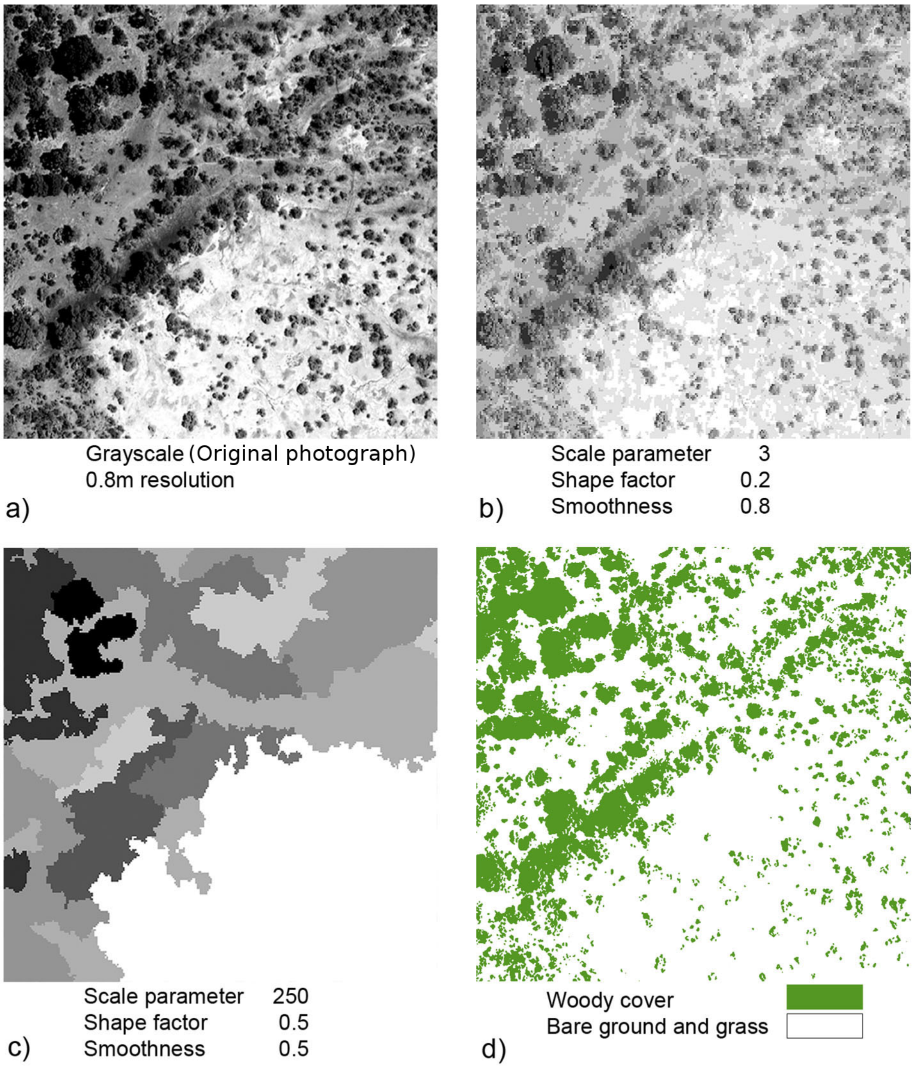


Figure 4.3: The advantage of object-based image analysis for woody cover classification in heterogeneous landscapes. The original image (a) was segmented to create fine (b) and large (c) image objects to enable context specific classification rules for accurate woody coverage extraction (d).

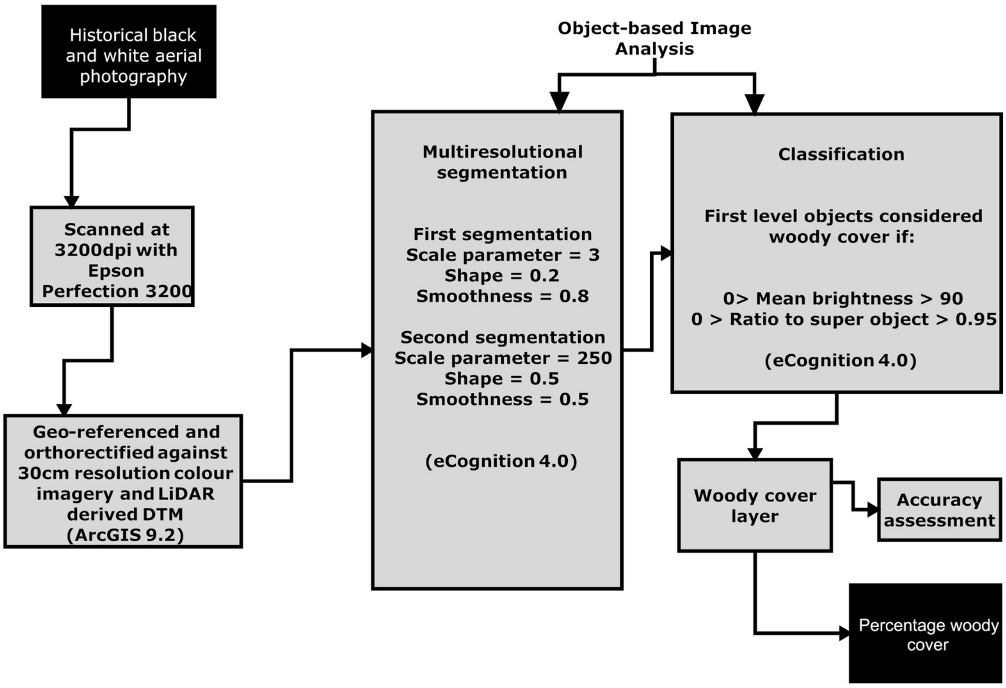


Figure 4.4: Object-based woody canopy classification procedure for black and white aerial photography.

sites. For each year of the temporal record, points were classed as either 'woody' or 'not-woody' by visual interpretation. The visually classified points were tested against the automated object-based classification results by means of an error matrix to assess the classification accuracy of the automated technique. The 1942 dataset produced an overall classification accuracy of 96% and the 2001 classification was 94% accurate. These two datasets provided a good platform from which to explore spatio-temporal dynamics, but the 1972 classification was only 64% and was therefore excluded from the analysis.

Binary rasters of woody coverage in 1942 and 2001, created in eCognition 4.0 (Definiens Imaging), were converted into floating point rasters of percentage woody cover in ArcGIS 9.2 (ESRI), to provide a basis from which to assess patterns and infer processes of change.

4.2.2 Woody dynamics-environment relationships at different scales

Patterns of change in percentage woody cover were explored in relation to environmental variables, at multiple spatial scales, to assess how woody dynamics-environment relationships changed with scale of analysis. The environmental variables fell into five broad categories of substrate, hydrology, topography, position and management (Table 3.1 on page 63 provides explanation and justification for variable selection).

The largest spatial scale of analysis for this component was determined by both the spatial-extent of sites selected for temporal analysis and the distribution of soil-types within the landscape. The largest circular plot that could adequately cover the different soil types, without overlapping different substrates, was 100ha in area. These large scale plots were distributed across the study area in a stratified random manner, using proportional allocation (Manly, 1992), to produce 59 plots across the spatio-temporal study site. Five 10ha plots were randomly placed with each of the 100ha plots, and five 1ha plots were randomly placed within each of the 10ha plots to produce the multi-scaled sampling design that maintained a constant scaling relationship (Figure 3.5 on page 65). The random placement of plots was achieved with Hawth's Analysis Tools for ArcGIS (Beyer, 2007). This sampling design ensured proportionate, multi-scaled coverage of the alluvial soils of the riparian zones and of the sand and clay soils of the upland areas, enabling spatial variation in woody dynamics to be assessed.

Canonical correspondence analysis (CCA) (section 3.2.2 on page 64) was conducted to elucidate spatial patterns of woody cover dynamics at different scales. Partial canonical correspondence analysis (PCCA) (section 3.2.2 on page 64) was run at the three different scales to explore the influence of changing scale on the amount of variation in woody dynamics that could be explained by environmental variables.

Change in percentage woody cover was reclassified into ten categorical classes and the abundance of each class was recorded in each plot to act as response variables in the CCA analysis, which requires categorical responses variables. The number of classes was limited to ten to enable clearer interpretation of the resulting ordination diagrams. Presence or absence of categorical environmental variables, and the mean values of continuous environmental variables, were also recorded in each plot, to test their explanatory power against the spatial distribution of woody cover dynamics, at the three scales of analysis.

4.2.3 Metastability of woody structure

Spatio-temporal variation of woody structure within a patch hierarchy

Change in percentage woody cover and heterogeneity were explored within a patch hierarchy to provide understanding of how patterns of woody cover vary with scale of analysis. Coughenour and Ellis (1993) suggested a hierarchy of constraint in savannas based on physical controls which determine the movement and availability of water within a landscape. Patterns of woody structure-environment relationships in this savanna riparian landscape (section 3.3.2 on page 71) revealed the influence of substrate on woody structure, and the distribution of woody structural classes differed between the major river systems. As such, the patch hierarchy was derived from substrate and hydrological characteristics (Figure 4.5). The total area of the spatio-temporal study site formed the largest patch. This patch was split amoungst the four major river catchments, which were then each divided according to granitic or basaltic substrates. These eight patches were then split again into alluvial riparian zones and their adjacent upland soil-types (sand on the granites and clay on the basalts), resulting in 16 patches at the lowest level of the hierarchy.

Within each of these patches the percentage change in woody cover, change in the number of woody patches present, and change in the mean size of woody patches present was calculated from the 1942 and 2001 datasets. All calculations

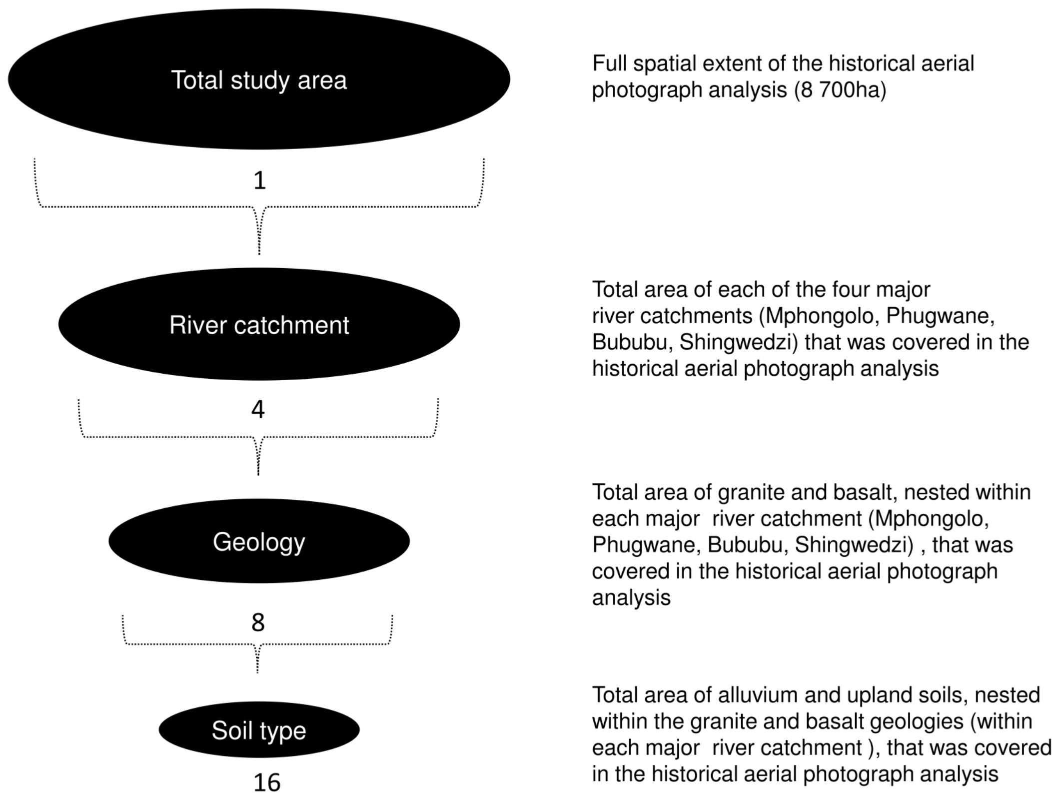


Figure 4.5: Patch hierarchy for the exploration of woody dynamics at different scales.

Table 4.5: Categories of historical dynamics used in the temporal context analysis.

Category	Woody cover dynamics between 1942 and 2001
Decreased	Woody cover decreased by more than 10%
Unchanged	Woody cover decreased or increased by less than 10%
Increased	Woody cover increased by more than 10%

were conducted in ArcGIS 9.2 (ESRI).

Exploring current woody structure in its temporal context to infer changes in the vertical component

In the same way temporal context influences ecological patterns and processes (Wiens, 1995; Harding et al., 1998), historical patterns of woody dynamics may be reflected in current woody structure. Such temporal context patterns have never been explored in savannas, but may provide an avenue for assessing how changes in woody cover, which can be derived from historical aerial records, relate to changes in woody vertical structure, which are difficult to determine from two-dimensional aerial records. Current woody vertical structure was therefore assessed within the context of historical cover dynamics. The raster layer of percentage change in woody cover was reclassified into three categories of historical dynamics (Table 4.5) and the ratio of tall (>10m) to short (<3m) woody canopy (derived from the woody canopy height layer 3.2) was calculated within each of the three categories to infer an understanding of how past dynamics may have influenced current woody structure.

4.3 Results

4.3.1 Inferring underlying processes of woody cover dynamics at different scales

Woody dynamics-environment relationships exhibited strong spatial trends at the broad-scale (100ha) (Figure 4.6a), where increases and decreases in cover occurred in different parts of the landscape. Decreases in woody cover were positively associated with the presence of alluvium, and negatively associated with the presence of clay and distance from main rivers (riparian zones), while increases in woody cover were most positively correlated with long fire return intervals.

The spatial separation between areas of increased and decreased woody cover became less distinct with decreasing scale of analysis, particularly in the smaller classes of change, as the spatial pattern weakened at the medium-scale (10ha) (Figure 4.6b) and further at the fine-scale (1ha) (Figure 4.6c) where classes of increased and decreased woody cover occurred in close proximity to each other. Environmental variables accounted for 65% of the variation in woody structural dynamics at the broad-scale (100ha), but only explained 33% at the medium-scale (10ha) and 16% at the fine-scale (1ha). This trend not only reveals that woody dynamics were highly variable at fine-scales, as would be expected from the HPDP, but the poor explanatory power of the gradient analysis technique indicates that fine-scale dynamics may be patchy in nature and result from the interaction of localized disturbances, feedbacks and contingencies.

The influence of "large and slow" bottom-up processes, such as substrate, contributed less to the explained variation in woody dynamics as scale decreased, but "small and fast" top-down processes such as the management variables (including fire) and position variables (including proxies for herbivory) became more important at finer-scales (Figure 4.7).

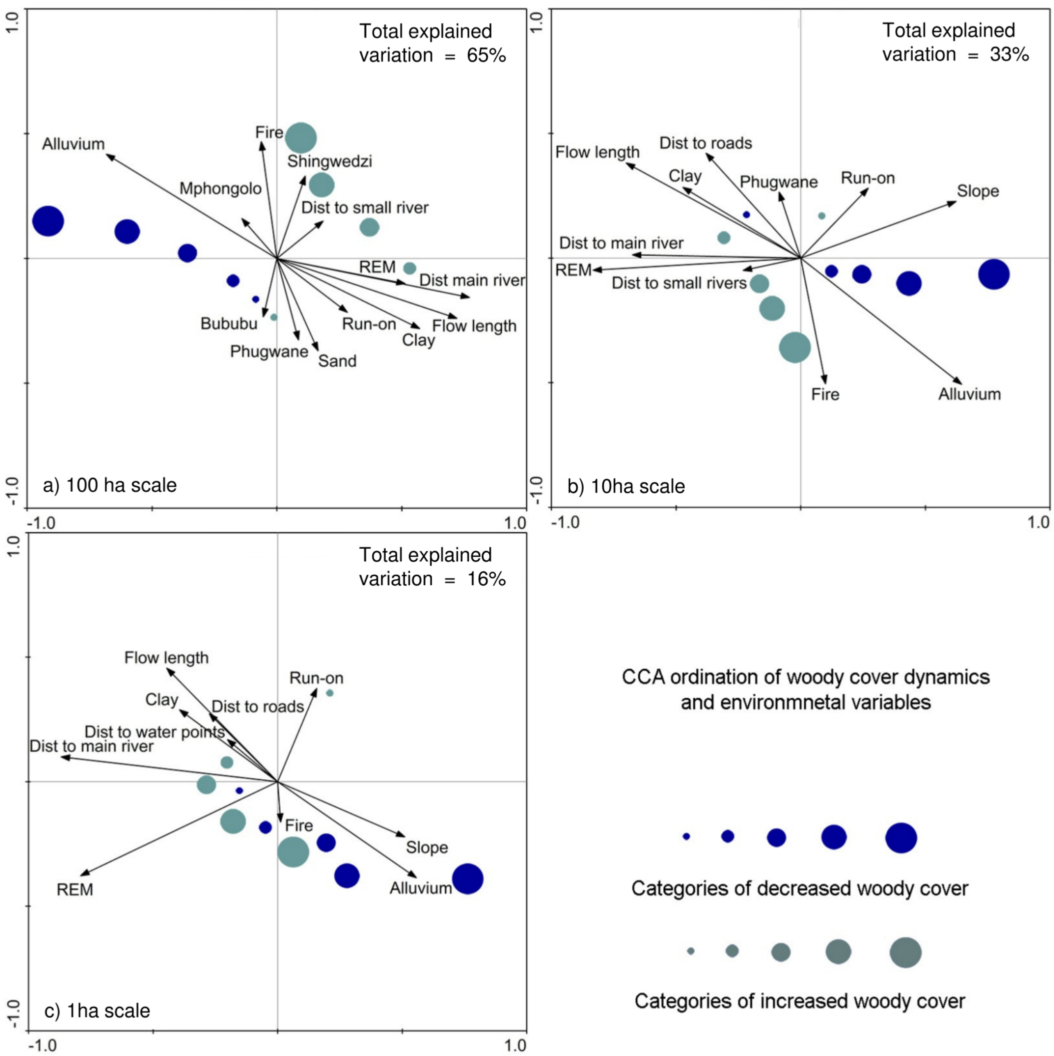


Figure 4.6: Multi-scaled patterns of woody cover dynamics in environmental space. Larger dots represent larger changes. Total explained variation was determined by the comparison of constrained and unconstrained Eigen values.

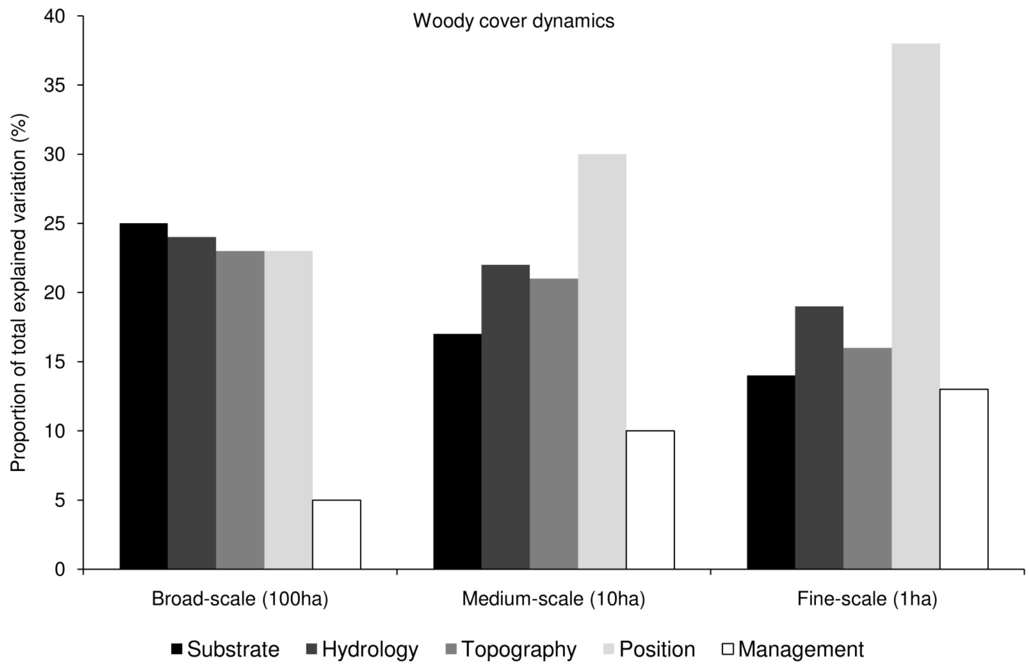


Figure 4.7: The effect of changing scale on the contribution of different environmental groups to the total explained variation in the distribution of woody cover dynamics.

4.3.2 Metastability of woody structure and heterogeneity within a patch hierarchy

Woody cover only showed a 2.8% increase between 1942 and 2001 at the scale of the entire study site (Figure 4.8). Cover decreased marginally in the sampled area of the Mphongolo and Phugwane catchments, but increased in the Bububu and Shingwedzi systems. Woody cover increased slightly on sampled granites and the basalts, but it was at the soil-type level that large changes in cover emerged, as cover decreased by 11% on the alluvial soils yet increased by 16% and 25% on sand and clay soils respectively. The changes in percentage cover were not consistent across all patch contexts, however, and the largest decreases in cover occurred on the alluvial soils in the basaltic setting of the Mphongolo (-22%) and Phugwane (-25%) systems. Therefore although opposite trends were observed on alluvial and upland soils, the degree to which they differed was strongly influenced by spatial context within the hierarchy, particularly between different river catchments.

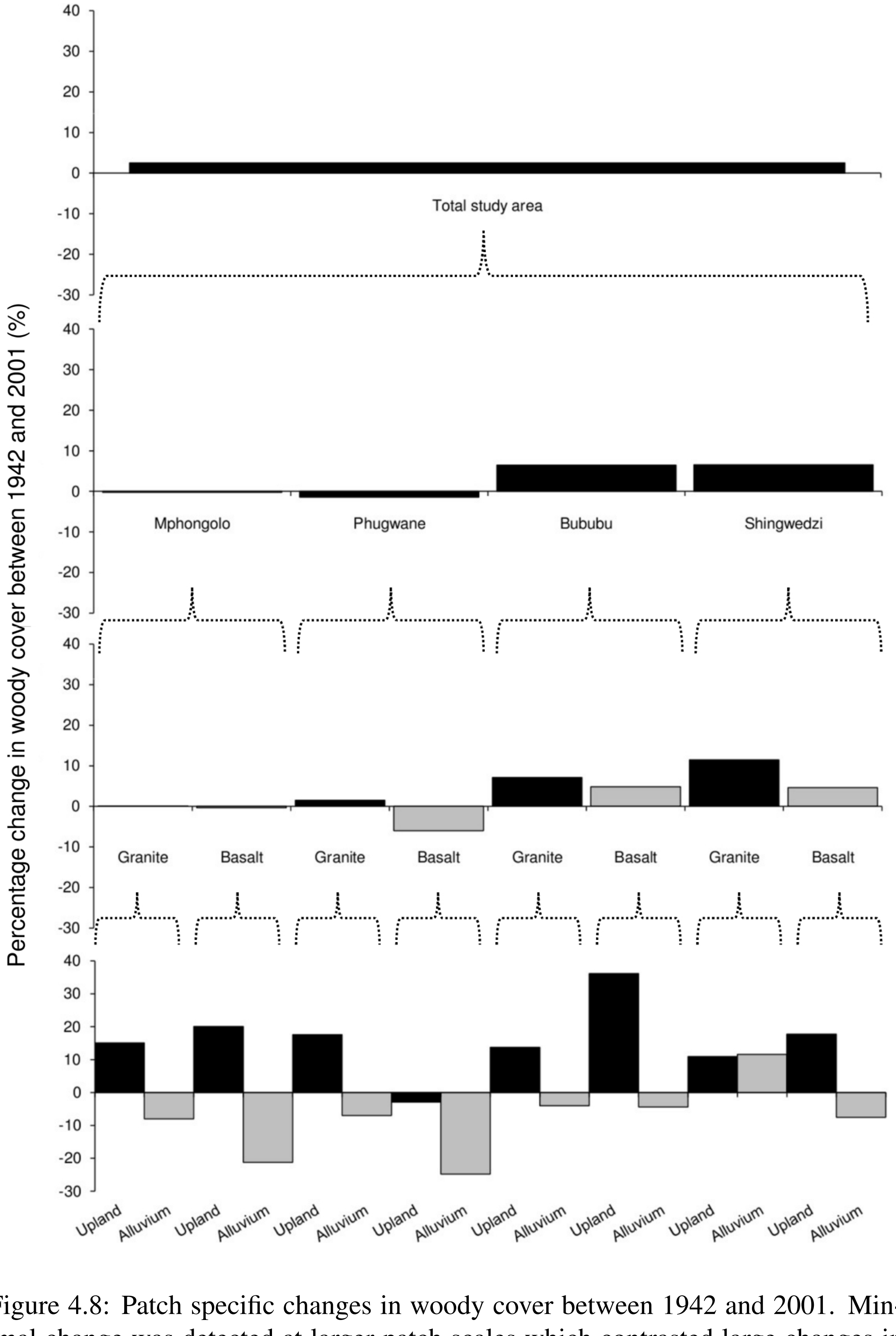


Figure 4.8: Patch specific changes in woody cover between 1942 and 2001. Minimal change was detected at larger patch scales which contrasted large changes in cover at the soil-type level.

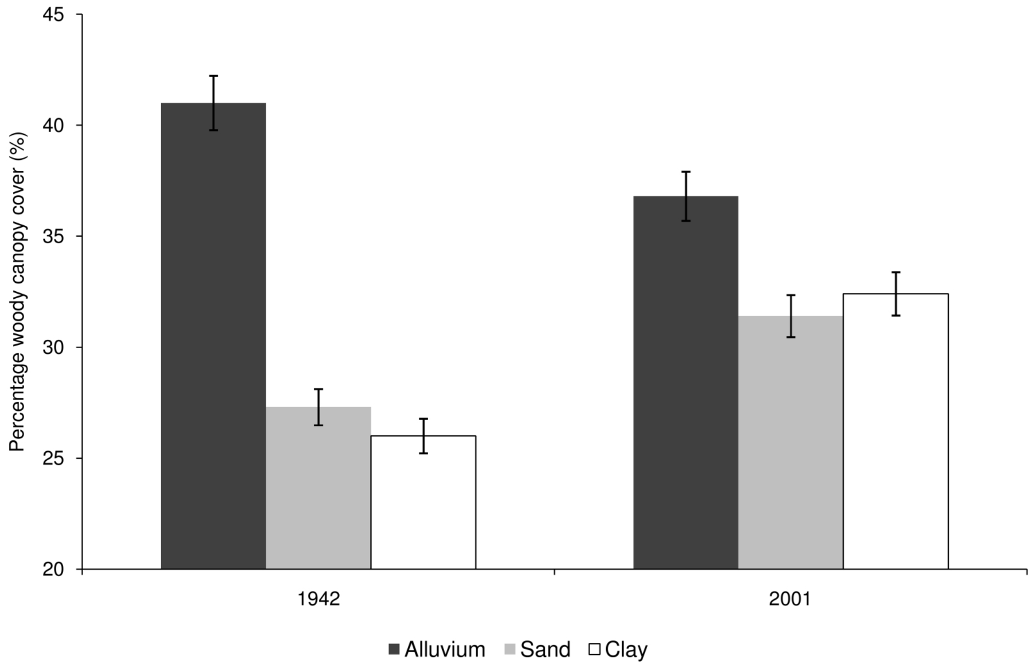


Figure 4.9: Temporal patterns of woody cover on different soil types between 1942 and 2001. Error bars represent the 4-6% error in classification accuracy.

This medium term (59 years) spatio-temporal pattern appears to support the metastability principle of the HPDP, as the percentage of total cover woody cover remained almost constant over time, despite high spatio-temporal variation at finer-scales. A broader consideration of woody structure, however, reveals that the principle is not applicable in this landscape. Changes in woody cover over time, on the three different soils types, led to a shift from a heterogeneous distribution of cover in the landscape (ranging from 26-42%) to a more homogeneous one (ranging from 31-36%) (Figure 4.9). Woody cover was 15-16% greater on the alluvium than on sand or clay soils in 1942, but this difference was reduced to just 4-5% by 2001. These changes indicate a loss of woody cover heterogeneity, and therefore structural biodiversity, across the savanna riparian landscape.

At a finer scale there was both an increase in the number of woody patches (Figure 4.10) and a decrease in the mean size of woody patches (Figure 4.11) between 1942 and 2001 across all levels of the hierarchy. Unlike changes in cover, where the direction and magnitude of change differed on different substrates and in different contexts, the direction of changes in patch structure were consistent across all substrates. However, the magnitude of changes in patch structure were context-dependent, as the largest increases in number, and the largest decreases in mean patch size, occurred in Mphongolo and Phugwane systems. These context specific differences suggest that processes driving woody dynamics are not stationary but vary considerably between the landscapes of different river systems.

Changes in patch number and size indicate the fragmentation of woody patch structure over time, but also represent an increase in finer-scale heterogeneity. Quantification of temporal change in heterogeneity is therefore scale dependent and the boarder scale homogenization of cover across soil-types does not preclude an increase of patchiness within a particular soil-type.

Although historical photographic analysis cannot provide direct insight into changes in the height component of woody structure, the exploration of current woody height within the context of historical change did provide insight into how three-dimensional structure was altered over time (Figure 4.12). The current ratio of tall canopy (>10m) to shrub canopy (<3m) was much lower (1:23) in areas that experienced an increase in woody cover over the previous 59 years, than in areas where cover decreased (1:14) or remained unchanged (1:7) over the same time period. These patterns show that although the decease of cover on alluvial soils was canceled out by increases in the uplands at the scale of the total study site, the areas in which increases occurred are now dominated by shrubs and not tall trees. The vertical structure of woody vegetation has therefore changed over time through shrub encroachment in the upland areas, while vertical height is likely to have been reduced on the alluvial soils. These patterns emerge clearly when current structure is viewed in conjunction with patterns of historical change (Figure 4.13).

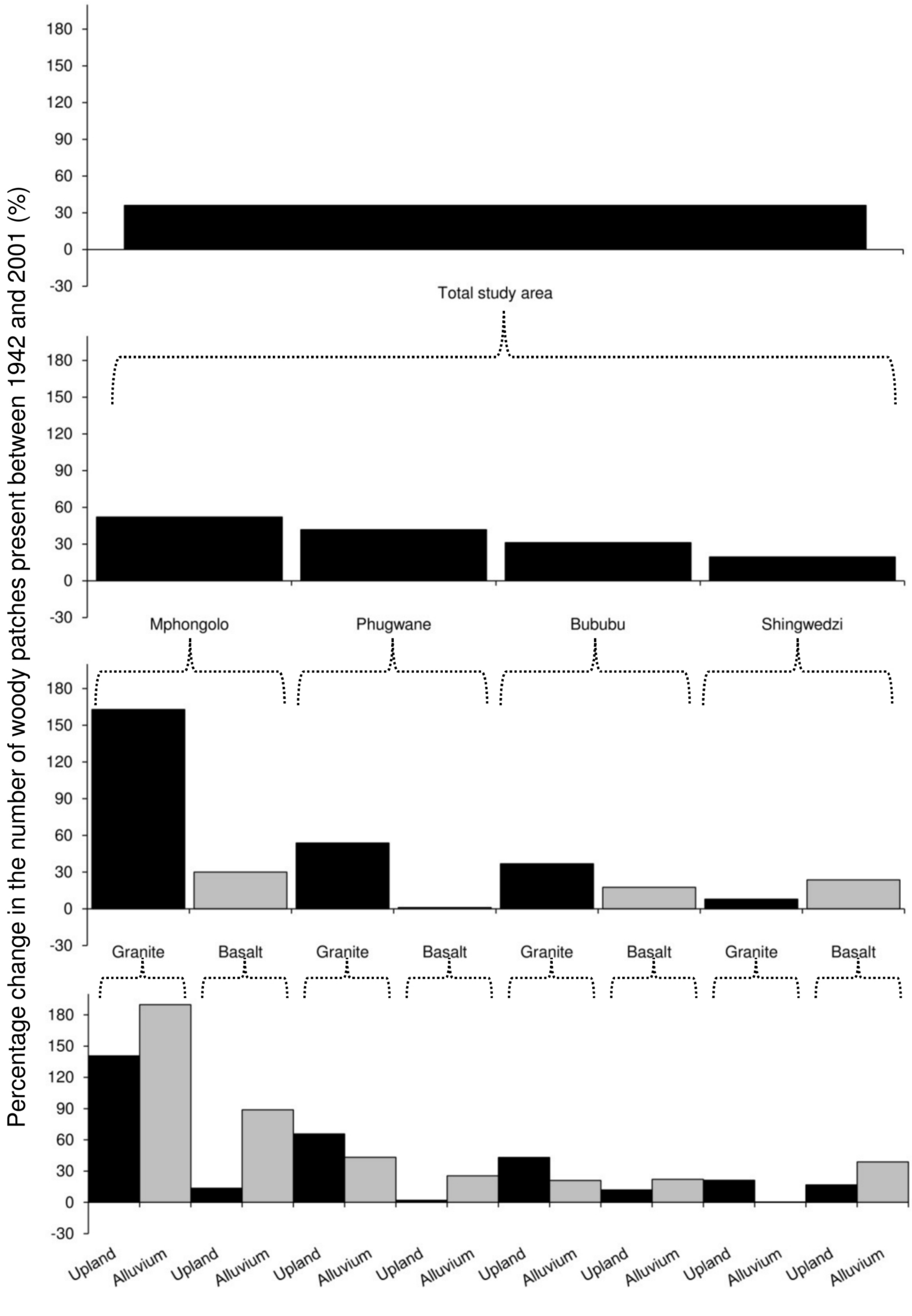


Figure 4.10: Patch and context specific changes in the number of woody patches present between 1942 and 2001.

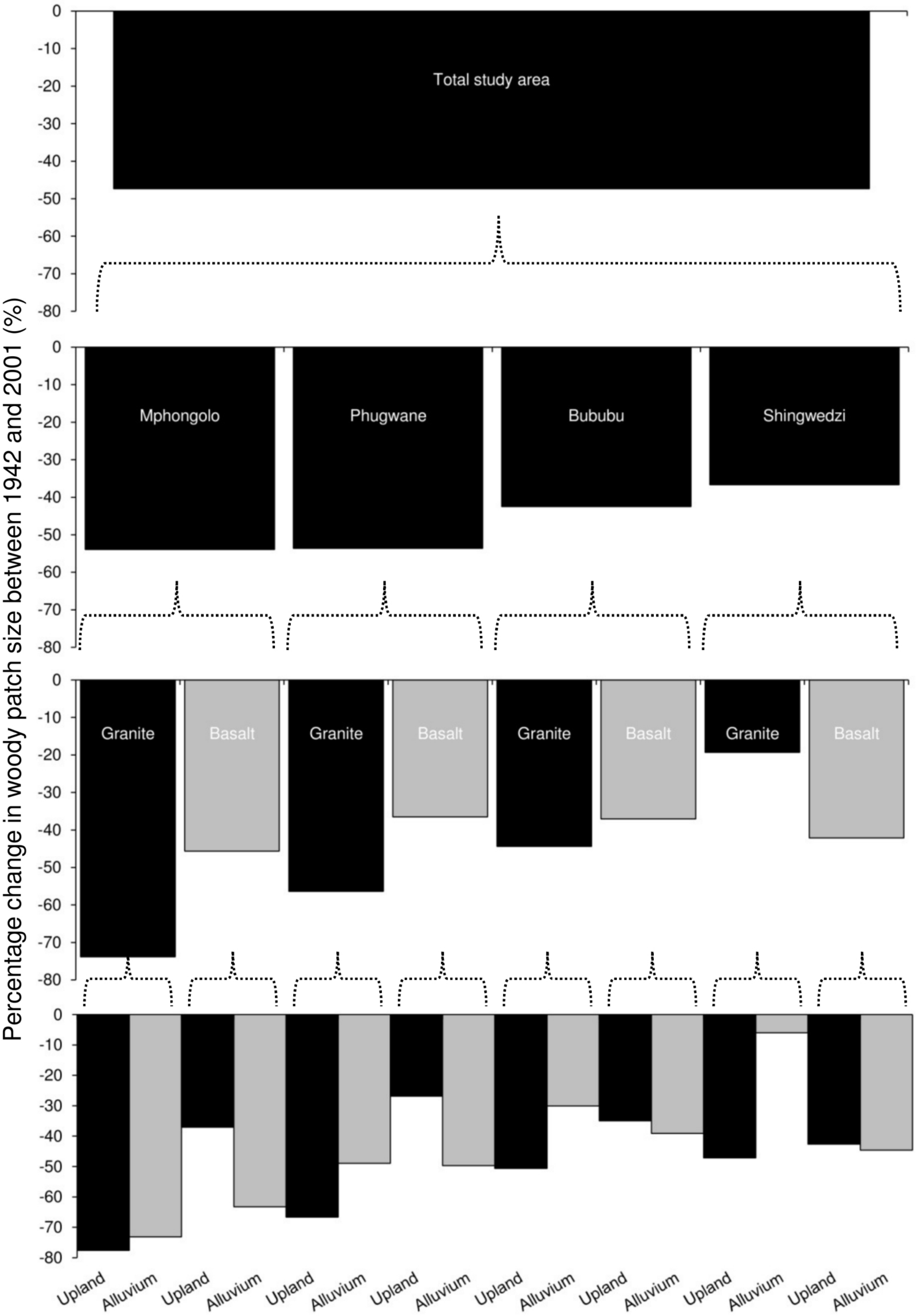


Figure 4.11: Patch and context specific changes in the size of woody patches present between 1942 and 2001.

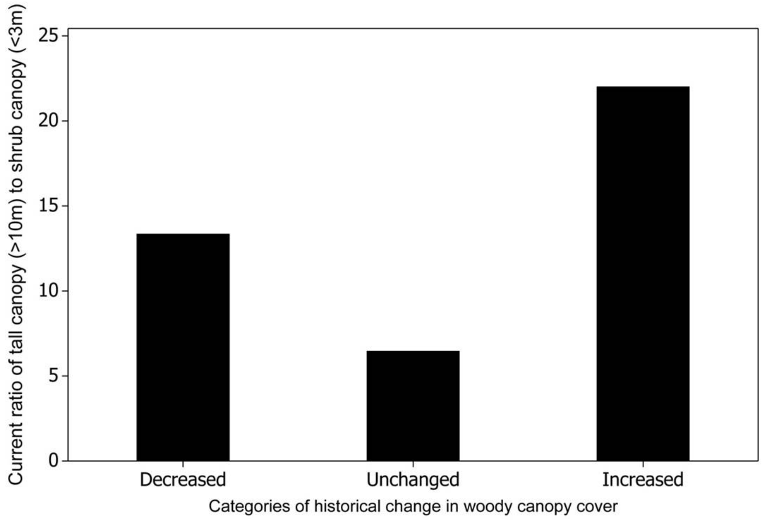


Figure 4.12: Current ratio of tall canopy (>10m) to scrub canopy (<3m) as a function of temporal context. Decreased = woody cover decreased by more that 10%. Unchanged = woody cover either decreased or increased by less than 10%. Increased = woody cover increased by more than 10% between 1942 and 2001.

4.4 Discussion

Temporal changes in woody structure are well documented in both southern and eastern African landscapes (Beuchner and Dawkins, 1961; Barnes, 1985; van de Vijver et al., 1999; Eckhardt et al., 2000), but spatial scale and location have been ignored in these analyses. The woody vegetation layer of this savanna riparian landscape exhibited scale and patch specific changes, between 1942 and 2001, and its cover component did not adhere to the metastability principle of the HPDP (Bormann and Likens, 1979; Wu and Loucks, 1995). Spatial patterns of change provide insight into the processes creating those patterns (Watt, 1947; Turner, 1989), therefore the spatial understanding developed here holds implications for understanding the processes underlying woody dynamics in savanna landscapes.

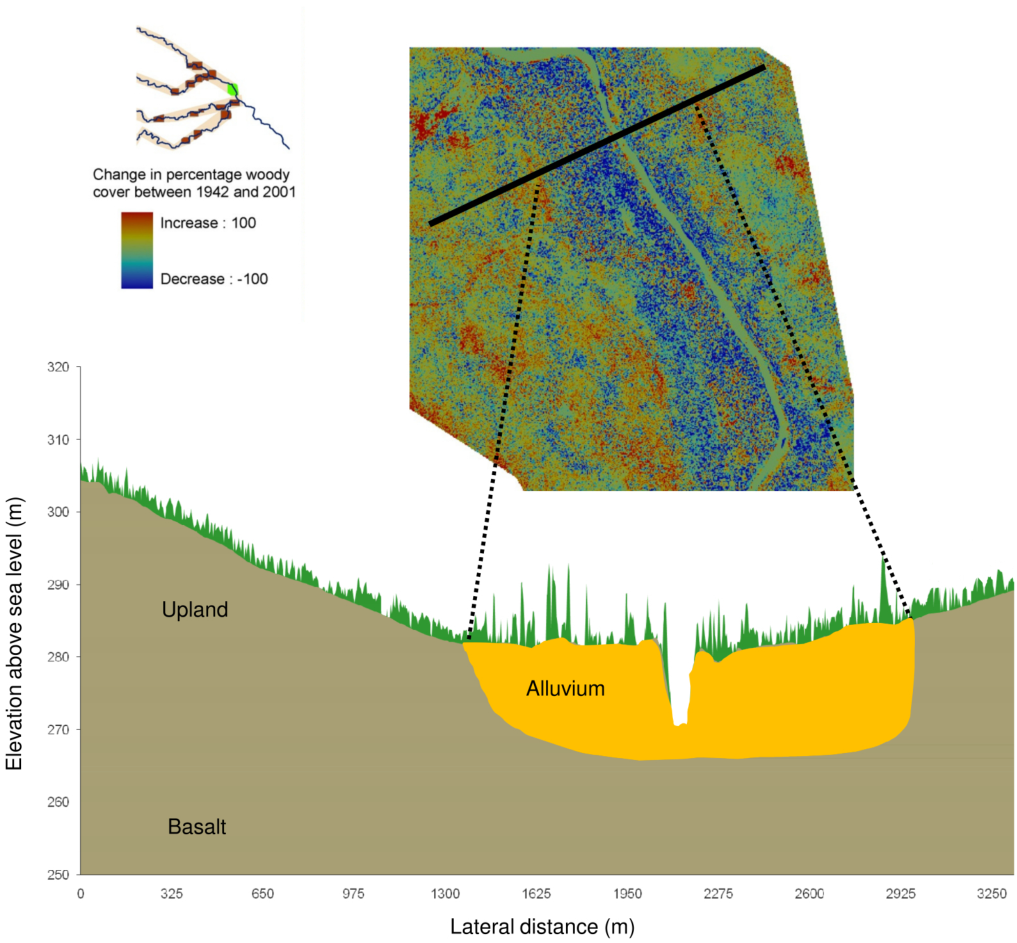


Figure 4.13: Cross-sectional profile of current woody structure in relation to historical dynamics. Decreases in woody cover (blue) were concentrated in the alluvial riparian zone, which currently supports tall trees and in structurally diverse. Increases in cover (red and orange) primarily occurred in the uplands, which currently support short, homogeneous woody patches. Occasional flooding events are confined within the deep (30m) macro-channel and do not impact vegetation on the paleo-floodplain.

4.4.1 Insights into drivers of woody dynamics through the explicit consideration of spatial scale and location

The encroachment of shrubs into grasslands and savannas is a worldwide phenomenon that has been attributed to a range of factors, including changes in broader climatic conditions, changes in fire regime, overgrazing, seed bank dynamics and combinations of these influences (Trollope, 1974; Vegten, 1984; Trollope and Potgieter, 1985; Archer et al., 1995; Witkowski and Garner, 2000; Password, 2001; Silva et al., 2001; Sankaran et al., 2005), including the interaction between woody response to fire and elevated CO_2levels (Bond and Midgley, 2000). However the underlying drivers of woody dynamics, and the relative influence of fire and herbivory in particular, remain the subject of much debate in savanna ecology (Dublin et al., 1990; Dublin, 1995; Prins and van der Jeugd, 1993; van Langevelde et al., 2003). The distinct spatial patterns of woody dynamics identified in this study suggest that different agents of change operate in the alluvial riparian zones, where cover predominantly decreased, and in the uplands areas, where cover increased over time in the shrub layer.

The alluvial zones of this system are paleo-floodplains (Venter, 1990), and the spatio-temporal analysis was conducted in the lower reaches of the major rivers where the channels are deeply incised (15-30m). Rare flood events are confined within the macro-channels and would not have impacted vegetation structure on the paleo-floodplains.

Large, mobile herbivores, however, discriminate spatially among variable food resources, thereby altering the structure of plant communities and the rates of ecosystem processes (Turner et al., 1997). In savannas, the impact of large herbivores on woody vegetation structure is spatially distributed amongst patches of different vegetation types in different parts of the landscape (Levick and Rogers, 2008). Most riparian zones provide a valuable forage and concealment resource for herbivores and are often heavily utilized components of the landscape (Naiman and Decamps, 1997; Naiman and Rogers, 1997). The sampled riparian areas support tall trees with dense foliage (Chapter 3) and their sodic soils have high concentrations of cations, such as sodium and calcium (Jacobs et al., 2007) which are valued by herbivores. Evidence of herbivore utilization is high within these alluvial zones (Figure 4.14), particularly by elephant which often concentrate their browsing close to river systems (Laws, 1970; Mosugelo et al., 2002; Nellemann et al., 2002; Gaylard et al., 2003). While artificial water-point placement influences grazer distribution within the Kruger Park, mixed feeders and browsers primarily concentrate along the major river systems (Smit et al., 2007). However they are not areas of high fire frequency or intensity, as the bare nature of the alluvial soils preclude, and act as boundaries, to the spread of fire (Figure 4.15). Although fires do occur in certain savanna riparian zones that are subject to the deposition of large woody debris (Pettit and Naiman, 2007a,b), in this landscape it is predominately the upland areas that support and sustain the spread of fire. Therefore herbivores are more likely to have caused, or contributed to, the decrease in woody cover on the alluvial substrates than fire.

In the upland areas of the savanna, however, the positive correlation between increased woody cover and fire return interval, suggests that a low fire return frequency has contributed to the increases in the woody component. Furthermore, the differential increases in cover on different upland soil-types (16% increase on sands and 25% increase on clays) suggest that different processes or interactions take place in different geological contexts. The basaltic clays are more nutrient rich than the granitic sands (Scholes et al., 2003a) and are therefore subject to heavier grazing. Higher grazing levels lead to a reduction in herbaceous biomass, which can promote the encroachment of woody shrubs by reducing both fire frequency and intensity (Bond and Midgley, 2001; Roques et al., 2001; Wiegand et al., 2005). Therefore the differential response in the uplands is likely the result of interactions between fire and grazing.

These inferences on the roles of fire and herbivory suggest that much of the

Figure 4.14: A mopane tree that was recently browsed by elephant in the alluvial zone.

Figure 4.15: Bare alluvial soils in the ripraian zone act as boundaries to the spread of fire. The spatial pattern of fire is heterogeneous within the upland. The circular patches with the upland are termite mounds.

debate surrounding the relative influence of fire and elephant on woody dynamics in savannas has been misdirected. Clearly in the northern Kruger, fire, elephant, and a host of other factors influence woody dynamics, but the influence of each is manifested at specific scales and in specific parts of the landscape. Processes influence the woody component differentially across heterogeneous landscapes and ecological relationships need to be interpreted in light of the context in which they were explored.

Furthermore, the exploration of multiple attributes of woody vegetation is critical to gaining comprehensive understanding of spatio-temporal dynamics. Patch specific exploration of woody dynamics revealed the homogenization of woody cover at the landscape level, but heterogeneity of woody cover increased over time at finer-scales, through an increase in the number of woody patches and the decrease in mean patch size. Such changes at the individual patch scale are then propagated upwards to reflect changes in cover at larger scales (Figure 4.16).

Increases in woody patch number, and decreases in woody patch size, represent the fragmentation of the woody cover layer over time. Such changes impact ecological functioning by altering the movement of water, rates of nutrient cycling and shading within a patch (Belsky and Canham, 1994). Ecosystem function is more likely to be affected at finer scales of fragmentation, through the intrinsic breakdown of functional interactions, and complex systems are more likely to be disrupted at a given scale of fragmentation than simpler ones (Lord and Norton, 1990). In addition, the fragmentation of vegetation at fine-scales may lead to irreversible changes in vegetation at broader scales, through the feedbacks between herbivores and resource distribution (van de Koppel et al., 2002). Thus, considering only one aspect of the woody component (such as cover) can mask changes in other woody components (such as height and heterogeneity) that have important implications for ecological functioning.

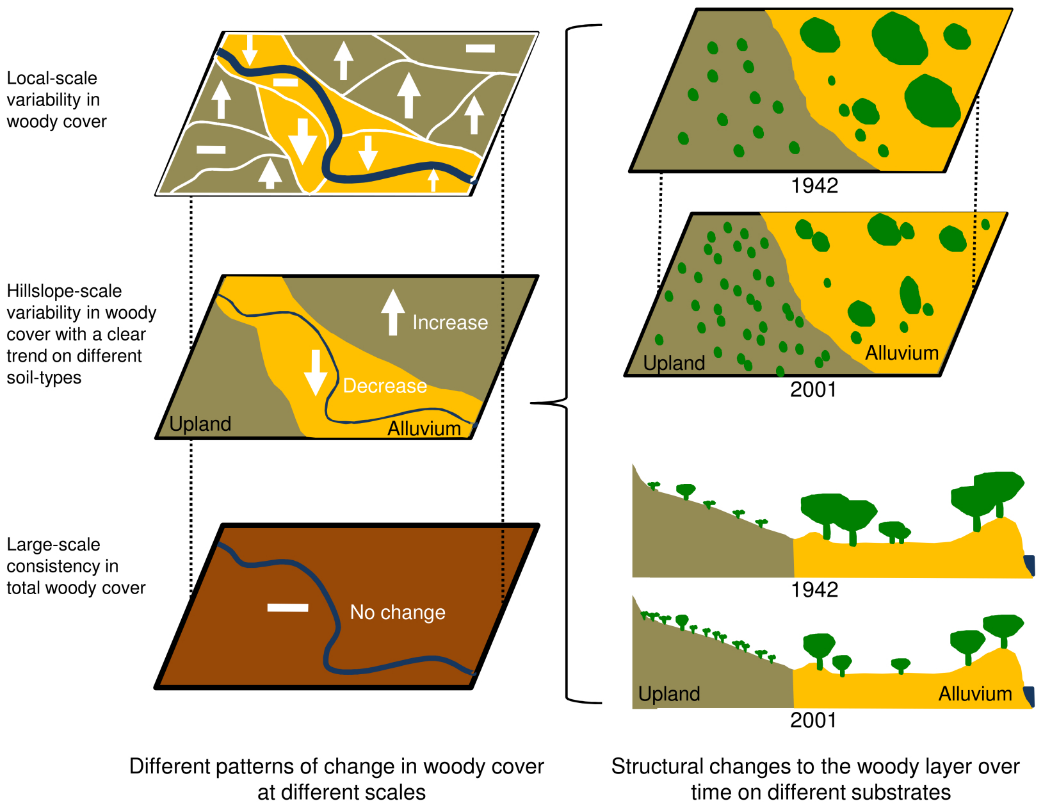


Figure 4.16: Schematic conceptualization of woody dynamics. Total percenatge woody cover remains constant at the large scale. At the hillslope scale, cover decreases in the allvial lowlands, but increases in the uplands. At a finer scale, different patches within the uplands and lowlands exhibit differential patterns of change. These patterns reflect individual woody patch level changes where the number of woody patches increases over time, but mean patch size decreases.

4.4.2 Implications for the metastability principle of the HPDP

Woody cover dynamics appeared to adhere to the metastability principle of the HPDP (Wu and Loucks, 1995) as spatio-temporal variation in percentage woody cover decreased with an increase in scale. These medium-term patterns (59 years) concur with Gillson's (2004a) paleo-ecological work in east African savannas, which indicated metastability of tree density over a long time frames (1400 years). However, the interpretation of metastability in both cases was derived from the measurement of single woody attributes, but shifting-mosaic and metastability concepts in landscape ecology were initially developed through the exploration of spatio-temporal patterns of vegetation seral or successional stages (Watt, 1947; Bormann and Likens, 1979), rather than single attributes of the vegetation.

A broader perspective of woody structural dynamics showed that changes in heterogeneity and height structure did not exhibit larger-scale consistency. Therefore the concept cannot be considered to be applicable in this landscape. The HPDP provides a useful means for considering spatio-temporal heterogeneity in ecological systems, but it is imperative that its core principles are not applied out of context to their origins, in the attempt to produce generalizable theory. Future investigations of metastability in savanna landscapes should therefore explicitly consider measures of successional stage, to provide holistic understanding of woody spatio-temporal dynamics.

The spatio-temporal dynamics explored here indicate that spatial context strongly influences the interpretation of metastability in a landscape. Pickett and White (1985) proposed that the shifting steady-state mosaic hypothesis (metastability) may only apply to relatively homogeneous landscapes that are subject to small and frequent disturbances. Furthermore, Turner et al.'s (1993) elaboration of this idea suggested that metastability could occur to differing degrees in natural systems, and that the level of stability was primarily a function of disturbance/recovery period and disturbance/landscape extent. In heterogeneous systems, such as this savanna riparian landscape, the large differences in substrate materials, which have such a prominent influence of woody structure, may preclude true shifting mosaic patterns (seral or successional stages resulting from disturbances) from occurring at the broader landscape scale. Patches of tall trees found on the alluvium, for example, could not establish on the clay soils of the upland. Rather, patches of vegetation are likely to exhibit a range of spatio-temporal dynamics, including metastability, within a particular substrate-type. Likewise the temporal scale at which different spatio-temporal patterns emerge may vary between different patch contexts, as both the disturbance and recovery interval are unlikely to remain constant across a heterogeneous landscape.

Issues of spatial variability in savanna pattern-process relationships, and the influence of spatial context, are explicitly addressed in Chapter 5.

Chapter 5

Context-dependency in savanna woody structure-environment relationships

5.1 Introduction

The central premise of landscape ecology is that pattern-process relationships are contingent upon where they are located in space (Wiens, 2002), yet ecology has historically focused on the identification and understanding of ecological patterns and processes without regard for the influence of spatial context. Spatial heterogeneity has often been excluded from the conceptual framework of analysis (McIntosh, 1991), and homogeneity and stationarity have been assumed in most ecological studies (Pickett and Cadenasso, 1995; Fortin et al., 2003).

Spatial context is of little relevance if a study area is locally homogeneous (Wagner and Fortin, 2005), but in heterogeneous landscapes, spatial context may strongly influence pattern-process relationships (Turner, 2005). Contextual influences on pattern were mathematically described by Yule (1903) and Simpson (1951), who found it possible for local subsets within a dataset to show opposite trends to the global dataset (Figure 5.1).

This pattern, termed Simpson's Paradox, has been observed in a wide range of fields including economics, social science, and health care (Blyth, 1972; Bickel et al., 1975; Wagner, 1982; Newson, 1991; Wardrop, 1995). Its implications for ecology are poorly established but are potentially profound as global analysis of ecological results may misrepresent patterns occurring in local subsets (Scheiner et al., 2000; Pineiro et al., 2006). I have already shown that the remotely sensed quantification of woody structure was dependent upon vegetation patch type (section 2.3.2 on page 49), and that spatial position was an important determinant of woody structure (section 3.3.2 on page 71) and woody dynamics (section 4.3.1 on page 95). As patterns vary spatially across different contexts, so too might the processes that create them. Such understanding is missing from the pattern-process-scale component of the hierarchical path dynamics paradigm (HPDP). The importance of context is implicit within the HPDP (section 1.2.2 on page 24), as the nested vertical arrangement of systems gives rise to constraint (O'Neill et al., 1989), but explicit understanding of how context influences vegetation pattern-process relationships is still lagging (Jones and Callaway, 2007).

The poor acknowledgment of spatial context in ecology stems from both the paucity of empirical evidence of its importance (Wiens, 1995) and the lack of suitable analytical techniques to explore spatially varying relationships. Recent advances in the field of spatial and geo-statistics (Fotheringham et al., 2002; Brunsdon et al., 1998; Wagner and Fortin, 2005) show much potential for furthering our understanding of the spatial nature of ecological patterns and processes in general, and the influence of context in particular.

Jones and Callaway (2007) recently called for a more explicit, comprehensive and integrative attack on the problem of context-dependency in vegetation pattern. In this chapter I support this need by exploring how woody pattern-process relationships vary across different spatial contexts, and evaluate if Simpson's Paradox

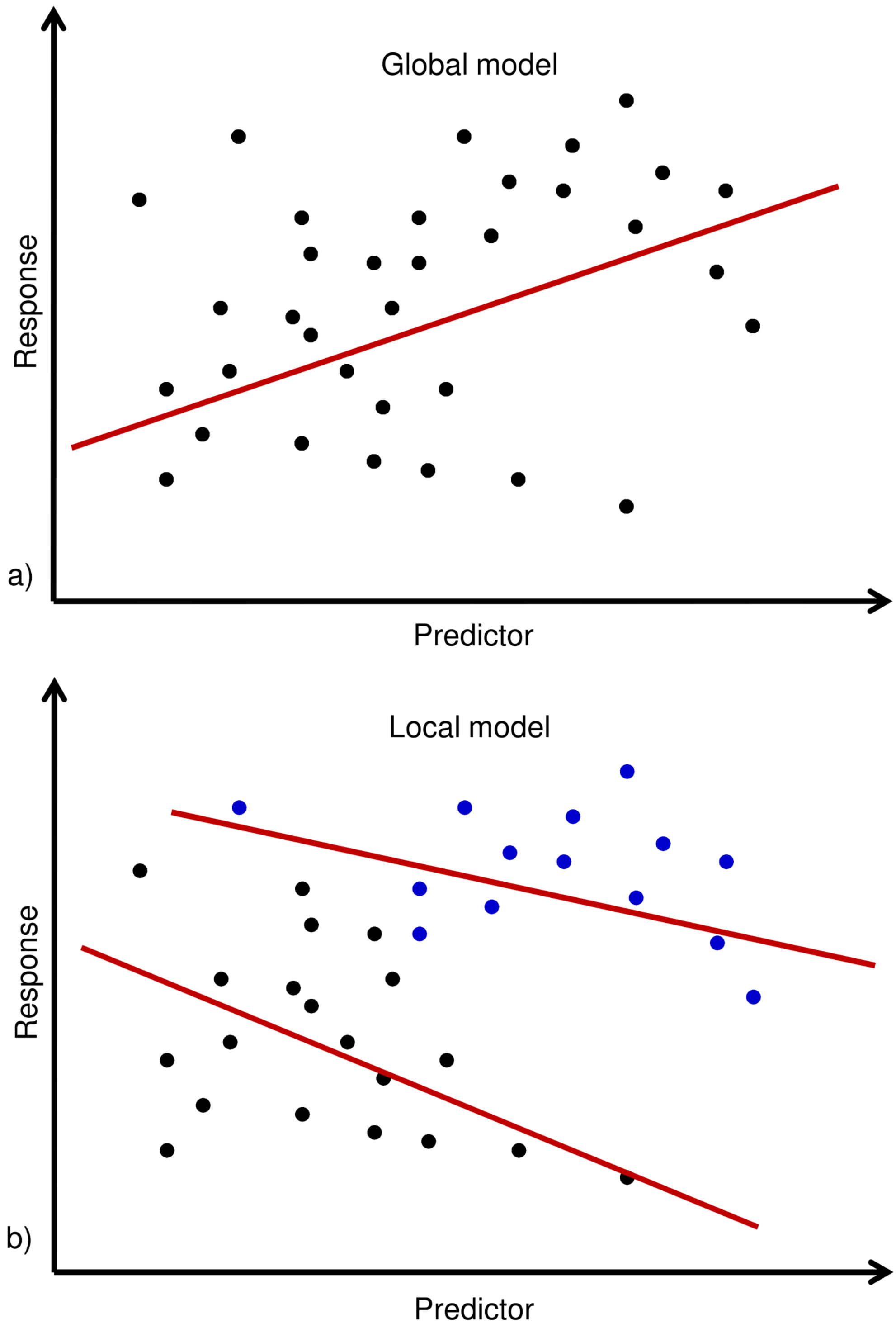


Figure 5.1: Simpson's Paradox. The global model (a) indicates a positive correlation between response and predictor variables. The trend is reversed when the same dataset is split amoung two different contexts (b).

is applicable to relationships in this savanna landscape.

5.2 Methods

Spatial variation in woody pattern-process relationships, and the emergence of Simpson's Paradox, were assessed from the perspective of woody structure across the savanna riparian landscape. Spatial variation in woody structure-environment relationships was statistically assessed through spatially explicit local analysis procedures, and the nature of woody structure-environment relationships was determined for different spatial contexts within a patch hierarchy.

5.2.1 Spatial variation in woody structure-environment relationships

Woody height and cover were extracted from LiDAR data and aerial imagery as described in Chapter 2 (Figure 2.7 on page 45). They were rendered as rasters to provide high-resolution (1m), spatially explicit representations of woody structural attributes (Figure 3.1 on page 57 and Figure 3.2 on page 58), from which to explore spatial variation in woody structure-environment relationships. The 12 continuous environmental variables, from the broader group of variables selected in Chapter 3 (Table 3.1 on page 63), were used to test for spatial variance in woody structure-environment relationships.

Statistical analysis of spatially varying relationships

The spatial relationship between woody canopy height, canopy cover and environmental variables was explored through geographically weighted regression (GWR) (Fotheringham et al., 2002) as it provides a spatially explicit means of exploring the relationship between response and explanatory variables (Brunsdon et al., 1998). Given the heterogeneity inherent in the study area, the spatial non-stationarity assumptions of standard global regressions are unlikely to be met. The standard global regression model can be expressed as follows:

$$\gamma_i = \beta_0 + \sum_{j=1}^{p} \beta_j \chi_{ij} + \varepsilon_i$$

where γ_i is the value of the response variable γ at location i, $\beta_0$is the intercept, β_j is the slope coefficient of the predictor variable j, $\chi_{ij}$is the value of the predictor variable j at location i, and ε_i is the random error term. Model coefficients are estimated by minimizing the squared error for each data point in ordinary least squares (OLS) regression. Unlike global models, GWR allows local coefficients for each of the predictor variables (Kupfer and Farris, 2007). The GWR equation is therefore as follows:

$$\gamma_i = \beta_0(\mu_i, \nu_i) + \sum_{j=1}^{p} \beta_j(\mu_i, \nu_i)\chi_{ij} + \varepsilon_i$$

where (μ, ν_i) are co-ordinate locations for each location i and $\beta_o(\mu, \nu_i)$,$\beta_1(\mu, \nu_i)$.... ,$\beta_p(\mu, \nu_i)$ are $p+1$ continuous functions of the location (μ, ν_i).The localized variable coefficients are based on a weighting matrix in which observations around a sample point are weighted using a distance decay function. Proximal observations therefore have greater influence on the resulting localized regression coefficients. Direct comparison of the R^2 values of geographically weighted and global regression models are often not valid due to the difference in the degrees of freedom of the two approaches. Improvement of a GWR regression model over a global model is therefore measured in terms of the Akaike Information Criterion (AIC). Following Hurvich et al. (1998), the Akaike Information Criterion (AIC) is defined as follows:

$$AIC_c = 2nlog_e(\sigma) + nlog_e 2(\pi) + n\left\{\frac{n + tr(S)}{n - 2 - tr(S)}\right\}$$

where n is the sample size, $\sigma$is the estimated standard deviation of the error term, and $tr(S)$denotes the trace of the hat matrix which is a function of the bandwidth.The AIC can be used to assess whether GWR provides a better fit than a global model, taking into account the different degrees of freedom in the two models (Fotheringham et al., 2002). Geographically weighted regression analyses were performed in GWR 3.0 (University of Newcastle). Spatial non-stationarity of processes was tested by regressing both of the response variables against the 12 environmental variables using the GWR approach. Bandwidth selection was determined through AIC minimization to ensure the best possible fit of the model. Spatial non-stationarity of underlying variables was tested statistically according to the Monte Carlo approach developed by Hope (1968).

Sampling design

Geographically weighted regression was chosen for its ability to elucidate spatial relationships between response and explanatory variables. In Chapter 3, the total explained variation in the distribution of woody structural classes was very low (10-20%) at the 1ha scale (section 3.3.2 on page 71), and I hypothesized that much of the unexplained variation at this fine-scale may be attributable to spatial variation in woody structure. As such, a sampling design was constructed to optimize the spatial coverage of 1ha sampling plots, within the computational limits of GWR. The circular sample plots were distributed across the entire LiDAR coverage, and each plot was positioned 150m apart from adjacent plots in a triangulated network. This design ensured comprehensive spatial coverage (27 000 plots) of the alluvial lowlands and their adjacent uplands, and provided an avenue for exploring spatial variation in woody structure-environment relationships. The mean of each response and explanatory variable was calculated for each plot for use in the GWR analysis.

5.2.2 Context-dependency in woody structure-environment relationships

Geographically weighted regression (GWR) results are well suited to identifying spatial variation in relationships, but the standard outputs do not provide a means of quantifying how relationships differ in different spatial contexts. As such, the localized woody height-environment relationships were examined further within a patch hierarchy (Figure 5.2).

The hierarchy was constructed from substrate and hydrological criteria as described in Chapter 4 (section 4.2.3 on page 92). The total area of the LiDAR coverage formed the largest patch. This patch was split amoungst the four major river catchments, which were then each divided according to granitic or basaltic substrate. These eight patches were then split again into alluvial riparian zones and their adjacent upland soil-types (sand on the granites and clay on the basalts), resulting in 16 patches at the lowest level of the hierarchy. Results from the GWR analysis were exported to ArcGIS 9.2 (ESRI), and the proportion of a patch in which each environmental variable exhibited significant positive and/or negative correlations with woody canopy height was then calculated, to assess how spatial context influenced woody structure-environment relationships. Exploration of woody structure-environment relationships within this hierarchy also provided a means for exploring the emergence of Simpson's Paradox in this landscape.

5.3 Results

5.3.1 Spatial variation in woody-structure environment relationships

The spatially variable GWR models showed significant improvements, in terms of AIC reduction, over the standard global regressions (Table 5.1), indicating that

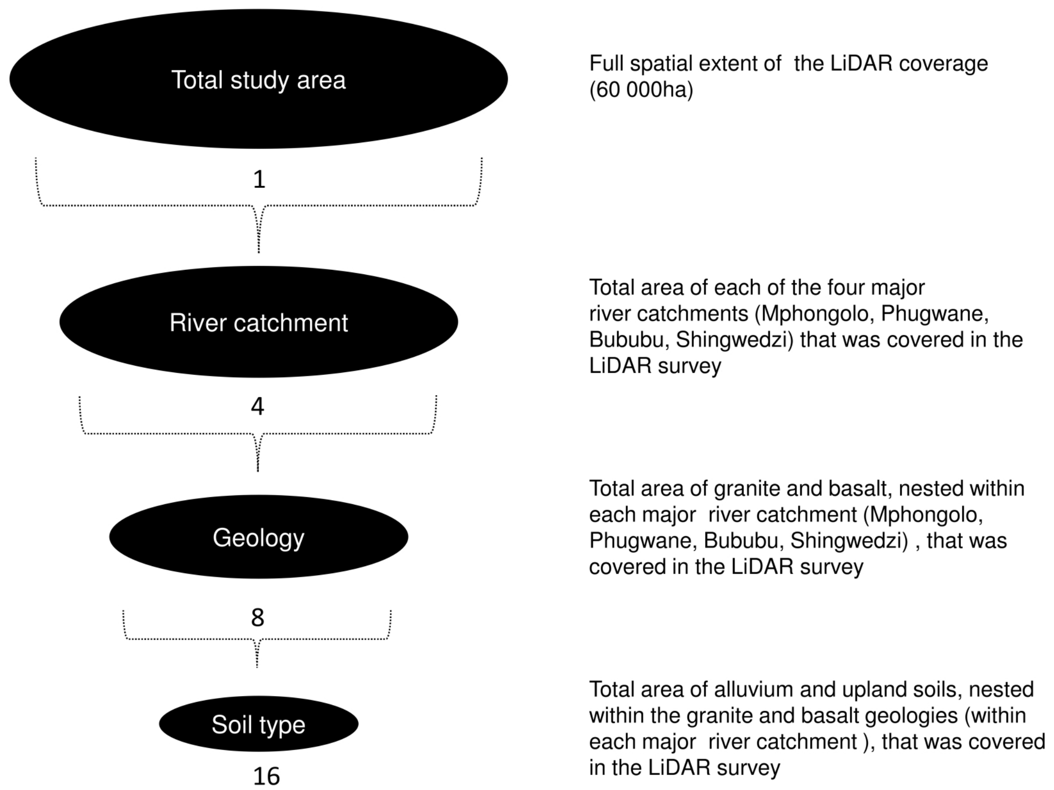


Figure 5.2: Patch hierarchy for the exploration of context-dependency in woody structure-environment relationships.

woody structure-environment relationships vary spatially across the landscape. This was confirmed through the spatial exploration of the model outputs, as the woody canopy height model produced a better fit in the eastern (downstream) portion of the study site and in the sampled area of the Shingwedzi and the Bububu catchments (Figure 5.3). However, the canopy cover model outputs were variable across the study area and showed no broader scale spatial trends (Figure 5.4). Woody canopy height was better correlated with the environmental variables than canopy cover, for both global and local models (Table 5.1). These patterns reveal greater non-stationarity in woody height-environment relationships and compliment the interpretation of results gained in Chapter 3 (Figure 3.11 on page 74 and Figure 3.6 on page 68) which suggested that height was more environmentally constrained than cover.

Table 5.1: Comparison of global and geographically weighted regression results for the relationship between woody height, cover and environmental variables.

	Canopy height	Canopy cover
Global R^2	0.265	0.095
Global AIC	35959	116504
GWR R^2	0.543	0.306
GWR AIC	31222	114905
F-value	5.703	3.353

All the environmental variables, with the exception of aspect, exhibited significant spatial non-stationarity across the study site (Table 5.3), therefore the GWR approach makes more ecological sense in this landscape than standard global approaches, as it allows for spatial variation in relationships. As such, limited confidence should be placed in the global model parameters (Table 5.5), despite them being the norm in most ecological analyses, as they assume stationarity.

Given the high levels of spatial non-stationarity shown here, standard global

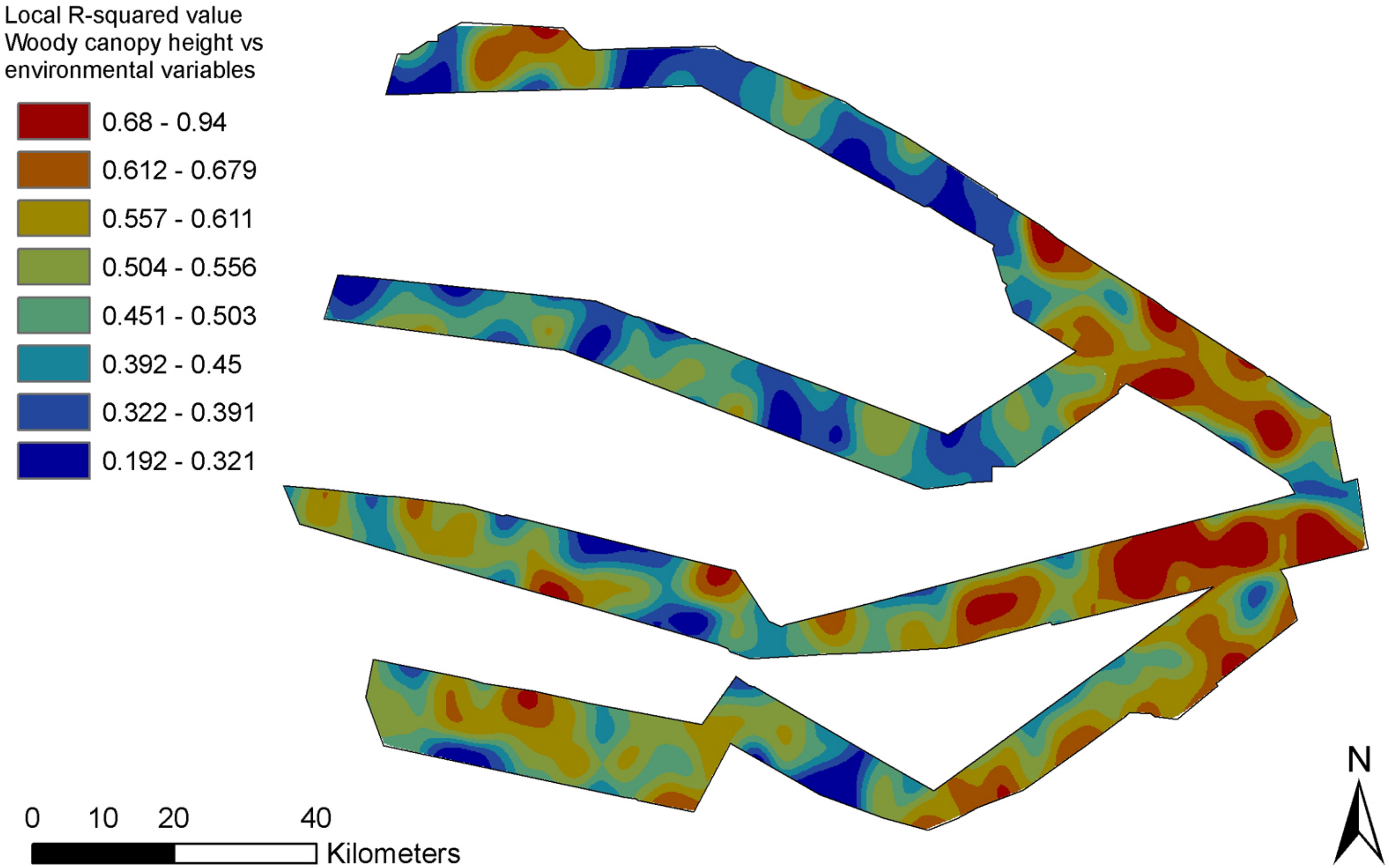


Figure 5.3: Spatial variation in the relationship between woody canopy height and underlying environmental variables.

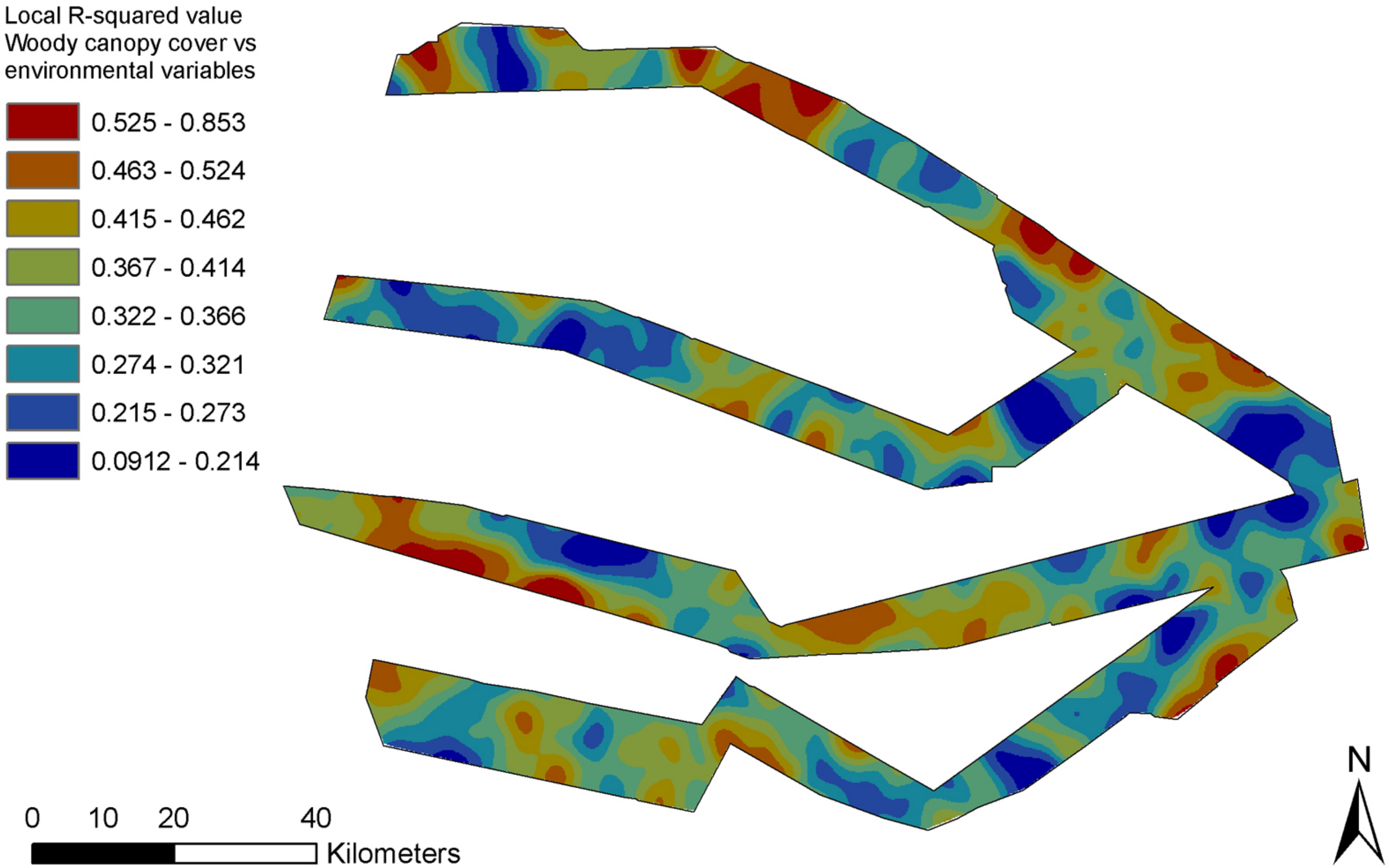


Figure 5.4: Spatial variation in the relationship between woody canopy cover and underlying environmental variables.

Table 5.3: Monte Carlo significance test for the spatial non-stationarity of environmental variables.

	Monte Carlo test for non-stationarity
Intercept	$p < 0.001$
Fire return interval	$p < 0.001$
NS aspect	$p > 0.05$
EW aspect	$p > 0.05$
Distance to main river	$p < 0.001$
Distance to roads	$p < 0.001$
Distance to small rivers	$p < 0.001$
Distance to water points	$p < 0.001$
Contributing area	$p < 0.001$
Flow length	$p < 0.001$
Relative elevation above river channel	$p < 0.001$
Elevation above sea level	$p < 0.001$
Slope	$p < 0.001$

Table 5.5: Global model relationships between environmental variables and woody canopy height and canopy cover.

	Woody canopy height			Woody canopy cover		
	Estimate	SE	T-value	Estimate	SE	T-value
Intercept	5.3118	0.1183	44.892*	44.7686	1.7481	25.609*
Fire return interval	0.0468	0.0050	9.366*	0.1545	0.0738	2.093*
NS aspect	0.1273	0.2153	0.591	5.6252	3.1815	1.768
EW aspect	0.2914	0.2121	1.373	3.8047	3.1334	1.214
Distance to main river	-0.3958	0.0251	-15.748*	-0.2036	0.3713	-0.548
Distance to roads	-0.0393	0.0144	-2.733*	0.6830	0.2124	3.214*
Distance to small rivers	0.0247	0.0177	1.395	-2.0598	0.2614	-7.880*
Distance to water points	-0.0523	0.0227	-2.310*	1.0575	0.3348	3.158*
Contributing area	0.3909	0.0233	16.755*	4.4334	0.3447	12.861*
Flow length	-1.2609	0.0389	-32.431*	-10.0071	0.5744	-17.422*
Relative elevation above river channel	-0.0063	0.0013	-4.740*	0.0230	0.0195	1.181
Elevation above sea level	0.0001	0.0002	0.322	-0.0137	0.0024	-5.674*
Slope	0.5289	0.0272	19.444*	8.1403	0.4019	20.255*

analyses may mask the true nature of processes operating across heterogeneous landscapes. For example, standard global regression indicated a negative correlation between relative elevation above the river channel and woody height (Figure 5.5a). The patch specific pattern (Figure 5.5b), however, revealed that the relationship varied in different soil-type contexts and provides empirical evidence of Simpson's Paradox in this system. Considering the relationship according to different river catchment contexts strengthens this pattern further, as although there was a negative correlation between woody canopy height and relative elevation on alluvial soils for all four rivers, the relationship differed on clay and sand soils across the river catchments, and was even positive in the upland areas of the Phugwane river (Figure 5.6).

Furthermore, although a linear trend was fitted to the global relationships between elevation above river channel and woody canopy height (Figure 5.5a), the pattern was distinctly nonlinear. The local representations of this pattern (Figure 5.5b and Figure 5.6) reveal that nonlinearity in the global pattern may emerge through the averaging of more linear relationships from different spatial contexts. Explicit awareness of spatial heterogeneity and context may therefore enhance current understanding of nonlinearity in ecological systems.

Whilst these results have illustrated both the presence of spatial variation in pattern-process relationships, and the emergence of Simpson's Paradox, the influence of spatial context on the relationships still needs explicit quantification.

5.3.2 Context-dependency in woody structure-environment relationships

The influence of spatial context on pattern-process relationships was quantified by determining the proportion of a patch (within the patch hierarchy - Figure 5.2) in which each environmental variable exhibited significant positive and/or negative correlations with woody canopy height.

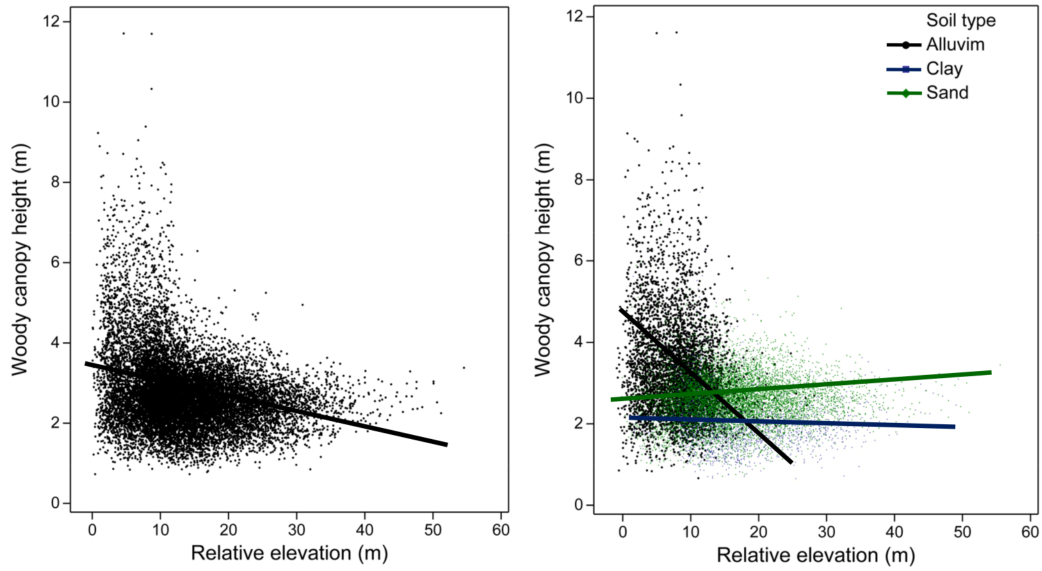


Figure 5.5: The emergence of Simpson's Paradox in the relationship between woody canopy height and relative elevation. The global relationship (a) differs considerably from the same relationship on different soil-types (b).

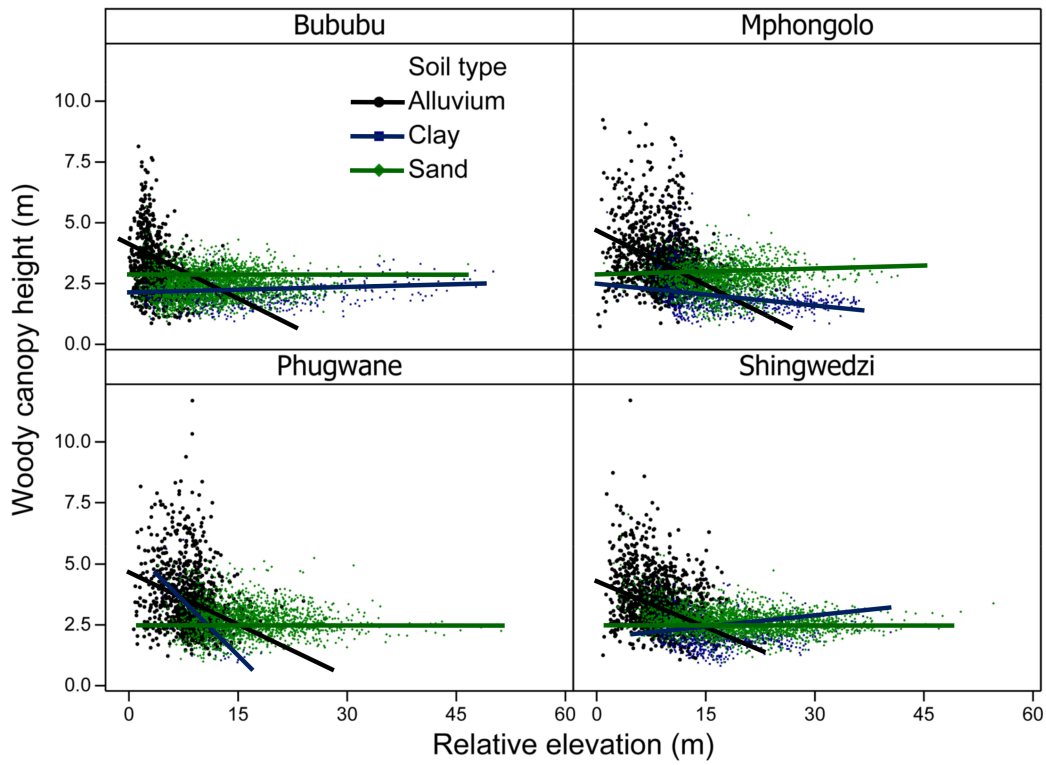


Figure 5.6: The emergence of Simpson's Paradox in the relationship between woody canopy height and relative elevation across four different river systems.

For example, relative elevation above the river channel exhibited both a positive and negative correlation with woody canopy height in a spatially variable manner across the landscape (Figure 5.7). The positive correlation occurred mostly in the lower reaches of the Mphongolo system, and the negative correlation was most prominent in the Bububu system. Summarizing these output for each patch in the hierarchy enabled clearer quantification of the influence of context on the relationship between woody canopy height and relative elevation, in terms of both magnitude (the proportion of the patch in which relative elevation was significant) and direction (positive or negative correlation) (Figure 5.8).

At the river catchment level of the hierarchy, relative elevation was positively correlated with woody height in the majority of the Mphongolo patch (67%), less than half of the Phugwane and Shingwedzi patches (40% and 35%) and only a small proportion of the Bububu patch (4%). At a finer scale, within the Mphongolo patch, relative elevation was positively correlated with woody height on 97% of the basaltic substrates and 37% of the granitic substrates (see Figure 5.7 for the spatial representation and Figure 5.8 for the quantification within the patch hierarchy). In the Bububu patch, however, relative elevation was negatively correlated with canopy height in 62% of the patch, 71% of its granitic substrates and 53% of its basaltic substrates (see Figure 5.7 for the spatial representation and Figure 5.8 for the quantification within the patch hierarchy). Similar spatially variable and context specific relationships held true for the majority of the environmental variables (Figure 5.9 and Figure 5.10). Hydrological flow length (FLW) and contributing area (CTA) were the only variables that maintained a consistent significant correlation with canopy height. This pattern highlights the importance of water availability for woody vegetation structure in savanna landscapes, as the potential for increased water supply (high contributing area, low hydrological flow length) was positively correlated with increased woody height. Importantly, this relationships held across all contexts, and although the strength of the relationship varied in different parts

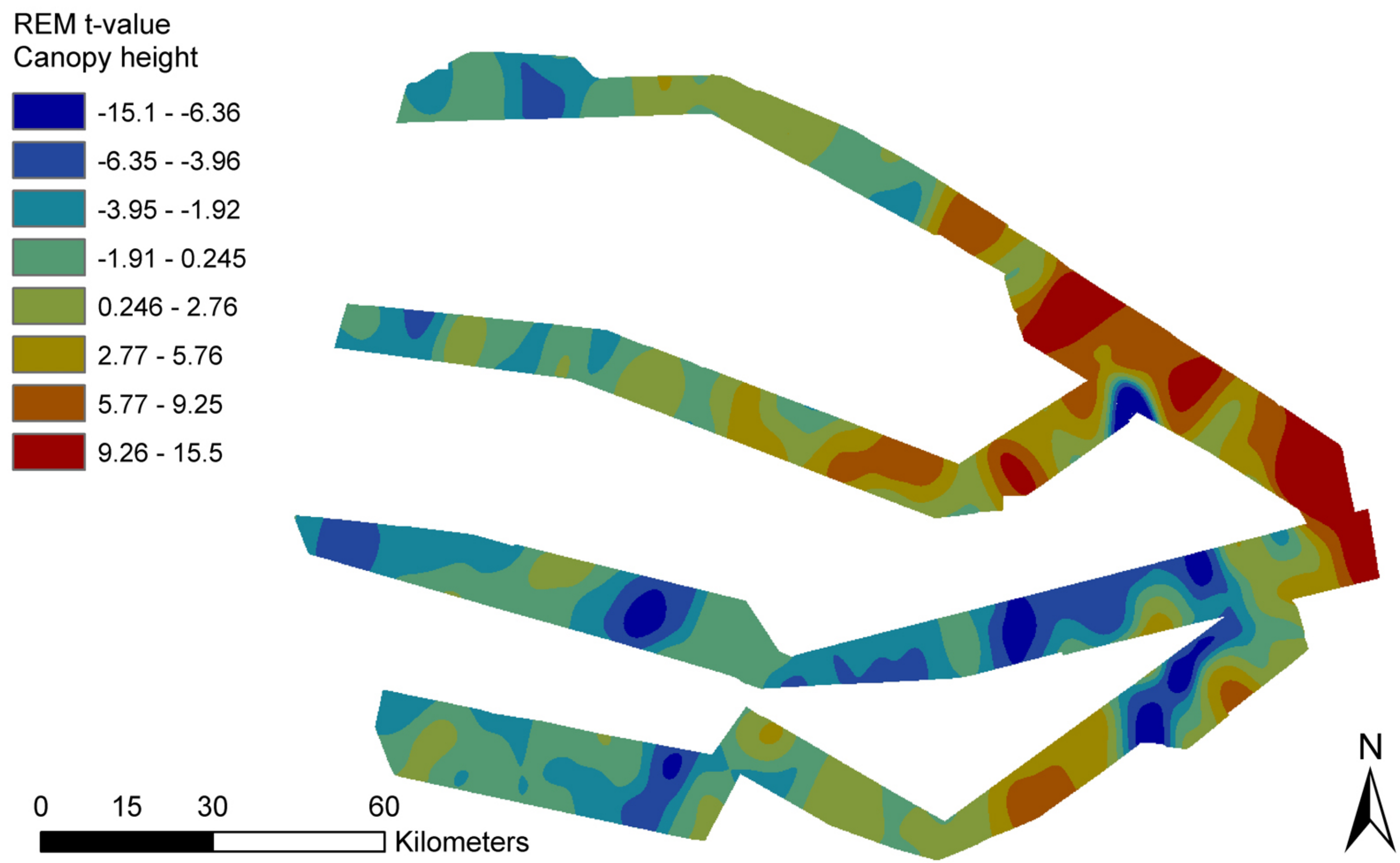


Figure 5.7: Spatial variation in t-statistic values for the correlation between relative elevation above the channel (REM) and woody canopy height.

	Positive	Negative
Mphongolo	67	9
Granite	37	17
Alluvium	37	17
Sand	38	18
Basalt	97	0
Alluvium	100	0
Clay	94	1
Phugwane	40	31
Granite	46	13
Alluvium	53	12
Sand	38	14
Basalt	35	48
Alluvium	28	54
Clay	42	42
Bububu	4	62
Granite	0	71
Alluvium	0	79
Sand	1	62
Basalt	8	53
Alluvium	6	59
Clay	10	46
Shingwedzi	35	22
Granite	20	29
Alluvium	33	28
Sand	7	31
Basalt	50	14
Alluvium	56	2
Clay	45	26
Total	37	31

Figure 5.8: The influence of spatial context on woody pattern-process relationships. The graph represents the proportion of patch in which there was a significant relationship between relative elevation above the channel (REM) and woody canopy height ($p < 0.05$). The length of the bars denote the proportion of a patch on a scale from 1 to 100. The patch hierarchy was derived from the total study area, the four river catchments, the two dominant geologies and the three prominent soil types.

of the landscape (both variables exhibited significant spatial non-stationarity), the direction of the relationship remained constant in both the uplands and lowlands of the different river systems.

5.4 Discussion

Woody structure-environment relationships varied considerably across the savanna landscape, to the extent that it was difficult to identify consistent patterns. The magnitude and direction of woody structure-environment relationships differed among the sampled area of the four different river catchments and varied differentially across the soil-types associated with different hillslope positions within each catchment. The context-dependent patterns shown here provide empirical evidence for the primary assumption of landscape ecology, that spatial context strongly determines ecological patterns and processes (Wiens, 1995), and have fundamental implications for both savanna and landscape ecology.

5.4.1 Implications of context-dependency for ecological understanding

Assumptions of homogeneity and stationarity limit ecological understanding in savanna systems where heterogeneity gives rise to context dependent relationships. High levels of spatial variability in woody structure-environment relationships, and the emergence of Simpson's Paradox (Simpson, 1951; Wagner, 1982; Newson, 1991) in this system, bring into question widely accepted interpretations of ecological phenomena that are derived from conventional global analyses.

Understanding the complexity of nature requires assumptions of homogeneity to be replaced by the explicit recognition of heterogeneity (Wiens, 1989; Wu and Loucks, 1995). Furthermore, without the explicit consideration of context, research in heterogeneous systems is likely to misrepresent ecological relationships, as the

	CTA	FLW	DTM	SLO	NS	EW	REM	DMR	DSR	FIRE	DWP	DRD
Mphongolo	74	0	15	72	8	2	67	2	23	48	16	27
Granite	50	0	20	71	0	5	37	3	36	22	16	21
Alluvium	51	0	14	69	1	6	37	3	37	23	19	21
Sand	48	0	27	73	0	3	38	2	35	22	14	21
Basalt	98	0	9	72	16	0	97	2	10	73	16	33
Alluvium	100	0	7	80	20	0	100	0	16	67	17	37
Clay	96	0	11	65	12	0	94	4	4	78	14	29
Phugwane	91	0	18	74	3	1	40	0	61	41	46	25
Granite	81	0	4	47	7	1	46	0	34	39	25	47
Alluvium	85	0	5	53	9	2	53	0	39	40	25	50
Sand	78	0	2	41	5	1	38	0	28	39	24	44
Basalt	100	0	32	100	0	0	35	0	89	43	67	4
Alluvium	100	0	26	100	0	0	28	0	96	52	75	0
Clay	100	0	38	100	0	0	42	0	82	35	58	8
Bububu	80	0	61	96	0	0	4	3	8	24	29	35
Granite	75	0	75	92	0	0	0	6	4	37	40	19
Alluvium	83	0	84	93	0	0	0	5	2	33	40	18
Sand	68	0	66	90	0	1	1	6	5	42	40	20
Basalt	85	0	47	100	0	0	8	0	12	11	19	51
Alluvium	97	0	49	100	0	0	6	0	5	5	7	53
Clay	73	0	44	100	0	1	10	0	18	17	31	50
Shingwedzi	92	0	8	56	0	12	35	4	17	33	44	11
Granite	86	0	16	55	0	13	20	1	18	25	53	14
Alluvium	94	0	18	61	0	23	33	0	32	28	51	22
Sand	78	0	14	49	0	4	7	2	4	22	56	5
Basalt	99	0	1	56	0	10	50	6	17	40	34	8
Alluvium	99	0	0	56	0	15	56	0	22	50	35	11
Clay	98	0	1	57	0	6	45	13	11	30	34	6
Total	84	0	25	74	3	4	37	2	27	37	34	25

Figure 5.9: Proportion of a patch (left-hand column) in which there was a positive relationship between environmental variables (column headings) and woody canopy height ($p < 0.05$). Length of bar denotes proportion of patch on a scale from 1 to 100. CTA = contributing area, FLW = flow length, DTM = elevation above sea level, SLO = slope, NS = north-south aspect, EW = east-west aspect, REM = elevation above river channel, DMR = distance o main river, DSR = distance to small river, FIRE = fire return interval, DWP = distance to water points, DRD = distance to roads.

	CTA	FLW	DTM	SLO	NS	EW	REM	DMR	DSR	FIRE	DWP	DRD
Mphongolo	0	88	44	3	4	0	9	70	27	8	39	37
Granite	0	77	25	1	7	0	17	57	18	9	31	27
Alluvium	0	78	29	1	5	0	17	56	17	6	27	26
Sand	0	76	20	1	9	0	18	58	20	13	36	28
Basalt	0	98	63	6	0	0	0	82	35	6	47	46
Alluvium	0	100	73	5	0	0	0	81	28	11	40	44
Clay	0	96	53	7	0	0	1	84	43	2	55	48
Phugwane	0	97	53	2	2	0	31	71	10	20	23	44
Granite	0	93	68	3	4	1	13	68	20	21	45	7
Alluvium	0	97	70	5	3	1	12	73	20	26	50	7
Sand	0	90	66	2	5	0	14	63	21	16	41	7
Basalt	0	100	39	0	0	0	48	75	0	20	0	80
Alluvium	0	100	30	0	0	0	54	85	0	19	0	95
Clay	0	100	47	0	0	0	42	65	0	21	0	65
Bububu	0	98	7	0	3	1	62	73	35	39	21	11
Granite	0	99	6	0	0	1	71	50	31	25	14	17
Alluvium	0	100	4	0	0	1	79	64	41	25	14	18
Sand	0	99	8	0	0	1	62	35	22	25	15	17
Basalt	0	97	7	0	7	0	53	96	39	53	27	5
Alluvium	0	100	2	0	12	0	59	100	32	75	32	3
Clay	0	94	13	0	2	0	46	91	46	31	22	7
Shingwedzi	0	93	56	5	3	0	22	66	29	20	17	30
Granite	0	86	33	0	6	0	29	75	40	23	14	19
Alluvium	0	95	44	0	10	0	28	81	32	29	14	16
Sand	0	78	23	0	1	0	31	69	48	18	14	22
Basalt	0	100	78	11	0	0	14	58	17	16	20	42
Alluvium	0	100	83	15	0	0	2	59	18	10	11	30
Clay	0	100	73	6	0	0	26	56	17	22	30	54
Total	0	94	40	3	3	0	31	70	25	22	25	31

Figure 5.10: Proportion of a patch (left-hand column) in which there was a negative relationship between environmental variables (column headings) and woody canopy height ($p < 0.05$). Length of bar denotes proportion of patch on a scale from 1 to 100. CTA = contributing area, FLW = flow length, DTM = elevation above sea level, SLO = slope, NS = north-south aspect, EW = east-west aspect, REM = elevation above river channel, DMR = distance o main river, DSR = distance to small river, FIRE = fire return interval, DWP = distance to water points, DRD = distance to roads.

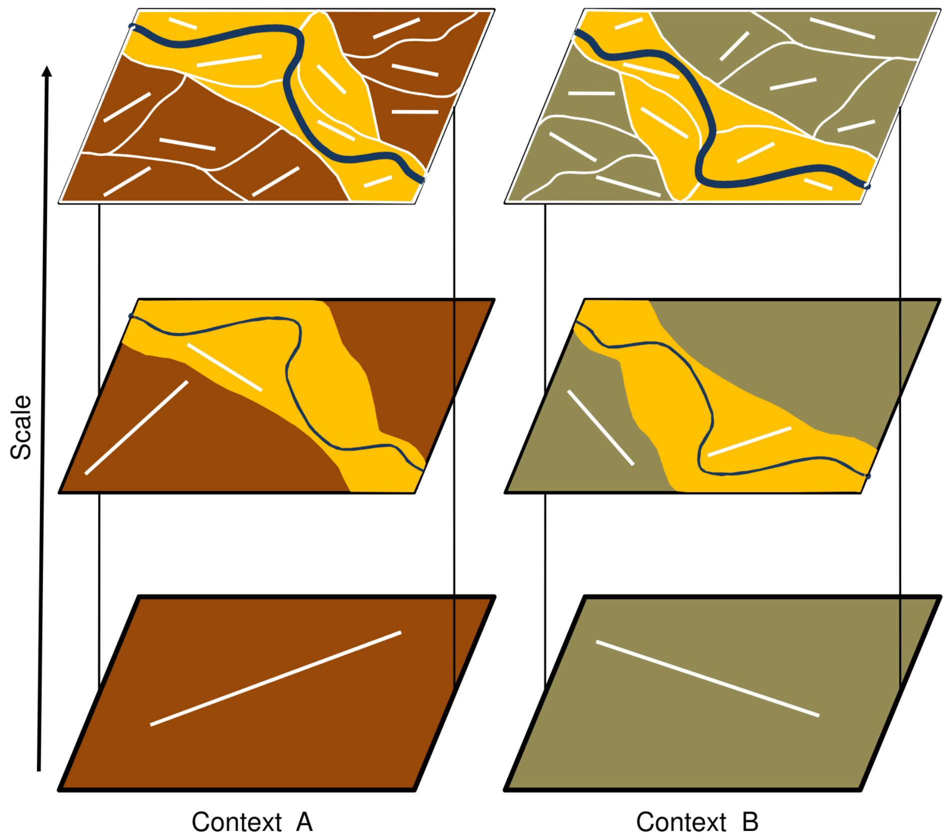


Figure 5.11: Schematic conceptualization of the influence of spatial context on pattern-process relationships. In context A there is a positive relationship between a response and an explanatory variable at the large scale (white lines represent the direction of the relationship). In context B, there is a negative correlation between the same two variables. The nature of the relationship changes and becomes more variable as scale of analysis decreases.

parameters of global models may not actually reflect the nature of a ecological relationship at any point in the landscape (Foody, 2004). In this heterogeneous system, the relationship between response and explanatory variables differed in both magnitude and direction in different spatial locations, thus interpretation of any directional trend in an ecological relationship becomes context-dependent (Figure 5.11).

It is critical that the current disregard for spatial influences in ecology is rectified, and that spatial context is explicitly incorporated into future research design, analysis and interpretation. Results obtained, or conservation objectives defined, in one spatial or temporal location are very likely to have little or no applicability in another. Although much thought has been given to problems of scaling in ecology (Turner et al., 1989; Wiens and Milne, 1989; Bradshaw, 1998; Cash and Moser, 2000; Gardner, 2001; Wu, 2004; Wu and Harbin, 2006), the problem of transferring results and management principles across different contexts also needs theoretical and practical exploration.

This is no easy task, but Jones and Callaway (2007) suggested that gaining better understanding of context-dependency in vegetation communities involves the combination of: (1) incremental sampling of local variation in vegetation pattern; (2) spatial and temporal measures of direct interactions; (3) locally parametrized versions of the general models; and (4) experiments manipulating the kinds of direct interactions and their intensities at appropriate spatial and temporal scales. I advise a slight modification to this approach, as the spatial analysis technique adopted in this study provides an excellent starting point for following their suggested approach. The initial spatial exploration of how pattern-process relationships vary across a landscape provides a means of stratifying that landscape to inform the next phases of investigation.

Whilst these findings are important in their own right, they also provided insight into understanding the roots of nonlinearity of ecological systems. The recognition of nonlinearity in semi-arid environments is not new (Hoffmann, 2002; Zeng et al., 2002; Manzoni et al., 2004; Peters and Havstad, 2006), but these patterns indicate that nonlinear relationships arise through spatial variation of processes across heterogeneous landscapes. Explicitly considering the spatial structure of landscapes, at different scales, will therefore enhance current understanding of nonlinearity in heterogeneous systems.

Spatial context was largely explored in terms of spatial location, but patch configuration has been found to nonlinearly affect sediment loss across scales in an Australian savanna (Ludwig et al., 2007). Future avenues of research should therefore consider a broader perspective of spatial context that incorporates spatial location, neighbourhood and adjacency. The quantification and description of landscape patterns remains an important element of landscape ecology, but generating understanding of how landscape heterogeneity influences ecological relationships becomes imperative.

Chapter 6

Conclusion

Exploration of the woody component of the broader Shingwedzi Catchment has revealed complex interactions between different attributes of woody structure, environmental variables, scale and spatial context. Landscape ecology has been criticized for being a purely descriptive science that focuses on pattern identification and quantification, without providing understanding of the implications of those patterns (Haines-Young, 2005). In this chapter I provide perspective of how the remotely sensed spatio-temporal quantification of woody structure, and subsequent multi-scaled spatial analyses, hold implications for understanding of pattern-process relationships and have made a meaningful contribution to the field of landscape ecology.

6.1 The influence of space, time and scale in heterogeneous systems

The primary contribution of landscape ecology to the recent paradigm shift in ecology, from assumptions of homogeneity to heterogeneity, has been the explicit consideration of spatial structure and spatio-temporal interaction of processes in ecological research (Wagner and Fortin, 2005). Patterns of woody structure and spatio-temporal dynamics exhibited strong spatial trends across the savanna riparian landscape. Tall, dense, structurally diverse canopies occurred on lowland alluvial soils. Decreases in woody cover also occurred in these locations whilst increases in cover took place in the upland areas. Although total percentage woody cover remained unchanged across the landscape, these patterns do not adhere to the metastability principle of the hierarchical patch dynamics paradigm (HPDP), as heterogeneity decreased over time and woody patches became fragmented.

Spatio-temporal patterns in vegetation reveal that this system is not randomly structured but organized by ecological processes. The HPDP suggests that such organization is hierarchically controlled through processes acting at different spatio-temporal scales (Wu and Loucks, 1995). This prediction was validated by the correlation of different environmental variables with woody structural attributes at different scales. Woody canopy height, canopy cover and cover dynamics exhibited scale variance in their relationships with environmental drivers, as predicted by the HPDP. However, woody canopy height diversity and cover diversity were scale invariant in their relations with environmental variables and were strongly influenced by substrate at all scales of analysis.

Woody structure-environment relationships varied not only with scale, but also with spatial location, particularly among different river catchments and hillslope positions, revealing that ecological relationships are contingent upon where they are located in space. System heterogeneity has gained increased attention through the field of landscape ecology, but understanding the implications and consequences of heterogeneity remains a fundamental challenge to ecologists (Pickett and Cadenasso, 1995; Turner et al., 1997; Wu and Hobbs, 2002; Turner, 2005). One such key consequence is the the high degree of context-dependency shown in woody structure-environment relationships.

6.1.1 Advancing understanding of pattern-process relationships in heterogeneous systems through the explicit consideration of context

Although the concept of context is inherent in the HPDP, in that upper levels constrain the processes at lower levels, spatial context within a level of organization is seldom considered. The hierarchical arrangement of processes influencing ecological systems is usually conceptualized as groups of processes acting at a particular scale, and the influence of each process is constrained by previous levels in the hierarchy. Gillson's (2004a) framework advanced this theory in savannas by illustrating the range of spatio-temporal scales across which different processes influence woody density (Figure 1.4 on page 28). However this framework does not account for the influence of spatial context in heterogeneous systems. Context-dependent variation in woody structure-environment relationships in the broader Shingwedzi Catchment demands the explicit consideration of context in ecology, as processes acting at a particular scale are more influential in certain spatial contexts, and the scale at which the influence of a process emerges is context-dependent.

The incorporation of context into ecological frameworks is somewhat overwhelming, as generalizations become difficult when variation in different spatial locations is considered, and complete stratification of heterogeneous landscapes is not logistically feasible (Turner et al., 1997). Context-dependent patterns bring into question the level of system understanding that field-based measurements can provide, through their limited spatial representation, and emphasize the need for large scale fine-resolution remote sensing to play a larger role in ecology. Although remote sensing holds much potential for furthering understanding (Turner et al., 2003), the enhanced resolution and spatial coverage of measurements also reveal greater variability that may hinder ecological interpretation (Wu and Hobbs, 2002). The scaled and context conscious approach adopted in this study provided a means of extracting meaningful information from this variability, but a framework is needed to address context-dependency in future research.

A catchment-based approach for advancing understanding of context-dependency

Context-dependency arises from the heterogeneous structure of landscapes, where processes act differentially across space. Thus, the ecologically meaningful delineation of landscape heterogeneity at different scales, in a process-based manner, will provide a solid platform for gaining better ecological understanding in systems where context-dependency is prevalent. The spatially explicit exploration of woody-structure environment relationships in this savanna landscape revealed that much of the context-dependency in vegetation pattern arose through variation in spatial location within and between different river catchments (Chapter 5). Hillslope position, and its associated soil-types, strongly influenced both woody structure (Chapter 3) and woody spatio-temporal patterns (Chapter 4). Hillslope morphology in this landscape varies between different catchments (Figure 6.1), with longitudinal position within a river (Figure 6.2) and between different stream orders (Figure 6.3). Hillslopes become longer and flatter as position downstream increases (Khomo, 2003), and the degree of alluvial deposition increases. The movement of water across the landscape, and the influence of context-dependent processes, changes with spatial location within a stream catchment.

Furthermore, hydrological flow-length and contributing area were the only environmental variables to maintain consistent significant relationships with woody structure in both the upland (sand and clay soils) and lowland (alluvial soils) positions of all four river catchments (section 5.3.2 on page 126). These patterns highlight the importance of understanding water movement through landscapes, and suggest that a catchment-based hierarchy will provide an ecologically meaningful way of exploring savanna heterogeneity (Figure 6.4). Many authors consider water to be the single most important driver in savanna landscapes, as it acts across a broad

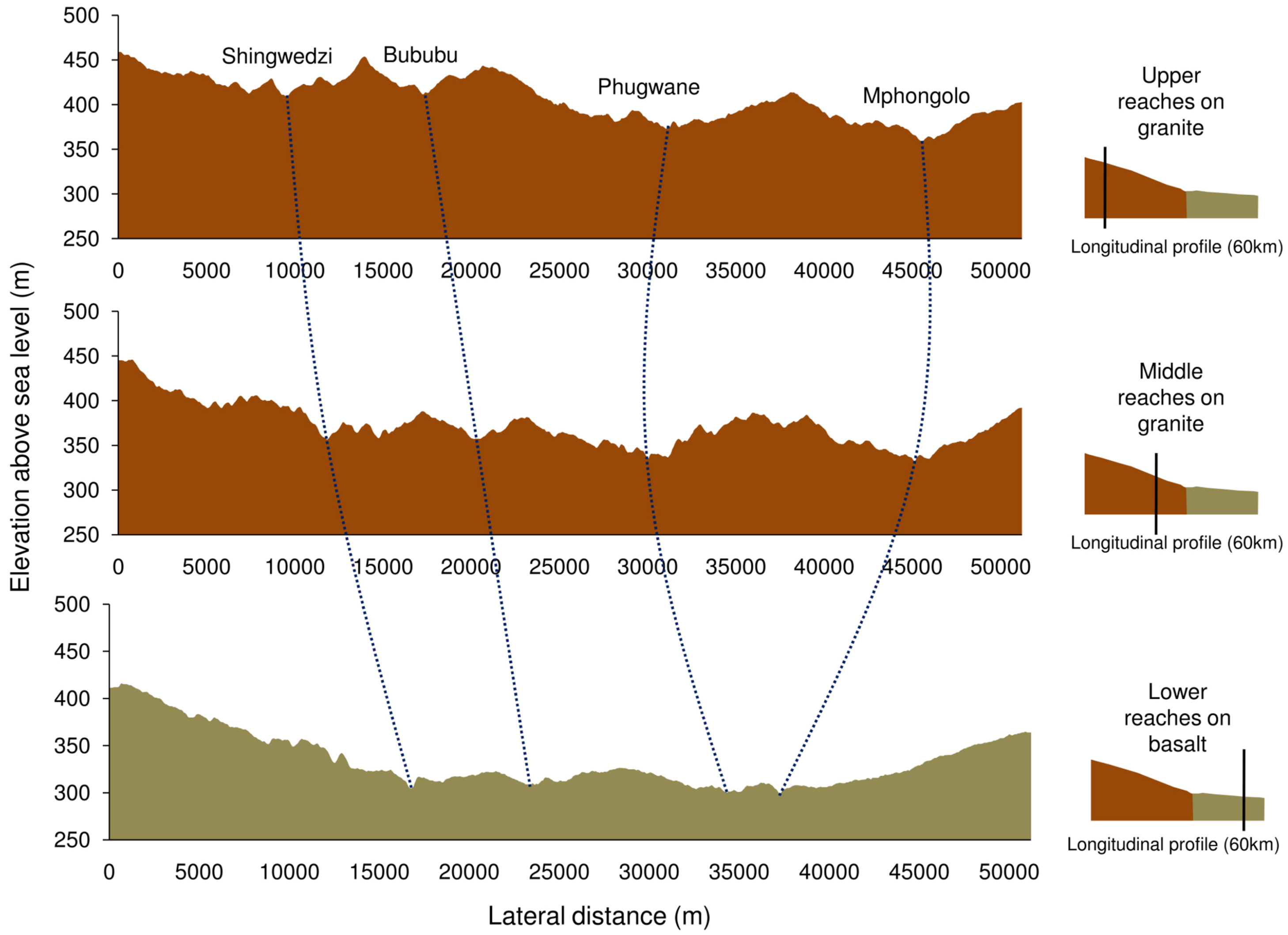


Figure 6.1: Cross-sectional profile of the four major river catchments, within the broader Shingwedzi Catchment, at different distances downstream. Profiles drawn from 90m SRTM data.

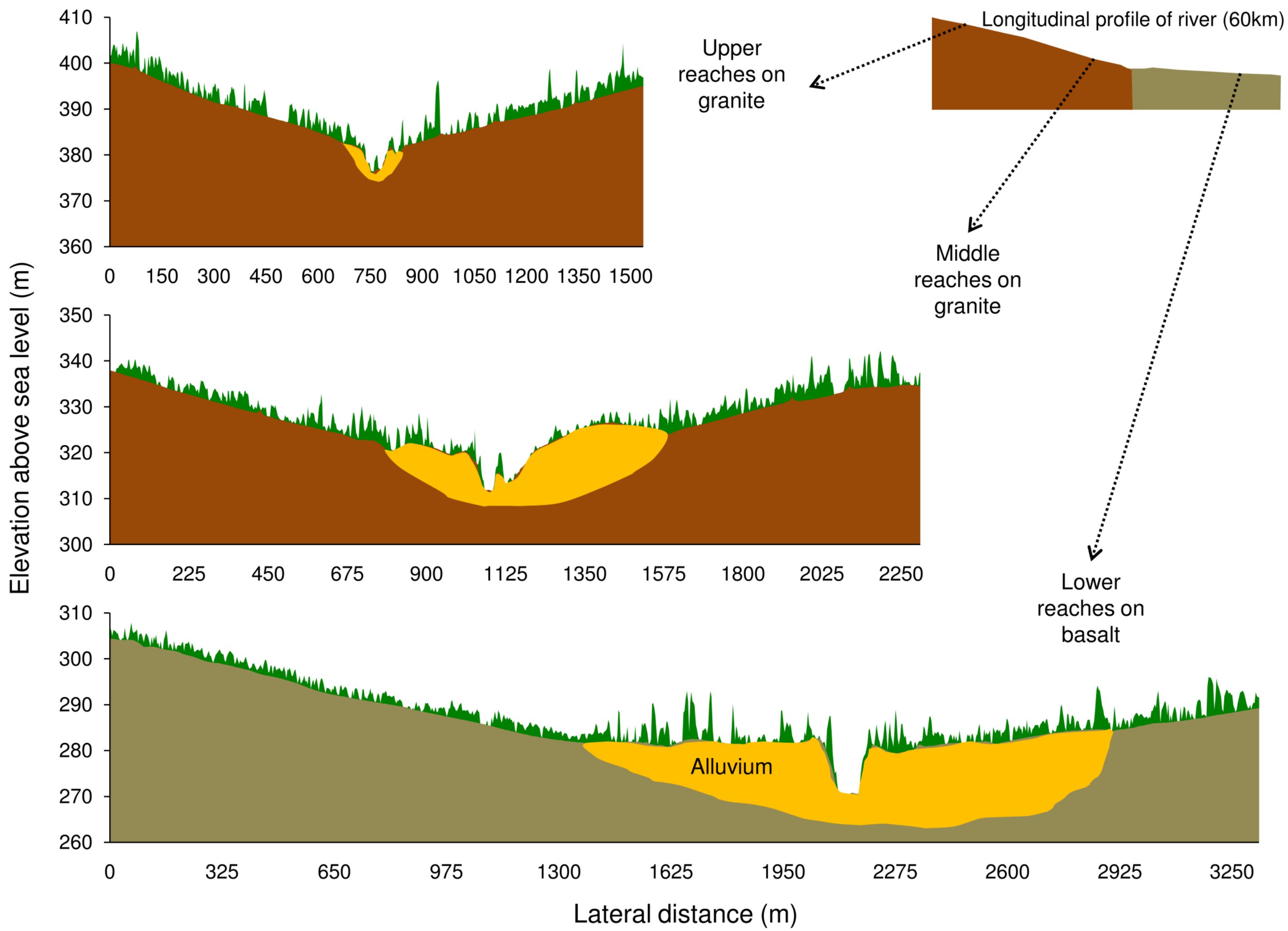


Figure 6.2: Cross-sectional profile of the upper, middle and lower reaches of the Mphongolo river, and its woody vegetation. Lateral slope decreases but hillslope length and alluvial deposition increase downstream. Profiles drawn from LiDAR derived DTM and nCM.

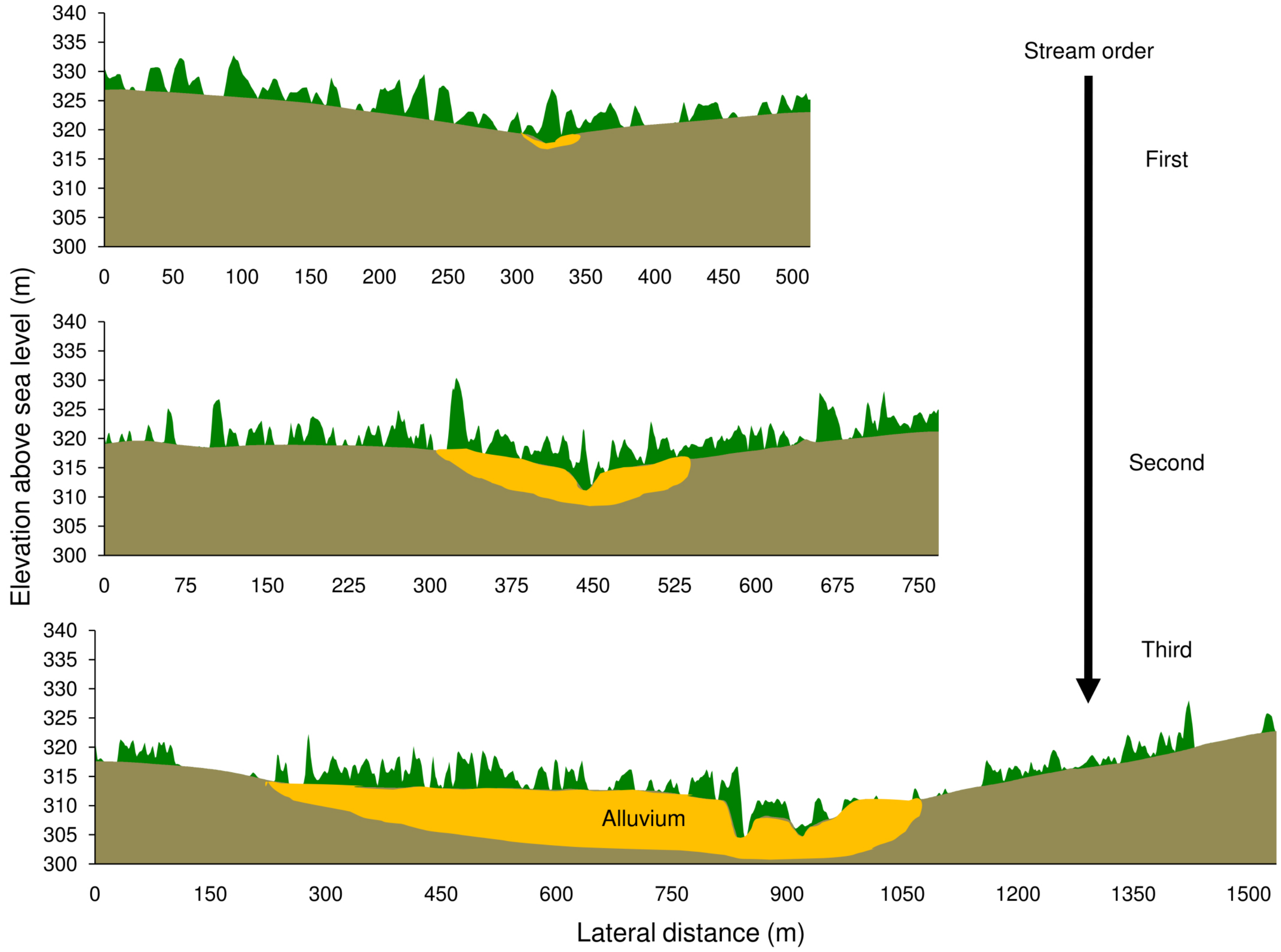


Figure 6.3: Cross-sectional profile of a first, second and third order stream, and its woody vegetation, within the lower reaches of the Mphongolo catchment. Lateral slope decreases but hillslope length and alluvial deposition increase with order. Profiles drawn from LiDAR derived DTM and nCM.

range of spatio-temporal scales, from weathering geological substrates, influencing the distribution of soil-types across a landscape, to controlling the mineralization rate and cycling of nitrogen needed for plant growth (Milne, 1935; Coughenour and Ellis, 1993; Scholes and Walker, 1993; Belsky, 1995; Ludwig et al., 1999, 2005). By explicitly considering the distribution and availability of water across a landscape at different scales, such a hierarchy will stratify the landscape according to the most dominant driver, and enable the influence of other more subtle drivers to be more clearly elucidated at different scales. Furthermore, the consideration of the landscape in this manner will provide a spatially explicit structure to help guide research and conservation efforts through the problem of context-dependency.

The limits of grain and extent of studies, organism perception of patchiness, disturbances and ecosystem drivers are usually defined by the spatio-temporal scales over which they act or exert an influence (Kotliar and Wiens, 1990; Rogers, 2003). In a context conscious hierarchy, the range of grain and extent for a particular factor will need to be redefined for different contexts as the scale at which a factor acts or exerts an influence will be context-dependent. The influences of scale, time and space are inextricably linked in ecological systems (Figure 6.5). Spatio-temporal patterns in heterogeneous systems should therefore only be interpreted in light of their context, and different outcomes should be expected at different scales and in different spatial locations .

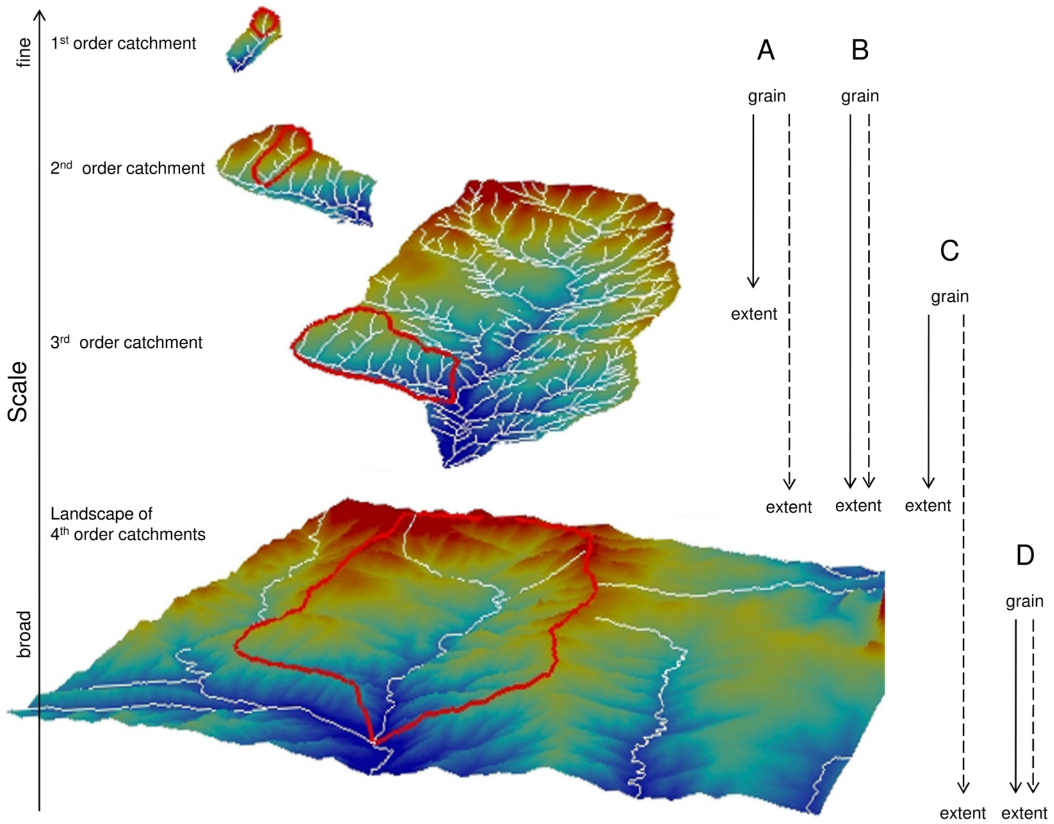


Figure 6.4: Delineation of catchments at different scales, based on stream order, to provide a process-based hierarchy for considering savanna heterogeneity. Factors A-D represent ranges of grain and extent of studies, organism perception of patchiness, disturbances, ecosystem drivers etc. The ranges of grain and extent of these factors are likely to be different in different spatial contexts (dotted lines).

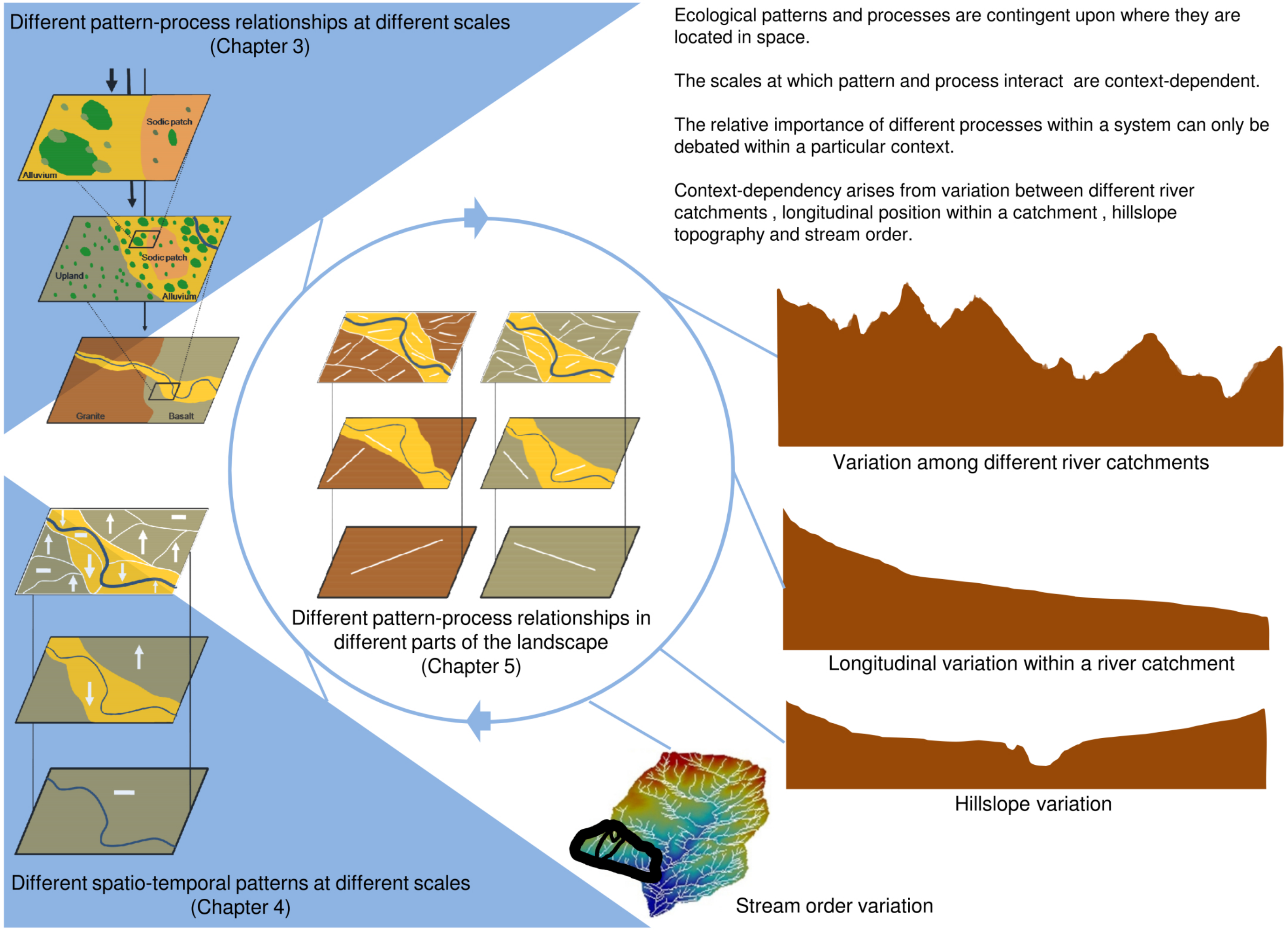


Figure 6.5: Schematic conceptualization of the key elements emerging from this thesis. Spatio-temporal patterns in heterogeneous systems can only be interpreted in light of their context, and multiple outcomes should be expected at different scales and in different contexts.

6.2 The further advancement of landscape ecology

Exploration of the influence of scale and context on pattern-process relationships in this heterogeneous savanna landscape has made meaningful contributions to the fields of remote sensing science, biodiversity conservation and landscape ecology.

A robust methodology was developed to integrate LiDAR and aerial imagery through object-based image analysis, which provides ecological researchers and conservation managers with a valuable tool for spatially quantifying vegetation structure in heterogeneous landscapes (Levick and Rogers, *in press*).

The pattern-process-scale principle of the HPDP (Wu and Loucks, 1995) was empirically explored in a savanna setting, and the observed patterns of change with scale validated some of the paradigm's assumptions and contradicted others. Ecological processes were found to shift with scale, as predicted, for woody height, cover and cover dynamics, but structural diversity measures were scale invariant in their relationship with environmental variables.

Although total percentage woody cover remained constant between 1942 and 2001, woody structure became more homogeneous at the hillslope scale and woody patch structure became fragmented over time. Therefore the metastability principle of the HPDP (Wu and Loucks, 1995) cannot be considered applicable in this savanna landscape. Pattern-process relationships varied spatially across the landscape and were strongly context-dependent, validating the fundamental premise of landscape ecology, that context influences ecological patterns and process (Wiens, 1995).

These findings have addressed the objectives of this thesis (section 1.3 on page 32), but have also raised some key challenges to ecological research. The spatio-temporal patterns and context-dependent relationships illustrated here represent exciting future opportunities for exploring landscape heterogeneity and for advancing landscape ecology.

The high levels of unexplained variation in woody structure and dynamics at fine-scales (1ha) suggest that interactions, feedbacks and contingency are important determinants of vegetation pattern. In complex systems, it is unlikely that fine-scale variation will ever be fully explained, but some of this variation is likely to arise from species variation and interactions. Future explorations of vegetation-environment relationships should aim to explicitly incorporate species variation across different contexts, as gaining better understanding of fine-scale interactions and feedbacks is fundamental to advancing current understanding of ecological dynamics (Agrawal et al., 2007).

Spatial context strongly influenced woody structure-environment relationships, but only the spatial location aspect of context was evaluated. The influence of patch neighbourhood and adjacency on pattern-process relationships should be explored in future work to provide a holistic perspective of the influence of spatial context on ecological patterns and processes. Gaining understanding of the influence of all three aspects of spatial context is imperative to understanding the functional implications of changes in system heterogeneity.

Woody structure-environment relationships varied between different river catchments and with longitudinal position within a catchment. The potential for exploring savannas as a hierarchy of catchments of different stream orders should be evaluated as a means of stratifying the landscape to further understanding of context-dependency and guide research and conservation efforts in heterogeneous systems.

Generalizable theory in landscape ecology

The hierarchical patch dynamics paradigm (HPDP) provided a robust conceptual construct in which to explore woody vegetation spatio-temporal dynamics. The spatio-temporal findings at different scales both supported and contradicted different aspects of the paradigm. Despite this, the HPDP fulfilled its role as a framework, as current understanding of woody spatio-temporal dynamics in savanna systems has been advanced through the explicit consideration of scale and context. The complexities and contingencies of landscapes make generalizations difficult, and those that do emerge often hold little operational value (Wiens, 2008). The principles of landscape ecology therefore need to be treated as guidelines, not concrete rules, to steer research and conservation efforts. Rather than searching for universal generalities, contingent principles need to be developed that can be applied across similar suites of landscapes or domains of scale (Hobbs and Lindenmayer, 2007; Wiens, 2008).

By creating awareness of the importance of scale, the field of landscape ecology has already made a major contribution to the ecological understanding and conservation of systems worldwide. Generating broader acknowledgment and awareness of the importance of spatio-temporal context is the next critical phase in this field, as assumptions of stationarity limit understanding of ecological systems.

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