DO MULTI-SCALED PATTERNS IN A SEMI-ARID SAVANNA SHOW EVIDENCE OF COMPLEX SYSTEMS DERIVED STRUCTURE?

Christopher Barichievy

School of Animal Plant and Environmental Sciences

University of the Witwatersrand

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Doctor of Philosophy.

DECLARATION

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

Signature: ______________________
Christopher Barichievy

Date: 10 October 2013

“*Drive, Drive, Driv*e...” Reg Barichievy-my dad

ABSTRACT

The detection of hierarchically nested structure in a semi-arid savanna as predicted by complex systems theory requires a method that detects context specific multi-scaled pattern in a proxy that represents the net effect of system processes. Statistical assumptions preclude the use of many traditional methods in the detection of hierarchical structure in heterogeneous landscapes so to circumvent statistical barriers to inference I developed a linear scale-space based application to represent multi-scaled woody vegetation structure in a spatially explicit manner. Analysis of a scale-space representation of woody cover across multiple scales explicitly recognizes landscape context and emergent pattern due to the causality principle inherent linear scale-space generation. As a proxy for process in scale and space I utilize the merge events of woody canopy cover, which should theoretically be considered the point at which processes shift domain.

Scale-space representations were analyzed using a spatially explicit discontinuity analysis that compares the distribution of structure across the dimension of scale to that of a neutral model specific to the landscape in question. The application was tested for rigor and ability to detect multi-scaled, context dependent pattern in test datasets. The effects of fire and herbivory on the multi-scaled structure of a semi-arid savanna landscape were compared using the merge events from scale-spaces generated from a 33 year herbivore browser exclosure.

No more hierarchical structure is present in real world savannas than can be expected from random. Hypotheses put forward to explain the results include: procedural and philosophical bias, errors in the application, or that the landscapes are not hierarchically nested. Each hypothesis is discussed in the light of the evidence and after synthesis I discuss that savanna landscapes may have more randomness within the pattern and process than previously acknowledged.

ACKNOWLEDGEMENTS

This thesis is supposedly the culmination of my formal training, but I hope it is only the start of my learning. It has been a long process during which many people have helped me in various ways; I would like to thank them.

BAREND ERASMUS: Thank you for the interest from the start and your open door policy which I used frequently. Thank you for many discussions; be they random ideas over a cold beer or serious debates. Thank you; I sincerely thank you, for taking me on when you did. I am genuinely grateful for all of your help and I have the utmost respect for the way in which you got me to this point. You have restored my faith and more importantly my enjoyment in research.

GRAHAM ALEXANDER: Thank you for the advice, well measured every time. Thank you for a place to live and for welcoming me into your family. Thank you for a desk when this homeless student needed it. Thank you for managing to teach me about science without ever saying a serious word. You're a remarkably generous man Prof. I am forever indebted to you.

NEIL O'LEARY, MARK DALTON AND DAVE RICE: Thank you for teaching me how to code, the basics of mathematics, and helping with the tricky aspects of MATLAB implementation. Neil-thank you for finding a computational solution to an analytically impossible problem. I could never have gotten this algorithm off the ground without all of your patience.

SAM: Sister-your passion about the world that is too small to see is contagious. Thanks for keeping me focused, for wise words over many meals, challenging debates, interesting parallels and of course, for being my number one fan.

MUM AND DAD: Thank you for all the help for all the years. Thank you for never doubting that I'd finish, or at least doing so silently.

LIAM: Shot.

SHANA SUNDSTROM: Thank you for the mind-bending questions that take me weeks to answer. Thank you for involving me in your work, the constant intellectual challenges and out-of-the-box thinking. Thank you for the constant support, for being my public relations officer and of course, thank you for the occasional stern word. Here's to many more years of collaboration.

KEVIN ROGERS: Thank you for your input.

WENDY MIDGELY: Thank you for facilitating everything through the years.

LINDSEY GILLSON: Thank you for your time, for the very poignant comments and words of encouragement on early drafts of this thesis.

Thank you to my post graduate faculty head *DAVE MYCOCK.* And to my colleagues through the years; *SHAUN LEVICK, BRIAN MARITZ, NICK TYE, MARCO VIEIRA, KATHLEEN MENNEL, JOLENE FISHER, PATRICK DWYER, SEAN BUCHANAN, GRAHAM PAUL, GLEN LAURENCE, KAERA COETZER, NIKKI STEVENS, LESEGO KHOMO, CAROLA CULLUM, KAREN KOTCHY* and the rest of the CWE.

The early years of this work and software costs were facilitated by the Andrew W. Mellon Foundation, via the Centre for Water in the Environment. I would like to acknowledge it for its funding.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

GLOSSARY OF TERMS

Absolute space: a term coined by Marceau (1999), to mean a fixed geometric scheme used to partition a geographic space to define the relevant units

Annihilation event: A linear scale space event that depicts the point at which significant data structure (A BLOB) is no longer evident at higher scales.

Bonferroni adjustment: A correction that can be used to correct confidence intervals in a test due to multiple comparisons increasing the likelihood of a rare event being witnessed.

BLOB: A Binary Large Object (BLOB) is an object which represents the structure of interest at the sampled scale within a scale-space. For the objectives of this thesis, BLOBs represent woody tree cover at a particular scale of observation.

Causality: Used primarily in this text in reference to the *principle of causality,* an important characteristic of a linear scale-space. No new information is created through the convolution of a dataset with a Gaussian kernel (Koenderink, 1984, Florack et al., 1994, Lindeberg, 1994).The importance for this thesis is that in a linear scale-space, analyzed in the manner done so here structure at higher scales can only have been generated by structure at lower scales. Causality of pattern is an important characteristic when testing for hierarchically nested woody vegetation structure and is the backbone of the spatially explicit discontinuity analysis technique developed.

Cross scale morphology: Pattern measured at and compared across multiple scales of observation is called the cross-scale morphology of a system (Holling, 1992, Allen, 2006, Stallins, 2006).

Discontinuity: Discontinuities are discontinuous distributions in a considered pattern when compared across scales of observation. Discontinuity research is in direct contrast to the traditional approaching of analyzing continuous distributions, (Allen 2006).

Entrainment: The capture of the spatio-temporal frequency of a pattern-process interaction and/or expression by that of another. This enforces similar spatial and/or temporal frequencies of pattern and process in the landscape.

Ecological memory: The degree to which an ecological process is shaped by its history is the strength of the ecological memory of that process (Peterson, 2002).

Extent: The largest possible range over which the samples are taken.

Grain: The smallest unit of measurement, often linked to the pixel size or resolution of an image.

Hierarchical Patch Dynamics Paradigm: The Hierarchical Patch Dynamics Paradigm (HPDP) is an integration of Patch Dynamics Theory and Hierarchy Theory, first described by Wu and Louks (1995). HPDP takes the concept of patches as a relatively discrete spatial pattern (White and Pickett, 1985) and makes it explicit that the patchiness observed is dependent on one's scale of observation, nested in a hierarchical manner.

Holon: A fundamental unit of a complex system in which a region of the system is relatively more coupled to each other than to the rest of the system(Koestler, 1967).

Kolmogorov-Smirnov test: A non-parametric statistical test which compares two distributions for similarity. The KS test statistic is calculated as: $K= max(|F_1(x)-F_2(x)|)$ and is compared to the alpha value in a standard hypothesis test. The null hypothesis is that the two distributions, F_1 and F_2 may be considered from the same continuous distribution.

Landscape context: Landscape context reflects that even at similar scales, different drivers may be responsible for different patterns under different landscape contexts, or configurations of processes (viz. Levick 2011).

Linear scale-space: Linear scale-space is a three dimensional representation of a dataset generated through the convolution of a Two dimensional X-Y dataset with a Gaussian Kernel of an ever increasing bandwidth/ The derived datasets are stacked sequentially on top of one another and structural units are linked between scales to generate the third dimension of scale (Z).

MAUP: The Modifiable Area Unit Problem (MAUP) is a sampling problem in spatial statistics in which changing the shape and/or size of the units on which data are mapped can change the resulting patterns or statistical models generated from the data (Dungan et al., 2002).

Merge Event: A linear scale space event that depicts where to regions of significant structure (BLOBS) merge into a single unit at higher scales of analysis.

Neutral models: A neutral theory in ecology is regarded as a set of rules which apply to all agents equally, which allows the variation of random chance to be understood and factored out (Hubbell, 2001). Neutral theory is the attempt to understand the amount of pattern that can be generated at random without needing to invoke the influence of process. Neutral models are often used as the basis of comparison in landscape ecology in which the ability to find control plots are limited.

Orthophotos: Orthorectified photographs, refer to images generally taken from an aircraft which are subsequently georeferenced (placed in a geographic coordinate system) and corrected to account for the distortion resulting from a single point of observation, on the aircraft.

Process domain: A range of scales over which a process operates and or dominates (Wiens, 1989).

Reify: To treat an abstraction as something with matrial existancy, in the context of this thesis it is when a throy set or conceptual framework is assumed to be real.

Relative space: Space that is not independent of the mass and energy within it and so any property is measured within the context of the spatial configuration of entities and the processes in the system (Marceau, 1999).

Scale: Scale has multiple meanings to a variety of people in different disciplines. I define scale for the purpose of this thesis as: the spatio-temporal extent over which pattern and processes operate.

Scale-space events: In a linear scale-space four types of scale-space events occur in which an object of interest undergoes a fundamental transition. This can be by way of splitting into two or more objects, merging into one, disappearing in an annihilation event or being created. The merge events, are used as the primary proxy for process in this thesis.

Stationarity: Spatial stationarity is the assumption that the mean and variance of the sample remain consistent across the entire data set (Fortin et al., 2005). The underlying assumption of stationarity is that the data structure is the same no matter where in the sample one observes a datum (Wagner and Fortin, 2005), thereby inferring that the process encapsulated by this pattern is equivalent.

Chapter 1 : GENERAL INTRODUCTION; THE PROBLEM AND A PROPOSED SOLUTION

Landscape ecology as a research field invokes a number of conceptual frameworks and models to understand landscape pattern and infer process. However, few if any, are actually rigorously tested for their legitimacy in real world systems (Levick and Rogers, 2008). This thesis is about validating a hypothesis, no different to testing whether or not exponential growth is an adequate description of animal population dynamics within a sampled population. Landscapes are visualized as complex systems, but are patterns predicted by complex systems theory an adequate description of a semi-arid savanna landscape?

1.1. THE IMPORTANCE OF THIS RESEARCH

Ecology as a science has very few predictive models that can be applied with confidence to landscapes. Complications introduced by scale and the contingency of pattern and variable processes render reductionist based techniques somewhat ineffectual. Landscape ecology requires a system level approach to allow for individual components to come and go, while retaining system level integrity, a central tenet to resilience theory (Gunderson, 2000).

System-level models in landscapes require an understanding of the relationship between feedbacks and spatial scale (Rietkerk et al., 2004) and current system level approaches proposed for ecosystems rely on measuring the variation in pattern in real-world landscapes between scales of analysis (HilleRisLambers et al., 2001, Rietkerk et al., 2002, Allen, 2006).

In these real world landscapes, as opposed to modeled systems, evidence of systems properties which can be used to make system level predictions have only been inferred from a handful of systems. For instance; power law distributions in vegetation patch size are inferred as evidence of self-organization (Scanlon et al., 2007) and deviations from these power law distributions can indicate imminent system change (viz. Kéfi et al., 2007a, Scanlon et al., 2007).

So far these power law models are confined to relatively homogenous landscapes such as the Kalahari Sands (viz. Scanlon et al., 2007) over large spatial extents, where I would argue, the entire landscape is affected by relatively similar processes. Other examples were investigated over small spatial extents where it is unlikely that too much spatial heterogeneity will affect the processes (viz. Kéfi et al., 2007a).

The potential of holistic, predictive models is large for application in system conservation. However spatial heterogeneity precludes the extrapolation of these models to more variable landscapes because the underlying processes are different across the sample and large scale pattern will not emerge. Evidence of this is to be found in the increasing awareness of context specific pattern–process relationships (Levick and Rogers, 2011).

Are there predictable system level properties in a system where there are varied processes interacting across space and across scale? There is as yet no theory which allows predictive powers from models similar to power law analysis to be applied to heterogeneous landscapes in a spatially explicit manner.

There are, however, predictive models for heterogeneous landscapes that are not spatially explicit. For example, the discontinuous distributions of parameters such as body mass can reflect "discontinuities" in the scale at which processes operate. Discontinuities are gaps in a considered pattern when compared across scales of observation. The position of individual components relative to these discontinuities has been shown to provide predictive power, indicating components of the system that are likely to change.

Discontinuities across a range of scales and systems have been used to assess system resilience (Allen et al., 2005) as well as a determinant of extinction or invasion (Allen et al., 1999, Sundstrom, 2009, Sundstrom et al., 2012). But as yet this model, known as the Textural Discontinuity Hypothesis (Holling, 1992), has not been made spatially explicit.

My broader research focus is primarily aimed at developing a spatially explicit predictive model for a heterogeneous landscape system. Before this can be done, however, an understanding of multi-scaled, spatially explicit pattern must be made, which is the focus of this thesis.

Much progress still needs to be made before a complete holistic theory can even be proposed, never mind applied to landscapes; especially one that encompasses the heterogeneity inherent in landscapes such as savannas. But to make headway in the quest for system level predictability, one must first test our representations of how the fundamentals of system dynamics translate into system level properties.

The configuration of any system that is by default only observed as a sample, is the result of a history of interactions that are contingent on one another, and a healthy dose of chance(Ulanowicz, 2008). Biophysical systems evolve through a combination of self-organization and natural selection (Kauffman, 1995). This interactive process of system evolution is encapsulated in the framework of ecosystems as complex adaptive systems (Levin, 1998).

Complex systems contain flows of energy which provide the interconnection between agents of the system (Levin, 1998). A differential distribution of interactions occurs across a system in space and time which results in parts of the system that are relatively more coupled to each other than to the rest of the system. Regions of similar rates which are tightly coupled to one another are termed *holons* (Koestler, 1967), the ecological unit at the scale of observation (Burnett and Blaschke, 2003).

Understanding and dissecting a landscape is unfortunately not as simple as measuring process rates and delineating holons. At different scales rates of processes may differ and these are termed *levels of organization* (Wu and Loucks, 1995). Current theory stipulates that holons and levels of organization are the structural units of a complex system and should form a nested hierarchy (Reynolds and Wu, 1999, Wu and Loucks, 1995, Wu, 1999).

In the hierarchy, the degree of looseness of vertical (between levels of organization) and horizontal (between holons) coupling is the reason for the decomposability of complex systems (Wu and David, 2002). In landscapes, the evidence of coupling in processes can be gathered via the distribution of patches in space and time. This has been formalized into the conceptual framework of the Hierarchical Patch Dynamics Paradigm (Wu and Loucks, 1995).

1.2. THE HIERARCHICAL PATCH DYNAMICS PARADIGM

The Hierarchical Patch Dynamics Paradigm (HPDP) is an integration of Patch Dynamics theory and Hierarchy theory (Wu and Loucks, 1995). HPDP takes the concept of patches as a relatively discrete spatial pattern (White and Pickett, 1985) and makes it explicit that the patchiness observed is dependent on one's scale of observation. Holons aggregate together as extent increases into separate levels of organization, which can themselves be considered as a holon at the next level (Figure 1.1).

The usefulness of HPDP is that it explicitly emphasizes the link between scale and heterogeneity and a patch is considered a fundamental structural and functional unit of the landscape. As patches should constitute holons (Burnett and Blaschke, 2003), applying HPDP should theoretically decompose the complex system of the landscape into fundamental units. Landscape dynamics and thus system dynamics due to changes in processes are then quantified as changes in ecosystem patches through time.

It is important to acknowledge that although the HPDP is proposed as a conceptual framework, fundamental units are argued to exist in complex systems (Reynolds and Wu, 1999). Reynolds and Wu (1999) do acknowledge that there is no generic recipe with which to simplify landscapes as yet, but point out that decomposition of a system into holons and levels of organization should be made at natural disjuncts and should reflect the self-organized nature of the pattern. In the following chapter I argue that by woody tree canopy cover I encapsulate just such a disjunct.

Many complex systems have been modeled as hierarchical patches. In non-landscape complex systems behavioral frequencies, relaxation time, cycle time, or response time (Wu and David, 2002) are used to decompose systems into their constituent parts. Spatially explicit patches of succession have been modeled in serpentine grasslands, where gopher mounds create islands of homogeneity and create a patch mosaic of different stages of succession (Wu and Levin, 1994).

In another practical landscape example the hierarchical patch dynamics conceptual framework was used to model the Arctic tundra (Reynolds et al., 1996). In the hierarchical tundra model the landscape was broken up into plant, patch, flow path and region. The smallest spatial unit was the individual plant, which was considered relatively homogeneous to one another due to various plant-soil-atmosphere-animal processes, such as soil water uptake, transpiration, herbivory, and nutrient uptake. Higher levels of organization units were patches and higher still were flow paths.

Process rates were used to dissect the landscape into fundamental units, inferring the degree of connectedness via the rates of transfer across the boundaries of the patches. The vectors of the material and energy flux between patches are water, atmospheric turbulence and animals. The tundra model dissects the landscape into a hierarchical patch mosaic of regions with higher homogeneity or coupling of materials/energy through various processes.

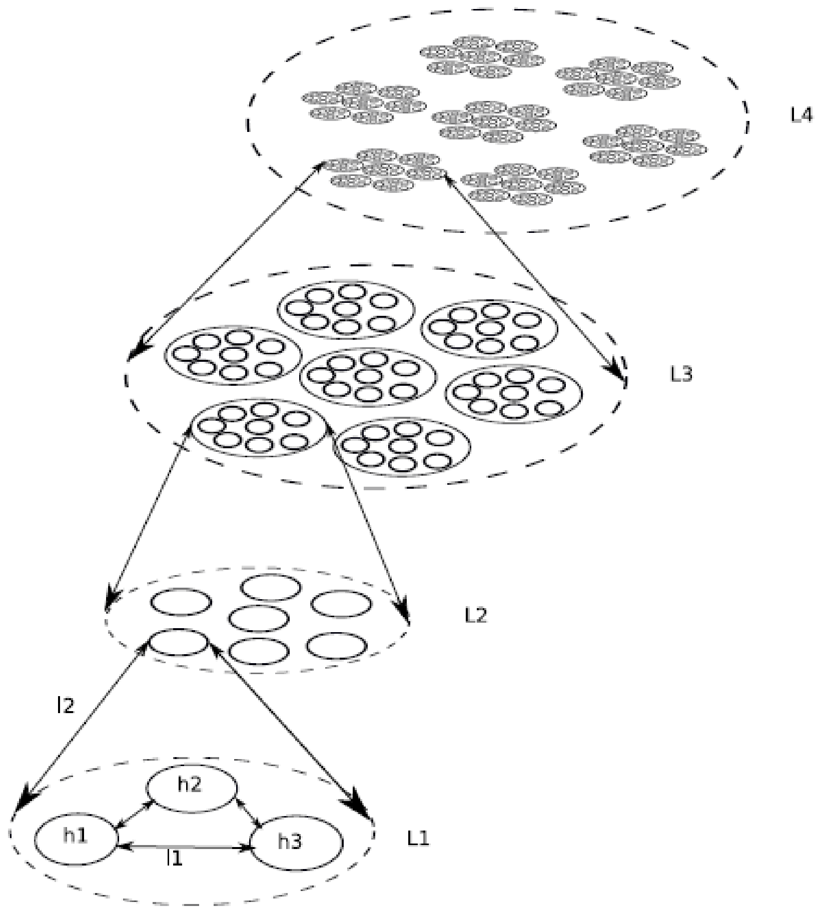

Figure 1.1: The conceptual framework of the Hierarchical Patch Dynamics Paradigm. At low levels of organization (L1), regions of tighter coupling called holons (h1-h3) interact non-linearly and emerge into higher levels of organization (L2). These levels of organization themselves interact with holons at the same level and subsequently create emergent entities at higher levels (L3-L4). Image adapted from Gillson (2004).

Another example more pertinent to this thesis; in an analysis of a savanna landscape, levels of organization have been inferred from differences in pollen carbon isotope assemblages in sediments which indicate that vegetation change is different at different scales (Gillson, 2004). It is clear that HPDP provides a useful framework to contextualize problems and to explain pattern in hindsight, but can it be reified? "The challenge is to find these scales and properly link processes and pattern" (Reynolds and Wu, 1999 pg. 289).

It is at this juncture that I fear the theory sets leave the scientist wanting and this is where this thesis aims to add value. Where do we delineate these gaps to ensure that the pattern we are measuring can be confidently attributed to the processes?

1.3. THE PROBLEM

"Pattern- be it spatial or temporal- is inseparable from scale"(Reynolds and Wu, 1999 pg.289). Because there will be tighter coupling among processes and components with similar process rates and overlapping spatial scales (Holling, 1992, Levin, 1992, O'Neill et al., 1989), scale is inextricable from a fundamental understanding of complex systems. In fact, one of the major elements of the HPDP is the *pattern-process-scale-perspective*. Processes may create, modify or maintain pattern and the pattern may constrain or modify the processes (Wu and Loucks, 1995) resulting in different processes dominating across different scales of observation (Wiens, 1989). These processes should be evident in distinct differences in pattern and the conceptual framework of HPDP predicts multi-scaled structure.

In this thesis I test **whether or not there is hierarchically structured woody vegetation pattern in a landscape, as predicted by Complex Systems theory and emphasized in the application of Hierarchical Patch Dynamics Paradigm** (Wu and Loucks, 1995).

The solution seems simple; simply take a landscape and assuming that vegetation patches can be considered as holons (an argument that will be much expanded upon in Chapter 2), if there is a hierarchically nested structure found, it would provide evidence that the HPDP is in fact a realistic representation of a savanna landscape. However the problem of generating unbiased descriptions of systems via the distribution of multi-scaled vegetation patterning is a lack of a method which can accurately describe the multi-scaled structure of a landscape while remaining ecologically meaningful.

Assumptions inherent in many methods render the results invalid, or at best, simply a reflection of the whim of the researcher. If a method becomes available to truly measure the multi-scaled structure of a landscape it becomes possible to test for complex system derived pattern explicitly. Evidence of holons in the landscape which are different across different scales will infer levels of organization and further our understanding of the relationship between spatial scales and positive feedbacks. The applicability of the HPDP to the landscapes in questions can then be discussed, or our understanding of the HPDP can be calibrated, or expanded upon.

Whether or not a conceptual framework or model can be reified is possibly "…a disaster of naïve realism" (Allen, 2011 pers. comm). However, the logic flow is as follows: system level models in landscapes require an understanding of the relation between feedback and spatial scale (Rietkerk et al., 2004). Multi-scaled analyses are now commonplace and there is a heightened awareness of the importance of multi-scaled study (Schneider, 2001). The scales selected, however, are generally arbitrary (Wheatley and Johnson, 2009).

Decisions about scale and extent and the hierarchical units to be studied may be done in a systematic and consistent way, but they are necessarily subjective (Kay and Schneider, 1994). They reflect the viewpoint of the analyst about which connections are important to the study at hand and which can be ignored. No observation is completely objective (Tainter and Lucas, 1983) and one cannot observe an absolute truth as it doesn't exist (Allen et al., 2001). However, rather than arbitrarily assigning scales, scales of observation should be justified within the context of the conceptual framework/model being utilized (Allen, 1998). It is not the reification of a conceptual framework that is important, but the validation that the framework being utilized is in fact applicable in the first place.

I aim to validate the framework of HPDP used in landscape analysis by testing for whether or not reifiying the HPDP is valid and combining it with a cross scale model that is used to predict systems change.

1.4. THE PRESENTED SOLUTION AND WHY IT IS NOVEL

The problem addressed in this thesis is whether or not **a hierarchically nested patch mosaic provides an accurate representation of a real world landscape.** There are no methods available to test for hierarchical structure in a landscape while remaining ecologically meaningful. The solution to the problem, therefore, is **to develop such a method, validate it, and subsequently test for hierarchical structure in a prototypical system in which the conceptual model of HPDP has been used.**

To generate such a method I turn to the image processing literature, particularly the linear scale-space literature which is focused on generating multi-scaled representation of scenes through methods that do not introduce any user defined bias into the analysis and allow patterns to emerge themselves. The novelty of this research is the use of linear scale-space to infer pattern-process relationships in a prototypical complex system.

Moreover I alter the traditional linear scale-space methods to allow for analysis of woody vegetation structure in a statistically unbiased sense. The novelty of the application and its differences from currently available techniques is explained in Chapter 2. It must be stressed, however, that this is a practical ecological research question, opposed to an academic study into image processing.

1.5. Outline and structure of the Thesis

The bulk of the thesis, bar this introductory chapter is divided into three major sections; each with particular objectives:

Chapter Two: Literature review, Theory and Synthesis aims to:

1. Develop an argument as to: *Why multi-scaled hierarchically nested structure is expected in landscapes*.
2. Develop an argument as to: *Why a semi-arid savanna landscape is a good study system to use to investigate the expression of complex systems properties.*
3. Describe: *What methods are available for multi-scaled pattern detection, and why they are not valid for the purposes of this thesis.*
4. S*ynthesize the literature review into a proposed solution; build a conceptual framework and present testable hypotheses*.

Chapter Three: Analysis and test for nested hierarchical structure in a semi-arid savanna has four main objectives, comprising the bulk of the thesis:

1. Objective 1: Generation of baseline landscape datasets.
2. Objective 2: Linear scale-space generation.
3. Objective 3: To demonstrate outputs of the linear scale-space application and to validate the linear scale-space application for repeatability of the algorithm and in detecting the scale of pattern expression.
4. Objective 4: Determine whether evidence of process can be detected in the 'Nwashitsumbe landscape?

Objective four is the culmination of the thesis in which I use the theory and methods developed up until this point to test whether or not complex systems pattern, expressed as hierarchically nested structure, can be detected in the woody canopy cover distribution in the 'Nwashitsumbe semi-arid savanna landscape.

Chapter Four: General Discussion discusses the findings of Chapter Three in the context of the broader ecological literature.

Chapter 2 : LITERATURE REVIEW, THEORY AND SYNTHESIS

In this thesis I present a test of whether or not **a hierarchically nested patch mosaic is an accurate representation of a real world landscape**. Before I do so, I briefly discuss complex systems theory and the concept of scale. I review the literature to explain why it is expected that hierarchical structure should be found in complex systems. I present the study system used in this thesis and I review why it would be expected to find hierarchical structure in such a landscape. I explore what methods are available for multi-scaled analysis and I review theory sets concerned with the detection of scales at which processes operate.

I highlight many of the shortcomings of these methods in the context of this thesis and explain why a novel method to detect hierarchical structure in a landscape is needed. I then synthesize the findings and present the concept of scale as a dimension and the use of linear scale-space as a method to measure pattern across scale that are developed in the methods Chapter 3.

Chapter Two objectives:

Chapter Two aims to review the literature in order to:

1. Develop an argument as to: *Why multi-scaled hierarchically nested structure is expected in landscapes*.
2. Develop an argument as to: *Why a semi-arid savanna landscape is a good study system to use to investigate the expression of complex systems properties.*
3. Describe: *What methods are available for multi-scaled pattern detection and why they are not valid for the purposes of this thesis.*
4. *Synthesize the literature review into a proposed solution; build a conceptual framework and present testable hypotheses*.

2.1. OBJECTIVE 1: WHY MULTI-SCALED HIERARCHICALLY NESTED STRUCTURE IS EXPECTED IN LANDSCAPES:

The reason we expect hierarchically structured pattern in landscapes is because landscapes are prototypical complex systems. Hierarchical structure is inherent in complex systems; inputs of solar energy and energy flows, within the constraints imposed by limitations within the landscape, will force the system away from thermodynamic equilibrium (Kay and Schneider, 2000) through the process of ascendancy and the adaptive process (Levin, 1998). Through selection based on the trade-off between efficiency and redundancy and a healthy dose of chance (Ulanowicz, 2008) hierarchical structure is generated to minimize the energy gradient (Jørgensen et al., 1998).

This is the current understanding of landscapes as systems, from which many theories, predictive models and frameworks have been developed and added to. This is contrary to the aged equilibrium theory. My question is whether or not this model can be reified into hierarchically nested patches of woody vegetation and used as a predictive tool. I argue here that it should. If it can be reified we have a ready measure of spatially explicit landscape process and can utilize this to make inference to resilience of the system to perturbation.

2.1.1. *LANDSCAPES AS COMPLEX SYSTEMS, FEEDBACK LOOPS AND THE GENERATION OF FUNDAMENTAL UNITS:*

Landscapes are spatially explicit ecosystems and ecosystems are considered prototypical examples of complex systems (Levin, 1998). I have already briefly referred to ecosystems as complex systems and that a conceptual framework used to dissect this complexity into manageable units is the Hierarchical Patch Dynamics (Section 1.2.). It should be born in mind that there is no single complex systems theory, but rather an amalgamation of commonalities from fields such as mathematics, computer science, physics, ecology, biology, epidemiology, economics and social sciences.

The literature is vast and the intricacies many, so for the purposes of generating context for why we expect hierarchical pattern, I draw together aspects of various research fields in a précis of landscapes as complex systems.

Historically, ecology has been primarily a descriptive science (Hobbs and Morton, 1999). Determining the processes that underlay the pattern we observe in nature is considered a fundamental goal in ecology (Habeeb et al., 2005). This is done through hypothesis testing to determine the rule sets or “laws” that may describe the interaction. These laws are not necessarily complicated; as Murray Gell-Mann (2007) so pertinently states: “You don’t need something more to get something more", and much of the complicated and complex patterns that are present on the planet may in fact be explained by a few simple rule sets.

Complex systems theory describes how if free energy is available, dissipative structures will form to take advantage (Nicolis et al., 1989). As energy is added to an open system the system shifts away from equilibrium, dissipating energy and entropy until the prevailing chaos gives way to new patterns of coherent events, order, and creating a new metastable equilibrium (Naveh, 2000). In other words, there is an inherent tendency for self-organization given the right conditions. (Gibson et al., 2000).

In the context of complex systems theory, ecosystems are understood as systems evolving in a self-organizing way towards a more efficient use of energy, to minimize the energy gradient created through the input of energy (Jørgensen et al., 1998). These systems are not necessarily spatially explicit, but the nature of self-organization and emergent pattern in dissipative systems has been put forward as an explanation of why there is life on earth, ecosystems development and patterns of biological evolution.

In fact, life has been termed "*…a manifestation of the second law of thermodynamics…"*, and that ecosystems should *"…increase their total dissipation, develop more complex structures with more energy flow, increase their cycling activity, develop greater diversity and generate more hierarchical levels, all to abet energy degradation*." (Schneider and Kay, 1994).

The importance in this line of study for scientists is that the very systems in which we live are complex systems and are thereby prone to sudden unpredictable shifts, regime changes, nonlinear dynamics and a resistance to reversal of change brought about by hysteresis (Levin, 1998, Kéfi et al., 2007b). The changes have major impacts on livelihoods and predicting these changes remains an avid field of research.

Many systems are termed to be on the edge of chaos and this reflects the tendency of the metastable systems to undergo rapid transitions and reorganize around another set of feedback loops. For example, overgrazing or climate change can push vegetated systems into a new metastable domain (desertification); generating positive feedback loops that maintain high temperatures and low water and nutrients and reinforce this state (Limburg et al., 2002, O'Neill and Kahn, 2000). It is translating this knowledge into predictive models that is imperative for our understanding and successful management of systems.

I have already suggested that the long term research goal is for a spatially explicit mechanism to measure system resilience. Non-spatially explicit models already exist and have been applied in landscapes, particularly the semi-arid to arid systems. Of particular interest is the concept of catastrophic shifts in ecosystem states, where a system reorganizes around a separate set of feedback loops, which may have devastating consequences for the occupants of that system.

Much research has gone into developing these predictive models and understanding state shifts in arid and semi-arid areas (Rietkerk and van de Koppel, 1997, HilleRisLambers et al., 2001, Rietkerk et al., 2002, van de Koppel et al., 2002, Rietkerk et al., 2004, Kéfi et al., 2007a). I will expand upon this in Section 0The organization of a system around the fundamental units of and the ability to use the positive feedback loops to predict change is at the heart of predictive systems models in ecology.

2.1.2. *COMPLEX SYSTEMS BASED CONCEPTUAL FRAMEWORKS IN LANDSCAPE ECOLOGY*

Landscapes themselves have been investigated using a number of conceptual models and paradigms. The field of rangeland ecology parallels landscape ecology in the transition from an equilibrium based paradigm through to one embracing non equilibrium dynamics inherent in complex systems. Many researchers in rangeland ecology use state and transition models to simplify landscape complexity (Milton and Hoffman, 1994, Bestelmeyer et al., 2003, Briske et al., 2008, Bestelmeyer et al., 2009). State and transition models, in the context of vegetation, are representations of alternative system "states" which are indicative of a number of environmental characteristics such as soils, vegetation type and each has a probability of transition to another state, which is then modeled under a variety of scenarios (Westoby et al., 1989, Bestelmeyer et al., 2010).

State and transition models are an interesting research field, however in this thesis I focus particularly on how the hierarchical nature of the complex system is investigated using

Hierarchy Theory (Allen and Starr, 1982, Allen and Wyleto, 1983, Urban et al., 1987, Kotliar and Wiens, 1990).Of particular relevance to my investigation, is the conceptual framework of Hierarchical Patch Dynamics Paradigm (HPDP) (Wu and Loucks, 1995). Before I defer to the Hierarchical Patch Dynamics Paradigm I investigate the basic framework of complex systems upon which these models are built.

Within a complex system, it is flows of energy that provide the interconnection between agents of the system (Levin, 1998). A differential distribution of interactions occurs across a system in space and time, resulting in parts of the system which are relatively more coupled to each other than to the rest of the system. These relatively tightly coupled components of a system are termed *holons* (Koestler, 1967) and can be considered the structural and functional units of a complex system (Blaschke et al., 2002, Wu and David, 2002).

The result is hierarchically structured complex systems, termed *constitutive hierarchies* (Gibson et al., 2000). Constitutive hierarchies are nested hierarchies composed of elements that interact non-linearly to emerge at higher levels of organization.

Urban and O'Neill (1987) describe how components in a hierarchical system are organized into levels according to a *functional scale* which reflects the natural frequency at which processes operate. The rates of interactions and processes are the key component in building hierarchical models of complex systems. The degree of coupling is used to decompose a system into holons (Wu and Marceau, 2002), with patches being spatially discrete entities whose internal structure or function is significantly different from its surroundings (Gillson, 2004).

According to HPDP landscapes have both a vertical structure that is composed of levels of organization and a horizontal structure that consists of holons (Wu and Loucks, 1995). Levels and holons exhibit *space-time separability* (Burnett and Blaschke, 2003 pg. 238), meaning that they are separated by the rates and strengths of interactions in space and time. It is the vertical and horizontal loose coupling or feedback that is the reason for the decomposability of complex systems (Wu and Marceau, 2002). Holons are not simply an abstract concept; for instance "…*when translating hierarchy theory to landscape ecology,* *holons are synonymous with patches: the ecological unit at a particular scale…"* (Burnett and Blaschke, 2003 pg. 238). The system is decomposed into *fundamental units*, which in an investigation of a landscape, are patches of difference pattern and process with the scale at which they are observed explicitly recognized by the HPDP (Wu and Loucks, 1995).

HPDP utilizes the concept of discrete patches, that differ in size, shape and successional stage and considers them the fundamental unit of a prototypical complex system. Each patch is scale and context dependent, lower scaled processes may be nonlinear and emerge into higher level pattern, reflected in pattern at higher levels of organization.

A fundamental premise of this thesis is that patches can be considered as fundamental units in a complex system and the multi-scaled nature of these patches to make inference around the nature of landscapes as complex systems. The fundamental units of the landscape are created through positive feedback loops in which pattern and process recursively interact. Such agents, which create agent-mediated nonlinear responses in a system, are often termed *ecosystem engineers* (Stallins, 2006). (The term "ecosystem engineer" has multiple definitions and so I limit my discussion to this particular definition). There are multiple mechanisms which generate ecosystem engineers; in order to illustrate a practical example of how a patch of vegetation is a fundamental unit, I use a semi-arid savanna landscape example.

Water infiltration is increased under canopies due to differences in soil porosity induced by root penetration. Shading reduces water loss from the soil and increased water runoff branches and stems during precipitation events increases the local moisture content. The increased available soil moisture increases the rate of nutrient cycling (Schlesinger et al., 1996, Agnew, 1997, Whitford et al., 1997). In addition, the accumulation of autochthonous leaf litter and sediments through wind trapping increases the local nutrient concentration, as does the use of vegetation by herbivores, which deposit dung in the vicinity of the tree either during foraging or during time spent ruminating in the shade (Agnew et al., 1993, Agnew, 1997).

The result is an increase in the growth of woody tree cover, creating feedback loops in which the conditions favorable for tree growth are facilitated by the tree growth itself. This is not just a local scale phenomenom; local forest patches facilitate their own well-being within the context of a regional non-forest supporting climate potential. As long as it is above a particular equilibrium area threshold (Da Silveira and Sternberg, 2001) the plants have *engineered* their own environment. However, control mechanisms may be in place to dampen feedback loops, such as if animal trampling under a tree reduces the nutrient cycling, water infiltration or growth mediated feedback loops of the tree itself.

2.1.3. *BUT WHERE DOES SCALE FEATURE?*

In landscape ecology, which is the focus field I am concerned with, an explosion of research occurred in the eighties and nineties. "*Pattern, generated by processes at various scales, is the hallmark of a landscape"* (Urban et al., 1987pg. 1). Research of scale in landscape ecology has a focus on the characteristic spatial and temporal scale of ecological events and how landscapes complexity can be simplified by using frameworks such as hierarchy theory and derivatives thereof (Allen and Starr, 1982, Allen and Wyleto, 1983, O'Neill et al., 1989, Kotliar and Wiens, 1990, Wu and Loucks, 1995).

Nowadays ecologists generally realize that it is of fundamental importance to recognize how patterns change across scales and how phenomena at different scales influence one another (Levin, 1992). Multi-scaled studies are now commonplace in landscape ecology and there is a heightened awareness of the need to account for the potential confounding effects of scale when interpreted out of context (Schneider, 2001). But what is scale really?

As an explanation of the importance of scale and how to link it to process, I utilize the concepts of incorporation and metastability discussed in the seminal HPDP paper (Wu and Loucks, 1995). If an ecologist is focused on individual trees there may be almost random fluctuations in the removal or recruitment of the trees. However, when looked at from a landscape perspective this is incorporated into a pattern that is "*…shifting mosaic steady state…"* (Watt, 1947). What we may observe is that the whole patch or landscapes may maintain a relatively constant average, but the individual components come and go. To obtain an adequate understanding of what is happening, therefore, it is vital to link the scale of observation to the processes under investigation.

Levick (2008) illustrated that in Northern Kruger National Park the overall percentage woody cover was stable over time, but dynamics were highly variable at smaller scales and displayed distinct spatial trends across the landscape. These were attributed to variable dominance of different drivers at similar scales but different positions in the landscapes, referred to as the "context dependency" to pattern.

Scale is not simply a consideration of the sample design and hindsight interpretation of pattern and process. Scale and the patterns at multiple scales have been proposed as one of the methods to generate a systems level model- one that measures a systems level property, while allowing the individual components to come and go. For instance, local level facilitation by plants is a positive feedback loop at relatively small spatial scales, which if left unperturbed can result in a measurable system level property.

This local level facilitation combined with resource competition, such as competition for water in semi-arid savanna systems, can result in power law relationships between woody vegetation cover and scale. As an example; in the Kalahari Sands it was shown that comparisons of vegetation cover versus scale of observation revealed power laws (Scanlon et al., 2007). The measured power laws are inferred to be evidence of self-organization (Rietkerk et al., 2002, Scanlon et al., 2007). This power law type analysis in landscapes is paralleled in many systems; scaling relationships provide interesting insight into many ecological phenomena.

The debate surrounding the supposed presence of allometric relationships such as the ¾ power of mass with metabolic rate, or the ¼ power law of time scales and/or sizes have been put forward as models which can be used to explain macro-ecological pattern from micro-ecological constraints (West et al., 1997, Brown et al., 2002, West and Brown, 2005).

In a separate landscape-vegetation cover study over a much smaller range of scales in the Mediterranean, vegetation patch size versus scale of observation also revealed power laws. Importantly though, it was shown that a power law relationship between patch size and scale of observation began to break down under increased grazing pressure (Kéfi et al., 2007a). This illustrates that if the feedback loop is unperturbed and self-organization occurs, the local level interactions result in a power law. However, if the interaction of process in space or time is perturbed, the self-organized pattern will break down over a range of scales, or it can flip into an alternate system state.

Flipping to an alternate state has been illustrated in the coupling between vegetation and drivers such as local climate change, fire and the hydrological conditions which favour forests versus savannas (Staver et al., 2011, Higgins and Scheiter, 2012). What this means is that a change in the amount of cover below a threshold can cause a catastrophic shift to savannas as opposed to a forest.

2.1.3.1. **What is scale? Explaining concepts and defining terms.**

Within the literature there are various definitions and interpretations of the term scale, the result of which is a somewhat multifaceted perception of scale. The term scale constitutes a meme, information that is copied from person to person along with subtle variations (Dawkins, 1989, Heylingen and Chielens, 2009). It is not my intention to redefine scale, but rather to explore a facet of the *science of scale* (Wu and Qi, 2000, pg.2) which is of interest in this thesis. Scale has been the subject of numerous papers over the last fifty years, a rather eloquent treatise of *the scale problem* by Marceau (1999) divides the problem into two fundamental questions:

1. What is the appropriate spatial scale for the study of a particular geographical phenomenon? - which is directly linked to space and the association between measurement and process, and;
2. How can we adequately transfer information from one spatial scale to another? - which is a subject known as *scaling*. In the following text I exclude scaling as a point of discussion as it is a technical process rather than an ontological argument.

To continue the eloquent framework of Marceau (1999), scale is defined in the context of one of two spatial frameworks. Firstly; *absolute space*; is a fixed geometric scheme used to partition a geographic space and define the relevant units. Interpreting scale in the context of absolute space is relatively straightforward and familiar to most people as the scale bar on a map. Although important, I am not concerned with absolute scale in this thesis, save for use during initial data handling. Secondly; *relative space*; harks back to Einstein's theory of relativity in which space is not independent of the mass and energy within it and so any property is measured within the context of the spatial configuration of entities and the processes in the system. Interpreting scale in the context of relative space is much more fundamental to the analysis of complex systems derived pattern, as *"...scale becomes a variable intrinsically linked to the spatial entities, patterns, forms, functions, processes and rates under investigation...*" (Marceau, 1999, pg 1.).

Based on this understanding of relative space, scale is similarly defined as the "*…spatial, temporal, quantitative, or analytical dimensions used to measure and study any phenomenon…"* (Gibson et al., 2000, pg.218); "*…the spatial dimensions at which entities, patterns, and processes can be observed and characterized…"* (Marceau, 1999, pg.2); "*… or the observer's measuring stick or viewing window size, a spatial or temporal characteristic of an ecological pattern or process, or a fundamental framework in which diverse ecological phenomena can be more effectively studied and understood individually and collectively…"* (Wu et al., 2000, pg.1).

This understanding of scale pertaining to relative space is the reason that we as ecologists may choose plots of a few meters in extent to study nutrient cycling within, but plots many hundreds of meters in extent to study fire effects on the landscape. The goal is to link the window of observation to the scale at which the process operates to allow for inference.

An important philosophical consideration is that because the scale at which an observation is made is defined by the filter or measuring tool with which a system is viewed and quantified (Allen and Starr, 1982, Hay et al., 2002); observations inherently contain an *a priori* assertion by the researcher as to the spatial and or temporal extent over which he/she measures or observes the world (Figure 2.1). In landscape ecology this assertion defines the grain and by proxy, the extent of data (Wu and Qi, 2000). The term *scale* is then often simply regarded as the grain and extent over which organisms perceive their environment (viz. Fritz et al., 2003), or over which we as ecologists take measurements.

As a result, the concept of scale has become focused on how relationships between measurements at different grains may vary. It is now widely accepted that in an ecosystem, patterns measured vary across scales of observation (Weaver, 1995, Gaston, 2000, Levick and Rogers, 2008), but the reasons for the variability in pattern at different scales may or may not be ecological in nature.

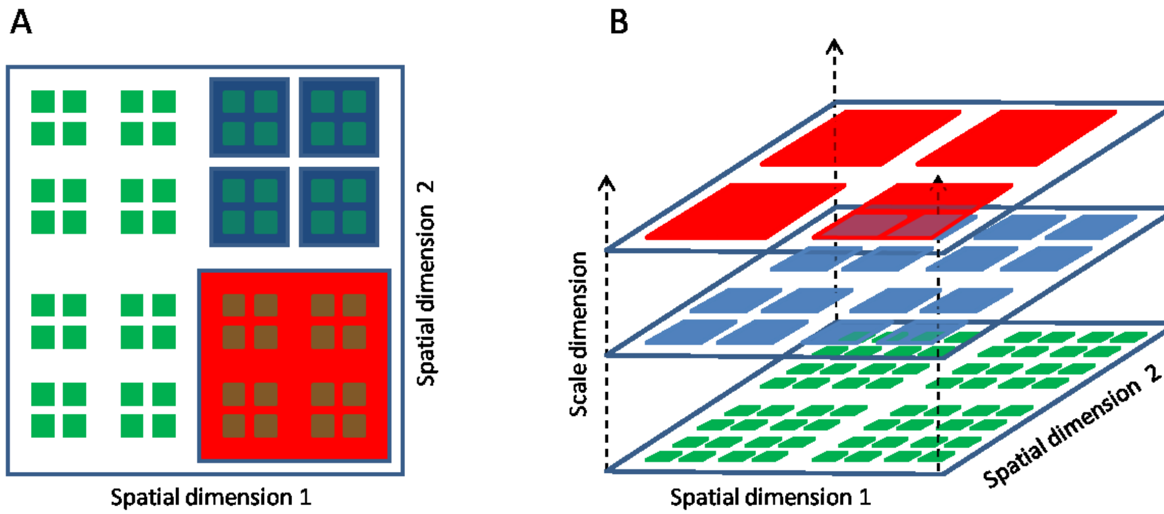

Figure 2.1: The pattern observed varies at different scales of observation. In image A, the patches of green will be observed as larger patches at higher scales, indicated as blue patches. At even higher scale the patches will be even larger, indicated as red patches. The scale of observation and therefore the pattern detected is the choice of the observer, which is somewhat arbitrary. If one considers scale as an explicit dimension (Image B), the patterns observed are simply slices across a continuous dimension of pattern. In this context it becomes explicit that pattern, and therefore process are only evident over a range of scales and that this range of scales may or may not be constant across space, thereby addressing issues of landscape context.

2.1.3.2. **So scale is a consideration, but why?**

A realization that scale is an important consideration in analysis and understanding of pattern and process has been evident in the literature for over seventy years. Earlier statements regarding scale were primarily statistical in nature; primarily concerned with the artifacts introduced by aggregating data at different spatial and/or temporal extents. For example, the Modifiable Areal Unit Problem (MAUP) represents the sensitivity of analytical results to the definition of data collection units (Hay et al., 2001).

Changing the shape and/or size of the units on which data are mapped can change the resulting patterns or statistical models generated from the data (Dungan et al., 2002). The potential for error in the analysis of spatial data resulting from the MAUP is significant (Fotheringham and Wong, 1991, Jelinski and Wu, 1996) and researchers need to be cognizant of issues relating to extrapolating relationships between scales of observation. However, the MAUP is an artifact and is not an inherent property of the system itself.

Considerations regarding the ecological inference that can be made from images that are bound by a particular gr

ain and extent are very important. Grain refers to the smallest possible unit of measurement, often linked to the pixel size of the image, but can just as well be linked to the sampling unit in a transect based field sample . Extent on the other hand is the largest possible space over which the samples are made (Allen and Hoekstra, 1991), for instance, the boundaries of the image or the length of the sample transect. How much inference can be made from a sample within these bounds remains a challenge to landscape ecologists and is of particular importance in this thesis.

I note here that the technicalities and difficulties of measuring and linking patterns at varying scales while avoiding statistical assumptions generated from sampling problems such as the MAUP are referred to as *scaling*, which is the science of extrapolating information up or down scales (Wu, 1999, Wu and Qi, 2000). Although interesting and of concern in methodology- scaling is not the primary focus of this thesis.

2.1.3.3. **How the reification of the HPDP leads to a spatially explicit predictive model**

The reification of the HPDP is part of the answer to the search of a spatially explicit measure of system for resilience. How do I intend to generate a predictive model therefrom?

For that I turn to resilience theory and the Textural Discontinuity Hypothesis (Holling, 1992, Holling, 2001) which uses the pattern of a system proxy measured across scales to make predictions regarding the likelihood of change in components of the system (Allen and Holling, 2002, Allen et al., 2005, Allen and Holling, 2008).

A generally accepted concept in many landscapes is that dominant processes are different at different scales and that this influences the observable pattern (Turner et al., 2001, Gillson, 2004). I consider this the *how/what* of scale; the statement does not infer why this phenomenon occurs. The *how/what* of scale is that patterns vary with scale of observation.

In this thesis I define this how/what aspect of scale as *the spatio-temporal extent over which pattern and processes operate*. However, this pattern process relationship is an effect of something more fundamental. W*hy* do these differences in pattern (and because pattern is a proxy for process, the underlying process) occur in the first place? I am well aware that it is because there are specific scales at which processes operate, but WHY do they only operate among limited ranges of scales in the first place?

The tighter coupling among processes and components with similar process rates and overlapping spatial scales (O'Neill et al., 1989, Holling, 1992, Levin, 1992) has resulted in scale being termed: "*…the time and space constants whereby it (a structure) receives and transmits information…"* (Allen, 1998, pg.17). I want to highlight that certain processes have a scale-related component and this affects the evolutionary potential of certain system components.

This co-dependency of scale at which process can influence the landscape and vice versa creates distinct ranges of scales over which pattern and process operate and ranges of scale where they do not. The ranges of scale over which different processes operate have been termed "*process domains"* (Wiens, 1989).

By way of illustration I revisit the example used by Allen (1998) of why there are no elephant-sized water striders. Although this anecdote was aimed at clarifying conceptual issues of scale versus level of organization, the example presents a profound insight into systems evolution. At the spatial extent experienced by an individual water strider, electrostatic forces are influential enough to allow the strider to be supported by the surface tension of water. The pressure of the water strider is ameliorated by the feathered structure of its feet dispersing its weight and the local pressure exerted by the insect does not overcome the cohesive electromagnetic forces which create the resistive surface tension of the water. However, if the water strider was the size of an elephant, the same would not be true - the local pressure would overcome the surface tension and the insect would sink.

The scale at which processes are interacting allows the system (the insect) to persist and is the root cause of a selection pressure against it, creating a boundary in the scale dimension across which the system cannot evolve. System interactions are not equivalent across scales and this heterogeneous distribution of interactions has implications for the potential of the system to evolve into various forms.

A further example of a boundary in the scale over which a system cannot evolve is that larger mammals have evolved with locomotor limb postures in which they move in an upright fashion relative to their smaller counterparts (Biewener, 1989) due to the relatively constant tensile strength of bone. The limbs of elephants are orientated so that the force is normal to the ground in order to increase load bearing, whereas a mouse has limbs that are at an angle from the pectoral and pelvic girdle in order to increase speed.

They may seem disparate, but the effect of water surface tension and the strength of calcium phosphate bones on the evolution of animal forms are qualitatively no different to the effects of certain ecosystem drivers on vegetation. In the context of physical constraints on individual trees for example; the above ground architecture of plants is influenced by environmental variables, for instance the wood density and the hydraulic architecture are affected by biomechanical demands such as canopy support and subsequent wind loading (Gartner, 1991).

Physiological responses which affect tree size and its ability to exploit resources include susceptibility to cavitation, which is the introduction of air embolisms into xylem conductive tissue. Increased hydraulic efficiency with increased vessel diameter increases vulnerability to cavitation (McElrone et al., 2004). Moreover, dense, larger diameter xylem may be more hydraulically efficient but is weaker mechanically than xylem dominated by smaller conduits (Tyree et al., 1994). This physical constraint of size of xylem and the risk of cavitation and weakening of structure, means that there is a risk in getting too big, as there are a host of physiological requirements that will not be met. As a result there have been a host of evolutionary responses (Meinzer et al., 2001).

The feedback between pattern and process in many systems makes these physiological relationships slightly more complicated, but still not fundamentally different. If there is a component of scale in the processes, it will be reflected in the evolutionary potential of particular forms of the system. The mechanisms driving the effects of process at various scales may be a seemingly absolute boundary imposed by the level of organization below such as the water strider example (although the boundary is not absolute and would be contingent on water temperature).

More pertinent to landscape ecology: if the transmission of energy forms a positive feedback loop which is constrained within the bounds of a specific scale, the coupling of processes and pattern through non-linear interactions can create positive feedback loops. These "*…self-reinforcing assembly states…"* (Stallins, 2006) can go by a variety of synonyms: "*attractors"* (Thompson et al., 2001, Baas, 2002, Harrison et al., 2006), "*stability domains"* (Gunderson, 2000) or "*domains of scale"* (Wiens, 1989) but in general, all of these terms refer to regions of scale in which pattern and process are tightly coupled relative to the other scales of the system.

The discontinuous nature of process in the system can be reflected and thereby measured in the patterns expressed. The Textural Discontinuity Hypothesis (TDH) proposes that certain keystone processes can entrain the spatial and temporal frequencies of the other processes in a system (Holling, 1992), which explains why this occurs in the first place. The entrainment creates a limited set of frequencies in both space and time at which drivers affect the landscape. According to the TDH, the limited scales at which processes are influential creates attractors in the scale domain that are reflected in the discontinuous distribution of pattern across scales (Figure 2.2).

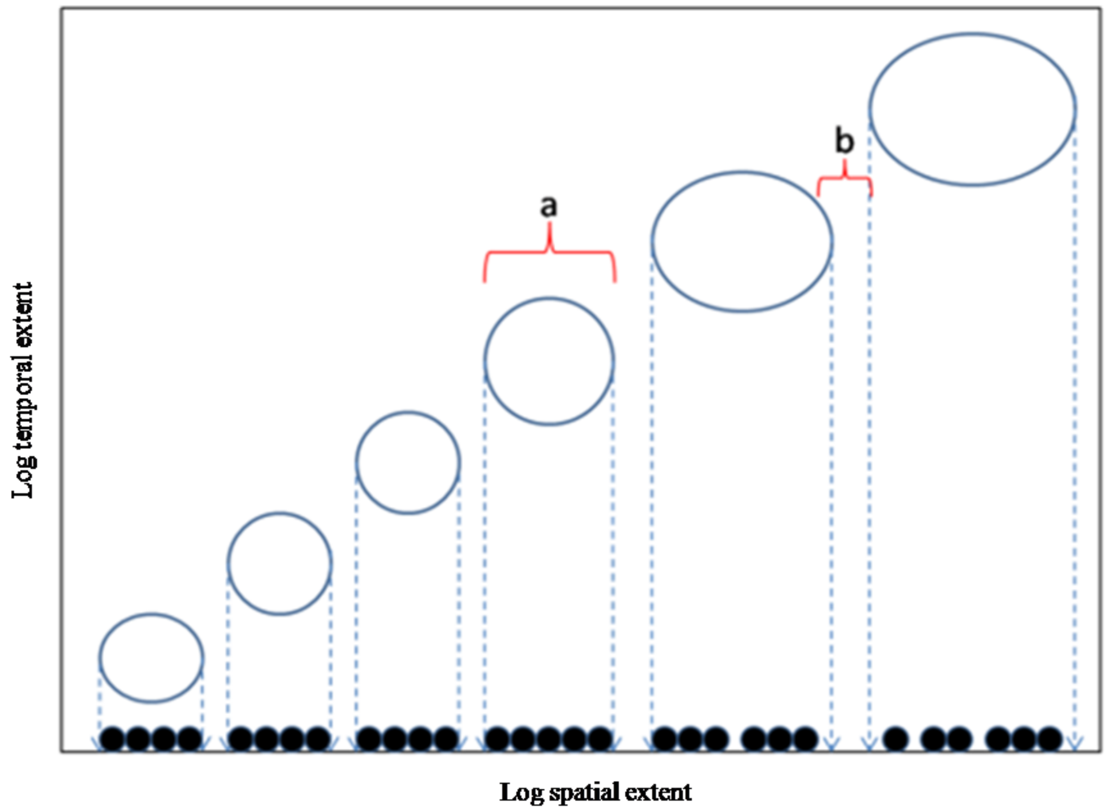

Figure 2.2: The Textural Discontinuity Hypothesis predicts that the entrainment of processes by keystone processes results in a limited spatio-temporal frequency of pattern: expressed in the system. These self-reinforcing regions are termed structural attractors (a) the areas between them are discontinuities, (b) regions where pattern is not expressed. Projected onto the spatial axis, the pattern can be viewed as a discontinuous distribution of pattern. This image is adapted from (Allen and Holling, 2002) in which Bird Body mass distributions are the dataset.

Predictions of the system components with increased likelihood of change are made relative to the edge of a discontinuity (Allen et al., 2005). I, should therefore, be able to detect process domains in a spatially explicit manner using a technique which can measure the pattern across scales (the cross scale morphology of a system) in a meaningful manner that reflects holons and process domains i.e. hierarchically structured vegetation as per the HPDP. I can perform a spatially explicit discontinuity analysis on the data and test whether or not it is possible to make predictions on where there are likely to be dynamics relative to other components. That is a long way off still, first one must detect hierarchical structure.

OBJECTIVE 2: WHY A SEMI-ARID SAVANNA LANDSCAPE IS A GOOD STUDY SYSTEM TO USE TO INVESTIGATE THE EXPRESSION OF COMPLEX SYSTEMS PROPERTIES

There is a vast amount of literature concerning the nature of vegetation pattern and representation of landscapes as complex systems. Much of the work on which this thesis is built derives from the fields of dry land ecology and the study of patterns in arid systems. Of particular interest in dry land ecological research is how systems may shift from one state to another and experience a hysteresis in the feedbacks, which means that even if the system is returned to the starting point, these non-reversible changes are often explored in the state and transition models (viz. Briske et al., 2005).

A major focus of dry land ecology is the presence of alternative stable states and the possibly catastrophic shifts from one state to another which have profound implications for livelihoods in marginal environments and the ability to manage such systems (Rietkerk and van de Koppel, 1997, Rietkerk et al., 2004, van de Koppel et al., 2002). Modeled systems (HilleRisLambers et al., 2001) and distinctive vegetation patterning (Rietkerk et al., 2002, Rietkerk et al., 2004) have been used to infer evidence of self-organized states and states that are possibly near a critical transition point. The self-organized nature of the system is inferred to be due to the spatial interactions such as the spatial exchange in water in maintaining an arid landscape (Van der Koppel 2004).

Models for alternative stable states in savannas and arguments highlighting the role of fire and herbivory in determining woody vegetation cover have been put forward (Sankaran et al., 2005, Sankaran et al., 2008, Staver et al., 2009, Staver et al., 2011), but not in such a spatially explicit context as the arid land models. For example, Higgins and Scheiter (2012) illustrate that increasing atmospheric CO_2 levels may force a shift in local vegetation to a more wood dominated savanna system. Staver (2011) showed that in savannas that receive between 1,000-2,500mm of rainfall per annum, two alternate states occur, those of open savanna and forest and that fire is the major controller of these two.

I refer to these models to illustrate that system model commonly uses woody vegetation cover as a proxy for process in the landscape which is used to infer system level properties. In the following section I review the feedback loops and processes that affect the woody canopy cover of a savanna in order to illustrate why I use woody canopy cover as a systems proxy.

2.1.4. *DRIVERS OF SAVANNA VEGETATION PATTERN*

The strength and the type of interaction in savannas varies in both time and space allowing a rich array of possible outcomes but no universal predictive model (Scholes and Archer, 1997). Woody and graminous plants interact by many mechanisms, both competitive and facilitative. There is abundant information on the drivers of tree-grass interactions in savanna systems, yet despite the large body of information, most investigations are still single driver focused, or investigate the combination of a few major drivers (viz. Bond and Keeley, 2005, Staver et al., 2009).

Although the outcome of particular drivers and driver interactions are well understood, the results and interpretations of pattern in savannas are plagued with issues of scale, exceptions and contingencies (Levick and Rogers, 2008, Levick and Rogers, 2011) leading to very few hard and fast rules in savanna dynamics.

Despite the lack of a universal predictive savanna model, there are some generalities which can be made, particularly when savannas are considered at broad spatial extents. The current understanding of the determinants of woody cover in African savannas is that systems which receive below 650mm ± 135mm of mean annual precipitation are constrained by water availability. In these "stable" systems, water availability constrains maximum woody cover and allows trees and grass to co-exist. It is disturbances such as fire and herbivory that influences the amount and distribution of woody cover, reducing it to below this potential maximum. These semi-arid systems are contrasted with mesic savanna systems in which it is the disturbances from fire and herbivory which allow the co-existence of trees and grass. (Bond and Keeley, 2005, Sankaran et al., 2005).

Fire and herbivory are two of the major disturbances/drivers which influence savanna dynamics, limiting tree cover and facilitating the co-existence of trees and grasses (Scholes and Archer, 1997, Eckhardt et al., 2000, D'Odorico et al., 2006, Staver et al., 2009). The general trend is that woody biomass usually increases with a decrease in fire frequency. Fire is inferred to play a role as a determinant of savanna structure through a reduction in young tree survival (Hoffmann and Jackson, 2000, Hoffmann et al., 2002). Herbivory too can decrease woody biomass, either through direct consumption, or via interactions with fire. For example, grazing can result in an increase in woody cover, via a decrease in grass cover and the subsequent decrease in inter specific competition and the reduced occurrence of fires. (Scholes and Archer, 1997).

Continuous fire may result in stunted "Gulliver" trees which stay in a stunted state for years until given an opportunity to escape the fire trap (Higgins et al., 2000). A "browse trap" can also form in which medium sized herbivores reduce the success of transition from saplings to adults (Staver et al., 2009).

Fire and herbivory are not the only drivers of savanna vegetation pattern and dynamics. The presence of termitaria (Levick et al., 2010), a history of human habitation (Scholes and Archer, 1997), the effect of nutrient cycling (Dougill et al., 1998, Hibbard et al., 2001, McCulley et al., 2004) or hydrological processes (Ludwig et al., 2005) are just a few factors which may influence the savanna vegetation distribution.

Not only do different drivers affect the savanna landscape at different scales (Gillson, 2004), but different drivers underlie vegetation dynamics in different *landscape contexts* (Levick and Rogers, 2011). Landscape context refers to multiple possible outcomes due to the configuration of numerous drivers of an inherently heterogeneous and complex system. For instance, in dry dystrophic savannas, Treydte, Heitkonig et. al (2007) recorded grass leaf N- and Pcontents up to 25% higher underneath tree canopies. However, there was no significant grass quality improvement by trees in moist and nutrient-rich savannas. In this example; the nutrient cycling was contingent on the available moisture of the soil.

Another example from dry lands ecology taken from a study of water balance associated with patterns of tree cover density in topographically heterogeneous semi-arid woodland found that the effect of one variable on tree cover density depends on the value of the other variables.

Any kind of synthesis of the dynamics of woody cover in savannas illustrates that many interactions are contingent on a number of factors, which themselves are part of feedback loops; examples of which I discuss later in this chapter. The last forty years of research into savannas have been fruitful and narratives generated about possible interactions and outcomes of differences in systems drivers (Scholes and Archer, 1997, viz. Sankaran et al., 2008, Staver et al., 2009). However, from a theoretical perspective, given the sensitivity of outcomes to initial starting conditions in complex systems (Kauffman, 1995) and given the possibly drastic effects of chance events (Ulanowicz, 2008); is a more holistic approach not better suited to the analysis of savanna systems?

Systems analysis is a concept borrowed from information theory and has been applied to determining the origin of the savanna biome (Beerling and Osborne, 2006). It is a method for assessing potential feedback loops within a system. In any system where the propensity for a positive feedback loop exists, it is likely that the loop will form. The feedback loop will become more entrenched and start to acquire resources from the rest of the system, until some form of constraint impedes its ability to grow any more (Ulanowicz, 2008) .

The systems representation presented below is by no means spatial, nor is it meant to be. In this thesis I utilize the spatial and scaled nature of woody cover to make an inference about the processes and feedback loops that affect the woody cover. The link between the system's representation (outlined here) and the multi-scaled distribution of woody cover in the landscape is fundamental to my thesis. I take advantage of the fact that trees are sessile and that feedback loops either aid or inhibit their proliferation into patches. This means that the spatial and scaled nature of woody cover can be used to infer the nature of certain processes, specifically processes which create feedback loops which either facilitate or inhibit the proliferation of woody cover. In the following section I discuss feedback loops in savanna systems from the point of view of process flow.

2.1.4.1. **Feedback loops influencing savanna vegetation structure**

A qualitative systems analysis of the drivers and interactions which affect woody tree cover in a semi-arid savanna was synthesized from the literature (Figure 2.3). Not all possible interactions are incorporated, but they are rather limited to the feedbacks likely to affect a single hill slope unit. I have focused on those interactions likely to significantly affect the woody tree cover of the hill slope. In this representation, therefore, it is assumed that climatic feedbacks such as CO_2 concentration, regional precipitation and subsequent drought, cloud formation and fire ignition probability are constant across the site.

In a simplified diagram, I qualitatively present the interactions that have the propensity to create a feedback loop resulting in an increase or decrease in woody biomass. Each loop is discussed independently in the context of the supporting literature.

2.1.4.1.1. *The interaction between fire, grass biomass and tree cover*
(Figure 2.3; Pathway A→B→C→D)

In a savanna, increased fire frequency reduces woody tree cover (Hoffmann et al., 2002). Grasses are likely to establish in the gaps between trees, as the grass patches expand they increase fire frequency as the grass biomass established in the wet season creates a plentiful fuel supply for dry season fires (Bond and Keeley, 2005, Keeley and Rundel, 2005, Beerling and Osborne, 2006).

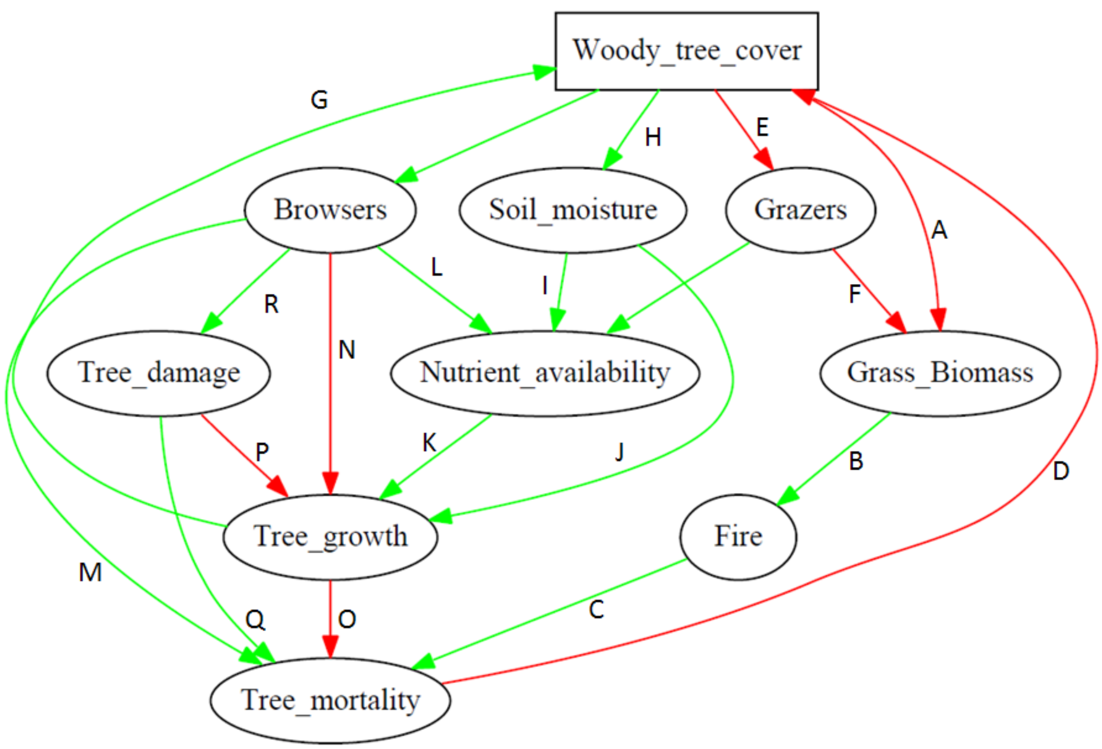

Figure 2.3: A qualitative systems analysis of interactions in a savanna system, focused on how the processes affect woody tree cover. Red arrows indicate a negative effect and green arrows indicate a positive effect. Letters label the interactions and feedbacks. Systems analysis allows for the detection of feedback loops, such as pathway A-B-C-D, in which an increase in fire frequency

causes a decrease in tree cover via an increase in tree mortality, which in turn increases the likelihood of grass biomass, which in turn increases the biomass available for combustion, closing the feedback loop. The diagram presented is not fully inclusive of all possible interactions; for example, fire may influence tree growth as well as tree mortality; these situations are however mutually reinforcing interactions and thus feedback loops will not be left out.

2.1.4.1.2. *The interactions between herbivory, fire and woody tree cover.*
(Figure 2.3: pathway E→F→B→C→D)

Interactions between fire and grazing are critical to structuring savanna landscape heterogeneity (Knapp et al., 1999, Fuhlendorf and Engle, 2001, Fuhlendorf and Engle, 2004, Kerby et al., 2007). Herbivores, most notably ungulates, influence the fire regime by altering the quality and quantity of fuels available for combustion (Hobbs, 1996). Large ungulates selectively graze recently burned patches for the high-quality regrowth forage (Coppedge et al., 1998, Coppedge and Shaw, 1998, Archibald and Bond, 2004). Patches not burned recently accumulate dead biomass because of reduced foraging pressure when ungulates focus on more recently burned patches (Fuhlendorf and Engle, 2004). The rapid re-sprouting initiated by fire presents ungulates with highly palatable grazing that consistently attracts herbivores to the same areas, creating a positive feedback loop (Fuhlendorf and Engle, 2004, Zavala and Holdo, 2005) which in turn reduces grass biomass and fire frequency.

Fire frequency is reduced as recently burned and grazed patches are unlikely to ignite and, if ignited, are unlikely to support fire spread. In contrast, patches not recently burned are very likely to support fire spread if ignited (Hobbs et al., 1991). This positive feedback interaction can be thought of as a form of ecological memory. In order for spatial self-organization to persist, there needs to be a relatively high level of ecological memory in a system (Peterson, 2002). In the absence of ecological memory a one-way relationship exists between landscape pattern and process (Peterson, 2008). This is an example of *ecosystem engineering*, a self-reinforcing pattern necessary for structural attractors to persist in the system.

2.1.4.1.3. *The feedback loops between soil-moisture, tree-growth and woody-cover.*
(Figure 2.3: pathways H→J→G, H→J→O→D, H→I→K→G and H→I→K→O→D).

Water availability affects tree distribution at multiple spatial extents. At local scales; water infiltration is increased under canopies due to soil porosity changes induced by root penetration. Shading reduces water loss from the soil and stem flow increases the local moisture content as vegetation patches serve to obstruct runoff (Ludwig et al., 2005). The increased available soil moisture increases the rate of nutrient cycling (Schlesinger et al., 1996, Agnew, 1997, Whitford et al., 1997), especially in the case of large trees (Treydte et al., 2009). In the space surrounding an individual tree; the accumulation of autochthonous leaf litter and sediments through wind trapping increases the local nutrient concentration, as does the use of vegetation by herbivores, which deposit dung in the vicinity of the tree either during foraging or during time spent ruminating in the shade (Agnew et al., 1993, Agnew, 1997).

The increase in water availability and nutrient cycling locally increase the growth potential of the plant and subsequently woody tree cover of the environment. This constitutes a feedback loop in which the trees facilitate the hospitality of their own environment. This feedback loop is an example of a self-reinforcing assembly state of pattern and process in a real world complex system, expressed in the distribution of vegetation pattern.

2.1.4.1.4. *The effect of browsers on woody-cover*
(Figure 2.3: pathway P→M→D, P→Q→S→G, P→N→G, P→N→O→D)
Not all feedbacks are positive and constitute self-reinforcing assembly states. Browsers directly affect the woody tree cover. Mega-herbivores such as elephants (*Loxodonta africana*) and giraffes (*Giraffa camelopardalis*) as well as a host of ungulates and insect browsers alter the structure of woody vegetation (Higgins et al., 2000, Bond and Loffell, 2001) through direct browsing or by increasing susceptibility of trees to fire (Holdo, 2007, Van Langevelde et al., 2008). An increase in browsing pressure will decrease the amount of available woody cover. This does not constitute a positive feedback loop but it is instead a density-dependent feedback between browsers and resource, a negative feedback. This will not create self-reinforcing assembly states. In traditional system models negative feedbacks can create an equilibrium state, cyclical response or even deterministic chaos, depending on the parameters of the response curves.

2.1.5. *THE 'NWASHITSUMBE ENCLOSURE SITE*

The northern portion of the Kruger National Park falls within a region of semi-arid/arid savanna systems (Figure 2.4). The study site chosen is the "'Nwashitsumbe semi-enclosure site", situated in the northern area of the Kruger National Park, on basaltic soils with a gentle gradient. The site receives between 400-450mm rainfall p.a. The Aridity Index (AI) is 4.8, defined as:

$$I = 100T/P,$$

where T is the mean annual temperature and P is the mean annual precipitation ($2 \geq AI < 3$, characterizes a semi-arid area, and AI>3 characterizes an arid system) (Kéfi et al., 2007a, Pueyo and Alados, 2007).

2.1.6. *HISTORY OF HERBIVORY IN THE STUDY SITE*

The 'Nwashitsumbe enclosure is an experimental enclosure which excludes all mammals larger than a springhare (*Pedetes capensis*). Constructed in 1968, the enclosure was then extended in 1986 to include a riparian section alongside the adjacent first order stream. The study site selected was in the oldest section, which at the time of the photograph, depicted in the figure below, was 33 years old. The enclosures have not excluded herbivory completely, rather they can be considered as browse, and mega-herbivore exclosures. The enclosures have been used since their inception for the breeding of rare antelope species; roan antelope (*Hippotragus equinuus*), sable (*Hippotragus niger*) and Lichtensteins hartebeest (*Alcelaphus lichtensteinii*). Outside the enclosure the dominant herbivores (in no particular order) include elephant (*Loxodonta africana*), buffalo (*Syncerus cafer*), giraffe (*Giraffa camelopardalis*), white rhino (*Ceratotherium simum*), impala (*Aepyceros melampus*), Kudu (*Tragelaphus strepsiceros*), Nyala (*Tragelaphus angasii*), bushbuck (*Tragelaphus sylvaticus*), blue wildebeest (*Connochaetes taurinus*), steenbok (*Raphicerus campestris*) as well as a host of other antelope species. The herbivores represent a range of mixed feeders, specialized grazers, and specialized browsers of which there are both concentrate selector species and bulk feeders.

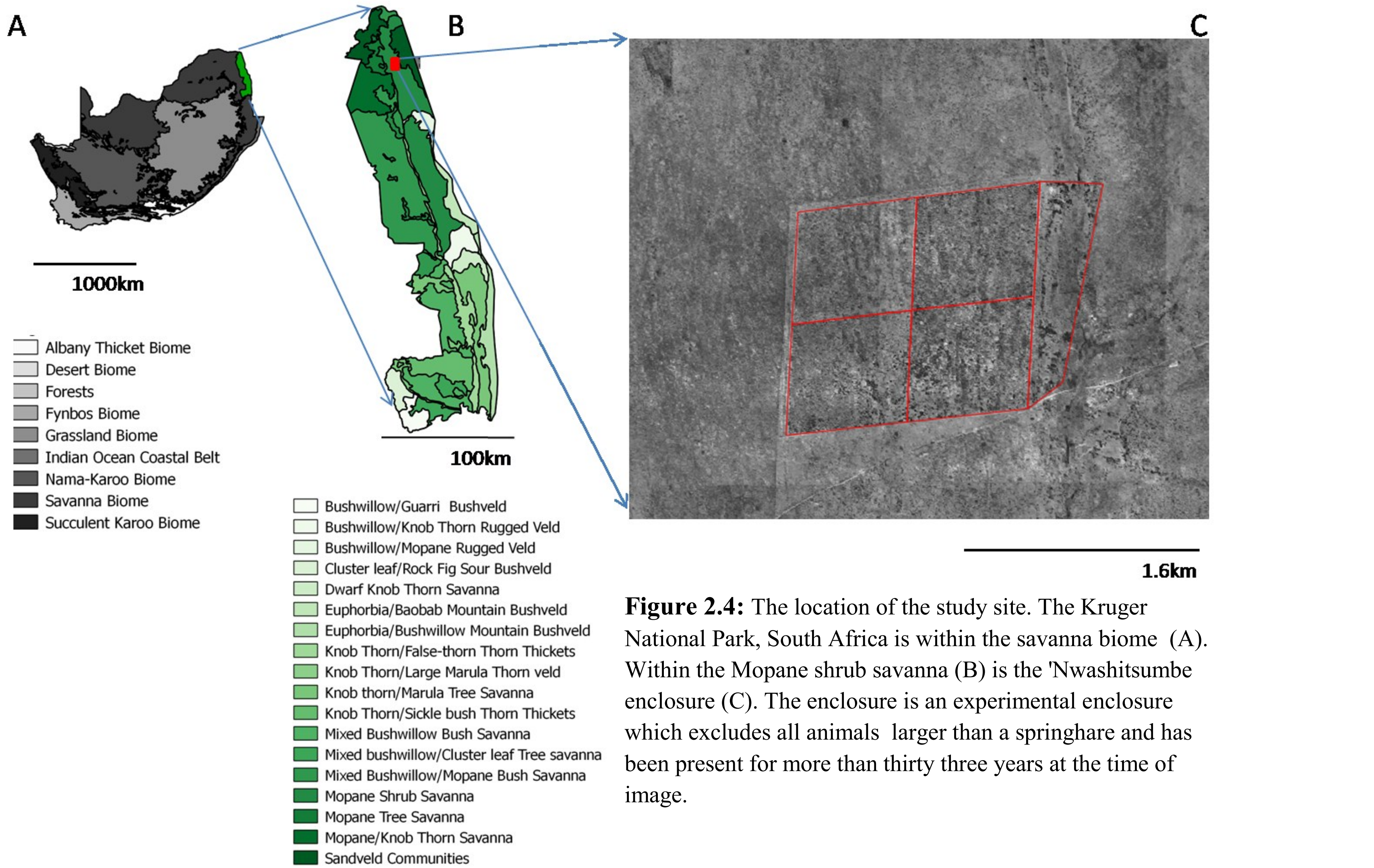

Figure 2.4: The location of the study site. The Kruger National Park, South Africa is within the savanna biome (A). Within the Mopane shrub savanna (B) is the 'Nwashitsumbe enclosure (C). The enclosure is an experimental enclosure which excludes all animals larger than a springhare and has been present for more than thirty three years at the time of image.

I acknowledge that the 'Nwatsitsumbe enclosure site is not a true herbivore exclusion site. Rather, the site has been used to breed rare antelope. Given that the herbivores within the enclosures are all concentrate selector species which are specialized grazers the assumption that they do not affect the woody vegetation via direct browsing is valid. Moreover, the enclosure site excludes mega-herbivores and abundant species such as nyala and impala and has done so for 33 years at the time of the photo.

Mega-herbivores have a major role as ecosystem engineers, mega-herbivores can shape vegetation over landscape scales (Owen-Smith, 1987, Owen-Smith, 1992). The removal of this major driver should influence vegetation and there is evidence from high resolution three dimensional LiDAR comparisons that there herbivory has had marked effects on canopy when inside and outside the enclosure are compared (Asner et al., 2009). Unfortunately large enclosures which totally exclude herbivores and that have been present for a long time are few and far between for the study of landscape ecology. Nevertheless, with all browsers excluded and all mega-herbivores, the difference between inside and outside of the enclosure indicate a 33 year difference in herbivore pressure.

2.1.7. *HISTORY OF FIRE IN THE STUDY SITES*

The 'Nwashitsumbe enclosure is divided into four burn treatments (Figure 2.5). The fire return frequency for each burn block has been accumulated from rangers' diaries and aerial photographs (Table 1;(Govender, 2009, unpublished data). There is no obvious periodicity in the fire return intervals and although fire intensity interval does affect vegetation structure (Govender 2006), fire intensity data are not available. I ranked the four sites based on time since the last recorded fire event: NW, SW, NE and SE respectively. The area outside of the enclosures has a fire return interval of approximately three years.

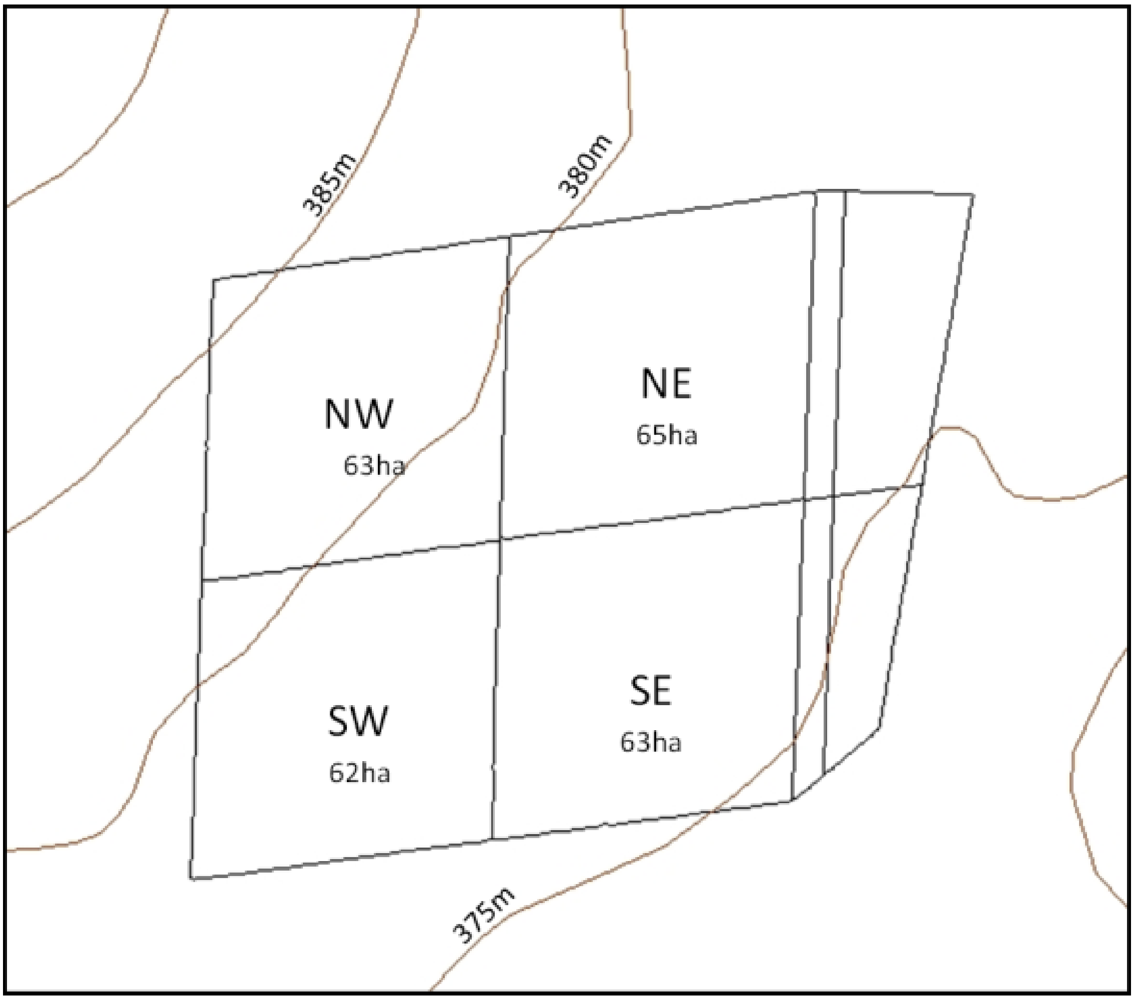

Figure 2.5: The 'Nwashitsumbe herbivore enclosure site, a 33 year browser enclosure. The enclosure is dived into four blocks which I have named based on their locations: NW NE, SW and SE. Each block has a different fire regime, expanded upon in Table 5. The sizes of the blocks are indicated in hectares. The topography is a gentle slope with a total drop of ten metres over a distance of approximately 1,800m.

Table 1: Recorded fire events for the four burn blocks of the 'Nwashitsumbe enclosure. Time since fire (tsf) between each event is indicated, with the time since last fire at the time of the photograph in 2001.

NW		tsf	**NE**	tsf	**SW**	tsf	**SE**	tsf
	1976		*1980*		*1978*		*1979*	
	1982	6	*1985*	5	*1984*	6	*1981*	2
	1985	3			*1986*	2	*1985*	4
	1987	2			*1990*	4	*1988*	3
	1990	3			*1999*	9		
	1998	8						
Photo	***2001***	**3**	***2001***	**16**	***2001***	**2**	***2001***	**13**

The 'Nwashitsumbe enclosure is situated on the uplands of a hill slope, dominated by *Colophospermum mopane* (Levick and Rogers, 2008). There is no steep incline or change in soil type within the site and differences in soil water availability are unlikely to be imposed by slope or aspect within the site. Changes have been documented with regard to the woody species composition and in the height class distributions of the wetland area adjacent to the sections of the enclosure used in this study (Levick and Rogers, 2008). Additionally, there has been a difference documented in the biomass accumulation within regions of the larger enclosure itself (Colgan, 2009, pers comm).

There have been documented differences in the canopy height of the 'Nwashitsumbe enclosure and the surrounds. The presence of herbivores severely reduces the amount of biomass and alters the vertical distribution thereof (Asner 2009). However, these studies did not compare the spatial distribution of vegetation cover in a non-stationary manner. The relationship between vertical distribution and the spatial distribution of woody canopy are related, but do herbivores, specifically browsers, affect the spatial distribution of patches? There are very few spatially explicit studies that document the effect of herbivory on the spatial configuration of vegetation. Herbivory has been shown to affect the cross-scale morphology of vegetation pattern by segmenting large patches and ultimately creating a regime shift (Kéfi et al., 2007a), but it remains to be seen whether or not the location of vegetation is driven by herbivory.

2.1.7.1. **Synthesis of Objective Two**

Savannas are complex systems with multiple interactions between biotic and abiotic agents. Some interactions result in distributions of vegetation that are self-reinforcing assembly states, while other interactions constitute classic density dependence responses. The spatial pattern of woody vegetation reflects the nature of feedback loops and has been used to infer system level properties. In addition, the distribution of vegetation is supposed to be affected at multiple scales by different drivers (Gillson, 2004). Vegetation distribution is a perfect test subject for complex systems properties as it should have multi-scaled pattern indicative of processes. By testing for hierarchically nested structure in a real world savanna system, it is possible to find the nested holons at varying levels of organization- from which further analyses may reveal system level properties commensurate with the power law type analyses but applicable to more heterogeneous landscapes.

2.2. Objective 3: What methods are available for multi-scaled pattern detection and why they are not valid for the purposes of this thesis

Ecologists strive to link spatial heterogeneity and ecological process; this requires a formal representation such as the Hierarchical Patch Dynamics Paradigm. In general, "…the *spatial configuration and composition of this patch mosaic typically describes using an assortment of landscape metrics to quantitatively link the dynamics of process and structure…"* (Castilla et al., 2008, pg. 1). However, there are a number of statistical artifacts and scale relationships inherent in the methods themselves which may preclude any ability to make ecologically meaningful inference. Linking datasets, or metrics between scales of observation has inherent bias which must be accounted for (O'Neill, 1986). Here I explain why.

2.2.1. *Statistical considerations in spatially explicit and multi-scaled analysis*

The spatial ecologist is confronted with a panoply of techniques which have been used to analyze the structure of landscape images. There are a multitude of caveats and possible errors introduced through linking pattern that have been captured through different windows of observation. I cannot hope to be completely comprehensive in the review, nor is it relevant, rather I review a subset of traditionally used methods for the purposes of generating an understanding of the pitfalls to be avoided in the process deriving the use of linear scale-space as a method for completing these analyses.

The traditional multi-scale methods in landscape ecology, which I review included; semi-variance analysis (Wu et al., 2000), wavelet analysis (McGarigal and Cushman, 2005, Saunders et al., 2005, Murwira and Skidmore, 2006), fractal analysis (Nikora et al., 1999, Alados et al., 2005) and lacunarity analyses (Plotnick et al., 1993, Plotnick et al., 1996, Dale, 2000, McIntyre and Wiens, 2000, Wu et al., 2000, Bastin et al., 2002). In addition I reviewed spectral analysis techniques (Couteron et al., 2006), cluster analysis (Scanlon et al., 2007) and multi-scaled object-based analysis approaches that have been developed for use with remotely sensed data (Hay et al., 2001, Hay et al., 2002). The wide range of methods reflects the diversity of data sets (Dale et al., 2002, Perry et al., 2002) as well as the variety of disciplines from which these methods are derived and vary from the very simple and easily applied to the very complicated and cumbersome. Results of pattern analyses using various techniques can show large variations, despite similar data and objectives, highlighting the necessity of understanding the different methods before applying them to the task at hand (Johnson et al., 2005).

2.2.1.1. **Statistical considerations:**

Across this full spectrum of methods exists a conflict between the statistical rigor of many techniques, introduced by the mathematical assumptions underpinning them and the ecological reality of accepting those assumptions. Not all methods reviewed necessarily fall foul of all assumptions and these are not necessarily comparable methods as they are aimed at answering different questions, but the four major assumptions and their consequent artifacts which pervade the reviewed statistical methods are: stationarity, subjective *a priori* scale selection, anisotropic sampling schemes and the Modifiable Areal Unit Problem. I briefly review the ecological implications of these assumptions and artifacts as I derive the use of linear scale-space as a superior method of multi-scale landscape analysis.

Table 2: Summary of the intrinsic statistical assumptions of the reviewed multi-scaled analysis methods. The review is limited to two dimensional applications as one dimensional applications naturally assume a gradient.

Multi-scaled analysis technique	Sensitive to the MAUP	Assumes Stationarity	Anisotropic sampling scheme	A priori scale assumptions	Ease of implementation	Retains local information
Semivariance Analysis	Yes	Yes	If 1D	No	Simple	No
Lacunarity Analysis*	Yes	Yes	If 1D	No	Simple	No
Fractal Analysis	Yes	Yes	If 1D	No	Simple	No
Spectral Analysis*	Yes	Yes	No	No	Simple using FFT	No
Cluster Analysis†	No	Yes	No	No	Requires some level of statistical sophistication	No
Wavelet Analysis*	No	No	If 1D	No	Not many	Yes

					applications available.	
Multi-scaled object based approaches$^{\phi}$	No	No	No	Yes	Requires object based software	Yes

Methods and reviews from Saunders et al (2005) and Ares et al (2003)*, Scanlon (2007)†, Dale et al (1998), Dale et al (2002), Dale (2000), Hay et al (2001)$^{\phi}$ and Wagner et al (2005).

2.2.1.1.1. *Stationarity*

Spatial stationarity is the assumption that the mean and variance of the sample remain consistent across the entire data set (Fortin et al., 2005). The underlying assumption of stationarity is that the data structure is the same no matter where in the sample one observes a datum (Wagner and Fortin, 2005). Stationarity is the spatial statistics equivalent of the assumption of independence in parametric statistics and implies that any variation that one observes across a dataset is a result of an anomaly in the distribution, as opposed to any difference in the processes creating the pattern.

The assumption of stationarity, however, is rarely kept in real landscapes, due to the presence of local variability, patchiness, spatial gradients and interactions which themselves are contingent on the underlying environmental and controlling biotic factors (Brown et al., 1996, Maurer, 1999, Fortin et al., 2003, Fortin et al., 2005). For instance, vegetation distributions in landscapes and in particular in semi-arid savannas are differentially influenced by different processes at different scales and at different places in the landscape (Gillson, 2004, Levick, 2008). By way of illustration, in a semi-arid savanna system, it is inferred that mammalian herbivory is the major driver of vegetation loss on lowland alluvial soils, whilst shrub encroachment on the upland hill slopes stems from changes in fire regime and climate (Levick and Rogers, 2011).

Stationarity cannot be assumed for landscape extent analyses which aim to extract pattern objectively in the context of patch delineation and process domains. Rather, when the assumption of stationarity is not fulfilled and spatial characterization should be performed using local spatial statistics (Boots, 2002) or wavelet analysis (Bradshaw and Spies, 1992, Dale and Mah, 1998). Local statistics and wavelet analysis are methods which preserve local information. Linear scale-space analysis can be considered a specific type of wavelet analysis and also preserves local information.

2.2.1.1.2. *A priori scale selection*

The scale of observation represents the window of perception of the data set representing the real world and is defined by the filter or measuring tool with which a system is viewed and quantified (Hay et al., 2002). Viewing spatial pattern through a relatively large filter reflects data pattern dominant at that large spatial extent. Similarly, small filters only allow for the relatively smaller spatial information to be represented in the outputs. Landscapes are inherently heterogeneous and the degree of variation observed will depend upon the temporal and spatial window of observation (Dungan et al., 2002, Chave and Levin, 2003, Levick, 2008).

Real world objects, represented as a sampled data set in whatever form, only manifest across a finite range of scales (Hay et al., 2002). The object will only be observed to the extent permitted by the spatial extent of the chosen filter sizes and therefore it is vital to specify the scale of interest before any methods for geo-statistical or boundary analysis can be applied (Kent et al., 2006). The choice of filter size that determines the scale of observation is either a subjective decision of the researcher, or a practical constraint of the dataset. For instance, to analyze pattern in the woody tree cover from an image at multiple scales, the image must be partitioned into windows for analysis. The relative size of the windows defines the scales of the analysis (Couteron et al., 2006) and therefore the emergent pattern. However, to link pattern and process one must accurately define the actual pattern that emerges from real process interactions, not those constrained by the *a priori* selection of a starting scale and/or window sizes as is the case in most of the reviewed methods.

2.2.1.1.3. *Anisotropic sampling schemes*

Anisotropy and isotropy refer to the direction of spatial analysis in a data set. Isotropic patterns contain no underlying directionality or trends in the dataset, whereas anisotropy refers to the case where the data characteristics are different, depending on the direction the samples are taken in. For example, oblong rather than circular patches of vegetation can be caused by directional wind or water flow (Dale, 2000). Transect based methods assume that any gradients or anomalies in the pattern will be parallel to the transect direction. Transect based methods present a bias in their application; in which direction does one place the transect? If one does not know anything about the nature of the process, choosing a direction may cause misinformation.

Many techniques applied to assess both spatial autocorrelation and spatial pattern assume anisotropic data (Kent et al., 2006, Ares et al., 2003) and may not be effective in detecting multi-scaled data structure when the shapes of patches vary greatly and are elongated with different orientations (Wu et al., 2000). In studies describing multi-scaled structure of landscapes, one must avoid sampling schemes that rely on, or fall foul of assumptions of anisotropy if the true ecologically meaningful pattern is to emerge.

2.2.1.1.4. *The Modifiable Area Unit Problem*

Remote sensing technologies are the primary data source for landscape analysis, but suffer from a sampling artifact termed the Modifiable Area Unit Problem (MAUP) (Hay et al., 2001). Changing the shape and/or size of the units on which data are mapped can change the resulting patterns or statistical models generated from the data (Dungan et al., 2002). The potential for error in the analysis of spatial data resulting from MAUP is significant and has been recognized in a number of studies (Fotheringham and Wong, 1991, Jelinski and Wu, 1996).

As a result of remotely sensed data being sampled without necessarily considering the ecological meaning, the outcome of aggregation of the data can have a great effect on the estimated covariance structure (Wagner and Fortin, 2005). Covariance structure of datasets is what is used to make inference regarding the process as it is a measure of the variability in pixels within a sample. Consequently changes to covariance structure induced by changing aggregation schemes at different scales can lead to an improper association of pattern and process.

A solution to the MAUP is to use object-based image analysis techniques (Hay et al., 2001), in which data are represented, not as an arbitrarily assigned association of pixels, nor in single pixels but in image objects which can be more ecologically meaningful than simple spectral representations (Baatz and Schäpe, 1999).

Methods used to analyze for multi-scaled landscape structure are numerous and scaling of the data is the subject of the field of scaling (viz. Milne and Johnson, 1993, Wu, 1999, Wu and Qi, 2000). I return to the analysis of multi-scaled pattern in landscapes; firstly I highlight a few other methods used to measure multi-scaled pattern upon which I draw when I develop my method.

2.2.2. *DISCONTINUITY ANALYSIS; THE SEARCH FOR BREAKS IN PATTERN ACROSS SCALE*

The Textural Discontinuity Hypothesis (TDH) predicts a discontinuous distribution of pattern in the cross-scale morphology of a system. According to the TDH the presence of a discontinuity is evidence that pattern and process entrain the scales over which one another are expressed. Entrainment refers to a dominant keystone process enslaving the spatio-temporal frequency of another process, resulting in a limited number of spatial and temporal frequencies over which processes operate (Holling, 1992, Allen, 2006). A number of methods have been used to identify *discontinuities* in datasets, reviewed by Skillen and Maurer (2008). In general, analysis for discontinuities is performed along the scale axis, comparing the size of the gaps between data points which reflect the scale at which processes are influential (Holling, 1992, Siemann and Brown, 1999, Allen et al., 2005, Stow et al., 2007).
A discontinuity is a gap in pattern measured across the scale dimension. But when measuring discrete units, as is necessary to take the measurement, what constitutes a gap that is sufficiently large to be considered a discontinuity? When considering a proxy such as body mass (viz. Holling, 1992) a five gram difference between two shrew species is more meaningful that a five gram difference between deer species. This is due to comparison of data across scales and the data must be detrended before it can be analyzed for discontinuities. Once the data are transformed, they are considered comparable and are tested for discontinuous patterns across multiple scales.

Most commonly the trend in scale is removed using a $\log_{10}$ transformation of the data (Holling, 1992, Holling, 2001, Allen and Holling, 2002, Allen et al., 2005, Allen, 2006, Allen et al., 2006, Stow et al., 2007, Skillen et al., 2008) or by transforming the data with a scaling factor (Holling, 1992). Earlier research into discontinuities utilized a body mass difference index:

$HI=(M_{(n+1)}-M_{(n-1)})/M_{(n)})^{\gamma,}$ where γ=1.3 for birds and 1.1 for mammals (Holling, 1992).

Siemann and Brown (1999) developed an index using $SB=log_{10}((M_{(n+1)})/(M_{(n)}))$. Both of these indices assume a single trend in the data, that is detrended by transformation exponent (1.3 or 1.1 in the case of Holling (1992) and $\log_{(10)}$ in the case of Siemann and Brown (1999)). A discontinuity constitutes a gap between two values of greater than a user defined criterion.

In more objective approaches a number of resampling methods have been developed in an effort to analyze for the presence of discontinuities. The Gap Rarity Index (Restrepo et al., 1997) utilizes a null model of uniform distribution that is repeatedly sampled as:

$$gap_{(n)} = log_{10}(M_{(n+1)}) - log_{10}(M_n).$$

The resampling creates a hypothetical distribution of gaps against which the gaps within the real data are tested. This constitutes a Monte Carlo Simulation approach in which the sample is tested against a population taken from a number of random replicates of known distribution. Standard hypothesis testing techniques are then used to determine the significance of any discontinuities.

A method developed by Stow et al. (2007) utilizes an overall discontinuity index, which indicates the "gappiness" in the dataset, done by calculating the vector norm of the dataset:

$$DI = \sqrt[2]{\sum_{i=1}^{N}(x_i)^2}$$

This discontinuity index (*DI*) is tested against a population of hypothetical discontinuity index values. The hypothetical population is created by resampling a hypothetical null distribution of uniform distances with the same sample size as the real dataset. The result of the test is a single value describing the probability that the discontinuity index of the data set is higher than that created through random chance.

Hierarchical cluster analysis; classification and regression trees as well as the Bayesian version thereof (Chipman et al., 1998) have been put forward as methods to detect the location of discontinuities in data (Stow et al., 2007, Skillen et al., 2008). However, the determination of what constitutes a significant cluster is a contentious issue and Stow, Allen et al.(2007) advocate finding consensus using a number of methods.

I must highlight here that detecting discontinuities in spatial data is novel at this point. In one dimensional datasets such as body mass distributions, a form of stationarity is assumed. It is implicitly assumed that the suite of processes affecting the body mass of all individuals of a species is equal throughout the sampled distribution. Therefore, any discontinuities in the data are assumed to be the result of an anomaly in process. In spatial data taken from a landscape however, stationarity assumptions are not valid. Contingency in landscape process and the resulting pattern renders this assumption of stationarity invalid. Detecting discontinuities in spatial data is novel and thus a novel method is needed to detect the presence of discontinuities in the dataset, which I develop later in this thesis. Firstly, I review other examples of multi-scaled analysis of landscape pattern.

2.2.3. *MULTI-SCALED ANALYSIS OF VEGETATION PATTERN*

The analysis of multi-scaled pattern and process found in a savanna landscape is by no means a novel field of research. A variety of methods have been used to quantify the structure of landscape variables at multiple scales, often involving some form of renormalization and scaling process in which data are sampled at multiple resolutions and variations in a quantity compared across resolutions (viz. Milne and Johnson 1993). I have divided the techniques used to analyze multi-scaled structure in datasets into four broad groups. Within the groups there are often a multitude of variations in the techniques which are not expanded upon here. I reiterate that the objective of this thesis is to detect hierarchically nested structure in woody vegetation cover of a semi- arid savanna.

2.2.3.1. **The search for translational invariance in scale**

A common technique in the search for multi-scaled structure in spatial data is the detection of regions of translational invariance in a comparison of scale of observation versus quantity of the observed variable. This type of analysis is often termed power-law analysis. The general form is:

$Y = \beta^{\alpha}$ where Y is a predicted variable, β is a normalization coefficient and α is the scaling exponent (Marquet et al., 2005).

Power laws have been studied extensively in various fields and a number of power law relationships have been found in natural systems (West et al., 1997, Brown et al., 2002, Brown et al., 2004, West and Brown, 2005).

Although the term power law has been used in a variety of similar ways, I confine the discussion of power laws to the analysis of the change in the measured value of a spatial attribute in a landscape as one changes the scale of observation. Power laws in this context are functions which define the relationship between the observed data across the scale axis. The philosophy of power law analysis is that the processes creating the pattern are constant across the entire range of observed scales. Any region across scale where a process predominates should follow a particular power law, implying that the same principles or processes are at work no matter what the scale of analysis.

A power law relationship implies that there is translational invariance in scale. The search for translational invariance in the landscape is well documented, (Wu, 2004, Saura and Castro, 2007). The search for a nested hierarchy is simply the search for multiple regions of translational invariance along the scale axis. In and of itself this does not violate any ecological assumptions; rather the problems lie in the ways in which data are collected to compare scaling laws. A number of methods exist for the determination of power laws in the landscape, of which I discuss three: measures of spatial autocorrelation, fractal analysis and cluster analysis.

2.2.3.1.1. *Measures of spatial autocorrelation*

Spatial autocorrelation exists when the process generating the pattern of interest is spatially weighted, there is a relationship between the pattern or strength of signal and the distance between points being compared. "*Everything is related to everything else but near things are more related than distant things".* (Tobler, 1970). There is a tendency for observations which are spatially close to each other to be more similar than that of a random sample (Dale et al., 2002, Rangel et al., 2006) i.e. variables co-vary in space (Kent et al., 2006). Spatially correlated data implies a coupling and dependence between pattern and process in the landscape. If one can determine the spatial extent at which the data no longer show dependency on one another, it is possible to determine the spatial extents at which process domains are evident in the landscape.

A number of methods, which observe both local and global patterns in a dataset, are used to determine the extent of spatial autocorrelation in the landscape. One of the most widespread tools for detecting spatial or temporal scales of variability is the sample variogram or semi-variogram (Dale et al., 2002). Variograms quantify the amount of spatial autocorrelation across differing lag distances, which typically increase from a theoretical zero until the spatial autocorrelation levels off at the maximum semi-variance, which occurs at and beyond a particular lag distance known as "the range".

1. Semi-variance measures

The spatial autocorrelation in a dataset is quantified by comparing data points at increasing distances from one another. The range identifies the distance beyond which pairs of objects no longer exhibit spatial autocorrelation (Meisel and Turner, 1998) and in terms of vegetation as a process domains the distance at which the coupling between pattern and process no longer occurs, i.e the patterns are independent. Evidence of multiple lag distances can be evidence of hierarchical structure in the dataset. The semi-variogram has been widely used in landscape analysis and the search for multi-scaled patterning. For example, semi-variograms have been used to study the correlation between scales of ungulate foraging strategies and resource availability in the landscape (Meisel and Turner, 1998), changes in forest canopy spatial pattern (Aguilar-Amuchastegui and Henebry, 2006), the study of the scaled nature of soil organism distribution (Ettema and Wardle, 2002) and to determine the scale-dependent spatial heterogeneity of vegetation (Chen et al., 2002).

The semi-variogram excels at describing a global pattern but fails in the detection of local features deviating from the mean (Bradshaw and Spies, 1992), due to the assumption of stationarity inherent in the method. In terms of the search for the presence of a nested hierarchy, besides issues concerning stationarity, the interpretation of the semi-variogram output becomes difficult when multi-scaled data is encountered (Bradshaw and Spies, 1992) Studies have indicated that in semi-variograms of real landscapes finescale variability can be affected by broadscale variability, so that multi-scale structure may be obscured (Meisel and Turner, 1998, Wu et al., 2000). In addition, the results of semi-variance analysis and their interpretations can also be significantly affected by changing the grain size, lag, and extent of the data sets, i.e. the MAUP (Dungan et al., 2002).

2. Lacunarity analysis

Lacunarity analysis is a "*…scale dependent measure of heterogeneity or texture…" (Plotnick et al., 1996)* and is used in landscape ecology to detect hierarchical structure within the data. There are many methods for calculating the lacunarity of an image, however a common method is the moving window method. This is done by calculating the mean and variance of the data of a gliding window over a number of filter sizes (scales of observation) (Plotnick et al., 1996, Dale, 2000, Saunders et al., 2005). Lacunarity analysis quantifies deviation from translational invariance by describing the distribution of gaps within the image at multiple scales of observation (Henebry and Kux, 1995, Cheng, 1999). The more lacunar an image, the more heterogeneous the spatial arrangement of data. In terms of landscape pattern, high degrees of lacunarity indicate a scenario in which different ecological processes generate pattern within restricted and strongly separated scaling regions (Keitt, 2000).

Lacunarity analysis is similar to semi-variance analysis, instead of an increasing distance (lag) between sample points, the filter size is increased. Lacunarity analysis calculates the mean and variance of a data set sampled at differing scales of observation. An analysis of lacunarity index value versus the window size reveals the scales of the ranges of scales across which the data structure is self-similar (Plotnick et al., 1996). It can provide power laws and be used similarly to the fractal dimensions in characterizing the regions of translational invariance.

Lacunarity analysis has been applied to vegetation structure in a number of applications (Plotnick et al., 1996, McIntyre and Wiens, 2000, Alados et al., 2005, Frazer et al., 2005), often from satellite imagery (Malhi and Román-Cuesta, 2008). Theoretically the regions of scale invariance should reveal the scale domains present in the landscape, but there is a loss of local information in the calculation of the lacunarity index. Although lacunarity analysis is in itself robust to non-stationary data sets (Saunders et al., 2005)the loss of local information implies an assumption of ecological stationarity in the pattern extracted. One can obtain little more than the average patch size or range of self- similarity out of traditional lacunarity analysis. Although a useful technique it is difficult if not impossible to translate the information back onto the landscape itself.

2.2.3.1.2. . *Fractals and multi-fractal based methods*

The fractal dimension ("D") of the dataset is a parameter which describes the relationship between measured size and measured scale. For a formal mathematical explanation of fractals see Mandelbrot(1982). Fractal analysis has been utilized to measure landscape structure and scales of pattern expression for many years (Krummel et al., 1987, O'Neill et al., 1988, Palmer, 1988, Nikora et al., 1999, Li, 2000, Wu et al., 2000, Despland, 2003), allowing ecologists to view landscape patch patterns and dynamics at multiple spatial and temporal scales (Li, 2000).

The essence of fractal theory is that it posits that concepts such as length (L), surface (L^2) and volume (L^3) are not discrete units as Euclidean geometry would have us believe, but that there is a continuum between the dimensions. Although it is intuitively easier to understand fractals in terms of lines, surfaces and volumes (D=1, D=2 and D=3;   for a point, surface and volume respectively) the data do not have to be physical and fractal analysis can be applied to statistical problems, which are a more common fractal problem in ecology.

Fractal analysis compares the magnitude of the observation, be it the size of the outline or mass of the object, across a number of scales of the measurement. This involves using different sized filters on the dataset and measuring the magnitude of the observation of interest. If the change in both variables is constant across a log-log plot, the fractal dimension

(D) indicates the degree of self-similarity in the data (Jelinek et al., 2006), which in turn can be an indication of the underlying biological process that leads to the observed pattern. The ranges of scale across which the slope of the log-log plot is constant implies that there is a single scale domain or dominant process or set of processes driving the pattern across this scale range (Keitt, 2000).

It must be remembered though that biological organisms are not true fractals (Shenker, 1994), so biological forms are at best statistically self-similar over a limited range. This range is often not wide enough for fractal tools to be utilized (Chen et al., 2002, Halley et al., 2004). Purely fractal landscapes can be derived as null models against which to test the real data or model process (Hill and Caswell, 1999) and possible process domains can and have been detected in vegetation distribution patterns within a landscape using fractal analysis (Hartley et al., 2004). A major use of fractal landscapes is as neutral models against which to test real world datasets, which I return to in the discussion of neutral landscapes (Section 2.2.4.

2.2.3.1.3. *Cluster Analysis*

Cluster analysis analyses the distribution of connected clusters, defined by neighbourhood relationships. Scanlon, Caylor et al. (2007) demonstrated the prevalence of self-organized vegetation patterns across a regional rainfall gradient in Southern Africa by finding translational invariance in the relationship between the cluster size of tree patches observed at differing observational window sizes. The method uses a cluster analysis technique in which the size distribution of connected patches of trees were calculated within a given lag distance (scale of observation) (Plotkin and Muller-Landau, 2002).

The probability that a cluster was smaller than the assigned scale of observation was then plotted against the size of the window of observation. A function was fitted to the data set allowing the fit of the power law to be calculated. A neutral model was developed to compare the observed power law against the power laws expected from a random with similar statistical properties. The results showed that the real world power laws infer a mechanistic understanding, implying that there is a suite of processes governing the scaling relationships within the study samples. The power law relationships were attributed by Scanlon, Caylor et. Al (2007) to internal feedbacks, rather than imposed spatial heterogeneity such as soil type differences or local topography.

2.2.3.2. **Quantifying spatial frequency**

A group of analysis techniques originates from signal processing and dissects the data into its constituent wavelengths. In a two dimensional dataset such as an image, the wavelengths constitute spatial frequency or spatial pattern. Techniques originating from signal processing applications use functions with varying scale or frequency parameters to approximate the dataset. Dissection of the dataset by a function with a varying parameter renders the data into a set of co-efficients relative to the strength of the parameter in the signal. There are a number of ways in which the spectral signatures of data can be dissected. I concentrate on the two most frequently utilized transforms: the Fourier transform and the wavelet transform.

2.2.3.2.1. *Fourier spectral analysis and textural ordination*

Spectral analysis examines periodicity in the spatial pattern of data. Although there are a number of techniques to do this, the Fourier transform is most commonly used for landscape imagery (Legendre, 1998).

1. Fourier transform

Any spatial frequency can be approximated in terms of sine and cosine functions of varying wavelengths. The Fourier transform fits sine and cosine functions of increasing frequency to the data and indicates which wavelengths best fit the data (Ripley, 1978). A coarse texture may be expected from a limited number of periodic functions having large wavelengths, whilst a finer texture is likely to be better described by functions with smaller wavelengths.

Spectral analysis can be useful in identifying multiple scales of heterogeneity and estimating the average patch size (Cullinan et al., 1997, Ares et al., 2003), but interpretation of the resulting spectral plots is difficult (Cullinan and Thomas, 1992). A major assumption of frequency analysis methods is that the spectra in the dataset are ecologically relevant; for instance, in a panchromatic image, the dark, low-value pixels are indicative of trees. Spectral analysis by Fourier transform plays a prominent role in signal processing but has not been widely adopted for landscape structural analysis. This may be due to the fact spectral analysis is perceived as only useful for studying genuine periodicity, a property that is not expected in most regions of the earth surface (Couteron et al., 2006). Fourier transforms are also integrative across the entire signal, which results in the loss of spatial information in the outputs. This constitutes a true assumption of stationarity and cannot render spatially explicit local information easily.

2. Textural Ordination

Textural ordination is a more sophisticated analysis method that has been developed incorporating Fourier analysis. The relative contribution to the Fourier approximation of large versus small wavelengths can be thought of as an expression of the relative importance of coarse versus fine textural components in a digital image (Couteron et al., 2006). A multi-variate analysis such as Principle Component Analysis (PCA) is used to categorize the significant structure in the data. The PCA is used to compare many Fourier spectra, where each image subjected to a Fourier transform is considered a sample and the spectra derived are considered the quantitative variables. The output of the textural ordination depicts the principle spectra that create the landscape structure and spectral differences from different areas can be compared. Assuming that the spectral bands represent similar ecological meaningful entities across the analysed image, dominant spatial scales of vegetation pattern expression can be detected.

Textural Ordination is a promising method in the analysis of multi-scaled data structure and can provide useful information in the search for the presence of a nested hierarchy. Textural ordination is superior to the global Fourier transform of an image, or even a windowed Fourier transform, which is used to try and avoid issues of stationarity. Textural Ordination does have a few problems in the detection of emergent vegetation patterns in the landscape. A major issue precluding its use in the search for a nested hierarchy is in the creation of the one dimensional spectra from the two dimensional Fourier transform. Couteron (2006) uses the notion of a radial spectrum, in which the spectra of all directions are averaged. Averaging all directions loses any directional information in the data and is mentioned as an area for future investigation.

Another problem with using textural ordination is that any information extracted cannot be related back to a GIS system, other than as a general pattern for the sampled area. Inverse Fourier transforms could possibly be used (see Sommerfeld et al., 2000) to depict areas of predetermined greyscale value in the image which will allow for spatially explicit data to be created. As much potential as textural ordination offers, it still suffers from assumptions of stationarity in the original Fourier transformation. Processes in a landscape are non-stationary and so inference about the reality of pattern extracted is not ecologically meaningful in terms of context specific pattern.

2.2.3.2.2. *Wavelet Analysis*
Wavelet transforms are similar to the Fourier transform but use functions parameterized by a scale factor rather than sine and cosine functions. Wavelet analysis can be used to find scale dependent regularities in data (Cho and Chon, 2006). Wavelet analysis offers distinct advantages over other methods when analysing non-stationary patterns (Keitt, 2000) as it preserves local information. Whereas the Fourier spectrum determines the magnitude of a certain frequency in the pattern, wavelet transforms decompose a pattern into a hierarchy of different scales of observation (Keitt, 2000). According to Chave and Levin (2003) "*…wavelet analysis is a very natural tool to detect spatial scales in an image …*".

A formal explanation of wavelet theory is inappropriate here. For a mathematical dissection of wavelet theory see (Cho and Chon, 2006). In brief, a wavelet is a mathematical function which oscillates around zero and is dilated by a scaling factor. The wavelet of known bandwidth is used as a filter across the dataset, which in simplistic terms gives a measure of how well the data correlate with the wavelet at that particular location and at that particular scale. The major wavelet function, known as the mother wavelet can take a number of forms, depending on the needs of the analysis. For example (Bradshaw and Spies, 1992) use the Mexican Hat wavelet to analyse tree canopies gap structure, while the Haar wavelet has been used to detect edges in natural images (Murwira and Skidmore, 2006).

Increasingly, wavelet transforms have become the preferred method to analyse pattern and scale in environmental data (Bradshaw and Spies, 1992, Dale and Mah, 1998, Csillag and Kabos, 2002, Rosenberg, 2004, Murwira and Skidmore, 2006, Cazelles et al., 2008). Yet wavelet analysis has, until recently, been mostly limited to one dimensional applications in the analysis of transect data. In landscape ecology wavelets have been used to analyse canopy gap structure (Bradshaw and Spies, 1992), soil variability (Lark and Webster, 1999), understory plant diversity (Brosofske et al., 1999, Chen et al., 1999, Perry et al., 2002, He et al., 2007), plant productivity (Csillag and Kabos, 2002), land cover (Dale and Mah, 1998) as well as to examine properties of neutral landscapes (Keitt, 2000).

2.2.3.3. **Object Based Image Analysis**
Pixel-based analysis deals with the three basic features of a single pixel, its position, its size and its value (De Kok et al., 2000). However, important semantic information necessary to interpret an image is not represented in single pixels but in meaningful image objects and

their mutual relations (Baatz and Schäpe, 1999). Pixels are simply the average spectral readings over a spatial area. These are often correlated with meaningful information; for example a green colour in a true colour image is likely to infer vegetation, but the pixel is itself not an ecological reality. This is the scale problem of the MAUP, in which the pixel scales are arbitrarily defined and are not ecologically meaningful entities. Up-scaling these can therefore create decreased confidence in the meaningful interpretation of the outputs.

A burgeoning field in landscape ecology is the use of image objects as an alternative to the traditional pixel based approaches (Baatz and Schäpe, 1999, Blaschke and Hay, 2001, Hay et al., 2001, Hay et al., 2003, Hay and Marceau, 2004). The concept is that instead of arbitrarily defined spatial units, the analysis is done on `basic entities'. For example, if we consider a tree-crown as a basic entity, it may be composed of, or is an aggregate of, leaves and branches, each of which individually belongs to classes which are themselves basic entities. In object based analysis image-objects rather than arbitrary spatial units are the basis for analysis and scaling. Image-objects are considered to be perceptual entities that visually represent objects in an image which is composed of similar digital numbers/grey-tones and which model realworld entities.

Such an object-based approach offers two main advantages. Object based analysis approaches reduce the effect of anisotropic data and avoid the MAUP. An additional advantage of the objectspecific approach is that it explicitly considers the hierarchical structure of the landscape by allowing the aggregation of smaller landscape components into the larger objects they are part of at their next scale of observation. In the method developed in Chapter Three of this thesis, I rely on an object-based approach.

2.2.4. *NEUTRAL LANDSCAPES IN LANDSCAPE ECOLOGY*

Hypothetical landscapes are often used as comparisons to infer process, or to test the effectiveness of landscape analysis techniques (Gardner and Urban, 2007, Hagen-Zanker and Lajoie, 2008). For instance, a hypothetical landscape (Figure 2.6A) has been used as a comparison against which we can infer process in a search for self-organization in a semi-arid savanna landscape (Scanlon et al., 2007). In another example, to test semi-variance analysis applications Meisel an Turner (1998) overlaid patches of different sizes (Figure 2.6B) to represent the effect of process at different scales.

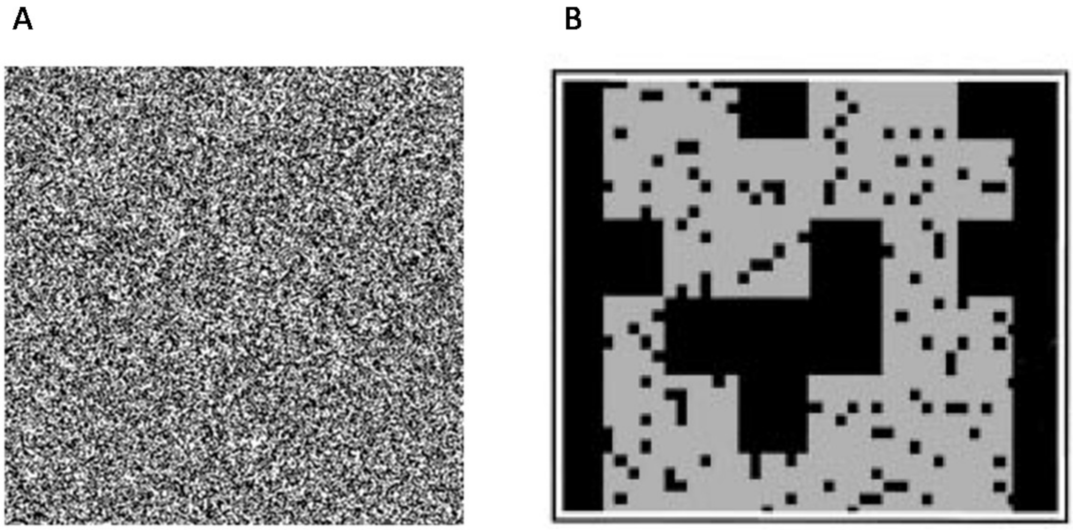

Figure 2.6: Two hypothetical landscapes that have been used in the validation of techniques used to detect multi-scaled structure in vegetation and subsequently infer process. Image A - a Global constraint image; randomly dispersed trees of a single pixel in extent and fifty percent cover. The only constraint on pattern is the global extent of the image, the image is analogous to that of Scanlon et al. (2007). Image B - Hierarchical landscape structure image created through the overlaying of 'Patches" of different sizes from Meisel and Turner (1998). These hypothetical landscapes were used as null models which have known pattern to allow for comparison to real world landscapes to allow for inference of process.

In this thesis I use images or hypothetical landscapes with known structure to both test methods and as neutral models to make inference of process. A neutral theory in ecology is regarded as a set of rules which apply to all agents equally; which allows the variation of random chance to be understood and factored out (Hubbell, 2001). Neutral theory is the attempt to understand the amount of pattern that can be generated at random, without needing to invoke the influence of process in one's argument. Deviations from predictions of a neutral model tell one where to look for the evidence of process (Hubbell, 2001). So, if the neutral model represents a process-free landscape and the real world data deviate from it, I can infer, given that all other statistical considerations are equal, it is due to the effects of process.

Neutral models are, in contrast mechanistic models which model a system from known relationships. Mechanistic models can be used to run scenarios of what would happen if particular drivers were made more or less influential, or removed completely, such as a model of climate limited vegetation distribution in the absence of fire (Bond et al., 2005). These models, as with the state and transition literature, are useful, but does not serve the purpose of this thesis, which is to detect hierarchically structured woody canopy cover in a landscape. I therefore do not discuss these mechanistic models in depth as I do not want to infer process *a priori*, but rather let the pattern emerge from the dataset.

Neutral landscapes have been utilized extensively in landscape analysis of various kinds. Generally, in the analysis of multi-scaled pattern, neutral models take the form of fractal landscapes. This is because fractal methods are based on the notion that the pattern varies with the scale of observation in a consistent manner. Deviations therefrom can be inferred to be evidence of a scale dependent process. For example, Milne (1992), used a fractal measure of patches to test the allometry of resource utilization by herbivores. By generating a fractal neutral landscape and comparing species resource utilization against the patterns, it was possible to distinguish between random associations and those affected by ecological constraints.

2.3. Objective 4: Synthesize the literature review into a proposed solution; build a conceptual framework and present testable hypotheses

In the previous two sections I have described why hierarchically nested structure is expected in a complex system such as a savanna ecosystem. I have described how vegetation pattern such as woody canopy cover can, and has been used to make inference about system properties. I have subsequently reviewed the methods available to measure these structures and illustrated a number of statistical problems which precludes the use of them as objective tests for the presence or absence of hierarchical structure in woody canopy cover.

In this section I synthesize all these seemingly disparate bits and pieces of information into a method to test the theory. Firstly, I discuss the concept of scale as a dimension in which one would test for patches in scale no differently to testing for patches in space. I then describe a method that can be used to do this, while allowing for the context specific nature for the pattern to be assessed by retaining local information.

I have articulated how fundamental units are the product of positive feedback loops and this occurs in space, time and scale. If fundamental units are patches, it is easy enough to analyze for patches in space, but how does one analyze for fundamental units in scale? Here I take the reader through the logic of using linear scale space to delineate patchiness in scale, no differently to how it would be done in space. In order to do this one must represent scale as a dimension.

2.3.1. *REPRESENTING SCALE AS A DIMENSION*

Visualize a hypothetical graph: the axes of the graph describe the relative strength of coupling in space versus relative strength of coupling in scale (Figure 2.7). If process and pattern are not interdependent, random pattern is expected (Figure 2.7a). In this instance stochastic models would describe the system better. If feedback loops form in a landscape, patches will occur as fundamental units and lacking any scale-related entrainment, scale invariant patterns will occur (Figure 2.7b). If feedback loops persist in the scale dimension, either through entrainment of processes or through process-pattern feedback, multi-scaled discontinuous structure in the scale dimension of the system will evolve (Figure 2.7c).

I propose that investigating the strength of coupling between pattern and processes in the system can explain much of the pattern we see in landscapes.

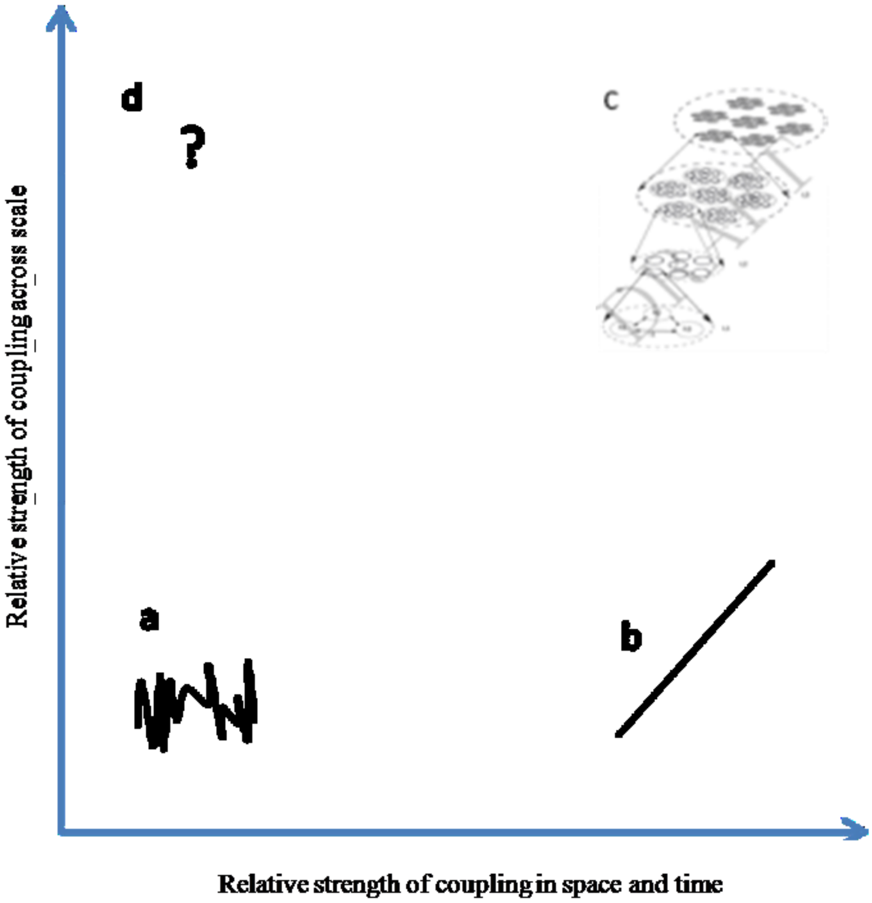

Figure 2.7: The conceptual framework of patterns generated by different amounts of coupling between processes. No persistent interaction in space or time results in random patterns (a); Coupling in space and time, without coupling across the scales investigated results in power law distributions as lower scale interactions' determine the cross-scale patterns (b); Coupling across scale-space and time results in hierarchically nested structures (c); So far it is not clear what will happen if there is coupling across scale and not space (d) In all likelihood it will simply be a random pattern within bounds.

The common thread that ties these terms together is the positive feedback, which I argue can generate the patchiness in scale that is necessary to generate discontinuous pattern. To explain the effect of a positive feedback loop in the dimension of scale I use the vehicle of "ecological memory" (Peterson, 2002, Peterson, 2008). The concept of ecological memory suggests that entrainment of pattern and process needs to occur for self-organization to take place. Entrainment is the co-dependency between pattern and process. The amount of entrainment can vary, but it has been shown that there needs to be a minimum amount of coupling between the pattern and the processes for the pattern to persist (Peterson, 2002) .

Just as there is a need for positive feedback loops to create patches in space, feedbacks between interactions between processes and between patterns and processes will affect the distribution of pattern across the dimension of scale. Put simply, I advocate that there can be patches in scale, in the same way there are patches in space. In some cases the distinctions of pattern among scales need not be sharp but may represent a continuous gradation across many orders of magnitude (Chave and Levin, 2003). But, if the pattern and process relationship has a scale component, discontinuities are likely to occur.

The following descriptive model is based on an ecological memory model that uses a contagious disturbance such as fire spread (Peterson, 2002). I use this model as an example to show how the strength of interactions between pattern and process influence the persistence of a pattern in space and time. I then expand upon this model to illustrate how the same can be said about the generation of patchiness in scale.

I generate a vector representing scale; $S=\{S_i \ldots S_N\}$.

Each element of the vector follows the form of:

$$Pr(\text{Fire Spread}|TSF)=(1+Pmax)(TSF/TPmax)^{\alpha}-1,\ TSF<TPmax$$

and

$$Pr(\text{FireSpread}|TSF)=Pmax,\ TSF>TPmax.$$

And the model iterates through time $t=\{1...5000\}$.

The model contains an entrainment function which is a distribution which affects the independence of the pattern and process across scale. Disturbances are introduced (ignitions, considering it is a fire model) when the time since fire (TSF) has reached an arbitrary threshold (TPmax). This would correspond to sufficient biomass of woody material.

For each value of $S=1\ldots N$:

$$Pr(\text{disturbance}|TPmax)=1,\ TSFs\geq TPmax$$

$$Pr(\text{disturbance}|TPmax)=0;\ TSF<TPmax$$

However, the scale at which the disturbance happens, S_d is randomly sampled from a normal distribution with the mean of all scales (S), For P(disturbance|TPmax=1)

S_d~dnorm(S,β),

Where; β is an indicator of the strength of the entrainment between scales.

Sampling from a normal distribution implies that there is a higher likelihood that processes will be affected at scales near to scales that have already had processes affecting them, and the variance of this distribution is a measure of how tightly entrained the processes will be. If there is a large β value this indicates a lack of any interaction between pattern and process at scale and the entire dimension of scale is independent.

I developed this model to describe the concept of entrainment of pattern and process in time and in scale, not to calibrate and test it. If there is tight entrainment, there is consistent pattern; when the entrainment breaks down, the consistency of pattern is more stochastic in time and in scale.

In Figure 2.8, at t=0, all of the scales of pattern are the same, randomly through time, patterns entrain one another and a relatively consistent set of patterns percolates through time, occasionally capturing another set of pattern and process, should they start to be found at the same scale. Whether or not this happens in reality is immaterial at the moment, the model is simply for the sake of explanation. Should the amount of variance break down (the image on the right) and there is a decrease in the amount of dependency between pattern and process, the individual patterns become much more stochastic in their behavior. Even more loss of entrainment results in almost random cross scale pattern, which is unstable through time (Figure 2.5).

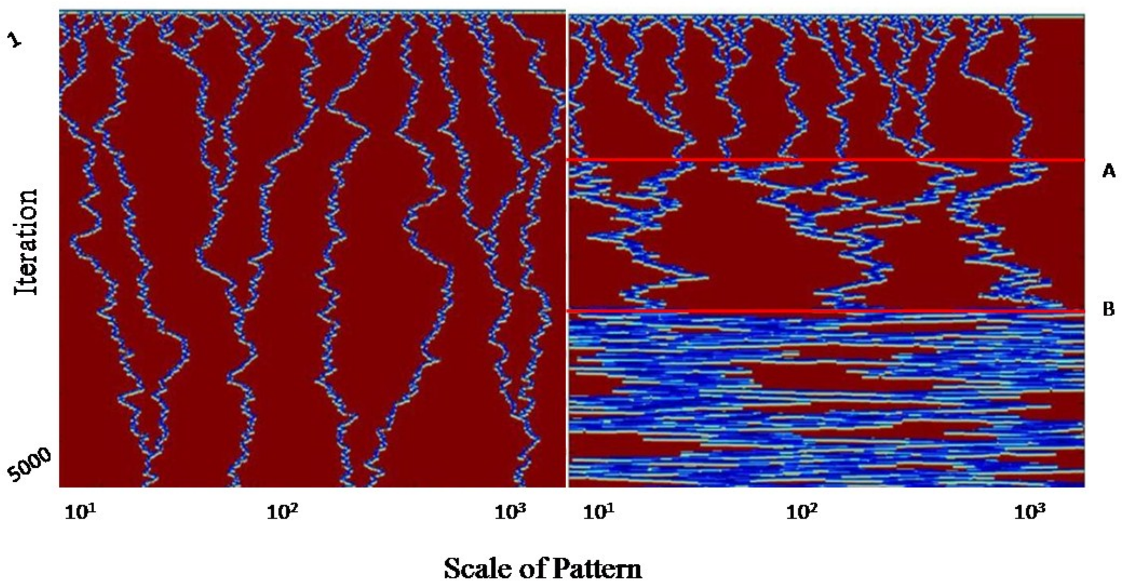

Figure 2.8: An entrainment model to explain the development of discontinuous cross-scale morphology through time. In both images; at t=0 (top of y axis), all scales have the same pattern. Through time, through entrainment of pattern and process, there develop process domains across scale. Entrainment is important in the consistency of pattern through time. Should there be a sudden change in the amount of entrainment in the system (Image on the left, t=1500, A or t=3000, B), there would be a change in the cross scale dynamics of the system, the cross scale morphology changes and pattern would become more stochastic over time.

The purpose of this model is to demonstrate how entrainment can affect the cross scale morphology of a system. Just as entrainment of pattern and process through time, termed *ecological memory* is necessary for patch structure to form and persist in space. Entrainment between pattern and process in scale is necessary for patchy structure in scale to persist. I advocate that this is the reason that systems generate what we term *holons* or *process domains.* This is why scale is represented as a dimension and linear scale-spaces are generated and this is why it is valid to look for patches in space and infer the entrainment of pattern and process in the dimension of scale.

The implication of viewing scale as a dimension is that one explicitly realizes that scale is not an absolute. A twenty square metre sample may not be equivalent to a twenty square metre sample on another hill slope, or in another landscape. Suites of processes are not necessarily equivalent across equal spatial extents in the landscape. Corroborating evidence lies in the recent recognition of the importance of context in landscape analysis (Levick, 2008). In much of landscape ecology the scales of observation selected in most scale explicit analyses are generally arbitrary (Wheatley and Johnson, 2009). By recognizing scale as a dimension across which processes are dynamic, it becomes explicit that the researcher needs to compare fundamental units of complex systems rather than simply compare similar spatial extents.

I am well aware that there needs to be empirical data to back up this assertion- this will hopefully come in time with further exploration and analysis. However, the idea is not without precedent; for instance, it has been said that if scale is used as an independent variable, scale may provide a surrogate for constraints that modulate ecological processes at specific levels of organization (Allen and Starr, 1982). Moreover, it is already advocated that to avoid the MAUP, investigators describe the fluctuations of spatial statistics across scale (Marceau and Hay, 1999) , which can only be done if analysed as a dimension. Visualizing scale as a dimension is conceptually simple, but transferring the philosophical argument into a practical experiment or statistical analysis requires the development of new tools in landscape ecology.

2.3.2. *Investigating scale as a dimension*

Pattern in a landscape can be considered as a snapshot in time, a result of the net effect of processes in the landscape. If the property of the system to be measured is adequately assigned and reflects the net effect of processes acting upon it, the multi-scaled patchy nature of the proxy will give evidence into the multi-scaled nature of process in the landscape. I propose to use vegetation distributions in a semi-arid savanna landscape as a measure of the result of certain system processes. Vegetation has been used to infer evidence of feedback loops in many systems (Rietkerk et al., 2002, Kéfi et al., 2007a, Scanlon et al., 2007) and provides easily measurable patterns across multiple scales in the landscape.

The method to do so at multiple scales while remaining spatially explicit is however another matter entirely. It may seem that if the assumptions of stationarity, ecologically relevant *a priori* scale selection, anisotropy are met or understood and the MAUP is avoided, the results from a landscape statistical analysis can remain valid. A philosophical circularity arises in that assumptions are based on *a priori* understanding of process in the landscape but there is not enough information available to say whether or not they are met. So in fact one sets out to test for pattern with the knowledge that the pattern will in fact be there.

What happens when there is no knowledge? This problem is paralleled in the disciplines of image analysis, where object detection is needed but *a priori* information about size, shape and context of the object are not. In processing an image dataset for which no *a priori* information is available the first stage of the processes should be as uncommitted as possible (Lindeberg, 1994, Lindeberg et al., 1994). An uncommitted analysis assumes no prior knowledge and no preference for how to analyze a signal (Florack et al., 1994). The researcher makes no assumptions and the pattern emerges out of the data. I advocate that if pattern and process are to be adequately linked in a heterogeneous environment, the structure must be allowed to emerge out of the data (Pickett et al., 1989), rather than be inferred by the user through assumptions made in the techniques used. Therefore if vegetation distribution is a reflection of landscape processes, a technique is required that objectively delineates the scaled hierarchy of vegetation distribution pattern, yet remains spatially explicit.

2.3.3. *PHILOSOPHY OF UNCOMMITTED ANALYSIS FRAMEWORKS*

In the synthesis of previously used methods I have expanded upon the assumptions that make the use of the many methods invalid in an objective search for the presence of a nested hierarchy. Prior knowledge, which allows for valid assumptions to be made, is not always available regarding the dataset to be analysed, so how does one assign a filter to detect the data structure?

In image processing and computer vision theory, when no *a priori* information is available, the first stages of visual processes should be as uncommitted as possible and have no particular bias (Lindeberg, 1994). The term "uncommitted framework" refers to observations made by a front-end vision system (i.e. an initial-stage measuring device) such as the retina or a camera that involves no knowledge or preference for anything (Hay et al., 2002). Not-committed frameworks are not novel; "Deep Structure" was a phrase first coined by (Koenderink, 1984) and refers to the analysis of an image at all scales simultaneously. The underlying principle is that data structure emerges rather than being inferred by the observer. Deep structure analysis was inspired by the fact that human recognition uses a similar technique when viewing a world scene (Lindeberg, 1994). The analysis of the deep structure of images by investigating a multi-scale image representation has become a valuable tool for feature detection and extraction in images (Klein and Ertl, 2005). Applications involving the use of scale-space and deep structure analysis range as widely as the imaging of CAT scans to search for anomalous growth patterns (Cachia et al., 2003, Coulon et al., 2000), to matching separate images containing the same scenes (Brown et al., 2005, Dufournaud et al., 2000, Rath and Manmatha, 2003). In recent years, ecologically focussed techniques are being developed (Hay et al., 2001, Hay et al., 2002, Castilla et al., 2008).

To measure the distribution I use linear scale-space; a form of "deep structure analysis". (Koenderink, 1984) which involves the analysis of all scales simultaneously, with no *a priori* assumptions about the scale of structure within data (Lindeberg, 1994, Lindeberg et al., 1994). A method proposed for use on complex landscape images is "linear scale-space" (Hay et al., 2002). Theoretically sound and mathematically rigorous, the highly mathematical nature of linear scale-space theory has precluded its use in the broader ecological community (Hay et al., 2002), of which an application for complex systems analysis in a semi-arid savanna landscape has been developed. Linear scale-space assumes no prior knowledge and no preference for how to analyze a signal (Florack et al., 1994), allowing emergent properties in the data to be delineated.

If the component of the system serving as a proxy is assigned correctly and its distribution across the scale dimension is a reflection of process, then I hypothesize that a linear scale-space representation can provide a means to objectively delineate woody vegetation structure in space and scale. By setting up experiments to change the configurations of the feedback loops in the landscape, it is possible to then test the effect of known perturbation of the fundamental units within a complex system.

What governs the dynamics of pattern and process in the "ecological theatre" (Hutchinson, 1965) remains a core question in ecology. Ecological processes occur over various scales of space and time (Wiens, 1989). "Pattern - be it spatial or temporal- is inseparable from scale. The challenge is to find these scales and properly link processes and pattern" (Reynolds and Wu, 1999 pg. 289).The use of linear scale-space should provide a mechanism to meet such a challenge in the face of ecological context (viz. Levick and Rogers, 2011). Given this mechanism, hopefully I will be able to provide insight into the question of "Does the landscape provide a discontinuous distribution of structure that is the theatre on which species interact?" (Allen, 2006, pg. 6084).

If it does, and we can measure it without violating ecological reality with our assumptions, then we are one step closer to finding spatially explicit predictive systems models.

2.3.4. *USING LINEAR SCALE SPACE TO MEASURE SPATIALLY EXPLICIT MULTI-SCALED STRUCTURE*

I present linear scale theory and methods in detail in the following chapter; in which I take the reader through the logic behind my method. A linear scale space generates a dataset that tracks the evolution of image structure across scales in a spatially explicit manner. For instance when viewing Figure 2.1, I am interested about what range patches are red, blue or green. A scale space will track the evolution of the woody vegetation cover through the dimension of scale and merge events and indicate the points in space and scale where the change occurs.

The logic for the use of merge events is as follows: By definition a patch of trees comprised of patches of trees at smaller scales of analysis. Merge events indicate the scale and spatial location where image structure (limited to woody tree cover in this thesis) merges together to become a larger patch. The principle of causality means that the larger scale patches can only be generated through the merging of patches at smaller scales, or according to the reviewer the creation at higher scales, but these are ignores as they have little ecological meaning in the test for hierarchical structure. Therefore the analytical technique follows the philosophical framework which is being tested without user bias regarding where the patches are generated. The objectivity in the delineation if patches and merging of patches together at higher scales is the reason linear scale space is used. Hierarchical structure is being tested for and therefore the merge event becomes the event of choice.

Assuming that the link between woody vegetation cover at different scales and differing process suites can be made, the merge events dictate the shift between process domains. In a stylized view of linear scale spaces of what would be woody canopy cover, I depict a hypothetical linear scale-space with three sets of hierarchically structured processes all created through different processes; Figure 2.9. By using a linear scale space in this manner, it becomes possible to trace which patches of woody cover merge to form larger patches, at what scales this occurs and where in the landscape this occurs. The merging of small patches of woody cover, synonymous with fundamental units, into larger patches can then be analyzed in a spatially explicit way and the spatial and scalar distribution of process debated. If landscape processes corresponded to a single domain, one would expect that a shift would occur at similar scales; however we know that processes across the landscape are likely to vary.

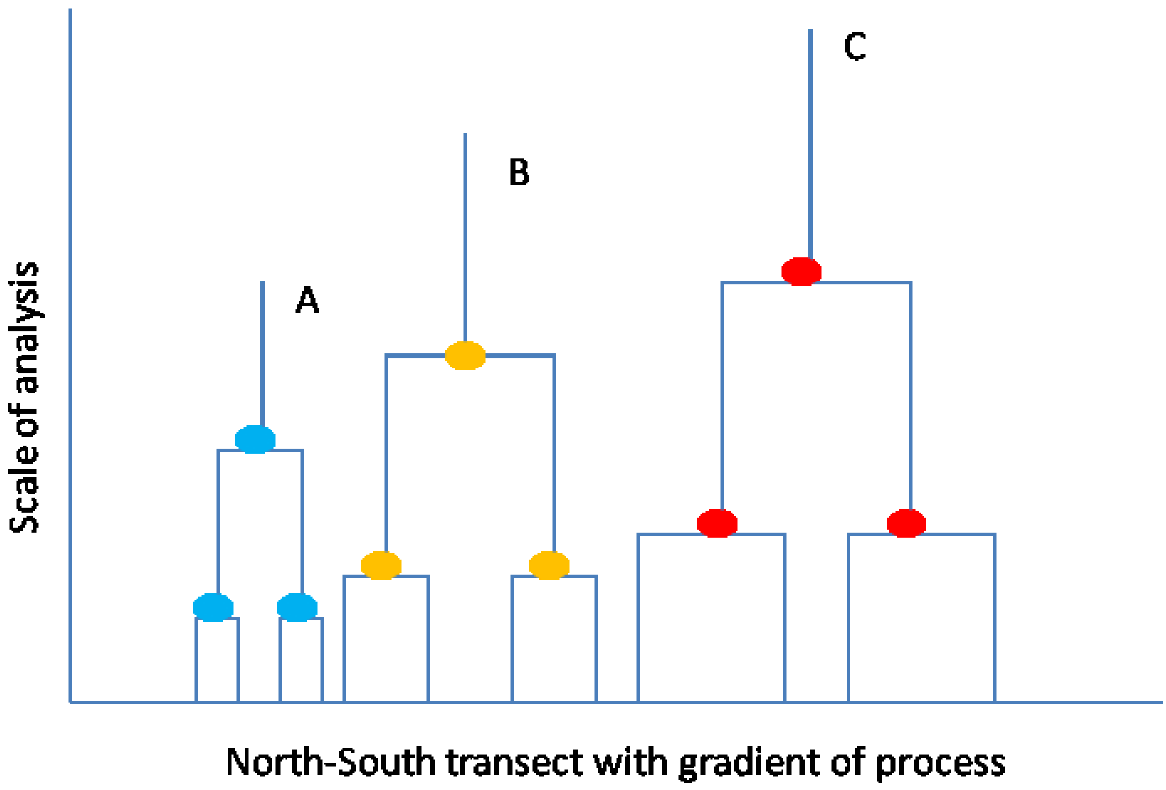

Figure 2.9: A stylized profile view of what a linear scale space would look like and how the scale at which patches of vegetation merge into other patches can be measured. A, B and C can be generated by different process suites and due to the local nature of the analysis, this information is retained.

I use linear scale-space as opposed to the other previously reviewed methods because processes vary across space and the context of vegetation distribution has been shown to be highly important in the linking of pattern, process and scale (Levick and Rogers, 2008, Levick and Rogers, 2011). Non-stationary comparisons are therefore needed to further understand the cross-scale morphology of the landscape. In Figure 2.9; if the distribution of vegetation patches in a landscape are context dependent, a nested hierarchy at an arbitrary location A in a landscape may not be created by the same process suite at the same scales as location B. Therefore there will not be hierarchical pattern evident at the same scales in a comparison between A and B. For instance A may correspond to the hilltop, B to the mid-slope and C to the valley bottom (viz. Levick and Rogers, 2011).

When the scales at which these merge events are represented on the scale axis (Figure 2.10), the merge events from individual primal sketches may be of discontinuous distribution, but the scales are overlapping and the integration of the entire dataset will result in a misleading signal. This mirrors the classic problem of Simpsons Paradox, in which grouped data can have different trends to the groups themselves (Simpson, 1951).This does not necessarily constitute evidence that there is a lack of hierarchically structured data, but rather the effect of context dependent process.

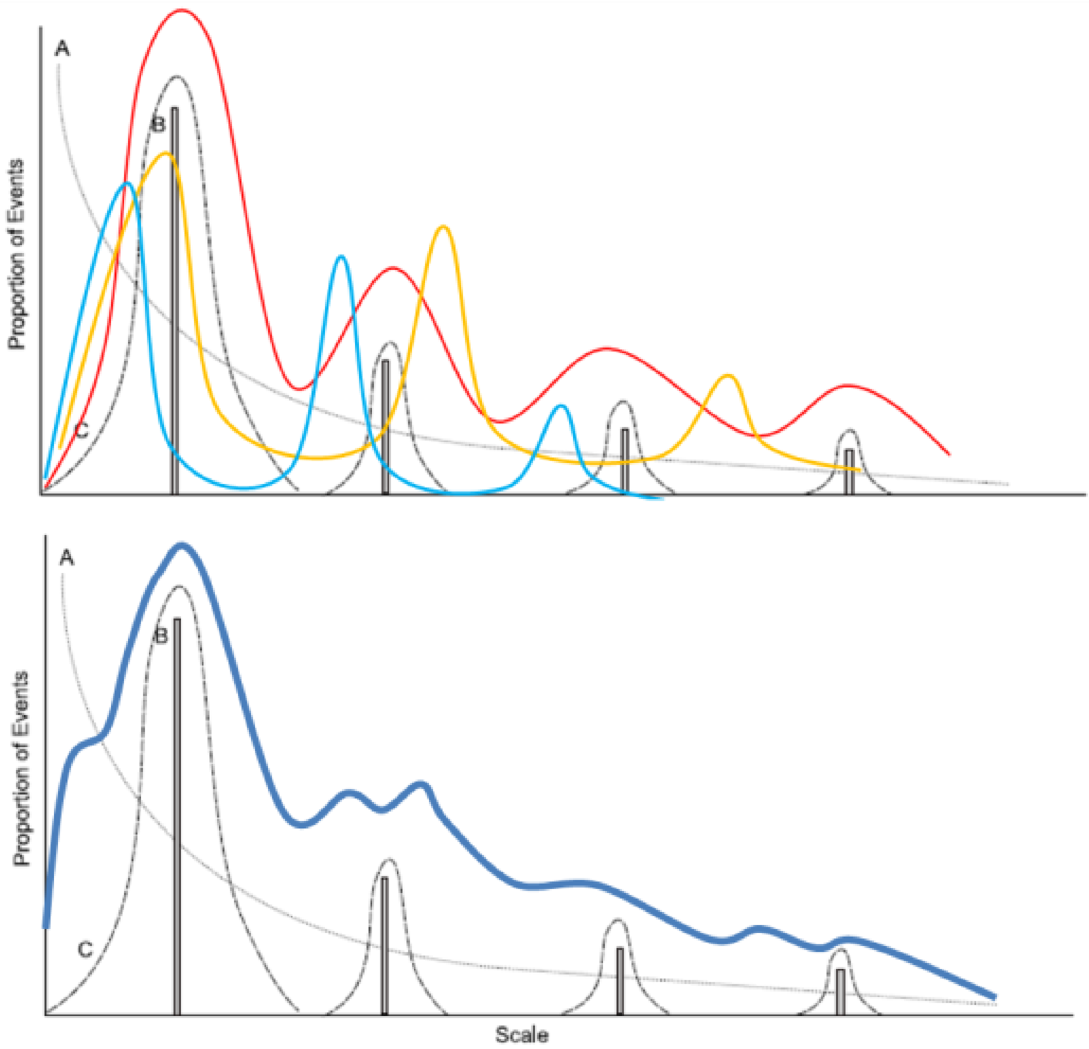

Figure 2.10. Individual nested hierarchies may be nested and projected on the scale axes (above). When overlaid and integrated (below), the merge event distributions' results can be a misleading distribution (below). This is a classic problem of Simpson's Paradox, in which dissection of a dataset can result in different trends. A local analysis approach is needed.

It is for this very reason that I utilize a linear scale space and as I will articulate in a later stage, use a spatially discontinuous discontinuity analysis that compares each of these primal sketches to a neutral model. In doing so, I circumvent issues of context dependent pattern and process and make inference around the nature of the pattern in that primal sketch.

A linear scale-space representation is purely a representation and makes no inference regarding process in the landscape. To make inference regarding process a comparison to a linear scale-space influenced by known process is needed. So, before inference about the nature of multi-scaled process can be made, a set of well validated neutral models are needed. The patterns of linear scale-space events found in linear scale-spaces derived from semi-arid savanna systems can be compared to those of the null model and the effect of process then inferred.

2.3.5. *TESTABLE HYPOTHESIS FOR CROSS-SCALE PATTERN IN LANDSCAPES*

Conceptualize a gradient between two end points; on one end there is a completely neutral landscape and pattern is completely random. On the other end of the gradient is a completely deterministic landscape, where the pattern is tightly constrained in space and in scale (Figure 2.11, cross scale morphology indicated by Block 1, landscape images in Block 2). In a neutral landscape, it can be expected that the shape of the distribution of merge events measured across the dimension of scale will be described by a function of space versus scale of observation. There are simply less large independent observations to be made relative to small observations in any given area.

The distribution of merge events will follow a form similar to $f(m) \sim (scale)^{-\gamma}$, where γ is a real number describing the shape of the curve (Figure 2.11 block 1, image A). On the other end of the gradient is a completely coupled pattern-process relationship in which the scale at which pattern is expressed at a few discrete scales (Figure 2.11 block 1, image B). This would be the case if there was some hypothetical driver that influenced process exactly and this process directly affected the spatio-temporal scale of the driver in return. In a landscape the transition is unlikely to be over a single unit of scale, but will rather be confined to a range. I hypothesize that a pattern of this nature will result in a multimodal distribution of merge events, when viewed across scales of analysis (Figure 2.11 block 1, image C).

When represented spatially (Figure 2.11, block 2), the end points are easily created; neutral landscapes are composed of randomly distributed vegetation (Figure 2.11, block 2, image A) and landscapes with strict coupling of pattern and process will have a perfect set type distribution of pattern (Figure 2.11, block 2, image B). The images representing multimodal distributions are somewhat more complex to develop; I depict an example here for the sake of completeness (Figure 2.11, block 2, image C), but the method used to generate these images is explained in the methods section.

Where does a real world savanna landscape fit in? (Figure 2.11, block 3). A multi-modal distribution is evidence of lumpy cross-scale morphology and is what I expect from a scale break due to discontinuous woody vegetation structure. It is important to remember that there may not necessarily be hierarchical structure in the entire landscape at the same time.

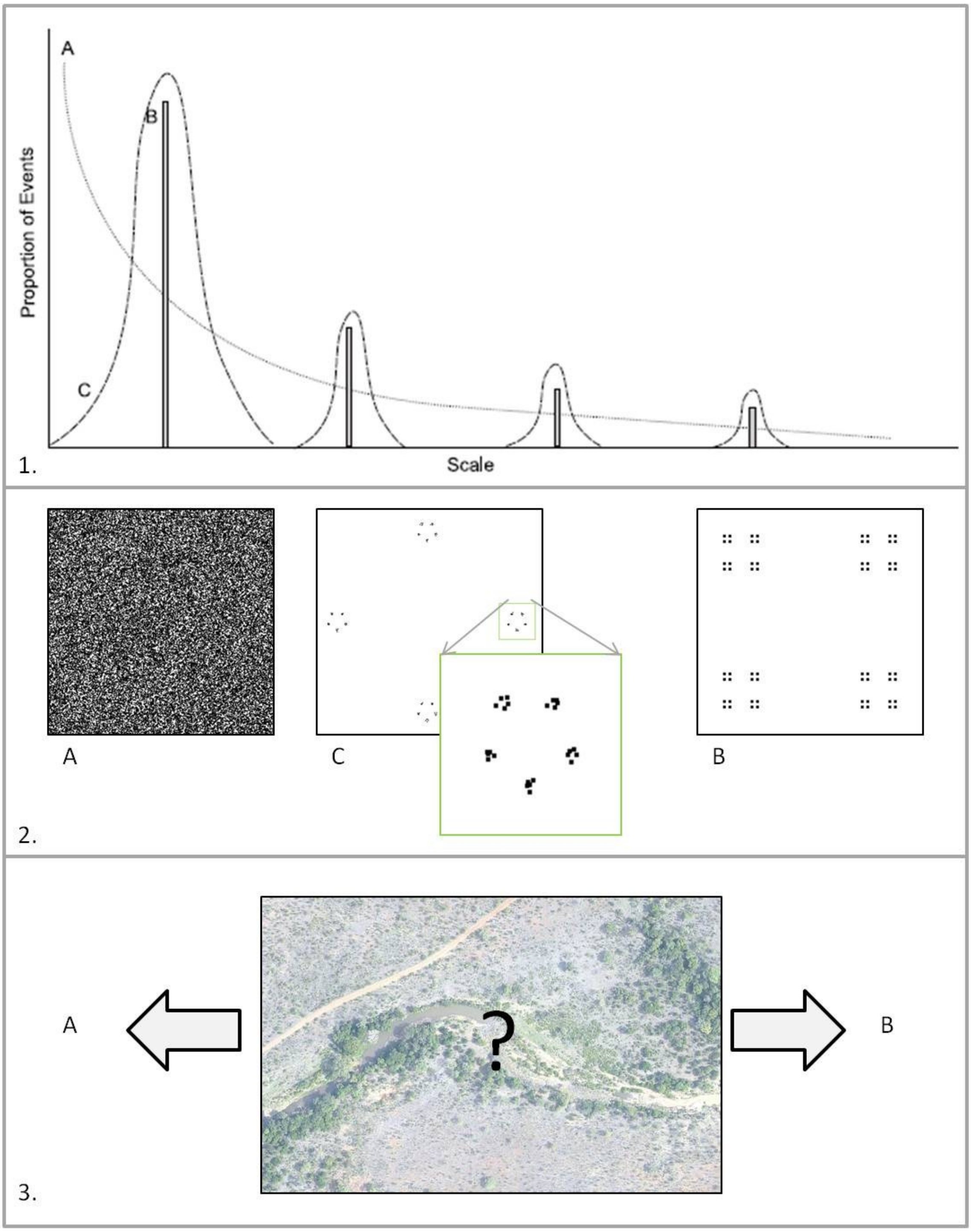

Figure 2.11: The cross-scaled architecture of three hypothetical landscapes (Block 1). A neutral landscape, which is constrained by the extent of the image (Block 2, image A) is an example of a neutral landscape against which the semi-arid savanna landscape is compared, to infer the effects of process. On the other side of the gradient is a perfect set (Block 2, image B), representing perfect coupling of processes in space, which creates a perfectly nested set of patches. A multi-modal distribution of merge events which occur in ranges of scale (Block 2, image C) are more likely to be

what would be found in a landscape, but it is unknown where a savanna landscape would be situated along this hypothetical gradient (Block 3).

I have reviewed the literature, generated an argument for the use of woody canopy cover as a proxy for system process and derived the use of linear scale space as the tool to do this. I have then presented a testable hypothesis for the detection of multi-scaled structure in woody canopy cover in a semi-arid savanna landscape. In the following chapter I outline the methods and how I aim to achieve this.

Chapter 3 ANALYSIS OF AND TEST FOR NESTED HIERARCHICAL STRUCTURE IN A SEMI-ARID SAVANNA

The premise of this thesis is that patterns in complex systems are a reflection of the configuration of processes that create them (Ulanowics 2008). Feedback loops between pattern and process and interdependencies of processes result in regions of a system which are more tightly coupled to one another than to the surrounding matrix, representing the fundamental units of the complex system (Reynolds and Wu, 1999). In the spatial and temporal dimensions of a landscape, some of these fundamental units are reflected as patches (Blaschke et al., 2002) and the hierarchical structure conceptualized in the Hierarchical Patch Dynamics Paradigm (HPDP) (Wu and Loucks, 1995). It should therefore be possible to detect hierarchically nested structure of vegetation in the landscape, if HPDP can be reified.

Savanna landscapes and the interactions which affect vegetation distribution and persistence provide an avenue for research into system level properties and this has been used in a number of studies. Different processes dominate at different scales (Wiens, 1989); process and pattern interact across scales and there is interdependence between processes at multiple scales (Holling, 1992, Allen, 2006). I propose that by investigating the hierarchically structured nature of a landscape it should be possible to attribute process to the pattern observed (if it is in fact there at all) and subsequently test the validity of the conceptual framework to develop spatially explicit predictive models.

The Hierarchical Patch Dynamics Paradigm makes scale an explicit consideration in landscape analysis; however, in practice, scale selection in landscape analysis is generally arbitrary (Wheatley and Johnson, 2009), possibly because to-date landscape ecology has lacked an adequate method to measure ecologically meaningful pattern at multiple scales in the landscape.

The search for multi-scaled structure in image is a possible avenue for addressing this problem; a technique or framework to explore and quantify complex landscape structures at multiple scales should:

- Generate a multi-scale representation of a scene from a single scale of fine resolution, remotely sensed, data;
- Exhibit hierarchical (i.e. multi-scale) processing and evaluation capabilities;

- Be spatially tractable through all scales, meaning that local information cannot be averaged and/or integrated into global information as it precludes the re-projection of the information back onto the landscape;
- Be mathematically sound and computationally feasible;
- Be capable of automatically defining dominant multi-scale patterns within the scene which are not biased by class definitional constraints; this will allow for scaling between defined patterns;
- Produce results that are spatially explicit and ecologically meaningful.

The above points adapted from (Hay et al., 2002)

One such method is linear scale-space and, although well accepted in the image processing and engineering disciplines, linear scale-space analysis as a method to analyze multi-scaled landscape structure is still in its infancy. There is no simple off the shelf linear scale-space application, particular with regard to analyzing multi-scaled vegetation patterns. In this chapter, I outline the method used to generate a linear scale-space representation of vegetation in the landscape which tracks the development of patchiness across scale, without invoking the ecologically invalid assumptions and statistical artifacts of other analyses.

The spatially explicit nature of this technique allows the scaled pattern to be projected back onto the landscape images and correlated with known distributions of drivers, hill slope units or experimental plots. For instance, I can now test if Hierarchical Patch Dynamics is an ontological characteristic of the landscape or simply a conceptual framework for savanna scientists. It should also be possible to dissect a landscape into regions of context specific pattern. To do so I can use the distribution of merge events in a linear scale-space to determine if in fact the vegetation in the landscape forms discrete process domains which correlate with known driver regimes, or if the patterns are inferred by the observer.

3.1. Outline of the methods

To test for hierarchically nested vegetation structure in a semi-arid savanna system:

Binary images depicting woody tree cover were generated for 8 x 800 m x 800 m, study plots from 2001 imagery of the 'Nwashitsumbe enclosure sites, (four inside and four outside the enclosures). Linear scale-space analysis was used to generate a three dimensional representation of the evolution of pattern through the scale dimension (as defined by increasing bandwidth of the Gaussian filter). I utilized merge events, the point at which pattern at smaller scales merges into pattern at larger scales, as the primary variable for further analysis. The distribution of merge events across scales was compared against treatments of fire, browsers and no browsers and the control sites with both fire and browsers. Furthermore the samples were compared to neutral landscapes which served as proxies for landscapes with no process. If, therefore, the distribution of the real world landscapes differs from that of the neutral landscapes it can be considered as evidence of process or no process at the scale considered.

Comparisons between the real world samples and between the real world landscapes and the neutral landscapes were made in two ways: firstly, the distribution of merge events was compared as a whole sample. Secondly, to avoid assumptions of stationarity and to implicitly test each and every part of the hierarchical structure, the individual patches and scales at which the lower scale pattern merges into larger pattern were tested against those of the neutral landscapes in a non-stationary manner.

The linear scale-space application I develop in this chapter is different from traditional linear scale-space analysis and written specifically for this thesis. It needs to be validated, any errors quantified and rectified and the patterns from datasets with known scales of pattern expression used to ensure that the technique can in fact extract hierarchically structured data. This validation is the first process to be undergone, before analyses are undertaken on real world samples.

3.2. CHAPTER STRUCTURE:

This chapter is divided into four broad objectives, within each of which is nested a number of sub-objectives:

1. *Objective 1: Generation of baseline landscape datasets.*

Objective 1 focuses on the generation of the datasets, both hypothetical and real world, upon which the analysis presented in the rest of the chapter is based. There are three sub-objectives; namely the:

   1.1. Generation of hypothetical landscapes with known cross scale structure;
   1.2. Generation of neutral landscapes;
   1.3. Extraction of tree canopy cover from aerial photographs.

2. *Objective 2: Linear scale-space generation*.

   Objective 2 is focused on presenting the method used to generate linear scale-space representations of the datasets set out by objective 1.

3. *Objective 3: To demonstrate outputs of the linear scale-space application and to validate the linear scale-space application for repeatability of the algorithm and in detecting the scale of pattern expression.*
   Objective 3 focuses on demonstrating that the linear scale-space application works and is effective in detecting pattern that would be expected in a hierarchically structured landscape.

4. *Objective 4: Can evidence of process be detected in the 'Nwashitsumbe landscape?*
   Objective 4 is the culmination of the thesis, in that I use the theory and methods developed up until this point to test whether or not complex systems pattern, expressed as hierarchically nested structure, can be detected in the woody canopy cover distribution in the 'Nwashitsumbe semi-arid savanna landscape.

3.3. METHODS

The chapter is divided into four objectives, each of which has its own sub-objectives and methods associated with it. A general outline is given in Figure 3.1, nested within this are flowcharts for Objectives 2-4,(Figure 3.4, Figure 3.11 and Figure 3.15 respectively) which outline the specifics.

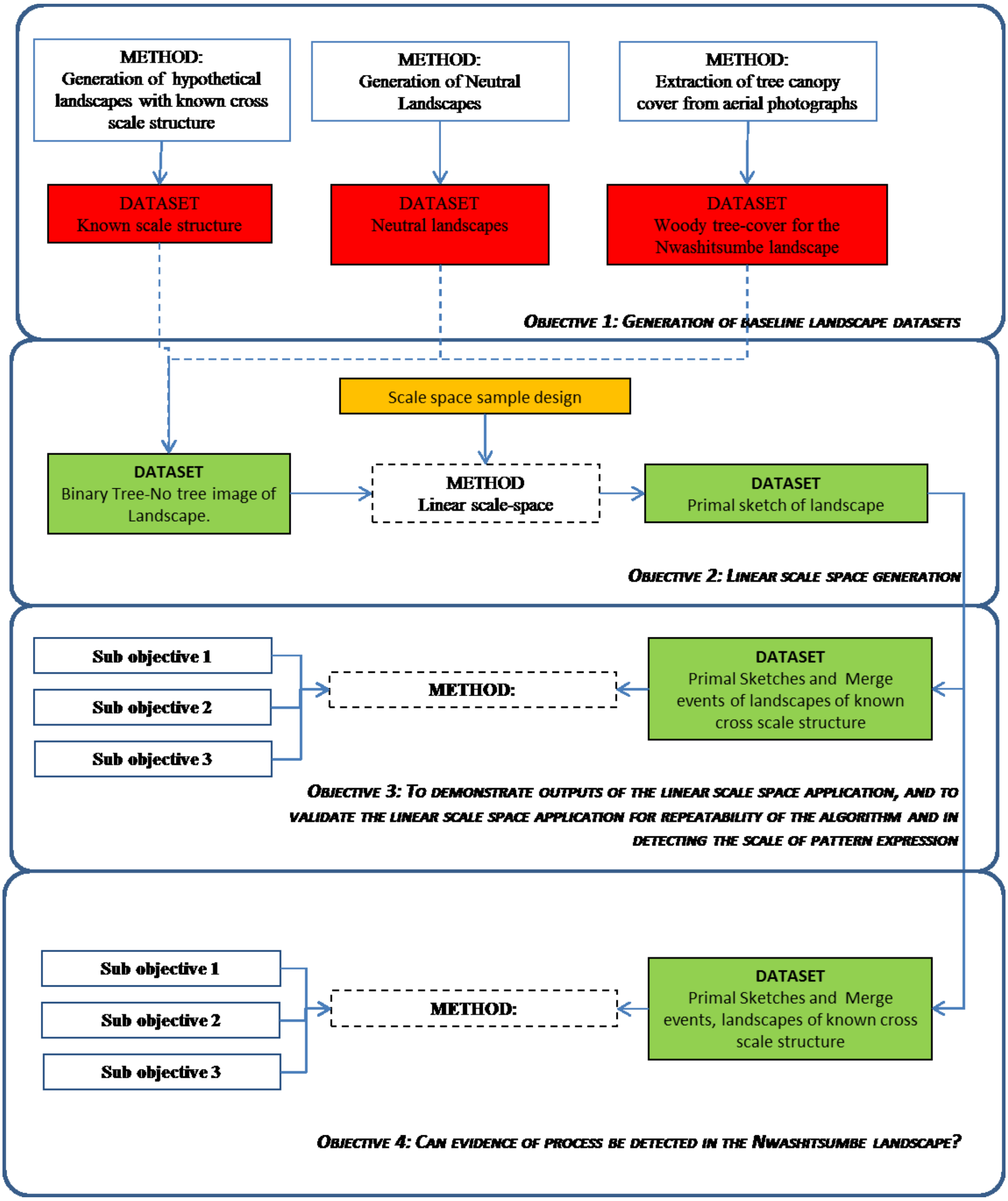

Figure 3.1. A flow chart outlining the methods used in this thesis. Each objective has a separate flow diagram outlining the specific methods used to reach the objectives.

3.3.1. *OBJECTIVE 1: GENERATION OF BASELINE LANDSCAPE DATASETS*

Baseline datasets were used to validate methods or as neutral models to infer process; three types of baseline datasets are generated for use in this thesis.

1. *Datasets with known cross-scale morphology*. These datasets were used late in the validation of the method and the application to illustrate that the method does in fact pick up multi-scaled pattern when expected. The datasets with known cross scale morphology are divided into three categories:
   a) *Random Landscapes* - these landscapes represent an ecologically "process-free" landscape in terms of vegetation distribution. They were used to analyze how parameters of the landscape such as tree size, density and image size affect the output in the validation of the process.
   b) Landscapes with *discrete cross scale-morphology* - these hypothetical landscapes represent a perfectly nested structure.
   c) Landscapes with *multi-modal cross-scale morphology* - hypothetical landscapes which are not perfectly nested were used to test how hierarchically nested structure at various scales will affect the cross-scale morphology of merge events of the primal sketch.
2. *Extraction of tree canopy cover from aerial photographs* - this section defines how the baseline data for the 'Nwashitsumbe enclosures was extracted from the aerial imagery to generate binary images which were used to generate scale-space representations for multi-scaled analysis.
3. *Generation of neutral models*- neutral models were generated to represent the 'Nwashtsumbe landscapes in which the effect of process has been removed.

3.3.1.1. **Datasets with known cross scale morphology**

All landscapes are binary, with trees valued as zero and the matrix as 1.

3.3.1.1.1. *Random landscapes*

Sixty eight hypothetical, neutral landscapes were generated with varying parameters of tree size, tree density and image size, with varying numbers of replicates (Table 3). The number of replicates was chosen based on the comparisons made in later sections. To generate a random landscape, the image size, the percentage canopy cover and tree size are defined. A uniform distribution was resampled to generate the X and Y locations in the image where the canopy cover is evident.

Table 3: Eleven neutral landscapes: Parameters of tree size, percentage woody cover and image size vary, with up to ten replicates per hypothetical landscape resulting in fifty eight individual landscape images which were analyzed. The merge events from the replicates are compared in various configurations to achieve objective 1.

neutral landscape	tree size (pixels)	percentage cover	image size (pixels)	number of replicates
a	10	25	500	5
b	10	50	500	5
c	10	75	500	5
d	20	50	500	5
e	5	50	250	10
f	5	15	800	10
g	5	25	500	10
h	1	25	500	1
i	1	50	500	1
j	1	50	300	1
k	5	50	500	5

3.3.1.1.2. *Discrete cross-scale pattern*

The creation of images with known variance surrounding the scale at which pattern is expressed is not a trivial problem and an analytical solution was not possible. Rather, a sample based approach was developed (O'Leary, Appendix). This sample based approach was developed specifically to create bottom up, controlled nested, structure while remaining top down constrained. The algorithm uses three scales of pattern generation: Z_1, Z_2 and Z_3, each an order of magnitude greater than the next. Each predefined scale of pattern expression was allocated a certain amount of variance around each of these scales, also input by the user. Patches, and patches within the patches were then distributed based on sample distances from a center point within each patch. The distance from the center point was sampled randomly from a normal distribution with the user defined input variances.

To generate images of discrete cross-scale pattern, two test images were created with the input variance around scale set as 0. These images represent woody cover in a non-woody matrix. Each hypothetical tree is perfectly nested within a hypothetical patch of woody cover at a larger scale, which is in turn nested at a larger scale. This approximates the conceptual framework of a nested hierarchy, in which the patterns are nested at distinct scales.

3.3.1.1.3. *Multimodal cross-scale pattern*

The same algorithm as was used for discrete pattern was used; three scales of pattern expression $[Z_1,Z_2,Z_3]$ were generated at 5, 50 and 500 pixels respectively for each test image. Variance was only allowed at one scale at a time for the purposes of understanding the cross-scale pattern generated by such images. Images were generated with variance around Z1, Z2 and Z3 of {0,0,0}- to create a perfect set and at {3,0,0} and {0,3,0} to create multimodal cross-scale pattern images with known variance. The cross-scale morphology of an image with variance input of {3, 0, 0} and {0, 3, 0} should be approximated by Figure 3.2 A and B respectively.

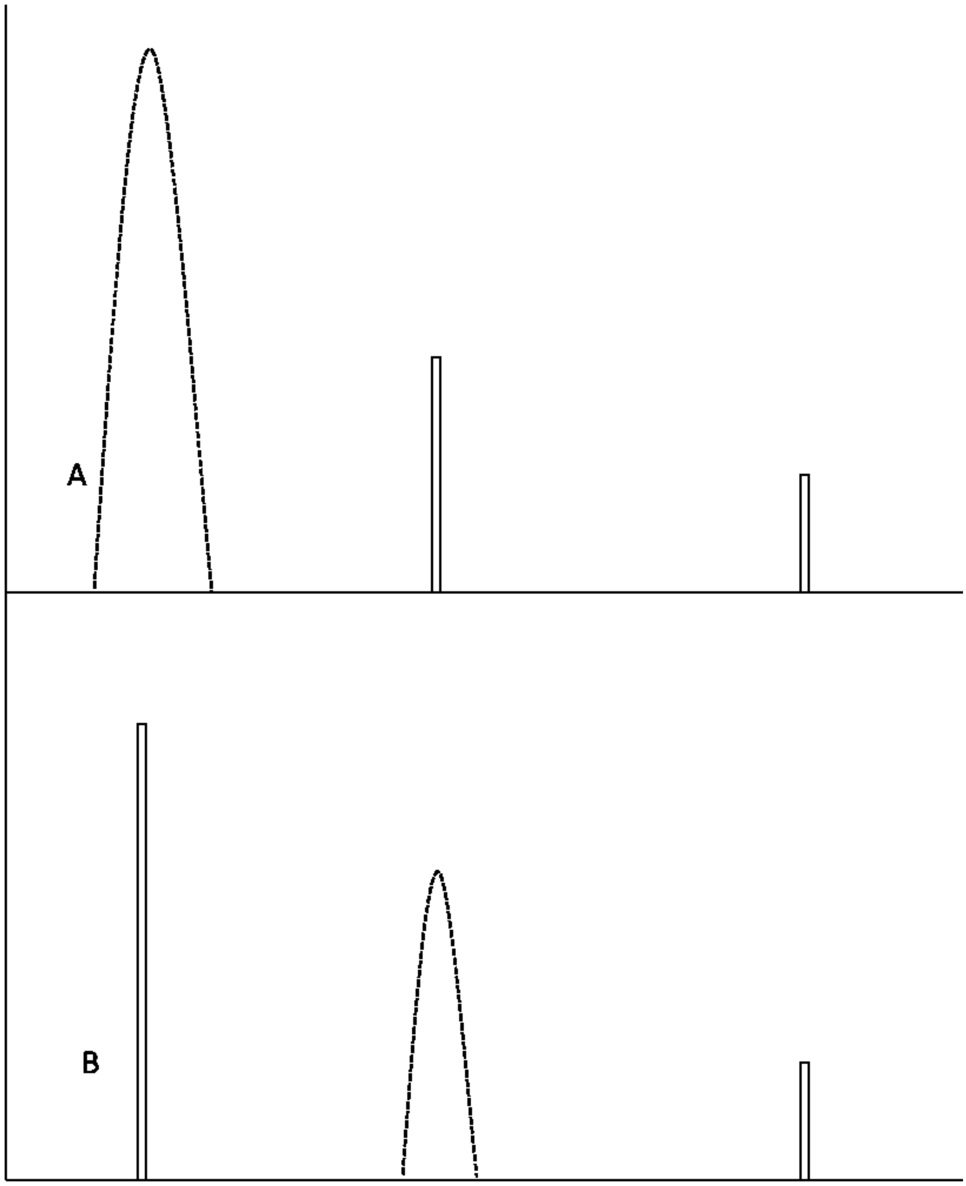

Figure 3.2: The predicted cross-scale morphology of an image with input variances of {3, 0, 0} and {0, 3, 0}. The images are created using a sampling algorithm which generated variance around a "scale" of pattern expression. The distance of the trees from the center point is sampled from a normal distribution with the variance input by the user.

3.3.1.2. **Extraction of tree canopy cover from aerial photographs**

A set of orthorectified imagery of the Shingwedzi River Basin, within which the 'Nwashitsumbe enclosure lies, taken during 2001 was used as a test dataset. The reason for using this dataset was that at the time of study, higher resolution imagery was being flown and the goal is to be able to eventually compare between the datasets over time.

3.3.1.2.1. *Imagery*

The eight samples from the 'Nwashitsumbe enclosures and surrounds were extracted from the orthorectified images, taken in 2001 (Figure 3.3). The original imagery was digitized in

2006. Printed images were digitized by a flatbed scanner to yield a resolution of 0.85m from the 1:20000 photographs. Scanning was done using Microtek ScanWizard Pro and Adobe Photoshop software and all subsequent processing was done using PCI Geomatics OrthoEngine Airphoto Edition version 8.0. (Bohenski, 2006). The "tiled" appearance of the image is due to unequalized images being stitched together during a mosaic, which complicated the process of extracting trees and resulting in the need for manual error correction in the woody canopy extraction, not an uncommon problem when dealing with this image set.

3.3.1.2.2. *Woody canopy extraction*

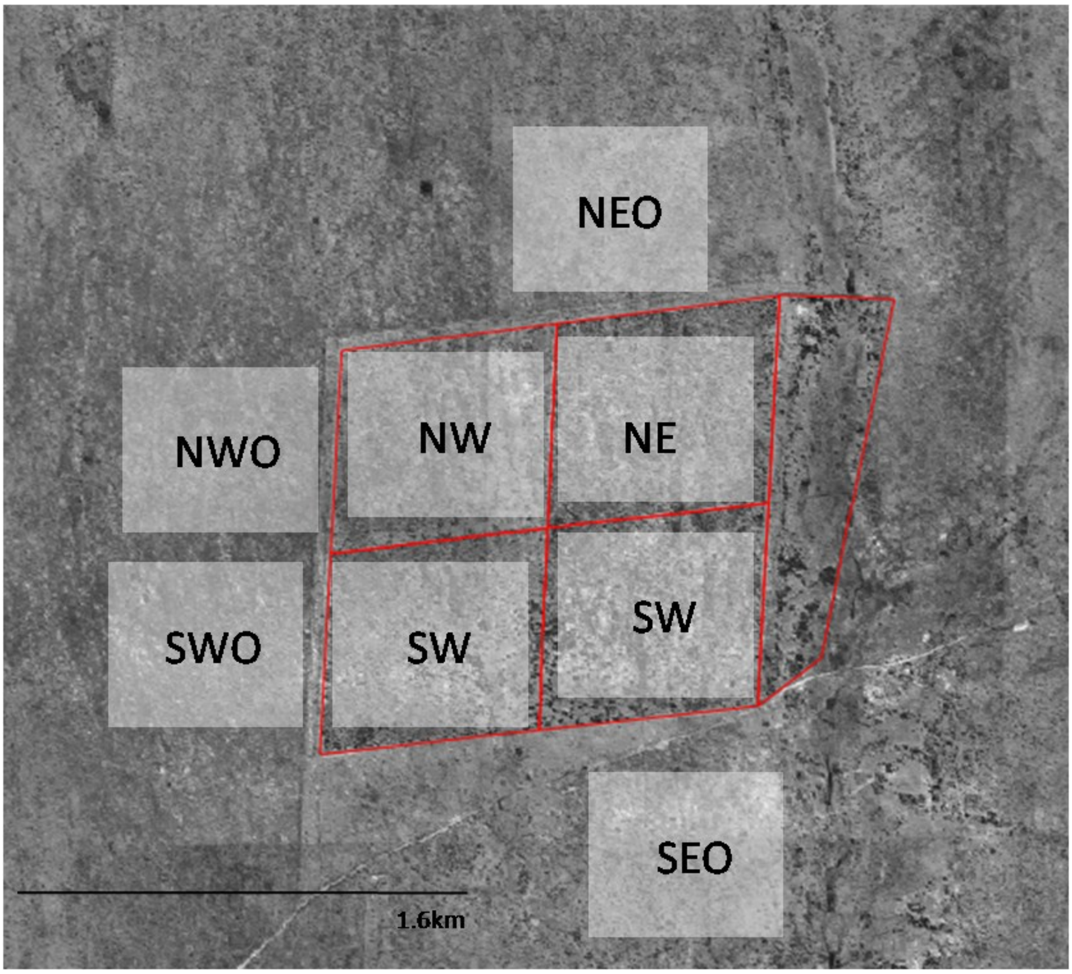

Figure 3.3: The samples taken from the orthophotos of the 'Nwashitsumbe enclosure site. NW, NE, SW and SE indicate samples inside the enclosures, within each of the four burn treatments. A suffix of O indicates a sample from outside the enclosure, NEO, NWO, SEO, SWO respectively. The tiled appearance of the image is due to the unequalized imagers being stitched together in the mosaic.

Woody canopy cover was extracted from imagery using the object-based classification software Definiens Professional 5. Pixels were aggregated into objects composed of equal variance defined using the *scale* parameter within the software. The parameter is hard coded within the software, but is part of a Fractal Net Evolutionary Approach (FNEA) used in the object based image segmentation program *Definiens*. Notwithstanding that it is termed a "scale" parameter, the parameter is a highly subjective parameter as it does not select for any shape or form. There have been subsequent developments in the form of *Estimations of Scale Parameter* (ESP) tools that can be used to more objectively define the scale parameter relative to the scene level (Drăguţ et al., 2010). However, these were not available at the time of analysis and their applicability to this particular segmentation procedure is limited.

In short, in the process of image classification, the scale parameter is a user defined threshold which defines whether or not homogenous image objects are fused into one. A simplified outline of this process is discussed by Zhang and Maxwell (2006). The potential change in the spectral heterogeneity before and after merging are calculated, these are then weighted according to a user defined weighting and subtracted to generate a *fusion* value. The fusion value defines the potential of the objects to be merged into one and it is this fusion value that is compared to the *scale* parameter of Definiens and the decision is made to use into an object or remain separate.

In the classification of woody canopy cover from the images, the homogenous units are pixels or groups of pixels that would be lumped together to what would be characterized by the user to be at least sub components of what is recognized visually as trees. Algorithms now exist which use super groups that benefit from multispectral imagery to extract woody canopy cover from imagery (Levick, 2008). However the greyscale imagery and lack of equalization between merged image tiles make true computer based classification unreliable.

To classify the orthorectified images into a tree binary image, the Definiens scale parameter was set very low to merge pixels into objects of similar spectral heterogeneity and shape heterogeneity at a spatial extent smaller than the individual trees. These small scale objects were then merged based on the mean spectral value of the objects associated with trees and visually checked for error. Once extracted from the original dataset, the woody canopy cover is assigned a value of 0 and "no trees" are assigned a value of 1. The binary image depicting woody canopy cover becomes the baseline dataset (I_0) for the linear scale-space analysis.

3.3.1.3. **Generation of Neutral Landscapes.**

The percentage woody canopy cover and average canopy size were measured for each of the eight 'Nwashitsumbe images from the BLOBs at scale = 1 in the linear scale-space stack. Based on the density of woody cover and the average size of woody canopy cover, ten neutral landscapes were generated. A uniform distribution was resampled to generate the X and Y locations in the image where the canopy cover is evident.

3.3.2. *OBJECTIVE 2: LINEAR SCALE-SPACE GENERATION*

For every one of the datasets generated a linear scale-space was generated. The output is a dataset termed a *primal sketch* of the landscape that shows the evolution of vegetation structure across scale, tracing where and at what scale each and every patch of vegetation occurs. To generate a primal sketch I followed a sequence of five sub-methods (Figure 3.4), excluding any for visualization, the intricacies of which are not of concern in this thesis.

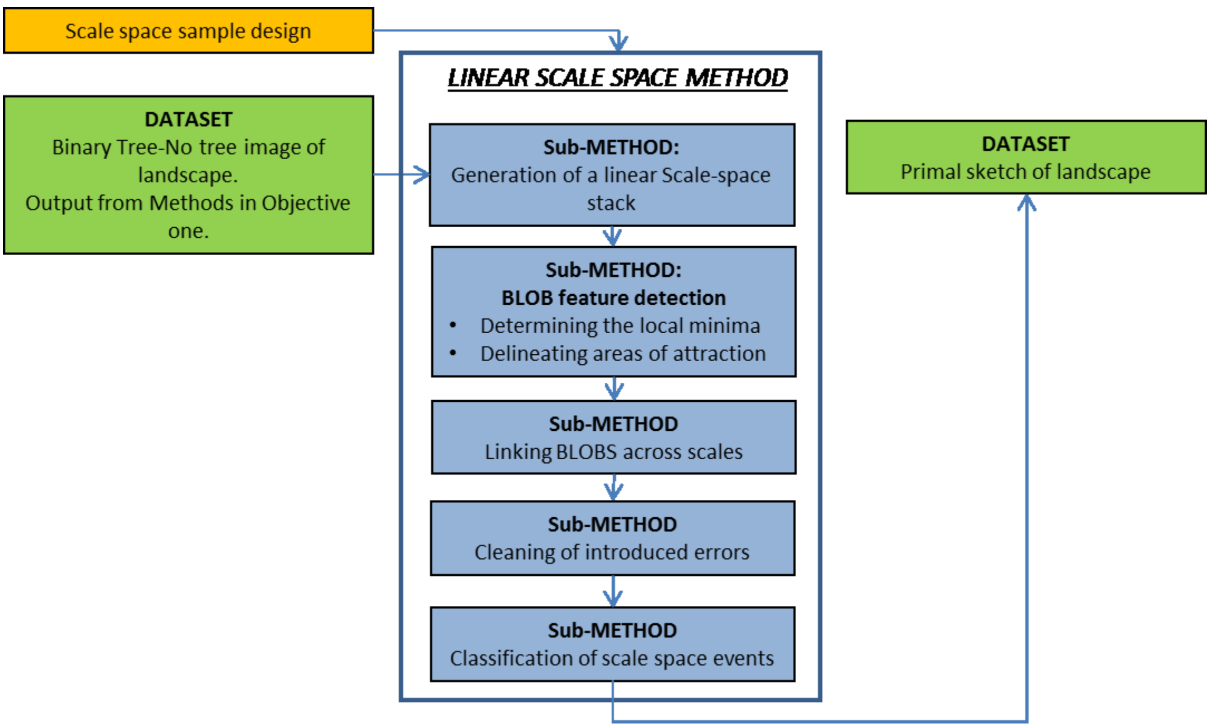

Figure 3.4: A flow diagram of the methods used to generate a linear scale-space sketch and the associated primal sketch, which is the dataset used to represent linear scale-spaces in this thesis. Five sub-methods are used in sequence to generate a primal sketch for each image.

The method I used in my thesis is different from traditional linear scale-space in a number of respects; I used only woody vegetation cover as my objects of interest, I utilized a linear sampling scheme of the scale space and I did not normalize the scale space stack.

3.3.2.1. **Scale-space sample design**

Linear scale-space results from the convolution of the original dataset, image=I_0, with a series of Gaussian kernels; $G(\vec{x},\sigma)$, of increasing width *(σ)*. The kernel is convoluted across each pixel across the original image I_0 and each image in the resultant set has the same resolution as the original image.

A two dimensional Gaussian kernel takes the form;

$$G(\vec{x},\sigma) = \frac{1}{2\pi\sigma^2} e^{\frac{\vec{x}.\vec{x}}{2\pi^2}}$$

where σ is the standard deviation of the Gaussian kernel.

3.3.2.1.1. *Sampling the scale-space*

Theoretically the standard deviation (σ) and therefore the scale of analysis is continuous, however it is practically necessary to sample the scale-space dataset at discrete intervals, i.e. $\sigma = \{\sigma_1; \sigma_2 \ldots \sigma_N\}$.

Generally when sampling a linear scale-space, to increase computational efficiency, a dimensionless scale parameter is used (τ), and the sampling scheme is derived by setting:

$d\sigma/d\tau = \sigma$ $\frac{d\sigma}{d\tau} = \sigma$, the lowest scale τ_0, being equal to the resolution (ρ) of the original dataset I_0 (viz. Platel, 2003).

To calculate the scale of analysis (τ); $\sigma = \rho e^{\tau}$ $\sigma = \rho e^{\tau}$ and so given ρ and σ; $\tau = \ln(\sigma/\rho)$, resulting in an exponential sampling scheme.

The number of events occurring in the scale-space decreases logarithmically with the scale of sampling (Lindeberg, 1994). The exponential sampling of a scale-space's scale axis is useful in image processing applications as it is computationally efficient. However, if the analysis of hierarchically nested vegetation in the landscape is to be a completely objective a linear sampling design is better suited (Hay et al., 2002).

I do not use an exponential sampling scheme as in other linear scale-space applications, rather I have chosen to use a sampling scheme which is linear across the scale dimension; $\tau_n=\sigma_n$, the window of observation being equal to the standard deviation of the Gaussian kernel. I sample across the set of $\sigma=\{\sigma_0;\sigma_1 \ldots \sigma_N\}$. The importance of the linear sampling scheme is that I create a scale axis with exactly the same resolution as the spatial dataset. The maximum scale of analysis (τ_N) and therefore σ_N is dictated by the extent of the original image dataset I_0. I set τ_N to half of extent of the original dataset to avoid overly large influences of edge effects, although these are still of concern and are discussed in section (3.5.2.2.)

3.3.2.2. **The generation of a scale-space stack**

A linear scale-space is created through the convolution of the Gaussian kernel with the input image:

$$I_n = G(\vec{x}, \sigma_n) * I_0$$

Convolution of the original image with Gaussian kernels parameterized by set σ results in a set of images I;

$$I = \{I_0; I_1 \ldots I_N\} = \{G(\vec{x}, \sigma_0) * I_0;\ G(\vec{x}, \sigma_1) * I_0 \ldots G(\vec{x}, \sigma_N) * I_0\}$$

The standard deviation of the Gaussian kernel (σ) was set to increase in integers to allow for the same resolution in the scale dimension as in the spatial dimension. Each of the images in Set *I* represents the extracted woody canopy cover at the sampled scale. The images of Set *I* were stacked sequentially on top of one another rendering a three dimensional volume with the three explicit dimensions being length (x), breadth (y) and scale (z) (Figure 3.5) This theoretically continuous three dimensional volume of data is a linear scale-space; I refer to the sequentially sampled images as a scale-space stack.

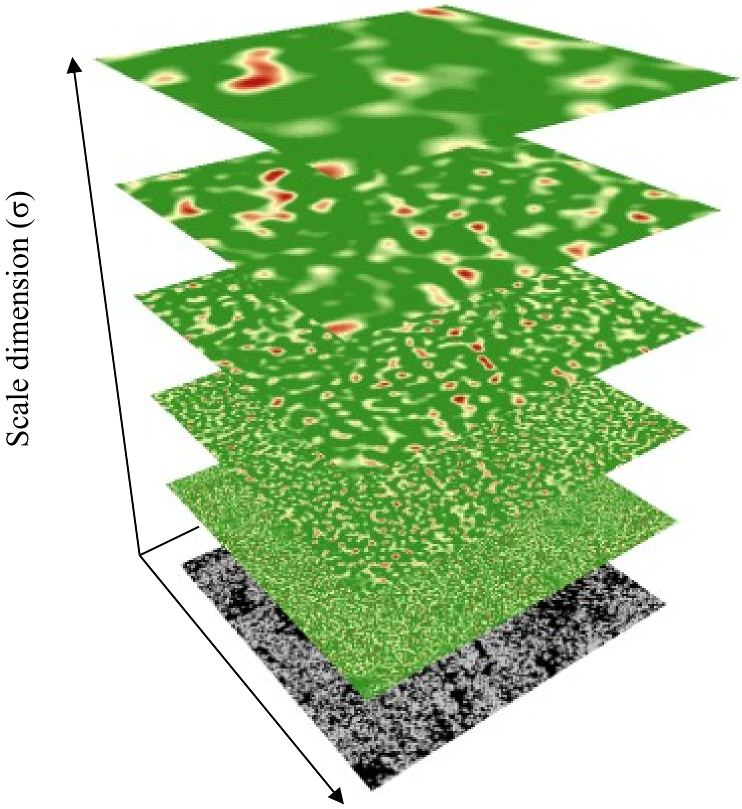

Figure 3.5: The creation of a linear scale-space stack. After convolution of the original binary image I0 with the Gaussian kernel with standard deviation of set σ, the images of Set I are stacked sequentially on top of one another. By sampling σ in a linear fashion, the resolution of the scale dimension (τ) is the same as the spatial dimensions.

3.3.2.3. **BLOB feature detection**

This thesis is an ecological thesis, albeit primarily a theoretical one, as opposed to a study in image analysis. Linear scale-spaces of images for image recognition and image matching, MRI's and complex image analyses of object orientated image analysis are different applications. The linear scale-space application I derive for use of analysis of woody canopy cover differs from these applications. I tested whether or not there was nested hierarchical structure within *woody tree cover* within a landscape. I therefore focus solely on the woody tree cover component and exclude other information. I discuss the implications further on in the text but must highlight here that the binary woody canopy cover classification remains the object of interest throughout.

Each image in a linear scale-space stack can be viewed as a landscape itself, the length and breadth of the image representing the extent of the landscape and the pixel value creating a virtual landscape of hills, valleys and saddle points (Figure 3.6). A linear scale-space stack is therefore four dimensional as it comprises length (x), breadth (y), the sampled scale (σ) and each image from Set I has pixel values. To remove this fourth dimension and link the data of interest across scales, the woody canopy cover is extracted in the creation of Binary Large Objects, BLOBS. I extract the regions of interest using the maximum attraction areas method, (Platel, 2003).

In contrast to a number of linear scale-space applications I do not normalize the linear scale-space stack. I do not feel it necessary in an application to trace woody vegetation cover through scales of analysis. The implications are discussed further at the end of this chapter.

Delineation of the BLOBs is a two part process for each image in the scale-space stack (Set *I*):

1. Local minima are derived from the image set, which indicates the locations of the valleys; and
2. The area of attraction surrounding each local minima is delineated by finding the contour polygon of largest area surrounding the single minima point.

3.3.2.3.1. *Determining local minima*

Critical points are where the local gradient equals zero (Florack et al., 1994), identified by the intersection of zero gradients of x and y ; where both $\frac{\partial I_n}{\partial x} = 0$ and $\frac{\partial I_n}{\partial y} = 0$ respectively; (Figure3.7)

Local extrema such as local maxima, local minima or saddle points are identified with the second derivative test at each critical point. Local minima, which represent the focus points of woody canopy cover in our analysis, are indicated by $\frac{\frac{\partial I_n}{\partial x}}{\partial_x} > 0$and $\frac{\frac{\partial I_n}{\partial y}}{\partial_y} > 0$.

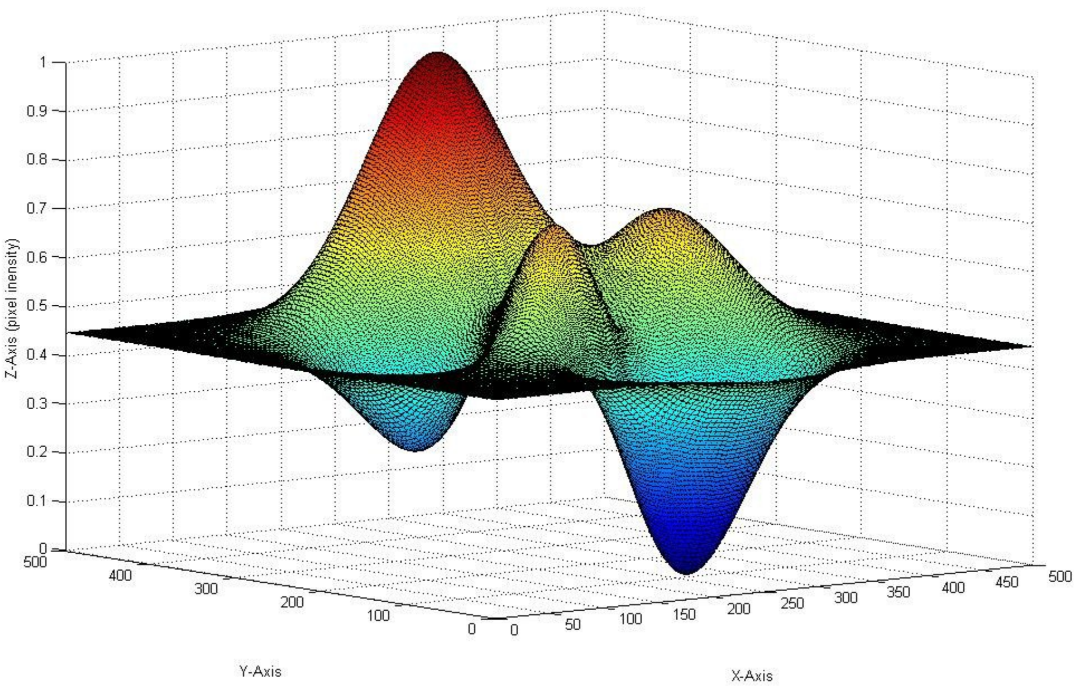

Figure 3.6: The topography of an individual image in a scale-space stack. Each image in the scale-space stack (Set I) has pixel values and can be viewed as a landscape of hills and valleys. This constitutes four dimensions in Set I, which must be reduced to three. To link the woody canopy cover across the scale dimension, the woody canopy cover needs to be extracted in the creation of Binary Large Objects (BLOBs).

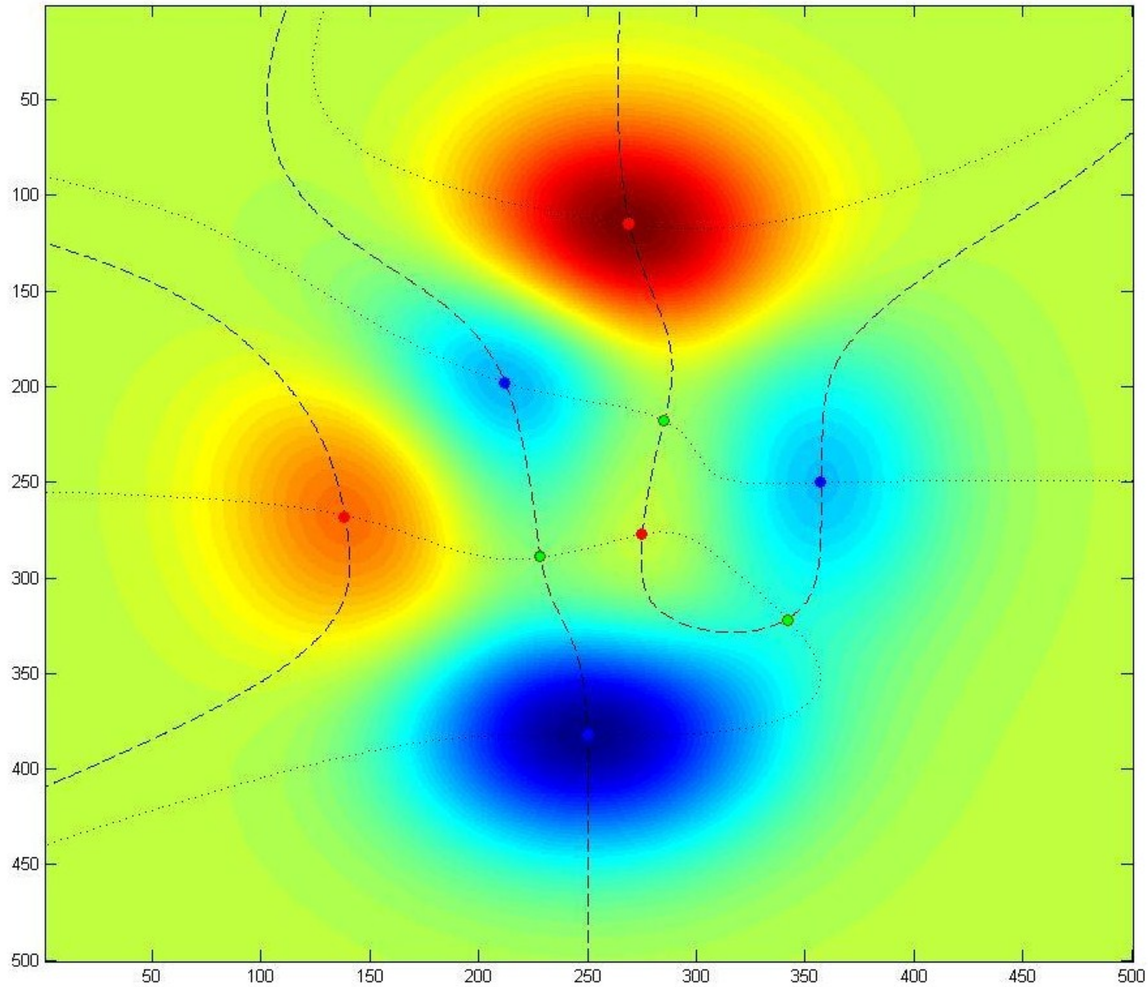

Figure3.7: Critical points reveal basins of attraction used to detect objects of interest: Intersections of ($\partial I\tau/\partial x = 0$) and ($\partial I\tau/\partial y = 0$) yield the critical points in an image of Set I for scale of observation τ.

The second derivative test indicates local minima, which represent woody canopy cover in our analysis, and local maxima are indicated by $(\partial In/\partial x)/\partial x > 0$ and $(\partial I\tau/\partial y)/\partial y > 0$.

In this image the blue dots indicate local minima, which are of interest in the application of linear scale-space to woody canopy cover. The green dots indicate saddle points and the red dots indicate the local maxima.

3.3.2.3.2. *Delineating Areas of Attraction*

Using the "areas of attraction" method, Platel (2003), for each critical minima point, a basin of attraction is delineated by defining the largest polygon which surrounds the single minima point (Figure 3.8A). The result is a number of image objects can be visualized as a flooded basin in the landscape of the image (Figure 3.8 B). Each of these objects represents a separate patch of woody canopy cover at the scale in question (Figure 3.8C) and is turned into a binary dataset as BLOB (Figure 3.8D).

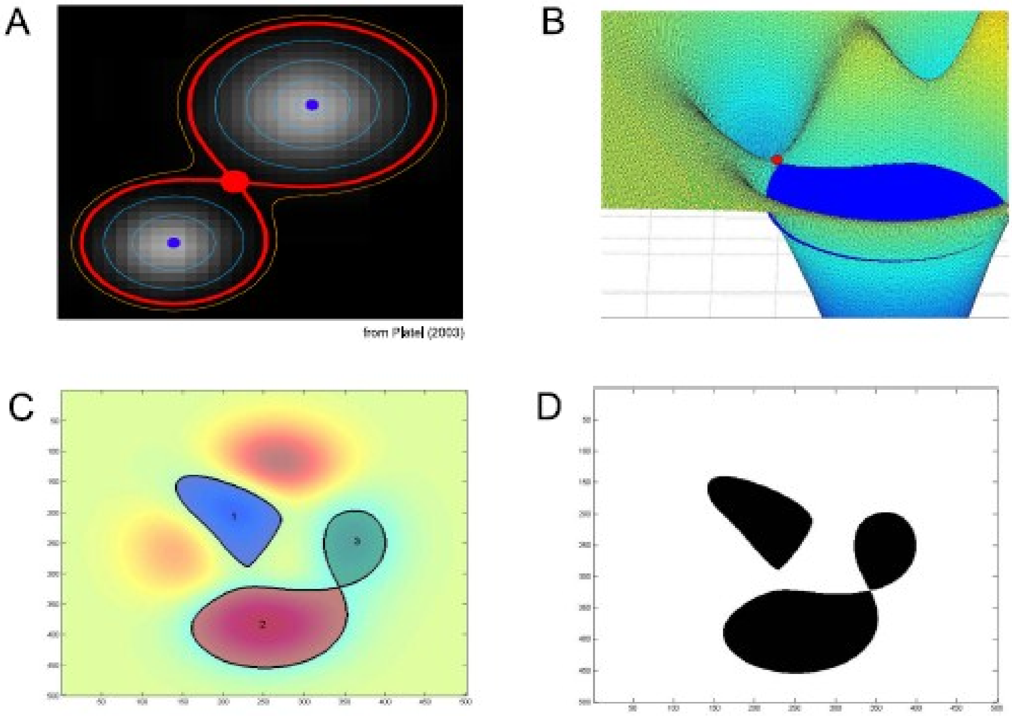

Figure 3.8: Binary Large OBject (BLOB) extraction via the areas of attraction method, viz. Platel (2003). Visualizing the topography of each image in a scale-space stack, the largest contour area surrounding a single minima point delineates the extent of a BLOB (A). The BLOBs can be viewed as flooded valleys in the hills and valleys of the image topography (B). Each BLOB represents woody canopy cover at the scale in question and each minima point is calculated separately, revealing the local structure in the image (C). Once all the BLOBs are calculated, the image is converted into a binary dataset, depicting woody canopy cover at the scale in question (D).

3.3.2.4. **Linking BLOBS across scales**

A scale-space primal sketch is a representation which gives a formal description of the hierarchical relations between structures at different levels of scale. The scale-space primal sketch is generally represented as three dimensional volumes of image structure, termed *scale-space BLOBs* or *grey level BLOB volumes* (Hay et al., 2002). Not only is the representation generated in this application not a typical grey level BLOB, but the three dimensional *scale-space BLOBS* are computationally cumbersome for our purposes, so I reduce the volumetric dataset of BLOBS into a three dimensional node graph which depicts what I term the *primal sketch* of the dataset in a linear scale-space.

As an illustration; if I use a perfectly nested dataset set as a test dataset (Figure 3.9A) at some scale the individual trees, represented as black dots, will merge to form a patch (blue box). At a higher scale these patches will merge to form a larger patch (red box). Drawn as a three dimensional node graph it becomes possible to view the development of woody vegetation structure across the dimension of scale (Figure 3.9B). Linear scale-space events such as merge events are indicated by the red dots (Figure 3.9B) which illustrate the points in space and scale where patches of woody vegetation merge into patches.

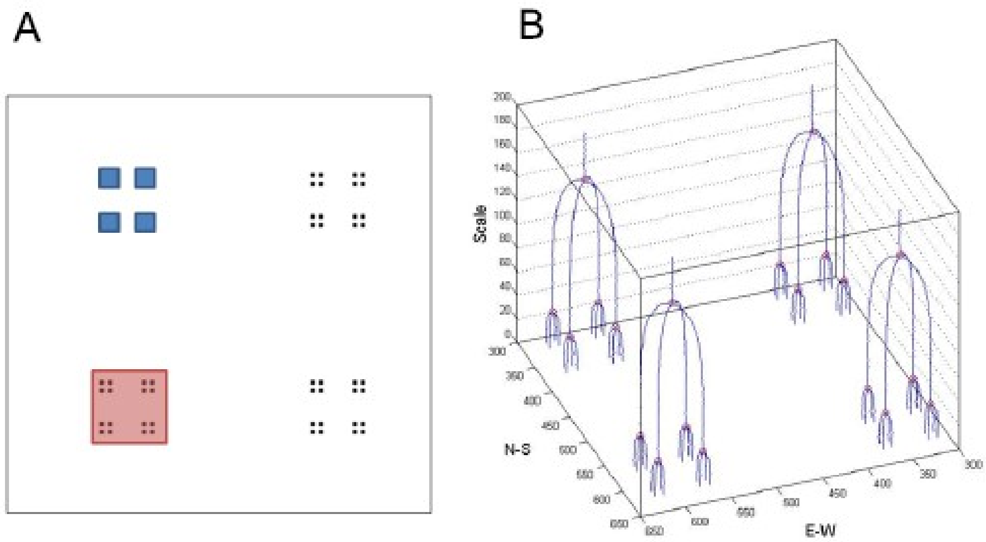

Figure 3.9: The rendering of a primal sketch. A primal sketch is a representation of the evolution of a dataset through scale. If I view a perfect set test landscape (A), the black dots represent the trees. At some scale, the trees merge into a patch, illustrated by the blue boxes. At a higher scale still the patches merge into a larger patch still, illustrated by the red box. Viewed as a three dimensional data volume (B), the node graph illustrates how individual trees merge to form patches in a linear scale-space.

To construct the primal sketch each minima point (*CR)* is considered as a node in a three dimension scale-space and each node has an associated polygon depicting woody canopy cover at the spatial location and scale of analysis. The linking of regions of support is done by testing whether BLOBS at differing sampled scales share spatial support (Cachia et al., 2003). I view each minima point as a node in the three dimensional scale-space of length (x), breadth (y) and scale (τ) and use the following basic element-wise algorithm.

For each critical point of set $Cr_{(\tau,i);}$ $i=\{1....N\}$:

1. Test for spatial overlap for the polygon representing point $Cr_{(\tau,i)}$ and all polygons in set $Cr_{(\tau+1,.)}$, beginning with the critical points closest to the one in question.
2. If there is spatial overlap between polygons, the nodes representing the polygons are considered to be connected.

3.3.2.5. **Cleaning of introduced errors**

In the early validation of the algorithm, errors were found in the primal sketches, which involved a break in the linkages between nodes in the linear scale-space. This break in linkage results in a break down in causality in the scale-space, small patches are no longer *owned* by large patches and later tests which do not assume stationarity would become impossible.

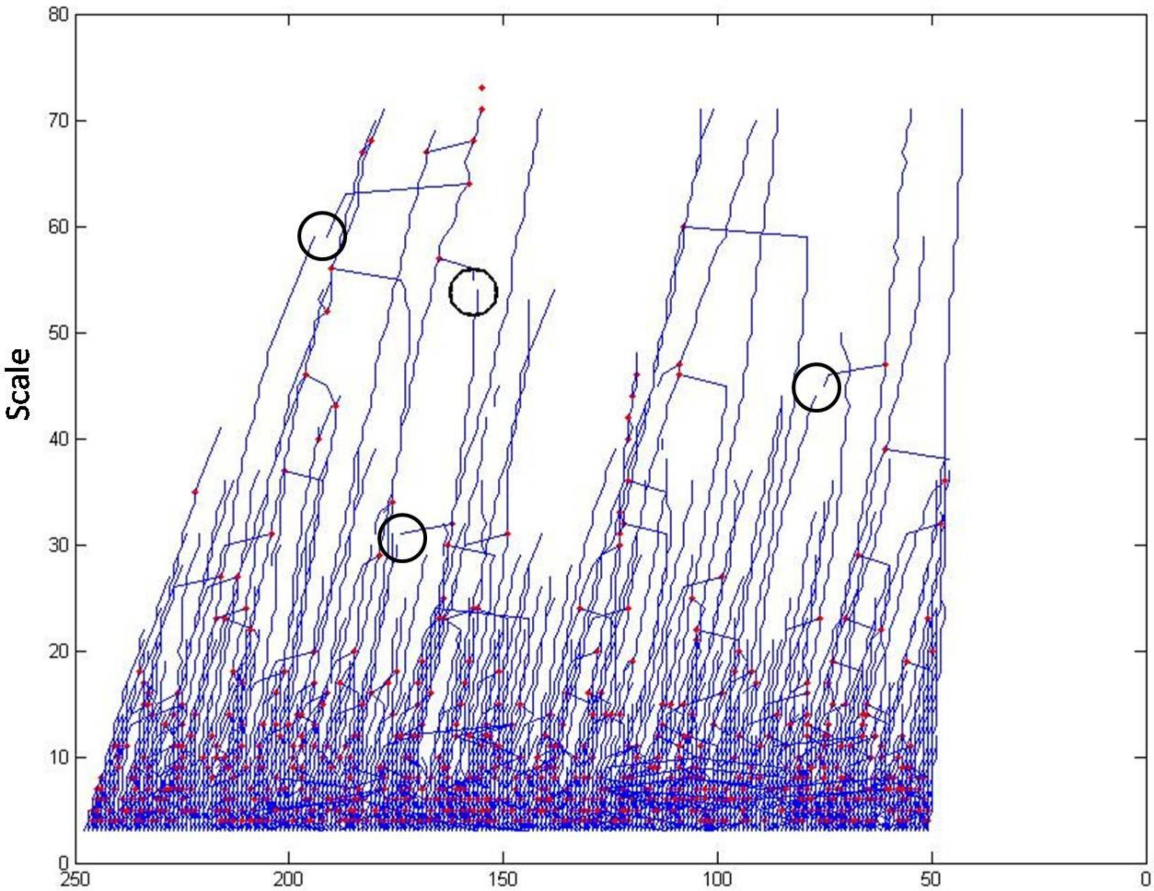

Figure 3.10: A profile view of a primal sketch of a neutral landscape. The circles indicate errors in the linkage algorithm where joins should be evident, but are not. The error is introduced because spatial support between BLOBs at adjacent scales becomes nonexistent once the BLOB becomes sub-pixel in extent. A simple cleaning algorithm was written to join the obvious gaps, but remains an avenue for future research.

The linkage of BLOBs across scales into scale-space volumes remains the major challenge, even outside of this application. Linking BLOBs between scales has been termed *"...practically difficult..."* (Coulon et al., 2000, pg. 770). BLOBs are linked if they overlap in the spatial dimension. The linear sampling scheme used in this application reduces the amount of lateral drift of BLOBs, which increases the chance of spatial overlap between

BLOBs at adjacent scales. However, as the BLOB tends toward a scale-space merge event, the area of an individual BLOB tends toward zero. At some point the BLOBS are smaller than an individual pixel. These sub-pixel BLOBs are not likely to share spatial support, introducing errors in the primal sketches as links are not made when they should be.

There are analytical methods which allow for the prediction of the linkage by using sub-pixel trajectories (Florack and Kuijper, 2000), however these techniques are based on true linear scale-spaces and not a scale-space optimized for binary imagery such as the imagery used here. Whether or not analytical methods are valid in these binary datasets which ignore the matrix structure is an avenue that needs further investigation and the errors and implications thereof are discussed in Section3.5.1. To remove the obvious errors caused by the sub-pixel BLOB problem, I use the following cleaning routine:

In an adjacency matrix which depicts a linear scale-space for a given image:

1. Define all creation, split and annihilation events by finding nodes with a single connection. As creation events should not theoretically occur in the linear scale-spaces of hierarchically structured vegetation, creation events above the first scale of analysis can be assumed to be a linkage error.
2. Define creations and splits as those which are connected to a node which is the scale above; annihilation events are connected to a scale below. Create 2 nx3 matrices, one containing the x, y, z values of the annihilation events and the other of the creation events (C).
3. For all error points ($C_{i...N}$):
    a. Find the closest annihilation event ($A_{i...N}$) by calculating the Euclidean distance between the points in the xyz scale-space.
    b. If the distance is less than the criterion value (z x 0.05), the points are considered connected.
    c. Index the connected nodes in the two matrices back to the major adjacency matrix.

The value of 0.05 is to allow a five percent increase in search radius; however it does increase the chance of errors at higher scales. The cleaned adjacency matrix then becomes the matrix used for the rest of analysis.

3.3.2.5.1. *Reporting on the errors cleaned:*

During the cleaning process I report the number of errors removed and broken linkages corrected.

3.3.2.6. **Classification of scale-space events**

Data were stored as adjacency matrices, if only one node is connected to any given node, the node is an annihilation or creation event. If there are more than two nodes connected to any node, this constitutes a split or merge event. Further analysis of the scales of the connecting nodes allowed the events to be determined as either annihilations or merge events. To remove the distortion of edge effects the top thirty percent of the scale space stack was discarded.

3.3.2.7. **Graphic representation of Primal sketches**

I present the primal sketch outputs of a sample for the following datasets with known cross scale structure:

a. Random landscape (a sub-sample)
b. Discrete cross scale pattern
c. Multi-modal cross scale pattern
d. Neutral landscapes.
e. 'Nwashitsumbe examples.

3.3.3. *OBJECTIVE 3: TO DEMONSTRATE OUTPUTS OF THE LINEAR SCALE-SPACE APPLICATION AND TO VALIDATE THE LINEAR SCALE-SPACE APPLICATION FOR REPEATABILITY OF THE ALGORITHM AND IN DETECTING THE SCALE OF PATTERN EXPRESSION*

Objective 3 focuses on demonstrating that the linear scale-space application works and is effective in detecting pattern that would be expected in a hierarchically structured landscape.

The objective has been divided into three sub-objectives, each of which is aimed at answering a question (Figure: 3.11). For each of these objectives, a separate set of statistical tests are undertaken on the test datasets presented on page 76.

The sub-objectives of Objective 3 aim to:

1. *Demonstrate the cross-scale morphology of landscapes of known cross-scale structure* - does the cross scale morphology of landscapes with known cross-scale structure conform to the conceptual framework presented in section 4?
2. *Demonstrate repeatability* - does the algorithm output show similar cross scale morphology for landscapes with similar scales of pattern expressions?

3. *Demonstrate sensitivity to variations in vegetation size and density, to inform the neutral models* - does tree size, tree density and the size of the input landscape dataset matter in the comparisons for neutral models?

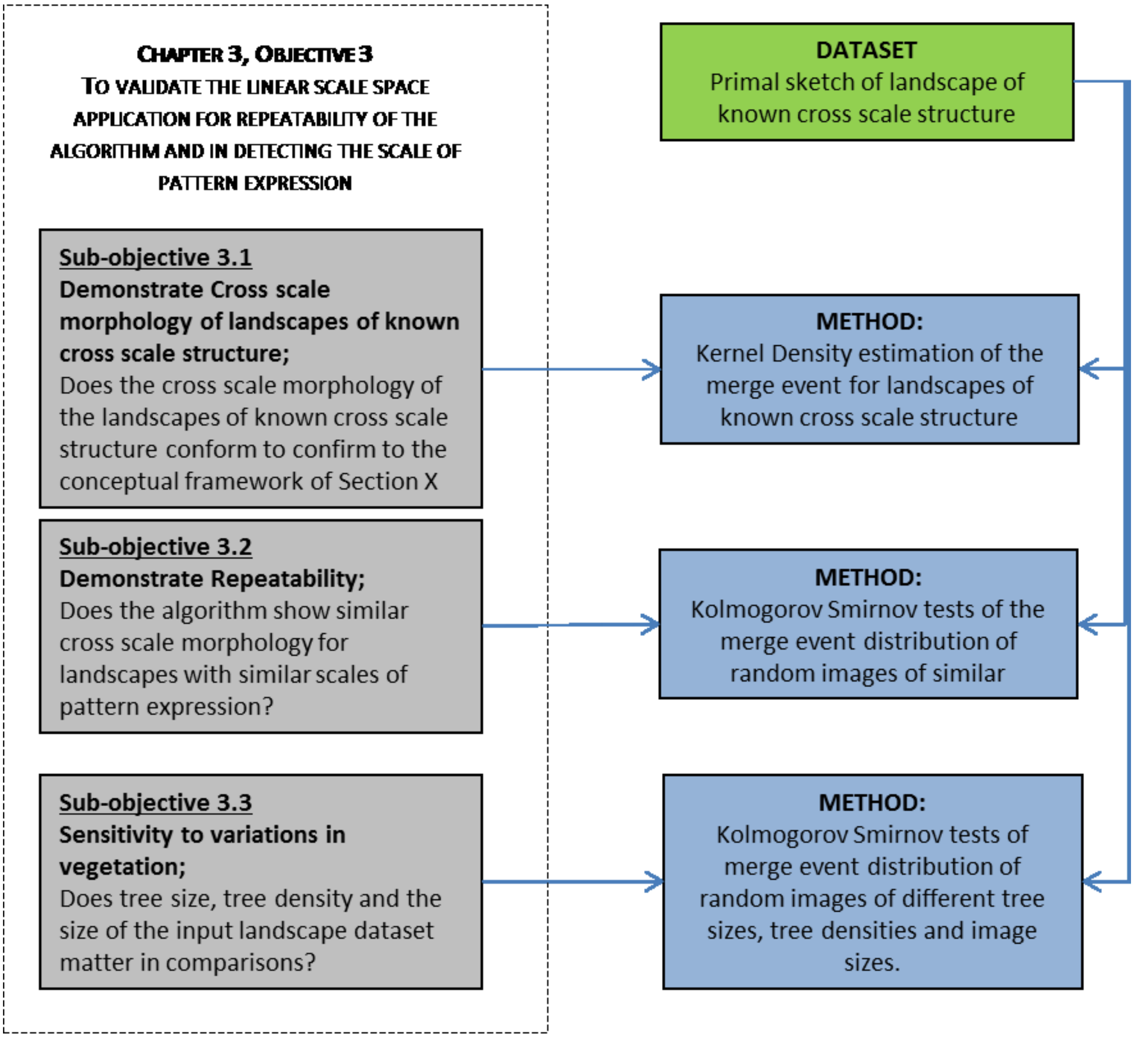

Figure: 3.11: A flow diagram of the methods used to achieve Objective 3. There are three sub-objectives which allow the linear scale-space application to be validated for the purposes of generating detecting representations in woody vegetation structure.

3.3.3.1. **Sub objective 3.1: Does the cross scale morphology of the landscapes of known cross scale structure conform to the conceptual framework of Section 4?**Error! Reference source not found.

I expect, based on the arguments of Chapter 2, that a multimodal cross scale morphology in merge events is evidence of hierarchically nested structure or distinct scales of process in the landscape. Landscapes without scaled processes however should display a negative exponential trend, inferring nothing more that the number of merges decreasing in relation to the area of analysis available.

Kernel density estimations are calculated on merge events of datasets with known cross scale structure, random datasets, discrete cross scale structure and multi-modal cross-scale structure. All primal sketches are grouped for the *entire* test landscape dataset. This constitutes a stationarity assumption as the pattern for the whole sample is integrated. Such an assumption is fair for the datasets of known structure; further analyses which do not assume stationarity are considered in later analyses. Kernel density bandwidth was kept to a single scale unit and the analysis bounded to the positive domain to allow for maximum resolution in the scale dimension. A diagram of the cross-scale morphology is presented below.

3.3.3.2. **Sub-objective 3.2: Demonstrate Repeatability; does the algorithm show similar cross scale morphology for landscapes with similar scales of pattern expression?**

Due to the lack of process the pattern of merge events across the random landscape can be assumed to be stationary. Merge events for all primal sketches within a landscape image are therefore grouped together to increase sample size and thereby sensitivity. The X and Y data are discarded, providing a distribution of *scales* where merges occur per replicate.

Kolmogorov Smirnov (KS) tests were used to compare the empirical cumulative density functions of the merge event distributions. The KS test statistic is calculated as:

$$K = max(|F_1(x) - F_2(x)|)$$

and is compared to the alpha value in a standard hypothesis test. The null hypothesis is stated as the two distributions F_1 and F_2 and can be considered from the same continuous distribution.

Comparisons were made between replicates of six neutral landscapes, (Table 3: replicate groups a, b, c, e, f, g and k). For instance, for neutral landscape “e”, there are ten replicates and each is compared to the other, generating 45 unique comparisons which are each tested using the KS test, with the null hypothesis that the two distributions being compared are from the same distribution (α=0.05).

3.3.3.3. **Sub-objective 3.3: Sensitivity to variation in vegetation; does tree size, tree density and the size of the input landscape dataset matter in comparisons?**

Kolmogorov-Smirnov (KS) tests (explained above) were used to compare the empirical cumulative density functions of the merge event distributions. The null hypothesis being that the two distributions F_1 and F_2 can be considered from the same continuous distribution.

For the purposes of demonstration, the cross scale morphology of the various datasets is presented, kernel density estimation of merge events, lumped for the entire landscape, bandwidth bounded to the positive domain and of a single scale unit in extent, are presented.

1. Test the effect of tree size on the distribution of merge events across scale.

Four neutral landscapes were compared, controlling for image size and canopy cover, but having varying tree sizes (Figure 3.12). The neutral landscapes with trees sizes of one pixel, five pixels, ten pixels and twenty pixels were compared to one another (a single replicate was used from each of the neutral landscapes Table 3; b, d, g and i) totaling six comparisons of images with differing tree sizes. Scale values of the merge events were compared using Kolmogorov-Smirnov tests (α=0.05), the null hypothesis assuming that they were from the same continuous distribution.

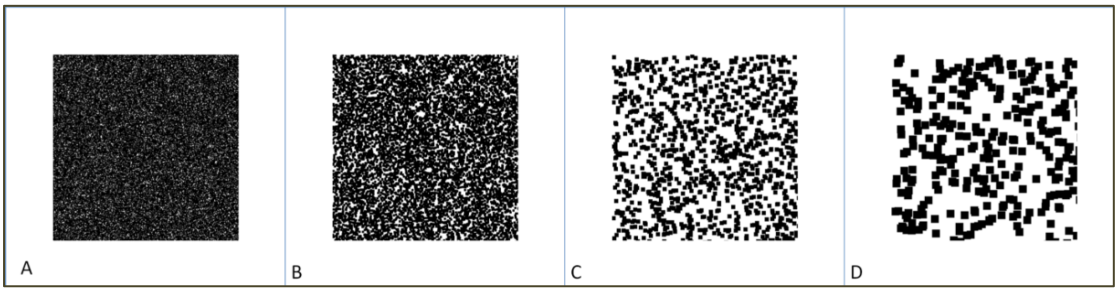

Figure 3.12: Images of neutral landscapes with differing tree sizes relative to the image extent, each image has fifty percent woody canopy cover overall but vary in pixel size. A, B, C and D represent trees of 1, 5, 10 and 20 pixels respectively. The distribution of merge events generated from these images are compared to one another, totaling six Kolmogorov-Smirnov tests (α=0.05), the null hypothesis assuming that they were from the same continuous distribution.

2. Test the effect of image size on the distribution of merge events across scale.

A neutral landscape of three hundred pixels (Figure 3.13A) was compared to a neutral landscape of five hundred pixels (Figure 3.13B) in extent. Scale values of the merge events were compared using Kolmogorov-Smirnov tests (α=0.05), the null hypothesis assumes that they are from the same continuous distribution. Only a single replicate was made to illustrate the point, as this is an expected and obvious difference.

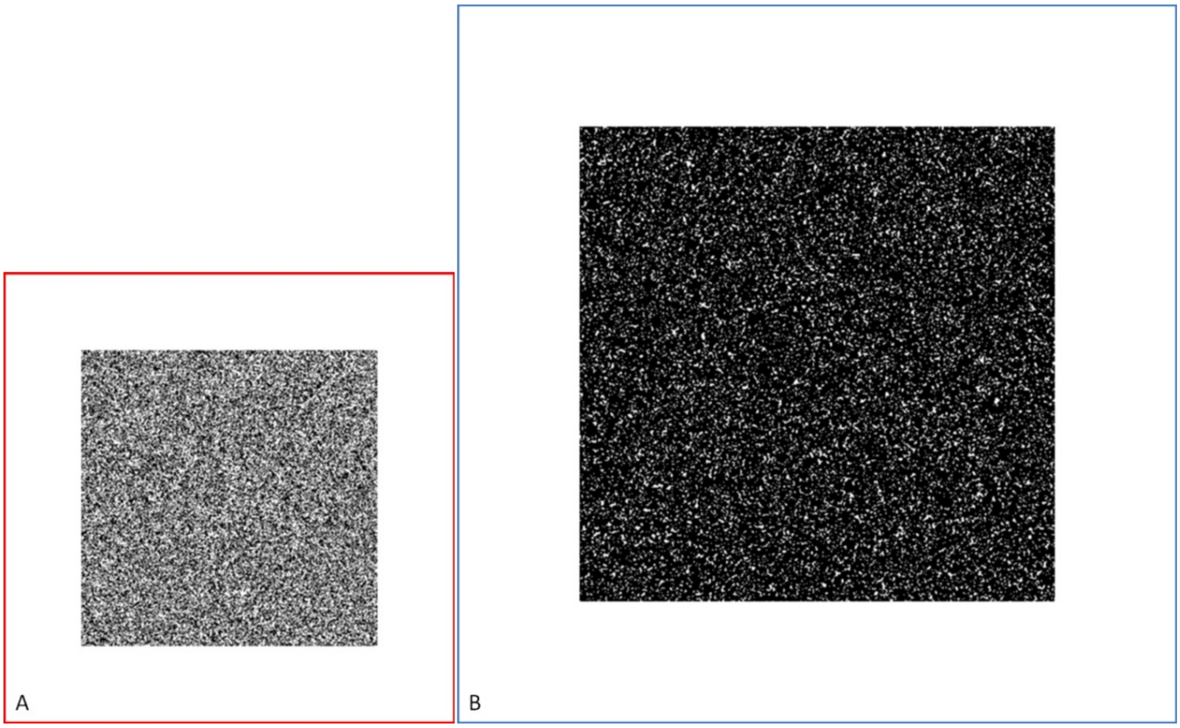

Figure 3.13: Neutral landscapes with different extents; both images have single pixel trees and fifty percent cover. A is 300 pixels in extent and B is 500 pixels in extent. Linear scale-spaces are generated and the distribution of merge events across scale is compared via a Kolmogorov Smirnov test (α=0.05), the null hypothesis assumes that they are from the same continuous distribution.

3. Test the effect of percentage woody cover (tree density) on the distribution of merge events across scale.

The distribution of merge events from five neutral landscapes with twenty five percent cover (Table 3, replicate group A, example in Figure 3.14A) were compared to five neutral landscapes with fifty percent cover (Table 3 replicate group B, example in images. Figure B) and five with seventy five percent cover (Table 3 replicate group C, example in Figure 3.14). Scale values of the merge events were compared pair-wise using Kolmogorov-Smirnov tests (α=0.05), the null hypothesis assumes that they are from the same continuous distribution. This constitutes 75 comparisons between images containing different canopy cover, nested into three replicates.

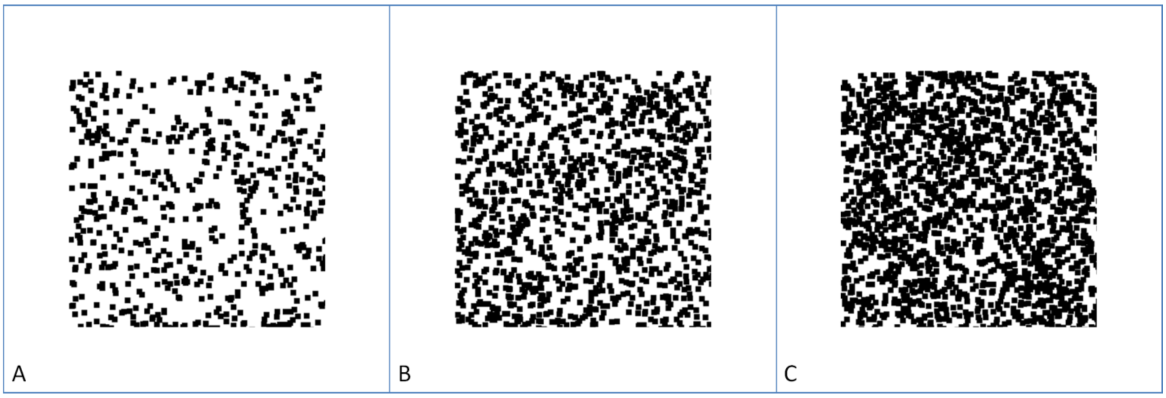

Figure 3.14: Neutral landscape images with differing tree densities; A, B and C represent 25%, 50% and 75% woody canopy cover respectively. Images are of the same extent and the trees are of five pixels in size for all images.

3.3.4. *Objective 4: Can evidence of process be detected in the 'Nwashitsumbe landscape?*

This objective is the crux of this thesis; to determine whether or not evidence of process can be detected in the woody cover of a real world savanna landscape in a way that can be considered to be nested hierarchical structure.

Objective 4 is achieved by achieving three sub-objectives:

1. *General cross-scale morphology* - to determine if the cross-scale morphology (determined by the scales at which mere events occur) of a real world landscape differs from a neutral landscape.
2. *Fire and Browse treatments* - the effect of the manipulation of two major savanna drivers on the system cross-scale morphology.
3. *Spatially explicit discontinuity analysis* - what I consider the point of this thesis, the section that all other sections have built toward, is to use the primal sketches of the 'Nwashitsumbe landscapes to perform a *spatially explicit discontinuity analysis of a complex system*. Spatially explicit discontinuity analysis, as far as the author is aware, is a completely novel analysis technique.

The process flow (Figure 3.15), outlines the tests structure of the tests undertaken to answer the two sub-objectives. Spatially explicit discontinuity analysis is explained as a sequence of four sub-methods. The datasets used as inputs are the primal sketches of the 'Nwashitsumbe landscape and the neutral landscapes.

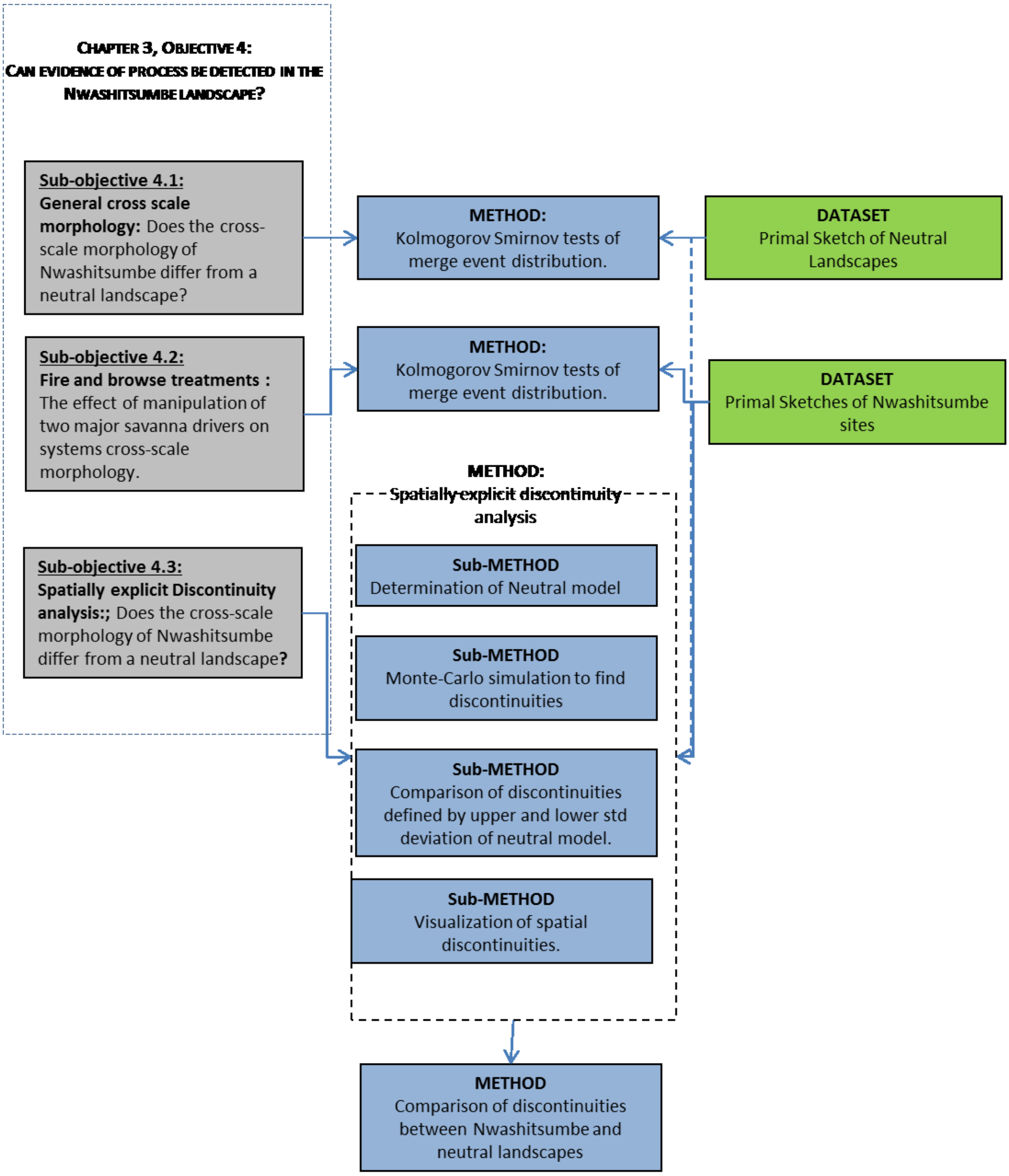

Figure 3.15: The process flow outlining the methods used to achieve Objective 4. To answer the question; "Can evidence of hierarchically nested structure be detected in the 'Nwashitsumbe landscape?" The objective has three sub-objectives, which are each tested using a specific method. Spatially explicit discontinuity analysis involves four sub-methods and a final comparison. The datasets used are the neutral landscapes and the woody canopy cover datasets presented in Objective 1.

3.3.4.1. Sub-objective 4.1:_General cross scale morphology: Does the cross-scale morphology of 'Nwashitsumbe differ from a neutral landscape?

The merge events for the entire landscape datasets were lumped together for this analysis. Kolmogorov-Smirnov tests (described in section 3.3.3.2.) were used to compare the distribution of the scales at which merge events occurred between the 'Nwashitsumbe images and the ten replicates of the neutral landscape (α=0.05). The null hypothesis states that the samples are from the same continuous distribution. I note here that the method here assumes that processes are equivalent across scales.

3.3.4.2. **Sub-objective 4.2: Fire and browse treatments: The effect of the manipulation of two major savanna drivers on systems cross-scale morphology.**

Comparisons of images under different treatments of fire and herbivory were undertaken. Kolmogorov-Smirnov tests ($K= max(|F_1(x)-F_2(x)|)$ were performed on the distribution of merges for the eight samples from 'Nwashitsumbe and the surrounds, with three comparisons, described below.

3.3.4.2.1. *Samples with uncontrolled fire and herbivores*

Kolmogorov-Smirnov tests of merge event distributions were conducted between samples from outside of the 'Nwashitsumbe enclosure (NEO, NWO, SEO and SWO). Pair-wise comparisons were made between each of the four samples, totaling six tests. The comparison tested for the effect of similar fire and herbivore intensity on the cross-scale morphology of woody vegetation in the landscape. The null hypothesis is that the samples come from the same continuous distribution (α=0.95).

3.3.4.2.2. *Samples with browser exclusion*

Kolmogorov-Smirnov tests of merge event distributions were conducted on samples from inside and outside of the 'Nwashitsumbe enclosure (NE, NW, SE and SW tested against NEO, NOW, SEO and SWO); pair-wise comparisons were made between all inside samples and outside samples, totaling sixteen tests. This comparison tested the influence of the herbivore exclusion on the samples that have been protected from fire for longer periods of time. The null hypothesis is that the samples come from the same continuous distribution (α=0.95).

3.3.4.2.3. *Samples with a known fire regime*

Kolmogorov-Smirnov tests of merge event distributions were conducted between samples from inside the 'Nwashitsumbe enclosure (NE, NW, SE and SW). Pair-wise comparisons were undertaken between each of the four samples totaling six tests. This comparison tested the effect of fire without the influence of browsers on the system. The null hypothesis being that the samples come from the same continuous distribution (α=0.95).

Any distributions considered from the same continuous distribution were correlated against the time since the last known fire and the time since the last known browsing.

3.3.4.3. **Sub-objective 4.3:Spatially explicit discontinuity analysis: Does the cross-scale morphology of 'Nwashitsumbe differ from a neutral landscape?**

I speculate that if discontinuous structure is evident due to the entrainment of pattern and processes in a landscape, then manipulation of the major drivers over a long period of time should result in changes in the discontinuities between treatments. But, given the importance of context in determining vegetation pattern–process relationships (Levick and Rogers, 2011), I must exploit the local nature of linear scale-space analysis.

Discontinuity analysis of a linear scale-space is novel and presents a number of unique challenges; analysis of scale-space events is not the equivalent to the analysis of the body mass distribution of species. To draw a parallel, a merge event is analogous to a single measure of an individual animal's body mass, where the species is unknown and so one cannot average the data. Merge events represent the raw values of pattern expressed in the system. However, the principle of causality inherent in the linear scale-space application allows for a convenient solution to the issue of stationarity in landscape analysis. By testing each individual scale-space volume for the presence of discontinuities independently, it becomes possible to test each area of pattern in the landscape.

This is the *fundamental reason as to why linear scale-space is used; due to the principle of causality, structure at large scales can only have been created through the merging of structure at smaller scales*. Each scale-space volume, described as a single connected node graph termed a *primal sketch* (Figure 3.16) contains merges specific to the hierarchically structured pattern in that region of the landscape. Each primal sketch is analyzed independently and the pattern at higher scales can only be generated from pattern at lower scales, stationarity is therefore not assumed.

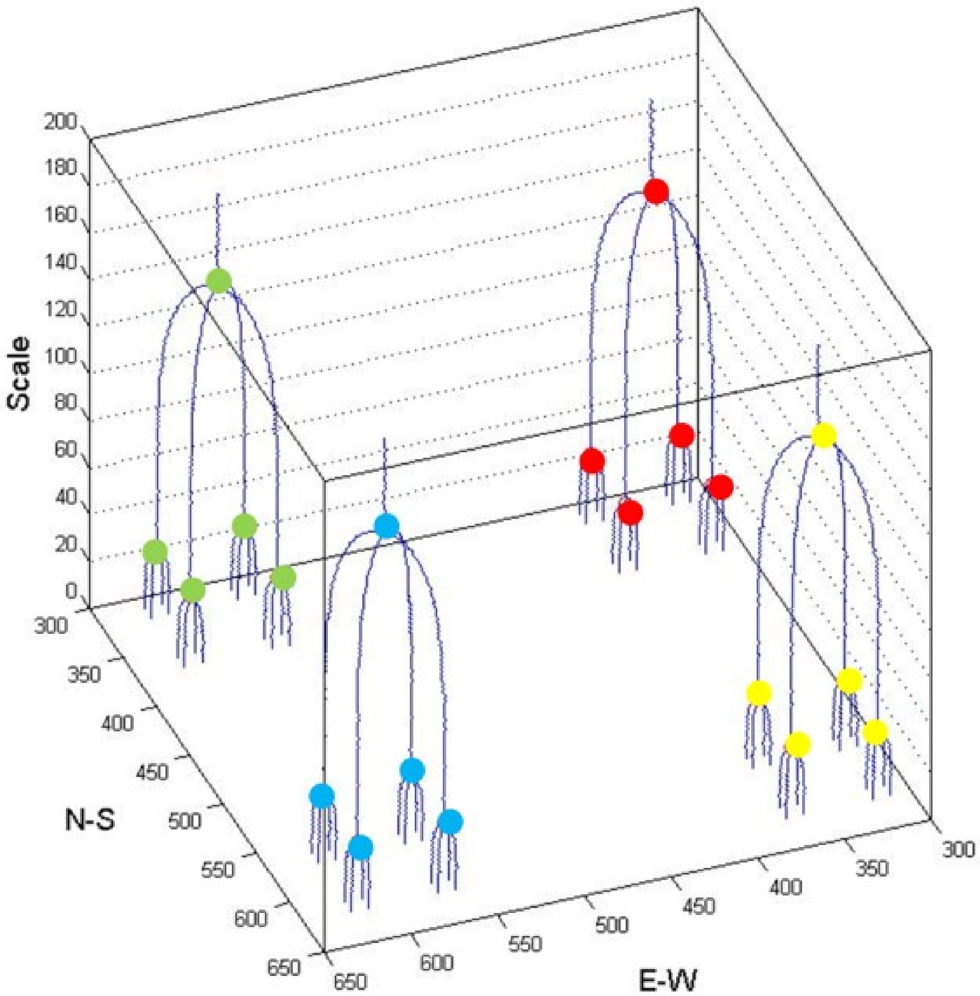

Figure 3.16: Causality of pattern; the structure at larger scales can only have been created through the merging of structures at lower scales. Each separate node graph in the scale-space contains merges specific to the hierarchically structured pattern in that region of the landscape. These merges are tested as a set, indicated as different colors, for the presence of discontinuities in the scale dimension.

Spatially explicit data derived from a linear scale-space introduce an additional trend to that due to scale. As methods are not available I developed one for use in this thesis. Based on resampling methods to detect discontinuities (Restrepo et al., 1997, Stow et al., 2007), I developed a method which allows for the probability that a gap between merge events from an individual primal sketch is larger than that predicted by random chance.

This method was applied to each gap of every single individual primal sketch within the linear scale-spaces derived from input images. Once the presence or absence of discontinuities was determined in a landscape, I had a spatially explicit measure of the cross-scale morphology of the system which indicates where and at what scales these occur. The discontinuities were then be overlaid over the original images to be depicted spatially. The proportions of discontinuities were compared between the 'Nwashitsumbe samples and against the neutral landscapes to infer the effect of processes on the nature of discontinuities in the landscape.

Spatially explicit discontinuity analysis is a novel technique. To perform the analysis I use the principle of causality and use each separate sketch in the 'Nwashitsumbe landscape and compare this to primal sketches of similar size, derived from the general form of the neutral landscapes. I reiterate, for the 'Nwashitsumbe samples I do not lump the dataset, rather each individual primal sketch is analyzed in the landscape.

3.3.4.3.1. *Spatially explicit discontinuity analysis*

There are three steps in the spatially explicit discontinuity analysis: determination of the neutral model specific to the landscape , a Monte Carlo based simulation to detect discontinuities and the subsequent visualization of those that are found.

1. Determination of the Neutral Model

For the neutral landscapes applicable to each image, the merges were lumped and distributions approximated by using the frequency distributions of the scale value for each of the ten neutral landscape replicates.

Kernel density estimation was used to calculate frequency distributions; with the kernel width kept to a single scale unit and analysis bounded to the positive domain to allow for maximum resolution in the scale dimension. To obtain the values for the null model comparison, the ten estimates were averaged and the upper and lower standard deviations are calculated. This constitutes the form of a neutral model, specific to the semi-arid savanna landscape image being analyzed, indicating what the cross-scale morphology of a similar landscape without the effect of process would be like.

2. Monte-Carlo based simulation to find discontinuities

Each primal sketch (p) is a vector of xyz values, depicting the locations in scale-space where merges occur. Each image contains a number of primal sketches; i.e.: $P= \{p_i....p_N\}$.

For each individual primal sketch (p_i) from the set of primal sketches derived from the test image (P), the following was performed on the scale-axis (the z-value) of the merge events;

1. The z value of the merge events for the test data set were ranked (let the z value of merge events from the primal sketch (p) be represented by μ) and the gaps between the merge events (γ), calculated as; $\gamma_i = \mu_{(i+1)} - \mu_i$
2. The number of gaps in the primal sketch of interest were determined (γ_N);
3. 5,000 hypothetical primal sketches were created by sampling from the known distribution of neutral landscapes created. Each neutral primal sketch has the same number of merge events as the test dataset (N) and was sampled with replication.
4. Each of the 5,000 neutral primal sketches was ranked, δ is equivalent to γ for process free images and the gap size between data points determined: $\delta_i = z - z_i$;
5. For each rank($i = \{1 \dots N\}$), there are 5,000 samples, each a gap indicating the scale-space blob lifetime of a primal sketch from a neutral landscape. For each rank an empirical cumulative distribution function (ecdf) is calculated, one per rank calculated from the 5,000 samples.
6. The density value from the ecdf is a percentile; a measure of the proportion of the neutral samples that the real world gap is greater than. To generate a measure of the percentile of the gap relative to the null model the gap value of the test primal sketch is compared to the corresponding value in the ecdf for rank = i.

The algorithm generated a percentile value for each gap, for each primal sketch, in each image. I have termed this value the *Discontinuity Probability Value* (DPV). The DPV is not a test statistic per se, but rather a proportion of gaps from the neutral sample that the test gap is larger than. The DPV is a measure of the proportion of gaps that it is greater than those gaps expected from random chance. Assuming that the same distribution will hold, a fair assumption given the 5,000 replicates, the DPV can be interpreted as a probability, analogous to a P–value. Gaps are considered to be discontinuities if their DPV value is greater than 0.95.

3. Visualizing discontinuities in the landscape

Although projected as a spatial entity, it must be remembered that this patch represents a volume in the scale-space. To project the gap spatially, the BLOB of approximately twenty percent of the height in the scale-space volume is projected (Figure 3.17). Patches were considered to be the gaps with a DPV value greater than 0.9. Nested discontinuities, as in hierarchically nested structure, will be represented by multiple nested patches with high DPV values.

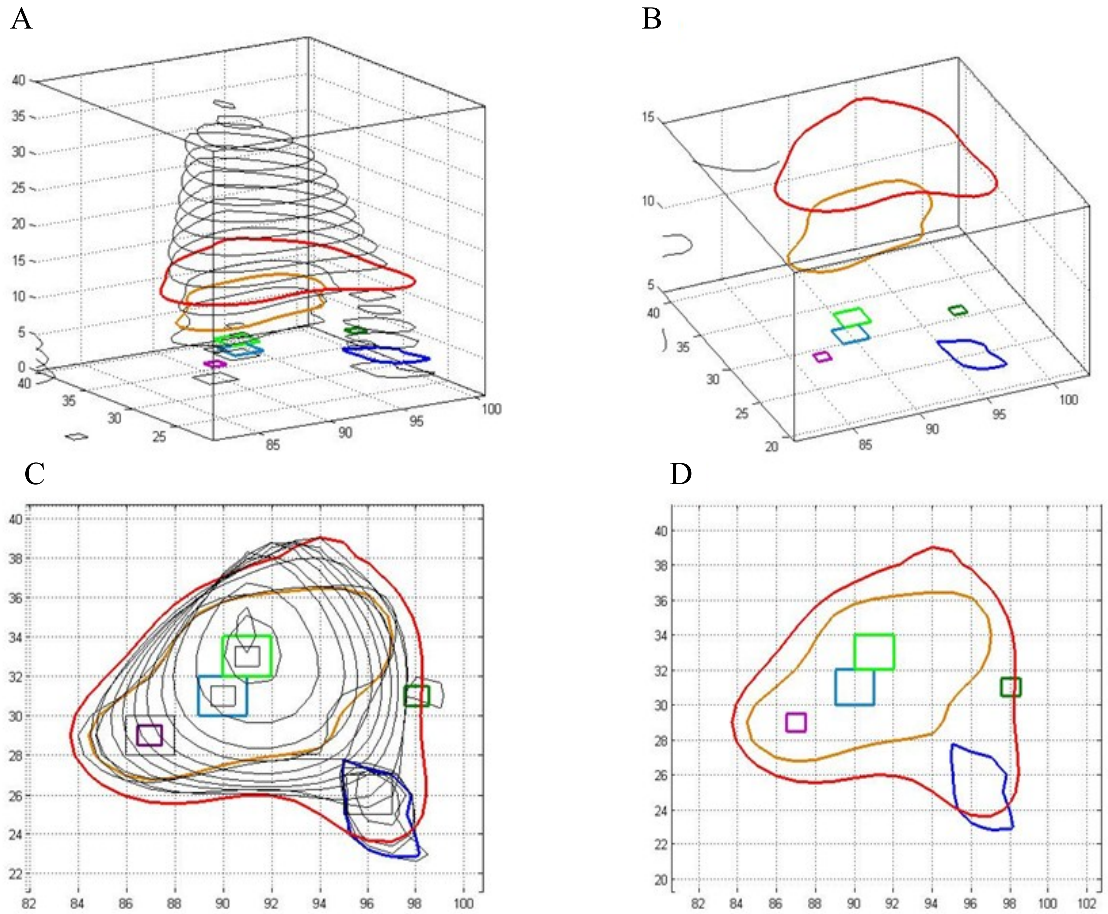

Figure 3.17: Spatially explicit discontinuity analysis; illustrating the re-projection of the discontinuities back onto the landscape. The scale-space volume (A) is represented by the BLOBs at 20 percent of the lifetime of the scale-space blob, B. From a bird's eye view this results in a hierarchically nested set of patches in the landscape (C-D).

For the purposes of interpretation I present visualizations of the following test landscapes:

1. A neutral landscape with 50% cover and single pixel trees analogous to the *global constraint* image of (viz. Scanlon et al., 2007).
2. A neutral landscape generated with 25 % cover, 5 pixel canopy cover and 500 pixels in image extent.
3. A perfectly hierarchically structured dataset.
4. Discontinuities from all eight images depicting woody canopy cover, extracted from the 'Nwashitsumbe enclosure sites are presented.

4. Test for robustness of the discontinuities

Concurrence between discontinuities extracted from null analysis using the neutral landscape, defined by the average, the upper and lower standard deviations will demonstrate that the pattern is robust. All comparisons were made using the average and the average plus one and minus one standard deviation.

3.3.4.3.2. *Comparison of results from discontinuity analysis between images and to neutral models*

Discontinuities were analyzed for neutral landscapes and the semi-arid savanna landscapes in all hierarchically structured datasets (as derived in Chapter Four). The proportion of all gaps in the dataset which are considered discontinuities (DPV>0.95) were calculated, for the average distribution of the neutral models and for the average plus one standard deviation and minus one standard deviation respectively. A box and whisker plot was used to compare the neutral landscapes and semi-arid savanna landscapes.

3.4. RESULTS

The results are presented per objective:

3.4.1. *OBJECTIVE 1: GENERATION OF BASELINE LANDSCAPE DATASETS*

Baseline datasets were successfully generated; due to the large number of replicates, only a subsample is presented in the text.

3.4.1.1. **Datasets with known cross scale morphology**

3.4.1.1.1. *Random Landscapes*

Examples of the random datasets generated have already been used to illustrate the comparative analyses in images Figure 3.12, Figure 3.13 and Figure 3.14. Although it is not generally accepted to present results before the result section, for the sake of brevity and clarity of explanation I chose to do so.

3.4.1.1.2. *Discrete cross-scale pattern*

Two separate images with discrete cross-scale structure were generated, one using an input variance of {0, 0, 0} with the algorithm derived by N. O'Leary (Figure 3.18A). The manually generated sample, used as an example already in this thesis is presented as comparison (Figure 3.18B). The images illustrate the perfectly nested sets of "trees" in a landscape of "no trees".

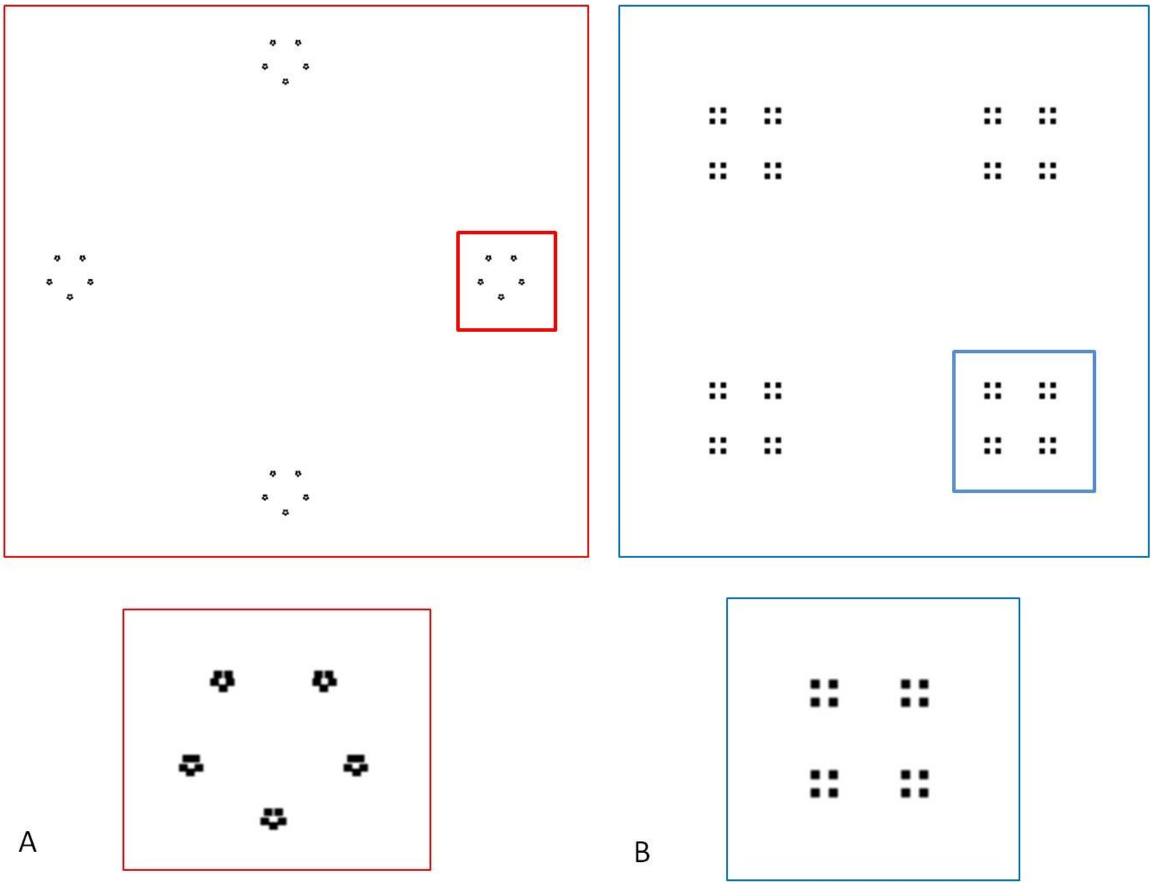

Figure 3.18: Linear scale-space representations of two hypothetical landscapes of perfectly nested trees, created as perfect sets. Binary "trees" are situated in a landscape matrix; each hypothetical tree is perfectly nested within a set at a larger scale, which is in turn nested at a larger scale. This approximates the conceptual framework of a perfectly nested hierarchy, in which patterns are entrained at distinct scales of analysis. A constitutes a radial pattern, which is isotropic; B constitutes the classic perfect square.

3.4.1.1.3. *Multi-modal cross-scale pattern*

Figure 3.19A was created using the O'Leary algorithm with input variance of {3, 0, 0}. Figure 3.19B, has input variance of {0, 30, 0}.

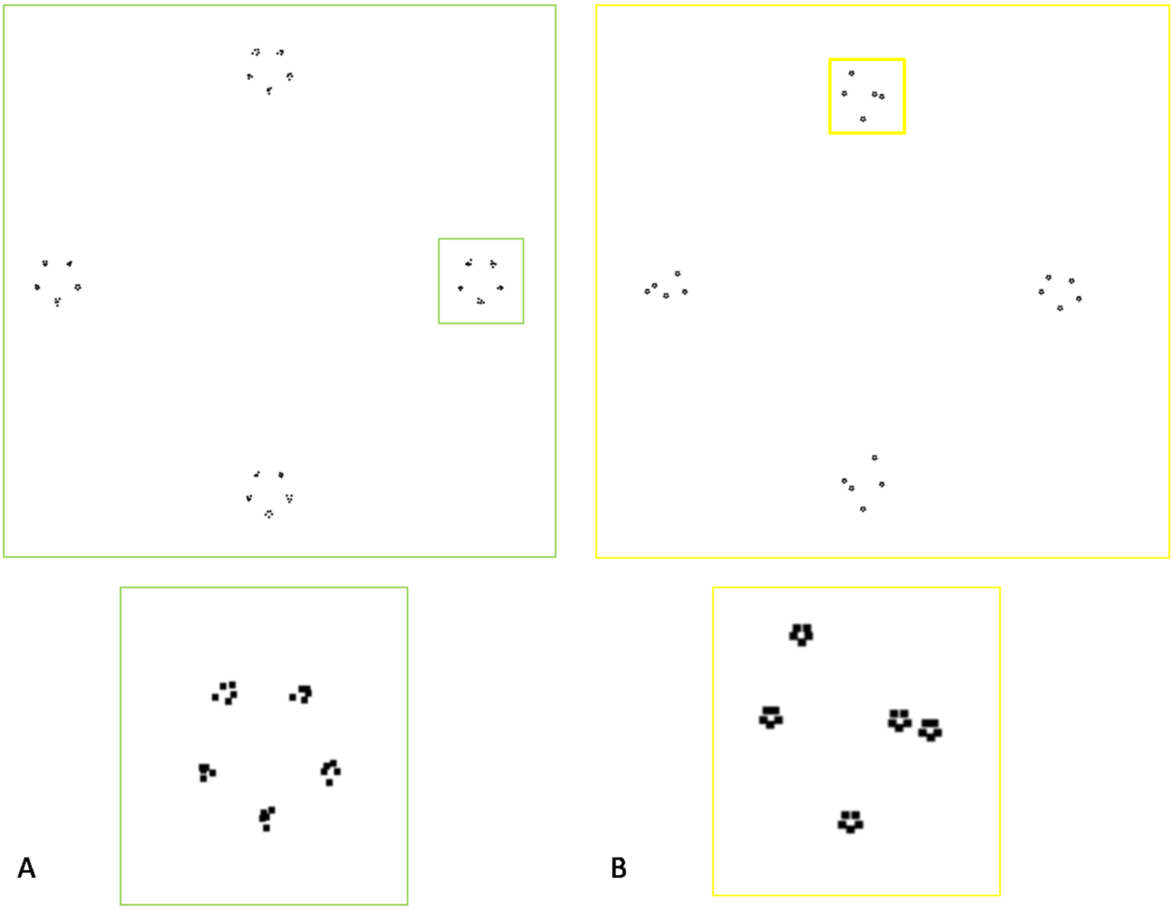

Figure 3.19: Images with three scales of pattern expression with allowed amounts of variance around the scales at which pattern is expressed. A has 3 units of variation around the first scale of pattern expression {3, 0, 0}; B has thirty units of scale around the second {0, 30, 0}. The inset images are zoomed in sections to illustrate the smaller scale pattern.

Replicate images for Figure 3.19 (A and B) were created using the same input variances. In addition, three replicates of a similar image with 300 units of variance at the top scale were constructed (image not shown here). Linear scale-spaces were created, the scale at which merge events occurs extracted and their distributions compared visually.

3.4.1.2. **Extraction of tree canopy cover from aerial photographs**

Woody vegetation cover was successfully extracted from the orthorectified images from 2001. The images are labeled according to their declination in the enclosure (

Figure **3.20**) with the suffix "O" being reference to the sample located outside of the enclosure (Figure 3.21).

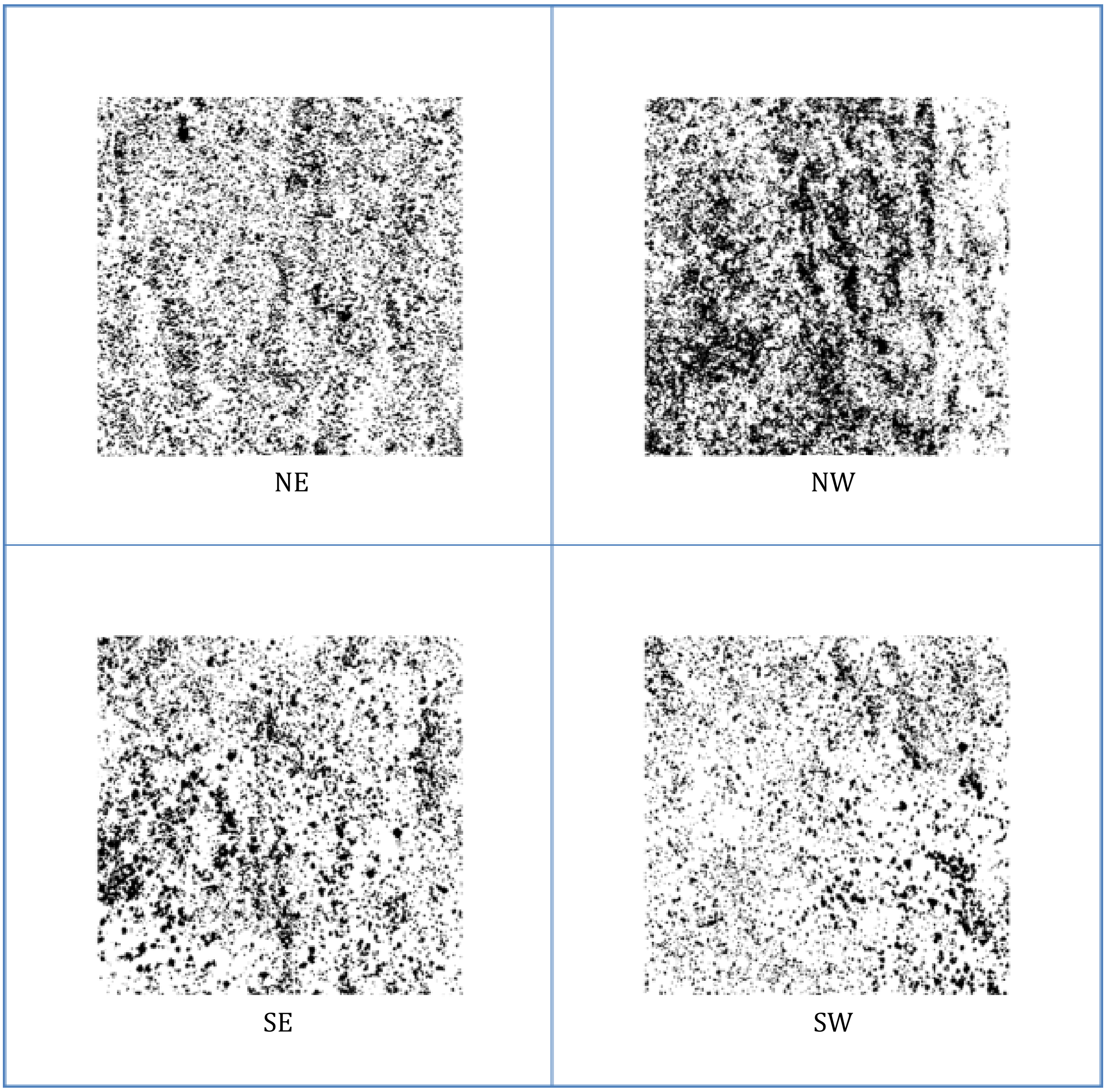

Figure 3.20: Binary images of woody canopy cover, extracted from inside the 'Nwashitsumbe enclosures.

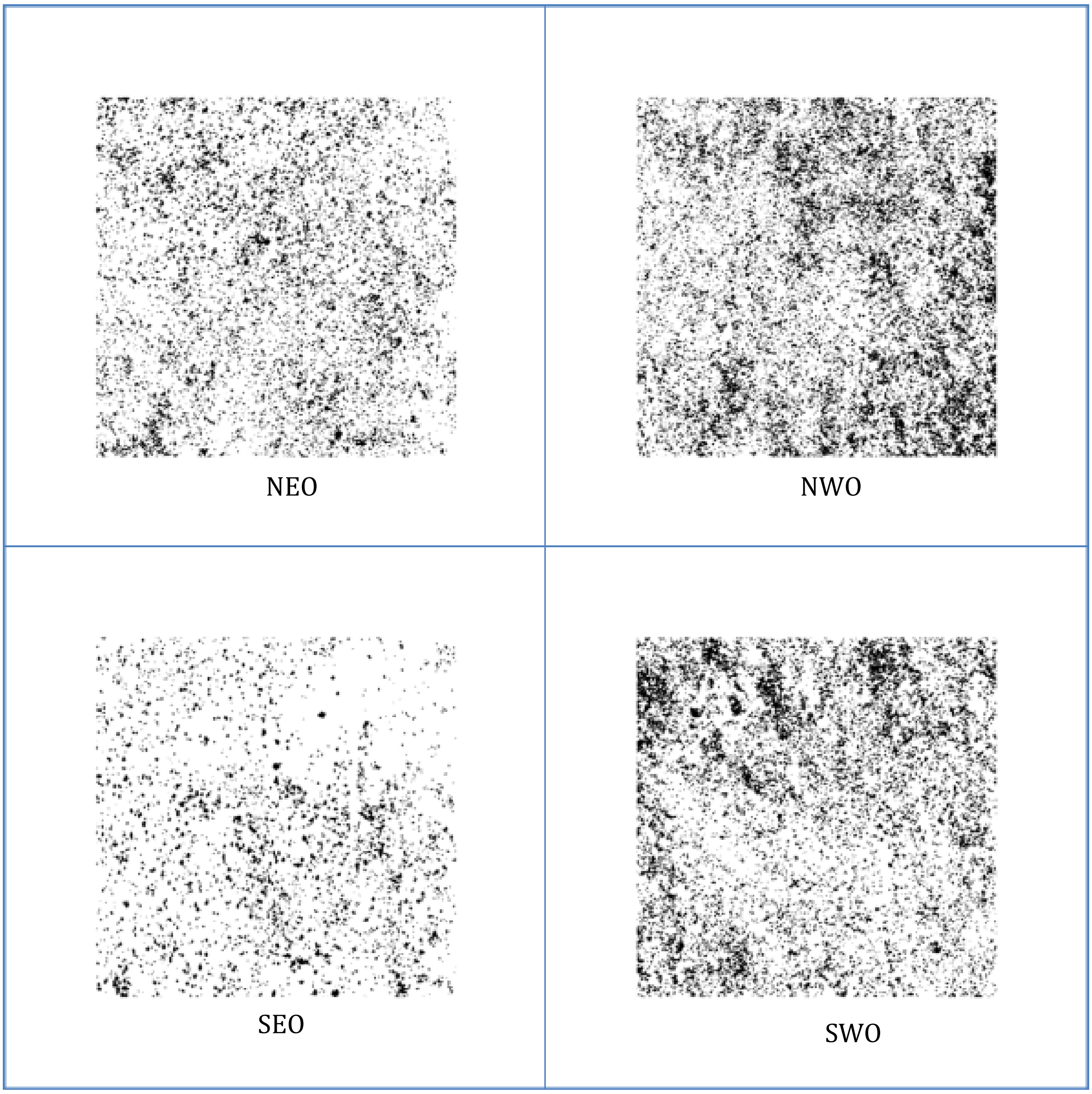

Figure 3.21: Binary images of woody canopy cover, extracted from outside the 'Nwashitsumbe enclosures.

3.4.1.3. **Generation of Neutral Landscapes**

Neutral landscapes that can be used to compare against the 'Nwashitsumbe samples were successfully created.

3.4.1.3.1. *Measurement of tree size and woody cover density*

The size class distributions of woody cover patches were determined from the first scale of BLOB detection in the scale-space stack, rendering a frequency distribution for each image, (Figure 3.22). Similarly the approximate percentage canopy cover was calculated for each of the samples (Table 4).

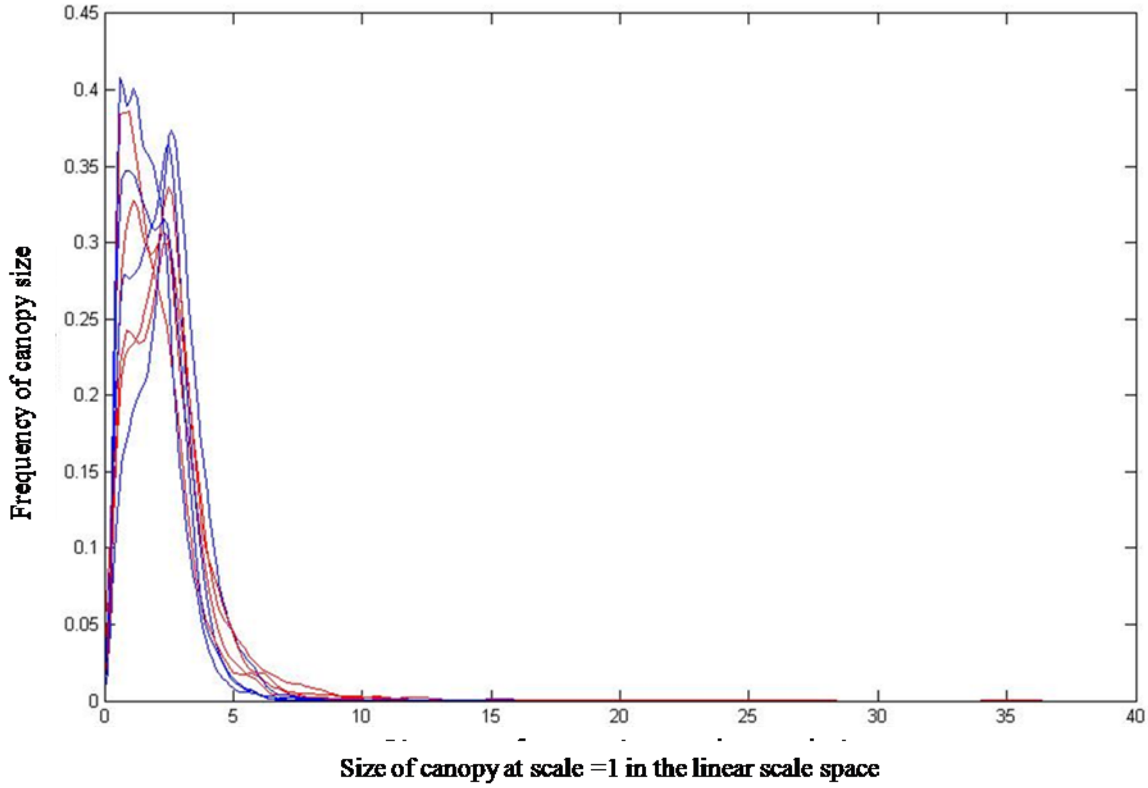

Figure 3.22: Size class frequency distributions for canopy size trees inside and outside of the 'Nwashitsumbe enclosure. Red lines indicate patch size distributions from inside the 'Nwashitsumbe enclosure, while blue lines indicate samples from outside the enclosure.

Table 4: Percentage canopy cover for semi-arid savanna samples, as determined from the first scale of BLOB extraction.

'Nwashitsumbe sample	Approximate percentage canopy cover
NE	25
NEO	20
NW	28
NWO	23
SE	24
SEO	15
SW	22
SWO	21

For seven of the eight 'Nwashitsumbe images, all parameters were within five percent and so a single set of ten process free images was used to compare those samples against. For a single process free image, the difference was greater than five percent in the average canopy cover and so a separate set of ten process free landscapes was generated. The size of woody canopy cover at the first scale of analysis was approximately 4 pixels in diameter.

3.4.1.3.2. *Creation of neutral landscape images comparable to 'Nwashitsumbe samples*
Based on the above results, ten images of twenty five percent canopy cover were created and ten images of fifteen percent canopy cover were created, with individual patches of 5 pixels in diameter. The images with 25% percentage canopy cover have less than 5% difference to seven of the samples from the 'Nwashitsumbe enclosures. A separate ten images with 15% cover were created to compare with the South East Outside sample, which had a 15% cover. This totals twenty sample process free images, ten for images of 25% cover, and ten for image of 10% cover.

For the sake of brevity, images are not presented here as they are included as insets in the primal sketch images in section 3.4.2.3.

3.4.2. *OBJECTIVE 2: LINEAR SCALE-SPACE GENERATION*

The following primal sketches are graphically represented here; these are not the entire dataset, rather samples for demonstration of the concept.

1. Datasets with known cross scale morphology:
    1. Random landscape (a sub-sample).
    2. Discrete cross scale pattern (a sub-sample).
    3. Multi-modal cross scale pattern (a sub-sample).
2. 'Nwashitsumbe Landscapes (a subsample).
3. Neutral landscapes (a subsample).

In the samples, the scale-spaces are represented as three dimensional node graphs, with merge events as red dots. The Z dimension represents the scale of sample (derived as the bandwidth of the Gaussian kernel) thereby tracing the evolution of woody tree canopy cover across scale.

3.4.2.1. **Datasets with known cross scale morphology**

3.4.2.1.1. *Random landscapes*
Linear scale-spaces were generated for all images but only four are presented here; four neutral landscapes with varying tree sizes from images with 1, 5, 10 and 20 pixels respectively (Figure 3.12).

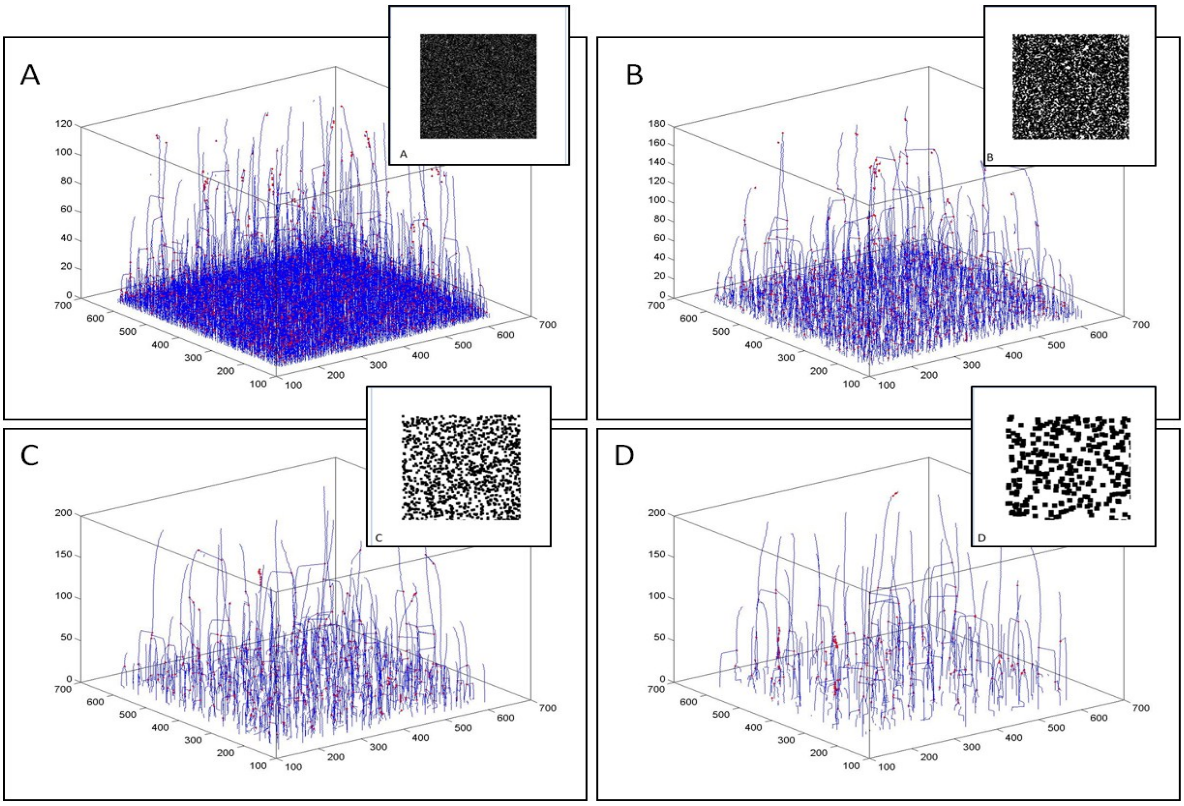

Figure 3.23: Linear scale-space primal sketches of neutral landscapes with varying tree sizes from inset image (Figure 3.12). Woody canopy cover across scales is represented as primal sketches drawn as 3D node graphs from images with 1, 5, 10 and 20 pixel sized trees in A, B, C and D respectively. The size of the trees affects the number of trees possible in a landscape and thereby the number of primal sketches and merge events which are possible. Small trees relative to the image size have much more dense primal sketches in a given linear scale-space.

3.4.2.1.2. *Discrete cross-scale pattern*

Primal sketches were generated of the hypothetical landscapes with perfectly nested tree structures (Figure 3.18 A and B). The primal sketch traces the evolution of pattern as scale increases. Trees merge into larger patches (Figure 3.24A, blue box), which themselves merge at larger scales into larger patches (Figure 3.24A, red box). This nested hierarchy of structure is illustrated in the three dimensional node graph of the primal sketch (Figure 3.24B)

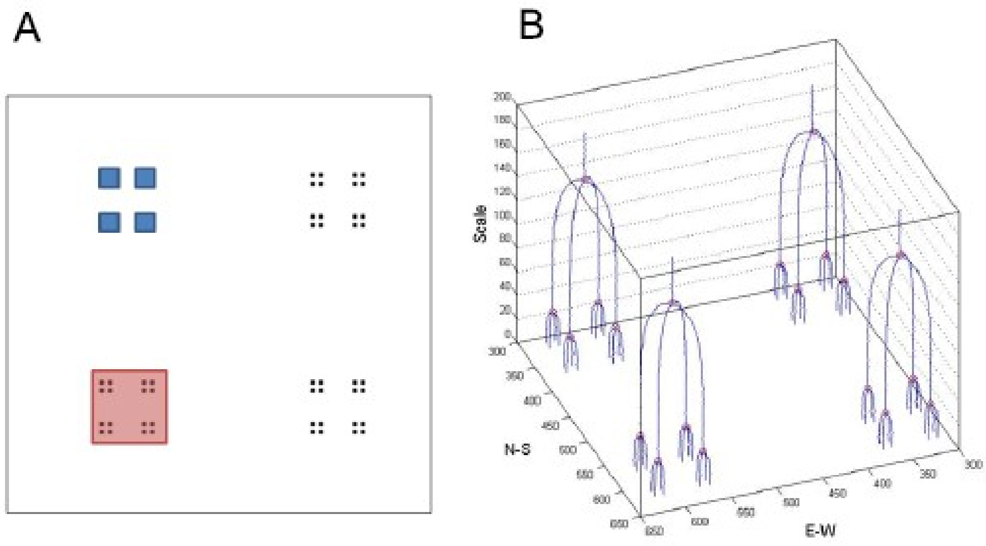

Figure 3.24: A linear scale-space primal sketch of a hypothetical landscape containing multi-scaled structure perfectly nested. Trees merge into larger patches (A, blue box) and these in turn merge into larger patches (A, red box). This evolution of pattern across scale is explicitly measured in the primal sketch of the image (B).

3.4.2.1.3. *Multi-modal cross-scale pattern*

The application succeeds in creating primal sketches of the hierarchically nested analysis. The primal sketches of the multi-modal distributions do differ from those from a perfect set as expected. The scales at which merge events occur are not confined to narrow a range of scales, resulting in asymmetry in the primal sketch itself (Figure 3.25). In a few instances, the merge events may not even occur, indicating that this structure is not actually part of the larger structure, but rather it annihilates out of existence and is not incorporated in larger scale pattern (Figure 3.26).

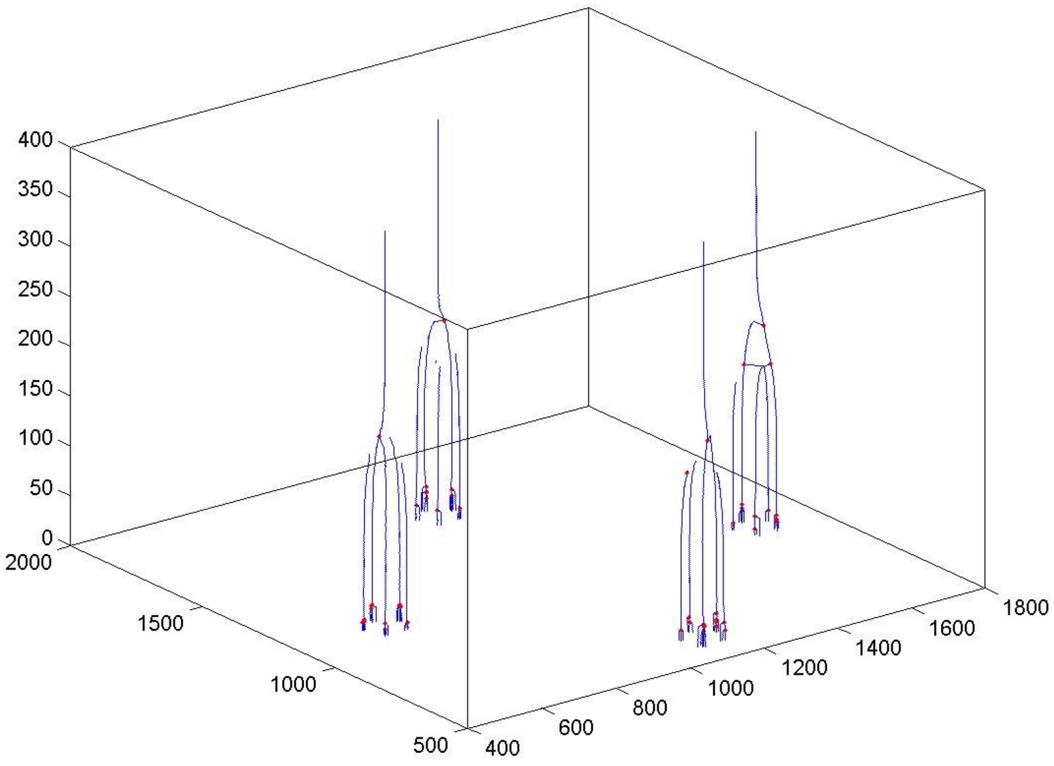

Figure 3.25: A linear scale-space primal sketch of a hypothetical landscape containing nested hierarchical structure. The input image Figure 3.19(A) was created by the algorithm developed by O'Leary (Appendix), with three units of variance around the lowest scale of pattern expression. Not all small scale pattern links into the larger patch. Some of the pattern terminates in annihilation events and does not merge.

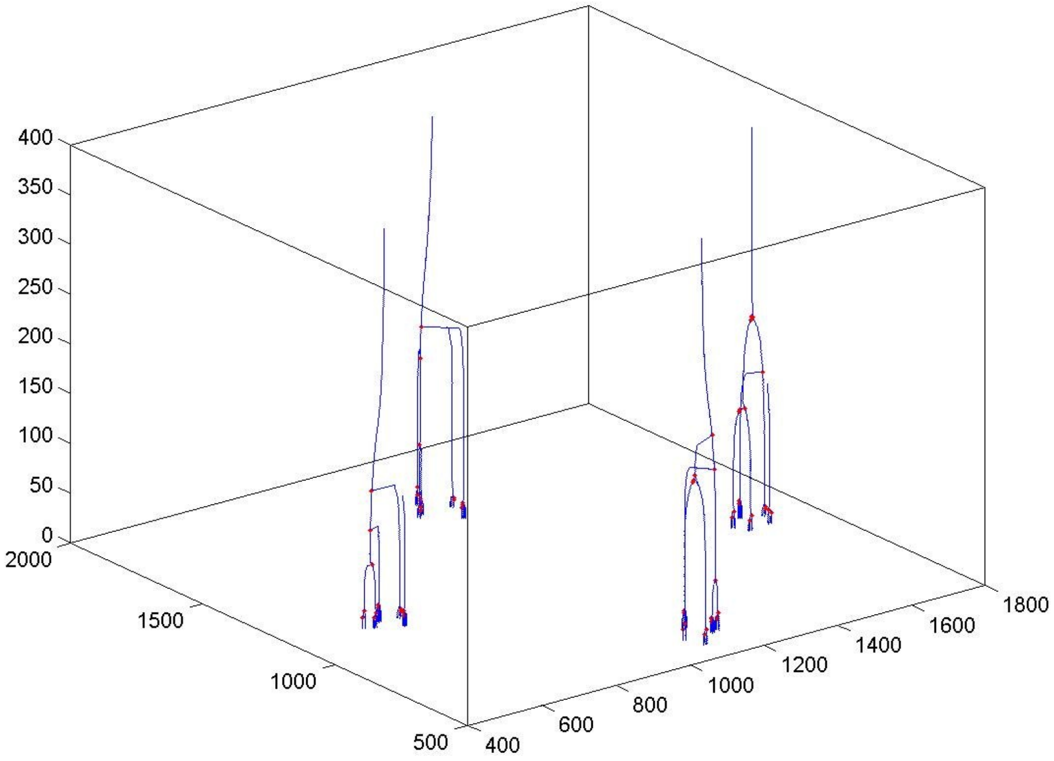

Figure 3.26: A linear scale-space primal sketch of a hypothetical landscape containing nested hierarchical structure. The input image Figure 3.19 (B) was created by the algorithm developed by O'Leary (Appendix), with thirty units of variance around the middle scale of pattern expression. Almost the entire pattern merges into the larger scale structure, with very few annihilation events.

3.4.2.2. **Linear scale-spaces of 'Nwashitsumbe samples**

Linear scale-spaces were generated for all eight images of the Nwashitsumbe enclosures. Only the primal sketch of the North West sample of the Nwashitsumbe enclosure is presented here.

The binary dataset depicting woody canopy cover (Figure 3.27 A) was extracted from aerial photographs, of the NW sample of the 'Nwashitsumbe enclosures (Figure 3.27A). A primal sketch was created after the linear scale-space creation, BLOB feature extraction and linking algorithms (Figure 3.27 C-E). The development of woody structure through scale was mapped in three dimensions. In Figure 3.27 C, D and E represent progressively increasing zooms of the primal sketch, illustrating the level of detailed information in a linear scale-space. Each individual tree and patch in the landscape was tracked across all scales and points at which trees merge with other trees to become larger patches and identified and marked

(Figure 3.27; Merges are indicated by red dots).

Viewed in profile (Figure 3.28); the primal sketch of the semi-arid savanna demonstrates how the woody cover changes across the scale-dimension. Each tree canopy, or patch of trees, traces through the scale-space and shows evidence of significant pattern at the scale in question. Where a patch of trees is no longer of significance at the scale in question, the primal sketch line terminates in an annihilation event (Figure 3.28 A: Figure 3.28 B is a zoomed view).

Where trees and patches merge, the primal sketch lines join (indicated by a red dot in Figure 3.28 C; Figure 3.28 D is a zoomed view). In sections of any particular primal sketch there are “zigzags” evident (two examples of which are circled in Figure 3.28 B). These zigzags are simply a graphical artifact. To draw the three dimensional graph the critical points of the BLOBS are used. The analysis is not sub-pixel therefore the X and Y co-ordinates of the minima points are rounded to the nearest integer. Rounding error means it may change to one of the four corners of the pixel. When zoomed in and at an oblique angle, this appears as a *wiggly* line. This does not affect the analysis; it is simply apparent in the graphical representation.

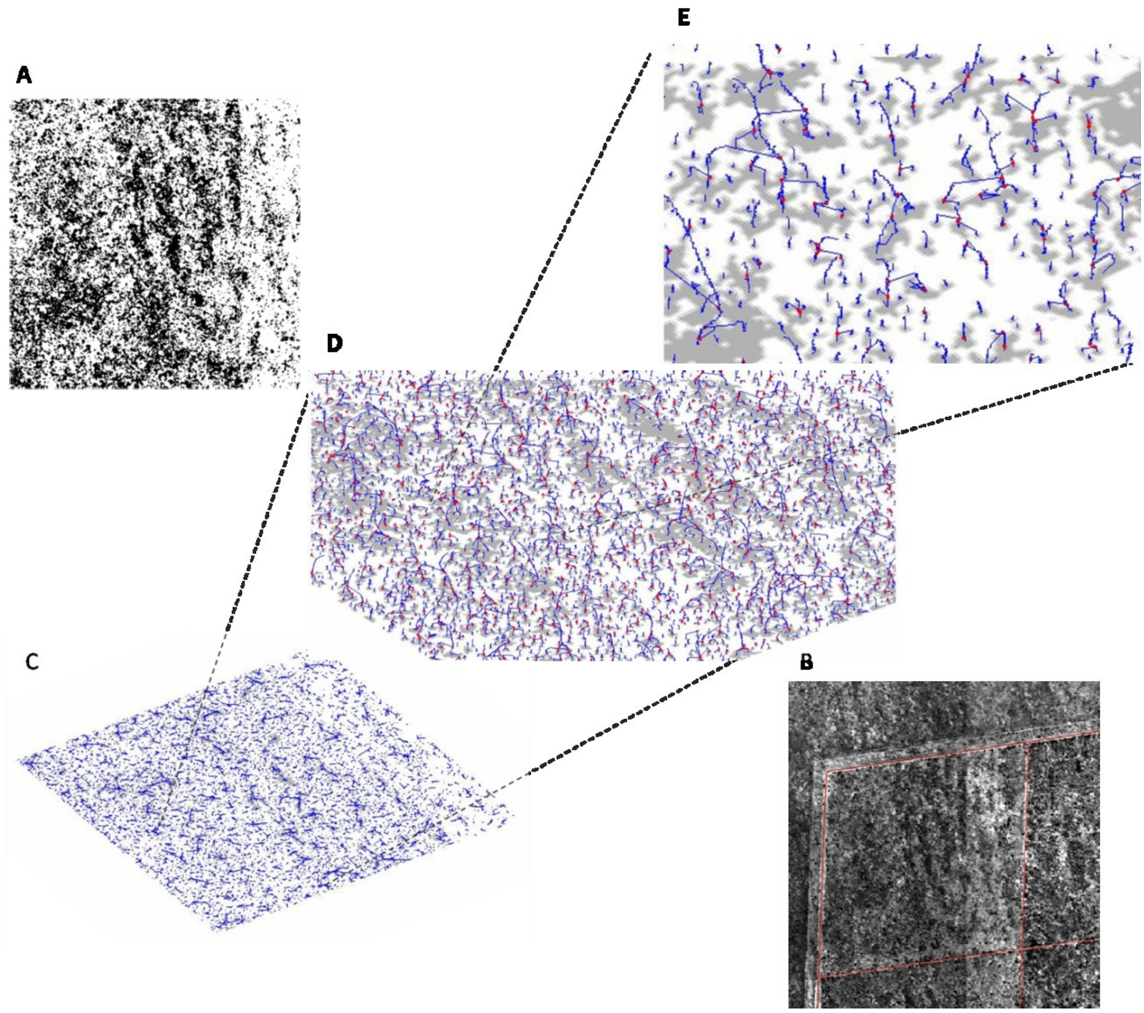

Figure 3.27: A linear scale-space primal sketch of a semi-arid savanna in Kruger National Park, South Africa. The binary data representing canopy cover (A), is extracted from the orthophotos (B) of an experimental browser enclosure experiment. All the trees in the landscape have their evolution through scale traced as a primal sketch, C-E showing successive zoom into the dataset. Points in scale-space where woody cover merges into patches are indicated as red dots.

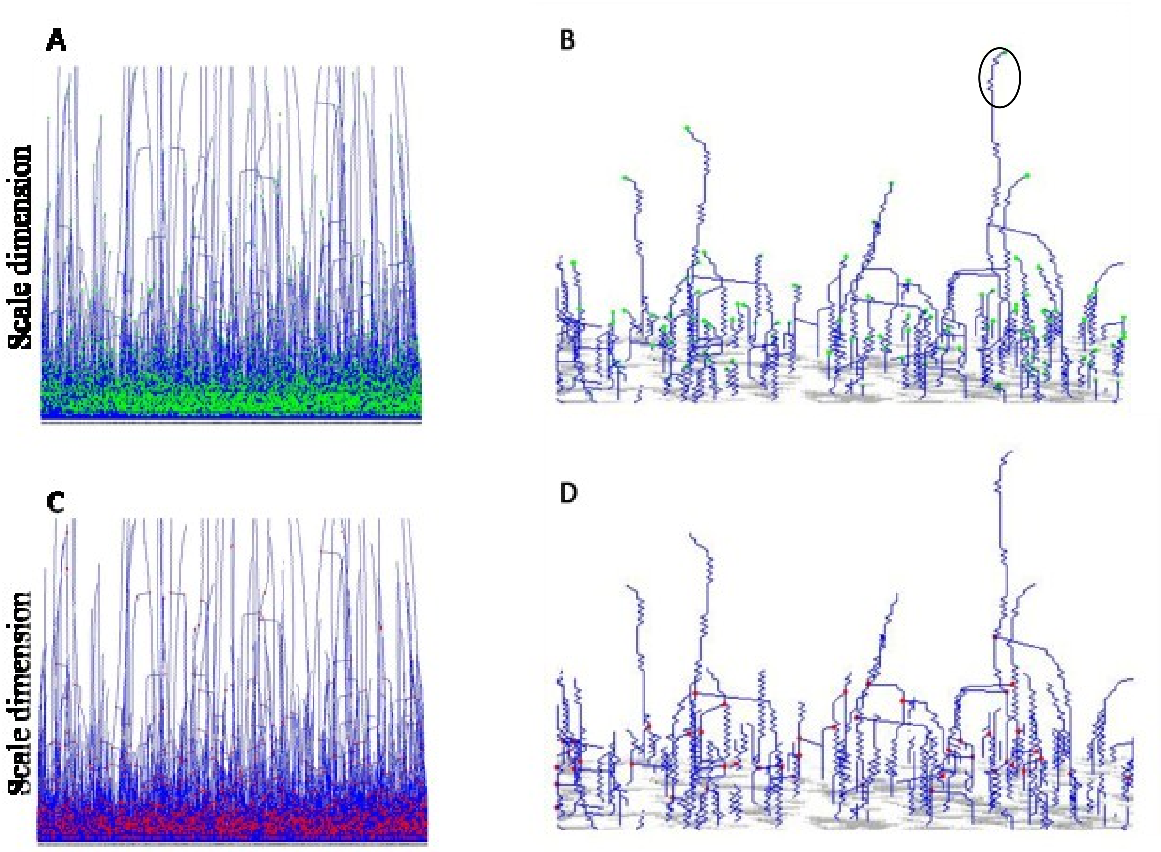

Figure 3.28 A profile view of the linear scale-space of a semi-arid savanna in the northern Kruger National Park, South Africa. The primal sketch is rendered from the same landscape image as Fig. 3.27. The profiles (A & C) of the linear scale-space illustrate how woody vegetation cover evolves across the scale dimension. Scale-space events are represented as annihilations (green dots) and merges (red dots). Annihilations indicate the scale at which woody canopy cover is no longer significant. Merges indicate the scales at which trees merge to form patches of trees. B and D are zoomed in regions of the linear scale-space, illustrating the annihilation and merge events. The circle in B indicates a graphical artifact, where rounding errors move the node in three dimensions and create the impression of a "wiggly" line. This does not affect the analysis, simply the representation.

3.4.2.3. **Neutral landscapes**

Linear scale-spaces were created for all twenty neutral landscapes that were to be used in comparison; only one example is illustrated here.

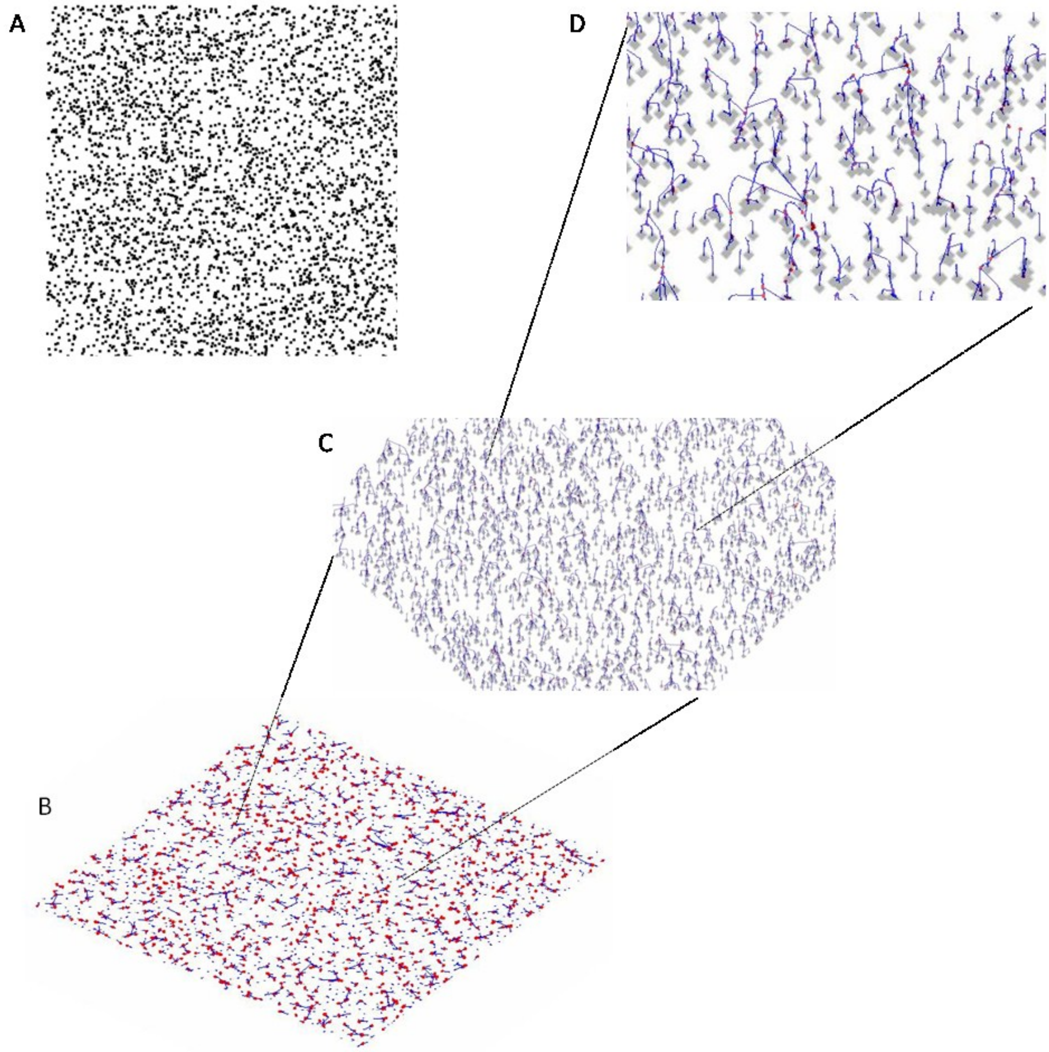

Figure 3.29: A linear scale-space primal sketch of a hypothetical, neutral landscape (A), with 15% woody cover and an average “tree” size of five pixels in diameter. All the hypothetical canopies and patches in the landscape have their evolution through scale traced and represented as a primal sketch, B-D showing successive zoom into the dataset. Points in scale-space where woody cover merges into patches are indicated as red dots.

3.4.2.4. **The error cleaning algorithm**

There are errors prevalent in the data, the total numbers of connections which can be considered an error are up to three percent when summed (Table 2). These were removed using the clearing algorithm.

Table 5: The number of errors detected in the linear scale-spaces of the 'Nwashitsumbe samples and the process free landscapes used as neutral models. The raw numbers are indicated, as are the total number of nodes in a scale-space, to allow for perspective. The numbers of errors are very small relative to the total number of connections that have been made in a graph. Creations split events constitute connections to nodes above, but not below, violating the principles of causality and therefore being classified as an error. Floaters constitute nodes which have not been assigned a connection. These are all removed by linking them within to the closest node within bounds.

	No. of nodes in the scale-space	No. of Creation events detected and removed	No. of Split events detected and removed	No. of Floaters detected and removed	Summed errors as a proportion of the total
Average for reps of 5 pixel trees, 15% cover (n=10)	98215.4	434.8	12.9	1170.5	0.016476
Average for reps of 5 pixel trees, 25% cover (n=10)	43949.6	413.2	2.4	769.2	0.026958
NE	122357	341	4	1465	0.014793
NEO	113949	85	1	737	0.007223
NW	117954	1263	6	2673	0.03342
NOW	144190	380	3	1740	0.014724
SE	95909	417	3	1128	0.01614
SEO	79085	45	17	410	0.005968
SW	98029	208	0	775	0.010028
SWO	118649	288	4	1349	0.013831

There are three percent less errors after the cleaning algorithm than before, this increases the likelihood of correct ownership of low scale BLOB’s by higher scale BLOBs. It is noted that the cleaning is not a hundred percent; not all of the errors are removed and a number of erroneous events may still occur. Moreover, the error cleaning algorithm does not clean BLOB errors.

3.4.3. *Objective 3: To demonstrate outputs of the linear scale-space application and to validate the linear scale-space application for repeatability of the algorithm and in detecting the scale of pattern expression*

The application does extract the pattern expected from the conceptual framework. There are, however, a number of errors in the application which may make interpretation of the results difficult.

3.4.3.1. **Sub-objective 3.1: Does the cross scale morphology of the landscapes of known cross scale structure conform to the conceptual framework?**

I expect that nested hierarchical structure would have a multi-modal distribution of merge events in the cross scale distributions. Random datasets would have no particular scale of high distribution and would follow a negative exponential curve which reflects the relationship between space and scale of analysis.

3.4.3.1.1. *Random Datasets:*

The cross-scale morphology of the discrete cross scale pattern images; illustrated as density of merge events against the scale of the merge events is multi-modal, as expected. The scales of merge events are constrained to scale 29 and between scale 145; 147 for the blue line, which illustrates the merges of the landscape presented in Figure 3.24. For the primal sketch illustrated in Figure.3.30 B the merges are all at scales 12; 13; 15; 16; 17; 19 and 204; 205.

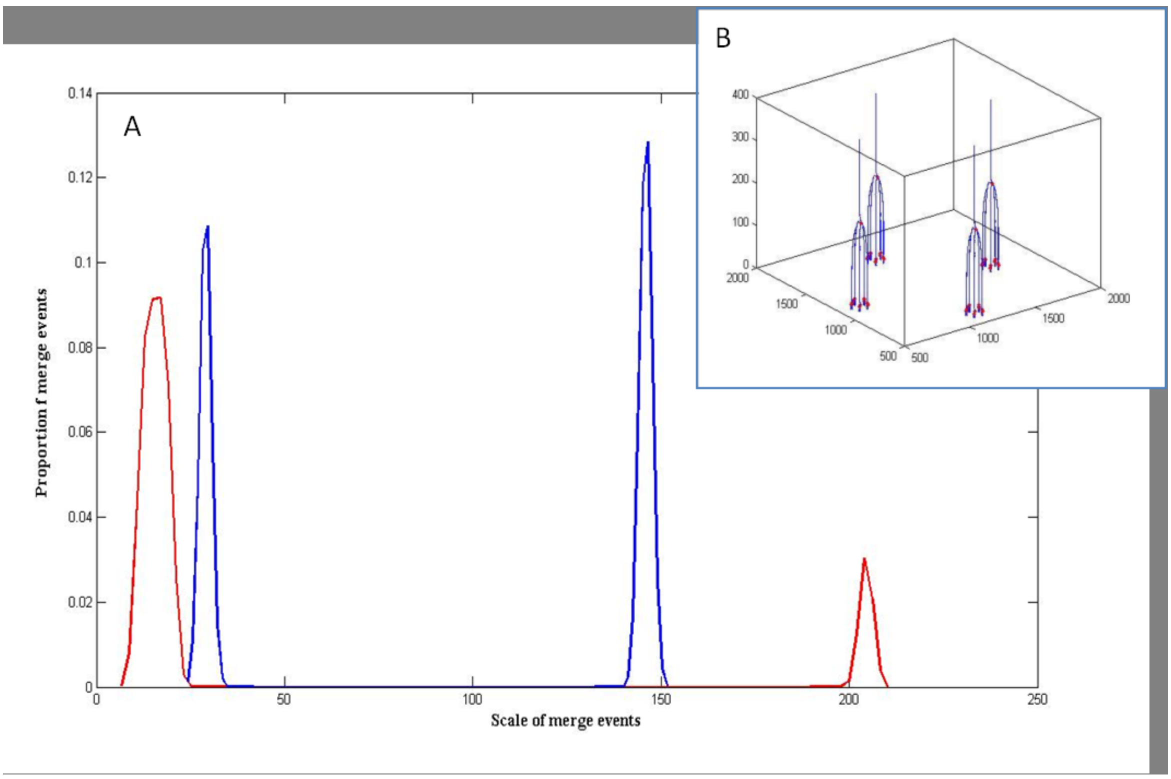

Figure.3.30: The cross-scale morphology of hierarchically structured landscapes is multi-modal. The blue line indicates the distribution of merge events from the image presented in Figure 3.24 The red line illustrates the distribution from the inset figure B which is a hypothetical landscape generated to have zero variance around the modes of pattern expression. The algorithm can detect multi-modal structure in linear scale-spaces.

3.4.3.1.2. *Multi-modal cross scale pattern*

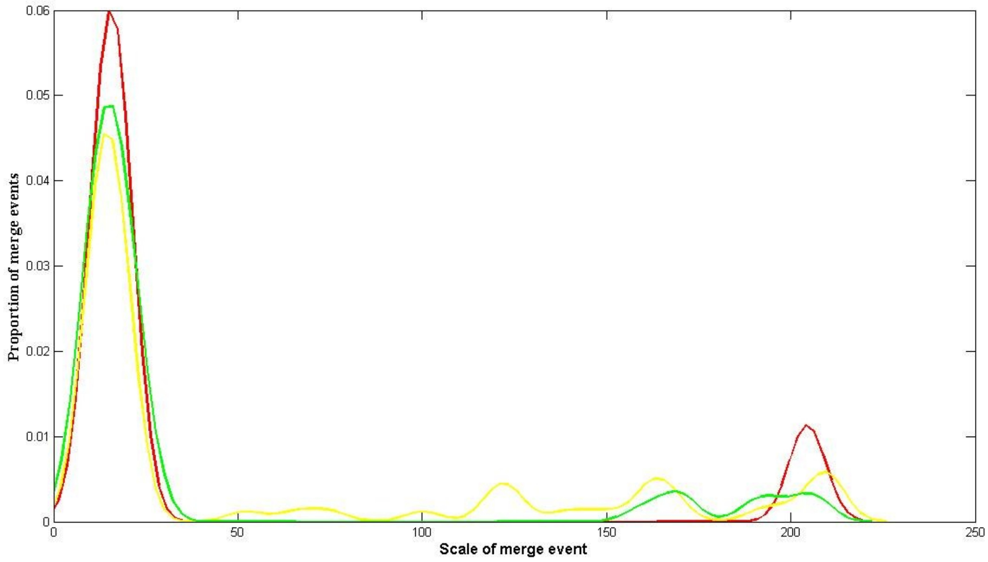

Figure 3.31: Scales at which merge events occur from images of nested hierarchies. The red line is a control plot, derived from an image with no variance around the scales of pattern expression (Figure.3.30, inset and red lines). The green line shows the scales of merges from an image with variance around the lowest scale of pattern expression (Figure 3.19 A, green box). The yellow line shows the scales of merges from an image with variation around the middle scale of pattern expression (Figure 3.19 B, yellow box) The distribution of the perfect set (red line) is distinctly multi-modal. The green and yellow lines are not as distinctly multi-modal, as the scales at which pattern is expressed varies, but there are still regions of scale over which there are higher densities of merge events.

The cross-scale morphology of the hierarchically structured landscapes shows a distinct multimodal pattern (Figure 3.31). Although not as neatly multi-modal as the perfect set, there are distinct zones in scale where merge events occur, with a larger amount of variation appearing as the zone becomes broader. Given that the cross-scale morphology of hierarchically structured datasets is multi-modal as expected, the application developed for this thesis can detect different configurations of hierarchically nested structure.

3.4.3.2. **Sub-objective 3.2: Demonstrate Repeatability; does the algorithm show similar cross scale morphology for landscapes with similar scales of pattern expression?**

P-values less than 0.05 indicate a rejection of the null hypothesis that the samples are from the same continuous distribution under a Kolmogorov Smirnov test. The majority of all the replicates demonstrated a low number of rejections (1/10 or 3/45; Table 6). However, there are four rejections out of ten possibilities in group *a* (these are samples comparing of the ten pixel tree size, twenty five percent canopy cover and five hundred pixels in extent), indicating that the pattern is not repeatable for this sample (acceptance of α=0.05). A post hoc test revealed that all rejections are between replicate two and the other four replicates.

Table 6: Replicate groups compared using Kolmogorov Smirnov tests. The null hypothesis is that they are from the same distribution. Each replicate group is a set of neutral landscapes, the distribution of scale values from merge events are compared pair-wise. The number of pair-wise comparisons within a replicate set is indicated and subsequently the number of times the null hypothesis is rejected, if rejected, the p-value is indicated.

neutral landscape	number of replicates	number of comparisons	number of rejections (α=0.05)	P-values of rejections
a	5	10	4	0.006; 0.024; 0.015; 0.017
b	5	10	1	0.024
c	5	10	0	n.a
e	10	45	3	0.003; 0.020; 0.014
f	10	45	1	0.031
g	10	45	3	0.005; 0.030; 0.039

There was an error in the application to generate the linear scale-space and erroneous merge events were created as the same BLOBs were linked multiple times during the linkage section of the algorithm. The linkages at low scales were effectively cleaned by the linkage cleaning, however, the influence of edge effects is a problem at higher scales. The convolution of data from outside the image area generates inverted BLOBS at high scales.

The result is important for two reasons; firstly, I realize that my application is not free of all error, even with the linkage cleaner. Secondly, although there is an error, it is not fundamental to the use of neutral landscapes as the patterns between all the other replicates in that sample were consistent.

There were other errors noted in the tests for repeatability, (Table 6), which were not introduced by an error in the algorithm and require explanation. Alpha values for all analyses are set at 0.95 rather than higher values to avoid a type one error (false positives). There is a risk of incorporating a type two error (false negatives); however, in the context of determining if a repeatable pattern is extractable from neutral landscapes it is more important to remove the likelihood of accepting different patterns as the same. Additionally, if forty five comparisons are made, each presenting an individual P-Value; by chance alone, between two and three samples are likely to reject the null hypothesis and be a false positive (a type one error).

In the right circumstances a Bonferroni adjustment can be used to remedy the effects of repeated measures (Rice, 1989). In cases where it is the global hypothesis of interest such as here, it is statistically valid. This analysis and application are a first attempt. Although statistically relevant, changing the P-value acceptance levels will not change the outcomes, but rather the audiences' perceptions of them. It is more useful for further research to realize that there are errors in the application; but be explicit that the errors are in the application and not the philosophy of using linear scale-space.

Given that some of the rejections (statistically most of them) of the null hypothesis (that the neutral replicates produce patterns that can be considered from the same distribution) may be due to chance alone; the application is remarkably repeatable. The errors that were brought to light by the lower acceptance values of alpha were generated by two sources, both of which pertain to the linkage algorithm responsible for linking BLOBs between scales into scale-space volumes.

3.4.3.3. **Sub-objective 3.3: Sensitivity to variation in vegetation; does tree size, tree density and the size of the input landscape dataset matter in comparisons?**

Cross-scale morphology of the subsample of the various datasets is presented for illustration purposes:

3.4.3.3.1. *Test the effect of tree size on the distribution of merge events across scale.*

The size of the trees in a hypothetical neutral landscape influences the distribution of merge event scale values (Figure 3.32). The larger trees (relative to the image extent) generate a right skewed distribution of merges relative to the relatively smaller trees.

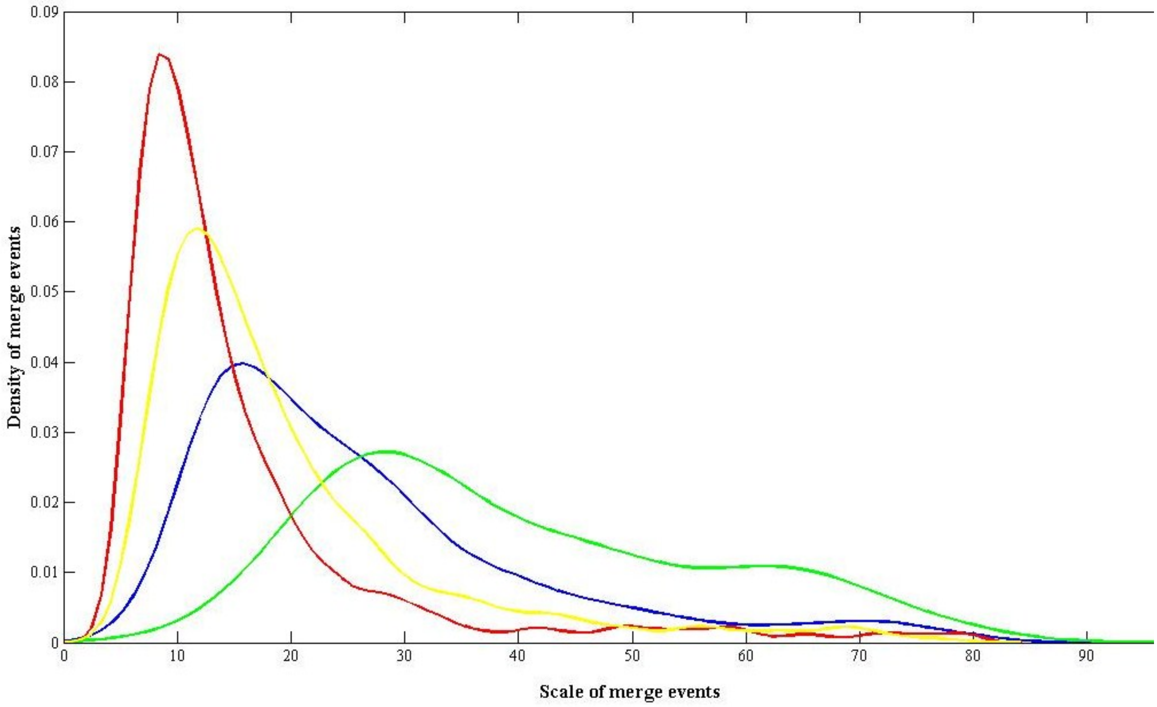

Figure 3.32: Cross scale morphology; the density of merge events at scales of analysis of hypothetical neutral landscapes with different tree sizes. Red, yellow, blue and green lines indicate example images with trees of one, five, ten and twenty pixels respectively (Figure 3.13 A, B, C and D).

The result of the Kolmogorov-Smirnov tests for *all comparisons* between images with differing tree sizes rejected the null hypothesis that they are from the same distribution ($P<0.05$). As the hypothetical trees increase in size relative to the pixels, the relative scales at which merges occur will be become skewed to the higher scales (Figure 3.32). The overall pattern may stay the same, but the lower and higher scales at which events occur will change relative to one another. This is an effect of arbitrarily changing the scale of interest, which is an example of the MAUP.

3.4.3.3.2. *Test the effect of image size on the distribution of merge events across scale.*
The size of the image influences the distribution of merge event scale values (Figure 3.33). The distribution of merges from the larger five hundred pixel image (Figure 3.13) is more right-skewed than that from the smaller 300 pixel image. Kolmogorov-Smirnov tests of the distributions of the scales at which merge events occur reject the null hypothesis that the samples are from the same continuous distribution ($P<0.05$). This is an obvious and expected effect of changing size in image as the relative proportions of merge events will change when image extent changes.

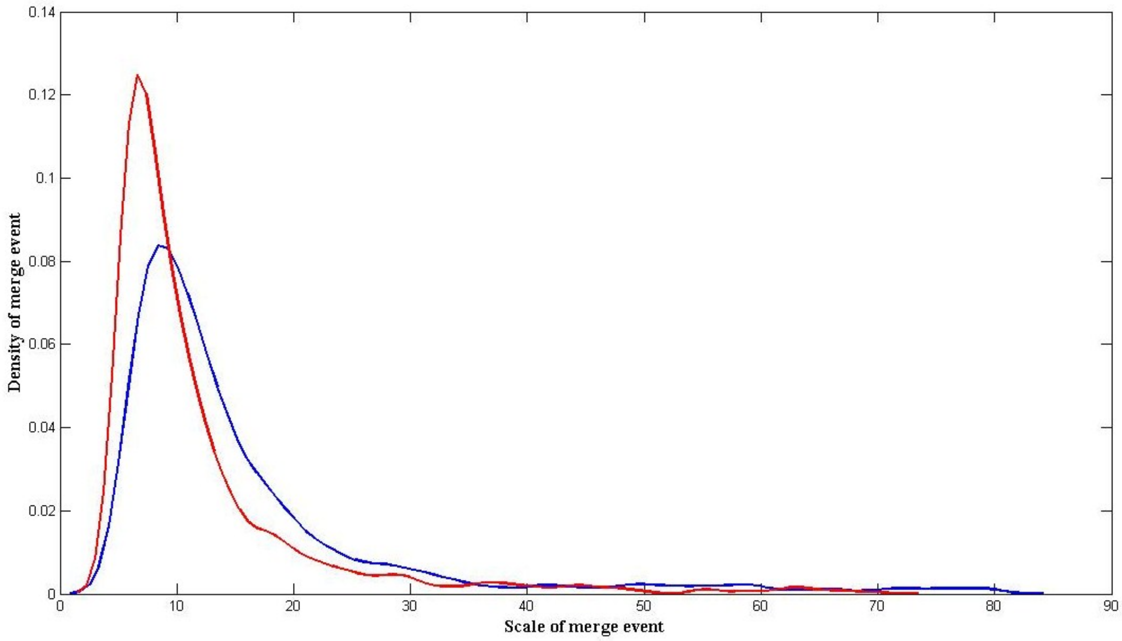

Figure 3.33: Cross-scale morphology; the scales at which merge events occur for two images of different sizes. The distribution from the larger image of 500 pixels in extent (blue) is right skewed relative to the 300 pixel image (red). Both images have trees of a single pixel and fifty percent cover.

All comparisons between images of different extents reject the null hypothesis that they are from the same continuous distribution, under a Kolmogorov–Smirnov test ($P<0.05$). This makes intuitive sense and is expected, because as images increase in extent, merges will be found at relatively higher and higher scales, assuming that woody cover is found across a larger and larger extent (Figure 3.33). This is also an example of the MAUP.

3.4.3.3.3. *Test the effect of percentage woody cover on the distribution of merge events across scale.*

The distribution of the scales at which merge events occur is influenced by the amount of vegetation cover in the image. The distribution becomes slightly right skewed under lower vegetation inputs (Figure 3.34). However, this is not ubiquitous (Table 7); Kolmogorov-Smirnov tests of the distributions of the scales at which merge events occur, reject the null hypothesis that the samples are from the same continuous distribution ($P<0.05$) for 25 samples in two of the three replicate groups. Samples with fifty percent cover and seventy five percent cover (b and c) are only significantly different in two of the twenty five comparisons made ($P=0.03$ in both rejected comparisons). In all other comparisons, there was a rejection of the null hypothesis and the samples can be considered different.

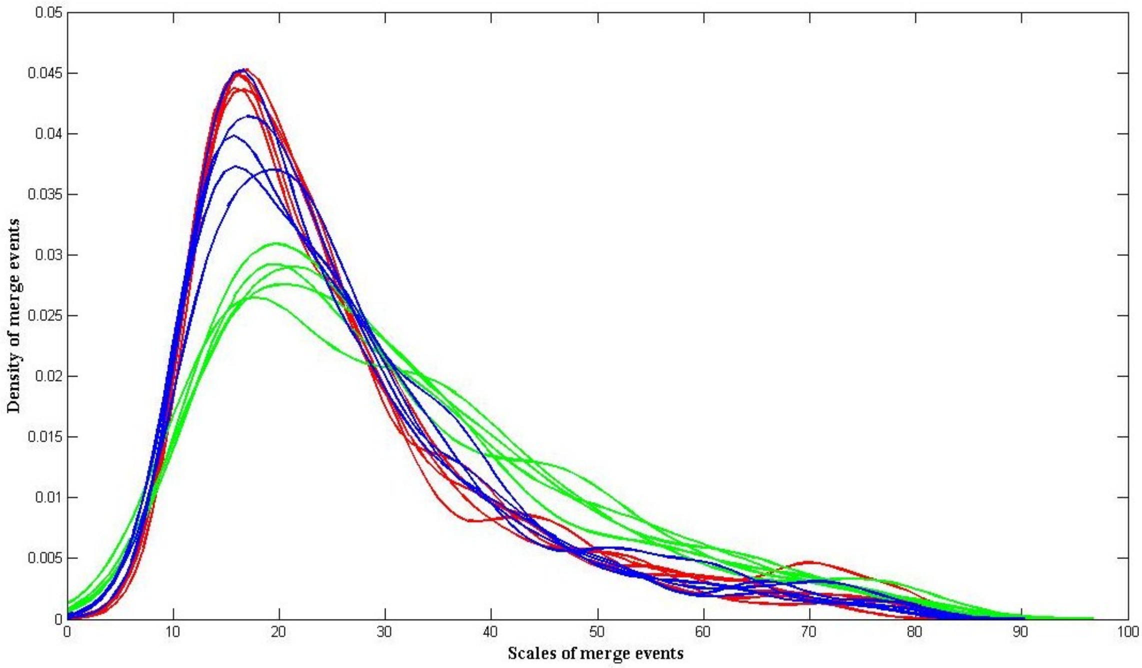

Figure 3.34: Cross-scale morphology; scales at which merge events occur compared between neutral images containing different percentage cover of woody vegetation. Red lines indicate three replicates of neutral images with seventy five percent woody cover; the blue lines represent a neutral landscape with fifty percent cover, and green lines indicate five replicate of neutral images with twenty five percent cover. All images are of the same extent, the amount of woody cover affects the distribution of merges in the scale dimension of the linear scale-space, lower cover being more right skewed.

Table 7: Results of Kolmogorov-Smirnov tests between distributions of the scales at which merge events occur between sets of replicates. Each replicate group has five replicates, and the number of rejections of the null hypothesis are indicated, H_0 being that the samples are from the same continuous distribution. P values for rejections are indicated in red in the top right diagonal.

Replicate group	a	b	c
a	.	P<0.001	0.03; 0.03
b	25	.	P<0.02
c	2	25	.

The percentage of woody canopy cover seemingly does not always affect the distribution of merge events. Despite that, comparisons of hypothetical landscapes of seventy five percent cover with landscapes of fifty percent cover yielded only two rejections (P=0.03). Other comparisons yielded rejections of the null hypothesis for all comparisons. Percentage canopy cover, at least under most circumstances, is an important consideration in the optimization of a neutral model.

3.4.3.3.4. *Sub-objective Synthesis*

Image size, tree size and percentage woody canopy cover affect the distribution of merge events relative to other neutral landscapes. Random landscapes of similar parameters do, on the whole, have repeatable patterns of the scales at which merge events are distributed. The replicates of the sample of twenty five percent cover resulted in four out of ten comparisons reject the null hypothesis that they are from the same continuous distribution. In these samples however, these four rejected comparisons were all between a single replicate and the other four, indicating that there may be an error with the replicate.

3.4.4. *OBJECTIVE 4: CAN EVIDENCE OF PROCESS BE DETECTED IN THE 'NWASHITSUMBE LANDSCAPE?*

The application, although successful at detecting discontinuous structure in test datasets, does not detect any more discontinuous structure in the 'Nwashitsumbe landscape than can be expected from random. This is under assumptions of both stationarity and non-stationarity.

3.4.4.1. **Sub-objective 4.1: General cross scale morphology: Does the cross-scale morphology of 'Nwashitsumbe differ from a neutral landscape?**

In the comparisons between each of the eight 'Nwashitsumbe samples and the ten neutral landscape replicates with fifteen percent woody cover and with twenty five percent woody cover respectively (Table 8), the Kolmogorov-Smirnov tests fail to reject the null hypothesis and they can be considered to be from the same distributions as the neutral landscapes designed to approximate the landscape characteristics ($P>0.05$).

Table 8: Maximum and minimum K-stats of comparisons between the 'Nwashitsumbe enclosure samples and the replicated neutral landscapes. All samples fail to reject the null hypothesis that they are from the same continuous distribution ($P>0.05$).

	Minimum K-stat	**Maximum K-stat**
	Neutral landscapes with 15% cover	
SE	0.224	0.257
	Neutral landscapes with 25% cover	
NE	0.114	0.176
NEO	0.090	0.144
NW	0.142	0.215
NWO	0.190	0.249
SEO	0.080	0.110
SW	0.072	0.131
SWO	0.146	0.210

The data do not reflect that the samples can be considered to be from different distributions. This implies that there is no need to invoke the effect of process when making inference on the creation of multi-scaled pattern in woody tree cover in the savanna landscape. There are a number of hypotheses that may explain why this is the case, including error in the application, the implicit assumption of stationarity when lumping all the merge events together for a sample and that the effect of process is not there because the landscapes approximate randomness. Results are discussed collectively at the end of this chapter given that the results presented next allow for many of these hypotheses to be teased apart.

3.4.4.2. **Sub-objective 4.2: Fire and browse treatments: The effect of manipulation of two major savanna drivers on systems cross-scale morphology.**

Of a possible 27 different comparisons between distributions of merges from the 'Nwashitsumbe sites, only three samples fail to reject the null hypothesis that they are from the same continuous distribution Table 9 (P>0.05).

Table 9: Kolmogorov-Smirnov test of merge event distributions for the real world samples. The bottom diagonal indicates a failure to reject (0) or rejection (1) of the null hypothesis that the compared distributions of merges are from the same continuous distribution. The upper diagonal contains the P-value for the K-S test.

	NE	NEO	NW	NWO	SE	SEO	SW	SWO
NE	x	0.19	0.01	0.00	0.01	0.00	0.01	0.02
NEO	0	x	0.00	0.00	0.04	0.00	0.07	0.00
NW	1	1	x	0.00	0.00	0.00	0.00	0.79
NWO	1	1	1	x	0.00	0.00	0.00	0.00
SE	1	1	1	1	x	0.00	0.92	0.00
SEO	1	1	1	1	1	x	0.00	0.00
SW	1	0	1	1	1	1	x	0.00
SWO	1	1	0	1	1	1	1	x

Within the treatments, the effects of fire and differing browser densities are investigated:

3.4.4.2.1. *Samples with uncontrolled fire and herbivores*

Comparisons between outside samples (NEO, NWO, SEO and SWO) indicate that even under the supposedly similar driver suite found outside the enclosure, all comparisons have a significantly different distribution of merges compared across scale Table 9 (P<0.05).

3.4.4.2.2. *Samples with browser exclusion*

Of the sixteen possible comparisons between samples from inside against those from outside the enclosures (NE, NW, SE and SW tested against NEO, NWO, SEO and SWO all perturbations; four inside against four outside); two samples fail to reject the null hypothesis that they are from the same continuous distribution **Table 9** (P>0.05). These are the comparisons between the NE and NEO sample, and between the SW and NEO sample. All other comparisons show significant differences **Table 9** (P<0.05).

3.4.4.2.3. *Samples with a known fire regime*

Comparisons between samples from inside the 'Nwashitsumbe enclosure (NE, NW, SE and SW all perturbations; 4+3+2+1 comparisons from inside enclosures equals 10), show no predictable pattern. Only one of the ten possible comparisons, the comparison between the SW and SE samples can be considered from the same continuous distribution **Table 9**, (P>0.05).

3.4.4.2.4. *Synthesis*

All except four of the comparisons between real world savanna samples were significantly different, **Table 9**; (P<0.05). The distributions that can be considered the same are comparisons between the NE and NEO sample, between the SW and NEO sample, between the SW and SE sample and between the NW and SWO sample. There is no obvious similarity in the fire and herbivore regimes of samples that can be considered to be from the same continuous distribution Table 10.

Table 10: Time since fire (TSF) in years and approximate time since herbivory (TSH) for the eight sample sites at the 'Nwashitsumbe enclosures. The "Similar to" column indicates which samples the KS test shows that the merge event distribution can be considered to be from the same continuous distribution.

Sample	TSF	TSH	Similar to
NE	12	33	NEO
NEO	±3	0	NE and SW
NW	4	33	SEO
NOW	±3	0	
SE	13	33	SW
SEO	±3	0	NW
SW	2	33	SE
SWO	±3	0	

1. The samples from the NE and NEO are considered to be from the same continuous distribution, but have different herbivore regimes and a different time since the last recorded fire of twelve and three years respectively.
2. The SW and NEO samples are considered to be from the same continuous distribution, but despite similar fire histories (three and two years respectively), the samples have experienced thirty three years of different herbivore pressures. This is to be seen in another example; the NW and SWO sample which are considered to be from the same continuous distribution, also have differing herbivore pressures for thirty three years and similar fire histories (four and three years respectively).
3. The SW and SE are considered to be from the same continuous distribution, despite samples having similar herbivore pressure due to the enclosure; their fire regimes are markedly different (two and thirteen years respectively since the last recorded fires).

The consistent difference between the samples indicates that there is no similarity between treatments, even those with similar drivers. There are a number of hypotheses that can be put forward to explain why, which I discuss in the chapter synthesis, including an error in the application, the nature of landscape context and that lumping of the samples implicitly assumes stationarity of the processes across the sample itself. These are discussed in the context of the next set of results which illustrate a non-stationary approach to the analysis of landscape patchiness.

3.4.4.3. **Sub-objective 4.2:Spatially explicit discontinuity analysis: Does the cross-scale morphology of 'Nwashitsumbe differ from a neutral landscape?**

A spatially explicit test for discontinuous structure in the landscape is the crux of this thesis. I present here the determination of the neutral models and then the test.

3.4.4.3.1. *Spatially explicit discontinuity analysis*

1. Determination of the Neutral Model

The distribution of merge events derived from the ten neutral-replicates for images with twenty five percent woody cover approximates a Gamma distribution (Figure 3.37). The average and the upper and lower standard deviations of the distribution are highlighted in red and green respectively. These distributions subsequently become the null distributions against which the primal sketches in the landscapes are tested for discontinuous structure in the scale dimension.

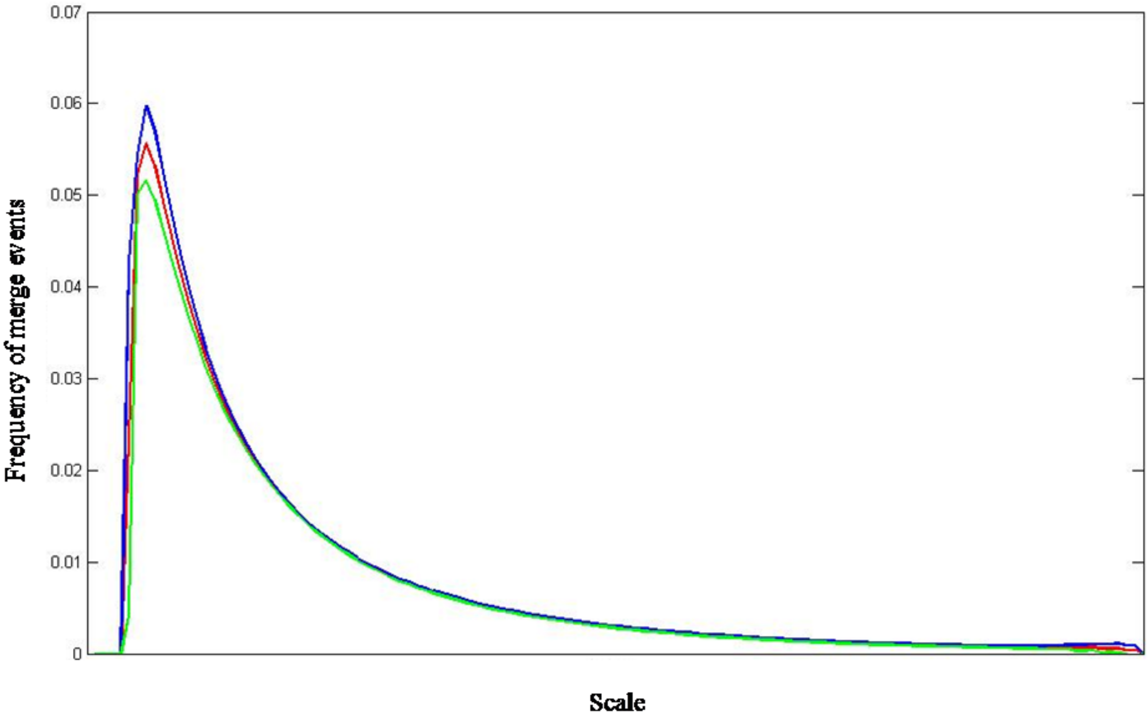

Figure 3.35: Cross scale morphology of neutral landscapes; the distribution of merge events from the ten neutral landscape replicates was calculated with kernel density estimation, rather than histograms. The analysis window bounded to a single scale unit and the positive domain. The average is calculated and used as the neutral model for analysis of discontinuities (red line). The upper (blue line) and lower bound (green line) were calculated; defined by the average plus or minus one standard deviation.

2. Monte-Carlo based simulation to find discontinuities

The simulation successfully generated distributions for each gap which were selected at an acceptance level of 0.95. These are visualized spatially below.

3. Visualizing discontinuities in the landscape

I present the visualizations of discontinuities in a subset of the test landscapes and the eight semi-arid savanna landscapes analyzed. Discontinuous structure is ubiquitous throughout datasets: Figure 3.36; even neutral landscapes contain discontinuous structure. The hierarchically nested structure forms nested discontinuities as expected.

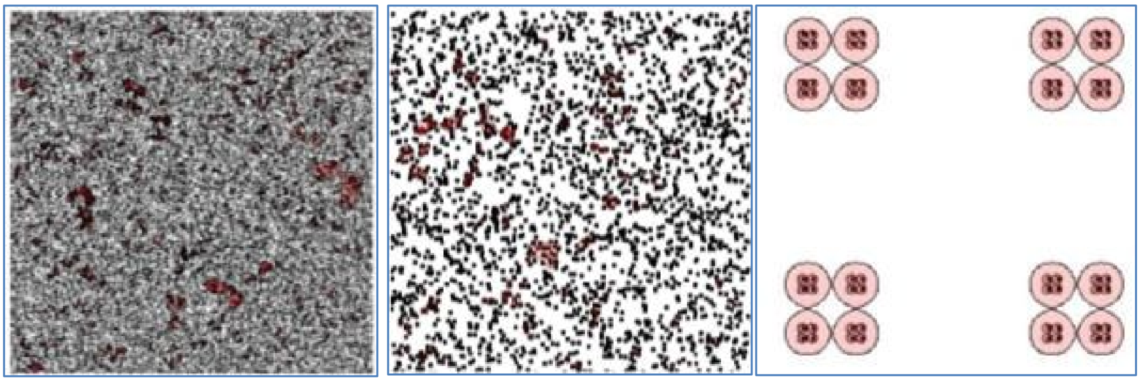

Figure 3.36: Discontinuities found in the neutral models. Global constraint image (left), a replicate of the neutral model used for the 'Nwashitsumbe comparisons (centre), and a perfectly hierarchically structured landscape (right). Discontinuous volumes are those whose gaps have a DPV value greater than 0.9 and are re-projected back onto the landscape.

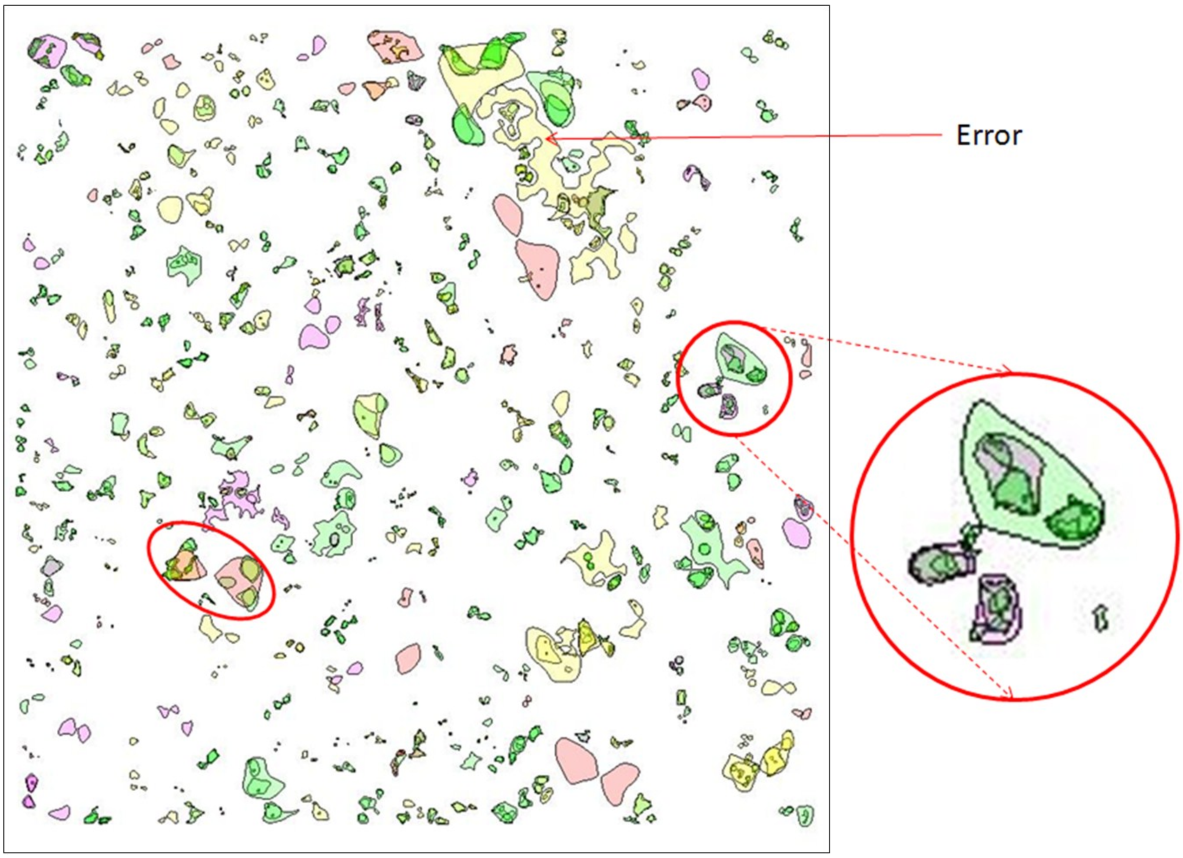

Figure 3.37: An example of discontinuities re-projected back onto a section of an analyzed semi-arid savanna landscape. Circles represent what can be considered classic hierarchical structure, where small patches are nesting into larger patches. Errors are found at higher scales, where the influence of edge effects becomes apparent. Colors indicate the different DPV-values between 0.9 and 1 (green to red).

I present an example of the results of this algorithm to allow for the interpretation of later examples: Figure 3.37. Hierarchically structured vegetation in real world landscapes is evident in certain primal sketches such as this sample section in Figure 3.37, highlighted in the circles. Individual patches are seen to merge into larger and larger patches in the landscape in what could be considered classical hierarchical structure. However, there is a lot of structure, which, although considered discontinuous, is not necessarily hierarchically structured.

The effect of errors at higher scales of analysis is the creation of anomalous patches (Figure 3.37, marked as an "error"). These are easily distinguishable from the hierarchically structured patches in the landscape. These are errors that are introduced at high scales when the influence of edge effect becomes apparent. These are seen in the results that follow, but they are few and far between and are found at relatively large scales.

Discontinuities are ubiquitous in all samples from the 'Nwashitsumbe enclosures, both inside and outside. Here I present all eight images with the discontinuities overlain (for these images a discontinuity is considered a gap with a DPV>0.9; Figure 3.38-Figure 3.45). All images presented here are real landscapes, with discontinuities in red derived by comparing to the average value from the neutral model, as opposed to the upper or lower standard deviation.

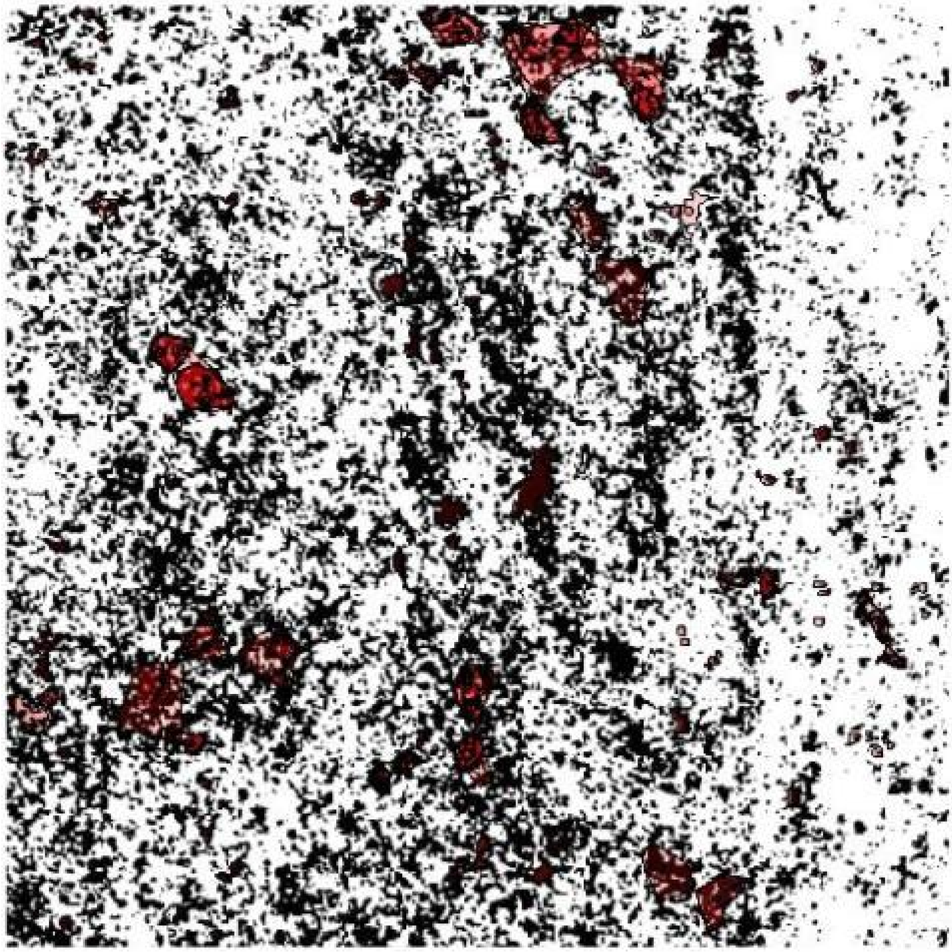

Figure 3.38: The north western sample from inside the 'Nwashitsumbe enclosure. The sample has been exposed to 33 years of herbivore exclusion and was taken four years after the last recorded fire event. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

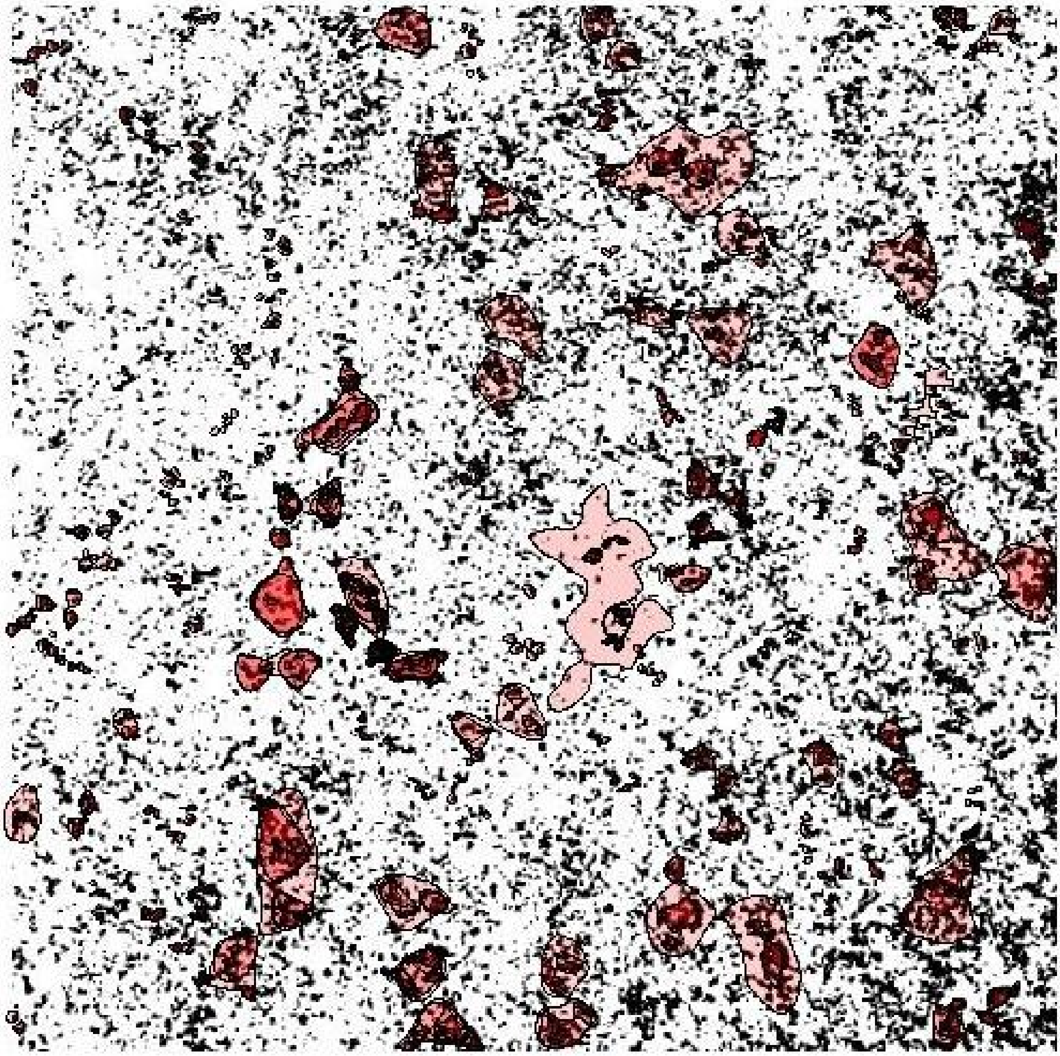

Figure 3.39: Discontinuities from the image outside the north western portion of the 'Nwashitsumbe enclosures. The landscape has been exposed to continuous herbivory exclusion and fires which have a return interval of approximately three years. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9. The large convoluted BLOB in the center of the image is an error created through an error in the linkage algorithm.

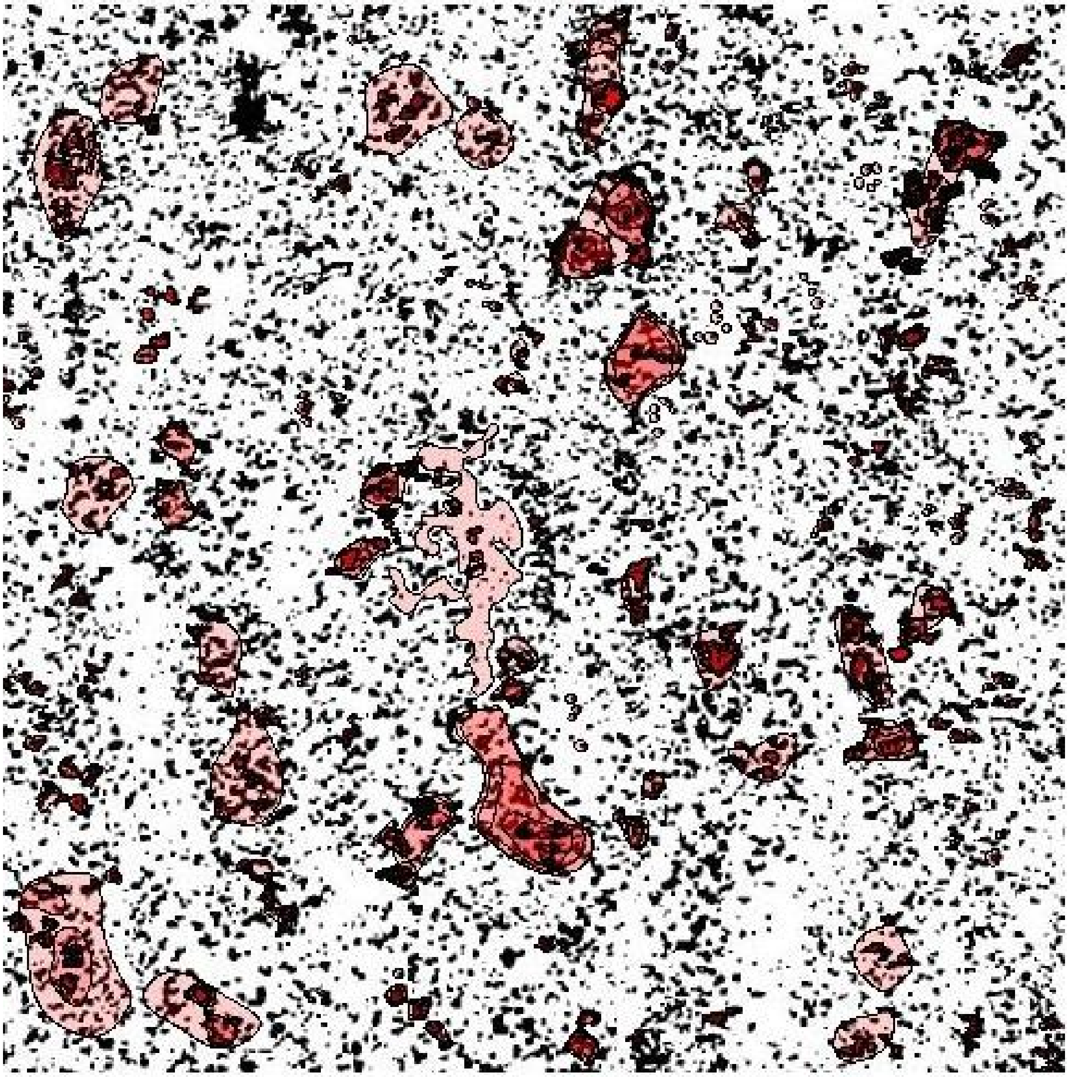

Figure 3.40: Discontinuities from the sample from the north eastern portion of the 'Nwashitsumbe enclosures. The sample has had active herbivore exclusion for 33 years and it has 16 years since the last recorded fire event. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9. The large convoluted BLOB in the center of the image is an error BLOB created through an error in the linkage algorithm.

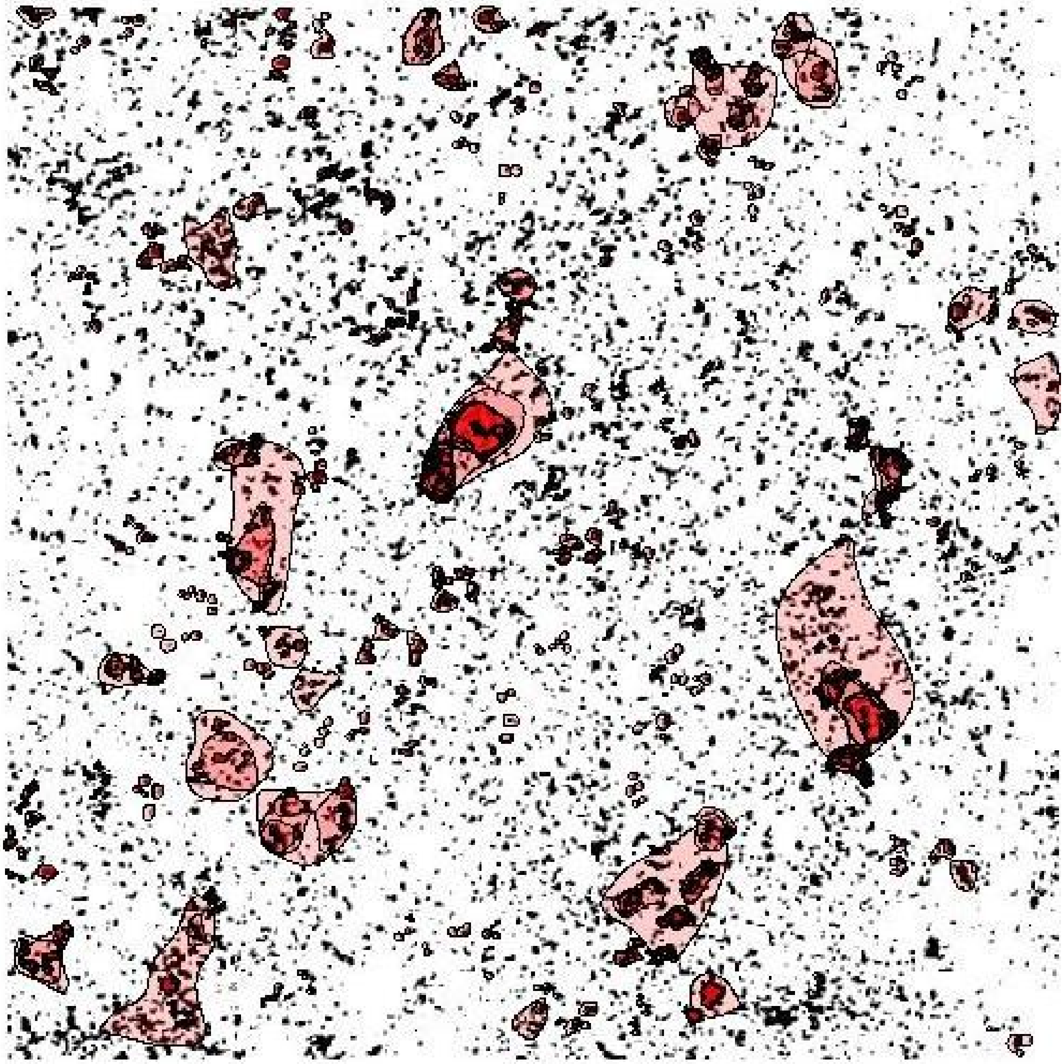

Figure 3.41: Discontinuities from the image outside the north eastern portion of the 'Nwashitsumbe enclosures. The landscape has been exposed to continuous herbivory exclusion and a fire return interval of approximately three years. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

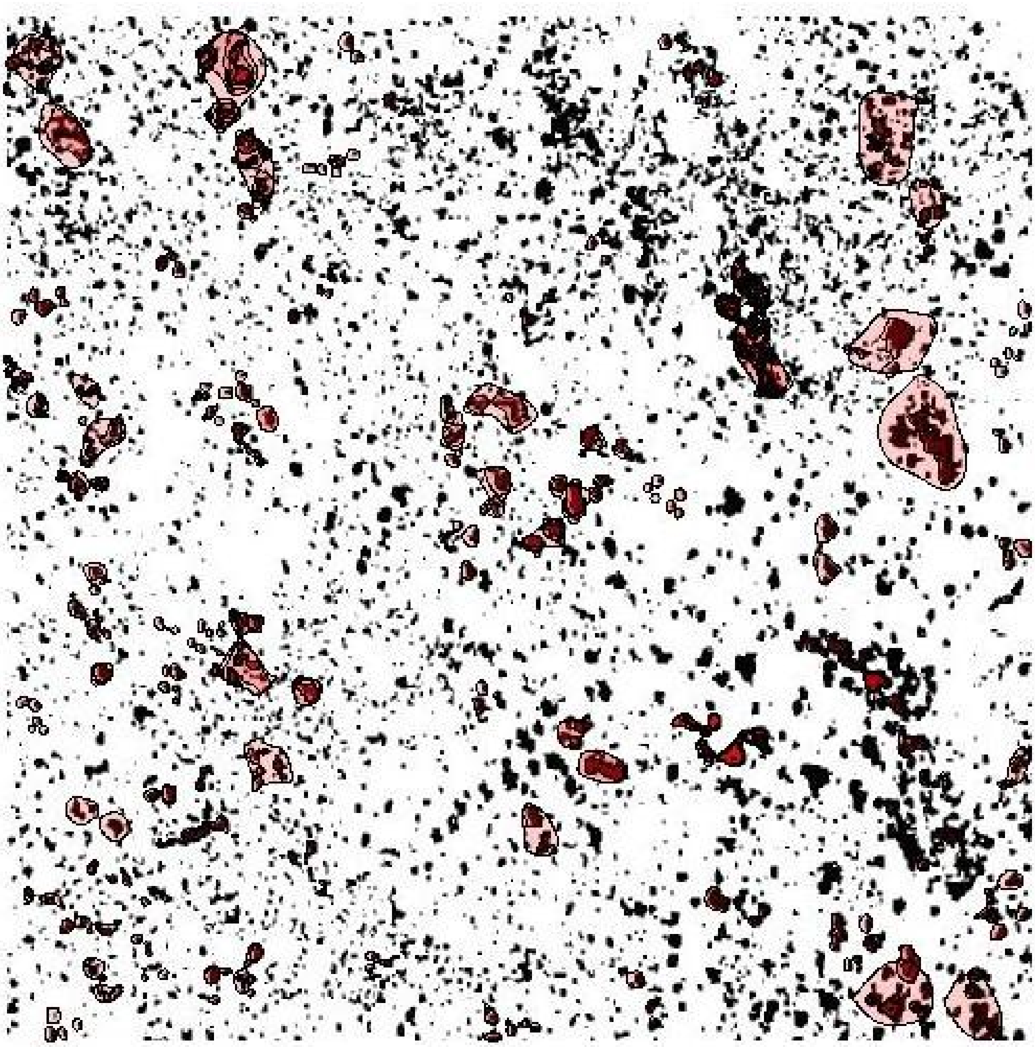

Figure 3.42: Discontinuities from the sample from the south western portion of the 'Nwashitsumbe enclosures. The sample has experienced active herbivore exclusion for 33 years and it has been 2 years since the last recorded fire event. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

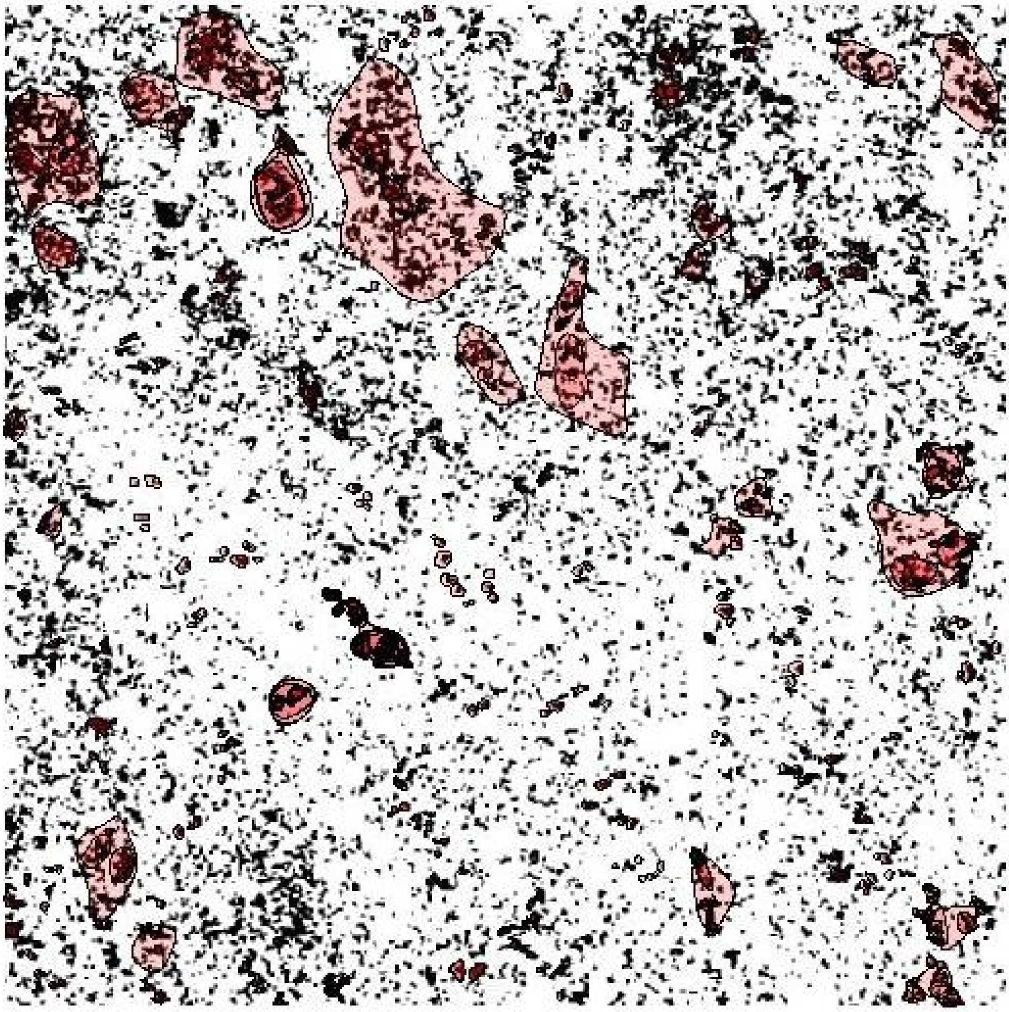

Figure 3.43: Discontinuities from the image outside the south western portion of the 'Nwashitsumbe enclosures. The landscape has been exposed to continuous herbivory exclusion and fire frequency of approximately three year periodicity. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

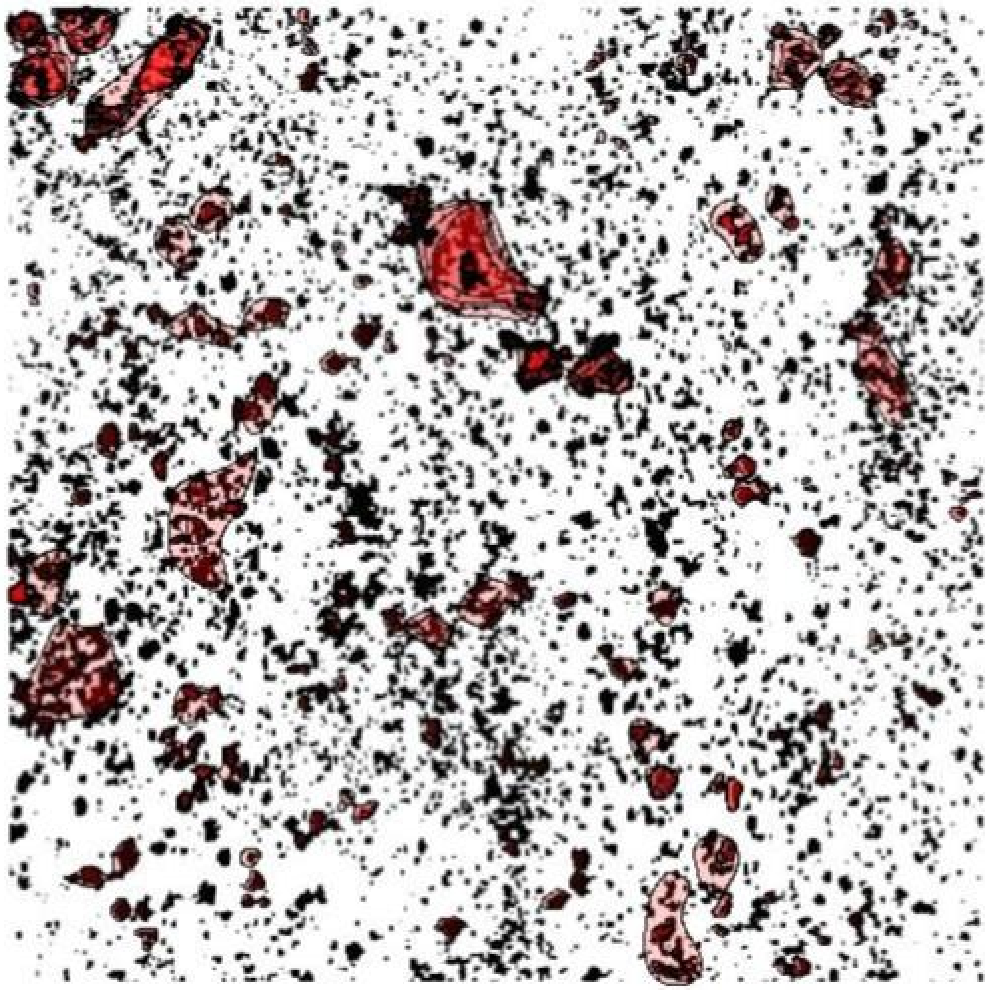

Figure 3.44: Discontinuities from the sample from the south eastern portion of the 'Nwashitsumbe enclosures. The sample has experienced active herbivore exclusion for 33 years and it has been 13 years since the last recorded fire event. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

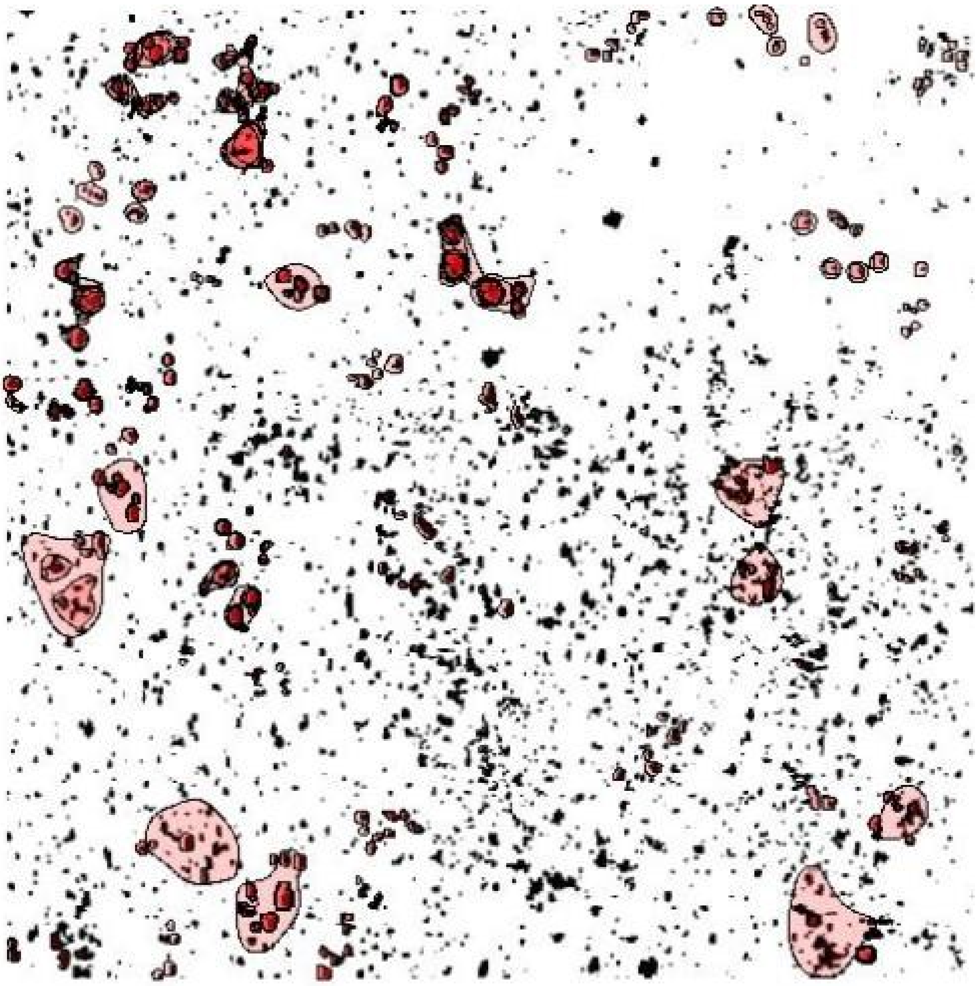

Figure 3.45: Discontinuities from the sample from outside of the south eastern portion of the 'Nwashitsumbe enclosures. The sample has had no active herbivore exclusion and has an approximate fire return interval of 3 years. The red patches indicate scale-space volumes that are considered to be discontinuities at an acceptance value of DPV>0.9.

4. Test for robustness of the discontinuities

The proportion of novel pattern generated, Table 11, using the different inputs are all below 0.05, bar a single sample of ≈ 0.7. Additionally, the consistency of differences between samples indicates robust discontinuities.

Table 11: Proportion of novel discontinuous structure. When using the average plus one standard deviation or the average minus one standard deviation as empirical comparison, only low amounts of novel structure are generated, compared to the average. The amount of novel pattern is generally very low. Secondly, the values are relatively consistent between samples indicating robust discontinuities.

	avg + std	**avg - std**
NE	0.04	0.02
NE O	0.05	0.02
NW	0.05	0.01
NW O	≈0.07	□.01
SE	0.04	0.02
SE O	0.04	0.02
SW	0.04	0.02
SW O	0.04	0.02

To illustrate that the pattern is robust, I present a sub-sample of discontinuities derived from the upper and lower standard deviations of the neutral model, in blue and green respectively; Figure 3.46, this consistency of pattern is ubiquitous across all eight images.

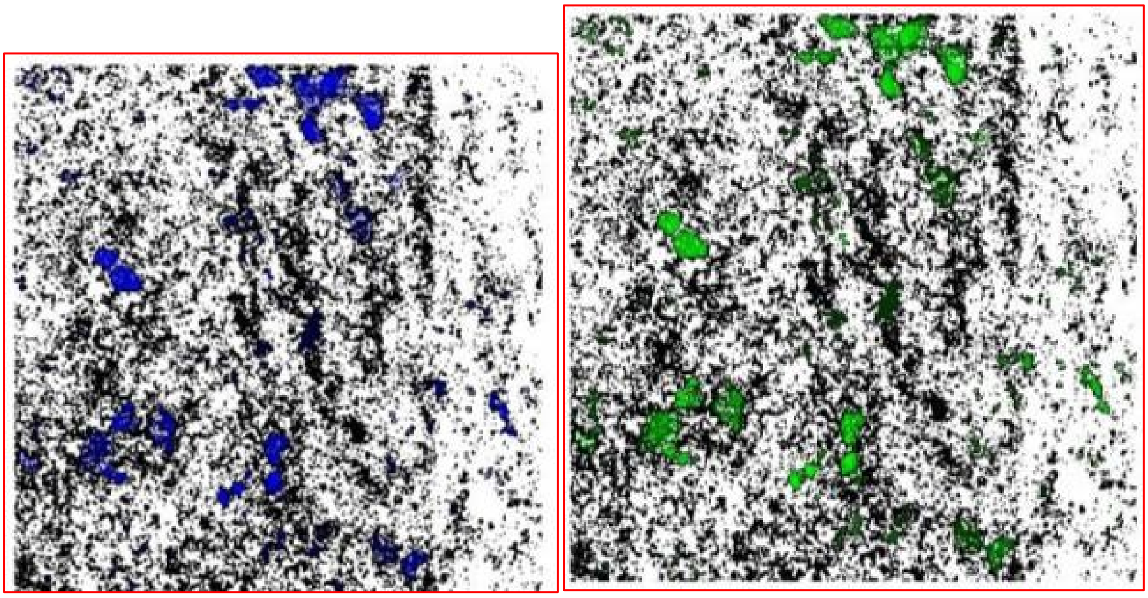

Figure 3.46: Discontinuities determined by analysis using the upper (left image) and lower (right image) standard deviations of the null model. Volumes are considered to be discontinuities at an acceptance value of DPV>0.9. The proportion of new structures is reported in Table 11: The distinctions are almost imperceptible, illustrating that the pattern of discontinuities is robust in the landscape.

3.4.4.3.2. *Comparison of results from discontinuity analysis between images and to neutral models*

In hierarchically nested datasets, (Figure 3.36; right hand side image) the proportion of discontinuities is equal to one. However, when compared to a population of proportion values generated from the neutral landscape replicates, only the sample from the south west (SW) and the south east of the 'Nwashitsumbe enclosure (SE) have a greater proportion of discontinuous structure than is expected from random. Both these samples fall within five percent of the upper extreme value of the neutral landscape ratios. The same pattern is found in the comparisons with the upper and lower standard deviations of the neutral null model.

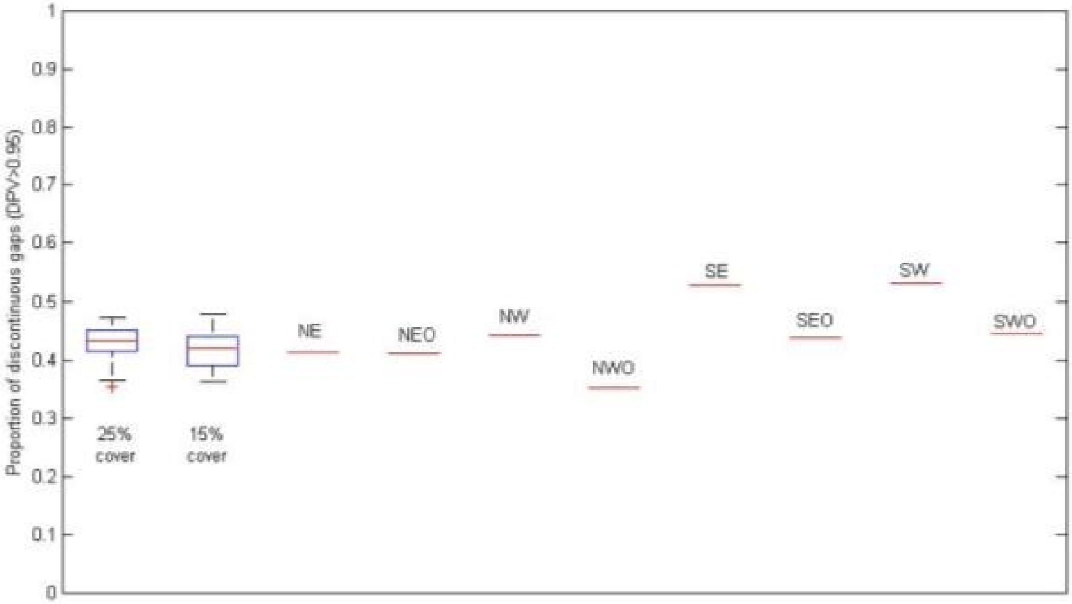

Figure 3.47: Proportion of the gaps in the primal sketches of the samples that are discontinuous, at an acceptance value of DPV>0.95, analyzed against the average of the neutral landscapes. The ten replicates of neutral landscapes, both 15% cover and 25% cover landscapes, andcreate a population of ratios against which the semi-arid savanna landscape ratios are plotted.
The distribution of the neutral landscape is plotted as a box and whisker plot; the red line indicates the median, upper and lower blue lines represent the upper and lower quartile respectively and the black lines indicate the extreme values.The semi-arid savanna samples are labeled by the letters indicating their coordinates, the O indicating a sample from outside the enclosure.
Only the south eastern and south western samples have a higher proportion of discontinuities than expected from a neutral landscape, although it is less than five percent higher than the distribution of neutral landscapes.

Discontinuous structure is evident in all the samples analyzed both in the hypothetical; Figure 3.36 and in the semi-arid savanna samples; Figure 3.38 - Figure 3.45. All of the samples show some proportion of discontinuous vegetation structure. Comparisons of the proportions of discontinuities indicate that there is not a realistically larger proportion of discontinuous structure in semi-arid savanna landscapes than in process-free landscapes; Figure 3.47. The south eastern and south western samples do have a slightly higher proportion of discontinuous structure than the process-free landscapes, but, this is less than a five percent difference from the maximum value in the random data.

Although this can be inferred to be statistically meaningful, I do not regard it as ecologically meaningful. I conclude that, within the bounds of inference set by the scales analyzed, none of the semi-arid savanna samples have a much higher proportion of discontinuous structure than can be expected than random. There is consistency in that the outside sample always has a lower amount of discontinuous structure than the paired sample from within the enclosure. The probability of this occurring by chance alone is ≈0.063 and begs explanation.

3.4.5. *SYNTHESIS OF RESULTS:*

Objective 1: Generation of baseline landscape datasets:

The objective was met; hypothetical datasets were generated, woody vegetation cover extracted from orthophotos with acceptable levels of error and neutral models derived.

Objective 2: Linear scale-space generation linear scale-spaces were successfully generated:

A number of errors in the linkage algorithm and the introductions of errors through edge effects remain a major problem in the ability to make uncontested inference around ecological process.

Objective 3: To demonstrate outputs of the linear scale-space application and to validate the linear scale-space application for repeatability of the algorithm and in detecting the scale of pattern expression.

The cross scale morphology expressed by the distribution of merge events analyzed across scale generated the patterns as expected. Multi-modal distributions are evident in hierarchically structured landscapes and a randomly distributed landscape generated a cross-scale morphology approximated by a gamma function. Tree size, density and image size all affect the distribution of merge events and therefore are crucial variables in creating neutral models for real world comparison.

Objective.4: Can evidence of process be detected in the 'Nwashitsumbe landscape?

There are three major findings related to this objective:

1. The cross-scale morphology of vegetation in semi-arid savanna landscapes is not significantly different to that of neutral landscapes.
2. There is no discernible effect of changes in the processes and the cross-scale morphology of the landscapes.
3. There is no more discontinuous structure in the landscape than expected from neutral landscapes when results from a spatially explicit discontinuity analysis are compared.

Accordingly there is no evidence that process affects the cross-scale morphology of woody tree canopy cover in the semi-arid savanna landscape of the 'Nwashitsumbe enclosure sites. This finding is in the context of the linear scale-space method used and the possible errors and shortcoming therein.

3.5. CHAPTER DISCUSSION

There are three options when faced with the results presented in this thesis; one can doubt the analysis method, one can doubt the philosophy of the investigation, or one can doubt the theory. More humbly put, rather than doubt the theory, we can at least realize that the preconceived ideas with which we as ecologists view savanna landscapes is unlikely to be able to explain all of the patterns that we see.

In Chapter 4 I discuss the findings in the context of the wider ecological field; here I present hypotheses for why the results may be what they are. I have broadly categorized three alternate hypotheses. The expected multi-scaled hierarchical structure is not evident because:

1. of *procedural and philosophical bias introduced by the study design;*
2. of *errors in the application* itself;
3. *landscapes are not hierarchically nested.*

3.5.1. *PROCEDURAL AND PHILOSOPHICAL BIAS INTRODUCED BY THE STUDY DESIGN*

This thesis is premised on the fact that the linear scale-space of woody canopy cover data is an ecologically meaningful representation of multi-scaled structure in a landscape. Throughout the sequence of methods, an effort has been made to ensure that reification has been supported by the literature and that any assumptions, both philosophical and methodological, do not bias the outcome. The nature of the investigation and many of the methods used are novel, so the assumptions require revisiting in light of the results to aid interpretation and future research.

3.5.1.1. **Is woody canopy cover a valid proxy?**

The objectives of this thesis are to detect hierarchical structure in woody canopy cover; but is this necessarily the best proxy for making inference that challenges systems theory? Traditional linear scale-space analysis uses greyscale imagery (Lindeberg, 1994, viz. Hay et al., 2002) as a baseline dataset, the image is not classified *a priori*. It may be that by classifying the trees out of the image and discarding all other ancillary information from the image, imperative non-tree information is lost. This may give a different picture of the scalar dynamics of structure in the landscape.

I do not, however, think so because although a large amount of information is lost, this is a measured action aimed at focusing pattern detection on the woody component. Woody components of a landscape have been used extensively as a reflection of processes in landscapes. Furthermore, although further more detailed investigations are warranted which use the entire aerial photograph (or even a mosaic of photographs), the problem of the primary classification cannot be circumvented. At some point, be it during the process of capturing the data spectrally, or in a subjective classification, a data point must be observed and categorized. Everything in science is an observation and that comes with a classification; all we can do is interpret the patterns of classified observations in the light of our models to describe them.

It may be that the two dimensional woody canopy cover in a savanna landscape may not actually be an adequate proxy for systems drivers. It may be the case that the entire argument presented in Chapter Two is in fact false and that tree distributions only give insight into system level properties in certain systems, such as the arid and Mediterranean systems used by Scanlon, Caylor et al (2007), Rietkerk, Dekker et al (2004), Van Der Koppel, Rietkerk et al (2002), Kefit, Rietkerk et al (2007) and the 'Nwashitsumbe landscape may not conform to such a model. It is perplexing that in my analysis the 'Nwashitsumbe sample shows no observable difference in the multi-scaled spatial pattern of woody canopy cover. Asner et al (2009) demonstrated that the 'Nwashitsumbe enclosure has a significant difference in the vertical structure of the vegetation when the inside and the outside of the enclosures are compared. How does this finding marry with the findings in my thesis?

My findings are seemingly contradictory; but Asner et al (2009) considered the vertical structure of the vegetation, integrated for the entire sample-not the spatial distribution of the patches. The lack of detectable change demonstrated in this thesis may be due to a number of factors:

1. It may be possible that the spatial distribution of vegetation is robust to even relatively heavy herbivory. The difference between the inside and outside enclosures may not have been great enough to induce a change in the system level properties as expected. This is not all that unexpected and I envisage it as a kind of hysteresis; once a tree has established itself in favorable conditions, it continues to facilitate these favorable conditions through the feedback loop outlined in previous chapters. Herbivores affect the feedback loops via browsing, but it is only once the disturbance pressure is large enough to create a fundamental shift in the feedback loop that the entire tree may be lost. The hysteresis property and sudden system shift has been shown in other studies of vegetation in savannas at larger scales (Higgins 2012,

Staver 2011) but not at smaller scales. Further support for the spatial position of vegetation being a poor indicator of process is anecdotal evidence from experimental burn plots that show that tree size structure (height) is affected by fire, but not species composition. Therefore once established, a tree can be smaller or larger due to fire, but the effect on the location (and there may be a less certain relationship with canopy size) will be small or negligible.

2. The method just did not work- as discussed separately.
3. It may be that the spatial distribution of patches in a savanna is not affected by herbivore impact and this may be influenced by fire and random assortment processes, while the vertical structure is affected by herbivore impact.
4. It may be that there are patches but that they are at different successional stages. meaning that they are not necessarily fully indicative of the set of process suites that generate them. i.e there is a time lag.

3.5.1.2. **The original classification of woody cover is biased**

Definiens uses the Fractal Net Evolution Algorithm to generate areas of homogeneous variance that are then classified based on the scale parameter of Definiens professional. There is a danger in the use of such a method as the parameter is unrelated to the scene in question and simply classifies based on pixel values which are an average measure of spectral strength received. The resolution of the imagery is dictated by the instrument used and not the ecological phenomena in question therefore the accuracy of the original data may be questionable as non-tree may become biased. This form of bias is reduced through the visual classification and comparison done during the data preparation process, outlined in section 3.3.1.2. In addition, the use of square trees as test datasets may introduce a bias when compared to real world landscapes, this remains to be quantified and is likely not of huge concern, but remains a consideration.

More importantly there is a philosophical circularity in that to generate an unbiased dataset, the user has to generate a biased classification of what they classify as woody cover. This is a point of departure between the traditional linear scale-space analysis and the application presented in this thesis. I am attempting to find complex systems derived pattern in a system proxy, this system proxy is woody cover and therefore there is already a classification made. I therefore attempt to use the smallest spatial units possible given the dataset. I acknowledge this bias, but the bias is made in order to allow for classification of the proxy of interest out of the image.

3.5.1.3. **The use of merge events as a proxy of system process**

The application that I have developed in this thesis uses only woody tree cover to depict the change in pattern across scale and thereby makes an inference about the savanna system. This inference is made assuming that wood canopy cover and the merge events derived therefrom are an adequate proxy.

Linear scale-spaces contain four critical events, I utilized only merge events. It is possible that no multi-scaled pattern was detected simply because merge events are not meaningful in ecological terms. I am doubtful that this is the case, the theory stating that scales at which patterns are evident is an inference of process, is well entrenched in the literature and has been well described in Chapter 2.

A possibility would be to use the midpoint of a scale-space volume, that is between two critical points, this would include annihilation events and merges and allow for *the scale at which maximum BLOB area* is evident to be analyzed.

My choice to use merge events follows the following logic: if woody canopy cover is a proxy for system process, as has been articulated and if in a linear scale space the merge event shows where patches merge to form bigger patches, which has been articulated and if HPDP dictates that patches are incorporated into other larger patches when process domains switch, then it follows that by using merge events of woody canopy cover I encapsulate the scale at which a process domain may occur, in a spatially explicit context.

3.5.1.4. **Sensitivity of analysis to variations between neutral models and real world samples**

Creation of the neutral models for this thesis is still in its infancy. Some questions which need further investigation are: how sensitive are the outputs are to the variations of the neutral landscape from reality? Also how sensitive is the result to the signal/noise ratio in the data? For instance, at present I accept a five percent difference in woody canopy cover density between the semi-arid savanna landscape density and the neutral model. This does not seem to affect the merge distribution and corroborating evidence is found in the determination of fits which illustrates that small differences in percentage canopy cover densities do not affect the distributions as much at tree size does.

But, the fact still remains that some of the samples are being compared to a landscape which has four or five percent more vegetation than they do and this configuration of trees is random and the trees in a neutral landscape are all uniformly the same size as the average of the real world landscape. How do these differences affect the statistical sensitivity of the outcome? The form of the semi-arid savanna landscapes still approximates random and I am confident of the results. However a more in-depth understanding of the statistical confidence that can be placed in various regions of the landscape would provide more insight and confidence in the findings.

3.5.1.5. **Simpsons Paradox**

The well-known statistical conundrum of Simpsons paradox describes how a trend appears in different groups of data, yet disappears when these groups are combined and the reverse occurs when data are aggregated (Simpson, 1951). Simpsons paradox disappears when causal relationships are linked to the data, yet without them the researcher is blinkered. In a landscape example; although the overall trend of the landscape woody vegetation cover can be relatively constant, upland and lowland vegetation dynamics can be vastly different from one another (Levick, 2008, Levick and Rogers, 2011). It has been proposed, through various discussions, that the lack of pattern detected could possibly be due to something similar, that different drivers dominate at different positions in the landscape and so one would not expect perfectly nested hierarchies.

This is true, however, the spatially explicit discontinuity method uses a neutral landscape and tests against that, not against the dataset as a whole and so does not assume stationarity of the processes. The entire point of the spatially explicit discontinuity hypothesis is to test for pattern while acknowledging Simpsons paradox and the confounding effects of context specific pattern process relationships. The Monte-Carlo simulation uses the neutral landscapes as the control to allow for inference to be made on each scale-space volume without considering the others and thereby circumventing the statistical ramifications of non-stationarity in landscape process.

3.5.1.6. **Lack of normalization of scale-space volumes**

When analyzing images for significant image structure normalization is an important step, which must be done to account for the structure inherent in the image. Hay et al (2002) normalize the scale space volumes of grey-level blobs by subtracting the mean volume of white-noise grey level volumes at each scale and then dividing by the standard deviation of white noise grey level BLOBS. White noise is a structure-less image in which there is no significant structure at any scale in particular. The mean and standard deviation are generated by analyzing a minimum of a hundred similar scale space BLOBS from a white noise image that are of the range in scales as the measured primal sketch to be normalized. The purpose of the normalization is to account for the structure inherent in even random images. The premise is that if the BLOB in a real world image is larger than that found in a structure less image, then it can be considered to be a significant structure.

It may be that by not normalizing the images, BLOBS which are insignificant are classified as significant and the extent of the structure in scale is exaggerated. However, in the application to analyze woody vegetation pattern, I do not deem the normalization of the scale-space stack important. I am interested in how the structure of woody vegetation evolves through scales, not in any other information. The non-normalized stacks successfully extract and depict the evolution of woody canopy cover across scales. These are then compared to similar scale primal sketches from neutral landscapes (analogous to the white noise) at a later stage to determine the significance of the structures relative to a neutral model.

3.5.1.7. **The scarcity of data at high scales due to the spatial nature of the data.**
When dealing with scale in a spatially explicit dataset, there is a confounding factor that the sample size decreases exponentially as one increases scale of observation. This is seen in the distribution of merge events in neutral landscapes following an approximate Gamma distribution. There are, by the very nature of hierarchical data, more small patches than large patches. The result is that comparisons at larger scales are inherently data deficient, especially when approaching the maximum extent of one's analysis.

Comparisons of the data deficient scales render the possible errors much higher and confidence in the results lower. Using large Monte Carlo simulations, as utilized in this thesis is one possible way to circumvent this issue. This allows for a large hypothetical distribution to be generated against which the data in question can be compared. The most rigorous test would be to increase the maximum extent of analysis and analyze a subsample, but the argument is circular as one then encounters a maximum scale in the next sample, with the same limitations.

3.5.1.8. **The small spatial extent of the analysis.**
In this study I was limited by two major factors in the maximum possible size to analyze. Firstly, the maximum size of the burn blocks in the 'Nwashitsumbe enclosures and secondly, the maximum possible computational size feasible in the written application.

3.5.1.8.1. *The maximum size of a burn treatment in the 'Nwashitsumbe enclosures*
The size of the burn plots is limited to approximately 65 hectares. However, when compared to other studies of the cross-scale morphology of the vegetation distribution this study

constitutes a comparable, if not larger spatial extent of analysis. Other studies of cross-scale morphology of savanna systems have studied 2 kilometre extent with 4m resolution (Scanlon et al., 2007) or between 32m and 16m (Kéfi et al., 2007a).

My thesis presents analysis of all scales, in a spatially explicit manner, not assuming stationarity, between $0.81m^2$ and the maximum scales of merge events used in analysis which were approximately 99 $225m^2$. This study is comparable to the other studies of cross-scale morphology in spatial extent and it is possible to expand the size of analysis with this application. However, larger experimental enclosures are not available.

3.5.1.8.2. *The maximum time scale of 'Nwashitsumbe enclosure experiment*

The time scale is 33 years which provides a relatively long term experimental set up, relative to other available landscape manipulation experiments. Longer time scale experiments of useful size for landscape analyses, be they limited to a relatively small extent, are not available in semi-arid savannas.

3.5.1.8.3. *The maximum feasible computational size*

The application was written for proof of concept in MATLAB, a higher order language. Although the application does work and works well for its purposes, the application is by no means as efficient or mathematically refined as possible, most likely due to the fact that I have had no formal training in either coding or mathematics. The application remains very computationally expensive and depending on the density of vegetation in the landscape, will exceed the maximum memory allowed by most programs in an image exceeding 1500 pixels. It is ironic that four years later, normal computers could in all likelihood deal with the computational load without a problem.

During the creation of the linear scale-space, convolution of the input image with the Gaussian kernel is easily transferred into a parallel computing application. The major memory problem at present lies in the creation of the adjacency matrices to analyze the three dimensional primal sketch datasets. Even using sparse matrices the data volumes of a large scale-space, in which every voxel constitutes a node, the data becomes cumbersome to analyze due to volume. Most of the analysis is, by its very nature, iterative and so the computational load becomes very time consuming. There are applications such as *scalespaceviz* (Kanters et al., 2004) which generate a linear scale-space, however the maximum image size possible still remains too limited for landscape analysis purposes.

From a more fundamental viewpoint, *scalespaceviz* and the different applications used by other researchers (Lindeberg, 1994, Florack and Kuijper, 2000, Hay et al., 2002, Platel, 2007, Kanters et al., 2004) are true linear scale-space applications. Critical paths can be calculated by analytical techniques such as the intersections of three dimensional iso-intensity surfaces and analytical techniques can be used to predict the position of critical points at sub-pixel level (Kuijper and Florack, 1999). The goal of this line of linear scale-space research is image segmentation and object identification, whereas the application written for this thesis is designed specifically for the detection and linking of woody vegetation. I ignore half of the original data in the image and thus many of the techniques designed and implemented in the true scale-space research, become invalid.

The use of linear scale-space analysis in ecology is in its infancy. With advances in computing power and, if the use of linear scale-space is taken further, the involvement of mathematicians and computational experts to increase the computational efficiency of the algorithm, will allow for more time to be spent dissecting the ecological problems within the dataset, rather than with wrestling with the problems of the application itself

3.5.2. *ERROR IN THE APPLICATION*

I have already discussed a number of philosophical or procedural issues which may have resulted in a lack of confidence in the results. These are a type of error, but in the next two paragraphs I confine the errors to those that are in the actual application which was written in MATLAB for this thesis, as opposed to an approach, such as normalization. There are two errors inherent in this application; errors in the linking of BLOBS between scales, and edge effects.

3.5.2.1. **Error in linking between BLOBs in space**

I have already briefly outlined the problem in Section 3.3.2.4. Linking BLOBs between scales has been termed *"...practically difficult..."* (Coulon et al., 2000, pg. 770). The current method used to link BLOBs across scale is to link those that share spatial support. However, as the BLOB tends toward a scale-space merge event, the area of an individual BLOB tends toward zero. At some point the BLOBS are smaller than an individual pixel. These sub-pixel BLOBs are not likely to share spatial support, introducing errors in the primal sketches as links are not made when they should be. I have used an error cleaning algorithm that removes these errors, however it will never be one hundred percent perfect unless the sampling scales of the scale-space become sub-integer, which is not practically possible.

The effect of missing a linkage is that woody cover at lower scales is no longer *owned* by larger patches of woody cover. Although this is of no concern when grouping merge events together in many of the analyses, it becomes a concern when undergoing spatially explicit discontinuity analysis. The entire point of the use of linear scale-space is causality, that pattern at larger scales is generated through the merging of pattern as smaller scales of analysis. The error in linkage violates this assumption as the larger scale pattern does not have all of the smaller scale data represented. This may mean that discontinuities are or are not detected erroneously. The proportion of these errors is low (between 0.007 and 0.033), particularly after the error cleaning algorithm has been run, but it is a source of noise in the signal, which, when combined with edge effects and sensitivity of the technique to signal/noise ratios may explain the lack of expected results.

3.5.2.2. **Edge effects**

At higher scales relative to the scale-space analysis, it happens that the data from outside the bounds of the sample will be introduced into the image and generate errors. This is noted in Figure 3.39 and Figure 3.40 as the irregular shape. It occurs at the point when the BLOB is inverted by the inclusion of zero data from outside the image where spatial support is assumed to be infinite. Edge effects occur in every spatial analysis where windows are used for calculations; in small spatial analyses such as the 800m samples used in the 'Nwashitsumbe comparisons, the edge effects can be profound and to circumvent their inclusion, the top 30 percent of the scale-space stack was discarded.

This effectively reduced the range of scales over which analysis is performed, which limits the scales over which inference can be made. Edge effects may also change BLOB shapes at larger scales, which will create noise in the signal at higher scales. The only solution to this problem is to have much larger images and analyze a sub-sample, however the size of the treatments was a limiting factor.

3.5.3. *LANDSCAPES ARE NOT HIERARCHICALLY NESTED*

The next hypothesis to explain the results, is that the expected pattern was not detected because landscapes are not hierarchically nested, as expected and derived in the arguments within this thesis. The implications of this finding are discussed in the following general discussion in Chapter 4 in which I put this finding in the context of current ecological theory and the broader ecological context. Of particular interest is that patches which are seemingly obvious to the user are not necessarily significantly entities in the scale space; in Figure 3.38

there are a number of these supposed patches. I acknowledge that there are patches that would seem distinct in the image, however the point of the algorithm is to analyze the dataset without user inference. Is the reader sure that those patches are really significantly different from what can be expected from random? And if not, is assigning a patch status not imposing a subjective assumption of process based on no evidence?

The question then remains why people see the patterns in the landscape in the first place if they are not necessarily really there. If one views the images of discontinuities one sees very definite patches. But are they really there? How does one prove that a patch is actually a patch generated through process and cannot be explained through random change alone? The method developed in this thesis did just that and assuming it worked, then those patches are not more patchy than can be expected from random.

Even if it is process related, yet can still be approximated through a neutral model- then why go through the trouble to invoke process at all? Let us assume that the algorithm is in fact sensitive enough and can in fact detect patches, something that the validation section does address. We must trust the data because the very fact that we are looking for patches as defined by the HPDP means that the observer cannot do so without being biased for patches.

One cannot challenge the fact that patches are not found because the observer who has been primed to look for patches found them. I agree that there are stark differences between the patch structure expected by the author and the outputs of the algorithm, but is it the algorithm that is wrong or could it be that we view landscapes through HPDP tinted glasses?

A possible explanation is that people have evolved to recognize pattern; it resides in our very consciousness. Psychological forcing is used by magicians to give the volunteer the illusion of free choice when they are in fact led down the road to the very end point selected by the magician himself. Our brains are full of pranksters which are quite capable of generating patterns that may not necessarily have any base in reality (Dennett and Weiner, 1993). The phenomenon of recognizing known patterns in inanimate objects is known as simulacrum; as children we find unicorns in the patterns of clouds, but not before we know what a unicorn is. Examples of simulacrum are plentiful when one looks at religious imagery. I unfairly pick Christianity as an example; this is simply due to the plethora of available examples rather than any bias in particular. How many inanimate objects have been hailed as holy? How many items from around the world have been claimed to contain the image of Jesus Christ himself? To list a few: toast (cooltoast.com), wall plaster (goldenpalaceevents.com) (Figure

3.48 A&B), family pets (getbehindjesus.net), dental x-rays (firstcoastnews.com), marble stones in church grounds (Sakyi-Addo, 2004), bricks (clickorlando.com) and even landscapes themselves (newslite.tv) (Figure 3.48 C).

A simple web search of "Jesus in everyday objects" yields hundreds of such examples. This is simply the result of dogma, we are primed to look for an image, in these instances a religious icon and we subsequently find it. An extreme and somewhat comical example, but it makes the point; ecologists are told that there are hierarchically structured patches in the landscape and we find them, no matter what the landscape. The simple act of finding patches in a landscape is by its very nature biased by the concept of a patch; there will be hierarchical structure in randomly distributed trees simply through chance, there is not necessarily process involved in all patterns.

Figure 3.48: Examples of pattern found in inanimate objects, a phenomenon known as simulacrum. Rising damp in the plaster surrounding a bath (A-B) (goldenpalaceevents.com), and a fire scar in a

landscape (C), (newslite.tv) when viewed at a particular scale superficially represents the face of Jesus Christ, even though there is no real religious significance to the image.

Another point of interest from the discontinuity results is that there is a consistently higher amount of discontinuous pattern in paired samples (i.e NEO and NE etc). It could due to chance, but why the outside samples have consistently less discontinuous structure than the paired sample inside is indeed perplexing. This pattern would allow for the inference that herbivory may have an effect on the discontinuous nature of cross scaled pattern. Herbivory as a driver of landscape pattern is commonly recognized and the finding at the 'Nwashitsumbe enclosures is in line with the findings of Asner, et. al.(2009).

I cannot exclude the effect, but given the lack of understanding of the sensitivity of the analysis technique and that it is not significantly different from random, I am unwilling to make broad statements based on the pattern and this remains a casual reference.

3.5.4. *FUTURE RESEARCH FOR THE APPLICATIONS*

3.5.4.1. **Annihilation events**

This thesis focused simply on merge events in the landscape; however additional information regarding processes occurs in a linear scale-space of a savanna. Linear scale-space represents a tool to generate multi-scaled descriptions of woody vegetation cover and other objects in a landscape for that matter, in an ecologically meaningful way. I have chosen to use the merge events to analyze the cross-scale morphology of the system and subsequently make inference about the nature of process in the landscape.

The possibilities for further analysis and generation of understanding of scale and space are immense. Annihilation events indicate the scale at which vegetation no longer persists and their distributions can be measured using Local Indicators of Spatial Autocorrelation (LISA). Preliminary tests using LISA statistics showed no pattern in the annihilation events for the 'Nwashitsumbe datasets, corroborating the merge event findings. However this was by no means exhaustive and much work remains to be done to examine the patterns generated by annihilation events in linear scale-spaces of savanna systems.

3.5.4.2. **The use of traditional linear scale-space analysis to measure multi-scaled structure of woody canopy cover**

In this thesis I present a method focused solely on the distribution of woody canopy cover. By utilizing the binary dataset of woody canopy vs. not I assume that this is representative of the savanna process. There is other information in the non-woody component which may also be hierarchical structures and information in the image which is lost when the image is made binary.

It would entail a completely different set of testable hypotheses and ways of analyzing the data, there may, however, be complimentary information gleaned from using the traditional linear scale space methods to analyze images of vegetation cover to ascertain whether or not there is hierarchically nested structure. Recently published literature on scale spaces may provide a promising avenue to this end (Hay, 2012)..

Chapter 4 General Discussion

This thesis presents a test of certain predictions made by complex systems theory applied to semi-arid savanna landscapes. I have tested whether or not the fundamental units of currently accepted models and conceptual frameworks from which we draw our knowledge are supported by empirical analyses. An argument from the available literature was built, expounding how scale can be viewed as a dimension across which ecological processes operate and, depending on the coupling of processes, may or may not result in structural attractors.

To test this philosophy I developed a novel application in landscape ecology, using linear scale-space analysis to describe the multi-scaled vegetation distribution in open canopy savanna woodland.

To understand the effect of process on patterns generated in a linear scale-space, I utilized neutral landscapes, by comparing the patterns in neutral landscapes against the semi-arid savanna datasets, the influence of process was inferred. In addition, comparisons of semi-arid systems exposed to different history of drivers were used to determine if there is any discernible effect of driver manipulation on the system. The cross-scale morphology of the scale-space was analyzed for the presence of discontinuities in a spatially explicit manner.

This thesis has taken me as a researcher through a labyrinth of intricately intertwined theory, conceptual frameworks, models, and explanations of system dynamics. The fundamental paradox remains; in the semi-arid system of the northern Kruger National Park; hierarchical structure, predicted by complex systems theory and advocated by the currently used paradigm of HPD, is not evident within the scales analyzed. Put simply; predictions of process domains cannot be demonstrated within the scales analyzed, yet the scales which were analyzed should have some level of discontinuous structure given our understanding of landscape dynamics.

I have explicitly looked for patterns of complex systems in a supposedly proto-typical complex system and I have not found it. The results contradict a widely accepted theory in landscape ecology and the results that the patterns observed in a landscape, need not be attributed to process is perplexing.

In the previous chapter I presented three hypotheses for why these results may be:

1. of *procedural and philosophical bias introduced by the study design;*

2. of *errors in the application* itself;
3. *landscapes which are not hierarchically nested.*

I have already discussed at length the first two points in Section 3.5. If there is a philosophical error or an error in the application, which I do not think there are enough of to completely disregard the findings, then this thesis has no implications for landscape ecology at large. However, if it is so that landscapes are not hierarchically nested, as I believe the data show, then it begs discussion. In the following discussion session let us assume that the perceived data are not influenced by the errors in the philosophy or algorithm itself.

4.1. CRITIQUE OF THESE FINDINGS IN THE CONTEXT OF CURRENT LANDSCAPE ECOLOGY THEORY

Not finding true hierarchical structure in a semi-arid savanna is in conflict with the currently accepted paradigm, but one must be cognizant of the limited nature of the study. The uplands of a single hill slope in the northern Kruger National Park are by no means representative of all landscapes. I must clarify that I am not dismissing hierarchical patch dynamics and constitutive hierarchies completely. There is a large body of evidence which dictates that hierarchical structure is the end point of complex system interactions.

What I am proposing is that this is not always the case in all complex systems and most certainly not in these examples of semi-arid savannas. What I do highlight is that our confidence in our mechanistic understanding of savanna systems may be misplaced.

There is profound insight in the question of Allen (2006, pg. 6064); "Does the landscape provide a discontinuous distribution of structure that is the theater on which species interact?". If it does, this has implications for the evolution of systems and our ability to use discontinuities as predictive tools for assessing system resilience, if not…then why are datasets discontinuous?

In the context of process domains; a discontinuous structure in the landscape would require the creation and maintenance of pattern by processes and the subsequent constraint of the processes by the generation by pattern. These concepts have been articulated in other, more theoretical works regarding system evolution (Ulanowicz 2008). But, just as the HPDP pattern-process-scale perspective asserts that these processes would need to be constant across the landscape, to create a discontinuous structure across the landscape would require that the processes that entrain pattern are entrained across similar scales.

Should the scales overlap spatially, then pattern and process becomes a local phenomenon, contingent on the particular suite of processes affecting that particular patch and generic observations and rules become difficult to apply. The answer to Allen's question is no, not in systems as heterogeneous as those found in the Northern Kruger National Park, and the same is likely for many other landscapes.

Other research is coming to the fore, in the realization that landscapes are not necessarily nested in structure and that the context of each section of the landscape considered is unique (Levick, 2008, Levick and Rogers, 2011). Many samples from different landscapes are by their very nature incomparable when trying to compare the effect of processes on pattern. For instance, analysis of soil on landscapes of ages of erosion due to rainfall differences, has illustrated that the properties of the soil itself vary with hill slope form and age, which varies stream order, which by its very nature vary with spatial scale.

The result is that as one increases scale one will not get an ontologically nested set of soil patches in a landscape, rather find that the soil properties are each contingent on a number of factors, which make them fundamentally different (Rogers pers comm, Khomo pers comm). In a thorough investigation of the woody vegetation cover across space and scale in the Northern Kruger National Park; Levick (2008) found that the results between response and explanatory variables differed in both magnitude and direction in different spatial contexts. This implies that the global model may not reflect the relationship evident at any point in the landscape (Foody, 2005). This finding called for a spatial exploration of how pattern and process relationships vary across the landscape (Levick, 2008, Levick and Rogers, 2011).

Processes do affect the pattern of vegetation in landscapes, this is not in question. But, what I have come to understand is that processes do not affect the spatial distribution of a landscape consistently. I propose that the patches which are observed in this particular landscape are not always ontological units, brought about by the influence of process. Rather they may simply represent a time slice in randomly distributed trees, which do not necessarily infer anything about the processes.

Patches are fluid in time under the influence of processes and cannot be used to infer either the effect of process or be explained by complex systems theory. If we are to reify patches as entities unto themselves, then we are assuming equilibrium in a different guise. This may be valid in particular instances, such as when ecological memory is high enough, in this instance the notion of a holon holds true and reification of the conceptual framework is possible. However, just as often it may not be the case as reification of the patch is invalid.

Complex systems theory has bounds to its application, it requires positive feedback loops in order for emergence to occur. What if the system in question is not replete with the feedbacks needed for holons to form? What if the feedback loops are disturbed before the emergence can in fact take place? The notion of holons and levels of organization have a strong undercurrent of equilibrium theory in them. That may be a heretical statement, but for holons to be reflected as patches and for ecologists to use patches as functional units, the pattern is assumed to be equilibrated to the processes. If not and ecosystems are actually a shifting mosaic of patches at various successional stages, then what specifics of process can be inferred from the pattern?

4.2. Conclusion

Hierarchical Patch Dynamics is a very good and useful framework; it is based on solid, empirically derived principles. However, it has not been demonstrated empirically in the very systems in which the conceptual framework is used. HPDP is left wanting in the ability to explain real world patterns in heterogeneous semi-arid savanna systems such as the Northern Kruger National Park. Contingency and context seem to be unshakeable companions in real world interpretation of pattern, rendering the pattern-process scale perspective ineffective at generating a working understanding (Levick, 2008).

In my opinion it is not because HPDP is flawed, it is simply not used with a full understanding of the underlying assumptions.

When considered from a fundamentalist viewpoint, the reification of patches in Hierarchical Patch Dynamics and the Textural Discontinuity Hypothesis can be viewed as a type of equilibrium theory. By looking for discontinuities and levels of organization we assume that the pattern and process have equilibrated to some steady state around a structural attractor. We assume that the feedback loop has reached the full potential of ascendancy and is in "equilibrium" with the other agents in the system.

While this may be so, in heterogeneous environments does the system ever actually reach the equilibrium, "stable" state or do they simply chase the illusive attractor *ad infinitum*? I think that Robert Ulanowicz and his multiple works, synthesized in the book "The Third Window" (Ulanowicz, 2008) has discovered something profound; that is the unrealized importance of chance in ecosystem evolution- the *Alleotoric* he calls it. How does one reconcile the viewpoints of Gardner, Milne et. al. (1987) that assert that natural landscapes are not random, and those of Ulanowicz (2008) and the findings of this thesis. I am not so bold as to assume my thesis is unequivocal evidence, but my assertion is that there is a lot more random in the landscape than previously appreciated.

4.3. A WAY FORWARD

I have come to realize that to understand systems one must understand flows, not patterns. If information flow is what drives complex systems, we need to measure flow. After all, we are simply an ever changing association of atoms, there is no "we". Process ecology is coming to the fore again and the acknowledgement that pattern is nothing more than a configuration of processes can go a long way to answering perplexing questions in ecology(Ulanowicz et al., 2006, Ulanowicz, 2008). Possibilities such as isotope and food web based methods (Fath et al., 2007, Ulanowicz et al., 2009) which trace the pathway of materials through a system have the potential to yield deep insight into the nature of information flow in ecosystems.

As yet there are no methods of determining the nature of process feedbacks in a spatially explicit context, nor at large enough scales in a landscape to glean an understanding of flows. However, with remote sensing technologies reaching a point where nitrogen levels, water levels and carbon can be accurately measured remotely at ever increasing resolution, it seems only a matter of time before the measurement of process becomes main stream. To achieve this understanding of complex systems then does require that we as landscape ecologists shake the yoke of purely pattern centered inquiry.

References

AGNEW, A. D. Q. 1997. Switches, pulses and grazing in arid vegetation. *Journal of Arid Environments,* 37, 609-617.

AGNEW, A. D. Q., WILSON, J. B. & SYKES, M. T. 1993. A vegetation switch as the cause of a forest/mire ecotone in New Zealand. *Journal of Vegetation Science,* 4, 273-278.

AGUILAR-AMUCHASTEGUI, N. & HENEBRY, G. M. 2006. Monitoring sustainability in tropical forests: how changes in canopy spatial pattern can indicate forest stands for biodiversity surveys. *IEEE Geoscience and Remote Sensing Letters,* 3, 329-333.

ALADOS, C. L., PUEYO, Y., NAVAS, D., CABEZUDO, B., GONZALEZ, A. & FREEMAN, D. C. 2005. Fractal analysis of plant spatial patterns: a monitoring tool for vegetation transition shifts. *Biodiversity and Conservation,* 14, 1453-1468.

ALLEN, C. R. 2006. Discontinuities in ecological data. *Proceedings of the National Academy of Sciences,* 103, 6083-6084.

ALLEN, C. R., FORYS, E. A. & HOLLING, C. S. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems,* 2, 114-121.

ALLEN, C. R., GARMESTANI, A. S., HAVLICEK, T. D., MARQUET, P. A., PETERSON, G. D., RESTREPO, C., STOW, C. A. & WEEKS, B. E. 2006. Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters,* 9, 630-643.

ALLEN, C. R., GUNDERSON, L. & JOHNSON, A. R. 2005. The Use of Discontinuities and Functional Groups to Assess Relative Resilience in Complex Systems. *Ecosystems,* 8, 958-966.

ALLEN, C. R. & HOLLING, C. S. 2002. Cross-scale structure and scale breaks in ecosystems and other complex systems. *Ecosystems(New York, NY. Print),* 5, 315-318.

ALLEN, C. R. & HOLLING, C. S. 2008. *Discontinuities in ecosystems and other complex systems,* New York, Columbia University Press.

ALLEN, T. F. H. 1998. The landscape "level" is dead: persuading the family to take it off the respirator. *In:* PETERSON, D. L. & THOMAS PARKER, V. (eds.) *Ecological scale: Theory and applications.*

ALLEN, T. F. H. 2011. *RE: Communications regarding paper submission on treating scale as a dimension.* Type to BARICHIEVY, C.

ALLEN, T. F. H. & HOEKSTRA, T. W. 1991. Role of heterogeneity in scaling of ecological systems under analysis. *Ecological heterogeneity.* Springer.

ALLEN, T. F. H. & STARR, T. B. 1982. Scales and filters. *Hierarchy.* Chicago: University of Chicago press.

ALLEN, T. F. H., TAINTER, J. A., PIRES, J. C. & HOEKSTRA, T. W. 2001. Dragnet ecology-Just the facts, ma'am: the privilege of science in a postmodern world. *BioScience,* 51, 475-485.

ALLEN, T. F. H. & WYLETO, E. P. 1983. A hierarchical model for the complexity of plant communities. *Journal of Theoretical Biology,* 101, 529-540.

ARCHIBALD, S. & BOND, W. J. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire,* 13, 377-385.

ARES, J., DEL VALLE, H. & BISIGATO, A. 2003. Detection of process-related changes in plant patterns at extended spatial scales during early dryland desertification. *Global Change Biology,* 9, 1643-1659.

ASNER, G. P., LEVICK, S. R., KENNEDY-BOWDOIN, T., KNAPP, D. E., EMERSON, R., JACOBSON, J., COLGAN, M. S. & MARTIN, R. E. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences,* 106, 4947-4947.

BAAS, A. C. W. 2002. Chaos, fractals and self-organization in coastal geomorphology: simulating dune landscapes in vegetated environments. *Geomorphology,* 48, 309-328.

BAATZ, M. & SCHÄPE, A. Object-oriented and multi-scale image analysis in semantic networks. 2nd International Symposium: Operationalization of Remote Sensing, 1999.
BASTIN, G. N., LUDWIG, J. A., EAGER, R. W., CHEWINGS, V. H. & LIEDLOFF, A. C. 2002. Indicators of landscape function: comparing patchiness metrics using remotely-sensed data from rangelands. *Ecological Indicators,* 1, 247-260.
BEERLING, D. J. & OSBORNE, C. P. 2006. The origin of the savanna biome. *Global Change Biology,* 12, 2023-2031.
BESTELMEYER, B. T., BROWN, J. R., HAVSTAD, K. M., ALEXANDER, R., CHAVEZ, G. & HERRICK, J. E. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management*, 114-126.
BESTELMEYER, B. T., MOSELEY, K., SHAVER, P. L., SANCHEZ, H., BRISKE, D. D. & FERNANDEZ-GIMENEZ, M. E. 2010. Practical guidance for developing state-and-transition models. *Rangelands,* 32, 23-30.
BESTELMEYER, B. T., TUGEL, A. J., PEACOCK JR, G. L., ROBINETT, D. G., SHAVER, P. L., BROWN, J. R., HERRICK, J. E., SANCHEZ, H. & HAVSTAD, K. M. 2009. State-and-transition models for heterogeneous landscapes: a strategy for development and application. *Rangeland Ecology & Management,* 62, 1-15.
BIEWENER, A. A. 1989. Scaling body support in mammals: limb posture and muscle mechanics. *Science(Washington),* 245, 45-45.
BLASCHKE, T., CONRADI, M. & LANG, S. S. Multiscale image analysis for ecological monitoring of heterogeneous, small structured landscapes. 2002. SPIE, 35-35.
BLASCHKE, T. & HAY, G. J. 2001. Object-oriented image analysis and scale-space: theory and methods for modeling and evaluating multiscale landscape structure. *International Archives of Photogrammetry and Remote Sensing,* 34, 22-29.
BOHENSKI, E. 2006. Creation of orthorectified aerial photography mosaics for the Sabie and Shingwedzi rivers, Kruger National Park. University of California, Berkley

River/Savanna Boundaries Programme-Kruger National Park Scientific Services.
BOND, W. J. & KEELEY, J. E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution,* 20, 387-394.
BOND, W. J. & LOFFELL, D. 2001. Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology,* 39, 286-294.
BOND, W. J., WOODWARD, F. I. & MIDGLEY, G. F. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist,* 165, 525-538.
BOOTS, B. 2002. Local measures of spatial association. *Ecoscience,* 9, 168-176.
BRADSHAW, G. A. & SPIES, T. A. 1992. Characterizing canopy gap structure in forests using wavelet analysis. *Journal of Ecology,* 80, 205-215.
BRISKE, D. D., BESTELMEYER, B. T., STRINGHAM, T. K. & SHAVER, P. L. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangeland Ecology & Management,* 61, 359-367.
BRISKE, D. D., FUHLENDORF, S. D. & SMEINS, F. E. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management,* 58, 1-10.
BROSOFSKE, K. D., CHEN, J., CROW, T. R. & SAUNDERS, S. C. 1999. Vegetation responses to landscape structure at multiple scales across a Northern Wisconsin, USA, pine barrens landscape. *Plant Ecology,* 143, 203-218.
BROWN, J. H., GILLOOLY, J. F., ALLEN, A. P., SAVAGE, V. M. & WEST, G. B. 2004. Toward a metabolic theory of ecology. *Ecology,* 85, 1771-1789.
BROWN, J. H., GUPTA, V. K., LI, B.-L., MILNE, B. T., RESTREPO, C. & WEST, G. B. 2002. The fractal nature of nature: power laws, ecological complexity and biodiversity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 357, 619-626.

BROWN, J. H., STEVENS, G. C. & KAUFMAN, D. M. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics,* 27, 597-623.
BROWN, M., SZELISKI, R. & WINDER, S. 2005. Multi-image matching using multi-scale oriented patches. *Computer Vision and Pattern Recognition, 2005. CVPR 2005. IEEE Computer Society Conference on,* 1.
BURNETT, C. & BLASCHKE, T. 2003. A multi-scale segmentation/object relationship modelling methodology for landscape analysis. *Ecological Modelling,* 168, 233-249.
CACHIA, A., MANGIN, J. F., RIVIERE, D., KHERIF, F., BODDAERT, N., ANDRADE, A., PAPADOPOULOS-ORFANOS, D., POLINE, J. B., BLOCH, I. & ZILBOVICIUS, M. 2003. A primal sketch of the cortex mean curvature: a morphogenesis based approach to study the variability of the folding patterns. *Medical Imaging, IEEE Transactions on,* 22, 754-765.
CASTILLA, G., HAY, G. J. & RUIZ-GALLARDO, J. R. 2008. Size-constrained Region Merging (SCRM): An Automated Delineation Tool for Assisted Photointerpretation. *PHOTOGRAMMETRIC ENGINEERING AND REMOTE SENSING,* 74, 409-409.
CAZELLES, B., CHAVEZ, M., BERTEAUX, D., MÉNARD, F., VIK, J. O., JENOUVRIER, S. & STENSETH, N. C. 2008. Wavelet analysis of ecological time series. *Oecologia,* 156, 287-304.
CHAVE, J. & LEVIN, S. 2003. Scale and scaling in ecological and economic systems. *Environmental and Resource Economics,* 26, 527-557.
CHEN, J., SAUNDERS, S. C., CROW, T. R., NAIMAN, R. J., BROSOFSKE, K. D., MROZ, G. D., BROOKSHIRE, B. L. & FRANKLIN, J. F. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience,* 49, 288-297.
CHEN, Y. F., YU, F. H. & DONG, M. 2002. Scale-dependent spatial heterogeneity of vegetation in Mu Us sandy land, a semi-arid area of China. *Plant Ecology,* 162, 135-142.
CHENG, Q. 1999. Multifractality and spatial statistics. *Computers and Geosciences,* 25, 949-961.
CHIPMAN, H. A., GEORGE, E. I. & MCCULLOCH, R. E. 1998. Bayesian CART model search. *Journal of the American Statistical Association,* 93, 935-948.
CHO, E. & CHON, T. S. 2006. Application of wavelet analysis to ecological data. *Ecological Informatics,* 1, 229-233.
CLICKORLANDO.COM. Available: http://www.clickorlando.com/news/4170720/detail.html [Accessed July 2010.
COLGAN, M. 2009. *RE: Woody vegetation biomass in the Nwashitsumbe enclosre sites, measured using LiDAR.* Type to BARICHIEVY, C.
COOLTOAST.COM. Available: <http://cooltoast.com/> [Accessed August 2010.
COPPEDGE, B. R., ENGLE, D. M., TOEPFER, C. S. & SHAW, J. H. 1998. Effects of seasonal fire, bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology,* 139, 235-246.
COPPEDGE, B. R. & SHAW, J. H. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management,* 51, 258-264.
COULON, O., MANGIN, J. F., POLINE, J. B., ZILBOVICIUS, M., ROUMENOV, D., SAMSON, Y., FROUIN, V. & BLOCH, I. 2000. Structural Group Analysis of Functional Activation Maps. *NeuroImage,* 11, 767-782.
COUTERON, P., BARBIER, N. & GAUTIER, D. 2006. Textural ordination based on Fourier spectral decomposition: a method to analyze and compare landscape patterns. *Landscape Ecology,* 21, 555-567.
CSILLAG, F. & KABOS, S. 2002. Wavelets, boundaries, and the spatial analysis of landscape pattern. *Ecoscience,* 9, 177-190.

CULLINAN, V. I., SIMMONS, M. A. & THOMAS, J. M. 1997. A Bayesian test of hierarchy theory: scaling up variability in plant cover from field to remotely sensed data. *Landscape Ecology,* 12, 273-285.

CULLINAN, V. I. & THOMAS, J. M. 1992. A comparison of quantitative methods for examining landscape pattern and scale. *Landscape Ecology,* 7, 211-227.

D'ODORICO, P., LAIO, F. & RIDOLFI, L. 2006. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist,* 167, 79-87.

DA SILVEIRA, L. & STERNBERG, L. 2001. Savanna-Forest Hysteresis in the Tropics. *Global Ecology and Biogeography,* 10, 369-378.

DALE, M. R. T. 2000. Lacunarity analysis of spatial pattern: a comparison. *Landscape Ecology,* 15, 467-478.

DALE, M. R. T., DIXON, P., FORTIN, M. J., LEGENDRE, P., MYERS, D. E. & ROSENBERG, M. S. 2002. Conceptual and mathematical relationships among methods for spatial analysis. *Ecography,* 25, 558-577.

DALE, M. R. T. & MAH, M. 1998. The use of wavelets for spatial pattern analysis in ecology. *Journal of Vegetation Science,* 9, 805-814.

DAWKINS, R. 1989. 11. Memes: the new replicators. *The selfish gene.* Oxford: Oxford University Press.

DE KOK, R., BUCK, A., SCHNEIDER, T., AMMER, U. & FREISING, T. U. M. 2000. Analysis of image objects from VHR imagery for forest GIS updating in the Bavarian Alps. *INTERNATIONAL ARCHIVES OF PHOTOGRAMMETRY AND REMOTE SENSING,* 33, 222-229.

DENNETT, D. C. & WEINER, P. 1993. *Consciousness explained*, Penguin London.

DESPLAND, E. 2003. Fractal index captures the role of vegetation clumping in locust swarming. *Functional Ecology,* 17, 315-322.

DOUGILL, A. J., HEATHWAITE, A. L. & THOMAS, D. S. G. 1998. Soil water movement and nutrient cycling in semi-arid rangeland: vegetation change and system resilience. *Hydrological Processes,* 12, 443-459.

DRĂGUŢ, L., TIEDE, D. & LEVICK, S. R. 2010. ESP: a tool to estimate scale parameter for multiresolution image segmentation of remotely sensed data. *International Journal of Geographical Information Science,* 24, 859-871.

DUFOURNAUD, Y., SCHMID, C. & HORAUD, R. 2000. Matching images with different resolutions. *IEEE COMPUTER SOCIETY CONFERENCE ON COMPUTER VISION AND PATTERN RECOGNITION,* 1.

DUNGAN, J. L., PERRY, J. N., DALE, M. R. T., LEGENDRE, P., CITRON-POUSTY, S., FORTIN, M. J., JAKOMULSKA, A., MIRITI, M. & ROSENBERG, M. S. 2002. A balanced view of scale in spatial statistical analysis. *Ecography,* 25, 626-626.

ECKHARDT, H. C., WILGEN, B. W. & BIGGS, H. C. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology,* 38, 108-115.

ETTEMA, C. H. & WARDLE, D. A. 2002. Spatial soil ecology. *Trends in Ecology & Evolution,* 17, 177-183.

FATH, B. D., SCHARLER, U. M., ULANOWICZ, R. E. & HANNON, B. 2007. Ecological network analysis: network construction. *Ecological Modelling,* 208, 49-55.

FIRSTCOASTNEWS.COM. Available: <http://www.firstcoastnews.com/news/usworld/news-article.aspx?storyid=28783> [Accessed July 2010.

FLORACK, L. & KUIJPER, A. 2000. The topological structure of scale-space images. *Journal of Mathematical Imaging and Vision,* 12, 65-79.

FLORACK, L. M. J., TER HAAR ROMENY, B. M., KOENDERINK, J. J. & VIERGEVER, M. A. 1994. Linear scale-space. *Journal of Mathematical Imaging and Vision,* 4, 325-351.

FOODY, G. M. 2005. Clarifications on local and global data analysis. *Global Ecology and Biogeography,* 14, 99-100.

FORTIN, M. J., BOOTS, B., CSILLAG, F. & REMMEL, T. K. 2003. ON THE ROLE OF SPATIAL STOCHASTIC MODELS IN UNDERSTANDING LANDSCAPE INDICES IN ECOLOGY. *OIKOS,* 102, 203-203.
FORTIN, M. J., KEITT, T. H., MAURER, B. A., TAPER, M. L., KAUFMAN, D. M. & BLACKBURN, T. M. 2005. SPECIES'GEOGRAPHIC RANGES AND DISTRIBUTIONAL LIMITS: PATTERN ANALYSIS AND STATISTICAL ISSUES. *OIKOS,* 108, 7-7.
FOTHERINGHAM, A. S. & WONG, D. W. S. 1991. THE MODIFIABLE AREAL UNIT PROBLEM IN MULTIVARIATE STATISTICAL ANALYSIS. *ENVIRONMENT AND PLANNING A,* 23, 1025-1044.
FRAZER, G. W., WULDER, M. A. & NIEMANN, K. O. 2005. SIMULATION AND QUANTIFICATION OF THE FINE-SCALE SPATIAL PATTERN AND HETEROGENEITY OF FOREST CANOPY STRUCTURE: A LACUNARITY-BASED METHOD DESIGNED FOR ANALYSIS OF CONTINUOUS CANOPY HEIGHTS. *FOREST ECOLOGY AND MANAGEMENT,* 214, 65-90.
FRITZ, H., SAID, S. & WEIMERSKIRCH, H. 2003. SCALE–DEPENDENT HIERARCHICAL ADJUSTMENTS OF MOVEMENT PATTERNS IN A LONG–RANGE FORAGING SEABIRD. *PROCEEDINGS OF THE ROYAL SOCIETY OF LONDON. SERIES B: BIOLOGICAL SCIENCES,* 270, 1143-1143.
FUHLENDORF, S. D. & ENGLE, D. M. 2001. RESTORING HETEROGENEITY ON RANGELANDS: ECOSYSTEM MANAGEMENT BASED ON EVOLUTIONARY GRAZING PATTERNS. *BIOSCIENCE,* 51, 625-632.
FUHLENDORF, S. D. & ENGLE, D. M. 2004. APPLICATION OF THE FIRE-GRAZING INTERACTION TO RESTORE A SHIFTING MOSAIC ON TALLGRASS PRAIRIE. *JOURNAL OF APPLIED ECOLOGY,* 41, 604-614.
GARDNER, R. H., MILNE, B. T., TURNEI, M. G. & O'NEILL, R. V. 1987. NEUTRAL MODELS FOR THE ANALYSIS OF BROAD-SCALE LANDSCAPE PATTERN. *LANDSCAPE ECOLOGY,* 1, 19-28.
GARDNER, R. H. & URBAN, D. L. 2007. NEUTRAL MODELS FOR TESTING LANDSCAPE HYPOTHESES. *LANDSCAPE ECOLOGY,* 22, 15-29.
GARTNER, B. L. 1991. STEM HYDRAULIC PROPERTIES OF VINES VS. SHRUBS OF WESTERN POISON OAK, *TOXICODENDRON DIVERSILOBUM*. *OECOLOGIA,* 87.
GASTON, K. J. 2000. GLOBAL PATTERNS IN BIODIVERSITY. *NATURE,* 405, 220-227.
GELL MANN, M. 2007. *BEAUTY AND TRUTH IN PHYSICS* [ONLINE]. AVAILABLE: HTTP://WWW.TED.COM/TALKS/MURRAY_GELL_MANN_ON_BEAUTY_AND_TRUTH_IN_PHYSICS.HTML.
GETBEHINDJESUS.NET. AVAILABLE: HTTP://GETBEHINDJESUS.NET [ACCESSED JULY 2010.
GIBSON, C. C., OSTROM, E. & AHN, T. K. 2000. THE CONCEPT OF SCALE AND THE HUMAN DIMENSIONS OF GLOBAL CHANGE: A SURVEY. *ECOLOGICAL ECONOMICS,* 32, 217-239.
GILLSON, L. 2004. EVIDENCE OF HIERARCHICAL PATCH DYNAMICS IN AN EAST AFRICAN SAVANNA? *LANDSCAPE ECOLOGY,* 19, 883-894.
GOLDENPALACEEVENTS.COM. AVAILABLE: <HTTP://WWW.GOLDENPALACEEVENTS.COM/AUCTIONS/JESUSWALL01.PHP> [ACCESSED JULY 2010.
GOVENDER, N. 2009. FIRE HISTORY OF THE 'NWASHITSUMBE ENCLOSURES. SANPARKS.
GUNDERSON, L. H. 2000. ECOLOGICAL RESILIENCE-IN THEORY AND APPLICATION. *ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS,* 31, 425-439.
HABEEB, R. L., TREBILCO, J., WOTHERSPOON, S. & JOHNSON, C. R. 2005. DETERMINING NATURAL SCALES OF ECOLOGICAL SYSTEMS. *ECOLOGICAL MONOGRAPHS,* 75, 467-487.
HAGEN-ZANKER, A. & LAJOIE, G. 2008. NEUTRAL MODELS OF LANDSCAPE CHANGE AS BENCHMARKS IN THE ASSESSMENT OF MODEL PERFORMANCE. *LANDSCAPE AND URBAN PLANNING,* 86, 284-296.
HALLEY, J. M., HARTLEY, S., KALLIMANIS, A. S., KUNIN, W. E., LENNON, J. J. & SGARDELIS, S. P. 2004. USES AND ABUSES OF FRACTAL METHODOLOGY IN ECOLOGY. *ECOLOGY LETTERS,* 7, 254-271.
HARRISON, S., MASSEY, D. & RICHARDS, K. 2006. COMPLEXITY AND EMERGENCE (ANOTHER CONVERSATION). *AREA,* 38, 465-471.

HARTLEY, S., KUNIN, W. E., LENNON, J. J. & POCOCK, M. J. O. 2004. COHERENCE AND DISCONTINUITY IN THE SCALING OF SPECIES' DISTRIBUTION PATTERNS. *PROCEEDINGS OF THE ROYAL SOCIETY B: BIOLOGICAL SCIENCES,* 271, 81-88.

HAY, G. 2012. VISUALIZING SCALE-DOMAIN MANIFOLDS. A MULTISCALE GEO-OBJECT BASED APPROACH. *IN:* WENG, Q. (ED.) *SCALING ISSUES IN REMOTE SENSING.* JOHN WILEY AND SONS.

HAY, G. J., BLASCHKE, T., MARCEAU, D. J. & BOUCHARD, A. 2003. A COMPARISON OF THREE IMAGE-OBJECT METHODS FOR THE MULTISCALE ANALYSIS OF LANDSCAPE STRUCTURE. *ISPRS JOURNAL OF PHOTOGRAMMETRY AND REMOTE SENSING,* 57, 327-345.

HAY, G. J., DUBÉ, P., BOUCHARD, A. & MARCEAU, D. J. 2002. A SCALE-SPACE PRIMER FOR EXPLORING AND QUANTIFYING COMPLEX LANDSCAPES. *ECOLOGICAL MODELLING,* 153, 27-49.

HAY, G. J. & MARCEAU, D. J. 2004. MULTISCALE OBJECT-SPECIFIC ANALYSIS (MOSA): AN INTEGRATIVE APPROACH FOR MULTISCALE LANDSCAPE ANALYSIS. *REMOTE SENSING IMAGE ANALYSIS: INCLUDING THE SPATIAL DOMAIN. KLUWER ACADEMICS*.

HAY, G. J., MARCEAU, D. J., DUBÉ, P. & BOUCHARD, A. 2001. A MULTISCALE FRAMEWORK FOR LANDSCAPE ANALYSIS: OBJECT-SPECIFIC ANALYSIS AND UPSCALING. *LANDSCAPE ECOLOGY,* 16, 471-490.

HE, Y., GUO, X. & SI, B. C. 2007. DETECTING GRASSLAND SPATIAL VARIATION BY A WAVELET APPROACH. *INTERNATIONAL JOURNAL OF REMOTE SENSING,* 28, 1527-1545.

HENEBRY, G. M. & KUX, H. J. H. 1995. LACUNARITY AS A TEXTURE MEASURE FOR SAR IMAGERY. *INTERNATIONAL JOURNAL OF REMOTE SENSING,* 16, 565-571.

HEYLINGEN, F. & CHIELENS, K. 2009. EVOLUTION OF CULTURE, MEMETICS. *IN:* MEYER, B. (ED.) *ENCYCLOPEDIA OF COMPLEXITY AND SYSTEMS SCIENCE.* SPRINGER.

HIBBARD, K. A., ARCHER, S., SCHIMEL, D. S. & VALENTINE, D. W. 2001. BIOGEOCHEMICAL CHANGES ACCOMPANYING WOODY PLANT ENCROACHMENT IN A SUBTROPICAL SAVANNA. *ECOLOGY,* 82, 1999-2011.

HIGGINS, S. I., BOND, W. J. & TROLLOPE, W. S. W. 2000. FIRE, RESPROUTING AND VARIABILITY: A RECIPE FOR GRASS–TREE COEXISTENCE IN SAVANNA. *JOURNAL OF ECOLOGY,* 88, 213-229.

HIGGINS, S. I. & SCHEITER, S. 2012. ATMOSPHERIC CO2 FORCES ABRUPT VEGETATION SHIFTS LOCALLY, BUT NOT GLOBALLY. *NATURE,* 488, 209-212.

HILL, M. F. & CASWELL, H. 1999. HABITAT FRAGMENTATION AND EXTINCTION THRESHOLDS ON FRACTAL LANDSCAPES. *ECOLOGY LETTERS,* 2, 121-127.

HILLERISLAMBERS, R., RIETKERK, M., VAN DEN BOSCH, F., PRINS, H. H. T. & DE KROON, H. 2001. VEGETATION PATTERN FORMATION IN SEMI-ARID GRAZING SYSTEMS. *ECOLOGY,* 82, 50-61.

HOBBS, N. T. 1996. MODIFICATION OF ECOSYSTEMS BY UNGULATES. *THE JOURNAL OF WILDLIFE MANAGEMENT,* 60, 695-713.

HOBBS, N. T., SCHIMEL, D. S., OWENSBY, C. E. & OJIMA, D. S. 1991. FIRE AND GRAZING IN THE TALLGRASS PRAIRIE: CONTINGENT EFFECTS ON NITROGEN BUDGETS. *ECOLOGY,* 72, 1374-1382.

HOBBS, R. J. & MORTON, S. R. 1999. MOVING FROM DESCRIPTIVE TO PREDICTIVE ECOLOGY. *AGROFORESTRY SYSTEMS,* 45, 43-55.

HOFFMANN, W., SCHROEDER, W. & JACKSON, R. B. 2002. POSITIVE FEEDBACKS OF FIRE, CLIMATE, AND VEGETATION AND THE CONVERSION OF TROPICAL SAVANNA. *GEOPHYSICAL RESEARCH LETTERS,* 29, 9-1.

HOFFMANN, W. A. & JACKSON, R. B. 2000. VEGETATION–CLIMATE FEEDBACKS IN THE CONVERSION OF TROPICAL SAVANNA TO GRASSLAND. *JOURNAL OF CLIMATE,* 13, 1593-1602.

HOLDO, R. M. 2007. ELEPHANTS, FIRE, AND FROST CAN DETERMINE COMMUNITY STRUCTURE AND COMPOSITION IN KALAHARI WOODLANDS. *ECOLOGICAL APPLICATIONS,* 17, 558-568.

HOLLING, C. S. 1992. CROSS-SCALE MORPHOLOGY, GEOMETRY, AND DYNAMICS OF ECOSYSTEMS. *ECOLOGICAL MONOGRAPHS,* 62, 447-502.

HOLLING, C. S. 2001. UNDERSTANDING THE COMPLEXITY OF ECONOMIC, ECOLOGICAL, AND SOCIAL SYSTEMS. *ECOSYSTEMS,* 4, 390-405.

HUBBELL, S. P. 2001. THE UNIFIED THEORY OF BIOGEOGRAPHY AND BIODIVERSITY. Á PRINCETON UNIV. PRESS.

HUTCHINSON, G. E. 1965. *The ecological theater and the evolutionary play*, Yale University Press New Haven.
JELINEK, H. F., JONES, C. L., WARFEL, M. D., LUCAS, C., DEPARDIEU, C. & AUREL, G. 2006. Understanding Fractal Analysis? The Case of Fractal Linguistics. *ComPlexUs,* 3, 66-73.
JELINSKI, D. E. & WU, J. 1996. The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology,* 11, 129-140.
JOHNSON, C. J., BOYCE, M. S., MULDERS, R., GUNN, A., GAU, R. J., CLUFF, H. D. & CASE, R. L. 2005. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. *Landscape Ecology,* 19, 869-882.
JØRGENSEN, S. E., MEJER, H. & NIELSEN, S. N. 1998. Ecosystem as self-organizing critical systems. *Ecological Modelling,* 111, 261-268.
KANTERS, F., FLORACK, L., DUITS, R. & PLATEL, B. Scalespaceviz: Visualizing -scale spaces. 2004. Citeseer.
KAUFFMAN, S. A. 1995. *At home in the universe: The search for laws of self-organization and complexity*, Oxford University Press, USA.
KAY, J. J. & SCHNEIDER, E. 1994. Embracing Complexity: The Challenge of the Ecosystem Approach. *Alternatives,* 20, 32-39.
KAY, J. J. & SCHNEIDER, E. D. 2000. Thermodynamics and measures of ecological integrity. *Ecological indicators.* Springer.
KEELEY, J. E. & RUNDEL, P. W. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters,* 8, 683-690.
KÉFI, S., RIETKERK, M., ALADOS, C. L., PUEYO, Y., PAPANASTASIS, V. P., ELAICH, A. & DE RUITER, P. C. 2007a. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature,* 449, 213-217.
KÉFI, S., RIETKERK, M., VAN BAALEN, M. & LOREAU, M. 2007b. Local facilitation, bistability and transitions in arid ecosystems. *Theoretical population biology,* 71, 367-379.
KEITT, T. H. 2000. Spectral representation of neutral landscapes. *Landscape Ecology,* 15, 479-494.
KENT, M., MOYEED, R. A., REID, C. L., PAKEMAN, R. & WEAVER, R. 2006. Geostatistics, spatial rate of change analysis and boundary detection in plant ecology and biogeography. *Progress in Physical Geography,* 30, 201-201.
KERBY, J. D., FUHLENDORF, S. D. & ENGLE, D. M. 2007. Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes. *Landscape Ecology,* 22, 507-516.
KLEIN, T. & ERTL, T. 2005. Scale-space tracking of critical points in 3D vector fields. *Topo-In-Vis 2005*.
KNAPP, A. K., BLAIR, J. M., BRIGGS, J. M., COLLINS, S. L., HARTNETT, D. C., JOHNSON, L. C. & TOWNE, E. G. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience,* 49, 39-50.
KOENDERINK, J. J. 1984. The structure of images. *Biological Cybernetics,* 50, 363-370.
KOESTLER, A. 1967. *The Ghost in the Machine,* New York, Random House.
KOTLIAR, N. B. & WIENS, J. A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos,* 59, 253-260.
KRUMMEL, J. R., GARDNER, R. H., SUGIHARA, G., O'NEILL, R. V. & COLEMAN, P. R. 1987. Landscape patterns in a disturbed environment. *Oikos*, 321-324.
KUIJPER, A. & FLORACK, L. 1999. Calculations on critical points under gaussian blurring. *Scale-Space Theories in Computer Vision*, 318-329.
LARK, R. M. & WEBSTER, R. 1999. Analysis and elucidation of soil variation using wavelets. *European Journal of Soil Science,* 50, 185-206.
LEGENDRE, P. 1998. *Numerical ecology*, Elsevier Science.
LEVICK, S. & ROGERS, K. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation,* 141, 489-498.

LEVICK, S. R. 2008. *A scaled, contextual perspective of woody structure across a savanna riparian landscape.* PhD, University of the Witwatersrand.

LEVICK, S. R., ASNER, G. P., KENNEDY-BOWDOIN, T. & KNAPP, D. E. 2010. The spatial extent of termite influences on herbivore browsing in an African savanna. *Biological Conservation*.

LEVICK, S. R. & ROGERS, K. H. 2011. Context-dependent vegetation dynamics in an African savanna. *Landscape Ecology,* 26, 515-528.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology,* 73, 1943-1967.

LEVIN, S. A. 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems,* 1, 431-436.

LI, B. L. 2000. Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecological Modelling,* 132, 33-50.

LIMBURG, K. E., O'NEILL, R. V., COSTANZA, R. & FARBER, S. 2002. Complex systems and valuation. *Ecological Economics,* 41, 409-420.

LINDEBERG, T. 1994. Scale-space theory: a basic tool for analyzing structures at different scales. *Journal of Applied Statistics,* 21, 225-270.

LINDEBERG, T., SPORRING, J., NIELSEN, M., FLORACK, L. & JOHANSEN, P. 1994. On the Axiomatic Foundations of Linear Scale-Space: Combining Semi-Group Structure with Causality vs. Scale Invariance. *Gaussian Scale-Space Theory: Proc. PhD School on Scale-Space Theory*.

LUDWIG, J. A., WILCOX, B. P., BRESHEARS, D. D., TONGWAY, D. J. & IMESON, A. C. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology,* 86, 288-297.

MALHI, Y. & ROMÁN-CUESTA, R. M. 2008. Analysis of lacunarity and scales of spatial homogeneity in IKONOS images of Amazonian tropical forest canopies. *Remote Sensing of Environment*.

MANDELBROT, B. B. 1982. *The Fractal Geometry of Nature*, WH Freeman.

MARCEAU, D. J. 1999. The scale issue in social and natural sciences. *Canadian Journal of Remote Sensing,* 25, 347-356.

MARCEAU, D. J. & HAY, G. J. 1999. Remote sensing contributions to the scale issue. *Canadian journal of remote sensing,* 25, 357-366.

MARQUET, P. A., QUINONES, R. A., ABADES, S., LABRA, F., TOGNELLI, M., ARIM, M. & RIVADENEIRA, M. 2005. Scaling and power-laws in ecological systems.

MAURER, B. A. 1999. *Untangling ecological complexity: the macroscopic perspective*, University of Chicago Press.

MCCULLEY, R. L., ARCHER, S. R., BOUTTON, T. W., HONS, F. M. & ZUBERER, D. A. 2004. Soil respiration and nutrient cycling in wooded communities developing in grassland. *Ecology,* 85, 2804-2817.

MCELRONE, A. J., POCKMAN, W. T., MARTINEZ-VILALTA, J. & JACKSON, R. B. 2004. Variation in xylem structure and function in stems and roots of trees to 20m depth. *New Phytologist,* 163, 507-517.

MCGARIGAL, K. & CUSHMAN, S. A. 2005. The gradient concept of landscape structure. *Issues and perspectives in landscape ecology*, 112-119.

MCINTYRE, N. E. & WIENS, J. A. 2000. A novel use of the lacunarity index to discern landscape function. *Landscape Ecology,* 15, 313-321.

MEINZER, F. C., CLEARWATER, M. J. & GOLDSTEIN, G. 2001. Water transport in trees: current perspectives, new insights and some controversies. *Environmental and Experimental Botany,* 45, 239-262.

MEISEL, J. E. & TURNER, M. G. 1998. Scale detection in real and artificial landscapes using semivariance analysis. *Landscape Ecology,* 13, 347-362.

MILNE, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. *American Naturalist*, 32-57.

MILNE, B. T. & JOHNSON, A. R. 1993. RENORMALIZATION RELATIONS FOR SCALE TRANSFORMATION IN ECOLOGY. *SOME MATHEMATICAL QUESTIONS IN BIOLOGY: PREDICTING SPATIAL EFFECTS IN ECOLOGICAL SYSTEMS*, 109-128.

MILTON, S. J. & HOFFMAN, M. T. 1994. THE APPLICATION OF STATE-AND-TRANSITION MODELS TO RANGELAND RESEARCH AND MANAGEMENT IN ARID SUCCULENT AND SEMI-ARID GRASSY KAROO, SOUTH AFRICA. *AFRICAN JOURNAL OF RANGE & FORAGE SCIENCE,* 11**,** 18-26.

MURWIRA, A. & SKIDMORE, A. K. 2006. MONITORING CHANGE IN THE SPATIAL HETEROGENEITY OF VEGETATION COVER IN AN AFRICAN SAVANNA. *INTERNATIONAL JOURNAL OF REMOTE SENSING,* 27**,** 2255-2269.

NAVEH, Z. 2000. WHAT IS HOLISTIC LANDSCAPE ECOLOGY? A CONCEPTUAL INTRODUCTION. *LANDSCAPE AND URBAN PLANNING,* 50**,** 7-26.

NEWSLITE.TV. AVAILABLE: <HTTP://NEWSLITE.TV/2010/07/05/GOOGLE-EARTH-REVEALS-IMAGE-OF.HTML> [ACCESSED JULY 2010.

NICOLIS, G., PRIGOGINE, I. & NOCOLIS, G. 1989. *EXPLORING COMPLEXITY*, FREEMAN NEW YORK.

NIKORA, V. I., PEARSON, C. P. & SHANKAR, U. 1999. SCALING PROPERTIES IN LANDSCAPE PATTERNS: NEW ZEALAND EXPERIENCE. *LANDSCAPE ECOLOGY,* 14**,** 17-33.

O'NEILL, R. V. (ED.) 1986. *A HIERARCHICAL CONCEPT OF ECOSYSTEMS*: PRINCETON UNIVERSITY PRESS.

O'NEILL, R. V., JOHNSON, A. R. & KING, A. W. 1989. A HIERARCHICAL FRAMEWORK FOR THE ANALYSIS OF SCALE. *LANDSCAPE ECOLOGY,* 3**,** 193-205.

O'NEILL, R. V. & KAHN, J. R. 2000. HOMO ECONOMUS AS A KEYSTONE SPECIES. *BIOSCIENCE,* 50**,** 333-337.

O'NEILL, R. V., KRUMMEL, J. R., GARDNER, R. H., SUGIHARA, G., JACKSON, B., DEANGELIS, D. L., MILNE, B. T., TURNER, M. G., ZYGMUNT, B. & CHRISTENSEN, S. W. 1988. INDICES OF LANDSCAPE PATTERN. *LANDSCAPE ECOLOGY,* 1**,** 153-162.

OWEN-SMITH, N. 1987. PLEISTOCENE EXTINCTIONS: THE PIVOTAL ROLE OF MEGAHERBIVORES. *PALEOBIOLOGY***,** 351-362.

OWEN-SMITH, R. N. 1992. *MEGAHERBIVORES: THE INFLUENCE OF VERY LARGE BODY SIZE ON ECOLOGY*, CAMBRIDGE UNIV PR.

PALMER, M. W. 1988. FRACTAL GEOMETRY: A TOOL FOR DESCRIBING SPATIAL PATTERNS OF PLANT COMMUNITIES. *PLANT ECOLOGY,* 75**,** 91-102.

PERRY, J. N., LIEBHOLD, A. M., ROSENBERG, M. S., DUNGAN, J., MIRITI, M., JAKOMULSKA, A. & CITRON-POUSTY, S. 2002. ILLUSTRATIONS AND GUIDELINES FOR SELECTING STATISTICAL METHODS FOR QUANTIFYING SPATIAL PATTERN IN ECOLOGICAL DATA. *ECOGRAPHY,* 25**,** 578-578.

PETERSON, G. 2008. SELF-ORGANIZATION AND DISCONTINUITIES IN ECOSYSTEMS. *IN:* ALLEN, C. R. & HOLLING, C. S. (EDS.) *DISCONTINUITIES IN ECOSYSTEMS AND OTHER COMPLEX SYSTEMS.* NEW YORK: COLUMBIA UNIVERSITY PRESS.

PETERSON, G. D. 2002. CONTAGIOUS DISTURBANCE, ECOLOGICAL MEMORY, AND THE EMERGENCE OF LANDSCAPE PATTERN. *ECOSYSTEMS,* 5**,** 329-338.

PICKETT, S. T. A., KOLASA, J., ARMESTO, J. J. & COLLINS, S. L. 1989. THE ECOLOGICAL CONCEPT OF DISTURBANCE AND ITS EXPRESSION AT VARIOUS HIERARCHICAL LEVELS. *OIKOS***,** 129-136.

PLATEL, B. 2003. *MULTISCALE HIERARCHICAL SEGMENTATION.* MSC, TECHNISCHE UNIVERSITEIT EINDHOVEN.

PLATEL, B. 2007. *EXPLORING THE DEEP STRUCTURE OF IMAGES.* PHD, TECHNISCHE UNIVERSITEIT EINDHOVEN.

PLOTKIN, J. B. & MULLER-LANDAU, H. C. 2002. SAMPLING THE SPECIES COMPOSITION OF A LANDSCAPE. *ECOLOGY,* 83**,** 3344-3356.

PLOTNICK, R. E., GARDNER, R. H., HARGROVE, W. W., PRESTEGAARD, K. & PERLMUTTER, M. 1996. LACUNARITY ANALYSIS: A GENERAL TECHNIQUE FOR THE ANALYSIS OF SPATIAL PATTERNS. *PHYSICAL REVIEW E,* 53**,** 5461-5468.

PLOTNICK, R. E., GARDNER, R. H. & O'NEILL, R. V. 1993. LACUNARITY INDICES AS MEASURES OF LANDSCAPE TEXTURE. *LANDSCAPE ECOLOGY,* 8**,** 201-211.

PUEYO, Y. & ALADOS, C. L. 2007. Effects of fragmentation, abiotic factors and land use on vegetation recovery in a semi-arid Mediterranean area. *Basic and Applied Ecology,* 8, 158-170.
RANGEL, T., DINIZ-FILHO, J. A. F. & BINI, L. M. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography,* 15, 321-327.
RATH, T. M. & MANMATHA, R. 2003. Word image matching using dynamic time warping. *Computer Vision and Pattern Recognition, 2003. Proceedings. 2003 IEEE Computer Society Conference on,* 2.
RESTREPO, C., RENJIFO, L. M. & MARPLES, P. 1997. Frugivorous birds in fragmented neotropical montane forests: landscape pattern and body mass distribution. *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. The University of Chicago Press, Chicago*.
REYNOLDS, J. F., TENHUNEN, J. D., LEADLEY, P. W., LI, H., MOORHEAD, D. L., OSTENDORF, B. & CHAPIN, F. S. 1996. Patch and landscape models of arctic tundra: Potentials and limitations. *In:* REYNOLDS, J. F. & TENHUNEN, J. D. (eds.) *Landscape Function and Disturbance in Arctic Tundra.* 120 ed. Berlin: Springer.
REYNOLDS, J. F. & WU, J. 1999. Do landscape structural and functional units exist. *Integrating Hydrology, Ecosystem Dynamics, and Biogeochemistry in Complex Landscapes. Wiley, Chichester*, 273-296.
RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution,* 43, 223-225.
RIETKERK, M., BOERLIJST, M. C., VAN LANGEVELDE, F., HILLERISLAMBERS, R., VAN DE KOPPEL, J., KUMAR, L., PRINS, H. H. T. & DE ROOS, A. M. 2002. Self organization of vegetation in arid ecosystems. *Am Nat,* 160, 524-530.
RIETKERK, M., DEKKER, S. C., DE RUITER, P. C. & VAN DE KOPPEL, J. 2004. Self-Organized Patchiness and Catastrophic Shifts in Ecosystems. *Science,* 305, 1926-1929.
RIETKERK, M. & VAN DE KOPPEL, J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos,* 79, 69-69.
RIPLEY, B. D. 1978. Spectral analysis and the analysis of pattern in plant communities. *The Journal of Ecology*, 965-981.
ROSENBERG, M. 2004. Wavelet analysis for detecting anisotropy in point patterns. *Journal of Vegetation Science,* 15.
SAKYI-ADDO. 2004. *Ghanaians flock to see 'miracle'* [Online]. BBC News. Available: http://news.bbc.co.uk/2/hi/africa/3976161.stm.
SANKARAN, M., HANAN, N. P., SCHOLES, R. J., RATNAM, J., AUGUSTINE, D. J., CADE, B. S., GIGNOUX, J., HIGGINS, S. I., LE ROUX, X. & LUDWIG, F. 2005. Determinants of woody cover in African savannas. *Nature,* 438, 846-849.
SANKARAN, M., RATNAM, J. & HANAN, N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography,* 17, 236-245.
SAUNDERS, S. C., CHEN, J., DRUMMER, T. D., GUSTAFSON, E. J. & BROSOFSKE, K. D. 2005. Identifying scales of pattern in ecological data: a comparison of lacunarity, spectral and wavelet analyses. *Ecological Complexity,* 2, 87-105.
SAURA, S. & CASTRO, S. 2007. Scaling functions for landscape pattern metrics derived from remotely sensed data: Are their subpixel estimates really accurate? *ISPRS Journal of Photogrammetry and Remote Sensing,* 62, 201-216.
SCANLON, T. M., CAYLOR, K. K., LEVIN, S. A. & RODRIGUEZ-ITURBE, I. 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. *Nature-London-,* 449, 209-209.
SCHLESINGER, W. H., RAIKES, J. A., HARTLEY, A. E. & CROSS, A. F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 364-374.
SCHNEIDER, D. C. 2001. The rise of the concept of scale in ecology. *BioScience,* 51, 545-553.
SCHNEIDER, E. D. & KAY, J. J. 1994. Life as a manifestation of the second law of thermodynamics. *Mathematical and computer modelling,* 19, 25-48.

SCHOLES, R. J. & ARCHER, S. R. 1997. TREE-GRASS INTERACTIONS IN SAVANNAS. *ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS,* 28, 517-544.

SHENKER, O. R. 1994. FRACTAL GEOMETRY IS NOT THE GEOMETRY OF NATURE. *STUDIES IN HISTORY AND PHILOSOPHY OF SCIENCE,* 25, 967-981.

SIEMANN, E. & BROWN, J. H. 1999. GAPS IN MAMMALIAN BODY SIZE DISRIBUTIONS REEXAMINED. *ECOLOGY,* 80, 2788-2792.

SIMPSON, E. H. 1951. THE INTERPRETATION OF INTERACTION IN CONTINGENCY TABLES. *JOURNAL OF THE ROYAL STATISTICAL SOCIETY. SERIES B (METHODOLOGICAL)*, 238-241.

SKILLEN, J. J., MAURER, B. A. & 2008. THE ECOLOGICAL SIGNIFICANCE OF DISCONTINUITIES IN BODY-MASS DISTRIBUTIONS. *IN:* ALLEN, C. R. & HOLLING, C. S. (EDS.) *DISCONTINUITIES IN ECOSYSTEMS AND OTHER COMPLEX SYSTEMS.* NEW YORK: COLUMBIA UNIVERSITY PRESS.

SOMMERFELD, R. A., LUNDQUIST, J. E. & SMITH, J. 2000. CHARACTERIZING THE CANOPY GAP STRUCTURE OF A DISTURBED FOREST USING THE FOURIER TRANSFORM. *FOREST ECOLOGY AND MANAGEMENT,* 128, 101-108.

STALLINS, J. A. 2006. GEOMORPHOLOGY AND ECOLOGY: UNIFYING THEMES FOR COMPLEX SYSTEMS IN BIOGEOMORPHOLOGY. *GEOMORPHOLOGY,* 77, 207-216.

STAVER, A. C., ARCHIBALD, S. & LEVIN, S. A. 2011. THE GLOBAL EXTENT AND DETERMINANTS OF SAVANNA AND FOREST AS ALTERNATIVE BIOME STATES. *SCIENCE,* 334, 230-232.

STAVER, A. C., BOND, W. J., STOCK, W. D., VAN RENSBURG, S. J. & WALDRAM, M. S. 2009. BROWSING AND FIRE INTERACT TO SUPPRESS TREE DENSITY IN AN AFRICAN SAVANNA. *ECOLOGICAL APPLICATIONS,* 19, 1909-1919.

STOW, C., ALLEN, C. R. & GARMESTANI, A. S. 2007. EVALUATING DISCONTINUITIES IN COMPLEX SYSTEMS: TOWARD QUANTITATIVE MEASURES OF RESILIENCE. *ECOLOGY AND SOCIETY,* 12, 26-26.

SUNDSTROM, S. 2009. *THE TEXTURAL DISCONTINUITY HYPOTHSESIS AND ITS RELATIONSHIP TO BIODIVERSITY, EXTINCTION RISK, AND ECOSYSTEM RESILLIENCE.* MASTER OF ENVIRONMENTAL DESIGN, UNIVERSITY OF CALGARY.

SUNDSTROM, S., ALLEN, C. R. & BARICHIEVY, C. 2012. SPECIES, FUNCTIONAL GROUPS, AND THRESHOLDS IN ECOLOGICAL RESILIENCE. *CONSERVATION BIOLOGY,* 26, 305-314.

TAINTER, J. A. & LUCAS, G. J. 1983. EPISTEMOLOGY OF THE SIGNIFICANCE CONCEPT. *AMERICAN ANTIQUITY*, 707-719.

THOMPSON, J. N., REICHMAN, O. J., MORIN, P. J., POLIS, G. A., POWER, M. E., STERNER, R. W., COUCH, C. A., GOUGH, L., HOLT, R. & HOOPER, D. U. 2001. FRONTIERS OF ECOLOGY. *BIOSCIENCE,* 51, 15-24.

TOBLER, W. R. 1970. A COMPUTER MOVIE SIMULATING URBAN GROWTH IN THE DETROIT REGION. *ECONOMIC GEOGRAPHY,* 46, 234-240.

TREYDTE, A. C., GRANT, C. C. & JELTSCH, F. 2009. TREE SIZE AND HERBIVORY DETERMINE BELOW-CANOPY GRASS QUALITY AND SPECIES COMPOSITION IN SAVANNAHS. *BIODIVERSITY AND CONSERVATION,* 18, 3989-4002.

TREYDTE, A. C., HEITKONIG, I., PRINS, H. H. T. & LUDWIG, F. 2007. TREES IMPROVE GRASS QUALITY FOR HERBIVORES IN AFRICAN SAVANNAS. *PERSPECTIVES IN PLANT ECOLOGY, EVOLUTION AND SYSTEMATICS,* 8, 197-205.

TURNER, M. G., GARDNER, R. H. & O'NEILL, R. V. 2001. *LANDSCAPE ECOLOGY IN THEORY AND PRACTICE: PATTERN AND PROCESS*, SPRINGER.

TYREE, M. T., DAVIS, D. D. & COCHARD, H. 1994. BIOPHYSICAL PERSPECTIVES OF XYLEM EVOLUTION: IS THERE A TRADEOFF OF HYDRAULIC EFFICIENCY FOR VULNERABILITY TO DYSFUNTION? *INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS JOURNAL,* 14, 335-360.

ULANOWICZ, R. E. 2008. *A THIRD WINDOW: NATURAL FOUNDATIONS FOR LIFE*, OXFORD UNIVERSITY PRESS.

ULANOWICZ, R. E., GOERNER, S. J., LIETAER, B. & GOMEZ, R. 2009. QUANTIFYING SUSTAINABILITY: RESILIENCE, EFFICIENCY AND THE RETURN OF INFORMATION THEORY. *ECOLOGICAL COMPLEXITY,* 6, 27-36.

ULANOWICZ, R. E., JØRGENSEN, S. E. & FATH, B. D. 2006. EXERGY, INFORMATION AND AGGRADATION: AN ECOSYSTEMS RECONCILIATION. *ECOLOGICAL MODELLING,* 198, 520-524.

URBAN, D. L., O'NEILL, R. V. & SHUGART, H. H. 1987. LANDSCAPE ECOLOGY. *BIOSCIENCE,* 37, 119-127.

VAN DE KOPPEL, J., RIETKERK, M., VAN LANGEVELDE, F., KUMAR, L., KLAUSMEIER, C. A., FRYXELL, J. M., HEARNE, J. W., VAN ANDEL, J., DE RIDDER, N. & SKIDMORE, A. 2002. SPATIAL HETEROGENEITY AND IRREVERSIBLE VEGETATION CHANGE IN SEMIARID GRAZING SYSTEMS. *AM NAT,* 159, 209-218.

VAN LANGEVELDE, F., VAN DE VIJVER, C., KUMAR, L., VAN DE KOPPEL, J., DE RIDDER, N., VAN ANDEL, J., SKIDMORE, A. K., HEARNE, J. W., STROOSNIJDER, L. & BOND, W. J. 2008. EFFECTS OF FIRE AND HERBIVORY ON THE STABILITY OF SAVANNA ECOSYSTEMS.

WAGNER, H. H. & FORTIN, M. J. 2005. SPATIAL ANALYSIS OF LANDSCAPES: CONCEPTS AND STATISTICS. *ECOLOGY,* 86, 1975-1987.

WATT, A. S. 1947. PATTERN AND PROCESS IN THE PLANT COMMUNITY. *THE JOURNAL OF ECOLOGY*, 1-22.

WEAVER, J. C. 1995. INDICATOR SPECIES AND SCALE OF OBSERVATION. *CONSERVATION BIOLOGY,* 9, 939-942.

WEST, G. B. & BROWN, J. H. 2005. THE ORIGIN OF ALLOMETRIC SCALING LAWS IN BIOLOGY FROM GENOMES TO ECOSYSTEMS: TOWARDS A QUANTITATIVE UNIFYING THEORY OF BIOLOGICAL STRUCTURE AND ORGANIZATION. *JOURNAL OF EXPERIMENTAL BIOLOGY,* 208, 1575-1592.

WEST, G. B., BROWN, J. H. & ENQUIST, B. J. 1997. A GENERAL MODEL FOR THE ORIGIN OF ALLOMETRIC SCALING LAWS IN BIOLOGY. *SCIENCE,* 276, 122-126.

WESTOBY, M., WALKER, B. & NOY-MEIR, I. 1989. OPPORTUNISTIC MANAGEMENT FOR RANGELANDS NOT AT EQUILIBRIUM. *JOURNAL OF RANGE MANAGEMENT*, 266-274.

WHEATLEY, M. & JOHNSON, C. 2009. FACTORS LIMITING OUR UNDERSTANDING OF ECOLOGICAL SCALE. *ECOLOGICAL COMPLEXITY,* 6, 150-159.

WHITE, P. S. & PICKETT, S. T. A. 1985. NATURAL DISTURBANCE AND PATCH DYNAMICS: AN INTRODUCTION.

WHITFORD, W. G., ANDERSON, J. & RICE, P. M. 1997. STEMFLOW CONTRIBUTION TO THE 'FERTILE ISLAND'EFFECT IN CREOSOTEBUSH, LARREA TRIDENTATA. *JOURNAL OF ARID ENVIRONMENTS,* 35, 451-457.

WIENS, J. A. 1989. SPATIAL SCALING IN ECOLOGY. *FUNCTIONAL ECOLOGY,* 3, 385-397.

WU, J. 1999. HIERARCHY AND SCALING: EXTRAPOLATING INFORMATION ALONG A SCALING LADDER. *CANADIAN JOURNAL OF REMOTE SENSING,* 25, 367-380.

WU, J. 2004. EFFECTS OF CHANGING SCALE ON LANDSCAPE PATTERN ANALYSIS: SCALING RELATIONS. *LANDSCAPE ECOLOGY,* 19, 125-138.

WU, J. & DAVID, J. L. 2002. A SPATIALLY EXPLICIT HIERARCHICAL APPROACH TO MODELING COMPLEX ECOLOGICAL SYSTEMS: THEORY AND APPLICATIONS. *ECOLOGICAL MODELLING,* 153, 7-26.

WU, J., JELINSKI, D. E., LUCK, M. & TUELLER, P. T. 2000. MULTISCALE ANALYSIS OF LANDSCAPE HETEROGENEITY: SCALE VARIANCE AND PATTERN METRICS. *GEOGRAPHIC INFORMATION SCIENCES,* 6, 6-19.

WU, J. & LEVIN, S. 1994. A PATIAL PATCH DYNAMIC MODELLING APPROAH TO PATTERN AND PROCESS IN AN ANNUAL GRASSLAND. *ECOLOGICAL MONOGRAPHS,* 64, 447-464.

WU, J. & LOUCKS, O. L. 1995. FROM BALANCE OF NATURE TO HIERARCHICAL PATCH DYNAMICS: A PARADIGM SHIFT IN ECOLOGY. *QUARTERLY REVIEW OF BIOLOGY,* 70, 439-466.

WU, J. & MARCEAU, D. 2002. MODELING COMPLEX ECOLOGICAL SYSTEMS: AN INTRODUCTION. *ECOLOGICAL MODELLING,* 153, 1-6.

WU, J. & QI, Y. 2000. DEALING WITH SCALE IN LANDSCAPE ANALYSIS: AN OVERVIEW. *ANNALS OF GIS,* 6, 1-5.

ZAVALA, M. A. & HOLDO, R. M. 2005. DELAYED EFFECTS OF FIRE ON HABITAT USE BY LARGE HERBIVORES IN ACACIA DREPANOLOBIUM SAVANNA. *AFRICAN JOURNAL OF ECOLOGY,* 43, 155-157.

ZHANG, Y. & MAXWELL, T. A FUZZY LOGIC APPROACH TO SUPERVISED SEGMENTATION FOR OBJECT-ORIENTED CLASSIFICATION. ASPRS 2006 ANNUAL CONFERENCE, RENO, 2006 2006.

Appendix 1

Developed by Neil O'Leary 2009 to create truly hierarchical vegetation distributions in a hypothetical landscape through bottom up organization combined with top down constraint.

I present the raw MATLAB code with the functions nested.

```
%Crogan Algorithm
%written by Neil O'Leary in October 2009 to create hierarchically
%structured vegetation in a hypothetical landscape

%inputs: input the values wanted into the square brackets, scales represented here are arbitrary.

[scales] = create Scales([400,70,10],[4 5 4]);
scaleVariance = [2,7,30];
%-----------------------------------------------------
%% Create the Scales object and display the matrix
displayMatrix = createDisplayMatrix(scales);
figure(1);
colormap(gray)
imagesc(~displayMatrix)

%% Move the scales randomly

moveScales(scales,scaleVariance);
displayMatrix = createDisplayMatrix(scales);
figure(2);
colormap(gray)
imagesc(~displayMatrix)

%%
function displayMatrix = createDisplayMatrix(scales)
displayMatrix = sparse(1500,1500);
midPoint = 750;
for k = 1:length(scales)
   displayMatrix =setPointRec(scales(k),displayMatrix,midPoint);
end

function dispMatrix = setPointRec(obj,dispMatrix,normFactor)
children = obj.getChildren;
for k = 1:length(children)
   if children(k).getLevel == 1
      dispMatrix = children(k).setPoint(dispMatrix,normFactor);
   else
      dispMatrix=setPointRec(children(k),dispMatrix,normFactor);
   end
end

%%
function [topScale,displayMatrix] = createScales(scaleDistance,scales )
%CREATESCALES Create a scale-space
%   Detailed explanation goes here

%TODO pass these as input params

%scaleDistance = [400,70,10]; %Make sure sum scalesDistance<midpoint
%scales = [4 5 4];
angles = linspace(0,2*pi,scales(1)+1);

%TODO, do we need to round here?


for k = 1:4
   [x,y] = pol2cart(angles(k),scaleDistance(1));

   topScale(k) = Scale(x,y,length(scales)); %#ok<AGROW>
   topScale(k).addChildren(scales(2:end),scaleDistance(2:end));
end
%%
function moveScales(scales,movementVar)

for k = 1:length(scales)
```

```
    moveScalesRec(scales(k),movementVar);
end

function moveScalesRec(obj,moventVar)
%Move the point
obj.movePoint(normrnd(0,moventVar(obj.getLevel)));
%Move my children
children = obj.getChildren;
for k = 1:length(children)
    moveScalesRec(children(k),moventVar);
end
%%
classdef Scale<handle
    %SCALE Summary of this class goes here
    %   Detailed explanation goes here

    properties

        X = [];             % X position in space
        Y = [];             % Y position in space
        Children = [];      % Vector of children objects
        Parent = [];        % Parent vector
        ScaleLevel = 0;     % Value for N to 1 where N is the largest scale
        ParentX = 0;
        ParentY = 0;        %Index of where parents live to avoid recursive movement
    end

    methods
        function this = Scale(x,y,scaleLevel)
            this.X = x;
            this.Y = y;
            this.ScaleLevel = scaleLevel;
        end
        function addChild(this,child)
            %ADDCHILD as a child scale
            if isempty(this.Children)
                this.Children = child;
            else
                this.Children(end+1) = child;
            end
            if isempty(child.Parent)
                child.setParent(this);
                child.setParentXY(this.X,this.Y);
            end
        end

        function xValue = getX(this)
           xValue = this.X;
        end

        function yValue = getY(this)
            yValue = this.Y;
        end

        function xyValue = getXY(this)
            xyValue = [this.X,this.Y];
        end

        function level = getLevel(this)
            level = this.ScaleLevel;
        end

        function setParent(this,parent)
            this.Parent = parent;
        end

        function setParentXY(this,X,Y)
            this.ParentX = X;
            this.ParentY = Y;
        end

        function parent = getParent(this)
            parent = this.Parent;
        end
```

```
    function children = getChildren(this)
        children = this.Children;
    end

    function addChildren(this,noChildren,distance)
        %Create angles at which to place the children, add one and
        %ignore, thinking about no angle itervals
        angles = linspace(0,2*pi,noChildren(1)+1);
        for k = 1:noChildren
            %TODO, do we need to round here?
            [childX,childY] = pol2cart(angles(k),distance(1));
            child = Scale(this.X+childX,this.Y+childY,this.ScaleLevel-1);
            this.addChild(child);
            child.setParent(this);
            if this.ScaleLevel>2
                child.addChildren(noChildren(2:end),distance(2:end));
            end
        end
    end
    %Method to move the points
    function movePoint(this,distance)
        if isempty(this.Parent)
            offsetXY = [0 0];
        else
            parentXY = this.getParent.getXY;
            offsetXY = [this.ParentX,this.ParentY] - parentXY;
        end

        theta = cart2pol(this.ParentX-this.X,this.ParentY-this.Y);
        [moveX,moveY] = pol2cart(theta,distance);
        this.X = this.X+moveX+offsetXY(1);
        this.Y = this.Y+moveY;+offsetXY(2);
        %Move my children rec


    end

    function movePointXY(this,XY)
        this.X = this.X+XY(1);
        this.Y = this.Y+XY(2);
    end

    %Method to display the scales
    function dispMatrix = setPoint(this,dispMatrix,normFactor)
        dispMatrix((round(this.X)-2:round(this.X)+2)+normFactor,...
            (round(this.Y)-2:round(this.Y)+2)+normFactor)=1;
    end
    end
end
```