Spatial pattern analysis of thicket expansion in a semi-arid savanna

by

RACHEL PUTZIER

Submitted in fulfilment of the academic requirements of

Master of Science

Department of Botany

Rhodes University

15 February 2024

Supervisors: Dr Tiffany Pillay & Professor Susanne Vetter

PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Botany, School of Botany of the Faculty of Science, Rhodes University, South Africa. The research was financially supported by the NRF Thuthuka (TTK200305508223).

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Rputzier

Signed: Rachel Putzier

Date: 15/02/2024

Signed: Tiffany Pillay

Date: 15/02/2024

SVetter.

Signed: Susanne Vetter

Date: 15/02/2024

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I, Rachel Rayne Putzier, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

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(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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DECLARATION 2: PUBLICATIONS

Chapter 2: Putzier, R., Pillay, T. and Vetter, S., 2024. Vegetation Structure Analysis of Thicket Encroachment Using High Resolution LiDAR Data. To be submitted to *Ecography*.

Chapter 3: Putzier, R., Pillay, T. and Vetter, S., 2024. Spatial Pattern Analysis of Thicket Clump Formation in a Semi-Arid Savanna. To be submitted to *Journal of vegetation science.*

Chapter 4: Putzier, R., Pillay, T. and Vetter, S., 2024. Inferring Competitive Interactions Using Spatial Pattern Analysis of *Vachellia karroo* Mortality. To be submitted to *African journal of range and forage science*.

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ABSTRACT

Woody thickening has negative economic and ecological impacts in savannas globally. While the increase of savanna trees as a form of bush encroachment has been well studied, less is known about the increase of thicket species in savannas, which is an important phenomenon resulting in the formation of closed-canopy clumps which may exclude the grass layer over time. The early stage of thicket expansion is often initiated by a nucleating savanna species which facilitates the establishment of woody thicket pioneer species, and as the thicket clump formation expands, bush clumps increase in dominance, thereby increasing the frequency of competitive interactions and leading to a possible switch from facilitative to competitive interactions. Spatial point pattern analysis provides a useful tool to elucidate these underlying patterns and ecological processes. I used high resolution LiDAR data combined with spatial point pattern analysis to understand tree-tree interactions in a semi-arid savanna in the Eastern Cape Province of South Africa. I conducted a cluster analysis based on vegetation structural variables to distinguish different stages of woody plant encroachment from open savanna to closed canopy thicket. Using the canopy height model, I quantified the change in the grass height from open savanna to closed canopy thicket clumps as an indicator of a possible biome shift. Additionally, I used spatial point pattern analyses to investigate the effect of thicket clump formation on the composition of savanna and thicket species, the overall patterns of trees, and the associations of small thicket species with large *Vachellia karroo* trees, which serve as clump initiators. Finally, I examined the mortality of savanna trees across increasing stages of thicket expansion using second order spatial statistics, namely the Mark- and Pair-Correlation Functions. Results confirmed that three vegetation states, influenced by elevation, are present at the study site, representing open canopy savanna (early-stage thicket encroachment), encroached savanna with low thicket dominance (intermediate-stage thicket encroachment), and highly encroached with dominant thicket clumps (late-stage thicket encroachment). These stages showed increasing tree height, canopy cover and canopy height density, as well as decreased (but not completely absent grass layer) as thicket encroachment progresses. Spatial point pattern analysis showed, as predicted, that there was an overall aggregation of trees at small-scales within early thicket clump formation, from which I inferred that facilitative relationships may exist between trees. Contrary to my predictions, at later stages of thicket clump formation I found dominant independent patterns between savanna adults and juvenile thicket species, which may result from a combination of facilitative and competitive effects. Lastly, as expected, I found that the density of *V. karroo* mortality increased as thicket encroachment increased, with an overall random spatial pattern of dead *V. karroo* across encroachment stages. As predicted, tree mortality was randomly distributed in space in the open savanna state, and as thicket clump formation increases, tree competitive mortality became more evident, as well as decreased tree performance. Overall, the study highlights the interplay between facilitation and competition in semiarid savanna where thicket clumps are expanding. Intervention strategies are suggested to target areas of intermediate thicket clump formation, as these areas provide an opportunity to remove *V. karroo* before the nucleation process has enabled the establishment and increase of thicket species and to ensure the grass layer is kept productive. I conclude that the use of remote sensing and LiDAR technology holds a wide range of possibilities for monitoring and managing woody encroachment in savanna systems, however these methods need to be further refined for effective use within African savanna and thicket context, which displays high spatial aggregation making typical segmentation methods difficult.

ACKNOWLEDGMENTS

I would like to take this opportunity to express my gratitude to a number of special people who have helped and supported me throughout my project. I would like to thank:

First and foremost, my supervisors, Tiffany Pillay and Susanne Vetter, without whom none of this would have been possible. You have guided and believed in me- I appreciate all the time and energy you have so generously given me and my project. Through all challenges you were there to encourage me and help me plan a path forward.

All those from the Davies Lab at Harvard University, especially Professor Andrew Davies, Dr Peter Boucher, and Dr Jenia Singh. Your help with collecting, processing and analysing the data was greatly appreciated.

My loved ones: Glenham, Debbie, and Hannah Putzier, as well as Stefan le Roux and all my wonderful friends and family, for all the love and support throughout my university journey.

The Botany Department at Rhodes University, specifically Riaan Strauss, Busi Goba and Barry Hartley for their help in ensuring my fieldwork was able to take place.

Rhodes University for providing me with funding through the Henderson Scholarship, which allowed me to pursue my MSc.

The Painter family for allowing me to collect my data and stay on their lovely farm.

And finally, thanks to God for blessing me with this opportunity and all these people in my life, who have made this possible.

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CHAPTER 1: INTRODUCTION

Savannas are characterised as open canopy ecosystems with a continuous grass layer and discontinuous tree layer (Charles-Dominique et al., 2015; Parr et al., 2012), distinguished by the co-dominance of these two distinct life forms (Staver et al., 2011a; Scholes and Archer, 1997), and maintained by environmental factors such as rainfall (Sankaran et al., 2005; Scholtz et al., 2014), nutrient availability (Riginos et al., 2005; Zhao et al., 2015), fire (Smit et al., 2010; Levick et al., 2012), herbivory (Asner et al., 2009; Levick et al., 2009), and the interactions between these ecological determinants (Jia et al., 2016). Tree-tree interactions are also important determinants of savanna composition and structure. High resolution spatial data, such as Light Detection and Ranging (LiDAR), coupled with spatial point pattern analysis can be powerful and effective tools for elucidating the underlying mechanisms of tree-tree interactions. In this thesis, the spatial patterns of thicket expansion in semi-arid savanna are characterized.

1.1 Woody plant encroachment in savannas

Woody plant encroachment is a widespread phenomenon, which is increasing globally in savannas and grasslands, and under multiple land-uses (Wigley et al., 2010). O'Connor et al. (2014) defined bush encroachment as a directional increase in the cover of indigenous woody species, with negative consequences for biodiversity conservation and ecosystem services (Gillson, 2015). Stevens et al. (2017) showed that in African savannas, encroachment occurs across several land uses, including commercial ranches, communal rangelands and conservation areas (except in the presence of elephants). Higgins et al. (1999) investigated the effects of differing land use systems on the woody community structure and composition in a semi-arid savanna, in South Africa, and found that communal grazing management had caused a change in the composition and structure of woody plant communities. Wigley et al. (2009) studied the effects of land-use practice on the rate and extent of bush encroachment in a mesic savanna in South Africa. They found that land-use practice had large effects on the process of bush encroachment within communal, commercial and conservation land-use systems. The effect of bush encroachment was the lowest in communal sites; with grass cover reduced (21 %) as well as tree cover (5 %), while shrub cover increased (13 %). Commercial sites however decreased in grass cover (46 %) and increased in shrub (10 %) and tree (36 %)

cover. Conservation sites had the greatest decrease in grass cover (47 %) and the highest increase in tree cover (66 %) and shrub cover (19 %). These changes were perceived to have significant negative connotations for commercial and conservation land users including the reduction of grazing land and decreased biodiversity, as well as secondary invasion of encroached areas by alien plant species. Belay et al. (2013) looked at the way a semi-arid savanna rangeland responded to woody plant encroachment in south-western Ethiopia. Their research found that woody encroachment causing the transition from an open savanna to a bushland state is most likely driven by a variety of factors. This may include the suppression of natural disturbances such as fire and herbivory, as well as climatic changes, or human disturbances, land use changes and livestock browsing (Belay et al., 2013).

Another factor which may influence woody encroachment within savannas is atmospheric CO_2 concentration. It has been shown that the global increases in atmospheric CO_2 favour C_3 plants over C_4 plants, as the photosynthetic pathway of C_3 plants is no longer limited by CO_2, which may translate into higher rates of growth and reproduction. Stevens et al. (2016) described woody encroachment patterns over 70 years in South African savannas and their results also indicated that a global factor, likely elevated CO_2, is driving encroachment. Buitenwerf et al. (2012) discovered that tree density had doubled at a semiarid savanna site from the mid-1990s to 2010, and also cited elevated CO_2 as a possible driver for increased tree densities in South African savannas. Aerial photography analysis on an adjacent site that had not been cleared also showed a 48% increase in woody cover, with large increases in *Vachellia karroo* (Buitenwerf et al., 2012). O'Connor and Crow (1999) aimed to describe the rate and pattern of this process of bush encroachment in the Eastern Cape of South Africa. They confirmed that substantial bush encroachment had occurred and that this trend is likely to continue. This change was found to be likely driven by increasing atmospheric CO_2 levels, in addition to environmental changes such as changes to the livestock and grazing systems (as well as an increased grazing pressure), decreases in fire frequency, and reduced demand for firewood as electricity was introduced (O'Connor and Crow, 1999). The combined effect of all these processes and the exclusion of herbivory and fire from sites such as this may promote the increased density of woody trees. Venter et al. (2018) mapped the change in woody plant cover (excluding closed forest) over Africa for the past 30 years, investigating the potential drivers of woody plant encroachment. They found that there were a diversity of drivers responsible for woody plant expansion, they confirmed global greening trends and they suggested that although global drivers such as climate and CO_2 may increase the possibility of woody plant expansion, fire and herbivory management may also provide an opportunity to help control this process at a local-scale.

The directional increase of woody plants in savannas is a negative phenomenon because of the resultant ecosystem, biodiversity and livelihood impacts. Woody plant encroachment significantly affects biodiversity and ecosystem services (Belay et al., 2013; Gillson, 2015). Wieczorkowsi and Lehmann (2022) performed a meta-analysis of field studies across tropical to temperate grassy ecosystems across six continents and quantified how encroachment (increases in woody cover) altered herbaceous species richness, and the richness of functional groups of forbs, C_3 graminoids and C_4 graminoids. They found that continued encroachment caused a large loss of herbaceous diversity and richness, as well as significant negative impacts on all functional groups, specifically forbs. Woody encroachment was found to be associated with undesirable processes such as desertification, and accelerated rates of water and wind erosion (Archer, 2010). Further, it has impacts for conservation biology, posing threats to endemic savanna and grassland ecosystems, plants, animals, and microbes (Archer, 2010). Declines in animal and plant diversity, in savanna and grassland communities were also reported as a result of woody plant encroachment (Ratajczak et al., 2012). Within a semi-arid savanna grassland in South Africa, woody plant encroachment was shown to decrease grass species richness and composition (Mogashoa et al., 2021). As woody encroachment increases, ecosystem services related to water resources may be threatened, as less water becomes available for savanna plants uptake, and water to recharge rivers and groundwater reserves is reduced (Honda and Durigan, 2016). There may also be consequences of woody encroachment for the carbon balance and biodiversity of grassy biomes, as encroachment was found to create an unfavourable environment for invertebrates, particularly termites, leading to decreased decomposition rates and potentially altering the functioning of African savanna ecosystems (Leitner et al., 2018). Smit et al. (2015) aimed to test some of the existing predictions on the effects of woody encroachment in African savannas. Their study found that an increased woody cover could affect fire regimes, reduce grass biomass and livestock production. These, among other effects may cause cascading consequences for livelihoods and industries which depend on the current conditions remaining unchanged. Gray and Bond (2013) researched the impact of woody plant encroachment on visitor experiences and on the economy of conservation areas within South African national parks. The visibility of animals was greatly reduced in areas that had undergone woody encroachment. They found that potential future visitors (particularly higher spending, often international visitors) would be lost if animals became more difficult to see, reducing the number of visitors to conservation areas and posing negative economic impacts (Gray and Bond, 2013).

1.2 Thicket expansion in savannas

In savannas, woody plant encroachment may occur as two distinct processes as described by Parr et al. (2012); savanna thickening and thicket expansion (Figure 1.1). Savanna thickening involves the cyclic increase of savanna tree species, usually the increase in woody density of a single or few typical savanna species, which importantly does not entirely exclude the grass layer. Conversely, thicket expansion involves the establishment of broadleaf thicket pioneers, which display different physiological characteristics, giving them unique functional traits (Parr et al., 2012), and resulting in the formation of bush clumps which may eventually reduce or eliminate the grass layer.

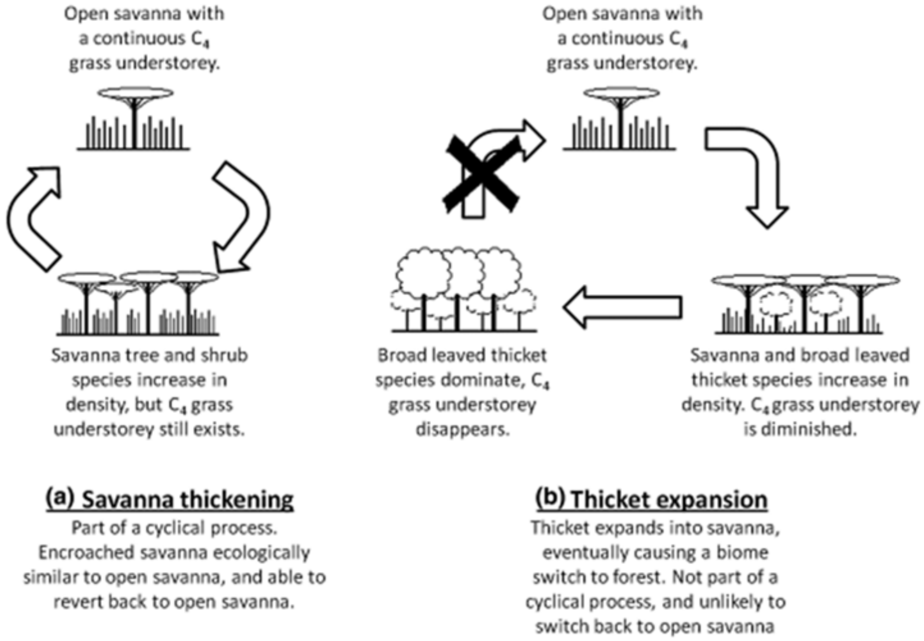

Figure 1.1 Schematic diagram showing two distinct woody thickening processes: (a) Savanna thickening occurs when densities of savanna tree and shrub species increase and is a cyclical process, and (b) Thicket expansion describes a shift in composition with increased densities of broad-leaved, shade-tolerant, fire-intolerant thicket and forest species. The latter process, which shades out the grass layer, may be difficult to reverse and is likely to alter ecosystem functioning and ecological processes significantly. It may lead to a biome switch to thicket, and even eventually, forest (Parr et al., 2012).

Recent global analyses, supported by theoretical work, have suggested that savanna and thicket or forest represent alternative stable states for some climates (Staver et al., 2011b, Parr et al., 2012), maintained by positive feedback between an open tree canopy and fire (Hoffman et al., 2012; Murphy and Bowman, 2012). Gillson (2015) studied the history of vegetation change in the savannas of the Hluhluwe-iMfolozi Park, KwaZulu-Natal, through stable carbon isotopes (δ13C) analysis from soil profiles. She discovered that areas which were previously open grasslands and savannas are now covered instead by C_3-dominated thicket and forest species. She found that the transitions from C_4 to C_3 are unidirectional towards increasing woody vegetation. Further, these sites were not simply returning to a previously C_3-dominated state, and there are no longer cyclic shifts between C_3 and C_4 dominance, but rather, the savannas of Hluhluwe-iMfolozi are at a tipping point between two alternate stable states (Gillson, 2015).

Charles-Dominique et al. (2015) described how the tree communities from thicket and savanna landscapes differ in their structure, composition and functional traits related to fire, grazing and competition for light. The thicket vegetation type is characterised by a dense, often closed canopy with low trees, a sparse understory of herbs, and a discontinuous layer of shade-tolerant grasses (Charles-Dominique et al., 2015; Vlok et al., 2003). Thicket species typically exhibit broad leaves that can form closed canopies that can shade the ground cover, reducing fuel load and preventing the fire from spreading. Therefore if these newly established woody thicket species form closed canopies as thicket encroachment increases, the likelihood of fires spreading as they historically do in savannas is reduced (Parr et al., 2012) (Figure 1.2). Archibald et al. (2009) studied the factors controlling the extent of fire south of the equator in Africa using burned area maps and spatial data from satellites. Their study found that across southern Africa, above a tree cover threshold of 40 %, fires might no longer be able to spread, and canopy closure would proceed. After this level of encroachment is reached it becomes unlikely that the closed-canopy thicket will be able to shift back to an open savanna (Charles-Dominique et al., 2018).

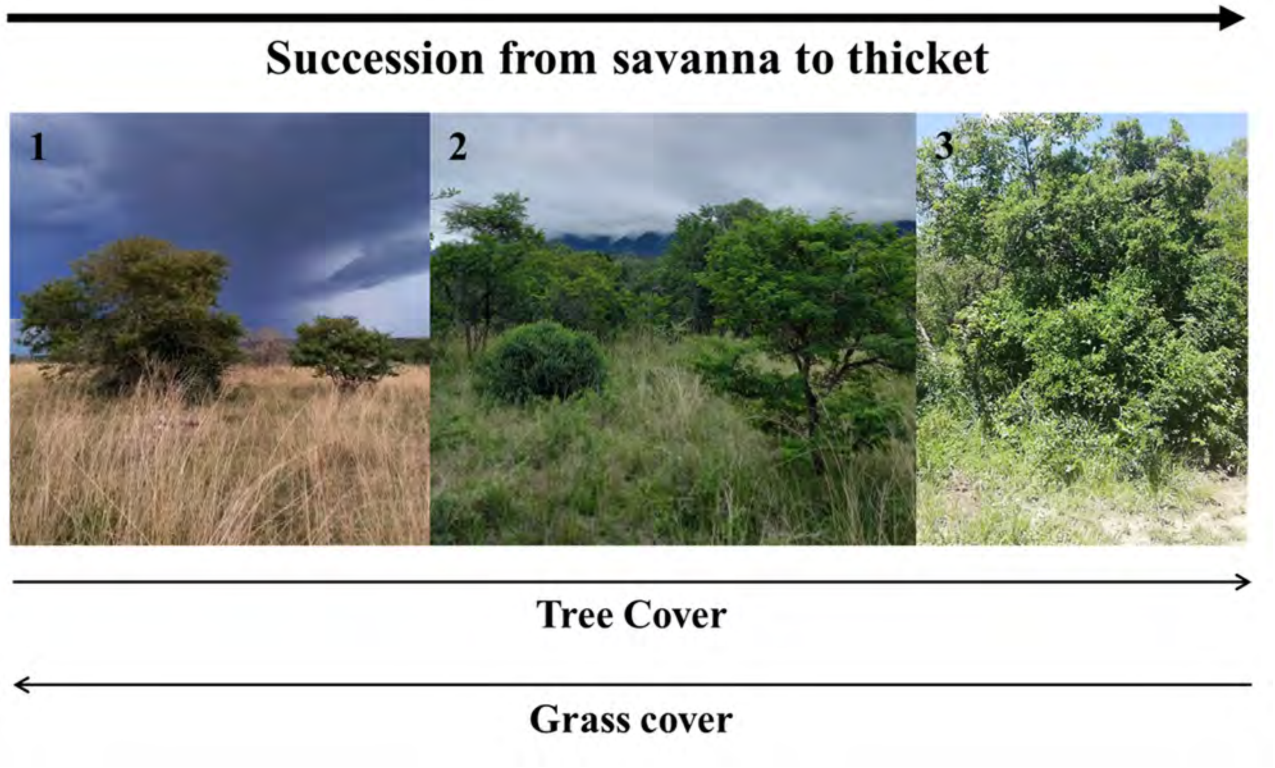

Figure 1.2 Biome vegetation structure: 1- savanna with a continuous grasses layer and a discontinuous and open tree cover; 2- transitional area displaying both savanna and thicket characteristics; and 3- thicket with dense closed canopies within thicket clumps and a discontinuous and patchy layer of grasses.

Parr et al. (2012) suggested that given the wide range and severity of woody thickening in southern African savannas (e.g., Skarpe, 1990; Hudak and Wessman, 1998; O'Connor and Crow, 1999; Moleele et al., 2002), it is possible that the trend observed in Hluhluwe may represent a broader-scale regional biome switch. In this biome shift, the savanna is being replaced by subtropical thicket. Within South Africa this process of thicket expansion into savannas has been documented (Gillson, 2015; O'Connor and Chamane, 2012, Jamison-Daniels, 2021), however more information is needed on the mechanisms and extent of this process, considering the probability of a biome shift from savanna to thicket, changing the structure, functional composition and system properties of savannas, which may have cascading consequences for savanna management and conservation (Parr et al., 2012). The introduction of thicket species would lead to shading (Charles-Dominique et al., 2018) and competition (Petritan et al., 2014) with a consequent reduction in savanna grass biomass, leading to the reduced likelihood of fires. This reduces the probability of maintaining an open-canopy tree layer (Murphy and Bowman, 2012) and results in a permanent biome shift towards thicket or forest, as the canopy cover cannot be re-opened (Parr et al., 2012). Biome shifts have negative economic and ecological impacts, causing serious conservation and rangeland problems regarding a reduction in biodiversity and grazing capacity impacting livestock potential (Khavhagali and Bond, 2008).

1.3 *Vachellia karroo* as a thicket-initiating species

Several studies have shown the important role of large savanna trees in the establishment of thicket pioneers. Savanna trees can establish in areas with harsh conditions and many commonly occurring savanna species are also described as important woody invader species capable of encroaching rapidly into grasslands and savannas (O'Connor, 1995; Wigley et al., 2010). Savanna tree species may act as nucleators or initiators, modifying local habitats and creating regeneration opportunities for seedlings which would otherwise not survive the harsh microhabitat conditions. This habitat amelioration of hostile conditions such as temperature extremes, limited moisture, nutrient stress or herbivory has been associated with early-stage thicket clump formation (Adie and Yeaton, 2013; O'Connor and Chamane, 2012). A recent study by Abreu et al. (2021) examined tree dynamics in the Brazilian Cerrado and found evidence that isolated trees cause nucleation and drive changes in the functional composition of savanna. Their study found that these nucleating species acted as perch sites favouring bird dispersed species, and then acted as nurse trees, facilitating the establishment of forest-adapted tree species and the eventual removal of savanna specialist species (Abreu et al., 2021). Likewise, Jamison-Daniels et al. (2021) studied the underlying determinants of bush clump formation (a form of encroachment) in a South African savanna. They found that woody encroachment is initiated by establishing a nucleating species, which then facilitates the establishment of new species. This causes a directional change toward forest-type species in larger and older bush clumps (Jamison-Daniels et al., 2021).

O'Connor and Chamane (2012) describe the pattern of bush clump formation in the Eastern Cape. They found that bush clumps (synonymous with thicket clumps in semi-arid savannas) formed due to the establishment of thicket pioneers under the canopies of established savanna species such as *V. karroo* as a result of nucleation via animal dispersal (O'Connor and Chamane, 2012). Similarly, Skowno et al. (1999) showed that the increased density of *V. karroo* may cause environmental conditions to become more favourable to new species, facilitating the later entry of thicket pioneer species. This may influence community structure over time. Pioneer thicket species such as *Scutia myrtina* are well adapted to growing within bush clumps and existing canopies left from the nucleator species, *V. karroo* (O'Connor and Chamane et al., 2012; Hester et al., 2006). The establishment of animal-dispersed species such as *S. myrtina* may perpetuate thicket expansion processes as these species provide natural sites for visitation by frugivorous birds and mammals, offering shade and forage sites for herbivores (O'Connor and Chamane, 2012). Preferential defecation beneath large savanna trees results in an increase in nutrients at that site, improves chances of directed seed dispersal and thus promotes the establishment of new species as thicket clump formation expands (Schleicher et al., 2011). In areas of later thicket clump formation, other thicket species are increasingly found within bush clumps. An increase in the abundance of these bush clumps therefore represents an important form of bush encroachment, prevalent in the Eastern Cape, in South Africa (O'Connor et al., 2014). O'Connor and Chamane (2012) studied the patterns of bush clump (synonymous with thicket clumps in semi-arid savannas) succession in the Eastern Cape, South Africa and found that bush clumps formed as a result of the establishment of thicket pioneers under nucleating savanna species such as *V. karroo*. This process of bush clump formation however is not specific to the Eastern Cape, and has been demonstrated throughout South Africa, within NE South Africa (Jamison-Daniels et al., 2021) and in KwaZulu-Natal (Adie et al., 2023), as well as within other parts of Africa (Jenik and Hall, 1976; Bloesch, 2008).

Finally, work by Nell et al. (2024) at the same site as this study has shown that *V. karroo* are recruited singly and in great numbers in open grassland and once these trees are mature they provided nucleation sites for thicket pioneers, which in this site was dominated by *Scutia myrtina*. These thicket pioneer species were found to recruit preferentially in close association with large *V. karroo*, forming thicket clumps with increased diversity of species and size classes, leading to multiple diverse associations within clumps. They found that these association patterns between large *V. karroo* and thicket pioneers such as *S. myrtina* were consistent with a successional sequence from open savanna to thicket clumps (Nell et al., 2024).

1.4 Savanna and thicket as alternate stable states

It has been reported that savanna and thicket can co-exist as alternative states where high tree cover can over time cause grass to be shaded out, and allow for fire-sensitive species to flourish (Ratnam et al., 2011). Parr et al. (2012) suggest that savanna, thicket and forest are alternative states defined by the switch in composition and function, with savannas being characterised by the dominance of grasses in the herbaceous layer. Positive feedbacks which promote the required environmental conditions to maintain one ecosystem state may be hostile towards the alternative ecosystem state, and therefore alternative states form distinct boundaries, often creating landscape-scale mosaics (Bond and Parr, 2010). Tropical savannas and forests have been found to act as alternate stable states, which are controlled by feedbacks with fire (Hoffmann et al., 2009). Where savanna and forest represent alternative stable states, extreme fires followed by repeated burning can result in a movement towards a savanna system "savannization" (Beckett et al., 2022). Savannas and forests are alternative biome states in the Neotropics and the Afrotropics, and for a range of environmental conditions, fire feedbacks and herbivory act to maintain these systems (Dantas et al., 2016).

Transitions between alternative stable states may be triggered by biotic interactions such as grazing or competitive interactions, which may cause a change in state as a threshold is crossed, further, abiotic conditions such as rainfall or soil nutrients may lower this threshold (Vetter, 2009). Abiotic triggers such as drought can act together with biotic interactions to affect the switch in states, by lowering the threshold, allowing the effects of biotic interactions to trigger transitions. Gillson (2015) studied the history of vegetation change in a savanna, studying the stable carbon isotopes (δ13C) from soil profiles within Hluhluwe-iMfolozi Park, South Africa, and found that there has been a shift from C4 grassland or open savanna to C3 dominated thicket, forest, and densely wooded savanna dominating these sites, supporting the idea of a biome shift between grass and tree dominated alternate stable states. Thresholds are important within these ecosystems, as once crossed there may be rapid, unstable transitions between these alternate states, and in a grass dominated system such as this, where woody vegetation increases threaten this threshold, management interventions such as burning and grazing may be necessary to preserve these grass-dominated habitats (Gillson, 2015). Where savanna and forest occur as alternative stable states on large portions of their range, Staver et al. (2011a) suggest that it is crucial to consider the transitions between these two stages, as it is fundamental to understanding past and future changes in the distribution of biomes at a global-scale.

At the same study site as my study, Khoza (2021) showed evidence for the existence of two alternative stable states, a savanna state dominated by *V. karroo* and few thicket species, and an alternate thicket state characterised by a more diverse thicket community with fewer *V. karroo*. They found that these savanna states existed at thresholds of canopy cover ~ 40% (LAI < ~ 0.5, light transmittance ~ 75%), at which stage many of the common grass and herbaceous species abundance began to become reduced, while the composition remained representative of the savanna state. At sites with a canopy cover of less than ~ 40% (Archibald et al., 2009) grass and forb species enable fires to burn and help maintain an open savanna system. The second threshold impacted species composition at ~50% light transmittance where a savanna state switches to a thicket (LAI ~ 1 and canopy cover ~70%). Here tree and herbaceous plant compositions are altered, grass layers were reduced, and fire is suppressed, allowing thicket encroachment to proceed causing closed canopy thicket. In my study, I aim to describe the spatial patterns of the proposed alternate stable states, open savanna, and closed canopy thicket.

1.5 Using spatial pattern analysis to understand tree-tree interactions

There has been an increasing interest in the study of savanna structure and spatial patterns in ecology, using the patterns of woody species to infer the existence of underlying interactive processes (Perry et al., 2002). Schleicher et al. (2011) used spatial statistics to examine the impact of shrub-shrub interactions and soil type (rocky or sandy) on the growth and spatial distribution of two savanna shrub species. They used the O-ring statistics (Wiegand and Moloney, 2004) to examine the spatial distribution of two shrub species and found a significant positive spatial association between the two species, suggesting that this association may have been the result of processes such as seed dispersal and facilitation.

Spatial patterns of plants may result from different processes such as seed dispersal, intraspecific competition, interspecific competition, facilitation, disturbance, herbivory, or environmental heterogeneity (Schleicher et al., 2011). When using spatial statistics, the position of a plant in a plot is represented by a point and the analysis of the spatial point pattern exhibits whether the distribution of the points is random, clumped, or regular by comparing the distribution to an appropriate null model (Wiegand and Moloney, 2004). Spatial statistics thus provide a quantitative description of biological variables distributed in space and time, allowing researchers to determine whether an observed pattern is caused only by chance or whether it results from specific causes (Szmyt, 2014).

In ecology, specific terms describe aspects of non-randomness in spatial data (Figure 1.3). Positive associations between points may be described as “aggregated”, “clustered”, or “clumped” (Perry et al., 2002). Terms such as “negatively auto-correlated”, “uniform”, “regular”, and “even” refer to negative interactions between points (Perry et al., 2002). First-order statistics explain large-scale variations in the intensity of points in a study region. Second-order statistics are summary statistics of all point-to-point distances in a mapped area, allowing one to determine different types and scales of patterns (Wiegand and Moloney, 2004). Wiegand and Hubbell (2013) found that second-order characteristics such as the pair correlation function play a crucial part in point pattern analysis and suggest that these are supplemented with additional summary statistic characteristics.

There are many factors which may influence the underlying mechanisms controlling the spatial distribution of trees throughout an ecosystem. Underlying mechanisms are synergic and they may act with or against each other to increase or reduce the effect of one another. Ben-Said (2021) and Goreaud (2000) summarize some of these drivers, which include natural processes, local environments of plants (biotic and abiotic), as well as human intervention. Natural processes include seed dispersal, which may involve seed characteristics, dispersal limitations and dispersal modes (Schleicher et al., 2011; Nguyen et al., 2016). Recruitment (Fajardo et al., 2006; Kraaij and Ward, 2006), growth (Meyer et al., 2008; Pillay and Ward, 2012), and mortality (Volkov et al., 2005; Hesselbarth et al., 2018) are also natural processes influencing the way that trees are spatially distributed. Biotic factors include the intra- and inter-specific relationships between trees, as competition and facilitation are major contributors to the spatial distribution of vegetation (Meyer et al., 2008; Ben-Said, 2021). Other biotic local environment variables include the presence of pests (Bassil et al., 2018) and herbivores (Asner et al., 2009; Levick et al., 2009), species niches (Martínez et al., 2010; Li et al., 2021) as well as seedling survival (LeMay et al., 2009). Abiotic local environmental factors include soil conditions (Fajardo et al., 2006; Zheng et al., 2017; Gupta and Pinno, 2018), nutrients (Riginos et al., 2005; Zhao et al., 2015), and moisture (Fajardo et al., 2006; LeMay et al., 2009). Topography (Baldeck et al., 2013; Scholtz et al., 2014), water availability (Sankaran et al., 2005; Scholtz et al., 2014), and light availability (Jia et al., 2016; Charles-Dominique et al., 2018), as well as fires (Smit et al., 2010; Levick et al., 2012) are also abiotic mechanisms. Human intervention has influenced tree spatial distributions through management practices such as thinning (Hare et al., 2021; Mndela et al., 2022) and land use change (Giannecchini et al., 2007; Wigley et al., 2010; Van Wilgen and Biggs, 2011; Western and Mose, 2021).

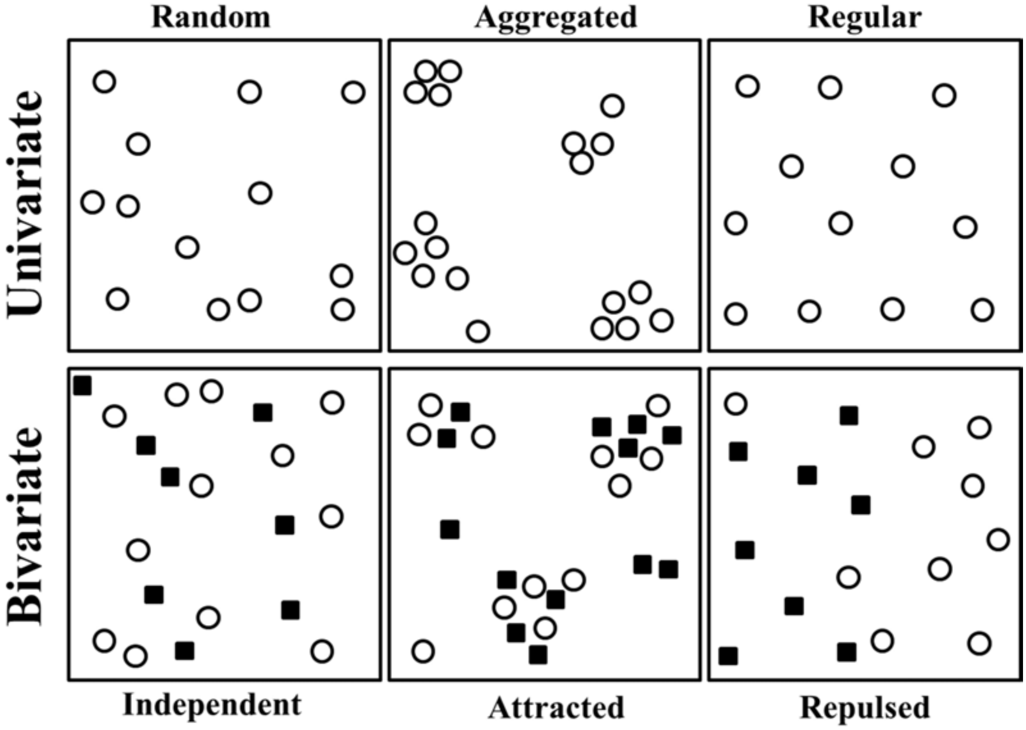

Figure 1.3 Spatial point patterns: Univariate patterns and bivariate patterns. Univariate patterns are random (no correlation), aggregated (positive correlation), or regular (negative correlation). Bivariate patterns show independence (no correlation), attraction (positive correlation), and repulsion (negative correlation).

Random or independent patterns of trees are usually expected to be formed from stochastic events, from a lack of dominant processes or a combination of processes such as limited seed dispersal and simultaneous competition (Hesselbarth et al., 2018; Wiegand and Moloney, 2013) (Figure 1.3). Alternatively, random patterns may be viewed as intermediate stages between regular and clustered tree patterns (Hesselbarth et al., 2018). Moustakas et al. (2008) investigated the tree spatial formations and nearest tree neighbour distances of *Vachellia erioloba* across large time and spatial scales in the Kalahari. They showed a cyclical transition from clumped tree spacing to a more random and then finally regular spacing. Random patterns of trees may be the result of randomly spaced regeneration sites where juvenile trees were able to establish (Caylor et al., 2003). Juvenile tree establishment can be reduced by environmental heterogeneity, disturbances such as fire, and shading from large trees with dense canopies (Muvengwi et al., 2018). This environmental heterogeneity affecting trees spatial distributions may be caused by diverse soil conditions and patchy rainfall within arid and semi-arid savannas (Schleicher et al., 2011). Natural or human induced disturbances such as prolonged droughts or selective species thinning may result in tree mortality, reducing overall tree competition and preventing a density-dependent shift from a clustered to a regular pattern, as well as segregation between small and large trees (Hesselbarth et al., 2018; Sea and Hanan, 2012). Gupta and Pinno (2018) studied the spatial patterns and competition-facilitation mechanisms of trees in early successional reclaimed and natural boreal forests in Alberta, Canada. They found that random patterns within 5-year-old study sites were possibly the result of random mortality caused by interspecific competition between juveniles and other understory vegetation (Gupta and Pinno, 2018).

Regular patterns are usually associated with competition between trees (Meyer et al., 2008) (Figure 1.3). As thicket expansion continues, savanna species are put under greater competitive pressure. When organisms rely on the same limiting resources and have similar ecological niches, they experience strong competition (Chesson, 2000; Johnson et al., 2017), which is exacerbated when it is present in sessile organisms such as trees (Silvertown, 2004). This may result in changes in the underlying mechanisms, spatial arrangement, species distribution, sizes and mortality of trees (Petritan et al., 2014). Under symmetric scramble competition, negative interactions such as competition are greatest in dense savanna vegetation, and over time mortality is predicted to cause clumps of dead trees to be segregated from living trees (Wang et al., 2017). However, Pillay and Ward (2012) found no evidence of regularity and competition with the spatial point pattern analyses (SPPA) tests, though smaller-scale competition was evident when nearest neighbour analyses were done to investigate the relationship between tree sizes and distance between neighbours. This indicated that although competition was present within the plot, it was not strong enough to change the vegetation from an aggregated arrangement (Pillay and Ward, 2012). Meyer et al. (2008) studied the spatial pattern of *Senegalia mellifera* along with other savanna woody species in a semi-arid savanna in South Africa. Across all investigated spatial scales, they found that young and reproductively mature shrubs showed decreasing aggregation as size or age increased. This study supported the idea that as trees grow and age, there is an increase in competition and a decrease in facilitation (Wiegand et al., 2006).

Clustered tree patterns may result from various factors driving vegetation structure; however one of the major causes of these patterns is the facilitation between adult and juvenile trees (Flores and Jurado, 2003). Facilitation is the major process dominating the early life stages, with competition becoming more dominant in later stages (Ledo et al., 2014) (Figure 1.3). Facilitative relationships are more common where conditions are high-stress according to the stress-gradient hypothesis (Maestre et al., 2009), and have been found to occur in open savanna vegetation (Hesselbarth et al., 2018). Muvengwi et al. (2018) performed a spatial pattern analysis of encroaching tree species after fire suppression in a semi-arid savanna. They found clustering in a savanna ecosystem, at scales of 6 to 18.5 m, which may have resulted from nurse plants, as small trees showed an association with larger trees. They found the species to be aggregated without any evidence of inter- or intra- specific species competition. They show that encroaching trees within this semi-arid savanna usually do not show self-organization during the early growth stages and they are able to co-exist as they lack significant competition. This is explained to likely be a result of roots and canopies not being fully developed, while the zone of influence of trees was still relatively small. Pillay and Ward (2012) use second-order spatial point-pattern analysis of *V. karroo* to help provide insights into the underlying processes which affect the individual trees in a mesic savanna. Their study showed that juvenile trees are more spatially aggregated than expected by chance. They further found that the overall spatial distribution of trees was aggregated without any evidence of regularity among large trees (Pillay and Ward, 2012). Disturbances such as browsing or fires are also able to reduce competition between trees and promote clustering (Sea and Hanan, 2012). Other possible factors causing a clustered distribution may include limited seed dispersal, vegetative propagation or the landscape showing heterogeneous intensity as a result of certain areas' favourability (Caylor et al., 2003; Meyer et al., 2008).

An interesting spatial pattern as thicket clump formation increases may be a switch from facilitation (resulting in clustering) to competitive interactions (reflected in a random or regular pattern) as the density of trees grows and the demand for resources increases (Stoll and Bergius, 2005). Furthermore, the greater competitive pressure faced by savanna species after the formation of bush clumps may lead to increased tree mortality, a fundamental process in ecosystem dynamics, as it influences the surrounding stand structure and species compositions (Petritan et al., 2014). Tree mortality is generally higher when neighbours are denser or closer (Adie and Yeaton, 2013), such as the conditions created when thicket species form clumps. This phenomenon known as competitive density-dependent mortality is commonly recognised as a major mechanism of species coexistence and community assembly (Volkov et al., 2005). Spatial point pattern analysis helps examine the effects of tree location on the probability of mortality of savanna species and may be used to infer competition. This is important to document as some studies have demonstrated that competitive density-dependent mortality ceased to play an important role for large trees because of their widely spaced distribution and permissive understory regeneration (Pillay and Ward, 2012). If encroaching species such as *V. karroo* are initiators or nucleators of thicket clumps, they may be expected to experience increased mortality in the later stages of clump formation due to competitive interactions.

1.6 Using LiDAR as a tool to detect spatial patterns

Light Detection and Ranging (LiDAR) is an active remote sensing technology which provides many advantages. LiDAR may be space-borne, terrestrial or airborne (Reutebuch et al., 2005). Light is emitted from the LiDAR device as a "pulse"; when this light is reflected from a surface, it is recorded as a "return" (Asner et al., 2007). This technology allows one to construct a three-dimensional (3D) image of the vegetation structure, as shown in Figure 1.4 (Staver et al., 2019; Joyce et al., 2019). This helps to build an accurate model of the ground and its features in that area (Crutchley, 2006).

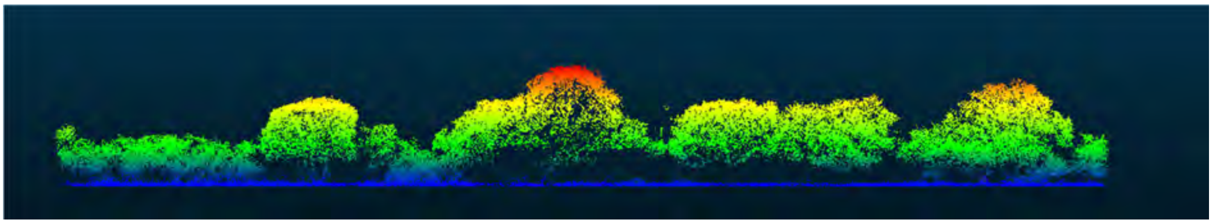

Figure 1. 4 Cross-section of LiDAR point cloud sampled from this study site showing the 3D image of the vegetation structure. Blue points represent a low height, with increasing heights from green, to yellow, and the tallest points represented in red.

There are four major components of an airborne LiDAR, including a scanner or sensor, a global positioning system (GPS) receiver, an inertial measurement unit (IMU), and a computer (Reutebuch et al., 2005). Sensors send out a pulsed emission of laser light, and these reflections are then detected and recorded. When the LiDAR sensor scans the site, some distortions may occur due to topography, altitude, aircraft motion (turbulence), and non-nadir laser emissions (Asner et al., 2007). Navigation and tracking hardware such as GPS receivers and IMUs are essential for generating information on the orientation and location of the sensors, which helps ensure accurate projections of the data (Crutchley, 2006; Asner et al., 2007). The GPS receivers track the altitude of the sensor and record the location of the drone or other vehicle transporting the LiDAR components; this information is used to calculate accurate terrain elevation values (Asner et al., 2007). The IMU tracks the orientation and speed of the drone as it flies, which allows for elevation to be calculated accurately and the precise position of reflectance points to be measured when the light is emitted (Reutebuch et al., 2005; Asner et al., 2007). The sensor generates great volumes of data, which need to be stored. Therefore, a high-performance computing system with specialised software for processing, storing and analysing the data is necessary (Reutebuch et al., 2005; Asner et al., 2007).

Guo et al. (2017) used airborne LiDAR systems to accurately and remotely measure 3D vegetation structure to help map and model species distributions for the forested areas of ten natural subregions in Alberta, Canada. They provided a novel method for processing regional-scale LiDAR data into categorical classes, which can represent natural groupings of habitat structure. They performed a cluster analysis on LiDAR-derived vegetation structural variables, where these classes were then compared across different areas (Guo et al., 2017). Baldeck et al. (2014) used LiDAR and hyperspectral data from Kruger National Park, South Africa. They used this data to remotely identify 500 000 trees and shrubs' crowns, allowing them to discover spatially complex patterns in woody plant communities across the landscape. This previously would have been a challenge, as field-based methods would not have been able to cover such a broad area. Their study shows that airborne species identification techniques can help map biodiversity to understand the ecological controls and processes taking place across much larger landscapes (Baldeck et al., 2014).

The purpose of LiDAR is not to completely replace fieldwork but rather to enhance and assist in this process, and the combination of using airborne laser scanner data and hyperspectral imagery helps offer extensive spatial coverage of measurements and can be used to help map vegetation at a provincial-scale (Torresan et al., 2016). Airborne LiDAR can help reduce the time taken for analysis, as measurements such as tree height can be calculated instead of measured in the field, which is often a difficult and time-consuming process. Levick et al. (2021) recognised that field-based and spaceborne satellite remote sensing methods alone are inefficient for monitoring and mapping highly dynamic vegetation such as savanna ecosystems over large areas and at regular time intervals. They evaluated the performance of mobile- and UAV-based laser scanning in conjunction with a traditional field-based inventory against terrestrial-based laser scanning within a savanna plot in Australia, and found that both these methods provide potential for rapid, larger area capture of savanna vegetation structure. Airborne remote sensing is important for managing land, conservation and earth science as, unlike satellite or terrestrial measurements, it can capture an ecosystem's structural and functional spatial heterogeneity (Asner et al., 2007; Joyce et al., 2019). LiDAR has the potential to enhance spatial point pattern analysis, as LiDAR point clouds can be used to derive the tree locations as well as variables such as tree structural properties, including tree height.

1.7 Rationale, aims and thesis structure

Savannas have great ecological, social and economic value, and the resources they provide are heavily relied on by rural villages (Shackleton et al., 2002), commercial livestock grazing and private and public conservation areas that contribute significantly to the tourism industry. Due to their high biodiversity, savanna conservation is a high priority research focus. Hesselbarth et al. (2018) highlight savanna dynamics need to be developed further, and they express the need to develop a greater insight into the spatial interactions and processes shaping the vegetation structure. The global negative phenomenon of woody plant encroachment has been well documented; however more research is needed on the spatial patterns and vegetation dynamics of thicket clump formation in savannas (Kgosikoma and Mogotsi, 2013).

By investigating vegetation structure and tree-tree interactions, the different stages of thicket encroachment can be better understood. Furthermore, studying the spatial patterns of these woody species will allow me to infer the existence of underlying processes (such as facilitation or inter-and intra- specific competition), which are crucial in determining the vegetation dynamics over time. The dynamics of thicket formation, including the vital role of savanna trees in facilitating the formation of thicket clumps, have been studied only to a limited extent, mainly in more mesic savannas (e.g. O'Connor and Chamane, 2012; Pillay and Ward, 2012, Jamison-Daniels et al., 2021). There have been several studies on the interactions between savanna and forest systems as alternate stable states (Aleman et al., 2020; Beckage and Ellingwood, 2008; Dantas et al., 2013; Staver et al., 2011a; Staver et al., 2011b) and how encroachment affects the shifts between these biomes (Aleman and Staver, 2018; Stevens et al., 2017). A few studies have considered thicket species as being a part of "forest" or combined "closed canopy" systems (Beckett and Bond, 2019; Gillson, 2015; Lehmann et al., 2011). There has, however, been far less research into the dynamics between savanna and thicket species (Charles-Dominique et al., 2015; Charles-Dominique et al., 2018) and how these biomes interact during encroachment processes (Parr et al., 2012). This study will add valuable insight into the dynamics of thicket clump formation in a semi-arid savanna system.

This study also aims to further the research on spatial pattern analyses in savannas and thickets. The use of spatial point pattern analyses in conjunction with LiDAR has been represented in the literature for forested areas (Packalen et al., 2013; Wang et al., 2020; Lin and Wiegand, 2021), as well as in plantations and agricultural landscapes (Tanada and Blanco, 2016). In contrast, there have been fewer applications in savanna systems (Staver et al., 2019). There have been few studies which investigate thickets and other non-forest dense vegetation using LiDAR and remote sensing methods, and even fewer using spatial point pattern analyses in conjunction with these systems (Mkheswa, 2021; Brede et al., 2022). Savannas are highly dynamic and diverse, providing many ecosystem services and benefits to human populations; however these systems face many challenges and are threatened by widespread degradation, and therefore require improved management strategies (Marchant, 2010; Geißler et al., 2024). It is therefore important to ensure that research tools to help analyse their structural complexity are developed further. Such methods would provide researchers with an efficient method to investigate vegetation structure and spatial distribution of trees, as well as enable them to map and model vegetation and topography. My study, therefore, set out to gain key and novel insights into the combined use of high resolution LiDAR and fine-scale point pattern analysis to study vegetation patterns in a landscape where thicket clump encroachment into a savanna is occurring.

This study took place at Endwell Farm, a semi-arid savanna in the Eastern Cape province of South Africa. The dominant savanna tree species present in this area is *V. karroo*, a common encroaching species which is known to increase in density during bush encroachment. This study aims to identify if the process of thicket clump formation in savannas can be distinguished into stages based on vegetation structure across the landscape, and how spatial point pattern analysis can be used to elucidate important ecological processes such as facilitation in early thicket clump formation and competition in later stages. This study also aims to quantify changes in the grass layer from open savanna to closed canopy thicket, as an important mechanism through which an irreversible biome shift occurs, as fire may be excluded from the system (Charles-Dominique et al. 2018). Remote sensing techniques including LiDAR and RGB imagery were used to investigate and map vegetation structure and spatial patterns of trees.

In **Chapter 2** I report on the use of LiDAR and remotely sensed RGB imagery to characterize the stages of plant encroachment in semi-arid savanna. I investigated whether stages of thicket clump formation from open savanna to closed-canopy thicket will exist as distinct clusters or present as a gradient of vegetation structure across the landscape. I hypothesized that distinct stages in the thicket clump formation would be evident, based on the proposed idea of savanna and thicket existing as alternate stable states, with significant clustering of vegetation structure variables from open savanna to closed-canopy thicket Clump stages. The six vegetation structural variables used for this analysis include maximum canopy height, mean canopy height, canopy cover percentage and canopy height densities at three height strata. I also quantified grass height in a spatially explicit manner using the LiDAR derived CHM and RGB imagery, to determine whether thicket clump formation resulted in a decrease in the grass layer. I predicted a significant decline in grass height as thicket clump formation increases, resulting in the reduction or elimination of the grass layer. Finally, I analysed whether thicket clump formation was influenced by elevation. I predicted that elevation had a significant effect on woody plant encroachment such that, at higher elevations open, lower vegetation was present, and as elevation decreased vegetation becomes denser.

In **Chapter 3** I performed a spatial point-pattern analysis on remote sensing data (LiDAR and RGB images) to investigate the vegetation pattern at three increasing stages of encroachment (early, intermediate and late-stage thicket clump formation). The spatial arrangements of trees were quantified to infer the underlying processes and interactions occurring in each stage. I aimed to compare the overall patterns of all trees at three increasing stages of thicket clump formation, as well as to investigate whether there was a positive spatial association of juvenile thicket species with adult *V. karroo* trees. I predicted that in the open savanna, under early stage thicket encroachment I would observe random spatial patterns due to both aggregation of juvenile trees and regular spacing of adult trees. I predicted that the spatial patterns within areas of intermediate- and late-stage thicket encroachment would be strongly aggregated as bush clump formation expands. Lastly, where thicket clump formation has expanded (intermediate- and late-stage thicket encroachment), medium and large trees would display a positive (i.e. clustered) spatial association with juvenile thicket pioneer plants, either due to facilitation, directed seed dispersal or environmental heterogeneity.

In **Chapter 4** I investigated the mortality of a key savanna species, *V. karroo*. The aim of this study was to characterise the spatial patterns of *V. karroo* mortality at Endwell Farm, a semi-arid savanna in South Africa using LiDAR-derived spatial point pattern analysis (Mark- and Pair-Correlation Functions). I used second-order spatial statistics to determine the pattern of mortality of *V. karroo* trees from open savanna to closed canopy thicket. I aimed to quantify the relative mortality of *V. karroo* in the three stages of thicket encroachment. I predicted that the density of dead *V. karroo* trees would be highest in late stage thicket encroachment (closed canopy thicket clumps) due to intense neighbour competition, and the lowest in early stage thicket encroachment 1 (open canopy savanna) due to agent-driven mortality primarily as a result of senescence. Spatial point pattern analysis (SPPA) was used to examine the overall spatial pattern of dead *V. karroo* trees. I hypothesized that the spatial pattern of *V. karroo* mortality would be regular or random where early stage thicket encroachment has taken place, representing mortality via senescence or environmental heterogeneity respectively, typical of open canopy savanna dynamics. Conversely I predicted that in late stages of thicket encroachment, Dead *V. karroo* trees would display a clustered spatial pattern of mortality with other dead *V. karroo* trees as a result of intense neighbourhood competition and due to the formation of closed canopy thicket clumps. I also investigated the relationship between living and dead trees under increasing stages of thicket clump formation. I predicted that competition-induced tree mortality would be evident as attraction between dead and living trees in high competition thicket clumps at late stages of thicket encroachment, while random mortality would be evident as segregation between dead and living trees in open savanna at early stages of thicket encroachment. Lastly, I examined the spatial distribution of dead and alive trees in relation to their height. I hypothesized that dead *V. karroo* trees would be shorter than expected when they were located close to living adults in areas of late stage thicket encroachment, and taller than expected when they were located close to living adults in the open savanna canopy at early stages of thicket encroachment.

In **Chapter 5** I integrated the work reported in Chapters 2-4 and provide overall conclusions. This chapter reflects on insights from the application of this methodology within a savanna under thicket encroachment, and highlights challenges faced when applying the techniques in this context. Further, this chapter offers recommendations for management and further research.

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CHAPTER 2: VEGETATION STRUCTURE ANALYSIS OF THICKET ENCROACHMENT USING HIGH-RESOLUTION LIDAR DATA

2.1 Abstract

Woody thickening can lead to a biome shift from open savanna to closed-canopy thicket, changing the structure, functional composition and ecosystem properties, and resulting in negative economic and ecological impacts. While the increase of savanna trees as a form of bush encroachment has been well studied, less is known about the increase of thicket species in savannas, which is an important phenomenon resulting in the formation of thicket clumps which exclude the grass layer over time. This study used a cluster analysis based on vegetation structural variables obtained from high resolution spatial data (LiDAR data and RGB images) to distinguish different stages of woody plant encroachment in a semi-arid savanna system. I studied the effect of advancing thicket clump formation on the grass layer. My findings suggest the presence of three main stages within the process of thicket clump formation: early-stage thicket encroachment (open canopy savanna), intermediate-stage thicket encroachment (encroached savanna with low thicket dominance), and late-stage thicket encroachment (highly encroached with dominant thicket clumps). I found significant and distinct vegetation structure within each of the clusters, with increasing tree height, canopy cover and density from open savanna to a closed canopy thicket. Structural variables with great ecological significance in distinguishing the overall stage of thicket clump formation were identified as canopy cover, canopy height density 3 (> 2 m) and mean height. As thicket clump formation increases there is an increase in canopy cover and a decrease in grass height. In areas where thicket clump formation had increased, the grass layer was found to be greatly decreased but not completely removed. I further found that elevation had a significant influence on the vegetation structure and stage of thicket clump formation which was present. At higher elevations, shorter and sparser vegetation was present, and as elevation decreased vegetation became denser, which may indicate the progression of thicket expansion begins at low elevations and over time spreads to valleys. This may provide useful management intervention for minimizing the formation of bush clumps.

Keywords: *savanna, thicket clump formation, LiDAR, vegetation structure, cluster analysis, grass height*

2.2 Introduction

Savannas have ecological, social, and economic value for land users globally and in South Africa (Shackleton et al., 2002). Savannas are characterised by the co-dominance of two contrasting life forms; a continuous grass layer and a discontinuous tree layer (Scholes and Archer, 1997; Staver et al., 2011; Parr et al., 2012; Charles-Dominique et al., 2015). The availability of resources such as water and nutrients, the impacts of disturbance such as fire and herbivory, and their interactions, are identified as key drivers of savannas which maintain the balance and coexistence between trees and grasses (Sankaran et al., 2005; Bond, 2008; Staver et al., 2009; Staver et al., 2011; Archibald et al., 2019; Hutley and Setterfield, 2019; Staver et al., 2021). Holdo and Nippert (2023) undertook a review of published models of tree–grass coexistence to link resource- and disturbance-based models to help explain tree–grass coexistence in savannas. They propose that functional rooting separation is necessary for tree-grass coexistence, and suggest that trees dominance through shading is prevented by ecohydrological constraints in arid savannas, and herbivores in mesic savannas. Further they argue that tree growth is limited by strong asymmetric grass-tree competition for soil moisture.

Contrastingly, the thicket vegetation type is characterised by a dense, closed canopy with low trees, and, a sparse understory of herbs (Charles-Dominique et al., 2015; Vlok et al., 2003). Thicket species are often evergreen, while savanna species are often deciduous which may add to the leaf area index (Mucina and Rutherford, 2006). These thicket species typically exhibit broad leaves that, when forming closed canopies can shade the grass layer, reduce fuel load and prevent fire from spreading (Parr et al., 2012). Archibald et al. (2009) found that across southern Africa, a tree cover threshold of above 40 % results in the inability of fires being able to spread, creating a feedback where fire suppression would lead to eventual canopy closure given sufficient rainfall (Sankaran et al., 2005). This important vegetation switch thus limits the ability of fire to reopen and reshape the vegetation and maintain these states (Charles-Dominique et al., 2018; Parr et al., 2012). This may result in a permanent biome switch from savanna to closed-canopy thicket (Skowno et al., 1999). This is an unfavourable outcome for livestock farming and ecotourism, and will have cascading consequences for savanna management and conservation (Parr et al., 2012) such as decreased biodiversity and reduced grazing capacity impacting livestock potential (Khavhagali and Bond, 2008). For land managers wanting to maximise grazing potential and limit tree cover, understanding the vegetation dynamics between savannas and thickets is important.

While vegetation state shifts between savanna and forest have been studied in a range of contexts (Hoffman et al., 2012), the savanna-thicket transition in semi-arid savannas is less explored (Parr et al., 2012; Charles-Dominique et al., 2015; Charles-Dominique et al., 2018). Charles-Dominique et al. (2015) found that savanna, thicket, and forest systems could be differentiated based on the distinct structure of their vegetation. They held that defining biomes based on their vegetation structure provided a useful general framework for interpreting ecosystem distribution and functioning. Bora et al. (2021) recommend that the management of ecological sites should consider the functional traits of individual woody species, composition, density coverage within height classes, and community structure. To successfully control encroaching woody species, there needs to be an understanding of the distribution, patterns and density of these woody species (Bora et al., 2021). At this study site, Khoza (2021) provided evidence for the existence of two alternative stable states, which included a savanna state dominated by *V. karroo* and few thicket species, and an alternate thicket state characterised by a more diverse community with fewer *V. karroo*. These states were controlled by thresholds of canopy cover, light transmittance, fire spread and suppression, and species composition.

Elevation is also an important determinant of vegetation cover and plant density. This study aimed to understand the effect of elevation on the spatial distribution of thicket expansion stages within the study site. Hottman and O’Connor (1999) used panoramic photographs to investigate the pattern and extent of vegetation change and bush encroachment from 1955 in KwaZulu-Natal, South Africa. They found an overall increase in woody cover over time, and this woody cover increase was greater on hill slopes than on plains, and higher on north-facing slopes than on south-facing slopes (Hottman and O’Connor, 1999). This woody cover included a shift in species composition, with *Vachellia karroo* found increasingly at higher elevations. They found that bush clumps began to develop, and that broad-leaf species dominated on moist south-facing slopes at higher elevations. They suggest that this change in vegetation may have resulted from the removal of fires from the system, as well as an opening of the system due to overgrazing. O'Connor and Crow (1999) also studied the rate and pattern of bush encroachment in savanna and grasslands within the Eastern Cape, South Africa through analysis of sets of aerial photographs from 1937 to 1986. They found that over this period, valleys demonstrated two to three times more woody cover than slopes or uplands, they discovered that there was a similar increase in woody cover over all these levels of elevation, indicating that encroachment was present and increasing at this site, and spreading from valleys to slopes and uplands – these areas were not immune to encroachment. They suggest that rainfall events, population processes such as seed dispersal and facilitative effects may have increased the encroachment of woody species at this site. This impact may also be influenced by a number of environmental changes such as livestock systems favouring grazers over browsers and previously combined cattle and sheep operations switching to become cattle dominated, changes from continuous to rotational grazing, decreased fire frequency, as well as a reduced demand for firewood. More recently, Bora et al. (2021) looked at encroacher woody species within separate height classes at different elevations within arid thorn bush savanna grassland and found that the elevation level was able to influence which encroacher shrub species were present (Bora et al., 2021). They determined that when the elevation was lower, there was more combined density of encroachment present than at higher elevation levels. Interestingly, they found that encroacher woody plant species from the *Fabaceae* family (*Vachellia*) were widely distributed across all elevation levels studied, and they were the most species-rich family at higher elevation levels – therefore suggesting the ability of this family to encroach across elevations. They suggest that these vegetation changes may result from environmental and anthropogenic factors (such as fire suppression and increased grazing pressure).

In this study I used LiDAR and remotely sensed RGB imagery to investigate the vegetation structure across a sequence of woody plant encroachment in semi-arid savanna, as well as to measure the grass layer changes during the transition from open savanna to closed canopy thicket clumps. I used a cluster analysis based on vegetation structural variables to group areas displaying similar structural characteristics representative of the stages in thicket clump formation. The six vegetation structural variables were maximum canopy height, mean canopy height, canopy cover percentage and canopy height densities at three height strata. The aims and predictions of this study are outlined as follows;

(1) According to evidence by Khoza (2021), alternative stable states do exist at this study site, therefore, I hypothesized that distinct stages of encroachment from open savanna to closed-canopy thicket would be revealed as distinct clusters, with an unstable intermediate stage determined by the density of adult *V. karroo* trees that are able to facilitate the entry of thicket pioneers.

(2) I predicted a significant decline in total grass height as thicket expansion increases (based on the 40 % canopy cover thresholds reported by Archibald et al., 2009), resulting in the reduction or elimination of the grass layer.

(3) I predict that thicket encroachment is dominant at lower elevations, and that higher elevations represent earlier stages of thicket encroachment, which, given the trends in thicket encroachment in this area, may gradually become encroached in the future (O'Connor and Crow, 1999).

2.3 Materials and methods

2.3.1 Study site

The study was conducted at a semi-arid savanna site at Endwell farm (32° 38' 26"S, 26° 22' 28.8"E), located in the Smaldeel region between Somerset East and Fort Beaufort, in the Eastern Cape province of South Africa (Figure 2.1). This study site has an elevation of between 728 - 831 m above sea level. This area has distinct wet (summer) and dry (winter) seasons (Martens et.al., 1996), with the farm receiving a mean annual precipitation of 730 mm (farm records 1927-2020). The soil in the area consists of a mixture of clay, sand, and loam (Martens and Morris, 1994). This area was previously classified as False Thornveld of the Eastern Cape (Acocks, 1953), and is now classified as a mixture of Bedford Dry Grassland and Bisho Thornveld by Mucina and Rutherford (2006). The study site is primarily used for commercial livestock farming, and cattle and game (such as bushbuck, impala, kudu, common duiker, and warthog) are present on the farm at low stocking rates. Fire and other bush control methods have not been implemented in the recent history of the farm.

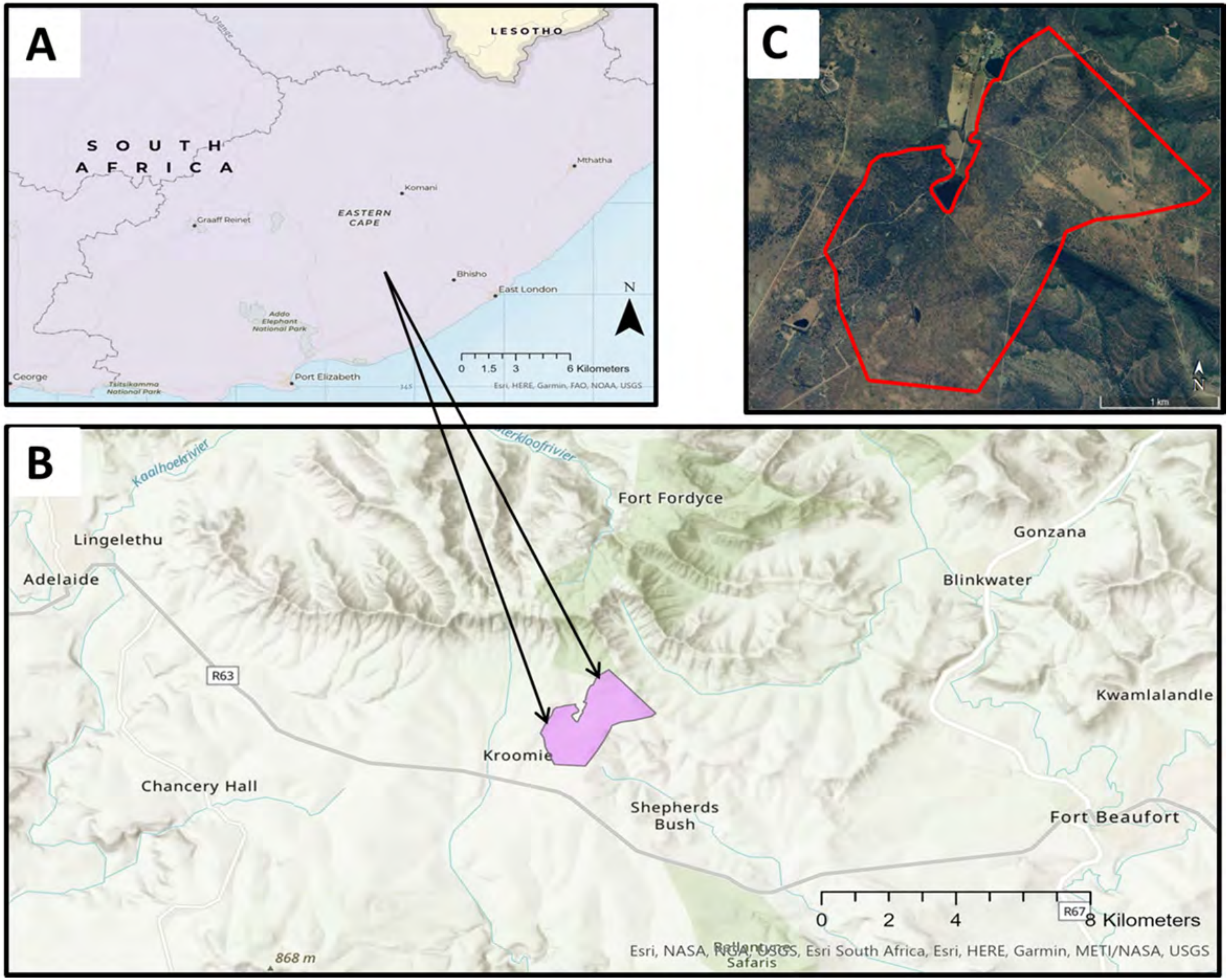

Figure 2. 1 (A) Endwell Farm location in the Eastern Cape, South Africa, where the study took place; (B) the study site over which area the LiDAR data and RGB images were obtained at Endwell Farm; (C) Google Earth images showing the vegetation cover over the study site.

Google Earth Pro was used to obtain historic imagery of the study site at Endwell Farm (Figure 2.2). Satellite images were used from 1985, 2013, 2016, and 2021 showing a visible increase in the amount of woody vegetation present over the years, particularly the increased density of bush clumps. *Vachellia karroo* is historically dominant in this region, and is the main encroaching tree species, and are described as one of the most important woody invader species of grasslands and savannas (O'Connor, 1995). In areas of later thicket clump formation, thicket species such as *Gymnosporia buxifolia, Brachylaena elliptica, Grewia occidentalis, Olea europaea spp africana, Ziziphus mucronata, Ehretia rigida, Afrocanthium mundianum and, Searsia longispina* are increasingly found within these bush clumps (Khoza, 2021).

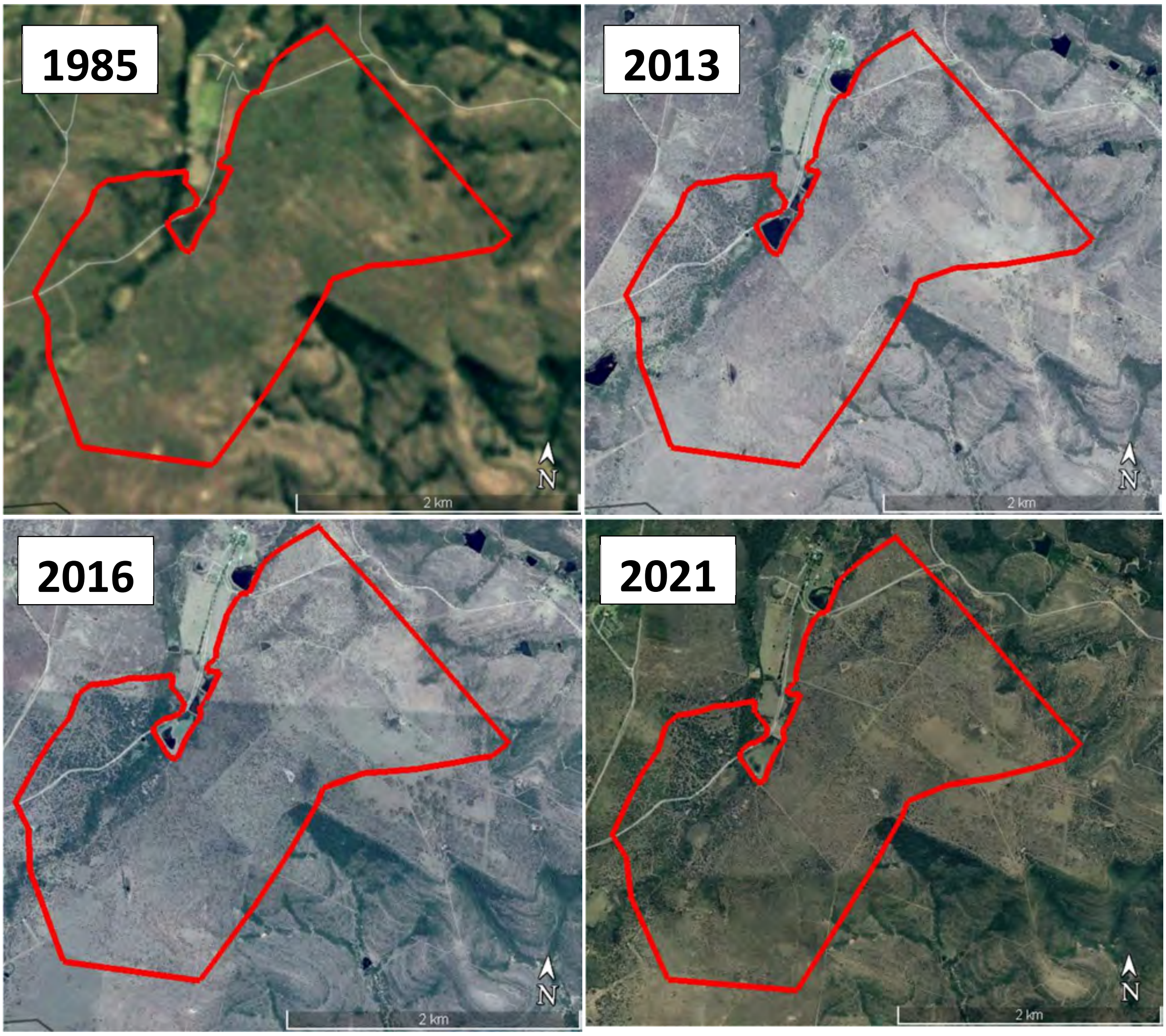

Figure 2.2 Historical imagery of the study site at Endwell Farm, taken over the years 1985, 2013, 2016 and 2021, from Google Earth. With the site boundary of the LiDAR flight data outlined in red.

2.3.2 Collection and processing of high resolution spatial data

The Harvard Animal Landscape Observatory (HALO) was used to collect LiDAR and RGB data. The HALO is a custom-designed multi-sensor remote sensing platform which integrates a LiDAR sensor, a thermal imager, an RGB camera, and a centralised data acquisition computer. On 26 March 2021, in conjunction with Professor Andrew Davies from the Davies Lab at Harvard University, the HALO system was mounted on a drone (unmanned aerial vehicle), and this was flown over the study site of 527 ha of land at Endwell Farm (Figure 2.1B). High-resolution, remotely sensed data was collected, including georeferenced RGB images and LiDAR point clouds.

The LiDAR point clouds were cleaned and processed, outliers and errors or interferences were removed, and data was saved in .las format by the Davies Lab at Harvard University. They normalized the LiDAR point clouds using R (R Core Team, 2021) (Figure 2.3A; Figure 2.3B) and created the canopy height model (CHM) using the first returns from the LiDAR point clouds by subtracting the height of the ground layer from the surface heights to ensure only the vegetation height is considered, without any influence from terrain and elevation (Figure 2.3C). This CHM of the study site was used in raster format as an image with a 25 cm resolution.

I used the grid creation function in QGIS (QGIS Development Team, 2022) to divide the study site into plots of 1 ha (100 m x 100 m). This choice of plot size was informed by consideration of previous studies where LiDAR data and RGB imagery were used to determine vegetation structure. Baldeck et al. (2014) used 0.25 ha plots to look at landscape-scale variation in plant community species composition of savannas in Kruger National Park from airborne species mapping using LiDAR data. Charles-Dominique et al. (2015) used 40 m × 10 m transects when defining South African savannas, thickets and forests structurally by their growth forms. The field calculator in QGIS was used to calculate the area of each plot, and plots along the edge of the study site which were incomplete (under 1 ha) were removed. All plots which contained inconsistencies and would not give a reasonable representation of the vegetation were removed, this included plots which had buildings, dams, or main roads present.

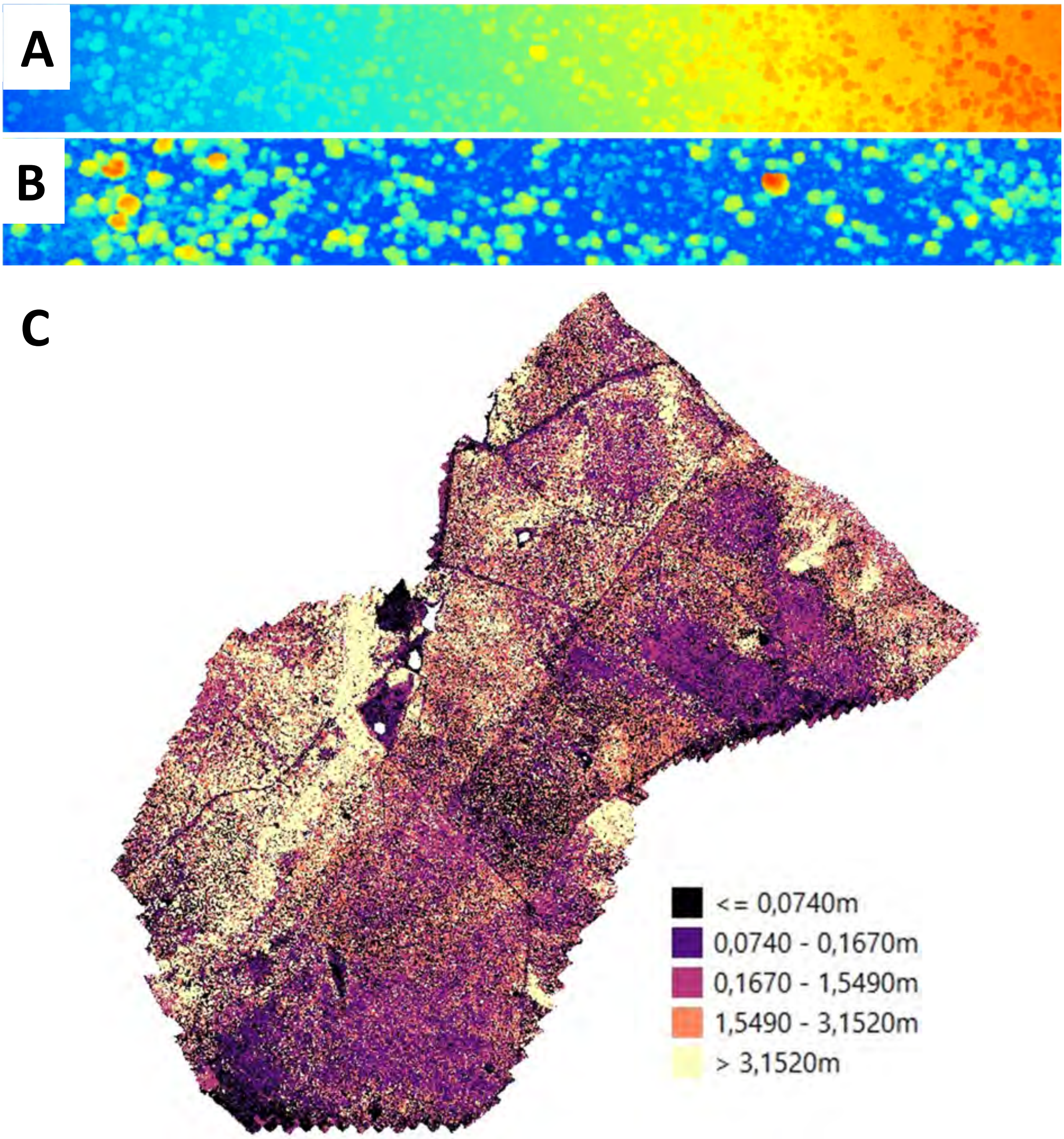

Figure 2.3 A) A cross section of the un-normalised point cloud which does not account for the effects of elevation. B) A cross-section of the normalised point cloud. Height increases as colours become warmer (move from blue to red indicates increasing height). C) The normalised Canopy Height Model (CHM) derived from the LiDAR point cloud for the study. Height increases as colour moves from black to yellow.

2.3.3 Calculation of vegetation structural variables

Guo et al. (2017) used airborne LiDAR data to calculate vegetation structural variables within forest areas in Canada, which included standard deviation of vegetation height, canopy cover percentage, and canopy height density at four increasing height categories. These vegetation structural variables were used to classify vegetation structure into classes representing different forest areas and they calculated these variables using a k-means cluster analysis at a 30 m spatial resolution (plot size). K-means clustering is a distance-based unsupervised clustering algorithm where data points that are close to each other are grouped in a given number of clusters/groups.

Similarly in my study, I selected six vegetation structural variables for this analysis: maximum canopy height, mean canopy height, canopy cover percentage and canopy height densities at three height categories (Table 2.1). I calculated these structural variables for each 1 ha plot over the entire study area. I used the Zonal statistics function in QGIS 3.22.3 (QGIS Development Team, 2022) to calculate the mean and maximum canopy height for each plot, using the 0.25 cm resolution CHM raster layer to get these measurements. I reclassified the CHM in QGIS 3.22.3 (QGIS Development Team, 2022) using the Reclassify function to form two classes representing "no canopy" (0 – 0.5 m) which was reclassified to give a value of zero, as well as "canopy cover" which was given a value of 100 (≥ 0.5 m). I used the Zonal statistics function in QGIS 3.22.3 (QGIS Development Team, 2022) to calculate the mean area covered by the tree canopy, and therefore the canopy cover, for each plot, with the use of this newly reclassified CHM raster. I used the function Lascanopy from Lastools (Isenburg, 2021) to create three height density categories from the first returns of the LiDAR point clouds (Guo et al., 2017; Alonso et al., 2020). The height categories that were selected here were: (1) 0 m to 1 m; (2) 1 m to 2 m; and (3) 2 m to 10 m. These height categories represent the height at which first returns were made, indicating the density of plant biomass present in each height category. I used these height density classifications of the LiDAR data to produce three new height density rasters for each height category, each with a resolution of 1 m for the study site. I divided the LiDAR point clouds in each height category by the total number of LiDAR points and scaled this to a percentage. I then loaded these relative height density rasters into QGIS and merged each separate raster from the different height categories across the study site (QGIS Development Team, 2022). I then used Zonal statistics to calculate the mean point density for each height category for each 1 ha plot. I, therefore, have the mean and maximum canopy height, the canopy cover percentage and the three height densities for each 1 ha plot across this study site (Table 2.1). The processes of calculating vegetation structural variables is summarised in Figure 2.4.

I then created an elbow graph to help determine the number of clusters best suited to capture the variation in the vegetation structural variables across the study site. I used the elbow method as a graphical indicator to help find the optimal K value for the k-means clustering. The elbow method is a graphical method for finding the optimal K value in a k-means clustering algorithm. The elbow graph shows the within-cluster-sum-of-square (WCSS) values on the y-axis corresponding to the different values of K (on the x-axis). The optimal K value is the point at which the graph forms an elbow. I used the attribute-based clustering function in QGIS to run a K-means cluster analysis across the study site (Table 2.1) (QGIS Development Team, 2022). This cluster analysis grouped 1 ha plots into three clusters based on the vegetation structural variables, as per the results of the elbow method.

Table 2.1 Variables used to cluster plots with similar structural vegetation across the study site

No.	LiDAR Variable	Description	Reference
1	Maximum canopy height	Highest mean height value of canopy	*Listopad et al., 2015; Lim et al., 2003.*
2	Mean canopy height	Mean height of canopy	*Listopad et al., 2015;*
3	Canopy cover	% of each cell covered by tree canopy (> 0.5 m height).	*Guo et al., 2017*
4a	Canopy height density 1	% of first return between 0 m and 1 m height.	*Guo et al., 2017.*
4b	Canopy height density 2	% of first return between 1 m and 2 m height.	*Guo et al., 2017.*
4c	Canopy height density 3	% of first return greater than 2 m height.	*Guo et al., 2017.*

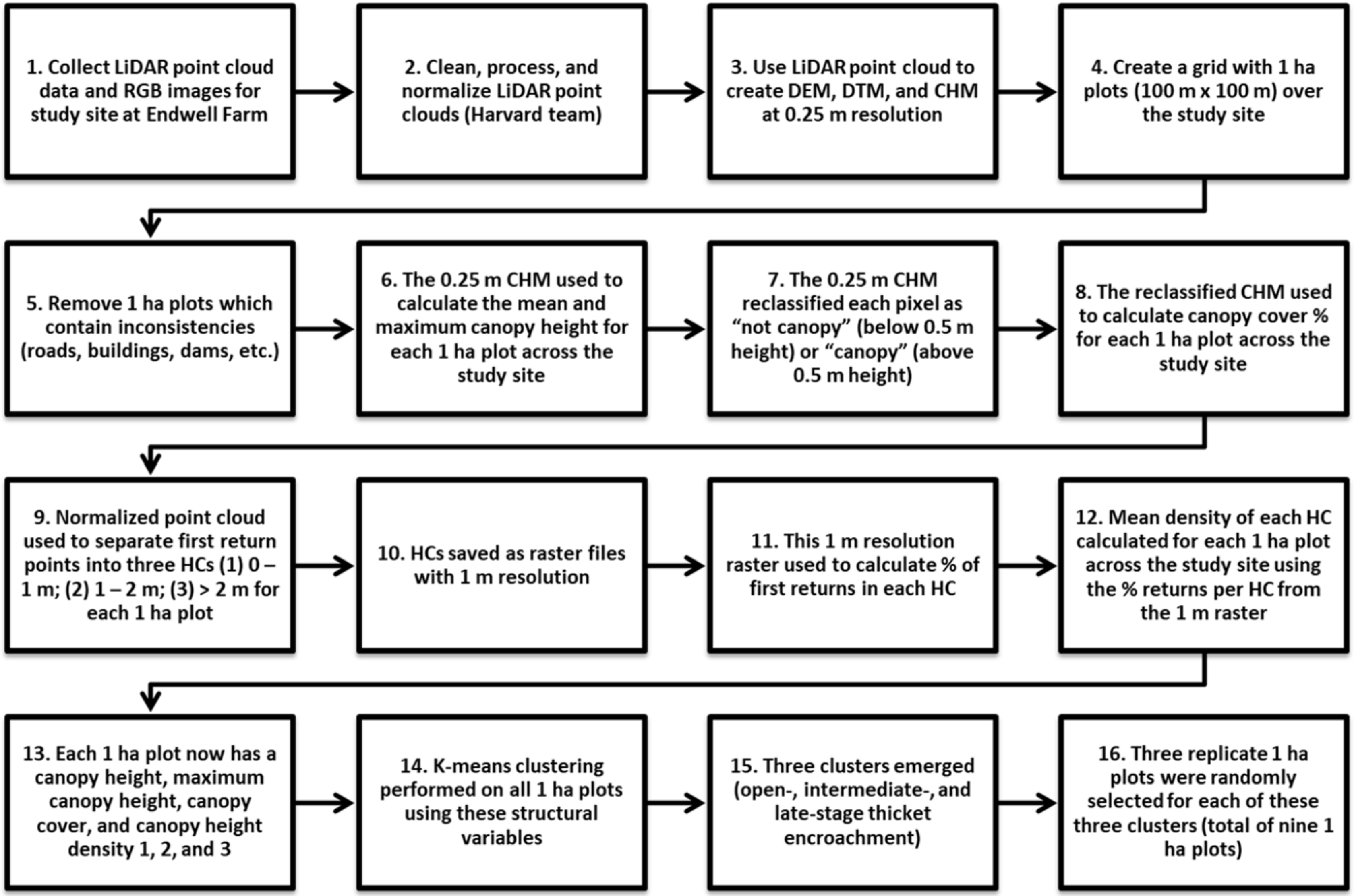

Figure 2. 4 Summary of the data processing procedure followed to calculate the six vegetation structural variables used to cluster plot: (1) mean canopy height; (2) maximum canopy height; (3) canopy cover; (4) height density (0 -1 m); (5) height density (1 – 2 m); and (6) height density (> 2 m).

2.3.4 Grass height quantification

I measured grass stand height using the RGB images and the CHM in QGIS 3.22.3 (QGIS Development Team, 2022). I created 1 m^2 hexagon sub-plots which were spaced randomly over the grass layer within a plot (50 to 65 hexagons per plot) representing each emerging cluster from the cluster analysis. I used zonal statistics in QGIS 3.22.3 to calculate the mean grass height within each hexagon (QGIS Development Team, 2022). I then substituted these heights into the disc pasture meter calibration equation by Trollope (1983) for grassland and thornveld areas of the Eastern Cape, South Africa, given as follows:

$y = 340 + 388{,}3x$

where: y = mean standing crop of grass (kg/ha)

x = mean disc height (cm)

To Ground-truth the study site, a disc pasture meter (DPM) was used to measure grass biomass, and a total of 30 DPM measurements were taken in December 2022. These points were taken in the same plots at the same sites as the LiDAR derived methods; within the early stages of thicket encroachment (Cluster 1, Plot 779), intermediate stages (Cluster 2, Plot 586), and late stages (Cluster 3, Plot 125). The corner closest to the access point was used as the starting place for DPM measurements, and from here a 100 m transect was set up across the plot. The DPM measurements were then taken every 2 steps (around 1.5 m) along that path. Where obstacles (such as a bush clump or fallen tree) occurred, another 2 steps after the obstruction were taken and the DPM was measured. DPM measurements taken in the field were substituted into the same disc pasture meter calibration equation by Trollope (1983) to calculate the mean standing crop of grass (kg/ha): $y = 340 + 388{,}3x$; where: y = mean standing crop of grass (kg/ha) and x = mean disc height (cm). I compared the grass biomass results derived from the LiDAR measurements with that taken in the field using traditional DPM measures to test whether the same trends in grass biomass between each of the three clusters would occur and whether this provides a potential method for grass layer estimations.

2.3.5 Elevation calculation and determination

I used Lastools (las2dem) to create a digital elevation model (DEM) of the study site using the LiDAR point clouds (Isenburg, 2021). This process allows visualisation of the terrain over the study site, showing changes in the elevation. I used QGIS 3.22.3 (QGIS Development Team, 2022) to overlay the resulting clusters over the DEM. I tested whether the resulting clusters are influenced by the elevation or whether there are any patterns resulting from changes in the topographic surface.

2.3.6 Data analysis

I used R to create boxplots demonstrating the vegetation structural variables within each cluster (R Core Team, 2021). I used Cloud Compare to create a cross-section of the point clouds within each of the three emerging clusters (CloudCompare, 2024). I used a Principal Components Analysis (PCA) to plot the three clusters against the first two discriminate axes with the strength and direction of each vegetation structural variable, as well as the eigenvalues indicated. The PCA analysis was performed in R (R Core Team, 2021), using the vegetation structural variables (mean and max heights, canopy cover, and canopy height density 1, 2, and 3) across each cluster. I analysed the percentage contributions of the variables in accounting for the variability of components for axis 1 (pair component 1) and axis 2 (pair component 2) as well as the quality of representation of the variables on the map of the clusters.

One-way analysis of variance (ANOVA) was used to compare the mean grass height within three plots representing each of the three clusters. An ANOVA test and the Coefficient of determination was also used to test whether grass biomass measurements differed when using the ground DPM and the LiDAR derived methods. Tukey post hoc tests were also performed to investigate whether there were any significant differences between grass heights for each of the three plots representing each cluster. I also used an ANOVA to compare the mean elevation across clusters, as well as a Tukey post hoc test to investigate the elevation between plots in each of the clusters. These significance tests were performed in R (R Core Team, 2021).

2.4 Results

2.4.1 Cluster analysis

The plots were separated into three clusters based on the vegetation structural variables; mean canopy height, maximum canopy height, cover and mean canopy height density at each height strata (0 to 1 m; 1 to 2 m; 2 to 10 m). Figure 2.5 shows the elbow curve graph which bends at three clusters, indicating that this is a suitable number of groups to separate the data into. The use of three classes allows each cluster to be separated with good homogeneity.

Each of these three clusters identified has a distinct vegetation structure, which may be representative of each of these stages of thicket expansion. These clusters appear to be arranged in a gradient across the study site, with Cluster 2 occurring as a transitional stage between Cluster 1 and 3 (Figure 2.6). Cluster 2 is the most commonly occurring, occupying 41.39 % of the study site (137 plots). This is followed by Cluster 1, which makes up 30.82 % of the site and consists of 102 1 ha plots. Cluster 3 is the least commonly occurring, with 92 plots over the study site, making up 27.79 % of the area.

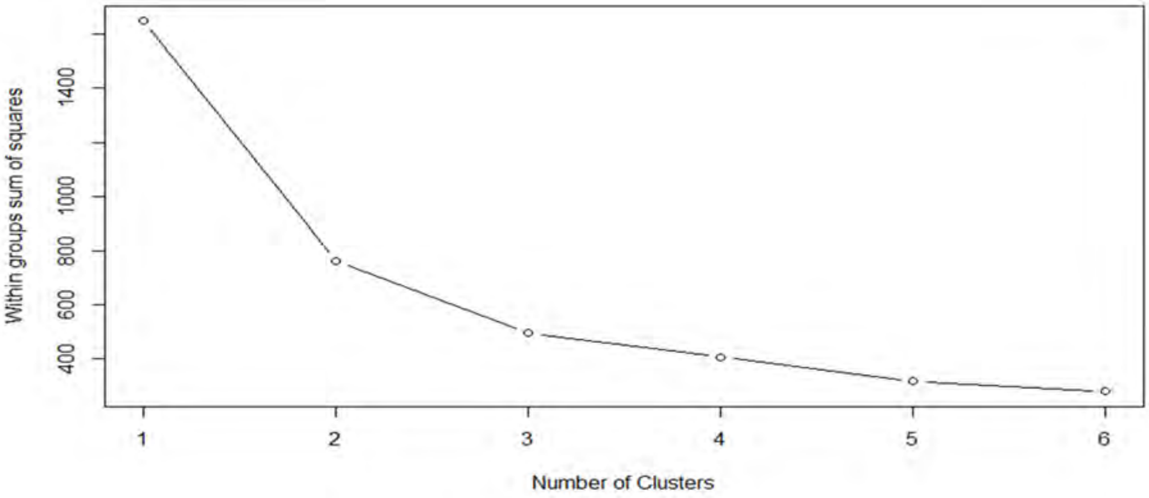

Figure 2.5 An elbow curve graph was used to identify the optimal number of clusters resulting from the K-means cluster analysis, which clustered areas based on vegetation structural variables: mean canopy height; maximum canopy height; canopy cover; (height density (0 -1 m); (5) height density (1 – 2 m); and (6) height density (> 2 m). The elbow bends at 3 clusters.

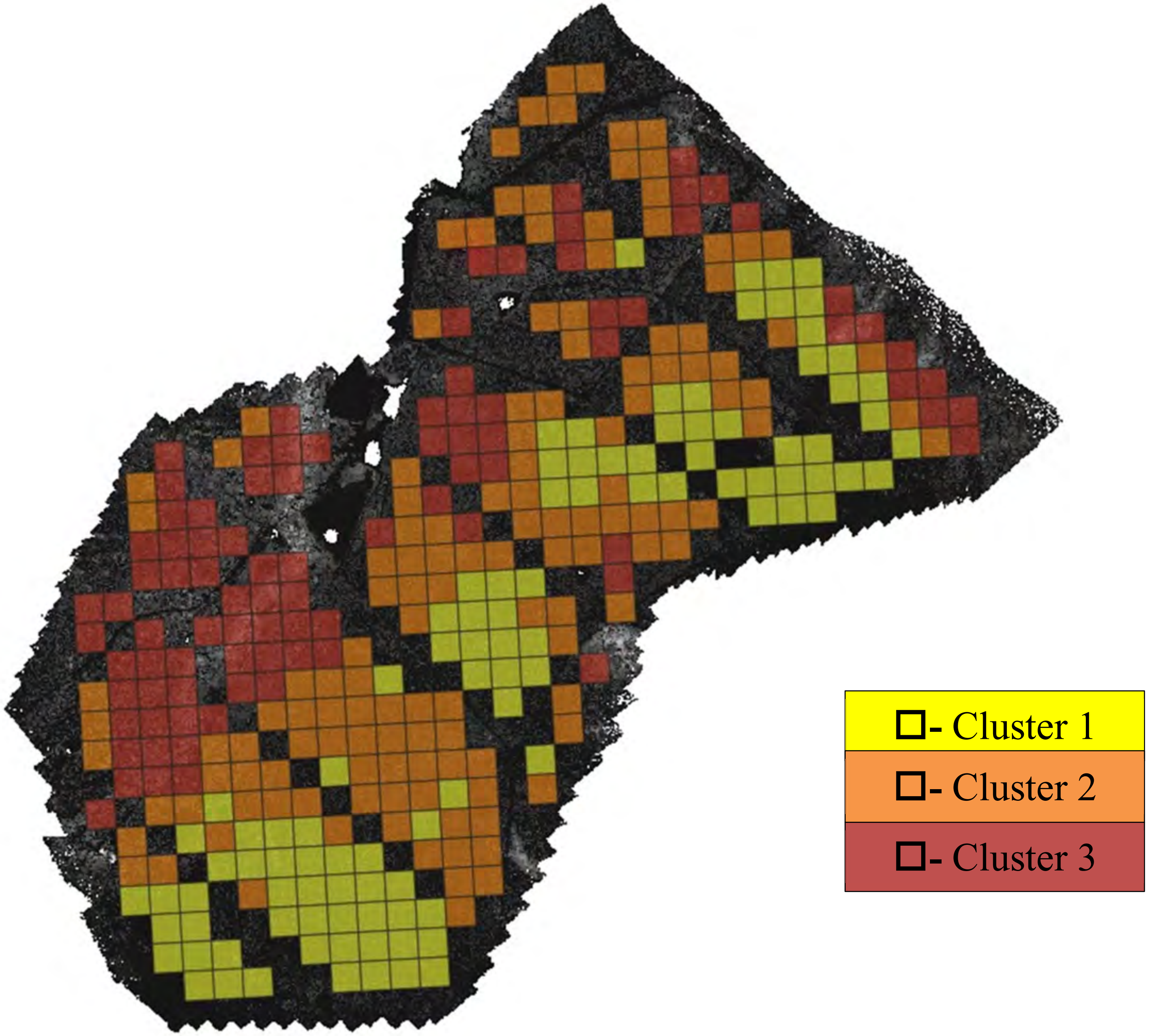

Figure 2.6 Plots (1 ha) are categorized into three clusters based on their vegetation structure Cluster 1 (Yellow); Cluster 2 (Orange); and Cluster 3 (Red). The distribution of these 1 ha plots are shown over the study site at Endwell Farm, with the plots containing roads, dams and housing removed.

2.4.2 Structure of vegetation within clusters

Figure 2.7A shows that the three clusters have an increasing mean height from Cluster 1 to Cluster 3. Cluster 1 has the lowest mean canopy height, at 0.62 m ± 0.22 SD, followed by Cluster 2 at 1.26 m ± 0.29 SD and then Cluster 3 at 2.82 m ± 0.91 SD (Figure 2.7A). Therefore Cluster 3, on average, has much taller vegetation cover than Cluster 1. The overall mean canopy height across all plots is 1.5 m ± 1.01 SD. The mean height data is positively skewed, resulting in most of the plots displaying mean values of less than 4 m, with outliers occurring at heights greater than this, with a peak at 1 m height.

Figure 2.7B shows that Cluster 1 has a mean maximum height of 5.48 m ± 0.98 SD, Cluster 2 has a mean maximum height of 6.40 m ± 1.21 SD, and Cluster 3 has a mean of 10.01 m ± 2.32 SD (Figure 2.7B). Therefore Cluster 3 has the tallest vegetation, followed by Cluster 2 and lastly, Cluster 1 has the lowest maximum canopy heights. Clusters 1 and 2 display more similar maximum heights, while Cluster 3 shows instances of vegetation almost double that height (Figure 2.7B). Most of the maximum canopy heights peak at 5 to 7.5 m.

Figure 2.7C shows that Cluster 1 has the lowest cover, with a mean canopy cover of 23.98 % ± 9.94 SD. This is followed by Cluster 2, with a mean canopy cover of 48.46 % ± 7.71 SD, while Cluster 3 has the highest canopy cover, with a mean of 75.5% ± 8.01 SD. The clusters show an increase in canopy cover from Cluster 1 to Cluster 3, as there is a shift from sparse, open canopies (Cluster 1); to a more frequent, semi-open/closed canopy (Cluster 2); and finally towards an almost continuous closed canopy (Cluster 3). The overall mean canopy cover is 48.43 % ± 21.48 SD across all sites, with the canopy cover having a reasonably normal distribution.

The mean canopy height density class 1 decreased from Cluster 1 to 2 and then to 3 (Figure 2.7D). Cluster 1 had a mean of 86.45 % ± 9.65 SD of points found between 0 to 1 m; Cluster 2, however, had a mean of 69.87 % ± 9.53 SD of its points found in this density class. Cluster 3 had the least of the three, with only 49.24 % ± 9.05 SD of the points making up the point clouds in these sites being found in this 0 to 1 m layer. An overall mean of 69.25 % ± 17.08 SD of points is found within this density stratum. This means that this canopy height density class is the most common for vegetation over this study site.

The mean canopy height density class 2 was 5.09 % ± 2.31 SD for Cluster 1; 10.73 % ± 2.51 SD for Cluster 2; while 11.83 % ± 2.91 SD of Cluster 3's points were found between 1 and 2 m (Figure 2.7E). Cluster 1 has vegetation with a low density between 1 and 2 m; clusters 2 and 3 have more dense vegetation present within this stratum. There is a great deal of variation within Cluster 3. Most of the points in this stratum occur at a mean point density of between 5 and 15 %, and outliers occur from above 20%. This canopy height density stratum contributes the least to making up the percentage of first returns indicating the structure of the vegetation.

The mean canopy height density class 3 increases in percentage from Cluster 1 (with a mean of 6.22 % ± 3.23 SD), to Cluster 2 (with a mean of 15.48 % ± 5.36 SD), and then to Cluster 3 (38.15 % ± 9.54 SD) (Figure 2.7F). Cluster 1 has a very low density, with very little vegetation structure falling into this canopy height density category. Cluster 2 similarly was found to display minimal vegetation within this stratum. For Cluster 3, however, this was different, as there were high rates of vegetation structure falling into this height density layer. The density of the percentages within this height density strata are positively skewed, with percentages higher than 50 % being outliers. Overall mean canopy height density 2 (9.30 % ± 3.83 SD) and 3 (18.93 % ± 14.07 SD) have much lower means than canopy height density 1, which has a mean of 69.25 % ± 17.08 SD. Therefore most of the first return points indicate vegetation between 0 to 1 m.

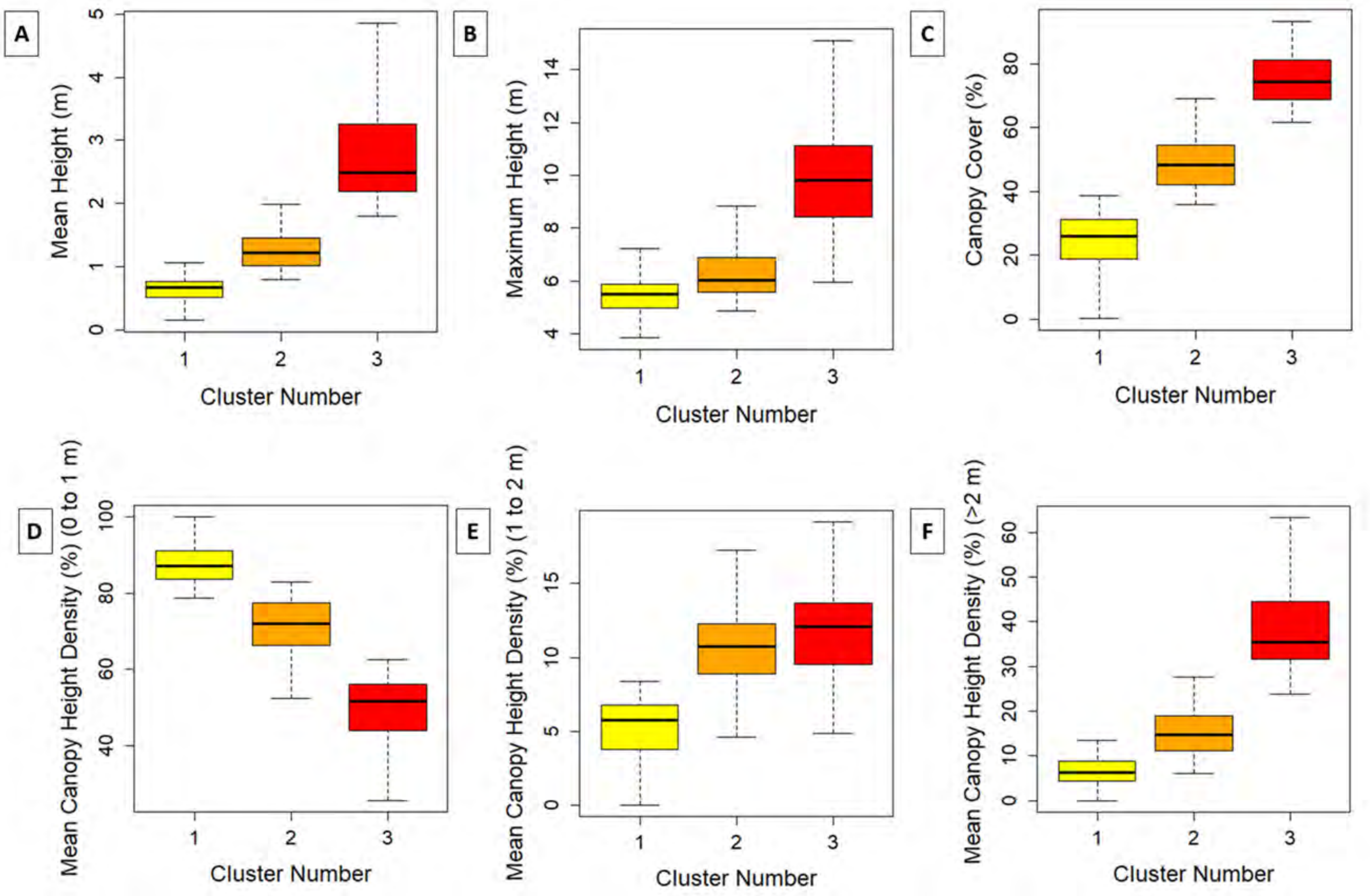

Figure 2.7 The vegetation structural variables for each cluster: (A) Mean canopy height (m); (B) Maximum canopy height (m); (C) Canopy cover (%); (D) Mean canopy height density 1 (0 to 1 m); (E) Mean canopy height density 2 (1 to 2 m); and (F) Mean canopy height density 3 (>2 m). Median value for each Cluster is indicated by a bold horizontal line within each box.

When clusters were plotted against the first two discriminate coefficient axes, axis 1 showed 80.5% of the variation in all variables, while axis 2 explained 13.9% of the variance (Figure 2.8). The PCA represented each cluster according to the vegetation structural variables selected, and these clusters were arranged in what appeared to be a continuous gradient, from Cluster 1 to 2 and then Cluster 3. The structure of vegetation seems to move from low, sparse vegetation to tall dense vegetation along axis 1. The variables which contributed the most in accounting for the variability in axis 1 were: Canopy cover (19.8 %), canopy height density 3 (> 2 m) (19.34 %) and mean height (19.16 %), however nearly all variables contributed fairly equally, except height density 2 (1 – 2 m), which was lower (8.08 %). These variables were found to also have the highest quality of representation of the variables on axis 1. Cluster 1 is located towards the left along the discriminate coefficient axis 2, while Cluster 2 is organised around the centre of axis 2 and axis 1, between Cluster 1 and Cluster 2. Cluster 3, however, is found primarily towards the right of axis 2, along the centre of axis 1 (Figure 2.8). Within Cluster 1, the top contributing variables for axes 1 and 2 (86.2 % variation of data) were Mean Height, Max Height, and Canopy Cover. In Cluster 2 Mean Height, Canopy Cover, and Canopy Height Density 2 (1 - 2m) had the highest discriminatory power, contributing to axis 1 and axis 2 which together explained 74.5 % of the variance within the data. Within Cluster 3, Mean Height, Canopy Cover, Canopy Height Density 1 (0 - 1m), and Canopy Height Density 3 (>2m) are the highest contributing variables for axes 1 and 2 (93 % variance). As they are primarily based on height and the development of vegetation, trees with greater height (Mean canopy height, maximum canopy height and canopy height density 3) displayed a strong positive correlation with canopy cover (R = 0.75). For the height density 1 (0 to 1 m) however there are strong negative relationships with mean height, maximum height and canopy cover.

This is illustrated in Figure 2.9, where cross-sections of the vegetation structure profile from the point cloud within each of the three clusters are displayed to show the defining structural characteristics. Within Cluster 1 the contributing variables are illustrated- with low canopy heights across the plot, and open canopy cover defining the vegetation structure. In Cluster 2 there is an increase in the canopy cover, as well as the height of trees, with a corresponding increase in the plant biomass occurring at greater densities within this now higher canopy layer. In Cluster 3 the trees are taller and canopy cover increases further, representing what is now a closed canopy thicket. The canopies contribute to a great deal of the plant biomass and therefore there is a decreased density in the lower herbaceous layers represented as the trees increase in height and canopy size.

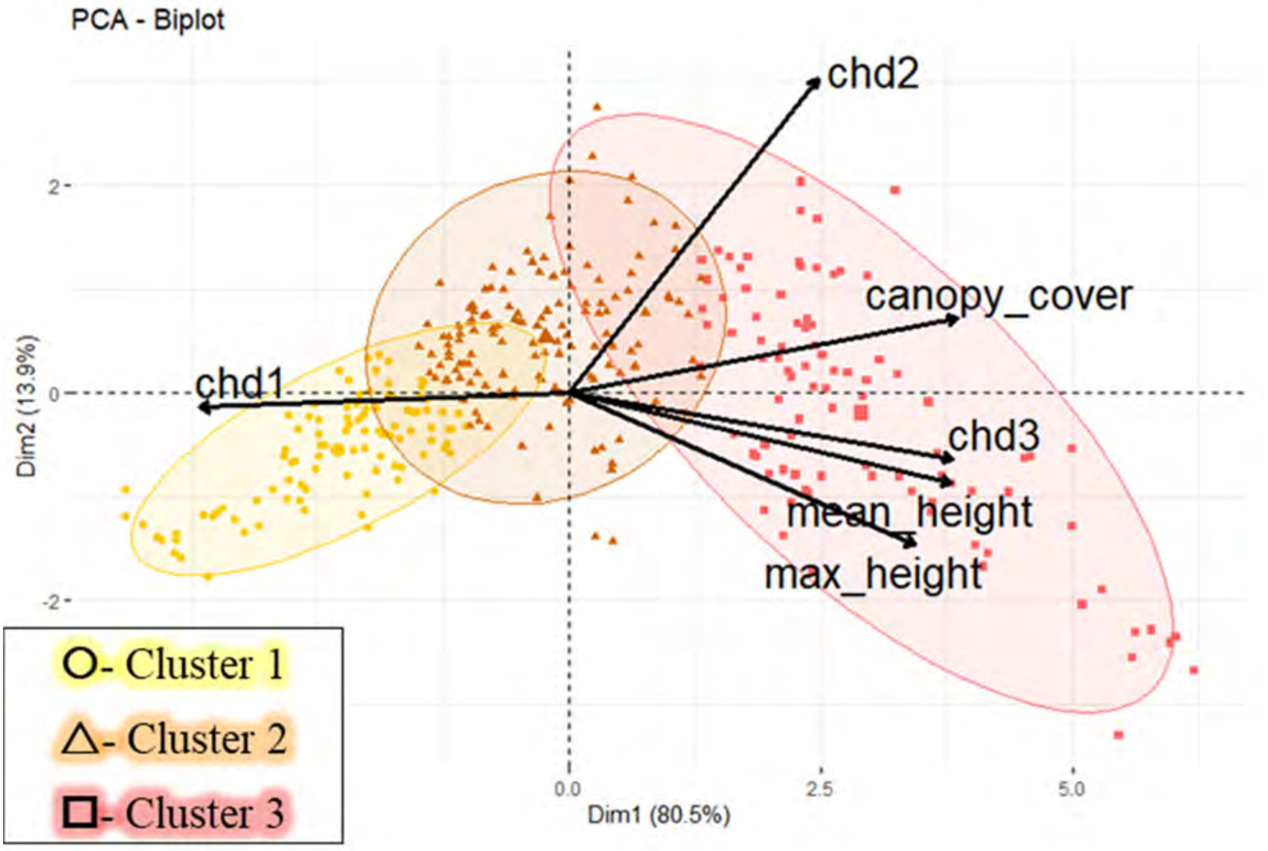

Figure 2.8 Vegetation structure variables plotted against the first two discriminate axes with arrows indicating the strength and direction of each variable. Individual plots plotted according to clusters, with a concentration ellipse around each group: Cluster 1- yellow dots, with a yellow ellipse; Cluster 2- orange triangles, with orange ellipse; Cluster 3- red squares, with a red ellipse.

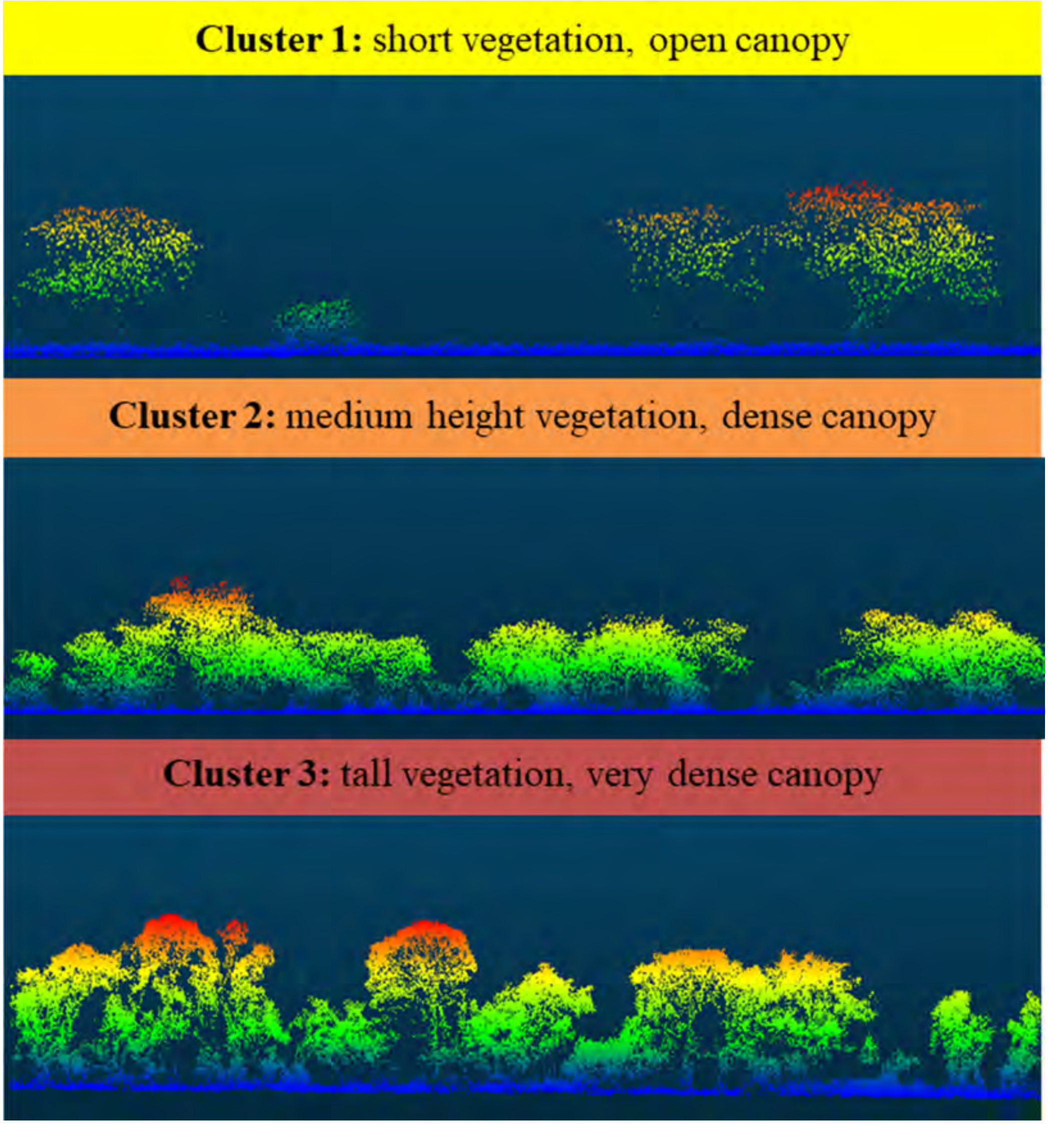

Figure 2.9 Cross sections showing the vegetation structure profile from the LiDAR point cloud within each of the three clusters: (1) Cluster 1 – yellow; (2) Cluster 2 – orange; (3) Cluster 3 – red. Height increasing as colour moves from blue (low vegetation) to green, with yellow and red indicating taller vegetation.

2.4.3 Effect of thicket clump formation on grass height

There was an overall statistically significant difference found in the grass height within these three clusters ($p < 0.05$, df= 2, F= 11.59). There was no significant differences found between the grass height within Cluster 1 and Cluster 2 ($p > 0.05$), or between Cluster 2 and Cluster 3 ($p > 0.05$). There was however a significant difference in the grass height between Cluster 1 and Cluster 3 ($p < 0.05$). In Cluster 1, the plot was dominated by grass cover (Table 2.2; Figure 2.10). The mean height of grass within this cluster was the tallest grass out of each of the three clusters (Table 2.2). Cluster 2 showed an almost even split between grass and tree cover (Table 2.2; Figure 2.10). The grass within this cluster had a medium height compared to other clusters (Table 2.2). In Cluster 3 the plot area was dominated by tree cover and the grass found within Cluster 3 was the shortest across clusters (Table 2.2; Figure 2.10). In Cluster 3 there was the least area covered by grass, and grass was the shortest, the total grass present is therefore the least grass present.

Table 2.2 Grass height measurements using LiDAR showing the mean ± SD and percentage canopy and grass cover within a sub-set of selected plots.

	Cluster 1	Cluster 2	Cluster 3
LiDAR Mean Grass Height (cm)	15.757 ± 1.60 SD	13.007 ± 1.53 SD	8.555 ± 2.31 SD
Canopy cover (%)	33 %	56 %	81 %
Grass cover (%)	67 %	44 %	19 %

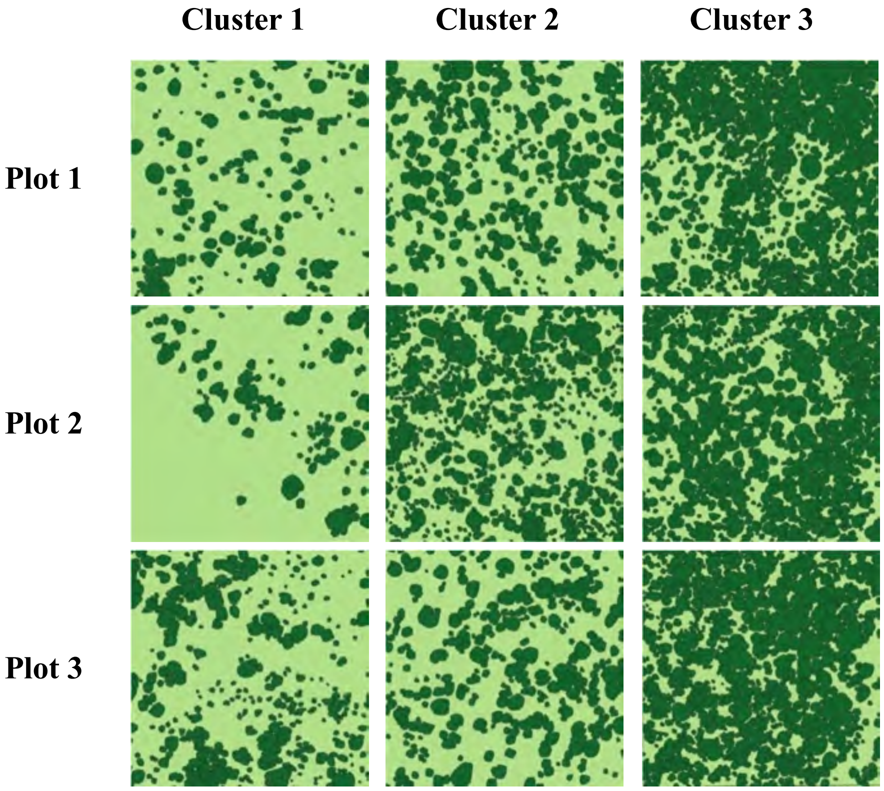

Figure 2. 10 Proportion of canopy cover within replicate plots from each of the three Clusters. Dark green areas represent tree cover; light green areas represent grass and ground layers.

The mean standing height of grass measured using the DPM was lower across all clusters than the mean heights obtained across clusters using LiDAR generated CHM (Figure 2.11). The same trend in the grass layer is followed however, with the greatest grass layer in Cluster 1, intermediate measurements in Cluster 2, and the lowest grass layer in Cluster 3 (Figure 2.11). There was no significant difference in grass biomass measurements when using the ground DPM and the LiDAR derived methods (p-value = 0.159, df = 1, F = 15.351). However, one can see a trend where the grass biomass is decreasing from Cluster 1 to Cluster 3, with a Coefficient of determination of $R^2 = 0.9817$ for ground measurements, and $R^2 = 0.882$ for LiDAR measurements.

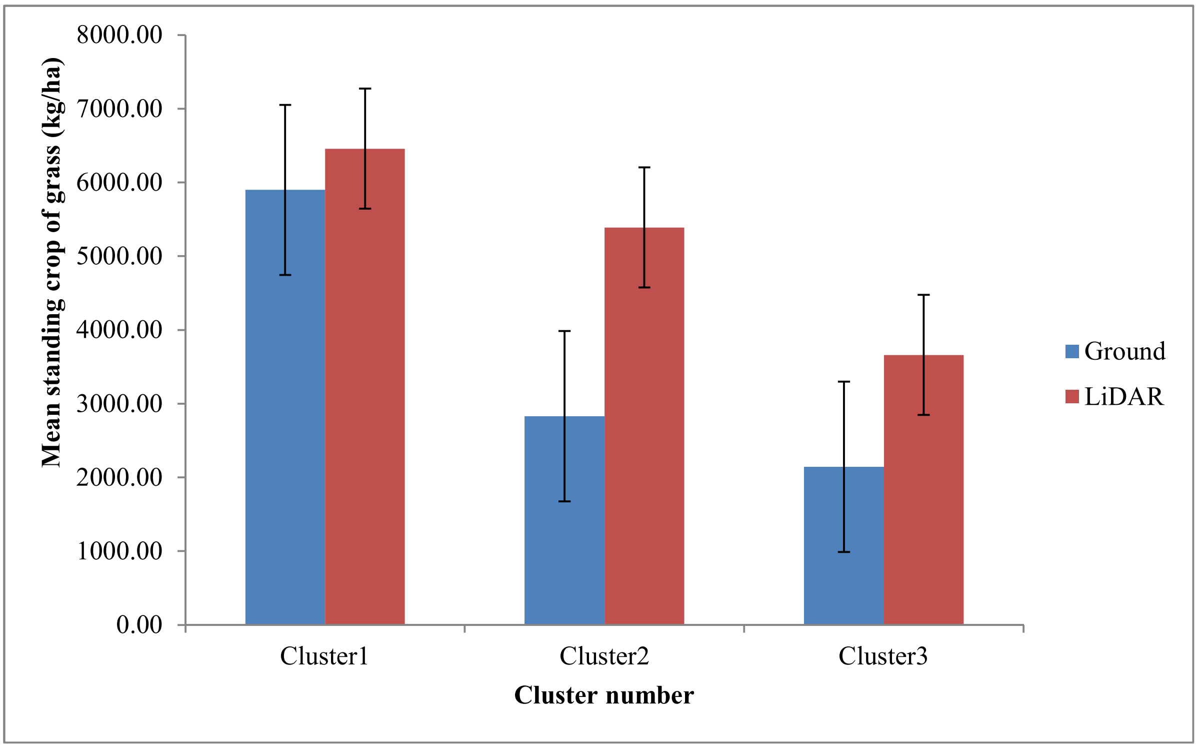

Figure 2.11 Grass biomass taken using traditional DPM measurements in the field (Ground measurements in blue) compared with grass biomass measurements made using LiDAR derived grass height (LiDAR measurements in red). Error bars are indicated on the graph; $R^2 = 0.9817$ for ground measurements, and $R^2 = 0.882$ for LiDAR measurements.

2.4.4 Elevation within clusters

The DEM (Figure 2.12A) shows how the terrain changes over the study site, with the elevation ranging from 722 m to 850 m. Figure 2.12 B1 shows the distribution of Cluster 1 over the DEM of the study site. Cluster 1 seems to be present predominantly in areas of higher elevations. Further, Cluster 1 appears to stretch over larger, flatter areas over the study site. Cluster 1 is also present along gradual declines in elevations as there is a smoother, natural decline in the topography. Cluster 2 (Figure 2.12 B2) is spread over a variety of elevations, with a high concentration of plots along the middle portion of the study site. Figure 2.12 B3 displays Cluster 3, which is dominant on the site's left side. Cluster 3 shows signs of increased presence in areas of lower elevation. These sites of lower elevation where Cluster 3 is frequent appear to be valleys or cuts in the landscape, where water may flow down the surrounding mountains. Cluster 3 occurs in lower elevations that decline more steeply, which differs from the gradual declines over which Cluster 1 is predominant. A one-way ANOVA test showed that there was a significant difference in elevation between clusters (p-value < 0.005, df= 2, F= 11.92), and a Tukey HSD test indicated that Clusters 1 and 2 did not have significantly different elevation, while Clusters 1 and 3 were significantly different and 2 and 3 had different elevations (Figure 2.13).

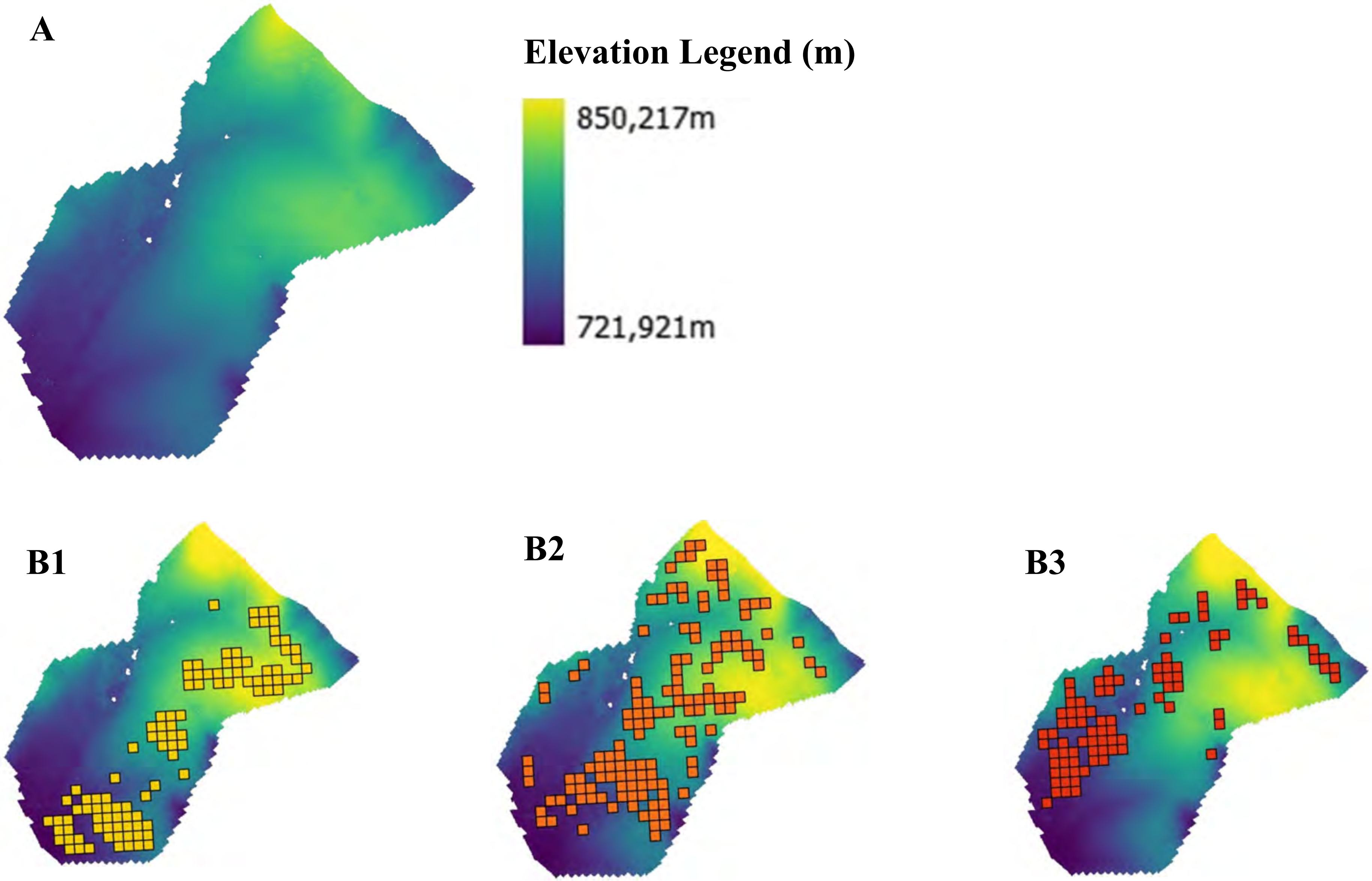

Figure 2.12 The digital elevation model of the study site: A) showing the levels of elevation of the terrain over the entire study site; B1) for plots in Cluster 1 (yellow grid); B2) plots in Cluster 2 (orange grid); and B3) plots in Cluster 3 (red grid) at these different elevations.

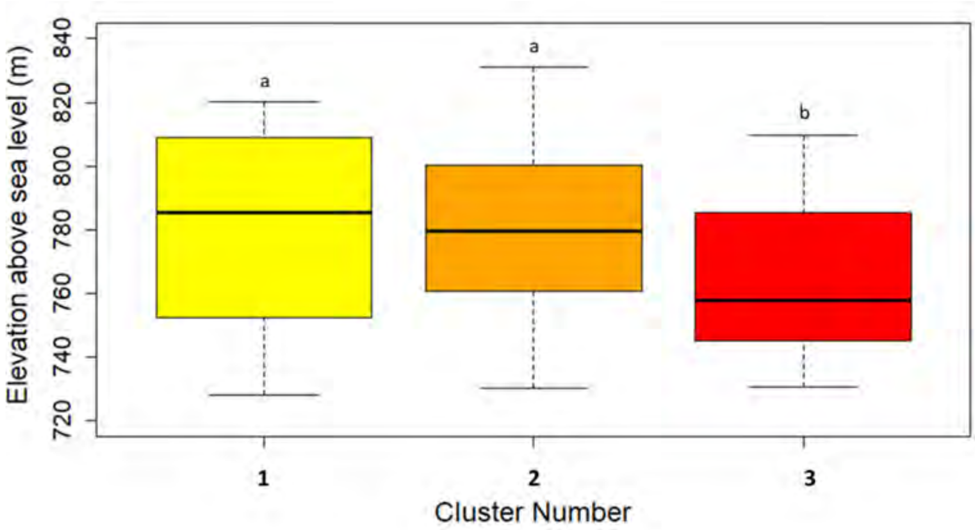

Figure 2.13 Elevation above sea level found at plots within each of the three clusters. Results of Tukey HSD test indicated using letters "a" and "b" to indicate significantly different elevations, with a p-value = 0.992 between Clusters 1 and Cluster 2, and a p-value = < 0.005 between Cluster 1 Cluster 3, as well as between Cluster 2 and Cluster 3. Median value for each Cluster is indicated by a bold horizontal line within each box.

2.5 Discussion

In savannas such as this study site, there has been an increase in thicket encroachment, with thicket species replacing savanna species (O'Connor and Chamane, 2012; Jamison-Daniels et al., 2021; Khoza, 2021; Nell et al., 2024). In this study I used LiDAR and remotely sensed RGB imagery to examine the vegetation structure of woody plant encroachment (Lim et al., 2003; Baldeck et al., 2014; Listopad et al., 2015). I used a cluster analysis based on vegetation structural variables to group areas displaying similar vegetation woody cover and vegetation structure and structure (Charles-Dominique et al., 2015; Marselis et al., 2018). As predicted, I found that distinct stages of thicket clump formation were evident along a gradient of thicket encroachment within this semi-arid savanna. Three unique clusters emerged, representative of increasing stages of thicket clump formation moving from savanna to thicket. Cluster 1 represented an open savanna with early stage thicket encroachment, while Cluster 2, the most commonly occurring cluster, represented intermediate stage thicket encroachment with thicket clumps starting to form. Cluster 3 represented late stage thicket encroachment with dominant thicket clumps. Meyer et al. (2008) studied the cyclical succession in semi-arid savannas in South Africa, using a spatial simulation model. Their study supported my findings of three dominant clusters, as they suggest that cyclical succession proceeds in three phases: (1) initiation phase characterized by facilitation and mass recruitment of shrubs under favourable environmental conditions, (2) build-up phase where the shrubs of a cohort increase in size and competition increases, and (3) break-down phase with die-back of the shrub cohort resulting from high competitive pressure and unfavourable conditions. My study found that each cluster of the three emerging clusters had distinct vegetation each with its own characteristic structure. Overall, the structural variables that were found most useful in predicting the thicket clump formation stage present within a site were found to be canopy cover, mean height, and canopy height density 3 (>2m).

These early stages of thicket encroachment can be easily identified by analysing the mean height, max height, and canopy cover within the area. At early stages of thicket encroachment the vegetation was found to be low, with open tree canopies and a high proportion of plant biomass below 1 m in height. This demonstrates that there is a great level of investment in small trees, as well as the herbaceous layer. This follows the characteristics of a savanna as described by Scholes and Archer (1997) who define savannas as having a mixture of contrasting life forms with a continuous grass layer and scattered trees. Ratnam et al. (2011); Parr et al. (2012); and Charles-Dominique et al. (2015) further help define savannas as having continuous grass understory and discontinuous tree cover.

I found that as areas become more encroached there is a shift from these open savannas towards a more closed-canopy thicket with thicket clump formation. As thicket clump formation expands, the vegetation structure changes, with increases in height, canopy cover and canopy densities (intermediate and late stage thicket encroachment). As the canopy cover and height increases, greater vegetation biomass occurring at increased heights, as the trees grow taller and more complex in structure. The vegetation within these later stages of thicket clump formation show a shift towards characteristic thicket structure, as explained by Woodward et al. (2004), Ratnam et al. (2011), and Charles-Dominique et al. (2015) who describe thickets as consisting of dense shrubs and small trees, with closed canopies and a variable understory. Tinley (1975) and Vlok et al. (2003) also characterised the thicket biome by dense closed-canopy vegetation consisting of an impenetrable tangle of broadleaf shrubs and low trees. Late stage thicket clump formation could be identified using ecologically significant structural variables such as mean height, canopy cover, canopy height density 1 (0 - 1m), and canopy height density 3 (>2m).

Based on these descriptions of thicket vegetation through the literature, I therefore found that the intermediate stage of thicket encroachment displayed a combination of traits and structures associated with both savanna and thicket systems and can therefore be seen as a transitional state between savannas and thickets (Staver et al., 2011, Parr et al., 2012). To help identify these areas of intermediate thicket encroachment, the mean height, canopy cover, canopy height density 2 (1 - 2m) of vegetation can be used. This intermediate stage may be important in determining the state change from savanna to thicket stable states, as this may act as the tipping point (Staver et al. 2011a) triggering this state shift. This unstable intermediate state may be governed by the density of available adult *V. karroo* trees that are able to act as nucleating species and facilitate the establishment of thicket pioneers.

As the thicket clump formation increased there was an increase in canopy cover and density. The trees showed less plant biomass density at lower heights as encroachment increased. This was further demonstrated by the grass height findings. My hypothesis that increasing thicket clump formation results in a significant decline in total grass biomass was supported. Using remote sensing (LiDAR derived CHM and RGB imagery), I found that early stage thicket encroachment within an open canopy savanna showed the highest grass layer height. The intermediate stage of thicket clump formation showed a slightly reduced grass layer, while late stage thicket clump formation displayed the most reduced grass layer. This is supported through the literature as it is found that savannas are characteristically comprised of shade-intolerant grasses, which are often reduced with the increase in canopy cover and density associated with woody encroachment (Charles-Dominique et al., 2015; Parr et al., 2012; Khoza, 2021). It is important to note, that in areas where thicket clump formation had expanded, the grass layer was found to be decreased but not completely removed, however open savannas provided far greater grass layers.

The mean standing height of grass measured using the DPM was lower across all clusters than the mean heights obtained across clusters using LiDAR generated CHM. This was likely due to the difference in sampling time between LiDAR and field data collection, as the LiDAR was collected before the ground truthing was performed. Further, the weight that the disc pasture meter places on grass as it descends reduces the recorded height in the field, therefore LiDAR derived biomass is often inflated as compared to field-based measurements. Nevertheless, the same trend of decreasing grass layer is followed, and similar coefficients of determination occur for LiDAR and ground derived grass biomass measurements- with the greatest grass layer in Cluster 1, intermediate measurements in Cluster 2, and the lowest grass layer in Cluster 3.

In open savannas, mechanisms such as fire are useful in maintaining the balance between trees and grass layers (Bond and Parr, 2010; Ratnam et al., 2011; Staver et al., 2011; Murphy and Bowman, 2012; Parr et al., 2012). Due to this increase in canopy cover and the resulting decrease in the grass layer as thicket clump formation expands, the ability of fire to burn and open up vegetation becomes reduced. Archibald et al. (2009) found that across southern Africa, this tree cover threshold was 40 %, at which fires might no longer be able to spread, and canopy closure would proceed. In areas of intermediate stage thicket encroachment there were increases in canopy cover (mean of 48.46 %) to just over this threshold. It is therefore at a tipping point where the change between savanna and thicket becomes irreversible. In areas of closed canopy thicket where late stage thicket encroachment is present, it is unlikely that without the natural spread of fire, this stage of thicket clump formation will be able to shift back to an open savanna (Parr et al., 2012; Charles-Dominique et al., 2018).

I found that woody plant encroachment was affected by elevation, and at low elevations open, lower vegetation (early stage thicket encroachment) was present, and as elevation decreased vegetation becomes denser (late stage thicket encroachment). There was therefore a significant influence of elevation on the vegetation structure and stage of thicket clump formation which was present at this site. This supports my prediction that thicket encroachment is dominant at lower elevations, and that higher elevations are dominated by earlier stages of thicket encroachment, which, given the trends in thicket encroachment in this area, may gradually become encroached in the future (O'Connor and Crow, 1999). The thickest portions of woody vegetation, characteristic of late stage thicket clump formation, appeared to run along the steeper valleys in the topography at lower elevations. In contrast, savannas with the more open vegetation appeared to be primarily located along smoother topography and at higher elevations. Unlike the findings of Hottman and O’Connor (1999) who found that bush clumps began to develop, and that broad-leaf species dominated on moist south-facing slopes at higher elevations, I found that the thicket encroached areas (with thicket species dominating) were dominant at lower elevations. O'Connor and Crow (1999) indicated that valleys demonstrated more woody cover than slopes or uplands, and found that there was a similar increase in woody cover over all these levels of elevation, indicating that increasing encroachment was possible at higher elevations. This however corresponds with Bora et al. (2021) who determined that when the elevation was lower, there was a greater level of encroachment present than at higher elevation levels. In their findings they held that trees from the Fabaceae family, such as *V. karroo* in this study site, were able to encroach at a variety of elevations, which may make them important species starting this thicket encroachment process first at lower elevations, and moving up to higher elevations as thicket clump formation expands and encroachment increases in the study site. Intermediate stage thicket encroachment was found across areas of medium elevation. At these medium elevations, open savanna and closed canopy thicket were able to establish, as the influence of elevation is less extreme and does not limit the vegetation structure as greatly.

Smit (2005), Hare et al. (2021), and Mndela et al. (2022) studied how tree thinning influenced grass and herbaceous layer production in semi-arid African savannas and rangelands. These studies found that as trees were thinned and thus woody cover reduced, grass biomass and forage production increased. There is therefore potential to implement intervention strategies aimed at reducing canopy cover and increasing grass biomass, ensuring the ability of the system to shift between savanna and thicket states. The intermediate stage of thicket encroachment is the most commonly occurring throughout the study site. These areas act as a transitional zone between savanna and thicket displaying a combination of these characteristics. The canopy cover and density increased at the intermediate stage of thicket encroachment; however these sites still have the potential to be opened up through burning, as they may have not fully lost the grass layer required for fire spread (Archibald et al., 2009). This stage of thicket clump formation is extensive throughout the study area and occurs at a mid-range elevation, which would allow for either open savanna or thicket species to dominate. I therefore suggest that it may provide the best potential stage at which to implement intervention strategies for managing thicket encroachment to prevent irreversible state changes, however further research is needed to test this.

2.6 Conclusions

In this chapter, the study site was clustered based on vegetation structure, and these vegetation structural variables were used to map areas of varying stages of thicket expansion. I found that distinct stages of thicket clump formation were evident from open savanna to closed-canopy thicket. Three main stages of thicket clump formation emerged: open canopy savanna (early-stage thicket clump formation), encroached savanna with low thicket dominance (intermediate-stage thicket clump formation), and highly encroached with dominant thicket clumps (late-stage thicket clump formation). Each of these stages was found to be significantly distinct with unique vegetation structure, showing increased tree height, canopy cover and density as thicket clump formation expands. Ecological significant structural variables useful for identifying the overall stage of thicket clump formation were canopy cover, mean height, and canopy height density 3 (>2m). I showed that as thicket clump formation increased there was a reduction in the grass layer. Grass height was found to be the highest in savanna areas lowest for late stage thicket clump formation. I further found that elevation had a significant influence on the vegetation structure and the stage of thicket clump formation. At higher elevations, shorter and sparser vegetation was present, and as elevation decreased vegetation became denser. I recommend that intervention strategies are potentially targeted within areas of intermediate thicket clump formation to ensure the most successful outcomes, in terms of reducing tree density and maximising grass biomass.

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CHAPTER 3: SPATIAL PATTERN ANALYSIS OF THICKET CLUMP FORMATION IN A SEMI-ARID SAVANNA

3.1 Abstract

Thicket expansion is often initiated by a nucleating savanna species which facilitates the establishment of woody thicket pioneer species. As thicket clump formation increases, dense bush clumps form which may increase the strength of competitive effects as size and density of individuals increase. This study used spatial point pattern analyses to infer the interactions occurring among woody individuals in three increasing stages of thicket encroachment. I examined the effect of thicket clump formation on the species composition, the overall spatial distribution, and the associations of small thicket pioneer species with large individuals of *Vachellia karroo*, the dominant savanna tree species at the study site. I predicted that the open savanna would be characterised by random spatial patterns among woody individuals due to a combination of aggregation of small individuals and regular spacing of large individuals, and that the spatial patterns of intermediate and late stage thicket formation would show increasing aggregation as bush clump formation progresses. Further, I predicted that in the intermediate and late stages of thicket formation, medium and large individuals would display a positive spatial association with small thicket pioneers, due to facilitation, directed seed dispersal, environmental heterogeneity or a combination of these factors. At early stages of thicket clump formation, tree density was low and *V. karroo* was dominant. As thicket clump formation increased to intermediate and late stages, there was a shift towards a higher tree density and an increase in the proportion of thicket pioneer species. Spatial patterns indicated positive aggregations between all trees at small-scales in the early and late stages of thicket encroachment. Furthermore, in early stages of thicket encroachment, large *V. karroo* trees and small thicket pioneers showed no dominant associations, which I suggest arises as a result of a combination of attraction patterns caused by *V. karroo* facilitative effect and repulsion patterns caused by competition. In the intermediate and late thicket encroachment stages, independent arrangements were most common, but there was also evidence of slight repulsion at small spatial scale. I suggest that this is likely arising from competition. The expected positive facilitative interactions between small thicket pioneers and large *V. karroo* individuals may have been overpowered if interspecific competition was strong enough to result in density-dependent mortality of large *V. karroo* trees. To understand the competitive interactions between trees and their effects on tree-tree patterns and mortality further analyses may be useful.

Keywords: *spatial point pattern analysis, semi-arid savanna, facilitation, thicket encroachment*

3.2 Introduction

Savannas have ecological, social, and economic value for land users globally and in South Africa (Shackleton et al., 2002). Savannas are characterised by the co-dominance of two contrasting life forms; a continuous grass layer and discontinuous tree layer (Staver et al., 2011; Scholes and Archer, 1997). Woody plant encroachment, defined as the increase in tree density, is a widespread phenomenon, predicted to increase over time as atmospheric CO_2 levels rise, coupled with other land use practices such as fire suppression and overgrazing (O'Connor and Crow, 1999).

Two distinct woody thickening processes can be characterised; savanna thickening and thicket expansion (Parr et al., 2012). Savanna thickening is the cyclic increase of savanna species, such as *Vachellia karroo*, accompanied by a decrease in, but not complete exclusion of the grass layer (Parr et al., 2012). Thicket expansion, contrastingly, introduces a new set of thicket trees and other species, which display different physiological characteristics, and giving them different functional traits (Parr et al., 2012). Thicket vegetation is characterised by a higher proportion of broad-leaved trees, forming a closed canopy with a sparse understory, and a discontinuous grass layer (Charles-Dominique et al., 2015; Parr et al., 2012; Vlok et al., 2003). Unlike savanna species which are typically found under conditions of high fire frequency and high light availability (Bond and Parr, 2010; Ratnam et al., 2011), these thicket pioneer species are shade-tolerant and fire-intolerant (Parr et al., 2012). Once these thicket pioneer species have been established, they may increase the favourability of the environmental conditions towards other thicket pioneer species, resulting in the formation of bush clumps (O'Connor and Chamane et al., 2012; Hester et al., 2006), and eventual replacement of savanna by thicket or forest. Here, savanna and forest or thicket ecosystems may be considered alternate stable states which are maintained and reversed through feedback processes between tree canopy and fire (Staver et al., 2011; Parr et al., 2012).

Jamison-Daniels et al. (2021) studied the process of bush clump formation in a mesic South African savanna. They found that nucleating species may initiate woody encroachment and thus the later entry of new species, as also documented in the Brazilian Cerrado (Abreu et al., 2021). This causes a directional change toward forest-type species in larger and older bush clumps (Jamison-Daniels et al., 2021). Savanna trees such as *V. karroo* can establish in harsh conditions, including seasonal water stress and frost. However, Botha et al. (2020) studied the resprouting and survival of seedlings under conditions of fire and frost in a greenhouse experiment, and they found that fire and frost prevent the persistent establishment and survival of woody species, such as *Scutia myrtina* along grassland-forest boundaries. Savanna species such as *V. karroo* may therefore be able to play an important role as facilitators or nucleators, allowing thicket pioneer species to establish preferentially under their canopies (Abreu et al., 2021, Nell et al., 2024). In arid environments, nurse-plants such as these savanna species modify their surrounding environment and create regeneration opportunities for seedlings which would have otherwise been vulnerable to hostile conditions created by biotic and abiotic factors, such as temperature extremes, limited moisture, nutrient stress or herbivory (Adie and Yeaton, 2013; Bertness and Callaway, 1994). Interestingly, many of the nucleator species for thicket clump formation are also characterised as important woody encroachers (O'Connor and Chamane, 2012; Abreu et al., 2021; Jamison-Daniels et al., 2021).

Due to thicket pioneer species typically exhibiting broad leaves, they form closed and often deep canopies that can shade-out the ground cover and grasses, as light is not able to easily pass through their canopy (Parr et al., 2012). Thicket expansion and the development of bush clumps reduce fuel loads and prevent the ability of fires to spread (Charles-Dominique et al., 2018; Parr et al., 2012). This, together with the increased competition for resources may negatively impact the presence of savanna tree and grass species. Thicket expansion thus has the potential to cause a shift from open savannas to closed-canopy thickets (Skowno et al., 1999), which will have cascading consequences for savanna management and conservation (Parr et al., 2012).

While thicket clump formation from open savanna to closed canopy thicket has obvious temporal features, there is also a dynamic spatial element which requires understanding. Spatial pattern analyses provide a statistical description of the distribution of points, thus revealing patterns indicative of different processes over an area of interest (Sankey, 2017). When using spatial statistics, the position of a plant in a plot is represented by a point and the analysis of the spatial point pattern indicates whether the distribution of the points is random, clumped, or regular by comparing the distribution to an appropriate null model (Wiegand and Moloney, 2004). Positive associations between points may be described as "aggregated", "clustered", or "clumped" (Perry et al., 2002). Terms such as "negatively correlated", “uniform”, “regular”, and “even” refer to negative interactions between points (Perry et al., 2002).

Random or independent patterns of trees are usually expected to result from stochastic events, from a lack of dominant interactions, or a combination of processes such as limited seed dispersal and simultaneous competition (Hesselbarth et al., 2018; Wiegand and Moloney, 2014). Alternatively, random patterns may be viewed as reflecting intermediate stages between clustered and regular tree patterns (Hesselbarth et al., 2018). Moustakas et al. (2008) examined nearest tree neighbour distances and tree spatial formations of *Vachellia erioloba* over large time and spatial scales in the Kalahari. Their study showed a cyclical transition from clumped tree spacing to a more random and sequentially regular spacing. Their study found that regular, clumped, and random pattern may be present, depending on the time and location, and that periods of high mortality often display reduced small-scale clumping. This work was supported by Jeltsch (1999) who compared real tree patterns obtained from aerial photographs, with patterns produced from computer simulation experiment in the southern Kalahari, who predicted that this cycle in time from clumped to random to regular spacing existed. They found that tree patterns in the transitional phase from an open savanna to a savanna woodland could indicate the underlying process, and that at periods of increased tree numbers, clumping increased, whereas during periods of decreasing tree numbers random or even spacing may be more prevalent (Jeltsch et al., 1999). Random patterns of trees may be the result of randomly spaced regeneration sites where juvenile trees were able to establish (Caylor et al., 2003). The establishment of new, smaller individuals can also be reduced by environmental heterogeneity, disturbances such as fire, and shading from large trees with dense canopies (Muvengwi et al., 2018). Such environmental heterogeneity affecting trees spatial distributions may be caused by heterogeneity of soil conditions and patchy rainfall within arid and semi-arid savannas (Schleicher et al., 2011).

Spatial pattern analysis can be used to elucidate important ecological interactions such as facilitation and competition. Facilitation has been shown to be an important process dominating the early life stages of many species, with competition becoming more dominant in later stages as individuals grow in size and resource requirement (Ledo et al., 2014). Facilitative relationships have also been shown to be more common where conditions are high-stress according to the stress-gradient hypothesis (Maestre et al., 2009), and therefore may occur commonly within open savanna vegetation (Hesselbarth et al., 2018), and in the early stages of thicket-clump formation. Clustered tree patterns may be the result of limited seed dispersal, vegetative propagation or the landscape showing heterogeneous intensity as a result of certain area's favourability (Caylor et al., 2003; Meyer et al., 2008), however clustered vegetation patterns may also imply the occurrence of facilitation between large and small trees (Flores and Jurado, 2003). For example, while investigating the spatial patterns of encroaching *Vachellia* species after fire suppression within a semi-arid savanna, Muvengwi et al. (2018) found clustering existed at scales of 6 to 18.5 m, which may have resulted from nurse plants, as small trees showed an association with larger trees. Pillay and Ward (2012) used second-order spatial point-pattern analysis of *V. karroo* to help provide insights into the underlying processes which affected individual trees in a mesic savanna. Their study showed that juvenile trees were more spatially aggregated than expected by chance, as well as that the overall spatial distribution of trees was aggregated without any evidence of regularity in the large trees (Pillay and Ward, 2012). They suggest that these patterns are the result of relatively weak competitive interactions between *V. karroo,* which result in decreased performance (reduced canopy diameter) instead of tree mortality which would normally cause a regular pattern to emerge. While several empirical studies have focussed on the shift between savannas to forest, relatively less is known about the spatial pattern of thicket clump formation that may result in a biome shift from savanna to thicket (Aleman and Staver, 2018; Jamison-Daniels et al., 2021; Stevens et al., 2017). Interactions between open canopy savanna species and broad-leaved, closed canopy thicket pioneer species may result in considerable vegetation change over time, however little is known in this regard.

In the previous chapter, I identified three stages of thicket expansion characterised by increasing woody plant size and density, namely, early stage thicket formation, intermediate stage thicket formation, and late stage thicket formation. The aim of this chapter is to characterise the spatial patterns of savanna and thicket pioneer species in these different stages of encroachment from an open savanna to a closed-canopy thicket ecosystem. I used second-order spatial statistics to determine the overall pattern of trees, as well as to investigate the differences in the spatial structure of small trees in relation to large trees in different stages of thicket encroachment. I set out to test the following predictions:

1. I predicted that the open savanna would be characterised by random spatial patterns among woody individuals due to a combination of aggregation of small individuals as a result of facilitation and regular spacing of large individuals due to competition. I predicted that the spatial patterns of intermediate and late stage thicket formation would show increasing aggregation as bush clump formation progresses.

2. I predicted that in the intermediate and late stages of thicket formation, medium-sized and large individuals would display a positive (i.e. clustered) spatial association with small thicket pioneers, due to facilitation, directed seed dispersal, environmental heterogeneity or a combination of these factors.

3.3 Materials and methods

3.3.1 Study site and species

The study took place at Endwell Farm (32° 38' 26"S, 26° 22' 28.8"E), a semi-arid savanna, in the Eastern Cape, South Africa, receiving 730 mm MAP with wet summers and drier winters (Martens et.al., 1996). The farm is used mainly for commercial livestock farming, and cattle and game are kept in relatively low stocking rates. Acocks (1953) classify this area as False Thornveld of the Eastern Cape, and Mucina and Rutherford (2006) describe it as a mixture of Bedford Dry Grassland and Bisho Thornveld. *Vachellia karroo* was the dominant savanna tree species in this area, while thicket pioneers include species such as *Scutia myrtina, Gymnosporia buxifolia, Brachylaena elliptica, Grewia occidentalis, Olea europaea* subsp. *africana, Ziziphus mucronata, Ehretia rigida, Afrocanthium mundianum and, Searsia longispina. Vachellia karroo* can act as a nurse plant for these thicket pioneers, enabling thicket encroachment (O'connor and Chamane, 2012).

3.3.2 LiDAR and RGB image data collection

The LiDAR and RGB images were collected in collaboration with the Davies Lab from Harvard University, United States, on 26 March 2021. The Harvard Animal Landscape Observatory (HALO) system was mounted on an unmanned aerial vehicle, and was flown over the 525 ha site (Figure 3.1). The HALO system consists of a LiDAR sensor, an RGB camera, and a centralised data acquisition computer, which recorded and stored the data as well as the GPS location. Using this system I obtained high-resolution georeferenced RGB images as well as point clouds which were cleaned, normalized, and processed to form a 25 cm resolution canopy height model (CHM) by data scientists at the Davies Lab (Harvard University).

3.3.3 Plot selection

I randomly selected three 1-ha plots in each of the three distinct stages of thicket expansion identified in Chapter 2 (Figure 3.1). These stages represent (1) an open canopy savanna with early stage thicket encroachment; (2) an intermediate stage of thicket encroachment, the conversion from savanna to thicket with the start of thicket clump formation; and (3) late stage thicket encroachment forming closed canopy thicket clumps (Figure 3.2). A minimum of at least 70 individuals is recommended to be used for statistical robustness when conducting point pattern analyses (Wiegand and Moloney, 2014). Therefore, for this study plots of 1 ha were found to be appropriate for spatial point pattern analysis in a savanna system as well as in more-closed canopy environments such as is represented by late stage thicket encroachment. The 1-ha plot size is similar to other related studies in the literature such as in Yao et al. (2016); Nguyen et al. (2016); Petritan et al. (2015); Gupta and Pinno (2018); and Ziegler et al. (2017).

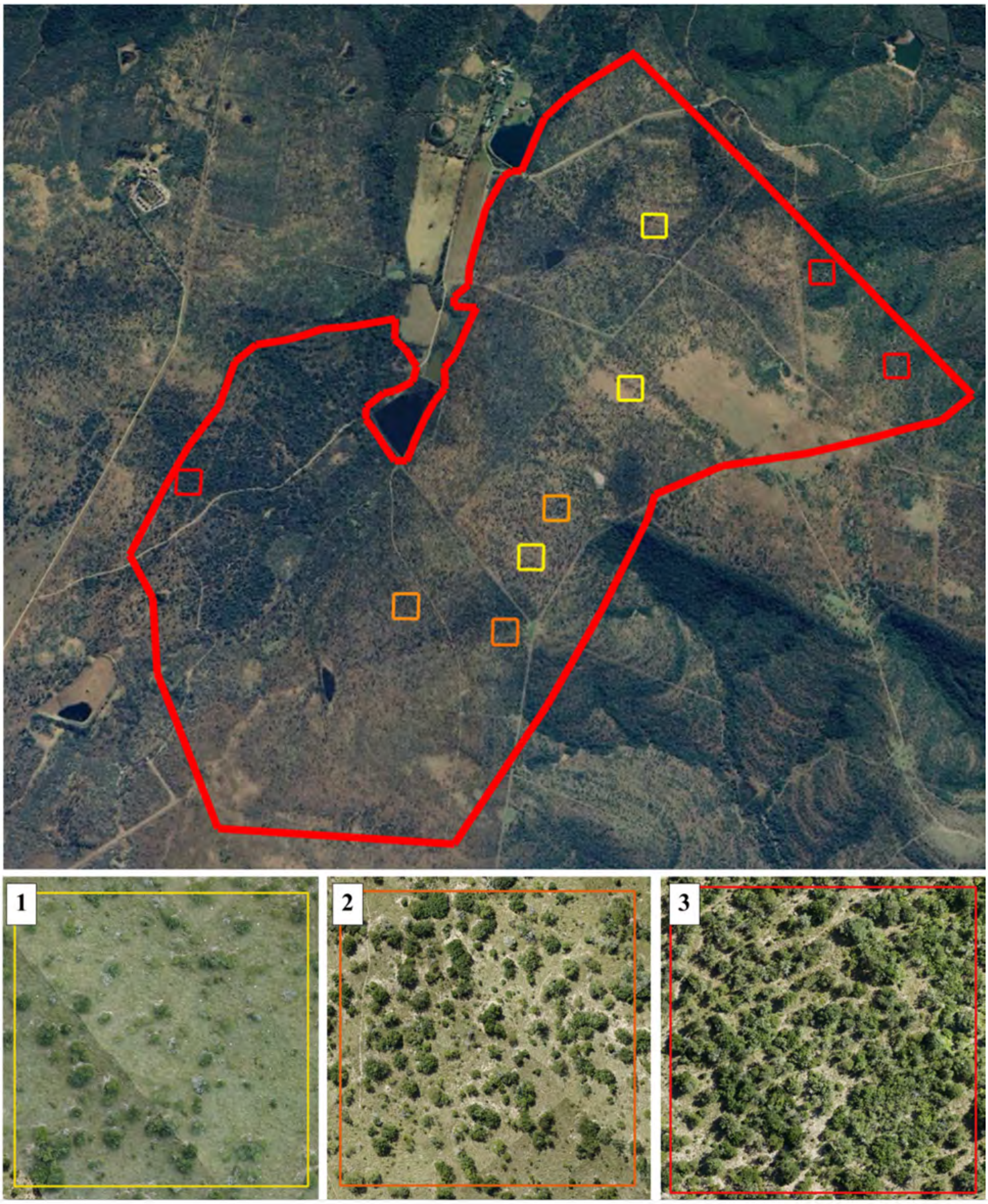

Figure 3. 1 Above: Study site showing the three 1 ha plots representing each of the three stages of thicket encroachment. Below: representative 1 ha plots demonstrating an aerial view of the typical vegetation within each of these stages. Stages of thicket encroachment: (1) early stage (yellow); (2) Intermediate stage (orange); and (3) Late stage (red).

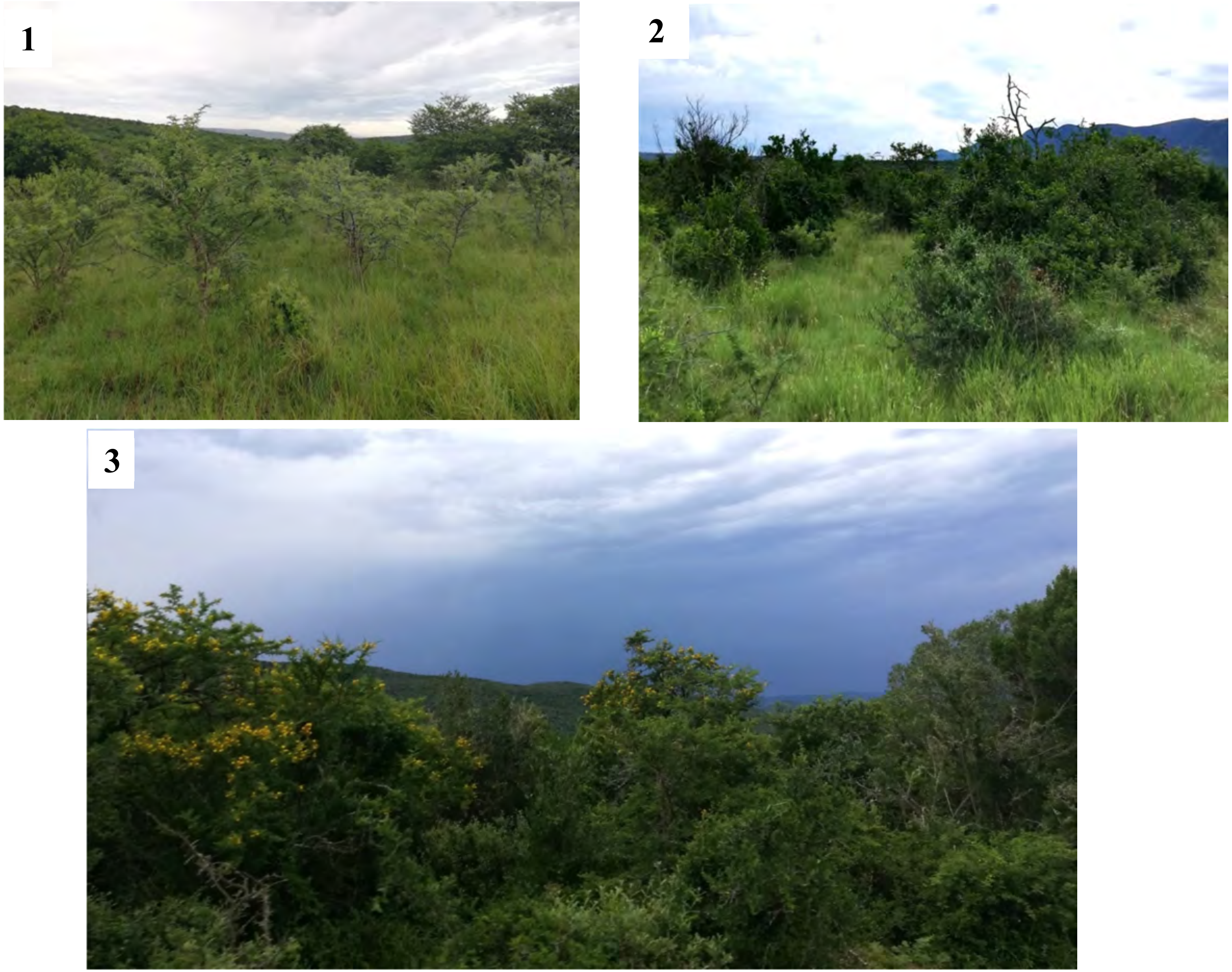

Figure 3.2 Vegetation structure of the three stages of thicket expansion in the study site: (1) open savanna with a continuous grass layer and scattered trees, (2) savanna-thicket transition with recruitment of thicket pioneer species close to large savanna trees, and (3) bush clumps with dominant thicket pioneer species and greatly reduced grass layer.

3.3.4 Tree identification and mapping of V. karroo and thicket pioneer species

For each plot, I manually identified every tree within each of the 1 ha plots using the RGB images as well as the Canopy Height Model (CHM) (Mayr et al., 2018; Ball et al., 2023; Popp and Kalwij, 2023). I decided to perform manual identifications due to challenges with the use of automatic tree segmentation tools given the combination of savanna vegetation with the dense thicket vegetation which often varies in structure and displays continuous tree cover, with multiple trees having overlapping and intermingled canopies. This led to the over- and under-segmentation of trees and false positives and negatives in the identification and delineation of trees. I created a point shapefile to represent each tree, with the point placed at the highest point of the canopy closest to the centre of the tree. I used the Geometry Tool in QGIS to determine and add the x and y coordinates to these tree points. I removed trees with a mean height of less than 0.2 m from the analysis (Hesselbarth et al., 2018; Petritan et al., 2015; and Ziegler et al., 2017). This was done to ensure accurate identifications were made, ensuring that grass and small shrub species were not inaccurately detected.

To identify different species, I created a point shapefile to overlay the pre-identified species of trees over the RGB images of the site.. I visually assessed each identified tree using the RGB images and I identified species based on the following trait variables: colour, branch spread, leaf size, openness of the canopy, and shape of the plant (Baldeck et al., 2014; Hastings et al., 2020; Norton et al., 2022). *Vachellia karroo* was the dominant savanna species in this area, and this plant was identifiable given the fine leaves and open canopies, however it proved difficult to visually distinguish and separate the broadleaf thicket pioneers into distinct species using the RGB imagery. Given the ecological similarity in the roles that these thicket pioneer species play in thicket encroachment and the development of thicket clumps, I grouped these woody thicket pioneer species together, referring to them as "thicket species". These thicket species included all thicket pioneers, though most frequently *S. myrtina,* followed by *G. buxifolia O. europaea* subsp. *africana,* and *Z. mucronata.* All tree identification and mapping was done using QGIS 3.22.3 (QGIS Development Team, 2022).

I used the Point Sampling Tool with the CHM (0.25 m resolution) to determine the height of each tree. This resolution gave a fine-scale representation of tree height, while reducing the chances of selecting a height within one of the canopy gaps (Guo et al., 2017; Hyyppa et al., 2001; Schardt et al., 2002). I used the height data to classify individual trees as "small" or "large". For *V. karroo*, I classified small individuals as being ≤ 2.5 m, while large individuals were > 2.5 m. I classified small thicket individuals as being ≤ 2 m and large individuals as > 2 m. I compared these height intervals to the tree canopy to test whether "small" and "large" based on height corresponded to the canopy size.

Tree species were identified in the field, their location was recorded, and key plant traits and features such as leaves and tree structure were recorded to aid in remotely sensed species identifications. From the tree identifications made remotely, a subsample of trees were selected and located within the study site using a handheld GPS device to allow for a comparison between trees on the ground and those remotely sensed across stages of encroachment. Refer to Appendix A1: Species identification: field and remote-sensed data validation technique for more information. The tree height was ground-truthed, with the highest point of each of these sub-sampled trees measured and recorded in field, and these heights were compared with those derived from the LiDAR-generated CHM for each of the tree points. Refer to Appendix A2 - Height measurement validation of tree size for further details on the ground truthing methods and results.

3.3.5 Data analysis

Testing the intensity (λ) of each plot using the L-function

Point patterns are usually influenced by two types of effect. First-order effects produce a variation in the intensity (λ) of point-pattern (the density) in response to some a causal variable such as environmental effects and is dependent on position, while second-order effects result from interactions or relationships between points (Wiegand and Moloney 2004; Wiegand and Moloney 2014; Velázquez et al., 2016; Ben-Said, 2021). Second-order analyses based on Ripley's K-function are frequently used in ecology to determine spatial patterns and help infer underlying processes, and detect first-order effects that result from the environment (Wiegand and Moloney, 2004; Wiegand and Moloney 2014). The widely used K-function is a cumulative version of the pair correlation function (Wiegand and Moloney, 2004).

I determined the intensity of each 1 ha plot in the study site using the L-function, a modified version of Ripley's K function, K(r), that applies a transformation which removes the scale dependence of K for independent patterns and stabilizes the variance (Ripley 1981; Pillay and Ward, 2012).

The estimation equation is:

$$L(r) = \frac{\sqrt{K(r)}}{\pi} - r$$

Where K(r) is Ripley's K function, and *r* is a given distance of an arbitrary point.

The L-function allows users to test whether patterns are homogeneous or heterogeneous (Wiegand and Moloney, 2004). For an unmarked Univariate analysis, Ripley's L function L(r) can be interpreted as: $K(r) = \pi r^2$; $L(r) = 0$ Points of the pattern are randomly distributed; $L(r) > 0$ Points of the pattern are aggregated; $L(r) < 0$ Points of the pattern are segregated (Ripley, 1977; Besag, 1977; Wiegand and Moloney, 2004; Ben-Said, 2021).

Homogeneous plots have the same statistical properties throughout the entire area observed, while in heterogeneous plots the intensity varies in space (Velázquez et al., 2016). Where areas are heterogeneous, first-order effects must be investigated before examining second-order effects, and appropriate null models must be selected to deal with those conditions (Wiegand and Moloney, 2004; Pillay and Ward, 2012). For plots with homogenous intensity (the pattern λ is constant in the plot), the most commonly used null model in ecology is that of complete spatial randomness (CSR), while under heterogeneous conditions, an alternate null model, the heterogeneous Poisson (HP) process, is employed (Pillay and Ward, 2012; Carrer et al. 2018; Ben-Said, 2021). A null model under antecedent conditions may be used where there is a hierarchy between two patterns (Pillay and Ward, 2012). In such cases, the antecedent pattern is fixed and the other pattern is randomized (Velázquez et al., 2016; Wiegand and Moloney, 2004). I used a null model under antecedent conditions when comparing large and small trees, keeping large individuals fixed and randomizing the small individuals.

In order to understand whether the data fits the null model or significantly deviates from it, it is compared to confidence envelopes (Wiegand and Moloney, 2004). In this study confidence envelopes were estimated using 1999 Monte-Carlo simulations of the point patterns under their relevant null models (Pillay and Ward, 2012; Schleicher et al., 2011). These simulations were run for points redistributed according to the chosen null model, and the summary statistic was then estimated. The same process was followed for points of the observed pattern, and I compared these patterns to discover whether the observed data occurred within or outside the usual range of the patterns created by the null model (Velázquez et al., 2016). Upper and lower confidence envelopes were estimated with the 5th lowest and 5th highest value for each distance r (Baddeley et al., 2014). If the observed summary statistic falls outside of the simulation envelope, it is taken as evidence of a departure from the null model hypothesis (Velázquez et al., 2016). To account for possible underestimation of type I error rate, a goodness-of-fit (GoF) test was used for each analyses within this study (Loosmore and Ford, 2006; Pillay and Ward, 2012).

Overall tree spatial patterns using the univariate pair-correlation function

To analyse the overall spatial patterns of all trees over each plot, I ran a univariate point pattern analysis (PPA) using the pair-correlation function (PCF), g(r), as the summary statistic (Stoyan and Stoyan, 1994). This is a second-order statistic which is closely related to Ripley's K-function (Ripley, 1977) (Carrer et al., 2018). In the PCF, the circles of Ripley's K-function are replaced by rings, giving the expected number of points at distance r from an arbitrary point, divided by the intensity of the pattern (Wiegand and Moloney, 2004). PCF have the advantage of being non-cumulative, and thus provide better quantification of the effects at specific spatial scales (Wiegand and Moloney, 2004; Perry et al., 2006; Velázquez et al., 2016).A null model of complete spatial randomness (CSR) was used for plots which displayed homogeneity, while in heterogeneous plots a heterogeneous Poisson (HP) process null model was employed. The 1999 Monte Carlo simulation envelopes were used to interpret the observed patterns. When values went outside of the confidence envelopes, the null model of CSR was rejected. When values were above the confidence envelopes, clustering or clumping was inferred, while values below the envelopes were inferred to indicate over-dispersion and a regular spacing (Carrer et al., 2018). Those values within the envelopes were accepted as fitting the null model of randomness.

Spatial relationships between large V. karroo trees and small thicket pioneers using bivariate pair-correlation function

I analysed spatial relationships between large *V. karroo* trees and small thicket pioneers by performing a bivariate PCF point pattern analysis. The null models used here were of CSR and HP for homogeneous and heterogeneous plots respectively. These null models were used along with antecedent conditions. The positions of the large individuals were kept fixed, while the location of the small trees was randomized. Values above the upper confidence envelope indicate significant association between large and small trees, while the values below the bottom confidence envelope indicate repulsion at that scale (Cordero et al., 2016; Pillay and Ward, 2012).

All analyses were performed in the grid-based software Programita 2014 (Wiegand and Moloney, 2004; Wiegand and Moloney, 2014) with a grid size of 1 m^2 and a ring width of 3 m. Hanisch Edge Correction was used to account for trees along the border of the plots (Wiegand and Moloney, 2014). I converted all coordinates to x-y Cartesian plane coordinates for each tree within each 1 ha plot for each stage of thicket encroachment; early stage, representing the open savanna, the intermediate stage, and the late stage with closed canopy thicket. The SPPAs were run for each plot (which results can be located in Appendix B), and the three replicates of each of the three stages were combined to show the overall patterns within each stage. Combining several smaller plots in one average function can provided an efficient strategy to detect small-scale spatial patterns, giving a more robust and stable view into the spatial patterns in that forest stand (Carrer et al. 2018; Ziegler et al. 2017; Erfanifard et al. 2019; Wang et al. 2020).

3.4 Results

3.4.1 Tree composition and density across the stages of thicket expansion

Early stage thicket encroachment had the lowest tree density of all the plots, while intermediate stage showed an increased tree density, however, as expected, late stage had the greatest tree density (Table 3.1). As expected in an open savanna under early stage encroachment, *V. karroo* was the most frequently occurring species, with small *V. karroo* individuals making up the greatest proportion (46 %) of trees in this stage (Figure 3.3). There was a similar proportion of savanna and thicket pioneer species in the late stages of thicket encroachment; *V. karroo* trees, made up 53.3% of trees, and 46.7 % of trees being thicket pioneer species (Figure 3.3). In intermediate stages of thicket encroachment, the greatest proportions of trees were large thicket pioneers, and small *V. karroo* individuals (each at 32 %). Species and age composition were the most equal within this stage. The mean tree height was the lowest out of all 3 stages, while trees in late stages of thicket encroachment were the tallest out of all three stages; with a mean height of 2.89 m ± 0.27. Results on the intensity of plots showed homogeneity across all plots in early, intermediate and late stage thicket encroachment, apart from one plot, plot 445 in the intermediate stage, which was heterogeneous (as shown in Appendix B, Section1).

Table 3.1 Tree composition and height classification for the three stages of thicket encroachment from open savanna to closed canopy thicket. Values are means ± SD.

	Early stage	**Intermediate stage**	**Late stage thicket encroachment**
Mean tree density (ha^{-1})	212 ± 120	466 ± 217	692 ± 40
Mean tree height (m)	2.4 ± 0.14	2.33 ± 0.2	2.89 ± 0.27
Quantile 1 height (m)	1.52	1.53	1.98
Quantile 2 height (m)	2.27	2.36	2.96
Quantile 3 height (m)	3.29	3.05	3.78
% of *V. karroo* trees	73.3	53.3	46.3
% of thicket trees	26.7	46.7	53.7

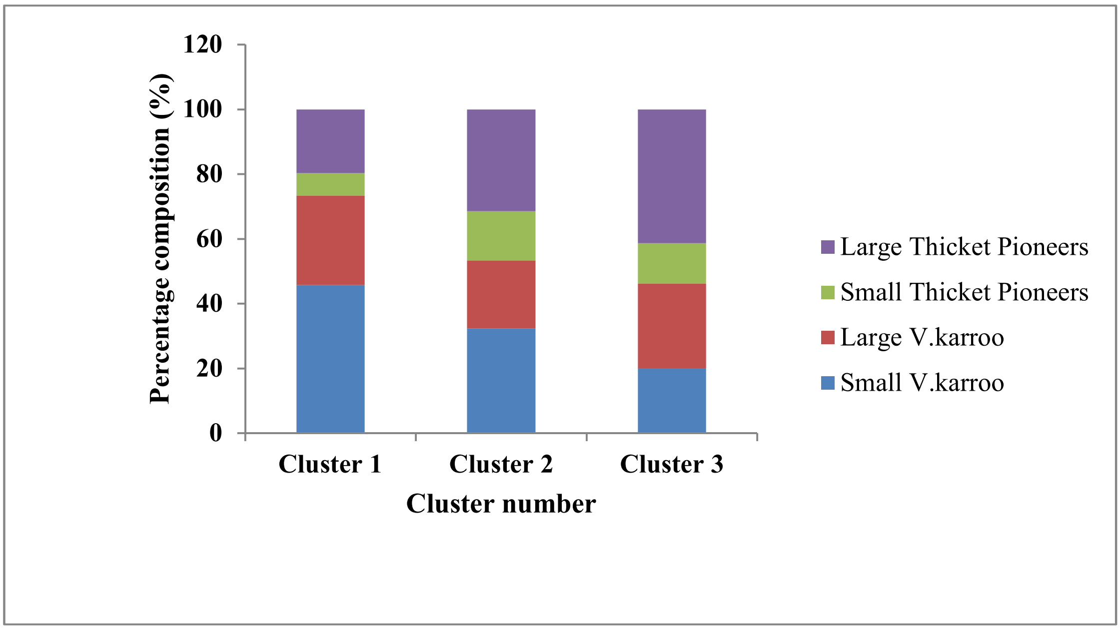

Figure 3.3 Large and small tree percentage composition of *V. karroo* and thicket pioneer species across early (Cluster 1), intermediate (Cluster 2) and late (Cluster 3) stages of thicket encroachment.

3.4.2 Overall pattern of dispersion of trees across three stages

At very small spatial scales (≤ 1 m) Univariate SPPA showed that all stages of thicket encroachment displayed negative associations between trees, with dominant regular spacing evident (GoF test, $p < 0.005$, Figure 3.4). After this regular pattern, there was a transition to random and then aggregated spatial patterns across all stages. Random arrangements such as these are often transitionary between these negative and positive associations. For the open savanna, I found that there was a dominance of positive associations with aggregation between all trees at small to medium-scales (GoF test, $p < 0.005$, Figure 3.4.1). As predicted for early stage thicket encroachment, this aggregation was followed by a random spatial distribution of trees at medium-scales (GoF test, $p = 0.16$, Figure 3.4.1). At the intermediate stage thicket encroachment there was a dominant random pattern of all trees (GoF test, p < 0. 0.15, Figure 3.4.2). As expected in this late stage of thicket clumps encroachment with increased thicket clump formation, there was a positive departure from the null model of CSR, indicating clustering (GoF test, $p < 0.005$, Figure 3.4). There was random spatial arrangements of trees at medium-scales (GoF test, $p = 0.145$, Figure 3.4), followed by regularly spaced trees at medium to large spatial scales (GoF test, $p < 0.005$, Figure 3.4). Regular patterns were the most dominant in late stage thicket encroachment.

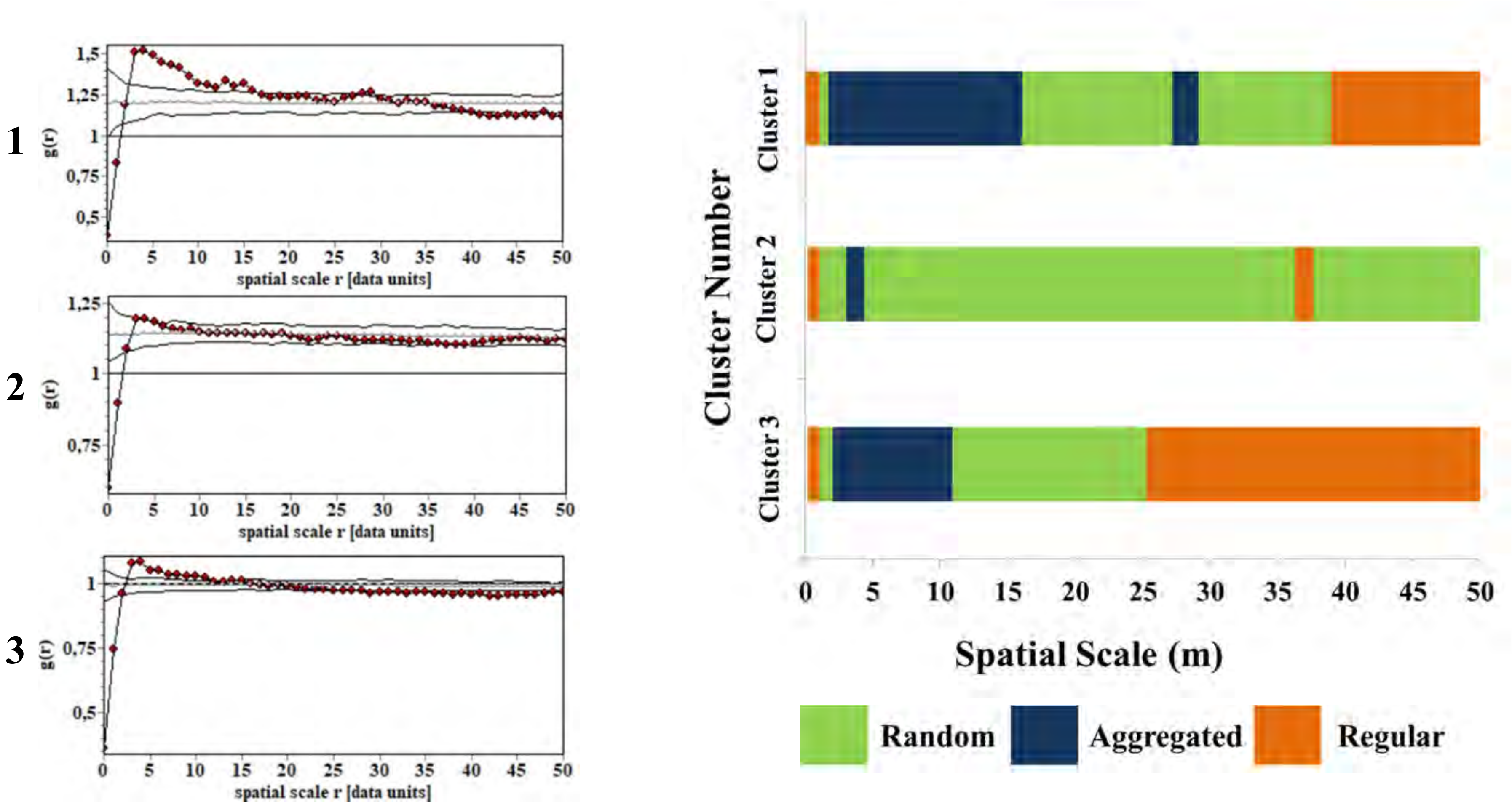

Figure 3.4 Univariate Pair Correlation Functions g(r): Spatial Point Pattern Analysis for all trees (thicket pioneers and *V. karroo* at all sizes) at early (Cluster 1), intermediate (Cluster 2) and late (Cluster 3) stage thicket encroachment. Simulation envelopes of 95% were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of CSR.

3.4.3 Patterns of small thicket pioneers in relation to large V. karroo individuals

A Bivariate PCF showed that within all stages of thicket encroachment, there was repulsion between large *V. karroo* and small thicket pioneers at small spatial scales (Figure 3.5). This repulsion spanned a greater spatial scale in late stage of thicket expansion, and was the most prominent in the intermediate stages, with dominant negative associations between small thicket pioneers and large *V. karroo* at distances of 0 to 8 m (GoF test, $p < 0.005$) (Figure 3.5). In early stage thicket encroachment, the trees appear to follow the null model of randomness, showing independence between small thicket pioneers in relation to large *V. karroo* trees (GoF test, $p = 0.24$). In intermediate stage thicket encroachment following the small-scale repulsion, there were random patterns between large *V. karroo* and small thicket pioneers at medium-scales showing a lack of dominant processes (GoF test, $p = 0.55$). At larger scales, patterns are less clear, with alternations between independence and attraction of small thicket pioneers and large *V. karroo* trees. In the late stage thicket encroachment, after the repulsion, there was independence between large *V. karroo* and small thicket pioneers from 6 to 50 m (GoF test, $p = 0.775$), and here they followed the null model of CSR, with small thicket pioneers occurring randomly in relation to large *V. karroo* trees.

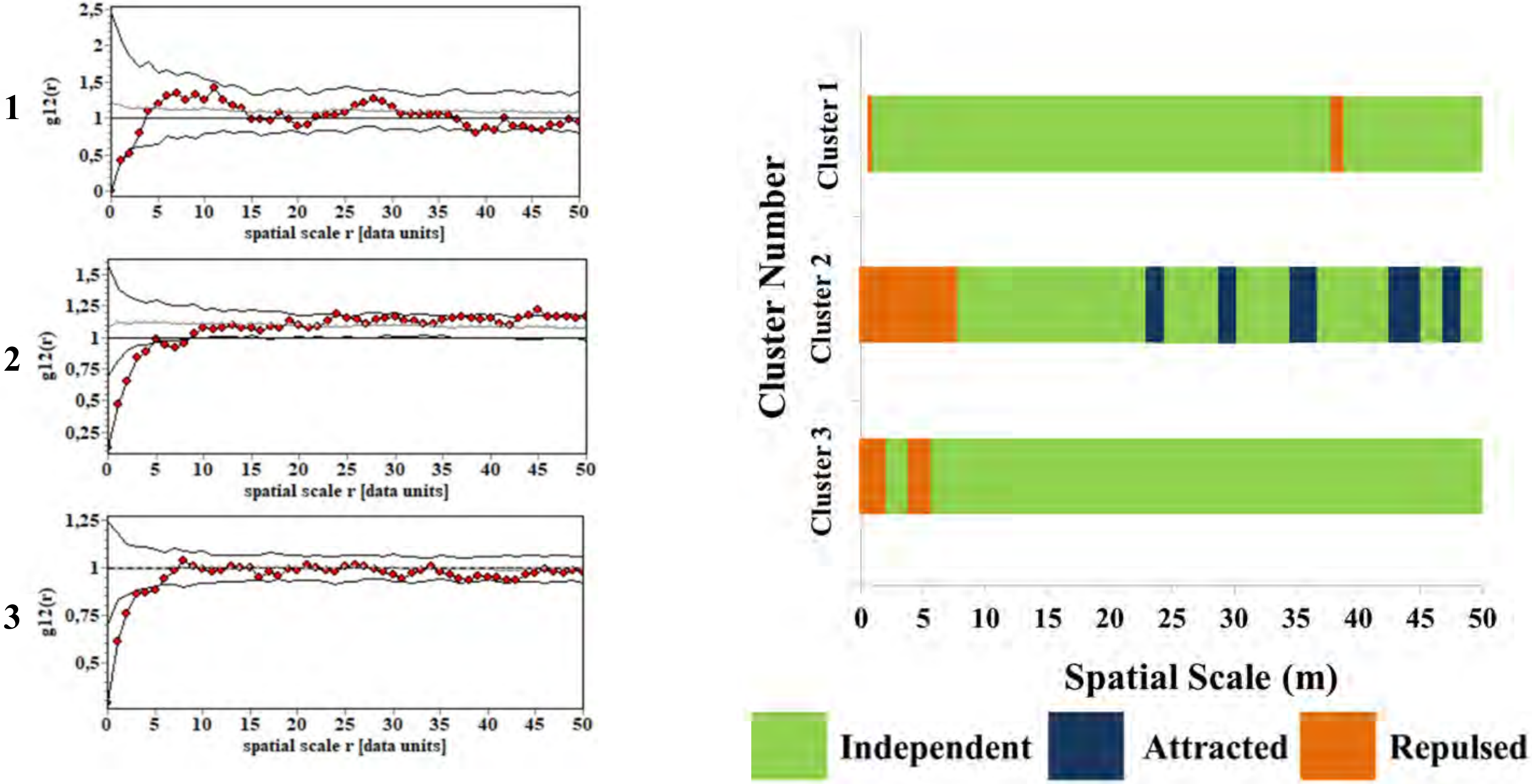

Figure 3.5 Bivariate Pair Correlation Functions g(r): Spatial Point Pattern Analysis for Large *Vachellia karroo* trees and small thicket pioneers across early (Cluster 1), intermediate (Cluster 2) and late (Cluster 3) stage thicket encroachment. Simulation envelopes of 95% were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of CSR.

3.5 Discussion

3.5.1 Tree composition and density across the stages of thicket expansion

The results of this study suggest a simultaneous savanna thickening and thicket expansion within this semi-arid savanna with evidence of a shift from savanna to thicket dominance. This follows the trend of increases in woody density and encroachment highlighted by O'Connor and Crow (1999), who used aerial photographs taken between 1937 and 1986 to show that canopy cover had expanded over time within the Eastern Cape. More recently Khoza (2021) used historical aerial photography over Endwell Farm to confirm that this increase in canopy cover continued into the 20th century. Parr et al. (2012) explain that increases in canopy cover may be the result of savanna thickening, which involves the increase in savanna species and maintenance of the grass layer, or alternatively, the result of thicket expansion, where broad leaf species increase and exclude the grass layer. Khoza (2021) suggest that the savanna thickening or thicket expansion can be distinguished through tree composition and herbaceous layer analysis. This study found an increase in the dominance of thicket pioneer species when studying the tree composition at late stage thicket encroachment, and in Chapter 2, grass layers were found to decrease as the stage of encroachment increased. I therefore suggest that while savanna thickening takes place, there is also evidence for thicket expansion.

As *V. karroo* trees increase in density through savanna thickening, this process is likely aiding thicket encroachment within this area, given the facilitative nature of *V. karroo*. Nucleating species may initiate woody encroachment and thus the later entry of new thicket pioneer species into bush clumps (Jamison-Daniels et al., 2021). Nucleating species can act as perch sites favouring bird dispersed species, and act as nurse trees aiding in the facilitation and establishment of forest-adapted tree species (Abreu et al., 2021). Within a savanna in the Eastern Cape, *V. karroo* have been found to act as the key species around which nucleation and bush clump formation occurr (O'Connor and Chamane, 2012). Once these thicket pioneer species have been established, they may increase the favourability of the environmental conditions towards other thicket species, resulting in the formation of bush clumps (O'connor and Chamane et al., 2012; Hester et al., 2006). These findings are supported by Nell et al. (2024) used association rules analysis to reconstruct thicket clumps and investigate the relationships between savanna (*V. karroo*) and thicket species along a gradient of increasing thicket encroachment at this same study site (Endwell Farm). They found association patterns following a successional sequence from open savanna to closed canopy thicket, with *V. karroo* providing nucleation sites for thicket species which led to thicket clump initiation and the establishment of a variety of species within these clumps.

3.5.2 Overall pattern of dispersion of trees across three stages

This study provides evidence of differing spatial arrangement, and varying ecological tree-tree interactions between trees as thicket encroachment and clump formation increases in semi-arid savanna. Hypothesis 1, which stated that the open savanna would be characterised by a combination of aggregation of small individuals and regular spacing of large individuals resulting in random spatial patterns among woody individuals and that the spatial patterns of intermediate and late stage thicket formation would show increasing aggregation as bush clump formation progresses was only partially supported by the data. Within the early stage thicket encroachment, trees showed aggregation with one another at small to medium distances, however at larger distances, simultaneous negative interactions may have increased, causing the predicted random pattern to become evident. Instead of the predicted increase in aggregation at intermediate stage, random patterns were most pronounced, while in late stages the distances of clustering decreased, with aggregation most pronounced in the early stage encroachment.

Within an open savanna (early stage thicket encroachment) I found that the overall spatial patterns within an open savanna displayed an aggregated relationship between trees at small to medium distance, and random patterns at larger distances. This aggregation is likely due to the dominance of *V. karroo* in open savannas under early stage thicket encroachment, as this is a nucleating species which can result in the formation of bush clumps where trees are aggregated (Skowno et al., 1999; O'Connor and Chamane, 2012). Open savannas may provide harsh conditions, thus facilitative relationships are expected here according to stress-gradient hypothesis (Maestre et al., 2009; Abreu et al., 2021). These positive associations between trees at small-scales are possibly also likely enhanced by the weaker competitive interactions between *V. karroo* in an open savanna, which may prevent regular patterns from dominating (Pillay and Ward, 2012).

At larger scales the trees became randomly spaced in open savanna (early stage). It is possible that this may be the result of stochastic events, from a lack of dominant processes or a combination of processes such as limited seed dispersal and simultaneous competition (Hesselbarth et al., 2018; Wiegand and Moloney, 2014). I suggest, however, that it is more likely that tree-tree interactions are often the dominant forces shaping the community at small spatial scales, however at medium to larger spatial scales other factors such as fire and herbivory may be of greater importance (Pillay and Ward, 2012).

I predicted that in stages of intermediate stage thicket encroachment, trees would be strongly aggregated as thicket clump formation expands. My findings, however, suggest that within this intermediate stage thicket encroachment random patterns between trees were most evident. I suggest that these random patterns may be viewed as intermediate stages between aggregated and regular tree patterns, which may result from the combination of opposing interactions such as facilitation of small individuals by *V. karroo* and competition resulting from the dominance of the large thicket pioneers (Hesselbarth et al., 2018; Wiegand and Moloney, 2014). At this stage *V. karroo* trees and thicket pioneers each make up around half of the species composition. Nell et al. (2024) found that *V. karroo*, are able to recruit individually, and can be involved in many types of associations, while thicket species such as *Scutia myrtina* recruited primarily in close association with *V. karroo*. I therefore suggest that this lack of one dominant pattern of aggregation or regularity may be the result of the different spatial associations between the species at this site. This result strongly supports the idea that the intermediate stage of thicket encroachment is a transition zone, where multiple ecological factors and climatic/ environmental heterogeneity may influence the outcomes of tree-tree interactions. I suggest that at the intermediate stage of thicket encroachment, this unstable state between savanna and thicket is maintained in part by the density of *V. karroo* the dominant savanna nucleating species. The presence of fire may also impact the thresholds being crossed as outlined in the literature (Hoffmann et al., 2009; Dantas et al., 2016; Beckett et al., 2022), however fire is not used as a management tool on this site, and therefore the impacts of fire are reduced within this system.

This study found overall tree aggregation existed at small-scales within late stage thicket encroachment. This late-stage thicket encroachment has undergone thicket clump formation processes and is characterised by a closed canopy with a sparse understory, and a discontinuous layer of grasses (Charles-Dominique et al., 2015; Parr et al., 2012; Vlok et al., 2003). Here, under the facilitative influence of *V. karroo*, thicket clumps are suggested to have formed, causing an aggregation of trees at smaller spatial scales. This is supported by O'Connor and Chamane (2012) who describe bush clump succession in the Eastern Cape, with thicket pioneers establishing under the canopies of savanna species such as *V. karroo*. Jamison-Daniels et al. (2021) further describe this facilitative process of bush clump formation with thicket pioneer species establishing within savannas. This aggregation is followed by a pattern of random distribution as the trees transition between the small-scale positive associations (aggregated) and large-scale negative associations (regular) (Hesselbarth et al., 2018). This study then confirms that bush encroachment in this semi-arid savanna site is a combination of savanna encroachment by species such as *V. karroo* as well as thicket expansion with the formation of bush clumps.

3.5.3 Patterns of small thicket pioneers in relation to large V. karroo individuals

Hypothesis 2 stated that in the intermediate and late stages of thicket formation, medium-sized and large individuals would display a positive (i.e. clustered) spatial association with small thicket pioneers, due to facilitation, directed seed dispersal, environmental heterogeneity or a combination of these factors, and this was not supported by the data. There was very little evidence of any prominent attraction at any stages of encroachment. Small-scale repulsion was present at these increased stages of thicket encroachment, and this shifted to a more a more pronounced independent spatial distribution of dead *V. karroo* and living thicket pioneers.

The findings of this study suggest that within the early stages of thicket encroachment, large *V. karroo* and small thicket pioneers displayed independent arrangements. This is supported by Nell et al. (2024) who indicated that at this study site, *V. karroo,* the tree I found to be dominant in open savannas (73 % of species composition), engaged in multiple types of associations and was able to grow without associations.

Thicket clump formation is often initiated by a nucleating species, which facilitates the establishment of new species, causing a change toward forest- or thicket-type species in bush clumps (O’Connor and Chamane, 2012; Abreu et al., 2021; .Jamison-Daniels et al., 2021). I therefore predicted that in the encroached savanna (intermediate and late stage), large *V. karroo* trees would display a positive spatial association with small thicket pioneers, either due to facilitation, directed seed dispersal or environmental heterogeneity. The *V. karroo* trees are documented as nurse-plants aiding in thicket encroachment (Skowno et al., 1999; O’Connor and Chamane, 2012, Nell et al., 2024). In this area, Nell et al. (2024) found that there were associations between *V. karroo* and thicket species, with thicket species showing preferential recruitment under *V. karroo*. This however was not supported by my study, as small-scale repulsion, and larger scale independence was found between large *V. karroo* and thicket species at these increased stages of thicket encroachment. This presence of repulsion and lack of evidence for facilitation in areas of thicket encroachment (intermediate and late stage) was unexpected. This may be the result of competitive interactions, which may be strong enough at small-scales to be evident, however which may weaken as distance increases, causing reduced (Pillay and Ward, 2012). I suggest that this facilitative association caused by *V. karroo* results in a pattern of aggregation, while competitive effects forming from increased encroachment cause negative associations, and independent patterns. These two patterns act simultaneously and may combine to display a random pattern of independence, which may prevent either of the associations taking place from dominating the spatial distribution of trees (Wiegand and Moloney, 2014).

However, it is possible that the stages of thicket encroachment are related to specific species, and since this study grouped the thicket pioneers into a single group for analysis, these patterns were undetected. For example, *Scutia myrtina* is a common thicket pioneer species which is noted to germinate under the canopy of large savanna trees. For this study, due to similar colour, leaf structure and architecture, segmentation and identification of thicket pioneers was not possible with the spatial data. More studies are needed to create RGB reference values for these key thicket pioneers in future.

3.6 Conclusions

This study used spatial point pattern analyses to examine the patterns and spatial arrangements of vegetation which can be used to infer the underlying processes and interactions occurring within three increasing stages of thicket clump formation. My findings suggest that *V. karroo* (savanna species) were dominant at all size classes at early stages of thicket clump formation however within later stages of thicket clump formation tree density increased and thicket pioneer species became more dominant. My findings show that overall there was evidence for facilitation within areas of early and late stage encroachment, which supports the idea that *V. karroo* acts as a nucleator for thicket clump formation. Large *V. karroo* trees and small thicket pioneers showed predominantly independent arrangements across all stages of thicket clump formation, likely as a result of a combination of facilitative and competitive effects, but also due to non-species specific identification of thicket pioneer species in the dataset.

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CHAPTER 4: INFERRING COMPETITIVE INTERACTIONS USING SPATIAL PATTERN ANALYSIS OF *VACHELIA KARROO* MORTALITY

4.1 Abstract

Tree mortality is an important determinant of savanna composition and structure. Mortality due to prolonged drought may be amplified by intense neighbourhood competition, such as that of dense, closed canopy thicket clumps formed during the expansion of thickets into savannas. Consequently, varying ecological interactions may result in differing spatial patterning of tree mortality. In this study I used point pattern analysis and second-order statistics to characterise the patterns of *Vachellia karroo* mortality in increasing stages of thicket encroachment: early stage (open savanna); intermediate stage (low thicket dominance); and late stage (dominant thicket clumps). I found that *V. karroo* mortality increased in density as thicket clump formation increased due to intense neighbour competition. In open savanna (early stage thicket encroachment), random mortality was evident, however, as thicket encroachment increases, competition-induced mortality combined with density-dependent mortality increases the competitive pressure on nucleating savanna species, causing dominant independent spatial arrangements. My findings suggest that dead *V. karroo* trees were taller than expected when they were located close to large living individuals in the open savanna canopy with earlier stages of thicket encroachment, indicating mutual stimulation and possibly previous facilitative relationships from the influence on *V. karroo*. As thicket encroachment progressed, dead *V. karroo* trees showed an absence of correlation with large living individuals, indicating possible effects of decreased tree performance from competition or tree canopy dieback resulting from an earlier drought. Overall, these findings support the idea that tree-tree interactions switch from facilitative to competitive as thicket encroachment progresses, and that tree mortality under drought conditions is more pronounced in high density stands. The implication for management is that tree mortality, while prevalent, may not be used as an effective form of bush control, especially if crown dieback is more prevalent than mortality.

Keywords: *tree mortality, competition, thicket encroachment, savanna, density-dependent mortality*

4.2 Introduction

Tree mortality is a fundamental process in ecosystem dynamics, as it shapes successional trajectories which influence the surrounding stand structure and species compositions (Petritan et al., 2014). Tree mortality may result from density-dependent processes, such as inter or intra-specific competition (Healy et al., 2008; Getzin et al., 2008b) or agent-driven mortality which can be caused by several factors such as resource availability and droughts (Gessler et al., 2017; Case et al., 2019; Swemmer, 2020), as well as the local neighbourhood conditions (Jeltsch et al., 1996; Wiegand et al., 2006). Tree mortality is generally higher when neighbours are denser or closer (Adie and Yeaton, 2013), such as the conditions created when thicket species form clumps. This phenomenon is known as competitive density-dependent mortality, commonly recognised as a major mechanism of species coexistence and community assembly (Volkov et al., 2005). Density dependence may modify and exacerbate non-competitive modes of mortality. For example, Fensham et al. (2009) studied drought-induced tree death in Australian savannas, and found that drought-induced mortality was more likely as the woody component of savanna increased, that is, when neighbourhood competition was more intense. Similarly, Dwyer et al. (2010) analysed the effects of neighbourhoods on drought-induced mortality of savanna trees in Australia and found that both limited plant available resources, as well as negative density-dependent effects predispose plants to drought-induced deaths. This demonstrates that the effects of agent-based mortality (such as drought) are increased by competition present under high tree density.

In semi-arid savannas, woody plant density may be increasing via two distinct processes; savanna thickening and thicket clump formation (Parr et al., 2012). In Chapters 2 and 3 I highlight the increasing presence of savanna thickening and thicket clump formation within the site used for this study, which shows a gradient of thicket encroachment with vegetation becoming more dense, and species composition changing from savanna to thicket pioneer species dominated, and eventually forming closed canopy thickets, with reduced grass layers. In this process of thicket expansion, savanna species, *V. karroo,* may act as nurse plants, enabling the facilitation of new species (Abreu et al., 2021). These trees have been found to enable the facilitation and establishment of thicket pioneer species and eventually cause the formation of closed-canopy thicket clumps (Jamison-Daniels et al., 2021). Savanna species, specifically *V. karroo*, are put under increased competitive pressure by these previously facilitated thicket pioneer species, which may lead to increased mortality of the savanna nurse plants (Petritan et al., 2014). Because of the key functional roles played by savanna trees, any ecological mechanisms resulting in significant mortality is an important determinant of community composition in these systems. Widespread tree mortality because of a changing climate, in conjunction with intense neighbourhood competition via thicket expansion may therefore have significant effects on the structure and function of savannas. This is particularly relevant for this study site, which experienced a severe and prolonged drought during 2016 -2018 (Swemmer 2020).

Tree-tree interactions, and specifically competitive interactions, can thus significantly affect the spatial distribution of tree mortality. Spatial point pattern analysis is a useful tool to elucidate the underlying ecological mechanisms (Shackleton, 2002; Getzin et al., 2006) and to describe the underlying ecological processes which may explain observed patterns of tree mortality. In general, open canopy savannas may display random or regular spatial patterns of mortality. Random patterns may be a result of resource heterogeneity or agent-based mortality due to age, disease or disturbance. Regular patterns can be attributed to a competitive-based mortality such as self-thinning over time which may occur in open savanna (Kenkel 1988; Wiegand and Moloney 2004). However, in late-stage thicket encroachment one may expect an aggregated pattern of dead trees due to the combined effects of agent-based mortality, amplified by intense neighbourhood competition resulting in aggregation of dead trees.

The aim of this study is to characterise the spatial patterns of *V. karroo* mortality of all size classes in a semi-arid savanna of South Africa using LiDAR-derived spatial point pattern analysis (SPPA). I used second-order spatial statistics to determine the pattern of mortality of *V. karroo* trees from open savanna at early stage thicket encroachment to closed canopy thicket, representing three progressive stages of thicket expansion into savanna. I set out to test the following hypotheses:

(1) With increasing thicket density, *V. karroo* mortality (via exacerbated effects of agent-based mortality and intense neighbour competition) would be increased. This would be evident as a higher density of dead *V. karroo* individuals in the later stages of thicket encroachment.

(2) The spatial pattern of dead *V. karroo* trees will be regular or random in early stages of thicket encroachment, representing mortality via senescence or environmental heterogeneity

respectively, typical of open canopy savanna dynamics. Conversely I predicted that in late stage thicket encroachment, *V. karroo* trees would display a clustered spatial pattern of mortality as a result of intense neighbourhood competition due to the formation of closed canopy thicket clumps in this stage of thicket encroachment.

(3) The relationship between living and dead trees under increasing stages of thicket encroachment was investigated. I predicted that tree competition-induced mortality would be evident (attraction between dead and living trees) in high competition thicket clumps under late stages of thicket encroachment, while evidence of segregation would be found between dead and living trees in open savanna with early stages of thicket encroachment.

(4) Lastly, the spatial distribution of dead and alive trees in relation to height was examined. I hypothesized that dead *V. karroo* trees would be shorter than expected when they were located close to large living individuals in late stage thicket encroachment within the closed canopy thicket clumps, and taller than expected when they were located close to large living individuals in the open savanna canopy with earlier stages of thicket encroachment.

4.3 Materials and methods

4.3.1 Study site and species

This study took place on Endwell farm (32° 38' 26"S, 26° 22' 28.8"E), between Somerset East and Fort Beaufort, in the Eastern Cape province of South Africa. This site is a semi-arid savanna with a mean annual precipitation of 730 mm (primarily summer rainfall) (Martens et.al., 1996) described as a mixture of Bedford Dry Grassland and Bisho Thornveld (Mucina and Rutherford, 2006), as well as False Thornveld of the Eastern Cape (Acocks, 1953). The focus species for this study is *Vachellia karroo,* a savanna species, which is dominant throughout the area, together with thicket pioneers, including species such as *Scutia myrtina, Gymnosporia buxifolia, Olea europaea ssp africana, and Ziziphus mucronata,* among others. Fires and bush control methods are not used as management tools on this farm, and browsing and grazing are kept minimal as a result of the lower stocking rates (cattle, sheep, goats, and game).

Plot selection

In this study I used 1 ha plots identified in Chapter 2 to represent early, intermediate and late stage thicket encroachment. I combined six neighbouring 1 ha plots (as identified in Chapter 2) which had the same stage of encroachment into one larger 6 ha plot (200 m x 300 m) for each stage of thicket encroachment (Figure 4.1). These 1 ha plots were combined to increase the statistical robustness of the spatial point pattern analyses, similar to work done by Hesselbarth et al. (2018) who performed a point pattern analysis of woody plants in a semi-arid and a mesic savanna in South Africa, using plot dimensions dependent on the density and distribution of trees, in accordance with the 70 individual requirement of spatial point pattern analysis as described by Wiegand and Moloney (2014). In this study, the three 6 ha plots included 363 dead *V. karroo* trees in the early stage 1, 425 dead trees in the intermediate stage, and 498 dead trees in the late stage thicket encroachment, therefore providing a sufficient number of individuals for analyses according to the literature (Getzin et al., 2008a; Hesselbarthet al., 2018; Carrer et al., 2018; Ribeiro et al., 2021).

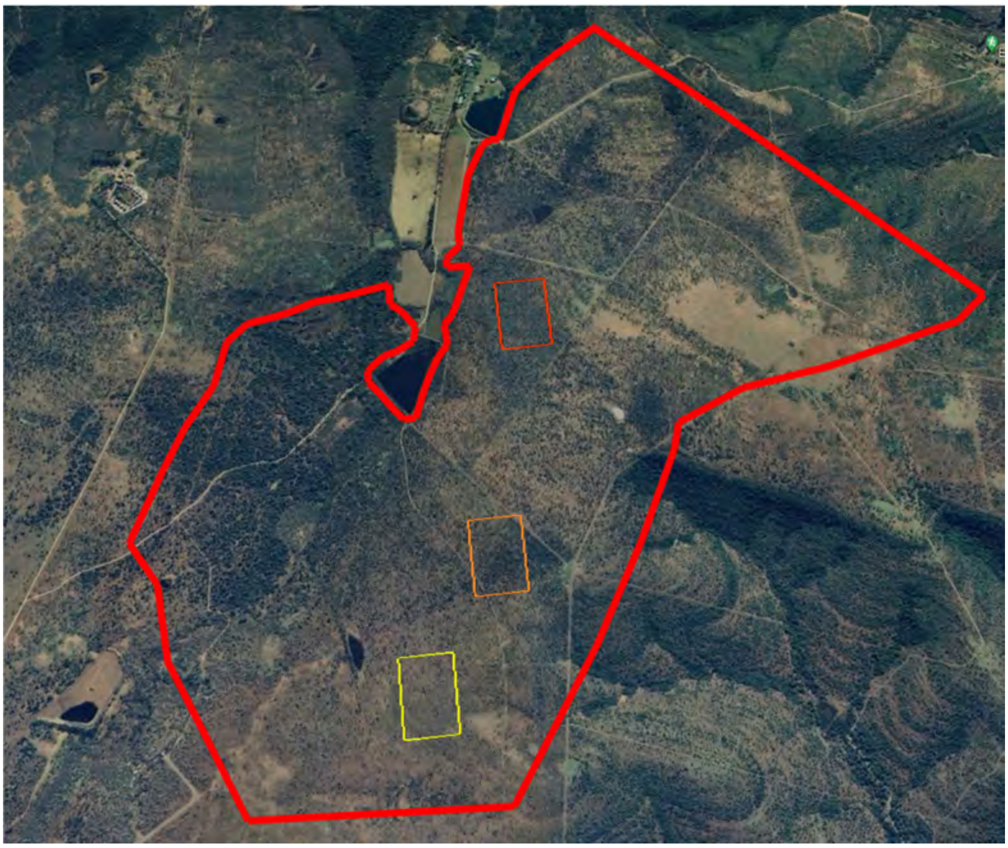

Figure 4. 1 The three 6 ha plots over the study site at Endwell Farm (Thick red outline), in the Eastern Cape. Yellow border box represents early stage thicket encroachment; Orange border box is intermediate stage; and the Red border box is late stage.

4.3.2 LiDAR and RGB image data collection

The Harvard Animal Landscape Observatory (HALO) system was (with the help of Professor Andrew Davies from the Davies Lab at Harvard University) used to collect high-resolution RGB images and LiDAR point clouds for this study site in March 2021. This was done using an unmanned aerial vehicle, which flew the HALO system over the study site of approximately 525 ha of land at Endwell Farm. This system includes a LiDAR sensor, an RGB camera, and a centralised data acquisition computer, which records and stores this data as well as the GPS location. The Davies Lab team helped clean and normalize the point clouds and georeferenced the RGB images. The LiDAR point clouds were used to develop a 25 cm resolution canopy height model (CHM) which is a raster image that contains the normalized heights of the vegetation (with the influence of the elevation and topography removed).

4.3.3 Characterisation of V. karroo mortality

The mortality of the savanna species *Vachellia karroo* was the focus of this study. Thicket pioneer mortality was observed to be rare and furthermore, because most dead thicket pioneer species occurred within thicket clumps their visibility in aerial images was obscured. I used the high resolution RGB images and 0.25 cm resolution CHM to visually detect dead *V. karroo* trees larger than 0.5 m in each of these three plots in QGIS 3.22.3 (QGIS Development Team, 2022). Dead *V. karroo* were easy to visually distinguish from living trees given their distinctive pale colour and lack of green leaves/ foliage (Figure 4.2). I created a shapefile with points at the centre of each identified dead *V. karroo* tree and used the Point Sampling tool plugin to determine the height of each tree based on the CHM. Similarly, I identified each living tree (*V. karroo* and thicket pioneers) and created a shapefile with points at the canopy centre, and calculated the heights for these living trees.

A sub-sample of trees over each of the three stages (early, intermediate and late stage thicket clump formation) was used for ground validation of tree mortality. These trees were located and their mortality was compared with that identified remotely. Groundtruthing revealed a high percentage success rate of remote identifications of dead trees (90.1 % of trees were correctly labelled as dead and 98.5 % of the trees were actually partially dead). Refer to Appendix A3: Validation of tree mortality for further details on the ground validation methods and results.

Figure 4.2 Tree mortality at the study site: (A) dead *V. karroo* tree in a thicket clump; (B) dead *V. karroo* tree surrounded by large living neighbours; (C) aerial view of dead *V. karroo* trees, visible from the RGB imagery collected at the study site.

4.3.4 Data analysis

Density of V. karroo mortality in the different stages of encroachment

For hypothesis 1, I analysed the density of dead *V. karroo* trees across the stages of thicket formation. I determined the number of living and dead *V. karroo* trees within each of the three plots which represented early, intermediate, and late-stage encroachment. I calculated the overall density of trees as well as the density of mortality within each of these stages and the mean heights of living and dead trees.

Spatial point pattern analyses

Patterns within plots may be caused by a variety of variables; first-order effects are often caused by environmental factors and will influence the intensity of points over a relatively large area of land, and these include factors such as topology, or mean annual precipitation (Wiegand and Moloney, 2004; Wiegand and Moloney 2014; Ben-Said, 2021). Second-order effects result from the interactions and relationships between the organisms within that particular area (Velázquez et al., 2016). The second-order effects are the major focus within this study, as I aim to explore the interactions taking place between living and dead trees within each of the three stages of thicket encroachment (early, intermediate, and late stage) (Wiegand and Moloney, 2004). I used second-order summary statistics to analyse the relationships between trees and describe the spatial characteristics of emerging patterns as a function of tree-to-tree distances (Velázquez et al., 2016; Ben-Said, 2021).

L-function and null model selection

The L-function, L(r) is a modified square-root transformation of Ripley's K-function K(r) (Besag, 1977), which uses a transformation to remove the scale dependence of K for independent patterns and helps stabilize the variance (Ripley, 1981; Wiegand and Moloney, 2004). This L-function assess the intensity of point patterns (Pillay and Ward, 2012; Velázquez et al., 2016) and whether the dependence revealed is caused primarily by first order heterogeneity or second order effects (plant-plant interactions) (Wiegand and Moloney, 2004; Muvengwi et al., 2017; Ben-Said, 2021). This is important to ensure that the correct tests and hypotheses are applied, with null models of complete spatial randomness (CSR) commonly used under conditions of homogeneous intensity, and alternate Heterogeneous Poisson process (HP) where the intensity was heterogeneous (Wiegand and Moloney, 2004).

The L-function equation is defined as:

$$L(r) = \frac{\sqrt{K(r)}}{\pi} - r$$

Where K(r) is Ripley's K function, and *r* is a given distance of an arbitrary point.

The L-function allows users to test whether patterns are homogeneous or heterogeneous (Wiegand and Moloney, 2004). For a homogeneous Poisson process (complete spatial randomness CSR), $K(r) = \pi r^2$ and $L(r) = 0$. Aggregation of the pattern up to distance r is indicated when $L(r) > 0$; while regularity of the pattern up to distance r is indicated when $L(r) < 0$ (Ripley, 1977; Besag, 1977; Wiegand and Moloney, 2004; Ben-Said, 2021).

Therefore in this study, I firstly tested the intensity of each plot using the L-function before undertaking the spatial point pattern analyses using the relevant statistical tests and null models (Table 4.1). I measured the intensity of all three plots (early, intermediate, and late stage encroachment) and found that early and late stages showed a heterogeneous pattern while intermediate stage thicket encroachment showed a homogeneous pattern of trees. Appropriate nulls models were thus applied and these can be located in Appendix B, Section 2.

For all spatial point pattern analyses, I used 1999 Monte-Carlo simulation envelopes to help explain whether the observed points fit the null model (Wiegand and Moloney, 2004). Summary statistics were run for the selected null model as well as for the data, and the 5th lowest and 5th highest values from the null model simulations were used to create simulation envelopes (Pillay and Ward, 2012; Velázquez et al., 2016). Where the observed summary statistics were not within simulation envelopes, this indicated the rejection of the null model within the dataset (Velázquez et al., 2016). If the data was found within these confidence envelopes, the data followed the null model chosen. To account for possible underestimation of type I error rate, a goodness-of-fit (GoF) test was used (Loosmore and Ford, 2006; Pillay and Ward, 2012).

Table 4.1 Summary of spatial point pattern analyses and corresponding null models used to test each study objective and prediction.

Objective	Predictions	Statistical test	Null model	Reference
Overall spatial distribution of dead trees	Dead trees show a regular or random distribution in the early stage and clustered distribution in the advanced stage of thicket encroachment.	Univariate Pair Correlation Function	Homogeneous: CSR Heterogeneous: HP	Carrer et al., 2018; Gupta and Pinno, 2018; Hesselbarth et al., 2018; Muvengwi et al., 2018; Pillay and Ward, 2012; Yao et al., 2016
Spatial distribution of dead and alive trees	Competition-induced mortality will be evident (attraction between dead and living trees) in high competition thicket clumps under late stages of thicket encroachment, while evidence of segregation will be found between dead and living trees in open savanna with early stages of thicket encroachment.	Bivariate Pair Correlation Function	Random labelling	Carrer et al. 2018; Gupta and Pinno 2018; Hesselbarth et al. 2018; Petritan et al. 2015; Pillay and Ward, 2012; Yao et al. 2016
Spatial and size related distribution of dead and alive trees	Dead *V. karroo* trees will be shorter than expected when they were located close to large living individuals in late stage thicket encroachment within the closed canopy thicket clumps, and taller than expected when they were located close to large living individuals in the open savanna canopy with earlier stages of thicket encroachment.	Quantitative Bivariate Mark Correlation Function: $k_{m1m2}(r)$	Random labelling	Hesselbarth et al., 2018; Velázquez et al., 2016; Gupta and Pinno, 2018; Muvengwi et al., 2018; Ziegler et al., 2017

Overall spatial distribution of dead V. karroo trees using the univariate pair correlation function (Hypothesis 2)

To investigate overall spatial distribution of dead trees I used the univariate pair-correlation function (PCF) g(r) (Stoyan and Stoyan 1994) to analyse the spatial patterns of only dead *V. karroo* within each stage of encroachment (early, intermediate, and late) (Table 4.1). I interpreted the results from the PCF as follows: points of the pattern are randomly distributed when $g(r) = 1$; points of the pattern are aggregated when $g(r) > 1$; and points of the pattern are segregated when $g(r) < 1$ (Stoyan and Stoyan, 1994; Ben-Said, 2021).

The PCF, g(r), is a second-order statistic which is closely related to Ripley's K-function (Ripley, 1977; Carrer et al., 2018). In the PCF, rings are used instead of the circles used by Ripley's K-function. This gives the expected number of points at distance r from an arbitrary point, divided by the intensity l of the pattern (Wiegand and Moloney, 2004). PCF's are non-cumulative, and better quantify the effects at specific spatial scales Wiegand and Moloney, 2004; Perry et al., 2006; Velázquez et al., 2016).

Spatial distribution of dead V. karroo and living trees using the bivariate pair correlation function (Hypothesis 3)

To analyse the relationship between all living trees and dead *V. karroo* within each stage of encroachment, I used a Bivariate PCF $g_{12}(r)$ (Table 4.1). This test allowed me to compare two separate patterns, which in this study were "dead trees" and a second pattern of "living" trees. I interpreted that (Stoyan and Stoyan, 1994; Ben-Said, 2021). I interpreted that where $g_{12}(r) = 1$, dead *V. karroo* and living trees are independent; where $g_{12}(r) > 1$, dead *V. karroo* and living trees were attracted; and finally, when where $g_{12}(r) < 1$, dead *V. karroo* and living trees are segregated.

Spatial and size distribution of dead V. karroo and living trees using the Quantitative Bivariate Mark Correlation Function (Hypothesis 4)

Marked analysis is a useful tool to help users investigate the distance- and density-dependent effects on trees (Ben-Said, 2021). I used a Quantitative Bivariate Mark Correlation Function (MCF) $k_{m1m2}(r)$ to analyse the spatial and size related distribution of dead *V. karroo* and living trees (Table 4.1). I used a quantitative mark of each tree's height (for living and dead trees), as well as a qualitative mark indicating whether the tree was dead or alive. I used a null model of Random labelling, where the spatial positions of all trees in the plot were kept fixed, and the quantitative marks (tree heights) were retained for each point, while the marks (labels) of the points (dead or alive) were randomly assigned to the overall pattern (Schleicher, et al., 2011; Wiegand and Moloney, 2014). I used this random labelling null model to investigate whether tree mortality was a random process (Getzin et al., 2006; Wang et al., 2017).

The MCF is calculated using the formula below:

$$k_{mm}(r) = \frac{\mathbb{E}[uv][m(u) * m(v)]}{\mathbb{E}(M,\ M')}$$

In this equation, *E[uv]* is the probability that two points are at location *u* and *v* separated by distance *r*, and *m(u)* and *m(v)* are the corresponding marks of the two points. The denominator *E(M, M')* includes random marks from an identical distribution and serves as a normalization factor (Baddeley et al., 2014; Hesselbarth et al., 2018).

Values within the confidence envelopes of the null model indicated independence or an absence of correlation ($k_{mm}(r) = 1$) (Hesselbarth et al., 2018; Wiegand and Moloney, 2014). In contrast, values of $k_{m1m2}(r) > 1$ indicated mutual stimulation and when or $k_{m1m2}(r) < 1$ there was inhibition between point marks. A positive departure from the null model thus signifies a positive correlation between dead *V. karroo* and living tree height and tree-to-tree distances (Hesselbarth et al., 2018; Muvengwi et al., 2018; Gupta and Pinno, 2018; Ben-Said, 2021).

I found the locations of each of these living and dead tree points from the shapefiles of living and dead tree points and heights, and I converted all coordinates to x-y Cartesian plane coordinates for each tree within each 6 ha plot for each stage of thicket encroachment. These were exported as CSV files and then formatted to be used within the grid-based software, Programita 2014, as set up in the User Manual for the Programita software by Wiegand (2014) (Wiegand and Moloney, 2004; Wiegand and Moloney 2014). I employed a bin width of 1 m^2, a ring width of 3 m, and a maximum radius of 50m, ecologically significant parameters for expected tree-tree interactions.

4.4 Results

4.4.1 Characterisation of V. karroo mortality (Hypothesis 1)

Early stage thicket encroachment displayed the lowest density of *V. karroo* mortality per hectare out of all three stages of thicket encroachment, as predicted. As the stage increased to intermediate and then late stage, there was a corresponding increase in the total tree density per hectare. As expected, late stage thicket encroachment had the greatest density of dead *V. karroo* per hectare (Table 4.2; Figure 4.3). In early stage thicket encroachment, the mean dead tree height was 2.2 m ± 0.94 SD, while the mean living tree height was 1.92 m ± 0.94, and therefore this stage had the lowest heights for living and dead trees. This increased at intermediate stages of thicket encroachment, with dead *V. karroo* displaying a mean height of 2.28 ± 1.03 m, while living trees had a mean height of 2.06 ± 0.97 m. The heights of living and dead trees were highest in late stage encroachment, with a mean height of 3 m ± 1.03 SD for dead trees and a height of 2.95 m ± 1.17 SD for living trees (Table 4.2), as expected for late-stage thicket clump formation over time.

Table 4.2 Densities of living and dead trees in one 6-ha plot in each of three stages of thicket encroachment: (1) Open Savanna; (2) Intermediate transitional zone; and (3) Closed Canopy Thicket. Height values are means ± SD

	Open Savanna	**Intermediate Transitional Zone**	**Closed Canopy Thicket**
Total number of trees per plot	1960	4128	4385
Percentage *V. karroo* mortality	18.5	10.3	11.4
Total tree density (ha^{-1})	327	688	731
Density of living trees (ha^{-1})	266	617	648
Density of *V. karroo* mortality (ha^{-1})	61	71	83

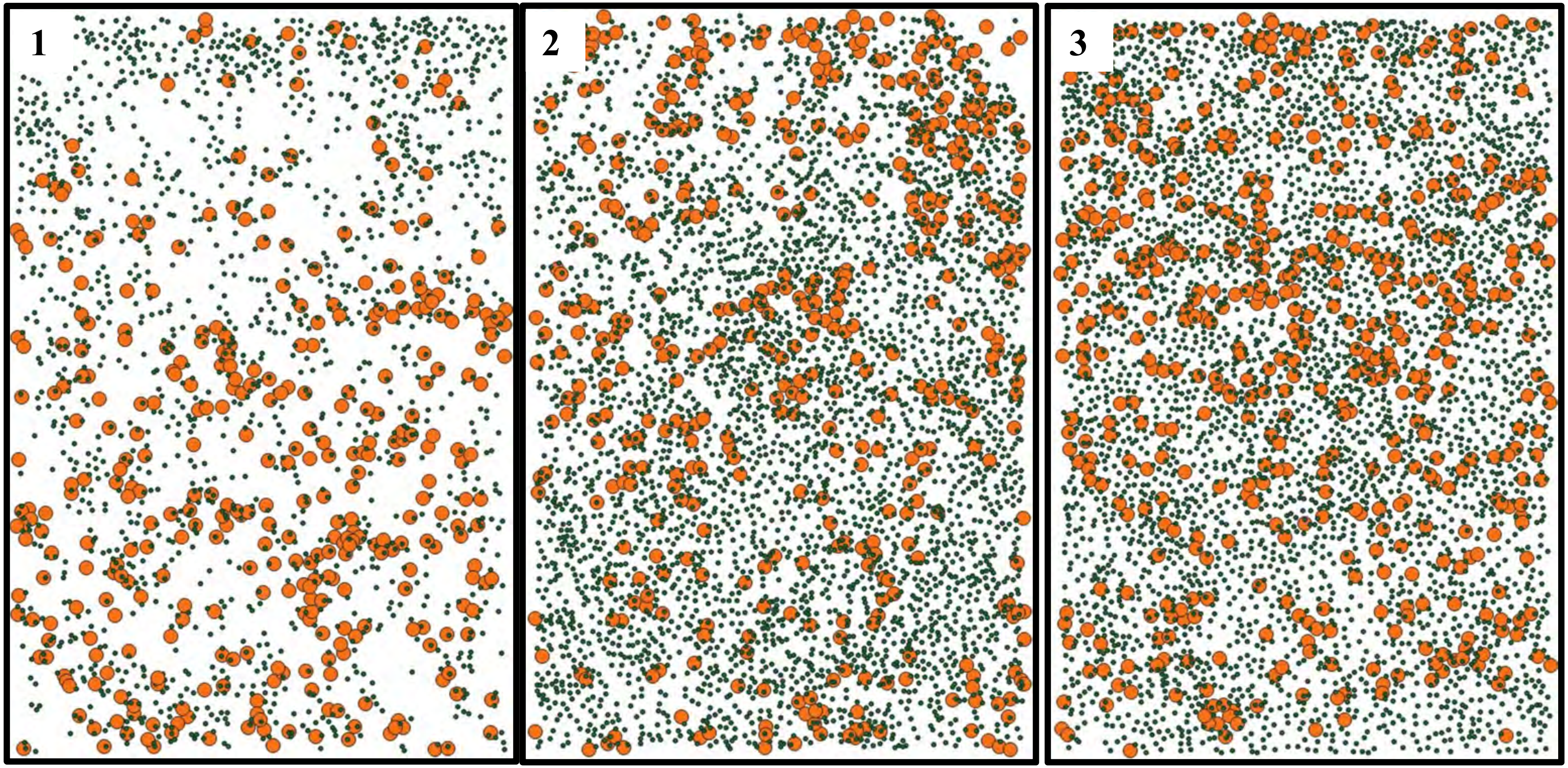

Figure 4.3 Dead *V. karroo* and living trees in (1) early encroachment - Cluster 1; (2) intermediate encroachment- Cluster 2; and (3) late-stage thicket encroachment - Cluster 3. Larger orange points represent dead trees, while smaller green points represent living trees. Sizes of points are not to scale and do not correspond to tree size.

4.4.2 Spatial point pattern analysis

V. karroo Mortality- Univariate PCF (Hypothesis 2)

Univariate pair correlations were used to analyse the spatial distribution of dead *V. karroo* trees at increasing stages of thicket encroachment. At all stages of thicket encroachment there was a significant negative deviation from the null model (0 to 1 m for early and intermediate stages, and 0 to 2 m for late stage) and dead *V. karroo* were therefore segregated from one another at short distances (GoF test, $p \leq 0.0020$, Figure 4.4).

In early stage thicket encroachment this small-scale segregation was then followed by a slight positive deviation, and *V. karroo* were aggregated between 3 to 4 m (GoF test, $p = 0.0025$, Figure 4.4.1). From 5 m there was no evident correlation and dead *V. karroo* trees were randomly distributed throughout early stages of encroachment (GoF test, $p = 0.6665$, Figure 4.4.1).

At intermediate stages of thicket encroachment (following the small-scale segregation patterns) there was an aggregation of *V. karroo* trees between 3 to 7 m (GoF test, $p < 0.0005$, Figure 4.4.2). This changed to a dominantly random distribution of dead *V. karroo* trees at larger spatial scales (GoF test, $p_{8 \text{ to } 9\text{m}} = 0.340.0940$, $p_{14 \text{ to } 50\text{m}}$, Figure 4.4.2).

Late stage thicket encroachment showed slightly increased segregation of dead *V. karroo* at small-scales compared to the other stages. Unlike the early and intermediate stage, in the late stage there was no evidence of aggregation, at distances greater 2 m, there was no evidence of significant deviations from the null model, and dead *V. karroo* trees were randomly spaced (GoF test, $p = 0.4735$, Figure 4.4.3).

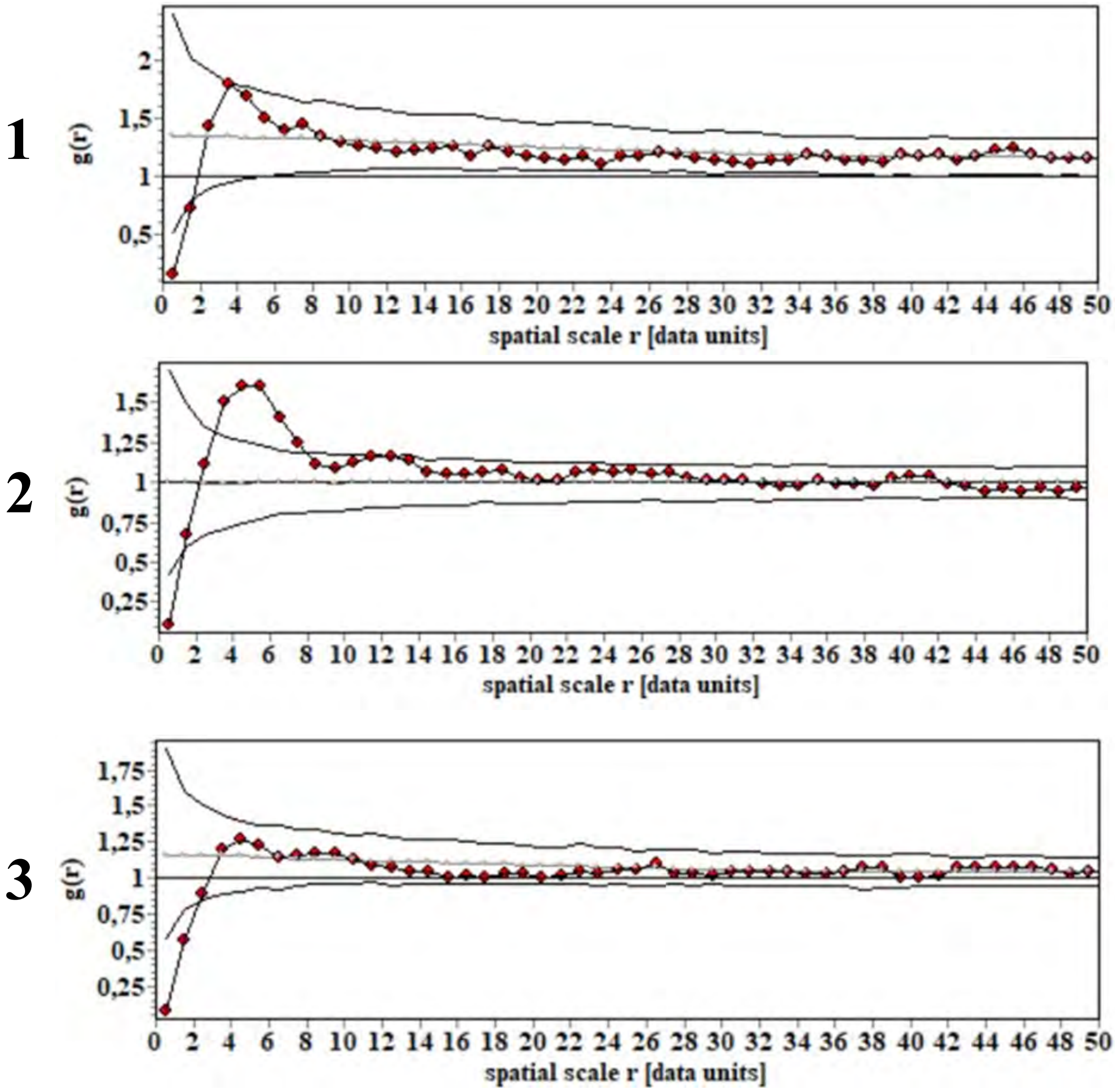

Figure 4.4 Spatial Point Pattern Analysis: Univariate Pair Correlation Functions g(r), were employed to analyse all the dead trees within: (1) early encroachment - Cluster 1, (2) intermediate encroachment- Cluster 2; and (3) late-stage thicket encroachment - Cluster 3. Approximate 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations. Clusters 1 and 3 were heterogeneous and used a Heterogeneous Poisson null model, while Cluster 2 was homogeneous and used a null model of CSR. Simulation envelopes are represented by the black solid lines, while the red dotted line shows the observed g(r). Where the observed summary statistics are not within simulation envelopes, this indicates the rejection of the null model within the dataset.

Dead *V. karroo* and living trees- Bivariate PCF (Hypothesis 3)

At early stages of thicket encroachment dead *V. karroo* and living trees displayed attraction at small distances of 0 to 2 m (GoF test, $p < 0.0005$, Figure 4.5.1). This was followed by independent patterns as the interactions transitioned from this small-scale attraction to a dominating pattern of segregation between dead *V. karroo* and living trees at larger spatial (≥ 6 m) (GoF test, $p < 0.0005$, Figure 4.5.1).

In intermediate stage thicket encroachment, at small spatial scales, dead *V. karroo* and living trees show repulsion followed by a dominance of independent spatial arrangements from ≥ 4 m (GoF test, $p = 0.2275$, Figure 4.5.2). The dead *V. karroo* and living trees within late stage thicket encroachment were spatially segregated at small-scales of 0 to 2 m (GoF test, $p < 0.0005$, Figure 4.5.3). From larger distances there was no longer any significant deviation from the null model and the trees within this encroached stage were independently arranged, with randomness patterns evident from ≥ 3 m (GoF test, $p = 0.8440$, Figure 4.5.3).

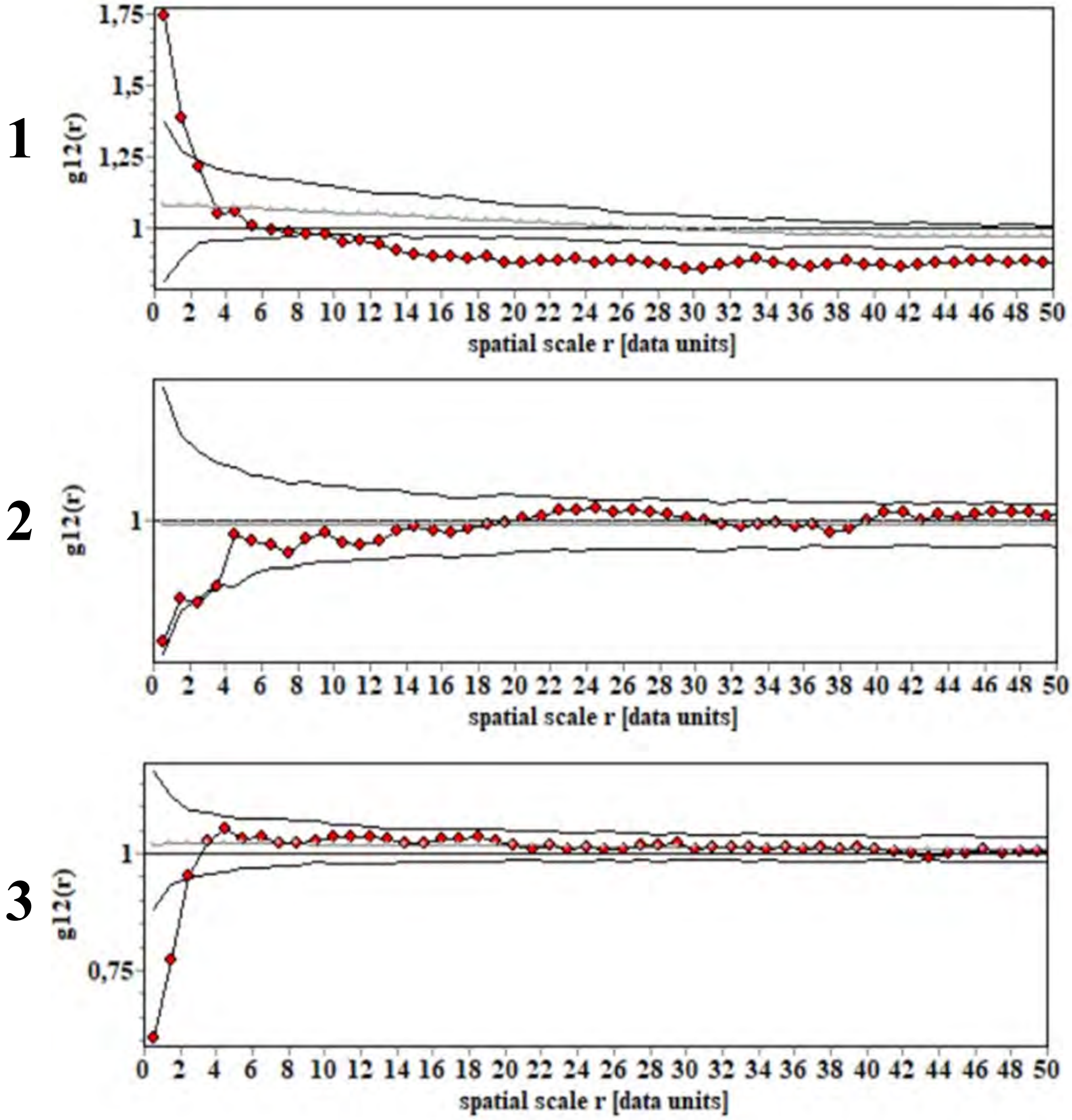

Figure 4.5 Spatial Point Pattern Analysis: Bivariate Pair Correlation Functions g(r), were employed to analyse the relationship between living and dead trees within: (1) early encroachment - Cluster 1, (2) intermediate encroachment- Cluster 2; and (3) late stage thicket encroachment -Cluster 3. Approximate 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations. Clusters 1 and 3 were heterogeneous and used a Heterogeneous Poisson null model, while Cluster 2 was homogeneous and used just a null model of CSR. Simulation envelopes are represented by the black solid lines, while the red dotted line shows the observed g(r). Where the observed summary statistics are not within simulation envelopes, this indicates the rejection of the null model within the dataset.

Dead *V. karroo* and living trees- Bivariate MCF (Hypothesis 4)

Qualitatively marked patterns with one quantitative mark (tree height) were analysed using mark correlation functions, where the trees were marked as “dead” or “alive”. The trees within early stage thicket encroachment showed positive deviations from the null model of Random Labelling at all spatial scales (GoF test, $p < 0.0005$, Figure 4.6.1). There was therefore a positive correlation between tree height and tree-to-tree distances, indicating mutual stimulation between dead *V. karroo* and living trees, with living trees having a greater mean tree height when growing closer to dead *V. karroo* trees.

In the intermediate stage of thicket encroachment there was a similar pattern to that within the early stage, although the positive deviation from the null model was not as great in this stage (GoF test, $p < 0.0005$, Figure 4.6.2). The clusters of trees within this intermediate stage were therefore taller than the mean tree height.

The late stage thicket encroachment displayed a significant positive deviation from the null model at small spatial scales of 0 to 2 m, where dead *V. karroo* and living trees neighbours close together were taller than the mean tree height, showing mutual stimulation (GoF test, $p < 0.0005$, Figure 4.6.3). At larger spatial scales (≥ 3 m) however, the null model indicated independence or an absence of significant correlation between dead *V. karroo* and living trees (GoF test, $p = 0.4700$, Figure 4.6.3).

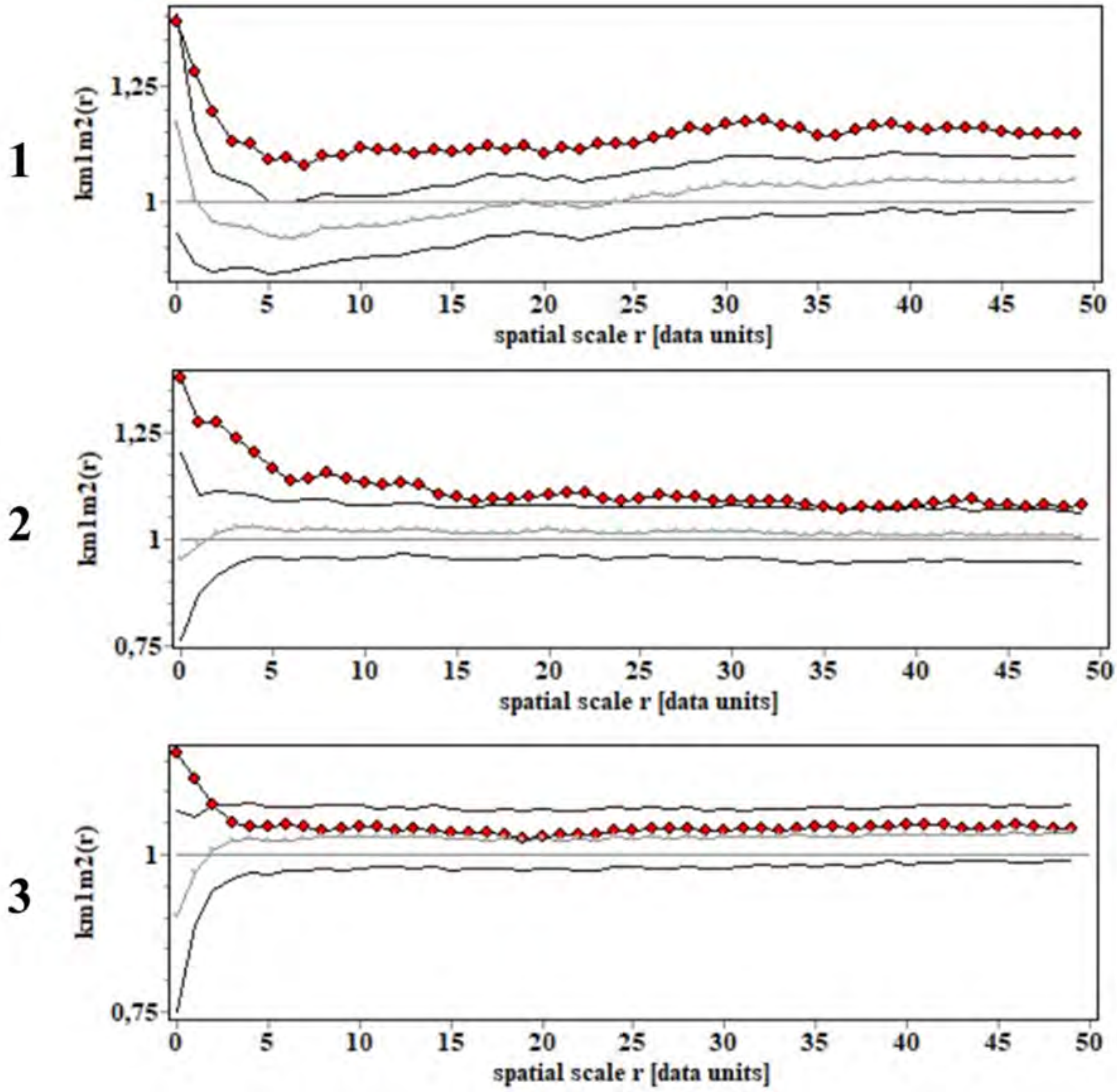

Figure 4.6 Bivariate Mark Correlation Functions (k_{m1m2}(r)): Analysis of patterns with one qualitative ("dead" or "alive") and one quantitative (tree height) mark (Data type 8 in Programita, 2014) within: (1) early encroachment - Cluster 1, (2) intermediate encroachment- Cluster 2; and (3) late stage thicket encroachment -Cluster 3. Approximately 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of random labelling. Simulation envelopes are represented by the black solid lines, while the red dotted line shows the observed k_{m1m2}(r). Where the observed summary statistics are not within simulation envelopes, this indicates the rejection of the null model within the dataset.

4.5 Discussion

4.5.1 Characterisation of V. karroo mortality

I predicted that with increasing thicket density, mortality (via exacerbated effects of agent-based mortality and intense neighbour competition) would be increased, evident as a higher density of dead *V. karroo* individuals in the later stages of thicket encroachment. This was supported by my findings, as there was an increase in the density of *V. karroo* mortality as thicket encroachment progressed. Meyer et al. (2008) studied the cyclical succession in semi-arid savannas in South Africa, and found increased mortality of shrubs due to the interaction of high competitive pressure and unfavourable conditions on large shrubs. *Vachellia karroo* are put under increased competitive pressure by these formerly facilitated thicket pioneer species, leading to increased mortality of the savanna nurse plants (Olff et al., 1999; Petritan et al., 2014). However, mortality of *V. karroo* across the plots may have been reduced as a result of high levels of crown dieback (which was not measured in this study) instead of death. Swemmer (2020) studied the impacts of this drought (2014 to 2016) on the mortality of woody plants in a semi-arid savanna in South Africa, and found that mortality was not extensive, however that some landscapes suffered some of the highest mortality values reported, with corresponding high levels of crown dieback. However this study provides evidence that *V. karroo* trees exposed to the drought did show a higher mortality expected by chance and, importantly that this effect was more pronounced in late stage thicket encroachment due to increased neighbourhood competition. This is supported by several Australian savanna studies such as that of Dwyer et al. (2010), who found that drought-induced mortality of savanna trees was highest in dense neighbourhoods, where density-dependent effects and limited resources predisposed plants to drought-induced deaths. Similarly, Fensham et al. (2009) showed that drought-induced death was more likely as the savanna increased in woody density. I suggest that this drought may play an important role as an abiotic trigger in the intermediate stage of thicket encroachment such that it is able to lower the threshold of tree density below a critical threshold, and enable transitions between states to take place (Vetter, 2009).

Furthermore, while the overall density of *V. karroo* trees did increase as shown, however, it would be useful to investigate the relationship between dead *V. karroo* and living thicket species, to single out the effects of inter-specific competition. Further, identifying the percentage of *V. karroo* mortality within each stage of thicket encroachment would be helpful as it would provide further insight into the proportion of dead *V. karroo,* rather than the density which may be a product of increased overall tree density.

4.5.2 Spatial point-patterns of tree mortality

I expected the spatial pattern of dead *V. karroo* trees to be regular or random in early stages of thicket encroachment, representing mortality via senescence or environmental heterogeneity respectively, typical of open canopy savanna dynamics, and that in late stage thicket encroachment, *V. karroo* trees would display a clustered spatial pattern of mortality as a result of intense neighbourhood competition due to the formation of closed canopy thicket clumps in this stage of thicket encroachment. My findings suggest that in the open savanna this is supported, with small-scale regularity and larger scale and random patterns of dead *V. karroo*. However contrary to predictions, this study found that there was similarly small-scale regularity of dead *V. karroo*, and a dominance of random spatial distributions at larger scales. These small-scale regular patterns can be attributed to a competitive-based mortality such as self-thinning over time which may occur in open savanna (Kenkel 1988; Wiegand and Moloney 2004). Thicket pioneer species grow densely, forming thicket clumps (O'Connor and Chamane et al., 2012), and causing an increase in overall competition (Stoll and Bergius, 2005) which results in the initiating species (in this case *V. karroo*) being unable to survive. This causes these nurse plants such as *V. karroo,* to die within the small-scales of these clumps, alleviating some pressure on neighbours, and resulting in a regular spacing of dead trees at small-scales within these clumps (Petritan et al., 2014). Inter- and intra-species competition taking place between trees may result in density-dependent mortality and an even arrangement of dead trees (Hesselbarth et al., 2018). These random patterns may be a result of resource heterogeneity or agent-based mortality such as the drought in this area (2014 – 2016) which may have increased dieback in the trees (Swemmer, 2020). The increase in tree density and the dominance of thicket pioneer species found within the later stages of thicket encroachment (Chapters 2 and 3) may cause these mortality agent effects to be stronger, causing an increase in the competition in this cluster, however, this may have led to increased dieback rather than mortality, causing random rather than regular patterns. These *V. karroo* trees also establish individually, and can be involved in many types of associations (Nell et al., 2024).

4.5.3 Spatial point-patterns of dead and living trees

This study found as predicted, evidence for random mortality, shown as segregation between dead and living trees, as the dominant pattern in open savanna (early stage thicket encroachment). Agent-driven mortality such as drought (Swemmer, 2020), may reduce the inter-tree competition by decreasing tree density and aiding in the co-existence of grass and trees such as is typically found within savannas (Asner et al., 2009; Levick et al., 2009; Holdo et al., 2013). As disturbances increase within a savanna, they result in greater random tree mortality (Sea and Hanan, 2012), which reduces the overall competition between trees remaining in the system (Hesselbarth et al., 2018).

Nucleating species, such as *V. karroo*, may initiate woody encroachment and thus the later entry of new thicket pioneer species into bush clumps (O'connor and Chamane et al., 2012; Jamison-Daniels et al., 2021; Abreu et al., 2021). These thicket pioneer species grow densely, causing an increase in overall competition which results in these initiator *V. karroo* trees being unable to survive (Olff et al., 1999; Petritan et al., 2014). This increased competition causes these nurse plants to die within the small-scales of these clumps, resulting in an aggregation of dead and living trees within these bush clumps. Nell et al. (2024) investigate the relationships between *V. karroo* and thicket species along a gradient of increasing thicket encroachment at this study site using association rules analysis. They found that *V. karroo* provide nucleation sites for thicket clump initiation, and once established, these thicket clumps are comprised of a variety of species, with association patterns at later stages of thicket encroachment less clear as a result of the increased number of individuals of mixed species and size classes. However, except in the small-scale of early stage encroachment (which I interpret as a result of senescence or a sampling artefact), there was no evidence of attraction between dead *V. karroo* and living trees within thicket clumps as thicket encroachment progressed.

Inter- and intra-species competition between trees may result in density-dependent mortality and an even arrangement of dead trees (Hesselbarth et al., 2018). Density-dependent mortality occurs most frequently in dense woody vegetation where neighbours are in close proximity to one another (Adie and Yeaton, 2013) as a result of the increased competition. This is also true for increased woody density in encroached and thickened savannas (Sea and Hanan, 2012; Wiegand et al., 2008). I therefore suggest that within sites of later thicket clump formation, the remaining effects of small-scale competition are caused by density-dependent mortality. Belay et al. (2013) looked at the way a semi-arid savanna rangeland responded to woody plant encroachment in south-western Ethiopia. Their research found that woody encroachment causing the transition from an open savanna to a bushland state is most likely driven by a variety of factors, including the suppression of natural disturbances such as fire and herbivory, as well as human disturbances or land use changes (Belay et al., 2013). As disturbances are reduced density–dependent mortality becomes more common (Sea and Hanan, 2012). Similarly, as this drought effect on mortality increased in late stage thicket encroachment as the tree density increased, this agent-based mortality caused an increase in random mortality, reducing the competition and resulting in more random spatial distributions of living and dead trees (Fensham et al., 2009; Dwyer et al., 2010; Swemmer, 2020).

4.5.4 The effect of competition on dead and living neighbours

Lastly, the spatial distribution of dead and alive trees in relation to height was examined. I hypothesized that dead *V. karroo* trees would be shorter than expected when they were located close to large living individuals in late stage thicket encroachment within the closed canopy thicket clumps, and taller than expected when they were located close to large living individuals in the open savanna canopy with earlier stages of thicket encroachment.

This was supported by my findings which suggested that as thicket encroachment progressed and thicket clumps formed, there was less of a facilitative effect between the sizes of dead and living trees. Within open savanna (early stage), trees which were in closer proximity were found to be above the mark mean, therefore positive relationships between dead *V. karroo* and living trees were most dominant (Wiegand and Moloney, 2014). This may indicate mutual stimulation (Gupta and Pinno, 2018) and that facilitation had previously taken place, as the larger dead tree (*V. karroo*) likely acted as a nurse plant for the living tree (Skowno et al., 1999; O'Connor and Chamane, 2012; Nell et al., 2024). This facilitative relationship would have continued until the new recruit was fully grown, at which time the facilitative tree senesced and was succeeded by the facilitated tree. It could however also indicate that both trees grew in that area occupying similar ecological niches (Chesson, 2000; Johnson et al., 2017), and as the now living tree grew, its demand for these limited resources (Yang et al., 2018) increased, putting increased competitive pressure on its neighbour. If this competition became strong enough, it could cause changes in the underlying mechanisms, spatial arrangement, species composition, sizes and mortality of trees (Petritan et al., 2014).

Under these conditions, the surviving tree would therefore have out-competed its neighbour, resulting in density-dependent mortality and thus the death of its neighbour. After the initiator, *V. karroo,* senesced, the facilitated tree which had established was able to occupy that ecological niche, with the immediate competition reduced in that area and resources made available (Martínez et al., 2010; Li et al., 2021).

The same facilitative pattern between dead and living trees was observed in intermediate stages of thicket clump formation, however the positive relationship here was less strong between the size of living and dead neighbouring trees at small spatial scales. As within early and intermediate stage of thicket encroachment, there is a positive correlation between the size of living and dead neighbouring trees at small spatial scales within later stages of thicket encroachment with increased clump formation. At slightly larger scales however (3 to 50 m) the trees showed independent heights, irrespective of neighbours. This seeming independence in tree size and distance between dead *V. karroo* and living trees may be as a result of a combination of positive and negative effects of different factors acting simultaneously (Hesselbarth et al., 2018; Wiegand and Moloney, 2014). This may include factors causing positive effects and mutual tree growth stimulation, such as is caused by the facilitative nature of *V. karroo* (Nell et al., 2024), while the negative influence of competition may result in the reduction of tree size, causing mutual inhibition rather than mortality between trees (Pillay and Ward, 2012). There were also likely effects caused by tree crown dieback as a result of the 2016 drought (Swemmer, 2020), which may have caused a decrease in tree size rather than mortality, which would cause the reduction of tree size, especially under increased tree density in later stages of thicket encroachment (Fensham et al., 2009; Dwyer et al., 2010; Swemmer, 2020).

It should be noted that the total density of dead *V. karroo* trees at the study site did not exceed approximately 12.3 % of the total trees present, indicating that this phenomenon of intense thicket competition cannot be relied upon by land owners as mitigation for bush encroachment. These results are in agreement with Swemmer (2020) who found that one cannot simply rely on agent-based mortality such as a prolonged drought to eliminate bush encroaching species, as this may not always happen. Rather, since *V. karroo* acts to facilitate thicket establishment in early stages, this study suggests that management efforts for controlling thicket expansion should target the early stage open savannas to prevent the facilitation of the thicket clumps.

4.6 Conclusions

Thicket expansion is an important process taking place in this semi-arid savanna site. *Vachellia karroo* initially acts as a nucleating species, facilitating the entry of thicket pioneer species into these savanna systems, which in turn increase in size, and place a greater demand on the limited resources available in that area, given their overlapping ecological niches. The increase in competition, coupled with climate change such as prolonged drought is shown to amplify the effects of density-dependent mortality of *V. karroo*, resulting in increased mortality as thicket clump formation increased. Overall there was a general pattern of random arrangement of dead trees – this likely is the result of a combination of processes. I infer that this random spacing across stages of thicket clump formation results from previous facilitation caused by savanna pioneer species, *V. karroo*, as well as density-dependent mortality resulting from competition. Findings suggest that at low rates of thicket clump formation in savannas, there is a positive correlation between short tree-to-trees and greater height, which may indicate a previously facilitative relationship between dead and living trees at short distances. This facilitative relationship decreases as thicket clump formation progresses. Competition which acted to reduce tree size and performance rather than mortality was found to be highest within later stages of thicket clump formation. Where encroachment has progressed, competition has increased and influences vegetation structure. The implication for management is that tree mortality, while prevalent, may not be used as an effective form of bush control, especially if crown dieback is more prevalent than mortality. A caveat of this study is that I combined all living trees to investigate a combination of inter- and intra-species competition; however it would be useful to investigate the relationship between dead *V. karroo* and living thicket species, as well as other *V. karroo* trees, to identify the effects of inter- and intra-specific competition independently.

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CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

5.1 Thesis summary

The aim of this thesis was to use high resolution spatial data coupled with spatial point pattern analysis to distinguish and infer the processes and mechanisms underlying the expansion of thickets into savanna. This study took place in a semi-arid savanna within in the Eastern Cape, South Africa. The vegetation across the study site is comprised of a combination of savanna tree and grass species and thicket pioneer. The dominant savanna tree species present in this area is *Vachellia karroo*. Vegetation structure was used to perform a multivariate cluster analysis to determine whether there are distinct stages or a gradient representative of thicket encroachment within a semi-arid savanna. Within these stages the spatial point patterns of association between savanna and thicket pioneer trees was investigated. The effect of increasing encroachment on underlying ecological mechanisms and interactions between plants was explored, as well as the impact of increased woody density associated with thickets on grass layers and tree mortality. The processes involved in this woody thickening from open savannas to closed canopy thicket that were highlighted throughout this study are shown in Figure 5.1.

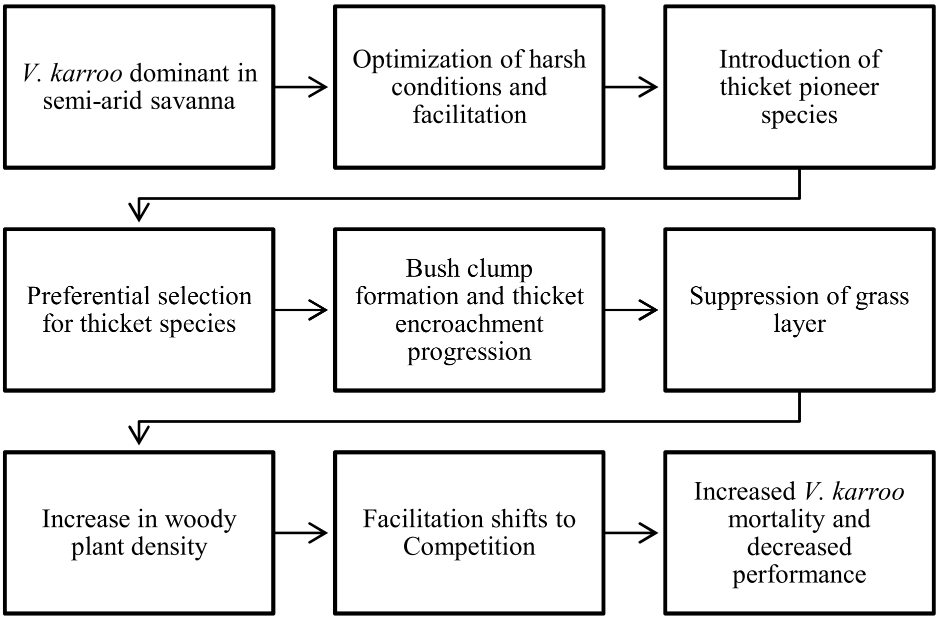

Figure 5.1 Schematic diagram of the shift from a savanna system with facilitative interactions dominant towards a closed canopy thicket system with dominant competitive interactions. Grass layer may be suppressed when tree density increases.

Hesselbarth et al. (2018) highlight that there is still an incomplete understanding of savanna dynamics, and they express the need for a better insight into the interactions and processes shaping the vegetation structure. Pillay and Ward (2012) used spatial point-pattern analysis of *V. karroo* trees to help provide insights into the underlying processes which affect the individuals in a mesic savanna population. This study therefore aims to contribute to this work, adding greater insight into the structure and dynamics of a semi-arid savanna, a system which has not been represented as well within literature on spatial point pattern analysis. The interactions between savanna and forest systems as alternate stable states have been well studied (Aleman et al., 2020; Staver et al., 2011a; Staver et al., 2011b) as has the effect of encroachment on biome shifts (Aleman and Staver, 2018; Stevens et al., 2017). There has been much less research into the dynamics between savanna and thicket pioneer species (O'Connor and Chamane, 2012; Charles-Dominique et al., 2015; Charles-Dominique et al., 2018; Jamison-Daniels et al., 2021) and how these biomes interact under encroachment processes (Parr et al., 2012; Khoza, 2021). This thesis aims to contribute towards this development of knowledge on thicket clump formation and expansion into savannas.

5.2 Management implications

Woody encroachment is a serious problem in savannas, both globally and locally, which results in negative ecological and economic impacts, affecting biodiversity and livelihoods. It is therefore important to ensure that this process is understood, as well as the best way to manage this encroachment. Studying the spatial patterns of these woody species allowed me to infer the existence of underlying processes, this may aid in determining the structure and, thus, the productivity of the land. This research will enable farmers or land users to recognise signs of state shifts and help inform the selection of intervention strategies- providing suggestions on when and where to implement these strategies.

The intermediate stage of thicket encroachment is extensive throughout the study area and occurs at a mid-range elevation, which would allow for either open savanna or thicket pioneer species to dominate. At intermediate stages, the canopy cover and density increases, however, these sites still have the potential to be opened up through tree thinning (Smit, 2005; Hare et al., 2021; Mndela et al., 2022) or burning (Archibald et al., 2009), as they have not yet lost their grass layer. This study therefore suggests that areas of early or intermediate stages of thicket clump formation may provide the best potential stage at which to implement intervention strategies for managing thicket encroachment to prevent irreversible state changes from savanna to thicket, however further research is needed to test this.

This study found that as the thicket clump formation progresses, bush clumps increase in dominance, thereby increasing the frequency of competitive interactions and leading to a possible switch from facilitative to competitive interactions (Meyer et al., 2008; Hesselbarth et al., 2018). This study therefore recommends that since *V. karroo* acts to facilitate thicket establishment (Nell et al., 2024), management efforts for controlling thicket expansion should be aimed at removing these *V. karroo* trees with the use of strategic clearing (Smit, 2004). Further, I suggest that earlier stages of thicket clump formation should be targeted, before thicket pioneer species have established and increased in dominance, starting the movement towards bush clump formation and thicket encroachment.

This study found that the density of *V. karroo* was highest under conditions of late stage thicket encroachment. However, the total density of dead *V. karroo* trees was only around 12.3 % of the total trees present. In agreement with these findings, after an intense drought in South Africa from 2014 to 2016, Swemmer (2020) suggested that agent-based mortality was insufficient to eliminate thicket encroachment. Even under late encroachment stages where the effects of the drought would be most pronounced (Fensham et al., 2009; Dwyer et al., 2010), I found evidence of tree crown dieback rather than purely mortality. I therefore suggest that further action needs to be taken by land owners to help mitigate thicket encroachment.

5.3 Limitations of research

In this study, I was able to calculate structural variables of vegetation and map the stages of thicket encroachment across 331 ha of land – which would not have been feasible using field-based methods. However, I faced challenges with the segmentation and delineation of trees, as well as the species identifications, given the highly multi-stemmed and intertwined nature of the woody species which made separating individuals difficult even with the use of LiDAR and RGB images. This study therefore manually identified trees and delineated tree canopies using the CHM and RGB imagery. This was time-consuming, and, like all other segmentation methods and remote identification processes, prone to some error given the overlapping nature of canopies as well as the similarity in the bands making up the RGB images for different tree species. This led to a smaller-scale analysis than initially planned, as it was time-consuming to identify these trees manually, even for plots of 1 and 6 ha. Methods such as ground truthing were used to ensure that results were as accurate as possible.

There were also challenges faced in the selection of “appropriate” sample and plot sizes (Ben-Said, 2021). In this study, plot size needed to be informed by the appropriate dimensions required for determining vegetation structure and composition using LiDAR data and RGB imagery, as well as sufficient individuals to undertake spatial point pattern analyses. This study therefore first attempted to use 30 x 30 m plots as used within a study by Guo et al (2017), which used airborne LiDAR data to map vegetation structure as in this study. However, it was found that for a semi-arid savanna system, this plot size was insufficient to pick up spatial patterns, as trees were not densely populated within the savanna biome. The decision was therefore made to use 1 ha plots to analyse the living trees, and to create 3 replicates for each stage of thicket encroachment (Carrer et al., 2018). In this study site there is a great deal of heterogeneity in vegetation structure. Given the aim of this study was to group areas based on similar vegetation structure, the plot size was also limited to help reduce the likelihood of each plot representing multiple different vegetation structures which would prevent accurate clustering as each plot would include a variety of stages of thicket encroachment present, rather than a dominant stage within the plot. At a 1 ha-scale, vegetation was fairly uniform, therefore the decision to use plots of 1 ha was supported. I then found that dead *V. karroo* were substantially more scarcely located within these plots, and to ensure that there were sufficient individuals, 1 ha plots were combined to form three 6 ha plots representative of each stage of thicket encroachment. I recommend testing out a variety of plot sizes to ensure that a sufficient sample size is selected; however, I suggest that within a system with highly variable vegetation structure, larger plots may be useful to ensure accuracy (Carrer et al., 2018; Wiegand and Moloney, 2004).

5.4 Future recommendations

The use of this technology within savanna and thicket systems is still relatively new, and this study contributes to the integration of these methods into these systems. Future developments in these segmentation methods designed to navigate such heterogeneous systems would enable future studies to investigate these tree-tree interactions on much larger scales. Machine learning and automatic tree detection and identification methods could also be implemented to improve these methods set out in this study. Automatic methods of segmentation were used within a number of other studies to train the machine learning methods which may provide future studies and monitoring programmes to up-scale and increase the area able to be analysed and managed (Mayr et al., 2018; Ball et al., 2023; Popp and Kalwij, 2023).

Rudge et al. (2021) modelled the diameter distribution of savanna trees within savanna woodland plots in northern Australia using drone-based LiDAR, and they suggest that segmentation accuracy is likely to improve with the development of more sophisticated segmentation algorithms. I support this finding and similarly suggest that more accurate tree detection and segmentation methods are required for use within savanna and thicket ecosystems. Further, Jansen et al. (2023) found that high-quality annotated and labelled training data required for supervised deep learning algorithms were curated mostly in Northern Hemisphere forests and settings with distinct, morphologically similar and easily distinguishable tree species. Their study presented a training dataset of tropical Northern Australia savanna woodland tree species using Remotely Piloted Aircraft Systems imagery and on-ground surveys to confirm species labels. Their study highlights the promising results that the use of deep learning algorithms may provide in classifying savanna tree species, even in the presence of significant inter- and intraspecific morphological variation (Jansen et al., 2023). I recommend that further developments of such data sets within a South African context would provide substantial aid to the classification of vegetation, and improve the efficiency of species mapping and land management.

This study measured the mean standing height of grass using values obtained from the LiDAR-generated CHM. A limitation of this study was that only fewer DPM measurements were taken to compare with this height value, and these measurements were taken over a year later – at which time the grass layer would have dramatically changed. The DPM heights were found to be lower across all clusters than the LiDAR mean heights. This was also likely due to the weight of the disc pasture meter pushing the grass down as it descends. The same trend of decreasing grass layer as thicket encroachment stage increases was followed. Integrating LiDAR and grass biomass measurements provides a great opportunity for land owners and users to determine their grass productivity and using remotely sensed species analysis could prove even more useful.

I conclude that the use of remote sensing and LiDAR technology holds a wide range of possibilities for more holistic and large-scale monitoring and managing thicket clump formation within savanna systems, however these methods need to be further refined for effective use within a South African thicket context. Further studies are suggested in order to better understand at what point within the stages of thicket clump formation encroachment can be best approached and managed for the greatest chance at successfully maintaining the important savanna biome. The development of intervention strategies to help farmers identify areas on their farms which have undergone state shifts, to deal effectively with thicket encroachment on their land within these different stages of thicket clump formation would be helpful.

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APPENDIX A: Ground validation of LiDAR data

High resolution spatial data such as that collected via airborne LiDAR has revolutionised the collection of vast amounts of vegetation data for large parts of the country, and indeed globally. Methods for the processing, analysis and validation of this data are constantly evolving. Nevertheless, ground truthing remains one of the most powerful validation tools for check height, elevation, species identification and vegetation status (such as mortality). This appendix highlights the specific validation techniques and field sampling which supported the studies represented in this thesis.

1. Species identification: field and remote-sensed data validation technique

The study site was visited in April 2021 and re-visited in December 2022. The locations and identity of 400 trees were recorded across the study site in April 2021. Tree species were identified in the field, and key plant traits and features such as leaves and tree structure were recorded to aid in remotely sensed species identifications (Table A1).

To determine the exact location of the trees being identified, a GNSS differential GPS (global navigation satellite system) Zenith 10 was used, which is a fully integrated satellite positioning system. This type of GNSS receiver is able to track satellite signals from GPS (global positioning system) and GLONASS (GLObalnaya NAvigatsionnaya Sputnikovaya Sistema). It is able to provide centimetre accuracy when the RTK Fixed solution is used. This precise location allowed me to match the trees recorded in the field to the same tree in the RGB images. The leaves and the branches often obstructed the satellite connection, giving a less accurate RTK Float reading when trying to record the tree location from the centre of the tree's canopy. The south-most readings were taken from the most central point of the canopy which was possible using the RTK fixed.

Table A1 Description of the leaves and structure of common tree species within this semi-arid savanna site to aid in identification through RGB imagery. *Scutia myrtina* *Gymnosporia buxifolia* and *Olea europaea* subsp. *africana* were grouped into the category of "thicket species" due to difficulty in correctly segmenting the species.

Species	Leaves	Structure
Vachellia karroo	• Fine, small leaves • Varied shades of green- dull to bright	• Open canopy with a fair amount of light able to travel through • Ground visible through parts of canopy • Canopy shape more asymmetric with branches protruding out of the canopy • Visible branching within canopy
Scutia myrtina	• Broad leaves • Dark green	• Closed canopy, with very little light able to travel through • No ground visible through the canopy • Canopy shape is more uniformly round and compact. It is usually symmetric
Gymnosporia buxifolia	• Broad leaves • Light green, similar in colour to *V. karroo*	• Partially closed canopy with little light able to travel through • Branches similar to *V. karroo*, but shorter and more compact
Olea europaea subsp. *africana*	• Broad leaves • Grey-green	• Closed canopy with little light travelling through • No ground visible through the canopy • Canopy is large, and they are often the tallest trees, with a fairly round canopy shape • The canopy appears almost fluffy and cloud like

From the tree identifications made remotely, 100 trees were selected and located within the study site using a handheld GPS device in December 2022. This was done to allow for a comparison between trees on the ground and those remotely sensed. Each of these tree's species was recorded within early stage thicket encroachment (Cluster 1, Plot 779), intermediate stage (Cluster 2, Plot 586), and late stage (Cluster 3, Plot 125).

Identifying the species of each tree was difficult as some species were clearly distinguishable (such as *Olea europaea* subsp *africana* and *S. myrtina*), but due to the great phenotypic variance in the *V. karroo* trees, it was often very easy to confuse this species with other thicket pioneer species. Of the sample of trees selected for ground truth validation, 79 % were found to be the same species in the field, as compared to the identification made using the RGB imagery in QGIS. In some instances, these trees form bush clumps, where canopies grow into one another. In these instances, it is often only the dominant or tallest canopy which could be used for identification purposes.

2. Height measurement validation of tree size

A sample of 100 trees was taken from the remotely sensed trees identified. These trees were located within early stage thicket encroachment (Cluster 1, Plot 779), intermediate stage (Cluster 2, Plot 586), and late stage (Cluster 3, Plot 125) within the study site using a handheld GPS. The highest point of each of these trees was recorded in field using a measuring tape. These heights were compared with those derived from the LiDAR-generated CHM for each of the tree points. Trees were classified using the height intervals "large" or "small" with a 2 m minimum for large thicket pioneer species and 2.5 m minimum height for large *V. karroo*.

On average 67 % of the measured heights in the field were within 0.5 m of the heights generated using a CHM of 1 m resolution, and 92 % of heights within 1 m of remotely sensed measurements. Some of this variability may be due to the time between LiDAR data collection and field measurements; over which time the trees would have grown slightly (74 % of trees were larger to some extent when measured in the field than the LiDAR measurements). Where plots were dense, the chances of identifying the wrong individual were also increased. Further, manually measuring trees at great heights becomes difficult and error-prone, leading to some differences in tree height.

Tree height and canopy area, were compared to determine whether both indicated similar determinations of "large" and "small" trees. The Spearman rank test was used to determine whether these variables were similar indicators of tree age (Table A2). Within early and intermediate stage encroachment (Clusters 1 and 2), there is a strong positive correlation between tree height and canopy size. In late stage encroachment (Cluster 3) however, there is a slightly weaker, but still positive correlation. The Regression Significance F p-value shows significant correlation between tree height and canopy size (Table A2).

Table A2 Correlation between tree height and tree size to determine a proxy for tree age across thicket encroachment stages

	Early stage	Intermediate stage	Late stage	**Mean**
Spearman Rank	0.74	0.77	0.64	0.71
Regression Significance F (p-value)	2.49884E-47	1.00212E-88	9.16155E-68	8.32946E-48
R Square value	0.46	0.43	0.34	

3. Validation of tree mortality

A sample of 71 trees over each of the three stages (early, intermediate and late stage thicket clump formation) was used for ground validation of tree mortality. At the study site, a handheld GPS was used to locate each of these trees which had remotely been identified as being dead. The focal dead tree was located as well as the cluster it was within, this dead tree species was recorded as well as whether the tree appeared to be dead. I found that 90.1 % of all trees located were correctly labelled as dead, while 98.5 % of the total trees were actually partially dead after ground validation.

APPENDIX B: Individual Spatial Point Pattern Analyses

1. Intensity of living trees in 1 ha plots across thicket encroachment stages (L-Function)

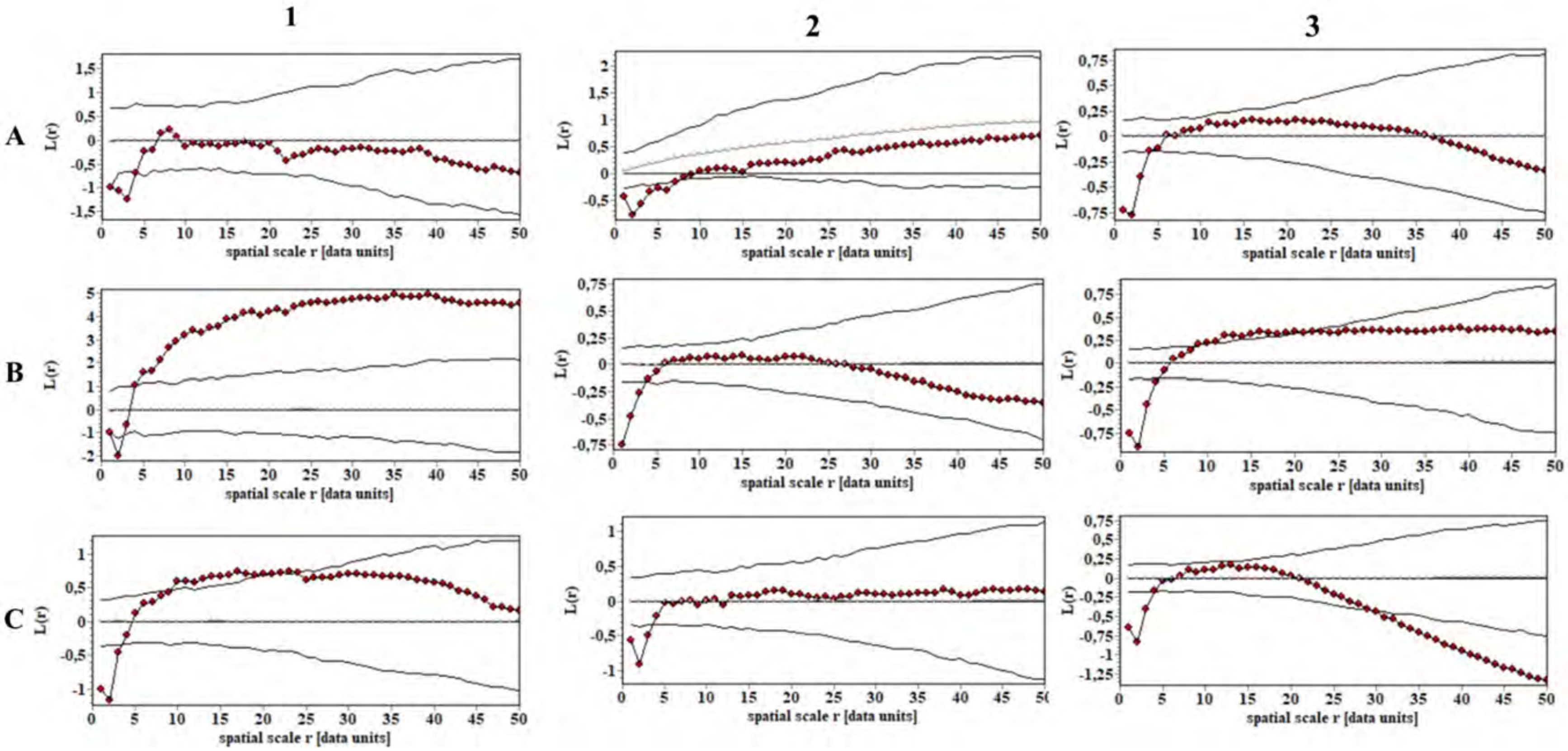

Figure B1 Intensity: A L-function L(r), a modification of Ripley's K, was run to analyse all the trees in each of the plots and classify them as homogeneous or heterogeneous. Approximately 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of Pattern 1 and 2 CSR. Plot 445 was heterogeneous and used a Heterogeneous Poisson null model. Column 1 represents Cluster 1, with a) Plot 618; b) Plot 751; and c) Plot 779. Column 2 represents Cluster 2, with a) Plot 445; b) Plot 586; and c) Plot 651. While Column 3 shows Cluster 3 and a) Plot 125; b) Plot 1026; and c) Plot 1135.

2. Intensity of trees in 6 ha plots across thicket encroachment stages (L-Function)

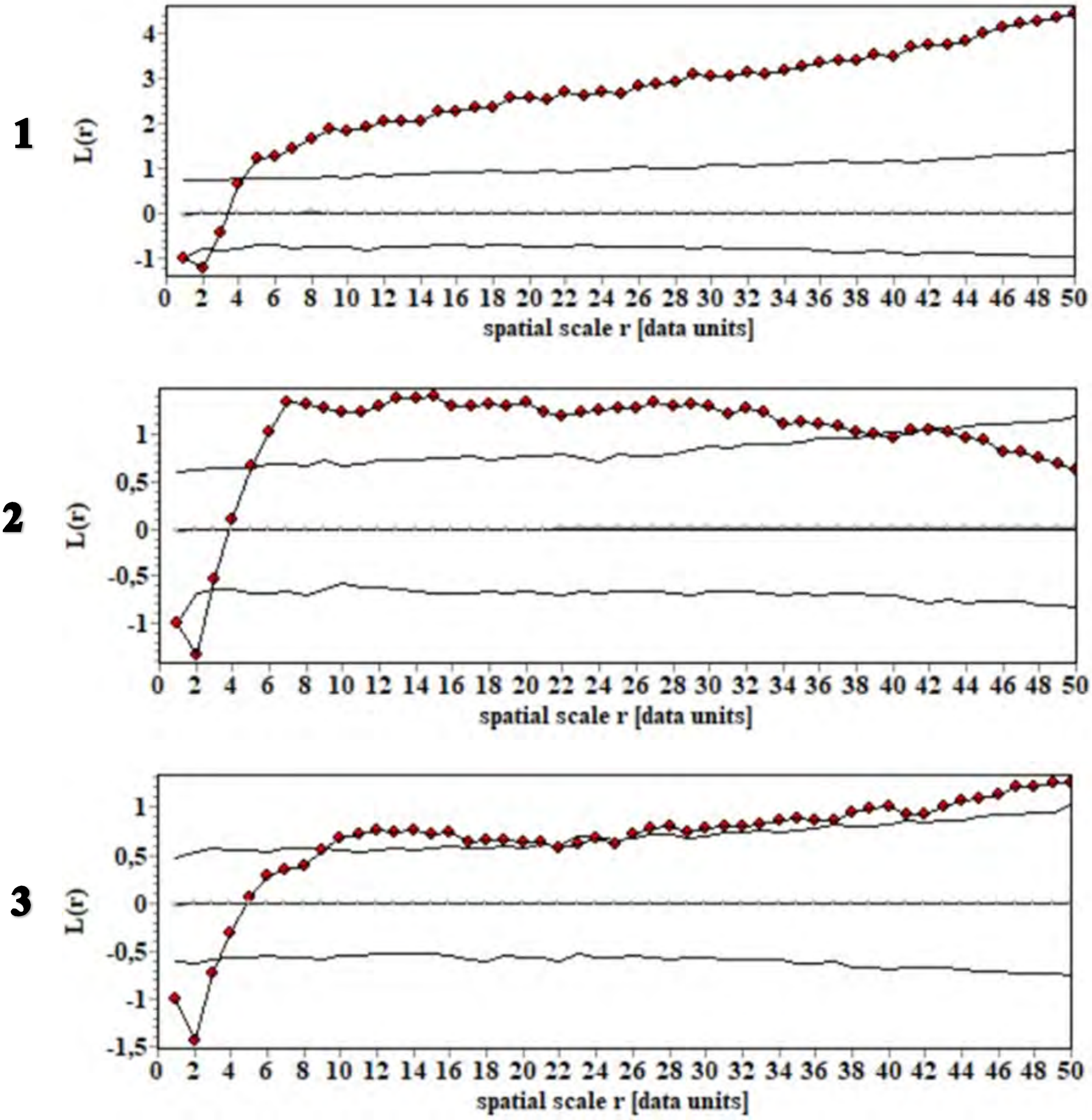

Figure B2 Intensity: A L-function L(r), a modification of Ripley's K, was run to analyse all the trees in each of the plots and classify them as homogeneous or heterogeneous. Approximately 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of Pattern 1 and 2 CSR. Cluster 1 and Cluster 3 were heterogeneous while Cluster 2 was homogeneous.

3. Spatial point pattern analysis of all trees across early, intermediate and late stages of thicket encroachment (Univariate PCF)

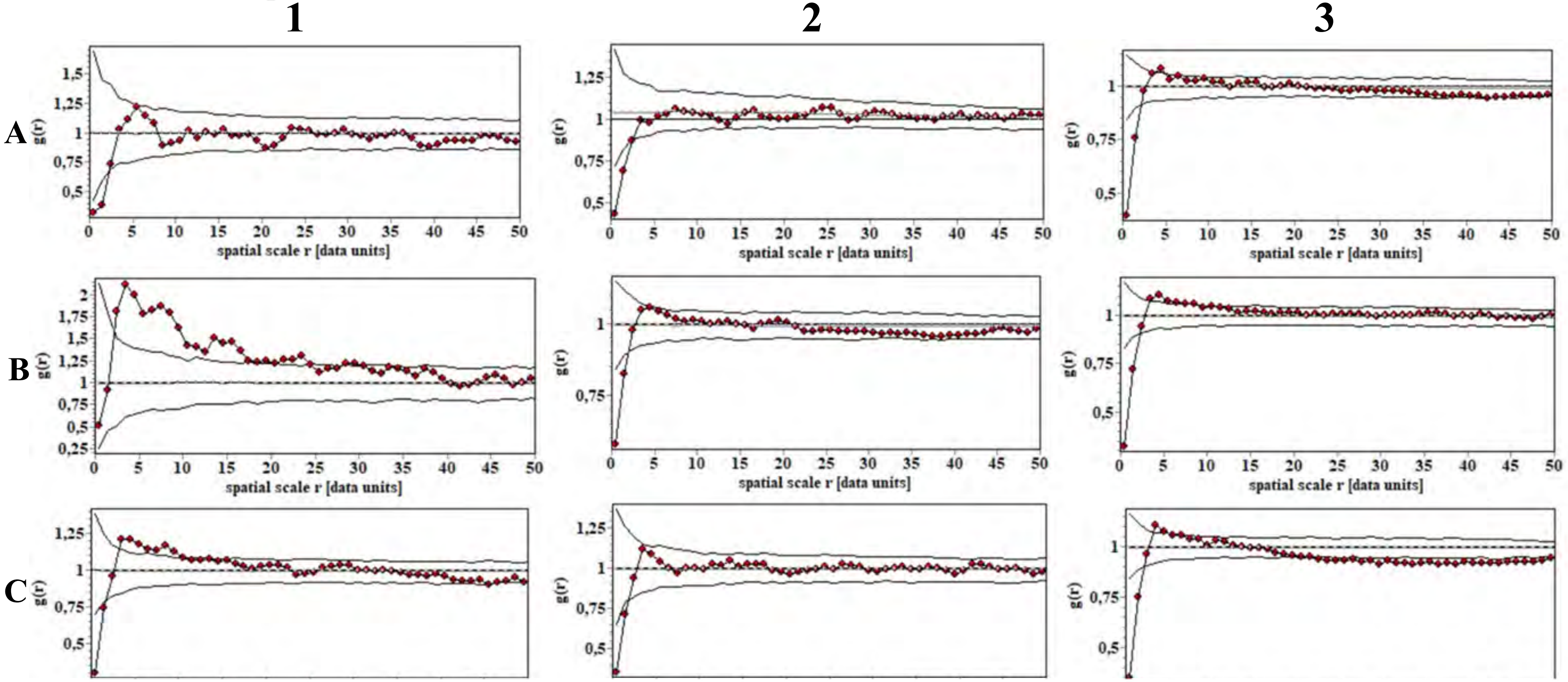

Figure B3 Overall SPPA: A Univariate PCF g(r), was run to analyse the trees in each of the plots. Approximately 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of CSR. Plot 445 was heterogeneous and used a Heterogeneous Poisson null model. Column 1 represents Cluster 1, with a) Plot 618; b) Plot 751; and c) Plot 779. Column 2 represents Cluster 2, with a) Plot 445; b) Plot 586; and c) Plot 651. While Column 3 shows Cluster 3 and a) Plot 125; b) Plot 1026; and c) Plot 1135.

4. Spatial point pattern analysis of large *V. karroo* and small thicket pioneer species across early, intermediate and late stages of thicket encroachment (Bivariate PCF)

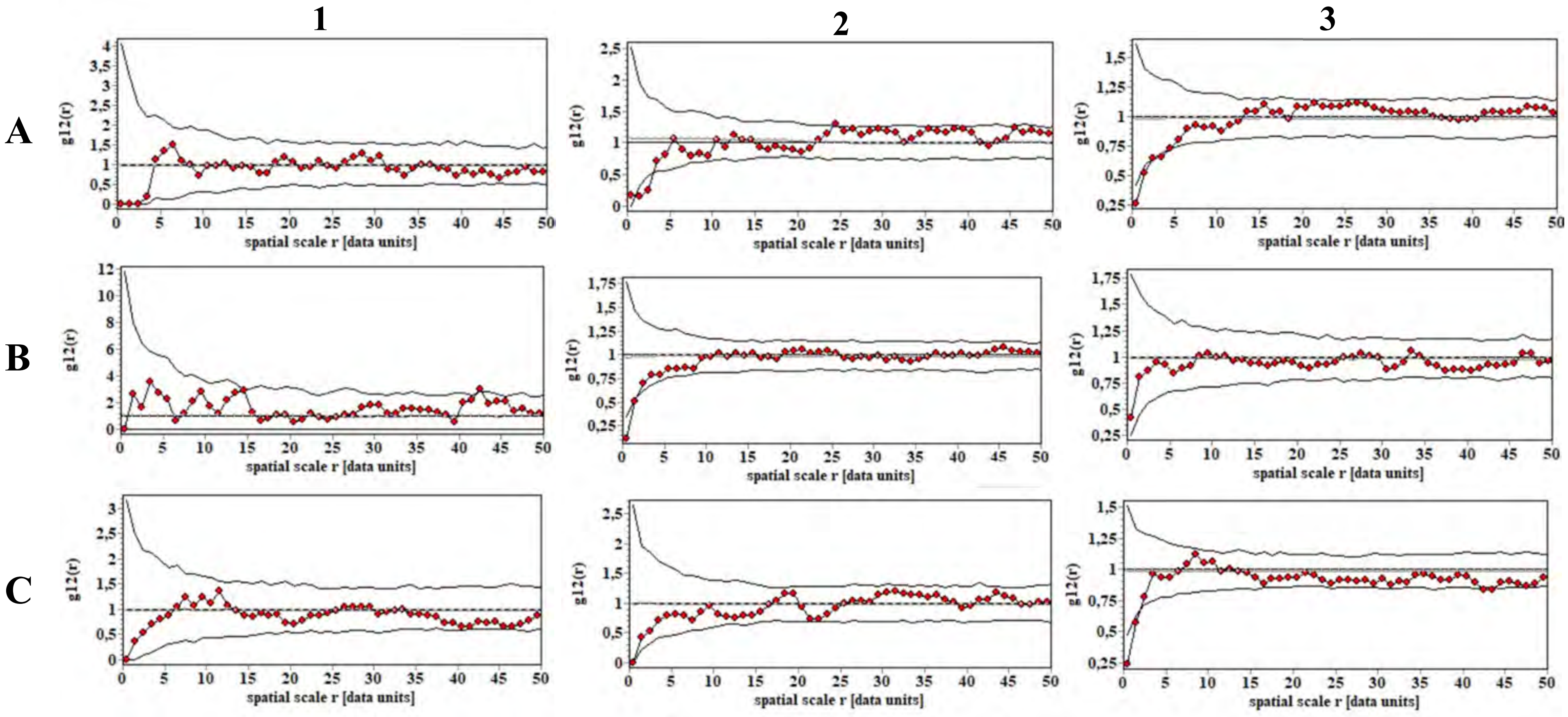

Figure B4 Large *V. karroo* and small Thicket pioneer species SPPA: a Bivariate PCF g12(r) was run to analyse the large *V.* and small Thicket individuals in each of the plots. Approximately 95% simulation envelopes were constructed using the fifth-lowest and fifth-highest values of 1999 Monte Carlo simulations, with a null model of antecedent conditions (large *V. karroo* fixed and small thicket trees randomized). Plot 445 was heterogeneous and used a Heterogeneous Poisson null model. Column 1 represents Cluster 1, with a) Plot 618; b) Plot 751; and c) Plot 779. Column 2 represents Cluster 2, with a) Plot 445; b) Plot 586; and c) Plot 651. While Column 3 shows Cluster 3 and a) Plot 125; b) Plot 1026; and c) Plot 1135.